UNIVERSAL
LIBRARY

OU_154903

UNIVERSAL
LIBRARY

OUP—786—13-6-75—10,000.

OSMANIA UNIVERSITY LIBRARY

Call No. 580 T27G Accession No. 42869

Author Taylor, William T and Webb, R

Title General Botany. 1959

This book should be returned on or before the date last marked below.

GENERAL BOTANY

WILLIAM T. TAYLOR, PH.D.
Professor of Biology, Georgetown University
AND
RICHARD J. WEBER, PH.D.
Professor of Biology, Georgetown University



ILLUSTRATED BY WILMA RILEY

D. VAN NOSTRAND COMPANY, INC.
PRINCETON, NEW JERSEY
TORONTO LONDON
NEW YORK

D. VAN NOSTRAND COMPANY, INC.
120 Alexander St., Princeton, New Jersey (*Principal office*)
257 Fourth Avenue, New York 10, New York

D. VAN NOSTRAND COMPANY, LTD.
358, Kensington High Street, London, W.14, England

D. VAN NOSTRAND COMPANY (Canada), LTD.
25 Hollinger Road, Toronto 16, Canada

COPYRIGHT, ©, 1956, BY
D. VAN NOSTRAND COMPANY, INC.

Published simultaneously in Canada by
D. VAN NOSTRAND COMPANY (Canada), LTD.

Library of Congress Catalogue Card No. 56-8223

All Rights Reserved

This book, or any parts thereof, may not be reproduced in any form without written permission from the authors and the publishers.

First Published April 1956
Reprinted July 1957, October 1959

PRINTED IN THE UNITED STATES OF AMERICA

PREFACE

THIS book is the result of some twenty years of teaching a course in general botany. It is designed primarily for a one-semester course. However, with some amplification on the part of the instructor, it can be made to form the basis of a year's course in the subject. The text embodies the physiological approach to plant organisms. Cell division (both equational and reductional), osmotic pressure, photosynthesis, and respiration—just to mention a few topics—are discussed concisely in terms of modern concepts, with background inserted wherever necessary. The great strides being made in molecular biology, especially in the study of plant respiration, are reflected on these pages in a manner quite different from that of comparable texts, but at the same time in a way that lends itself to comprehension by the serious student. The authors do not undertake to simplify nature nor are they tolerant of the dilettante attitude in the presentation of this basic discipline.

The algae and fungi, often superficially treated in semester texts of this type and sometimes neglected, are presented with the fullness of treatment which they deserve. The fungi are considered not only in their pathological aspects but, more importantly, in the light of their economic contributions to industry and medicine. The usual and sometimes incorrect rehash of the algal and fungal organisms will be found to be conspicuously absent from the text.

The art work is fresh and original. It mirrors wherever possible the textual matter and will, we are sure, be significantly helpful to the student in pursuit of a subject that has again taken its place among the basic biological disciplines.

The book is suitable for use in the introductory course for biology majors or for pure botany majors. It can be readily employed as a text for the first course in either agricultural or pharmacy schools. It may

also be utilized in the strictly cultural type of course in which the student should be, but rarely is, the recipient of at least a really scientific insight into the subject itself.

Acknowledgments for the use of certain electron micrographs of both bacteria and viruses are indicated in specific legends. We would be remiss if we did not take this opportunity of expressing our thanks to Mr. Thomas O'Keefe for his part in proofreading much of the manuscript.

It is a great pleasure to acknowledge the artistic ability of the illustrator, Miss Wilma Riley. The favorable comments which it has drawn from all quarters are richly deserved. Strange as it may seem, there is little that we can say here; her artistry speaks for itself.

The authors wish to take this opportunity to express a token of their sincere gratitude to Dr. Paul Alanson Warren, Professor of Botany and Chairman of the Department of Biology at Tufts College, for his thorough and constructive criticism of the manuscript.

Last but by no means least, the authors feel greatly indebted to Mrs. Miriam Campbell, the departmental secretary, who typed, assembled, and did more than her share of proofreading of the manuscript. Above and beyond all this, we would thank her for her great patience with, or perhaps her forbearance of, the eccentricities of the two authors.

W. T. T.

February 1956 R. J. W.

TABLE OF CONTENTS

CHAPTER		PAGE
	Preface	iii
	INTRODUCTORY CONCEPTS	
1.	Botany and Its Subsciences	1
2.	Chemical Principles and the Constitution of Protoplasm	6
3.	Plant Cells	17
	Structure	17
	Functions	25
4.	Taxonomy of Plants	41
	Traditional Method of Classification	41
	Modern Method of Classification	44
	Classification Used in This Text	45
	PHYLUM TRACHEOPHYTA: PTEROPSIDA. ANGIOSPERMAE	
5.	Plant Tissues and Stems	47
	Plant Bodies	47
	Definition and Classification of Buds	48
	Deciduous Plants	50
	Plant Tissues	51
	Stems	56
	Functions of Stems	74
	Subterranean Stems	75
6.	The Root	77
	External and Internal Anatomy	77
	Soil	83
	Functions of Root	95
7.	The Leaf	98
	External Anatomy	98
	Internal Anatomy	102
	Opening and Closure of Stomata	105
	Abscission	105
	Tropistic Behavior	106
8.	Functions of the Leaf	107
	Photosynthesis	107

CHAPTER PAGE

Transpiration 115
Secondary Functions 118
Functions of Stem Incidental to Forces Operative in Leaf 118

9. Plant Metabolism 121
Enzymes 121
Reactions Catalyzed by Enzymes 122
Biological Oxidations 123
Synthesis of Chemical Compounds in Higher Plants 128
Aerobic and Anaerobic Respiration 132

10. The Flower 138
External and Internal Morphology 138
Inflorescences 146
Seed and Fruit Development 147
Meiosis 150
Histogenesis of Anther and Microsporogenesis 160
Histogenesis of Ovule and Macrosporogenesis 161

11. Fruit, Seed, and Seedling 163

PHYLUM THALLOPHYTA

12. The Thallophytes 173

THE ALGAE

13. Class Cyanophyceae: Blue Green Algae 177

14. Class Chlorophyceae: Green Algae 182

15. Class Bacillariophyceae: Diatoms 200

16. Class Phaeophyceae: Brown Algae 206

17. Class Rhodophyceae: Red Algae 213

THE FUNGI

18. Class Schizomycetes: Bacteria 218
Structure and Reproduction 218
Nutrition and Metabolism 223
Importance to Man 226
Human Infection and Immunity 233
Agencies for the Control of Pathogenic Bacteria 236
Bacteriophage 238

19. Viruses and Rickettsiae 240

20. Class Myxomycetes: Slime Molds 245

21. Class Phycomycetes: Algal Fungi 250

CHAPTER PAGE

22. Class Ascomycetes: Sac Fungi . . . 261
23. Class Deuteromycetes: Imperfect Fungi . . . 283
24. Class Basidiomycetes: Club Fungi . . . 286

THE LICHENS

25. Lichenes . . . 300

PHYLUM BRYOPHYTA

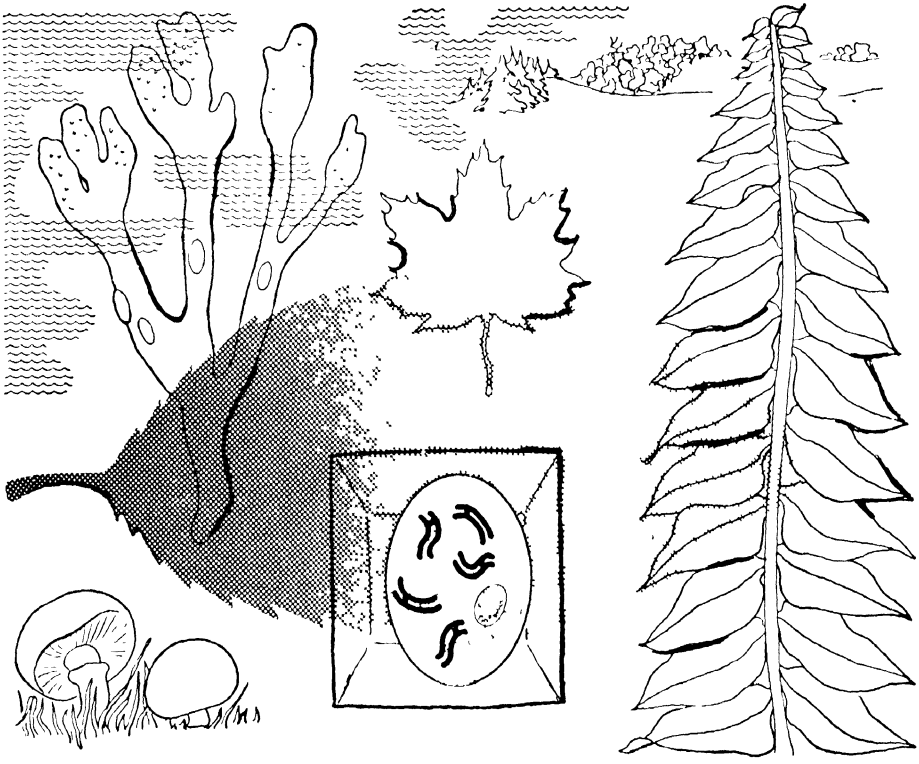
26. Bryophytes: Liverworts and Mosses 305

PHYLUM TRACHEOPHYTA: OTHER SUBPHYLA

27. Subphylum Sphenopsida: Horsetails 314
28. Subphylum Lycopsida: Club Mosses . . 317
29. Subphylum Pteropsida: True Ferns . . 322
30. Subphylum Pteropsida: Gymnosperms Only . 327

GENETICS AND EVOLUTION

31. Plant Genetics . . . 335
32. Plant Evolution 348
Index 359



Chapter 1

BOTANY AND ITS SUBSCIENCES

THE science which deals with the study of living things is called biology (Greek *bios*—life, *logos*—discourse). Living things may be classified as either plants or animals, and thus there are two subdivisions of the science of biology. These are botany and zoology. Botany (Greek *botanē*—plant) is that branch of biology which treats of plants. Zoology (Greek *zōon*—animal) is that branch of biology which deals with animals.

Since our knowledge of plants is so extensive, there exist today numerous phases of botanical study. The three fundamental botanical subsciences are plant morphology, plant taxonomy, and plant physiology.

Plant morphology or **plant anatomy** is the study of the external form and internal architecture of plants. It may be subdivided into macroscopic or gross plant morphology, plant histology, plant cytology, and plant embryology. *Gross plant morphology* deals with plant form and structure which can be discerned with the naked eye. *Plant histology* is a study of the plant tissues. *Plant cytology* is a study of the structure of plant cells. *Plant embryology* treats of the changes which a plant undergoes in form and structure during development.

Plant taxonomy or **systematic botany** is that study which is concerned with identification, correct nomenclature, and placing of individual plants or groups of plants into categories related by descent. Modern plant taxonomists, in order to establish a more satisfactory system of classification, must gather and synthesize data obtained from such sciences as plant morphology, plant genetics, phytogeography, paleobotany, and plant biochemistry.

Plant physiology deals with the physiological or functional processes associated with plant life. It explains how the different parts of plants function or how they perform their work. The plant physiologists

deal with such problems as the translocation of water and solutes, osmosis and osmotic pressure, photosynthesis, respiration, plant hormones, and plant movements. Necessary prerequisites for the study of plant physiology are the sciences of physics and chemistry. The scope of plant physiology has become so vast that a number of limbs have broken off from the parent tree and started independent existence. These limbs are the sciences of plant biochemistry and plant biophysics. *Plant biochemistry* deals with the chemical constitution and the chemical reactions of plant cells and organisms and the chemical laws which govern them. *Plant biophysics* studies the phenomena of plant life which are governed by physical laws. Plant physiology includes not only the physical and chemical principles but also the physiological principles which govern the phenomena of plant life and thus forms one coherent aspect of botanical inquiry.

The definitions and general content of other botanical subsciences are now presented.

Plant genetics is the science which seeks to account for the likenesses and differences between plant organisms related by descent. In short, it deals with heredity and variation. Though genetics is the youngest of the biological sciences, it has done much to remove the antagonism that originally characterized the relations between botany and zoology. In fact genetics has welded together these two basic biological sciences in its work on genes and chromosomes. Genetics was conceived in the work of a botanist, Gregor Mendel, but gave real meaning to the evolutionary concepts that integrated the whole field of zoology. Genetics took the quibbling out of plant taxonomy and made it a real discipline. The ramifications of genetics took the geneticists in each of the basic biological sciences into embryological, morphological, and physiological studies and posed for them in these fields problems of mutual interest. The fundamental principles of genetics, and even its more profound concepts, could be demonstrated with the same facility in corn as in the fruit fly. In short, cytology, one of the great pillars of genetics, forged the unbreakable link that now joins these two basic biological sciences into a continuum. Without genetics both plant and animal evolution would lose much of their appeal as scientific theory.

Plant pathology is a study of the diseases of plants and the methods used to combat these diseases. Plant diseases are caused by viruses, bacteria, and other fungal organisms, by certain parasitic nonseg-

mented roundworms, by a limited number of seed plants, and by adverse environmental conditions. In the last-named category are included nutrient deficiencies and excesses, excess of hydrogen or hydroxyl ions, water deficiency, oxygen deficiency, frost injury, and smoke injury. The development of means to reduce the amount of damage to crops by plant diseases has resulted in the saving of millions of dollars each year. Control of plant diseases caused by plant and animal organisms involves such procedures as exclusion or eradication of the pathogenic agent and the development of disease-resistant varieties of plants.

Plant ecology is a study of plants in relation to their external environment. The nonliving environmental factors include light, temperature, air movements, water supply, and the texture and chemical composition of the soil. The living environmental factors are other plants and animals. In ecology one learns of the effects of these factors on plant behavior.

Plant geography or **phytogeography** is a consideration of the distribution of the various individual types of plants and plant associations which cover the land surface of the earth, together with those found in water and in soil. It also includes a study of the factors which determine plant distribution.

Geological botany or **paleobotany** is a science which deals with the study of extinct plants that exist today as plant fossils. Knowledge obtained from a study of these plants has been of unique assistance in supplying evidence for organic evolution.

Economic or **applied botany** is the study of plants and plant products as related to the welfare of mankind. Because the field of economic botany has become so vast, it has been divided into numerous branches. Examples of such branches are: *agronomy*, the study of field crops and of soil management to increase their production; *horticulture*, the study of garden crops (*olericulture*), fruit production (*pomology*), and flowering plants used for ornamentation (*floriculture*); *forestry*, the study of forest and timber plant management; and *pharmaceutical botany*, which is a study of plants from which are obtained various drugs used in the treatment of disease in man and other animals.

The enormous number of plant organisms and the tremendous expansion of botanical experimentation have now made it impossible for any one man to acquire a comprehensive knowledge of the whole subject of botany. For this reason specialization has become essential.

The botanist who wishes to specialize chooses a specific group of plants and acquires all the information he can obtain from the field he has selected. Special studies have led to the development of such sciences as phycology (algae), mycology (fungi), bryology (liverworts and mosses), bacteriology (bacteria), bacterial physiology, bacterial genetics, physiological genetics, and plant biometrics (mathematical statistics in relation to botanical research).

WHY STUDY BOTANY?

Botany, a basic scientific discipline, gives a man a real appreciation of both the morphological and physiological complexities that obtain in the vegetative life surrounding him on every side. In fact, animal life, inclusive of man himself, depends for its existence upon the photosynthetic processes that occur in the green plants which man takes so much for granted. His dependency upon even so lowly a thing as bacterial decomposition in the soil will never make any impression upon him unless he has studied botany to some extent; nor will he ever know of the wonderful antibiotics which have been derived from the soil bacteria and the part they play in the maintenance of his health and that of those dear to him. Truly it has been said that an educated man is one who makes the most of his environment; and obviously plants, whether they be of the unicellular variety or as complex as those which are grown in the field to feed him, constitute a most important part of man's environment. Much of what he wears and of what he uses to build the home in which he lives stems directly or indirectly from the plant life that he takes so much for granted.

Much of the real art that man is privileged to see in the architectural wonders of the world may be traced to beauty and symmetry that were expressed first in plants. A great deal of our poetry seems to underline the artistic handiwork embodied in a flower or even so prosaic a thing as a tree.

But botany, though it makes for a full man as far as education is concerned, is nevertheless a science that carries with it a practicality. If a student is to become an agronomist he must know plants. Many of our drugs are derived from plants, and so botany takes a great place in the curriculum for pharmacy. Time was—and that not so long ago—when many people thought that botany had practically ceased to exist as far as scientific education was concerned. Now, with the discovery of antibiotics and the new hypotensive principles in plants, botany

once more takes its place in the preprofessional education of the student for medicine. As a matter of fact, some medical schools are now giving lectures in medical botany to fill the gap in the education of those who did not have the good fortune to take an adequate course in botany in their undergraduate days.

The fields which ramify from a study of botany are almost boundless. We shall only mention some of the practical fields that are open to those who take undergraduate training in botany: bacteriology, agriculture, horticulture, pharmacy, forestry, plant genetics, and pharmaceutical chemistry. The list could go on endlessly. The use of botany to man is obvious. It needs no apology here.

Chapter 2

CHEMICAL PRINCIPLES AND THE CONSTITUTION OF PROTOPLASM

CHEMICAL PRINCIPLES

Atoms, Molecules, and Ions. The *atom* is the smallest possible particle of a chemical element. It is also the smallest portion that can take part in chemical combination. A chemical *element* is a form of matter, all the atoms of which have the same nuclear charge. A *molecule* is the ultimate or most minute particle of any element or compound as it exists under ordinary conditions. A molecule of an element may consist of two or more atoms. The molecule of oxygen as present in the atmosphere is made up of two atoms. A molecule of a compound consists of atoms of two or more different elements. Sodium chloride, a compound of two different elements, is written NaCl. *Ions* are atoms or groups of atoms which have a positive or negative electric charge.

Atoms are built up from several kinds of elementary particles called protons, electrons, and neutrons. The *proton* is an elementary particle with a positive charge equivalent to the negative charge of the electron, but with a weight approximately 1845 times as great. The *electron* is a minute, negatively charged particle. The simplest of all atoms is the hydrogen atom. It consists of a single proton, which forms its nucleus, and a single orbital or planetary electron. Hence a proton is in effect the positive nucleus of the hydrogen atom. The nucleus is the heavy central part of an atom in which most of the weight is concentrated. The electron of the hydrogen atom revolves about the proton.

In elements heavier than hydrogen, another type of elementary particle called the *neutron* is a constituent of the atomic nucleus. It is an uncharged particle. It is convenient to consider it as a combination of a proton and an electron, although its mass is not exactly equal

to the sum of the masses of these two subatomic particles. The nucleus of an atom consists of a definite number of protons and neutrons—according to a simplified version. A definite number of planetary electrons revolve in concentric rings or shells around the nucleus.

The atom of sodium (Fig. 2.0) has an atomic weight of 23 and an atomic number of 11. The *atomic number* of an element is the number of positive charges in the atomic nucleus, and it is this charge of the nucleus which distinguishes one element from another. The *atomic weight* of an element is the relative weight of the atom of that element on the basis of oxygen as 16. The nucleus of the sodium atom contains 11 protons and 12 neutrons, making an atomic weight of 23. The 11 planetary electrons are distributed in three shells, 2 in the first shell,

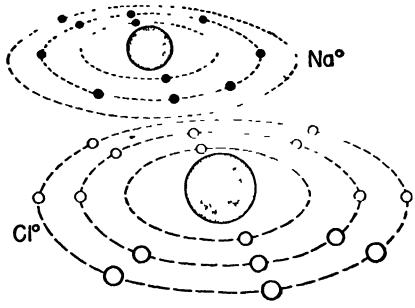


FIG. 2.0 Sodium (Na) and chlorine (Cl) atoms. The nucleus and planetary electrons of each atom are shown.

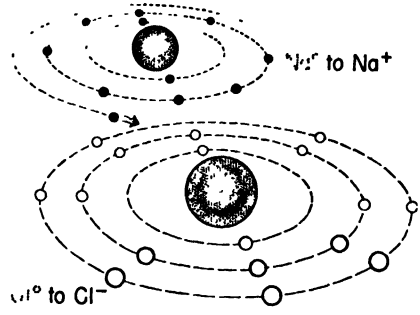


FIG. 2.1 Electron transfer. Sodium (Na) is visualized as giving up an electron to chlorine (Cl). As a result each atom becomes an ion. Na becomes Na^+ and Cl is changed to Cl^-.

8 in the second, and 1 in the third. Electrons in the outermost shell of the planetary system are termed *valence electrons*. The chlorine atom (Fig. 2.0) has a nucleus and 17 planetary electrons distributed in three orbits.

All atoms of a given element do not necessarily have the same weight. Atoms of the same element which have different masses are called isotopes. The architecture of the ordinary hydrogen atom has been given. Heavy hydrogen, or deuterium, an isotope, is constituted of a nucleus with one neutron and one proton, which accounts for its atomic weight of two.

Some atoms combine to form compounds by transferring valence electrons (Fig. 2.1) from one atom to another; others, by simply shar-

ing electrons. When electrons are shared, one electron may be contributed by each atom or both electrons may be contributed by the same atom. When one or more electrons have been transferred from one of the atoms in a compound to the other, the compound is said to be *electrovalent*. Sodium chloride (Fig. 2.2) is such a compound. Deelectronation of an atom causes it to become a positive ion or *cation*. Electronation of an atom causes it to become a negative ion or *anion*. Sodium chloride is a compound which results from the transfer of an electron from the outer shell of the sodium atom to the outer shell of the chlorine atom, with the resultant production of sodium and chloride ions. The electrical charge carried by an ion indicates its valence or

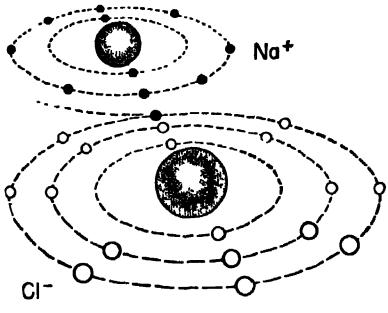


FIG. 2.2 Sodium chloride ($Na^+ Cl^-$), an electrovalent compound.

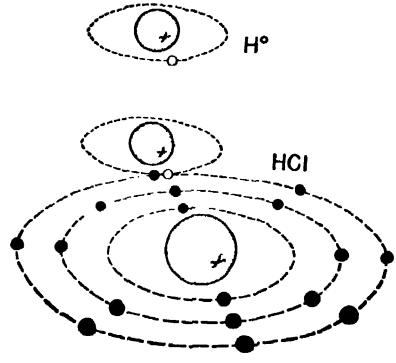


FIG 2.3 ABOVE. Nucleus and planetary electron of a hydrogen atom. BELOW: Hydrogen chloride (HCl), a covalent compound.

combining capacity. Electrovalent compounds are ionized even in the solid state.

Covalent compounds involve no transfer of electrons from one atom to the other. Hydrogen chloride (Fig. 2.3) is an example of such a compound. The sharing of electrons between the atoms forms the covalent bond. The sharing usually involves two electrons per valence bond. If both electrons are contributed by one atom, we have a special type of covalence which is termed coordinate covalence. It is the type of valence bonding found in the ammonium ion and in the hydronium ion.

The Colloidal State. Some of the substances in protoplasm (e.g. proteins) are in the colloidal state or in colloidal solution. In a colloidal solution the solute particles are molecular aggregates whose diameter

varies from 1 millimicron to 200 millimicrons. (A micron is 1/1000 millimeter and a millimicron is 1/1000 micron.) In a true or crystalloidal solution the solute particles are either molecules (e.g. glucose) or ions (e.g. sodium chloride). In a suspension the solute particles are molecular aggregates greater than 200 millimicrons in diameter. A colloidal solution is a heterogeneous system consisting of two phases, the *dispersion medium* and the *dispersed phase*. A phase is a physically distinct portion of matter.

Colloidal solutions are classified as lyophobic colloids or *suspensoids* and lyophilic colloids or *emulsoids*. In *lyophobic* colloids there is no affinity between the dispersed particles of solute and the dispersion medium. In *lyophilic* colloids the particles of dispersed solute have a high affinity for the dispersion medium. When the dispersion medium is water, the lyophilic colloids can be termed *hydrophilic colloids*. Each dispersed particle has a shell of water surrounding it. Aqueous solutions of proteins are hydrophilic colloids or emulsoids and are of great biological importance since the cellular solvent is water and the chief protoplasmic solute is protein.

A colloidal solution in which the mixture is liquid is called a *sol*. A colloidal solution which is firm or semisolid in consistency is termed a *gel*. A very dilute aqueous solution of a protein such as gelatin is a sol. However, if a very concentrated aqueous solution of the same protein is made and allowed to stand, it is converted into a gel. Apparently, long chains of gelatin molecules interlace to form a meshwork, and water is entrapped in the interspaces to form the gel, which is thus a liquid dispersed in a solid. In this case the change from sol to gel would be due to phase reversal.

Hydrogen and Hydroxyl Ions. Knowledge concerning the concentration of hydrogen and hydroxyl ions (H^+ and OH^-) in aqueous solutions is of great import in biological studies. The hydrogen ion concentration of pure water is 1×10^{-7} gram per liter or 1/10,000,000 gram per liter. Since the water molecule separates into two ions, the concentration of hydrogen ions must be balanced by the same concentration of hydroxyl ions. Inasmuch as the above method for expressing hydrogen ion concentration is awkward, the negative exponent with its sign changed to positive is used and is termed "pH." The pH of water or of a neutral solution which contains equal concentrations of hydrogen and hydroxyl ions is 7.0, and the pOH is thus also 7.0. The term pOH is seldom used.

If hydrochloric acid is added to pure water, the hydrogen ion concentration is increased and the pH is decreased. Hence the pH of acidic solutions is less than 7.0, and the more acidic the solution, the less the pH. The pH of an alkaline solution is greater than 7.0. In all aqueous solutions, the sum of the pH and pOH always equals 14.0. Hence a solution whose pH is 6.0 would have a pOH of 8.0.

The pH of protoplasm in the cells of an organism and, when present, of fluids which bathe them approaches neutrality. Hydrogen and hydroxyl ions are involved in cellular chemical processes, and cellular function is profoundly modified by differences in pH. Relatively small changes in cellular pH produce alterations in function which may result in cellular death. Chemical devices called *buffers* are present in protoplasm and extracellular fluids, which tend to maintain a constant pH when hydrogen or hydroxyl ions are added. A buffer system usually consists of a weakly dissociated acid and the salt of that acid, or of a weak base and its salt. For example, carbonic acid and sodium bicarbonate constitute a buffer system. The addition of hydrochloric acid to this buffer system might be expected to produce a profound rise in hydrogen ion concentration, but the acid reacts with a weak base to yield a neutral salt and a weak acid and the pH is not appreciably raised:

$$NaHCO_3 + HCl \rightarrow NaCl + H_2CO_3$$

Sodium diacid phosphate and disodium acid phosphate also constitute a buffer system. If a strong base such as sodium hydroxide is added to such a system, the reaction occurs as symbolized below. The weakly acid sodium diacid phosphate buffers the strong base by yielding the weakly alkaline disodium acid phosphate:

$$NaH_2PO_4 + NaOH \rightarrow H_2O + Na_2HPO_4$$

CONSTITUTION OF PROTOPLASM

The term "protoplasm" implies living material. Since most methods of chemical analysis lead to death of living material, one can obtain for the most part only information about that which was once alive. Hence the exact chemical constitution of protoplasm is unknown. It can be said that it is an aqueous solution of three main types of organic constituents—proteins, carbohydrates, and lipids—and of inorganic salts.

The chemical elements present in every living organism are carbon,

hydrogen, oxygen, nitrogen, sulfur, phosphorus, sodium, potassium, magnesium, calcium, and chlorine.[1] In addition to these macronutrient elemental constituents of protoplasm, a number of other elements are required in "trace" amounts in the metabolism of certain organisms. Of the micronutrient elements, iron and probably zinc and manganese are required for all living systems. Cobalt, iodine, copper, boron, molybdenum, aluminum, vanadium, and silicon are other trace nutrilites known to be essential for certain forms of life but not for others. Other elements for which a vital role has been suggested are bromine, gallium, nickel, chromium, rubidium, strontium, fluorine, lithium, tin, tungsten, and columbium. The chemical elements present in living systems can be termed *biological elements.*

Inorganic Constituents. The inorganic constituents of protoplasm are water, small amounts of gases such as oxygen and carbon dioxide in solution, and inorganic salts.

The chief chemical substance of protoplasm and the universal biological solvent is water. It occurs mostly in the free state, but probably a small fraction is bound chemically to other protoplasmic constituents. The percentage of water varies from a low of approximately 8 per cent in dormant seeds to a high of over 90 per cent in certain species of fruits and vegetables. Water has certain physicochemical properties which make it especially suited to be an essential medium for the existence of life. It has a remarkable solvent power; it is an electrolyte and not only dissociates itself, but has high dissociative power on most solutes; it has a high surface tension and a low viscosity; and finally, it has a great capacity to absorb heat, which enables it to act as a protective mechanism for protoplasm against extreme variations of temperature.

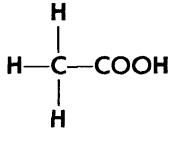
The inorganic salts are electrolytes which are composed chiefly of the following cations and anions. The cations are sodium, potassium, magnesium, calcium, and ammonium. The anions are chloride, bicarbonate, carbonate, sulfate, phosphate, nitrite, and nitrate. Some of the ions listed are linked in part with the organic constituents of protoplasm, as are also copper, iron, zinc, and others.

Organic Constituents. The three principal types of organic compounds present in protoplasm are proteins, carbohydrates, and lipids.

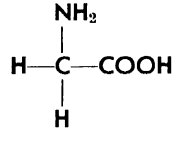
A. PROTEINS. The proteins are complex nitrogenous organic compounds of high molecular weight which on hydrolysis (decomposition

[1] Chlorine as a macronutrient element in plants is debatable.

on reaction with water) yield amino acids. The elements found in proteins are carbon, hydrogen, oxygen, nitrogen, and at times sulfur, phosphorus, and iron. An amino acid is an organic acid in which an amino group (NH_2) has been substituted for a hydrogen atom attached to a carbon atom other than the carbon atom of the carboxyl group (COOH). The first amino acid to be obtained from the hydrolysis of a protein was aminoacetic acid or glycine. To date over twenty amino acids have been isolated from various proteins. Certain amino acids may be lacking in this or that particular protein.

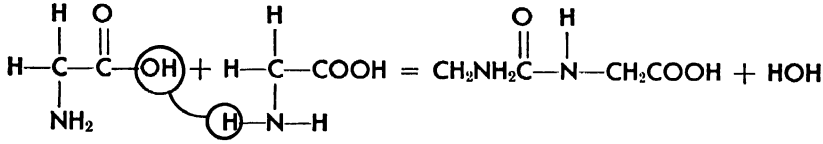


Acetic acid



Glycine

The principal type of union between amino acids in proteins is called the peptide or carboxylamino linkage. In this type of linkage, the amino acids are joined by the union of carboxyl groups to amino groups with the elimination of a molecule of water at each linkage. A dipeptide (a derived protein) is formed by the union of two amino acids, as illustrated:



Glycine **Glycine** **Glycylglycine** **Water**

The proteins are divided into three general categories:

1. SIMPLE PROTEINS. These are proteins which on hydrolysis yield amino acids or their derivatives. On the basis of solubility and coagulability by heat, the simple proteins are further subdivided into albumins, globulins, globins, prolamins, histones, glutelins, protamines, and albuminoids. To illustrate, globulins are insoluble in salt-free water, but soluble in neutral salt solutions such as sodium chloride, and are coagulable by heat. Gamma globulin, a blood plasma protein, and thyroglobulin, from the thyroid gland, are examples of globulins.

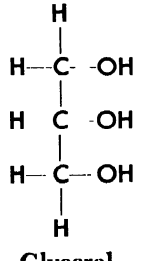
2. CONJUGATED PROTEINS. These are proteins whose molecule consists of protein combined with some nonprotein substance (the *prosthetic group*). They are classified according to the nature of the prosthetic group into nucleoproteins, glycoproteins, phosphorproteins,

chromoproteins, and lipoproteins. Nucleoproteins are compounds of one or more protein molecules with nucleic acids and are present in the cell nucleus and in the cytoplasm. The prosthetic group in a glycoprotein is a carbohydrate. In phosphoproteins the prosthetic group is phosphoric acid. Chromoproteins are compounds of proteins with a metal-containing prosthetic group and they are colored; the hemoglobins from vertebrate blood are illustrative of this group. Lipoproteins are compounds of protein with a lecithin, cholesterol, or some other lipid.

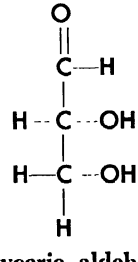
3. DERIVED PROTEINS. These are divided into the primary and secondary protein derivatives. The primary protein derivatives are proteans, metaproteins, and coagulated proteins. They are compounds formed from proteins when they are subjected to certain physical and chemical agents which bring about intramolecular rearrangement. The secondary protein derivatives are hydrolytic cleavage products of proteins. They are, in order of decreasing complexity, proteoses, peptones, and peptides.

Proteins are fundamental components in the molecular organization of protoplasm and are indispensable for vital processes. They act as buffers in cells and help to keep lipids in emulsion in cell protoplasm. Enzymes are protein in nature. Most plant organisms can synthesize proteins from inorganic nitrogenous salts. On the other hand, the animal organism must ingest protein, hydrolyze it to amino acids in the digestive process, and from them form its own proteins. Various proteins contain different proportions of their constituent amino acids with a special architecture for each protein. The properties of proteins are determined by their amino acid pattern.

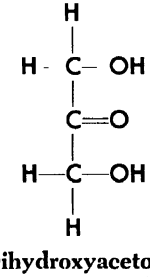
B. CARBOHYDRATES. These are for the most part simple sugars or substances which on hydrolysis yield simple sugars. A simple sugar is an aldehyde or ketone derivative of a polyhydric alcohol (—CHO = aldehyde group; —CO = ketone group; and —OH = alcohol group).



Glycerol
(a polyhydric alcohol)



Glyceric aldehyde
(an aldotriose)



Dihydroxyacetone
(a ketotriose)

The carbohydrates may be classified as follows:

1. MONOSACCHARIDES OR SIMPLE SUGARS. The simple sugars cannot be hydrolyzed into simpler substances. They are further classified according to the number (3 to 10) of carbon atoms they contain into trioses, tetroses, pentoses, hexoses, and so on. The commoner simple sugars of functional importance are the pentoses (e.g. xylose, ribose, desoxyribose) and the hexoses (e.g. glucose, fructose, galactose, mannose).

2. DISACCHARIDES. These are carbohydrates which on hydrolysis yield two molecules of simple sugars. The commoner ones are those composed of hexoses, and they have the empirical formula $C_{12}H_{22}O_{11}$. Examples are sucrose or cane sugar, maltose or malt sugar, and lactose or milk sugar. The products of hydrolysis of the disaccharides listed are:

Sucrose + water = glucose + fructose
Maltose + water = glucose + glucose
Lactose + water = glucose + galactose

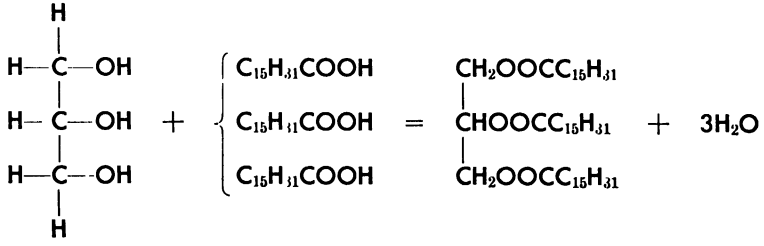
3. POLYSACCHARIDES. These are carbohydrates which on hydrolysis yield more than two molecules of simple sugars. It is a group that includes starches, glycogens, celluloses, hemicelluloses, and dextrins. Starch is found in many plant cells in the form of granules. Glycogen is stored in some plant cells. Cellulose is found in the cell walls of plant cells. The dextrins are intermediary compounds formed in the course of the hydrolysis of starch.

The most important carbohydrate in nature is D-glucose or dextrose. All carbohydrate is converted to it before oxidation in the tissues to furnish energy to carry on cellular activities. Glucose is readily fermented by yeasts and most bacteria. Alcoholic fermentation yields ethyl alcohol (grain alcohol) and carbon dioxide. Lactic acid fermentation yields lactic acid.

C. LIPIDS. These are a heterogeneous group of substances occurring in plant and animal tissues and characterized by their insolubility in water and their solubility in such organic fat solvents as boiling ethyl alcohol, ether, benzene, and chloroform.

1. SIMPLE LIPIDS. The lipids are classified as follows:

(*a*) *Neutral Fats and Oils.* These are compounds of fatty acids and glycerol. The oils differ from the fats in that they are liquid at body temperature. An example of a fat is tripalmitin or glyceryl palmitate:

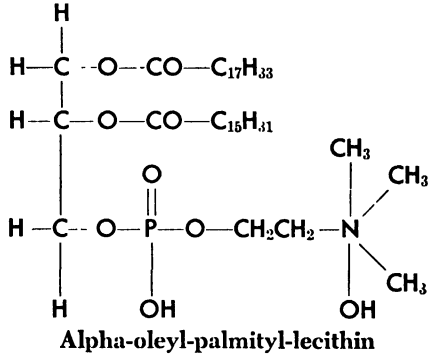


Glycerol **Palmitic acid** **Glyceryl palmitate (an unmixed neutral fat)** **Water**

Some of the commonest fatty acids found in vegetable and animal fats are palmitic acid ($C_{15}H_{31}COOH$), oleic acid ($C_{17}H_{33}COOH$), and stearic acid ($C_{17}H_{35}COOH$).

(*b*) *Waxes.* These are compounds of fatty acids with long-chain monohydric aliphatic alcohols and with monohydric aromatic alcohols. An example is beeswax.

2. COMPOUND LIPIDS. These are lipids which on hydrolysis yield compounds other than an alcohol and fatty acids. Examples are phospholipids (lecithins, cephalins, and sphingomyelins), glycolipids or cerebrosides, aminolipids, sulfolipids. To illustrate the complexity of many of the compound lipids, the formula for a specific lecithin is given. The hydrolysis of a lecithin yields glycerol, phosphoric acid, choline (an organic nitrogenous base), and two molecules of fatty acid.

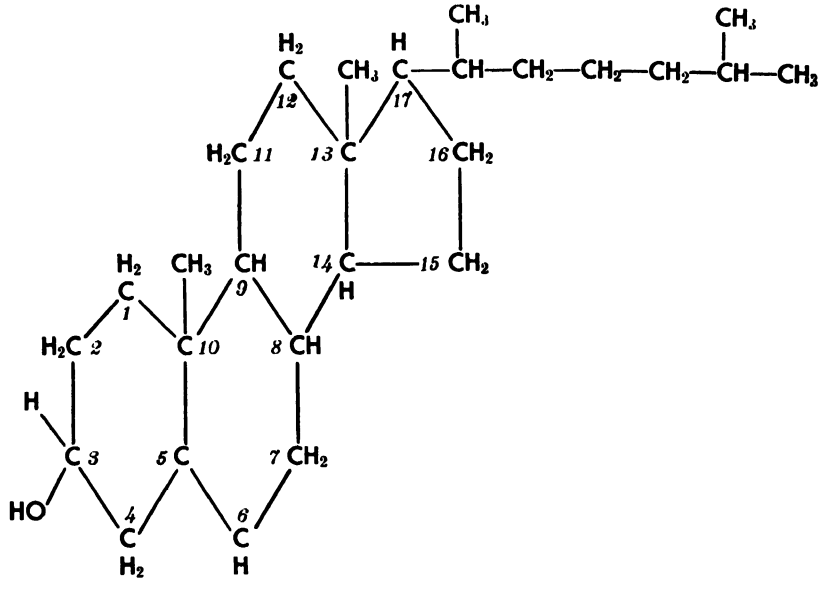


Alpha-oleyl-palmityl-lecithin

The phospholipids are probably present in all cells and appear to be essential protoplasmic constituents.

3. DERIVED LIPIDS. These are substances possessing the general physical characteristics of lipids which are obtained by the hydrolysis of simple and compound lipids. Examples are fatty acids, aliphatic alco-

hols, and sterols such as cholesterol and ergosterol. Cholesterol is an



Cholesterol

essential protoplasmic constituent. It is an aromatic monohydric alcohol containing the cyclopentano-perhydrophenanthrene nucleus (also called the *steroid* nucleus). This nucleus is also found in the sterol vitamins, the sex hormones, the adrenal cortical hormones, and many other compounds of plant and animal origin.

Chapter 3

PLANT CELLS

ALL living things, whether plant or animal, are constituted of a complex living material called protoplasm, the chemical aspects of which have been previously considered. Generally this protoplasm is organized into minute morphological units called cells. The protoplasmic components of each cell are collectively designated as the *protoplast.* This protoplast is generally enclosed by a cell wall. In the protoplast there is generally present a spherical body called the *nucleus.* The nucleus is denser and more refractive than the surrounding protoplasm. The peripheral limits of the nucleus are defined by a film-like nuclear membrane. The undifferentiated protoplasm of the nucleus is called *karyolymph.* The extranuclear protoplasm is commonly referred to as the *cytoplasm.* In this cytoplasm are contained organoids and inclusions. The *organoids* are formed cytoplasmic particles concerned with the accomplishment of various functions in the cell. The *inclusions,* often called *ergastic substances,* are passive, lifeless, temporary constituents in the cytoplasm and in the main represent materials requisite for, or resulting from, the process of cellular metabolism.

On the pages that follow we shall devote ourselves to a more detailed study of the morphology and physiology of the plant cell (Fig. 3.0).

CELL STRUCTURE

Cell Wall. The cell wall (Fig. 3.0B) is the product of the protoplast which it encompasses. Initially the cell wall consists of calcium pectate and is termed the *middle lamella.* Subsequently the protoplast overlays the middle lamella with cellulose so that the mature cell wall presents a laminated aspect. On the other hand, the cellulose may also be impregnated with lignin to give it tensile strength, as in mechanical tissue; or with suberin, a fatty substance, to render it impervious to water

and gases, as in cork tissue. In general, the chemical composition and structural architecture of the cell wall will vary according to the physiological requirements of the plant tissue in which it occurs.

Organoids. The organoids include the mitochondria (chondriosomes), the plastids, and the centrosome.

MITOCHONDRIA. The mitochondria (Fig. 3.0B) are filamentous, granular, or spherical in shape and require special microtechnical methods to be rendered microscopically visible. The literature ascribes a variety of functions to mitochondria: involvement in the synthesis

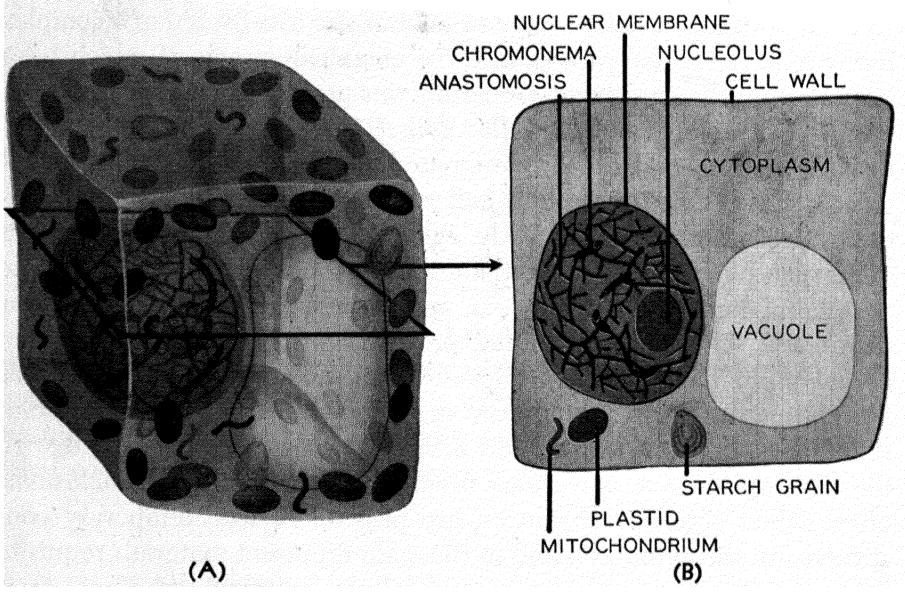


FIG. 3.0 (A) Stereoscopic view of a plant cell. [The anastomoses in the figure are considered by some cytologists to be artifacts; if this is true, the nuclear reticulum does not actually exist.] (B) Optical section through a plant cell.

of cytoplasmic nucleoprotein; reducing agents in protoplasmic respiration; centers of enzyme systems related to oxidations in the cell as well as a mechanism for energy liberation. Recent experimental reports point up the importance of the last function. Obviously such a diversity of function indicates that the mitochondria are far from being completely understood. We do know, however, that the division (*chondriokinesis*) of the mitochondria does take place during cell division; that they are hypersensitive to adverse conditions affecting the cell; that they are composed largely of lipid and protein.

PLASTIDS. Plastids (Fig. 3.0B) are specialized cytoplasmic bodies concerned with definite functions in the cell, such as the elaboration of glucose and its conversion into starch. In contrast to the mitochondria, plastids are microscopically discernible both in the living cell and in fixed preparations. Plastids have no homologue in the animal cell and are absent from blue-green algae and from bacteria and other fungal organisms. There are three types of plastids: green plastids or chloroplastids; colorless plastids or leucoplastids; and red, yellow, and orange plastids collectively grouped as chromoplastids.

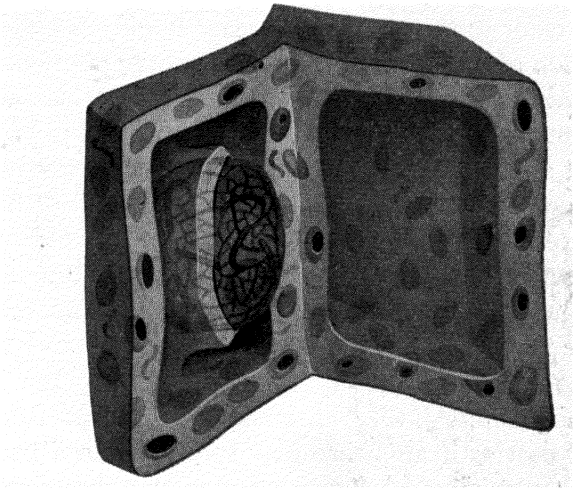


FIG. 3.1 Stereoscopic view of a plant cell sectioned so as to show the large central vacuole. Some of the cytoplasm vicinal to the nucleus has been removed.

The *chloroplastids* vary in shape from a common disc-like aspect to being either spiral or reticulate in form. Each chloroplastid is structurally composed of granules, called *grana,* contained in a colorless matrix or *stroma.* Two green pigments, chlorophyll *a* and chlorophyll *b,* occur in the grana together with two yellow pigments, carotene and xanthophyll. Because of their abundance, the green pigments mask the expression of the yellow pigments. With the disappearance of the chlorophyll from the leaves, the yellow pigments become manifest. Physiologically the chloroplastid is the center of food manufacture or *photosynthesis,* a process whereby carbon dioxide and water are synthesized in illuminated chloroplastids into energy-rich organic compounds such as glucose or sucrose. Thus in the chloroplastid, light energy, a form of kinetic energy, is converted into chemical or poten-

tial energy that finally becomes chained in the glucose or sucrose molecule. A detailed consideration of photosynthesis will be found in the chapter on the leaf.

The *leucoplastids* are the nonpigmented or colorless plastids which occur in the protoplasts of the plant cells not exposed to light, as in the roots of crop plants and underground stems. These plastids are the centers of starch formation from glucose. When a leucoplastid becomes a starch-bearing body, it is referred to as an *amyloplast*. Leucoplastids, upon illumination, may change to chloroplastids.

Chromoplastids may occur as spherical, lobed, or elongated bodies. They owe their color to the presence of *carotenoids*, a collective term for the designation of certain red, yellow, or orange pigments. Chromoplastids are found in the protoplasts of leaves, roots, fruits, and flowers. In spite of their close association with the chlorophyll pigments in the chloroplastids, it cannot be said with any degree of certainty that these pigments are involved in the photosynthetic processes of the plant. Of physiological interest, however, is their relation to color changes in leaves, flowers, and fruits. For example, in the green tomato the color is due to chlorophyll of the chloroplastids, but as the tomato ripens into its characteristic redness, the chlorophyll disappears and the red carotenoid, lycopin, appears. This, of course, points up the fact that a chloroplastid can change into a chromoplastid. Aside from the fact that the chromoplastids in this case play some role in a fruit-ripening process, the real physiological significance of the chromoplastids still remains a problem for the botanist.

Centrosome. The microscopically discernible centrosome occurs in the majority of animal cells (Fig. 3.2) and in the cells of the lower plant groups. The centrosome lies, in the cytoplasm, closely vicinal to the nucleus and usually coincides with the axis of the cell. The morphology of the centrosome varies according to the functional activity of the cell. During the interphase (the period between two successive mitotic divisions of a cell) the centrosome consists of a small granule, the *centriole*, in an area of condensed cytoplasm called the *centrosphere*. During cell division the centriole divides into two centrioles, each centriole becoming surrounded by a halo of radiations. These radiations, aptly termed *asters* because of their stellate disposition around the centriole, are thought by some to be hollow filaments enclosing liquid material and by others to be solid fibrillae resulting from the paralleled disposition of molecules or micelles in this region.

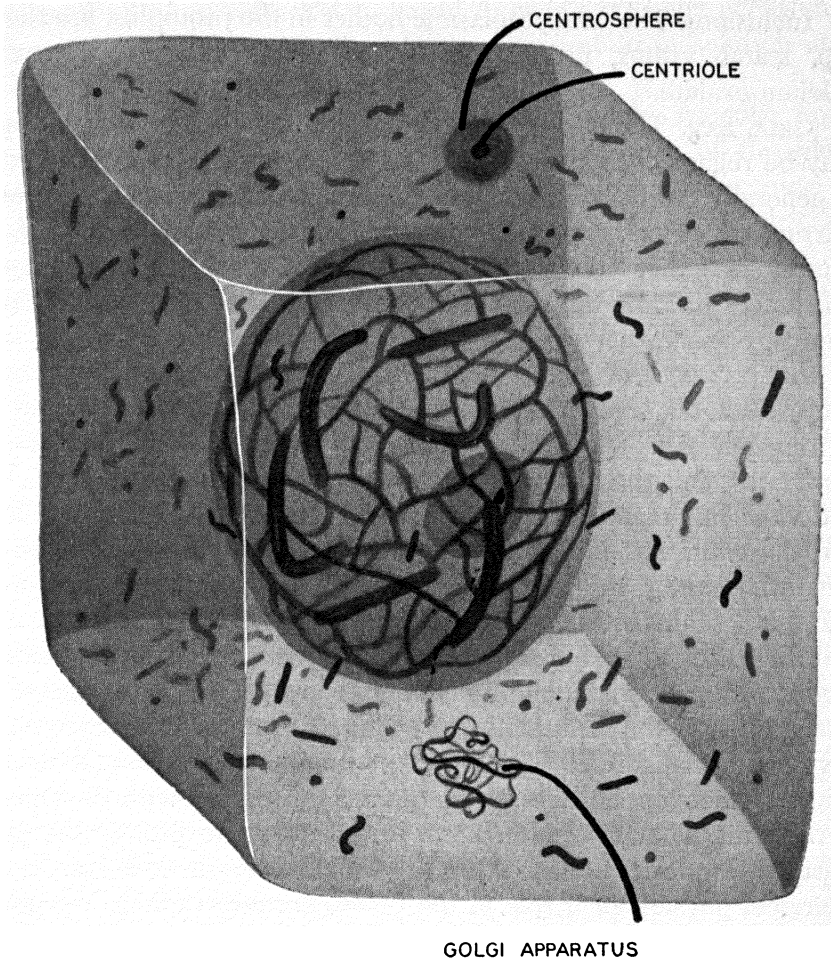


FIG. 3.2 Stereoscopic view of the animal cell, showing the centrosome.

The centrioles are functionally concerned with the orientation of the spindle fibers or with the polarization of the spindle. In those animal cells, as well as plant cells, in which there are no centrosomes, the centriolar mechanism is believed to occur in diffuse form or to be submicroscopic. In short, the spindle implies some sort of organizing center, formed or unformed. As to the physiological significance of the asters, experimental evidence indicates that the relative positions of the asters in the dividing cells determine the locations of the planes of cleavage. Cleavage of the cytoplasm is suppressed with the disappearance of the asters.

Inclusions. The noncytoplasmic bodies in the protoplast are the cell sap, starch grains, proteins, carbohydrates, lipids, and crystals of calcium oxalate.

CELL SAP. Though any space in the cytoplasm of the protoplast may be regarded as a vacuole (Figs. 3.0B and 3.1), the term *vacuole* is generally employed to denote those spaces containing an aqueous mixture called *cell sap.* This vacuolar fluid contains a variety of substances in either true solution or colloidal suspension. Elementary substances in ionic form, such as sodium, magnesium, calcium, phosphorus, occur rather commonly. In solution in the cell sap are many of the products of plant metabolism:[1] glycosides, tannins, organic acids, alkaloids, and pigments. The *pigments* are glycosides dissolved in the cell sap. The yellow pigments, referred to as *flavones* and *xanthones,* and the *anthocyanins,* a collective term for the red, blue, and violet pigments, are generally localized in the cells of the flower and the fruit. The great range of flower color is due in large part to the anthocyanins, the color determined by the latter depending on the pH that obtains in the vacuolar fluid. The *tannins,* aromatic compounds possessing many phenolic hydroxyl groups, seem to abound in regions of great metabolic activity and are astringent to taste. The astringency of the tannins is the common experience of anyone who has eaten unripe fruit. The fact that tannins can be metabolized is evident, since a great deal of the tannins disappears with the ripening of the fruit. Though tannins have been thought to protect the protoplast against desiccation or injury by animals, very little is known as to their real physiological role in the plant. Because tannins are protein precipitants, they are utilized for that purpose in the commercial tanning of leather. The *alkaloids* are not as common in their distribution through the plant as are the tannins. Alkaloids occur especially in seeds and fruits: in solution in the vacuoles of young parenchymatous tissue and in solid form in the cytoplasm of older tissues. What function alkaloids perform in the plant is not known. On the other hand, the importance of alkaloids such as morphine, quinine, and atropine in chemotherapeutics need hardly be stressed at this point. Soluble carbohydrates, such as the hexose sugars, are to be found in the

[1] Metabolism is a term employed to denote the physicochemical processes taking place in living cells. It is conventional to refer to the constructive phase of metabolism as *anabolism* and to the destructive phase as *catabolism.* Thus food manufacture in the plant organism would be anabolic while the oxidation of protein, carbohydrate, or fat would be catabolic.

vacuoles of all plant cells. Fat in liquid form is a common occurrence in the vacuoles of spores and seeds. Storage protein in solution may also be found in the vacuolar fluid.

Not all the ergastic substances are confined to the vacuolar fluid. Perhaps the most common inclusion in the cytoplasm of the plant protoplast is the *starch granule*. Each starch granule has a central or eccentric point surrounded by concentric lamellae. These starch granules represent a storage product in the cytoplasm. Protein in either amorphous or crystalline form is generally distributed throughout the plant body, but is relatively more abundant in the cytoplasm of the cells of the tubers, seeds, and roots. Fat in solid form occurs characteristically in the seed, where it often replaces the carbohydrate as the main source of nutrient and energy for the development of the embryo upon seed germination.

Wastes of cellular metabolism in the form of calcium oxalate crystals may occur in the cytoplasm. Since the cells of crop plants are not generally in contact with liquid water in their external environment, there is no outlet by which the plant cells can rid themselves of such waste products by simple diffusion; nor is there any elaborate excretory mechanism in any of the higher plants for elimination of such metabolic wastes. Actually, in the cell the precursor of the calcium oxalate is oxalic acid, a substance rather toxic to the protoplast. The oxalic acid, however, is quickly combined with calcium to render it inactive insofar as toxicity to the cytoplasm is concerned. Thus here is exemplified one of the ways in which the protoplast takes care of the excretory products of cellular metabolism.

As to the origin of vacuoles, there is a great deal of controversial literature. Two schools of thought on the subject are worthy of mention. One group postulates the dissociation of certain colloids from the cytoplasm and their subsequent conversion into cell sap because of their affinity for water. The other group maintains that the vacuolar system in a cell takes its origin from small units in the cytoplasm. These units, morphologically similar to mitochondria and assumed to be permanent and capable of perpetuation by division from cell to cell, absorb water and form small vacuoles which subsequently fuse to form a large vacuole. Functionally vacuoles are reservoirs of substances potentially useful in the metabolism of the plant cell, as well as depositories for certain by-products of metabolism.

Cytoplasmic and Vacuolar Membranes. Where the cytoplasm comes

to approximate the cell wall or where it limits a vacuole, there it is modified physiologically to function as a selectively semipermeable membrane. Such a membrane may be simply defined at this time as a membrane which permits the passage of water and some dissolved substances, but restricts the passage of other dissolved materials. The selectively semipermeable membrane which controls the uptake of a substance from the external environment is termed the cytoplasmic or plasma membrane, while the membrane which regulates the interchange between the cytoplasm and the cell sap in the vacuole is the vacuolar membrane or *tonoplast*. These membranes will be considered more fully in this chapter under cellular absorption.

Nucleus of the Plant Cell. The metabolic nucleus (Figs. 3.0 and 3.1), briefly one which is not in the process of division, is demarcated from the cytoplasm by a delicate, almost film-like membrane called the nuclear membrane. The undifferentiated protoplasm or ground substance of the nucleus is termed *karyolymph* or nuclear sap. Embedded in this karyolymph are variously shaped threads of *chromatin*, a deep-staining substance. These threads of chromatin are designated as *chromonemata* (Figs. 3.0 and 3.1) and are actually the filamentous constituents of structures which we shall come to know as chromosomes. Arranged in linear sequence along each chromonema are submicroscopic bodies or units, called *genes* or factors, which are the causative agents or determinants in the development of hereditary characters. In the fixed preparations of the nucleus, the chromonemata (Fig. 3.0B) are observed to be interconnected by strands (*anastomoses*) so that they collectively present the aspect of a network termed the *nuclear reticulum*. (The anastomosing strands, however, are considered by some cytologists to be artifacts.) In the karyolymph of the nucleus also occur rather distinct smaller bodies called *nucleoli*. On the basis of their Feulgen staining reaction[1] there are two types: the pseudonucleoli (frequently called the chromocenters of chromatin nucleoli) and the true nucleoli (Fig. 3.0B). The pseudonucleoli, Feulgen-positive in staining reaction, are coarser masses of chromatin that occur at several points of the nuclear reticulum. Some cytologists believe these pseudonucleoli represent areas of chromonemata that remained condensed instead of despiralizing to take part in the forma-

[1] *Feulgen reaction.* A staining reaction positive (intense coloration) for those nuclear entities that contain thymonucleic acid and negative (no coloration) for nuclear material containing ribonucleic acid.

tion of the nuclear reticulum. On the other hand, the true nucleoli, generally Feulgen-negative in staining reaction, are more dense and viscous than the surrounding karyolymph and may at times be vacuolated. As to the function of the true nucleoli, nothing definite can be said except that the nucleoli disappear and are re-formed respectively during the prophase and telophase of cell division, in an area vicinal to the ends of certain so-called nucleolar chromosomes.

Functionally the nucleus is the control center of the physiological activities of the cell. A denucleated protoplast can no longer grow nor reproduce; its continued viability at the most extends over a short period of time. The nucleus itself is incapable of autonomous existence, for the nucleus and cytoplasm complement each other in the normal metabolism of the entire protoplast. In other words, there is a continuous reciprocation of substances between the nucleus and the cytoplasm —an interchange that sustains normal cellular activity. Finally, in the nucleus are the chromosomes which are composed of genes that play such an important role in the transmission of hereditary characteristics.

FUNCTIONS OF THE PLANT CELL

The functions of the plant cell are absorption, food synthesis, digestion, assimilation, respiration, growth, and reproduction.

Absorption. The passage of water into a cell and the differential uptake of dissolved substances by the cell constitute absorption. To understand absorption, it is necessary to have a working concept of diffusion. When a small lump of hydrated copper sulfate (blue vitriol) —the *solute,* or substance to be dissolved—is dropped into water—the *solvent,* or dissolving substance—the ions of the solute become uniformly dispersed throughout the solvent, with the result that there finally exists a blue-colored solution of copper sulfate. This uniform distribution of ions or molecules, as the case may be, throughout the solvent to form a solution is termed *diffusion.* But what has actually happened? The ions in this case pass from the region where they are more abundant (the lump) to the region where they are less abundant (the solvent). Now diffusion may take place through membranes, but obviously, what passes through a membrane depends on the nature of the membrane. Filter paper, an example of a permeable membrane, will allow water and the substances dissolved therein to pass through. On the other hand, there is a type of membrane which will permit the passage of water and some dissolved substances, but will restrict

the passage of other dissolved substances. Such a membrane is commonly referred to as a *selectively semipermeable membrane* or a differentially permeable membrane.

Osmosis. To obtain some insight into the action of a selectively semipermeable membrane, visualize, as in Fig. 3.3, a U-tube between the arms of which has been interposed a selectively semipermeable membrane, one which is permeable to water molecules but impermeable to glucose molecules. Let us say, further, that we have put in one arm of the U-tube a 10 per cent aqueous solution of glucose and into

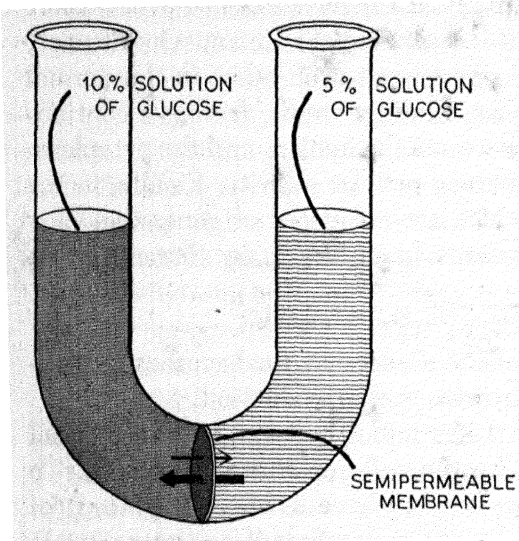


FIG. 3.3 Before dynamic equilibrium: The membrane is permeable to water only. The thickness of the arrows is in direct relation to the rate of passage of water through the membrane.

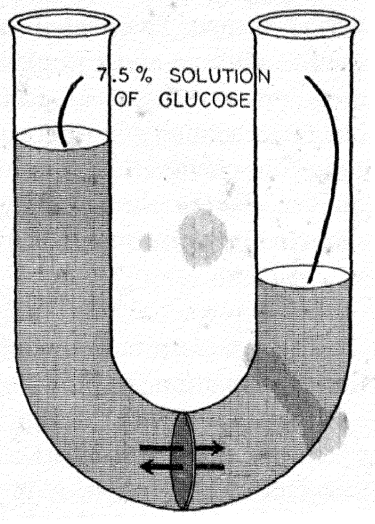


FIG. 3.4 At dynamic equilibrium.

the other arm a 5 per cent solution of glucose. After a while we will notice, as in Fig. 3.4, that the column of solution in what was originally the 10 per cent solution is higher and that the column of what was previously the 5 per cent solution is correspondingly lower. Evidently water has diffused through the semipermeable membrane from the region of its greater concentration (5 per cent solution) to the region of its lesser concentration (10 per cent solution). This passage of a solvent, such as water, through a semipermeable membrane from a region of greater solvent concentration to a region of lesser solvent concentration is known as *osmosis*. Osmosis will continue until there

is established between the two solutions a dynamic equilibrium; that is to say, until the rates of passage of the water molecules in opposite directions are the same.

Osmotic Pressure. Osmotic pressure is often defined as a pressure which a solution exerts when separated by a semipermeable membrane from either pure solvent or a less concentrated solution. According to this concept, the hydrostatic pressure (product of the height and density of the fluid) which a solution possesses at the time of dynamic equilibrium is equivalent to, and is a measure of, the osmotic pressure of the solution. However, here it must be emphasized that the osmotic pressure thus determined is in relation to the concentration of the solution after it has undergone dilution through osmosis; that is to say, it is the osmotic pressure of the solution after dilution through osmosis. The osmotic pressure which the solution exerted before its dilution through osmosis is greater. The latter osmotic pressure is experimentally ascertained by determining how much pressure would be necessary to prevent the influx of solvent through the semipermeable membrane into the concentrated solution. A 15 per cent solution of glucose, since it contains more molecules, will exert a greater osmotic pressure than a 10 per cent solution of the same substance. Basically, therefore, the osmotic pressure of a solution is directly proportional to the concentration of the solution. In our example, the 10 per cent solution of glucose possesses, just before osmosis, a greater osmotic pressure than the 5 per cent solution of glucose. However, as osmosis goes on, the osmotic pressure of what was originally the 10 per cent solution decreases as its hydrostatic pressure increases (Fig. 3.4). This reciprocal relation between the osmotic pressure and the hydrostatic pressure will continue until there is established, between the two solutions of originally different concentrations, a dynamic equilibrium. In other words, the hydrostatic pressure of the originally more concentrated solution will increase until it causes as many water molecules to pass from one side of the semipermeable membrane as are coming in from the other side, or from the originally less concentrated solution. The hydrostatic pressure that finally obtains on the side of the originally more concentrated solution is just sufficient to prevent further osmosis and is termed the osmotic pressure. The latter osmotic pressure, it should again be emphasized here, is NOT the osmotic pressure of the original 10 per cent solution, since dilution has occurred through osmosis, but

it is the osmotic pressure in relation to the concentration of the solution that ultimately exists at the time of dynamic equilibrium. In summation, therefore, osmosis takes place from a region of greater solvent concentration (less solute concentration) to a region of lesser solvent concentration (greater solute concentration). Hence, the greater the osmotic pressure of a solution, the greater will be the degree of osmosis into such solution when it is separated from pure solvent or a solution of lesser concentration by a semipermeable membrane.

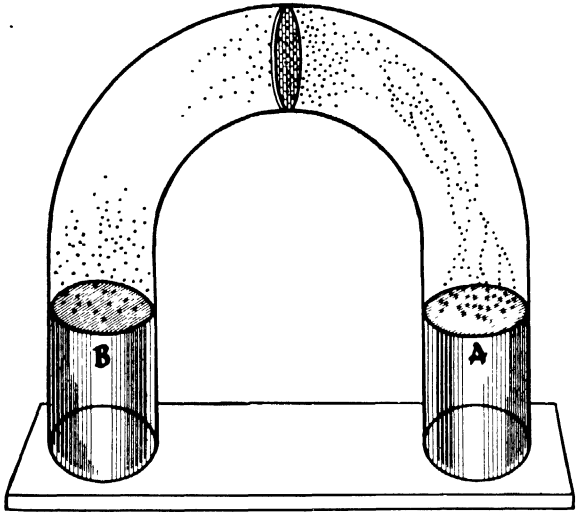


FIG. 3.5 The possible cause of osmosis. *A* is the beaker containing the less concentrated solution. *B* is the beaker containing the more concentrated solution.

CAUSE OF OSMOSIS. Perhaps the best idea put forth as to the cause of osmosis is that it represents an attempt to equate the vapor pressures[1] of two solutions of different concentrations, separated by a semipermeable membrane. The mechanism by which this equalization of vapor pressures is realized may now be considered. For the purpose of illustration (Fig. 3.5), visualize two small beakers bridged and interconnected by a U-tube in which has been interposed a semi-

[1] Liquids evaporate. The molecules which escape from the evaporating liquids constitute the vapor. If the evaporating liquid be put in an evacuated chamber connected to a manometer, the pressure of the vapor can be measured. At a given temperature within the chamber, the vapor will come into dynamic equilibrium with the liquid. The pressure exerted by this vapor in equilibrium with the liquid, the temperature of both the liquid and the vapor being the same, is termed vapor pressure.

permeable membrane. The small beakers aforementioned contain two solutions of different concentrations. The membrane is, of course, impermeable to the solute particles of either of these solutions. Now then, the less concentrated solution has fewer solute particles to interfere with the vaporization of the solvent and therefore will vaporize more rapidly than a more concentrated solution. The semipermeable membrane, consequently, becomes saturated with vapor from the less concentrated solution, but is at the same time supersaturated in reference to the more concentrated solution on the other side of the membrane. Hence, the water vapor will be distilled, as it were, through the semipermeable membrane from the less concentrated to the more concentrated solution until the hydrostatic pressure of the originally more concentrated solution is able to reciprocate in terms of the same quantity of water vapor in unit time.

Thus far we have considered the diffusion of water through a semipermeable membrane and discussed a possible cause of osmosis. Let us now turn our attention to the diffusion of solute through a semipermeable membrane.

Diffusion of Solutes. Visualize again, as in Fig. 3.6, a U-tube in one arm of which we have a 10 per cent solution of glucose and a .025 per cent ($^1/_{10}$ per cent) solution of sodium chloride, and in the other arm of which we have a 5 per cent solution of glucose and a .050 per cent ($^1/_{20}$ per cent) solution of sodium chloride. Let us say that the semipermeable membrane between the opposite arms of the U-tube is impermeable to the glucose but permeable to the water and the ions of the sodium chloride. Again, osmosis of the water molecules will occur from the side of greater solvent concentration, or the arm in which we have the 5 per cent solution of glucose and the .050 per cent solution of sodium chloride. This osmosis will take place until there is again established between the solutions in the two arms of the U-tube a dynamic equilibrium. But what about the ions of the sodium chloride? The ions of the sodium chloride will diffuse through the semipermeable membrane at a much faster rate from the region of their greater concentration, the .050 per cent solution, and will continue to do so until there obtains between the ions on the opposite sides of the semipermeable membrane an equal rate of passage; that is to say, there will be as many sodium and chloride ions passing through the semipermeable membrane from one side as from the other—and at equal rates of speed. On the establishment of equi-

librium (Fig. 3.7) between the solutions in the opposite arms of the U-tube, the respective concentrations of the glucose and the sodium chloride in each arm of the U-tube will be 7.5 per cent and .0375 per cent. The osmotic pressures of the solutions at this time will be the same, since each solution has the same concentrations of both the glucose and the sodium chloride. In general, therefore, molecules or ions will diffuse through a semipermeable membrane (one permeable to those ions or molecules, of course) from the area of their greater

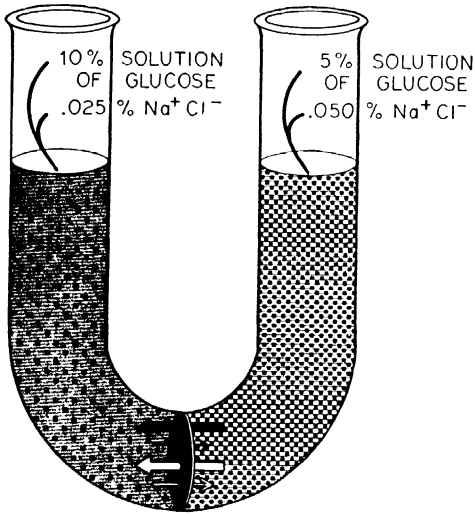


FIG. 3.6 Before dynamic equilibrium: The black arrows indicate the rate of water passage. The white arrows refer to the rate of passage of the sodium and chloride ions. The membrane is impermeable to the glucose molecules.

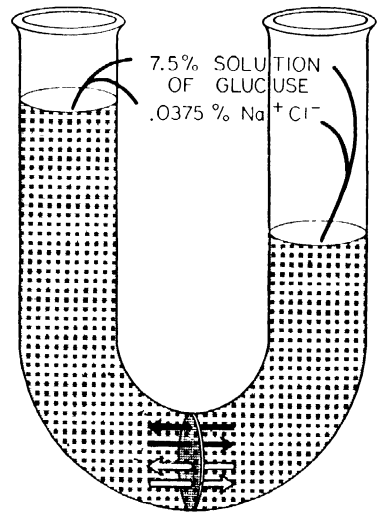


FIG. 3.7 At dynamic equilibrium (see text).

concentration to the region of lesser concentration. Further, ions or molecules will diffuse through a semipermeable membrane independently of each other, the direction of their diffusion being determined by the relative concentrations. Gas molecules also follow this pattern of diffusion through a semipermeable membrane if the latter is permeable to them.

STRUCTURE OF THE CYTOPLASMIC MEMBRANE. Before considering osmosis and the differential uptake of substances in reference to the plant cell, some knowledge as to the structure of the cytoplasmic membrane would seem desirable. From a fairly large mass of indirect

evidence, it has been theorized that the cytoplasmic membrane (also the vacuolar membrane) is composed of a bimolecular layer of lipid molecules, adsorbed to both surfaces of which is a protein layer. The lipoidal nature of the membrane is based on the observation that the cytoplasmic membrane is freely permeable to lipid-soluble substances and that it is dissolved away or destroyed by lipid solvents such as chloroform or ether. The rapid passage of water molecules through the membrane, an indication of its sieve-like nature, forms the main reason for the assumption that the membrane possesses a protein component. Whatever elasticity and mechanical resistance the cytoplasmic membrane possesses are also attributed to the protein layer.

Osmotic Relations of the Cytoplasmic Membrane. The passage of water into and out of the cell is regulated by osmotic principles, the direction of the movement being determined by the solute concentrations either within or without the cell. Should endosmosis into the cell be great because of its osmotic pressure, the great part of the influx of water will lodge in the vacuole, which will of necessity become commensurately large. Thus the hydrostatic pressure of cell content against the cell wall, or the turgor pressure, becomes correspondingly greater. The cell wall, being elastic to a limited degree, exercises a restraining influence on the pressure of the cell content and thus exerts a back pressure equal in magnitude to that of the turgor pressure. This back pressure exerted by the cell wall is called *wall pressure*. If endosmosis continues, the turgor pressure increases and tends to force water out of the cell. Now on the one hand there is continued endosmosis because of the osmotic concentration of the cell, and on the other hand the tendency for the outward movement of water becomes greater because of the increased turgor pressure. Ultimately there will be established a final dynamic equilibrium, at which time endosmosis, because of the osmotic pressure of the cell content, will equal water outgo due to the turgor pressure. It is pertinent to recall here that the osmotic pressure of the cell content decreases as the turgor pressure increases, and it is more important to realize that the turgor pressure established at the time of dynamic equilibrium is actually the hydrostatic pressure which causes as many water molecules to pass out of the cell as are coming into the cell from the external aqueous medium.

If we represent the turgor pressure by T and the osmotic pressure by P, then at the attainment of dynamic equilibrium, conditions in

the cell may be represented in the simple equation: $P - T = 0$. Obviously when $P - T$ has a positive numerical value, there must still obtain an excess of osmotic pressure to attract water into the cell. This excess of osmotic pressure is generally termed the *suction pressure* of the cell and represents the water-absorbing capacity of the cell. Suction pressure becomes a useful concept when we are confronted with the problem of water passage between two adjacent cells. Let us say that cell X lies in contact with cell Y and that the respective osmotic and turgor pressures are P_x and P_y and T_x and T_y. Upon establishment of dynamic equilibrium between the two cells, we have $P_x - T_x = P_y - T_y$. If, on the other hand, the value of $P_x - T_x$ should exceed that of $P_y - T_y$, then the cell will absorb water from X notwithstanding the absolute values of the osmotic pressures in the cells X and Y. The following example will serve to make the latter conclusion a bit clearer:

	Cell X		Cell Y
P	14 atm[1]	P	11 atm
T	8 "	T	3 "
SP	6 "	SP	8 "

Cell Y, since it has the greater suction pressure (SP), will absorb water from cell X notwithstanding the greater osmotic pressure in cell X.

Cytoplasmic Membrane and Nonionic Solutes. Nonionic solutes pass in and out of the cell according to the simple laws of diffusion. The rate of diffusion of nonionic substances seems to be governed by two factors: lipid solubility and molecular size. Lipid-soluble substances move into the cell at a much faster rate than those which possess little or no lipid solubility. Smaller lipid-soluble molecules traverse the cytoplasmic membrane at a faster rate than the larger molecules with equal lipid solubility. Water and water-soluble substances of nearly similar molecular dimensions are able to penetrate the cell at a rate faster than that anticipated on the basis of lipid solubility; in this case molecular size in reference to the porosity of the cytoplasmic membrane would seem to be the dominating factor.

[1] Pressure (force per unit area) is measured in terms of atmospheres. One atmosphere is that force which supports a column of mercury 760 millimeters (29.9 inches) in height against a vacuum. One atmosphere at sea level is equal to a force of 14.7 pounds per square inch or 1.0336 kilograms per square centimeter.

CYTOPLASMIC MEMBRANE AND IONIC UPTAKE. In contrast to the passive diffusion process which attends the absorption of nonionic substances into the cell, ions may be concentrated within the cell contrary to the simple laws of diffusion. In other words, a cell may continue to take up ions from the external medium when the concentration in this external medium is far lower than that concentration within the cell itself. Such a process of ionic accumulation against the concentration gradient is commonly referred to as *active absorption*. Since the cell must do work in the movement of ions against a concentration gradient, active absorption is a process requiring the expenditure of energy on the part of the cell. The energy to drive the process of active absorption is obtained from cellular respiration, or more simply, from the oxidation of hexose sugars in the cell.

Further, the absorption of a particular cation, say K^+, may be greater than the uptake of the corresponding anion from a particular salt, or the absorption of an anion, such as NO_3^-, may exceed the uptake of a slowly absorbed divalent cation like Ca^{++}. In any event electrical neutrality must be maintained both intracellularly and in the extracellular fluid in order to preclude the development of large electrical fields. Thus, upon the unequal uptake of a particular cation, the electrical neutrality is insured through the formation within the cell of organic acids. The organic anions stay within the cell to neutralize the absorbed cations, while the hydrogen ions from the organic acids pass into the extracellular fluid to balance the excess of anions therein that results from excess cation absorption.

On the other hand, if there should obtain an excess anion uptake from the extracellular environment, the excess anions in the cell must be balanced by ions of the opposite charge, and the excess cations in the extracellular fluids must be also compensated. When excess anions obtain within a plant cell, organic acids in that cell disappear, as a result of which the carbonic acid content of the external environment becomes proportionately increased. The carbonic acid dissociates to a limited extent into hydrogen ions and bicarbonate ions. The water of the extracellular fluid also dissociates (only slightly of course) into hydrogen ions and hydroxyl ions. The hydrogen ions from the carbonic acid and water migrate into the cell to balance the excess anions therein, while the bicarbonate and hydroxyl ions remain in the extracellular medium to compensate excess cations therein. Monovalent

cations undergo more rapid active absorption than divalent cations; similarly monovalent anions like NO_3^- are absorbed more rapidly than divalent anions such as $SO_4^{=}$.

Thus the whole process of active absorption, especially the unequal uptake of cation or anion, as the case may be, points to the flexibility of the plant cell's metabolic mechanisms whence stems the energy to drive the process of active absorption and through which adjustment of the intracellular and extracellular ionic imbalances is accomplished for the maintenance of electrical neutrality both inside and outside the cell.

Plasmolysis. Before bringing to a close our work on absorption, a few words on plasmolysis would seem desirable at this point. However, before any discussion of plasmolysis, it will be necessary to define rather briefly three types of solution in reference to the cell. First, an *isotonic solution* is one which has the same osmotic pressure as that exerted by the contents of a particular cell. Second, a *hypertonic solution* is one which has a greater osmotic pressure than the cell content. Third, a *hypotonic solution* is one which has a lower osmotic pressure than the cell content.

Now then, if we immerse a plant cell in a hypertonic solution, exosmosis exceeds endosmosis and there is a shrinkage of cell content because of the loss of water. The shrinkage of cell content which results when exosmosis exceeds endosmosis is called *plasmolysis*. In a plasmolyzed cell the turgor pressure falls to zero while the osmotic pressure increases. If, on the other hand, we place a plasmolyzed cell in a hypotonic solution, endosmosis exceeds exosmosis, with the result that the turgor pressure increases while the osmotic pressure decreases. Thus a plasmolyzed cell can be restored to its normal degree of turgor; that is to say, it has been deplasmolyzed.

Food Synthesis. After the absorption of substances from the external environment, the plant cell which possesses chlorophyll pigments is able to synthesize the raw materials of carbon dioxide and water into glucose—a process involving the transformation of radiant energy into chemical energy through the agency of chlorophyll. This represents the initial step in food synthesis and is called photosynthesis, a detailed consideration of which will be found in our discussion of the leaf, Chapter 8. The glucose which results from photosynthetic activity may be changed into proteins, fats, or other carbohydrates.

Digestion. Insoluble storage products, such as starch, fats, and certain types of protein, cannot pass from cell to cell. These molecules are too large to be diffusible. Secondly, such molecules must be soluble in water if they are to pass from one cell to another. Through the agency of enzymes, the protoplast is able to accomplish the hydrolysis of these insoluble storage products into soluble and diffusible substances. The process of rendering insoluble foods soluble and diffusible is called digestion.

Assimilation. The transformation of lipids, carbohydrates, and proteins into protoplasm is termed assimilation. Practically nothing is known as to how nonliving material is made into living substance except the fact that the conversion can only occur where living material already exists.

Respiration. The energy required to sustain the synthesis of protein and fat, to accomplish the active absorption of ions, to bring about the growth and division of the cell itself, is obtained from the oxidation of glucose and other substances. In this oxidation of glucose, oxygen is consumed; water and carbon dioxide are formed. This biological combustion of sugar involves a series of chemical reactions, a detailed description of which will be found in the chapter on plant metabolism.

Growth. Growth in reference to the plant cell is the irreversible increase in size of the cell which is effectuated by the formation of new protoplasm, accompanied by the deposition of new cell material and by the stretching of the cell under the influence of turgor pressure. Growth in the multicellular plant involves not only irreversible increase in size of the individual cells but also their multiplication by division.

Reproduction. When the volume of an embryonic cell begins to exceed the absorbing capacity of its surface area, the cell divides into daughter cells, as a result of which there is effectuated in each daughter cell a reduction in volume in reference to its surface area. This type of cell division, commonly referred to as *somatic cell division* or *equational cell division,* consists of two processes: *karyokinesis* (mitosis[1]) or division of the nucleus, and *cytokinesis* or division of the cytoplasm.

KARYOKINESIS. Karyokinesis is arbitrarily divided, for the purpose

[1] Mitosis in its loose sense is employed by some biologists to denote both the division of the nucleus and the division of the cytoplasm.

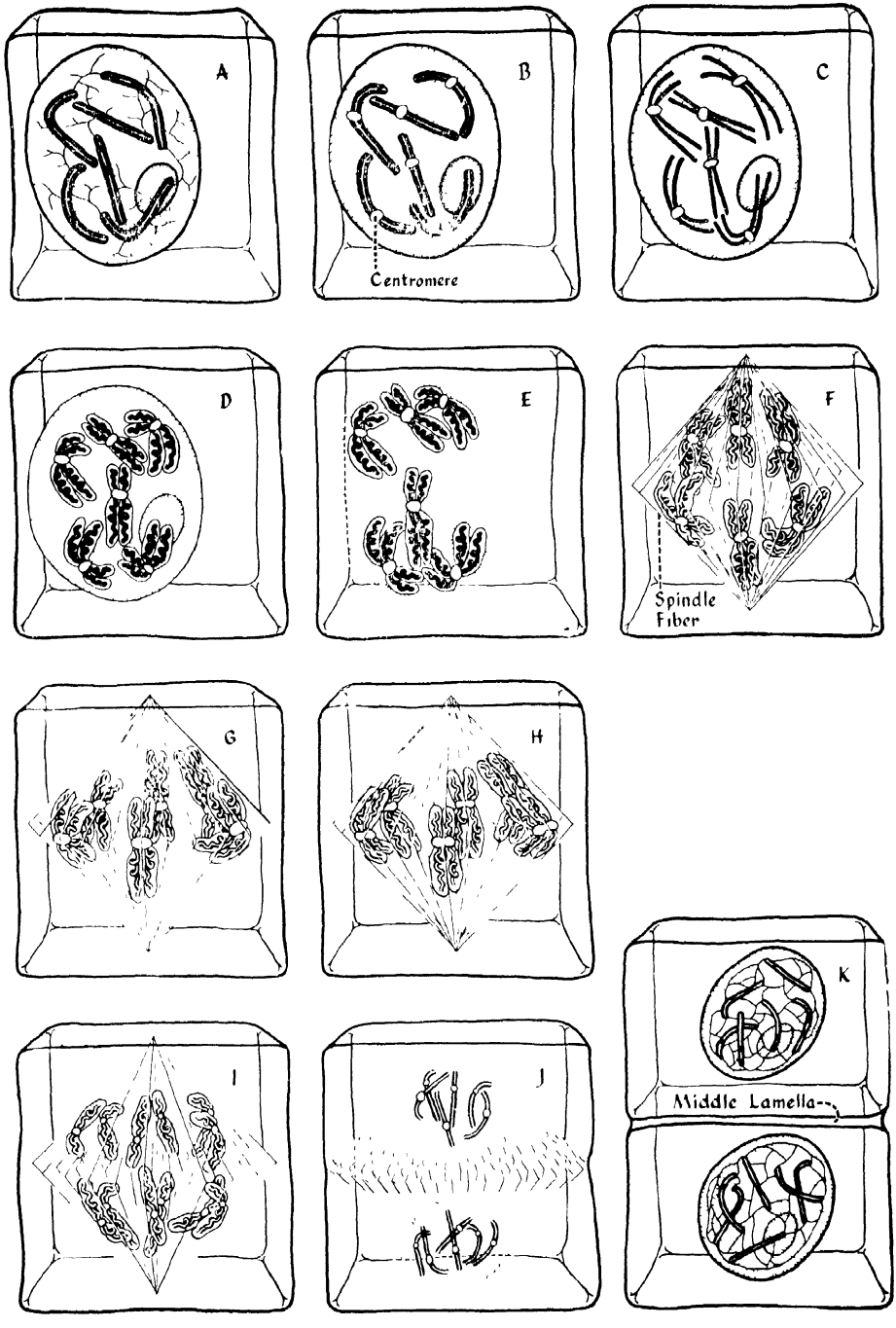


FIG 3 8 Karyokinesis (mitosis) and cytokinesis in the plant cell. (*A*) Cell with metabolic nucleus, (*B–E*) prophase, (*F*) prometaphase, (*G–H*) metaphase; (*I*) anaphase, (*J*) telophase, (*K*) formation of the middle lamella.

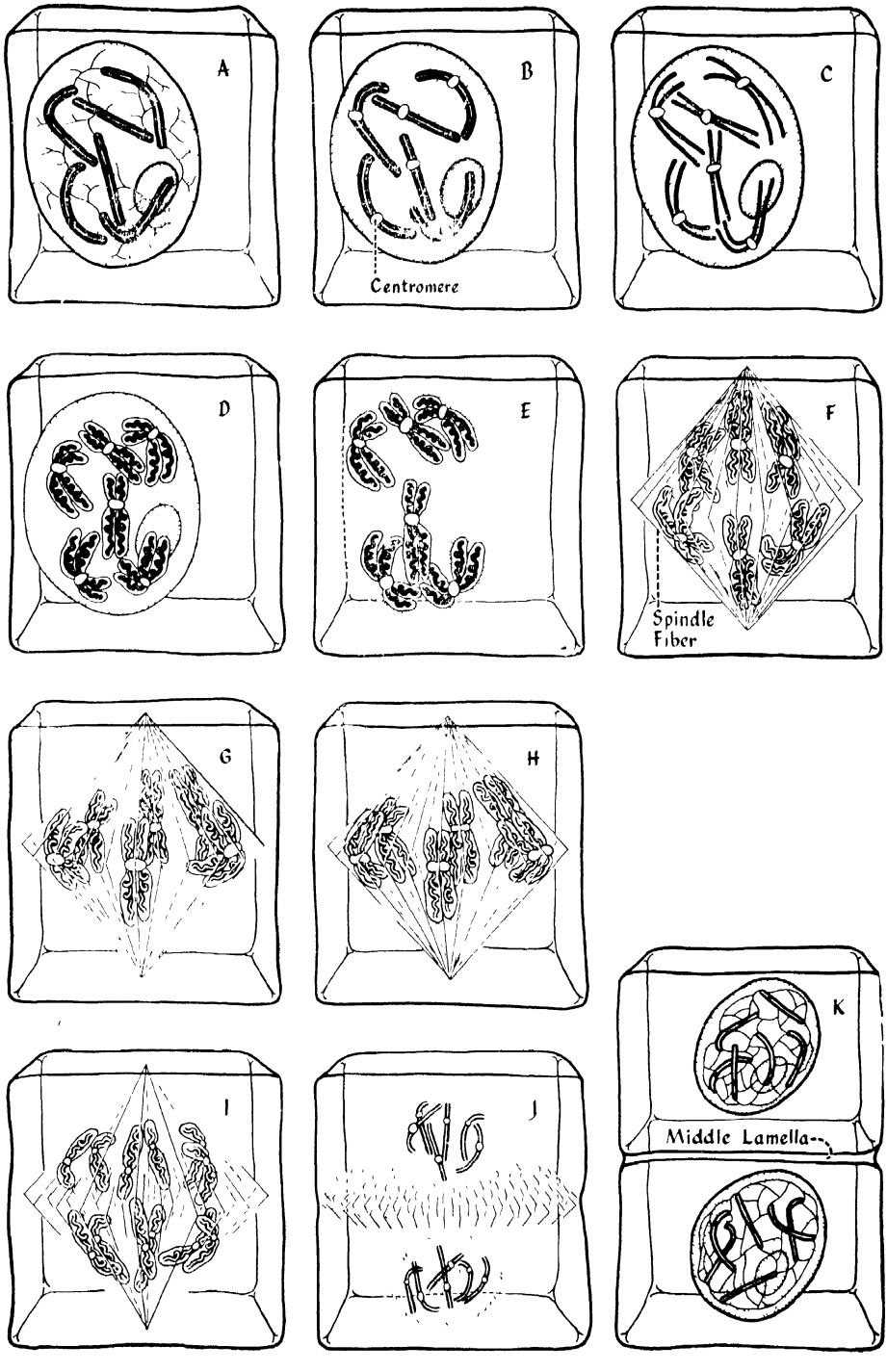


FIG. 3.8 Karyokinesis (mitosis) and cytokinesis in the plant cell. (A) Cell with

chromonemal constituents, the nuclear membrane (Fig. 3.8J) is being reconstructed; at this time the nucleoli will reappear.

CYTOKINESIS. Division of the extranuclear protoplast may occur through the formation of a cell plate (Fig. 3.8K) through the equatorial plane of the cell or by means of peripheral furrowing. The cell plate type of cytokinesis is characteristic of the somatic cells of the plants in the phylum Bryophyta and the phylum Tracheophyta. The furrowing method of cytokinesis is exemplified among certain algal and fungal organisms.

CELL PLATE. Previously it was thought that the spindle fibers remaining in the region of the equatorial plate after karyokinesis thickened to form an intermediate body called the cell plate. This plate then became longitudinally divided, it was thought, each half of the cell plate becoming the cytoplasmic membrane of the daughter protoplast to which it was adjacent. Into the intervening cleft between the cytoplasmic membranes thus formed was deposited, by the daughter protoplasts, calcium pectate to constitute the middle lamella (Fig. 3.8K). More recently, this cell plate is believed to be a transverse cleft or fluid film formed as the spindle fibers disappear from the central to the marginal area of the equatorial plate of the cell. This fluid film is believed to be formed through the fusion of many small vacuoles or droplets in the equatorial plane. Be the case as it may be, the daughter protoplasts secrete the necessary salts in the cleft or the fluid film to form the middle lamella.

FURROWING. This method of cytokinesis involves the formation of a peripheral cleavage furrow so that the cell appears to undergo a progressive constriction midway between the two poles. The potential daughter protoplasts secrete cell walls as the cleavage furrow knifes its way across the cell. What physiologically initiates the cleavage furrow is unknown at this time.

SUMMARY OF SOMATIC CELL DIVISION

Karyokinesis

(*a*) PROPHASE: Dissociation of nuclear reticulum into chromonemata, each of which is longitudinally double except at the centromere. Embodiment of the sister chromonemata with matrix to form two sister chromatids.

(*b*) PROMETAPHASE: Disappearance of the nucleoli and the nuclear membrane. Formation of the spindle. Duplication of the chromonema in each chromatid.

(*c*) METAPHASE: Arrangement of the chromosomes at the equatorial plate. Division of each centromere into two daughter centromeres. Connection or approximation of each daughter centromere to a spindle fiber.

(*d*) ANAPHASE: Movement of sister chromatids to respective poles.

(*e*) TELOPHASE: Disappearance of the matrices from chromatids. Despiralization and subsequent anastomosis of the chromonemata in each chromatid to form the nuclear reticulum. Reappearance of the nucleoli and the nuclear membrane.

Cytokinesis

By formation of the middle lamella and subsequent deposition of cellulose.

By cleavage furrowing of the cell.

Other Functions. Plant cells have other functions in addition to those already discussed. The plant cell's capacity for secretion as exemplified in the formation of enzymes and hormones, its motility as shown by certain bacteria, its capacity for reaction to external stimuli as reflected in its tropistic behavior—these functions will be considered in subsequent chapters.

Chapter 4

TAXONOMY OF PLANTS

PLANT TAXONOMY is the science which deals with the identification, nomenclature, and classification of plants. Plant taxonomy is often referred to as *systematic botany.* The recognition of an organism as similar to another of known identity or as one new to science is identification. Nomenclature is concerned with the application of the correct scientific name to an organism according to a nomenclatural system. Classification in actual practice consists of the placing of a group of organisms in its proper place within the modern plan of classification, which is based on the theory of evolution. To bring related groups of plants together in categories demands a knowledge of the gross anatomy, histology, cytology, embryology, ecology, biochemistry, and geographical distribution of extant and extinct organisms.

The method of naming organisms is called the binomial system of nomenclature. The Swedish botanist Carolus Linnaeus (1707–1778) is regarded as the father of this system, although he was not the first to employ binomials (two names). In the scientific name of an organism, the first word is the name of the genus to which the organism belongs, and it is followed by the name of the species. For example, the scientific name for the onion is *Allium cepa.* It belongs to the genus *Allium* and the species *cepa.* The generic name is capitalized and the specific name usually begins with a small letter. Thus a Latin name composed of two words is the binomial.

The scheme of classification begins with the concept of a species. Every individual plant belongs to a species, every species to a genus, every genus to a family, every family to an order, every order to a class, and so on. A species is a group of individual plants which are essentially similar in form and function and which can interbreed among themselves but not with members of other closely related species.

A group of closely related species constitutes a genus. For example, the plants which we identify as northern white pine, pitch pine, scrub pine, red pine, and ponderosa pine belong to the genus *Pinus*. An assemblage of genera which have many characters in common constitutes a family. The pine genus (*Pinus*), the fir genus (*Abies*), the spruce genus (*Picea*), the hemlock genus (*Tsuga*), and the cedar genus (*Juniperus*) belong to the pine family (Pinaceae). A group of related families constitute an order. The pine family and the yew family (Taxaceae) belong to the order Coniferales. A class is a still higher category of organisms composed of related orders. The order Coniferales belongs to the class Gymnospermae (flowering plants with naked seeds). Any collection of organisms may be divided into subordinate groups intermediate between it and that of the next lower rank. A subclass is an example of such a subordinate group.

A number of related classes constitute a subphylum or subdivision. A phylum is composed of related subphyla. The plant kingdom is composed of a number of phyla. (Some botanists prefer the term *division* to phylum.)

Summarizing, the complete classification of the northern white pine is as follows:

KINGDOM: Plant
PHYLUM: Tracheophyta[1]
SUBPHYLUM: Pteropsida[1]
CLASS: Gymnospermae
ORDER: Coniferales
FAMILY: Pinaceae
GENUS: *Pinus*
SPECIES: *strobus*
SCIENTIFIC NAME: *Pinus strobus* L.[2]

TRADITIONAL METHOD OF PLANT CLASSIFICATION

The plant kingdom, according to the system of classification in use for many years, is divided into four phyla or divisions.

A. Phylum Thallophyta. This division includes plants which are relatively simple in structure, without true roots, true stems, or true leaves and with reproductive organs which are characteristically uni-

[1] Term to be defined later.
[2] L. = Linnaeus.

cellular. The plant body is called a *thallus*. There are two subdivisions of thallophytes, the algae and the fungi. Some higher thallophytes exhibit alternation of generations. Their life cycles involve the alternation of a gametophyte generation with a sporophyte generation. The gametophyte generation reproduces sexually by fusion of sex cells or gametes. The sporophyte generation reproduces asexually by means of spores. The gametophyte produces the sporophyte by means of gametic fusion, and the sporophyte gives rise to the gametophyte by means of spores. The gametophyte generation is the conspicuous generation in the thallophytes.

1. SUBPHYLUM Algae. The algae are thallus plants which contain chlorophyll and manufacture their own food. This group includes diverse microscopic and macroscopic forms having a wide distribution. Some are aquatic, others are terrestrial. The pond scums and the seaweeds are algal organisms.

2. SUBPHYLUM Fungi. The fungi are thallus plants without chlorophyll which, with the exception of certain bacteria, cannot make their own organic foodstuffs. Bacteria, yeasts, molds, rusts, and mushrooms are fungal thallophytes.

B. Phylum Bryophyta. Bryophytes are thallus plants characterized by multicellular reproductive organs. Two classes constitute this phylum, the class Hepaticae (liverworts) and the class Musci (true mosses). The gametophyte generation is the conspicuous portion of the life cycle in the members of both classes.

Mosses are more familiar flora than liverworts, and almost all of them have a diminutive gametophyte generation with apparent stems and leaves (the apparent stems and leaves of mosses are not structurally like those of the vascular plants). A small capsule in which spores are produced, together with a long stalk and a foot embedded in the gametophyte plant, constitutes the sporophyte generation. In all bryophytes the sporophyte is dependent throughout its existence on the gametophyte. Liverworts are usually diminutive plants largely confined to moist situations, where they grow on the soil, on rocks, and on the trunks of fallen trees. Some have a thallus or plant body which is flat and leaf-like, whereas others resemble small creeping mosses in their appearance.

C. Phylum Pteridophyta. This phylum includes the ferns, the horsetails, and the club mosses. In the members of this phylum, the sporophyte generation possesses vascular tissues (aggregations of

different cells specialized for the conduction of various substances) and is the conspicuous generation. The sporophyte of the familiar fern plant is differentiated into an underground stem called a *rhizome,* leaves or fronds, and roots, and when mature leads an independent existence. It produces cells called *spores* which on germination give rise to green, flat, heart-shaped plants which reproduce sexually. The production of two types of spores (heterospory), microspores and megaspores, occurs in some members of this phylum.

D. Phylum Spermatophyta. Spermatophytes or seed plants constitute the greater and most conspicuous part of the flora of the earth. This phylum is divided into two classes, the Angiospermae and the Gymnospermae.

Vascular spermatophytes which bear cones in which are produced naked seeds are termed gymnosperms. Examples are pine, hemlock, redwood, spruce, and cedar. The pine tree with its true roots, stem, leaves, and cones is the sporophyte. It produces two morphologically different types of spores which form two kinds of gametophytes, each of which produces only one type of sex cell or gamete. The gametophytes are small and parasitic. The gametes are brought together by means of a pollen tube as in the flowering plants. The fusion cell or zygote through cell division develops into the embryo sporophyte enclosed in a naked seed.

The outstanding characteristics of the angiosperms or flowering plants are as follows: wide distribution over the earth; conspicuous sporophyte with true roots, stems, and leaves, and with flowers; heterospory; two gametophytes, male and female, which are small and inconspicuous; pollination and pollen-tube production; production of two types of gametes and their fusion or fertilization; and the production of seeds enclosed in fruits. The class Angiospermae is subdivided into two subclasses, the Monocotyledoneae and the Dicotyledoneae.

Monocotyledons have an embryo with a single cotyledon or seed leaf. Other characteristic features are: leaves with parallel veins in most species, scattered bundles of vascular tissue, absence of a true cambium, and flower parts in threes or multiples of three. Examples are the tulip, lily, onion, and corn.

Dicotyledons possess an embryo with two cotyledons. Other distinguishing features are: leaves with net venation, arrangement of the vascular bundles of the stem in a circle or of the vascular tissues

in the form of a cylinder, usually the presence of a true cambium, and in most species floral parts in fours or fives. Familiar examples are the pea, bean, rose, sunflower, oak, and birch.

MODERN CLASSIFICATION OF THE VASCULAR PLANTS

The traditional classification of plants is natural or *phylogenetic* (based on evolutionary history) only in part. The distinction between the members of the phylum Pteridophyta and the phylum Spermatophyta has been broken down by recent paleobotanical studies. Numerous researchers have established that the Pteridophyta are not a phylogenetic group. A study of the fossils of seed ferns reveals that the ferns and their allies are of polyphyletic origin and that the ferns are more closely related to the gymnosperms and angiosperms than they are to the horsetails and club mosses. All vascular plants are, therefore, grouped into a single division, the phylum Tracheophyta. The term Tracheophyta refers to the fact that all plants in this phylum have *tracheids* (a type of vascular tissue) or tracheid derivatives. The members of this phylum are distributed among four subphyla: Psilopsida, Sphenopsida, Lycopsida, and Pteropsida. All possess a dominant sporophyte and a reduced gametophyte.

The subphylum Psilopsida includes primitive vascular plants with a plant body consisting of a dichotomously branched erect stem, no roots, and no leaves or only incipient leaves. Underground stems or rhizomes which bear rhizoids may be present. The spores are of only one type. The wood or xylem consists only of tracheids, which in the more primitive types are all of the annular variety. A cambium is lacking. The Psilopsida are for the most part extinct (fossils only) with only a few forms extant (living forms).

The subphylum Sphenopsida corresponds to the class Equisetineae, or horsetails in the traditional classification, and includes fossils and living forms. True roots, stems, and leaves are present. Small wedge-shaped leaves occur in whorls at the nodes of the jointed and hollow aerial stems. Sporangia are borne in groups on stalked structures which form cones. Most horsetails exhibit homospory.

The sporophytes of the subphylum Lycopsida, or club mosses, have a plant body which is differentiated into true roots, stems, and leaves. The vegetative leaves are usually small and spirally arranged. The spore-bearing leaves or sporophylls are condensed into homosporous or heterosporous cones which are usually borne at the tips

of the stems. The sporangia or spore cases are borne singly on the top surfaces of the sporophylls. Lycopodium and Selaginella exemplify this subphylum.

The classes Filicineae (ferns), Gymnospermae (conifers and their allies), and Angiospermae (flowering plants) constitute the subphylum Pteropsida of the phylum Tracheophyta. The distinguishing characteristics of the Pteropsida are: sporophytes with true stems, roots, and leaves which are usually large; both homosporous and heterosporous forms; gametophytes independent only in the ferns; and sporophytes large and independent at maturity.

The following outline represents the system of plant classification utilized in this text:

PHYLUM Thallophyta[1]

SUBPHYLUM Algae

CLASS Cyanophyceae: blue-green algae
CLASS Chlorophyceae, green algae
CLASS Bacillariophyceae: diatoms
CLASS Phaeophyceae: brown algae
CLASS Rhodophyceae: red algae

SUBPHYLUM Fungi

CLASS Schizomycetes: the fission fungi or bacteria
CLASS Myxomycetes: the slime fungi or slime molds
CLASS Phycomycetes: alga-like fungi
CLASS Ascomycetes: sac fungi
CLASS Basidiomycetes, club fungi
CLASS Deuteromycetes, imperfect fungi

PHYLUM Bryophyta

CLASS Hepaticae, liverworts
CLASS Musci: mosses

PHYLUM Tracheophyta: vascular plants

SUBPHYLUM Psilopsida: primitive vascular plants
SUBPHYLUM Sphenopsida: horsetails

[1] In the light of modern research on the algae and fungi, some botanists regard the phylum Thallophyta as an unnatural collection of classes of unrelated organisms. They speak of the subkingdom Thallophyta and divide it into seven phyla of algae and four phyla of fungi.

SUBPHYLUM Lycopsida: club mosses
SUBPHYLUM Pteropsida:

CLASS Filicineae: ferns
CLASS Gymnospermae: conifers and their allies
CLASS Angiospermae: flowering plants

SUBCLASS Dicotyledoneae
SUBCLASS Monocotyledoneae

Chapter 5

PLANT TISSUES AND STEMS

Plant Bodies. The bodies of plants are either unicellular or multicellular in nature. A unicellular plant consists of a single cell or a colony of cells. Plant colonies are aggregations of unicellular organisms of the same species, the individual cells of which can carry on their vital activities even when separated from all the other cells of the colony. Most colonies show no architectural differentiation, but in a limited number the cells are differentiated into vegetative and reproductive cells. The bodies of most plants are composed of innumerable cells, and there is extensive differentiation in morphology and function among the component cells; that is, various types of tissues are present.

The shoot and the root constitute the principal parts of the plant body of the flowering seed plant. The shoot is usually aboveground, is generally branched, and is composed of the stem and its appendages, the foliage leaves, and the reproductive structures (flowers). Roots, stems, and leaves are the vegetative organs of the body of the flowering seed plant and are concerned with the intake of water and inorganic salts, the fabrication of foodstuffs, and their utilization for maintenance and growth. Flowers, in the strict sense, are aggregations of reproductive structures concerned with the fundamental process of sexual reproduction which leads to seed formation.

The stem is typically an aerial organ, which may be erect and unbranched, bearing leaves and reproductive organs on a single vertical axis, or may be much branched, with several axes of approximately equal size. It serves as a mechanical support for the leaves, flowers, and fruits, and furnishes a path of conduction between these organs and the roots. Externally, the stem is recognizable by the nodes and internodes. The usually slightly enlarged portions of the stem from which leaves and buds arise are called *nodes*. The interval of

stem between two successive nodes is an *internode.* Foliage leaves are usually expanded and dorsiventrally flattened lateral protuberances from the stem which perform the photosynthetic function.

Roots are primary organs of the vascular plant which are typically subterranean and whose primary functions are anchorage and the passive and active absorption of ions and molecules from the soil. They are not divided into nodes and internodes, and branches arise irregularly.

Definition and Classification of Buds. A bud (Fig. 5.0) is a short segment of undeveloped stem with nodes and internodes and with rudimentary leaves in various stages of development compactly arranged around it. The most important feature of a bud is the small mass of meristematic tissue, the growing point, which constitutes the very tip of stem within the bud, together with the leaf primordia about it. Scaly buds (Fig. 5.0) have their outer rudimentary leaves transformed into scales to protect them from climatic changes. Buds which lack these scales are said to be naked and are generally limited to the tropical regions.

According to their position on the stem, buds are classified as terminal, axillary, and adventitious. A *terminal bud* (Fig. 5.0) is one which is located at the tip of a stem. It is largely through elongation of the internodes of this bud that the stem increases in length. An *axillary bud* (Fig. 5.0) is one which arises in a leaf axil, that is, in the upper angle between the leaf stalk and the stem. It may give rise to a leafy branch, to a flower, or to both. Axillary buds may be classified according to the number at a node into (1) alternate, with a single bud at a node, (2) opposite, with two buds at a node on opposite sides of the stem (Fig. 5.0), and (3) whorled, with more than two buds at each node. Buds which arise anywhere on the plant except at the tips of stems or in the axils of leaves are called *adventitious buds*

Buds may be classified according to the nature of the structures produced by them into (1) leaf buds, (2) flower buds, and (3) mixed buds. Leaf buds develop into a leafy shoot. When a leaf bud is an axillary bud, it is properly called a branch bud (Fig. 5.0). A flower bud produces one or more flowers. A branch bearing both foliage leaves and flowers develops from a mixed bud.

On the basis of their activity, buds may be divided into (1) active buds and (2) dormant buds. Buds which grow are said to be active,

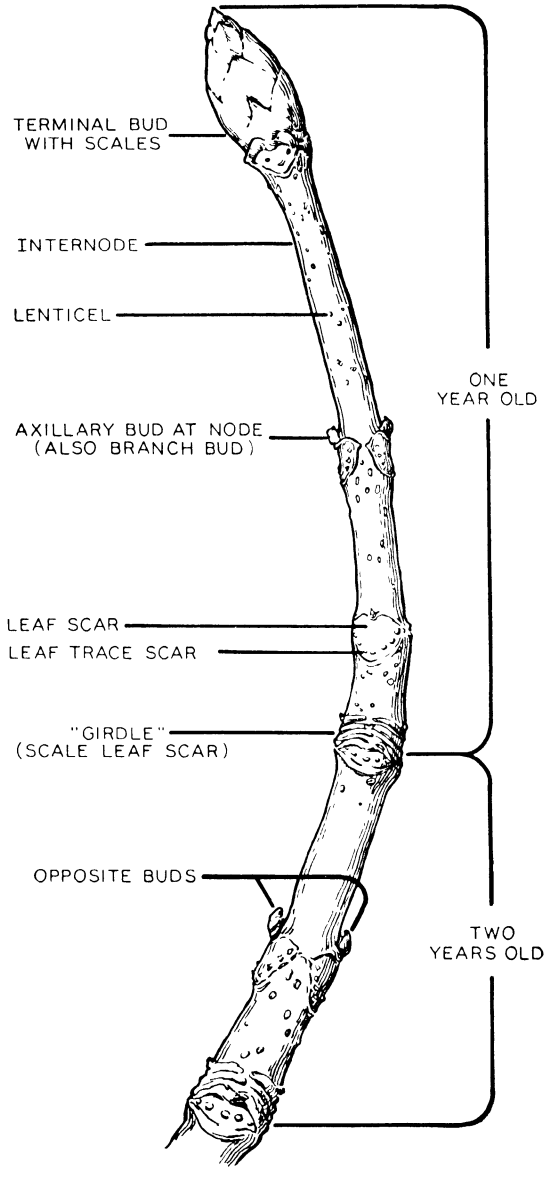


FIG. 5.0 Stem of horse chestnut (*Aesculus hippocastanum*) in winter condition.

while those which remain inactive are said to be dormant. Very often, dormant buds remain inactive throughout their existence.

Deciduous Plants. A deciduous plant is one whose shoot sheds its leaves each fall and so remains bereft of foliage throughout the winter. The oak (*Quercus*), the maple (*Acer*), and the elm (*Ulmus*) exemplify such deciduous plants. Most of our forest trees, with the exception of the gymnosperms such as the spruce (*Picea*), pine (*Pinus*), and fir (*Abies*), are deciduous.

A deciduous plant in winter condition, as illustrated by the woody stem of the horse chestnut (*Aesculus hippocastanum*), is presented in Fig. 5.0. A large, scaly, resin-coated structure, the terminal bud, is located at the tip of the twig. Arranged in alternating pairs on the sides of the twig are the axillary buds, and below each one is a large shield-shaped mark, the *leaf scar*. These marks were left by the breaking away of the leaf stalks from the twig during the preceding autumn. Near the margin of each leaf scar are seven small dot-like raised areas called the *leaf-trace scars*. They are the broken ends of the leaf traces or vascular bundles which ran from the twig into the leaf stalk.

When the scales of the terminal bud are shed in the spring as the bud develops into a new shoot, a ring or girdle of terminal-bud-scale scars is left. The segment of the twig between two successive girdles indicates a year's growth.

Scattered over the surfaces of the twig are slightly raised areas called lenticels. They permit an exchange of gases between the atmosphere and the tissues of the stem.

Life Span of Seed Plants. On the basis of length of life and the time required to complete the life cycle, seed plants may be classified as annuals, biennials, and perennials.

An *annual* is a plant which completes its life cycle within a single year. Corn (*Zea mays*) and wheat (*Triticum vulgare*) are examples of annual plants. Fruit and seed are produced in one growth season, and thus the species is maintained from generation to generation. In a *biennial* plant such as the cultivated beet (*Beta vulgaris*) the life cycle is normally completed within two years. For biennials the vegetative period extends through two growth seasons, but seed production occurs only during the second growth season. Plants which have a life span of more than two years duration are called *perennials*. After a period of one or more years of vegetative activity, reproduction occurs, and thereafter both vegetative and reproductive activities nor-

mally occur each year of the plant's existence. The privet plant (*Ligustrum*), a shrub commonly used for ornamental hedges, is a perennial plant.

PLANT TISSUES

Before entering upon a study of a seed plant or any vascular plant in the phylum Tracheophyta, whether the organ of the plant be stem, root, or leaf, it will be necessary to have some knowledge of the tissues that compose these organs.

A plant tissue is an aggregation of structurally similar cells with a common function. The sporophyte generation of the multicellular vascular plants begins its existence as a single cell, the *zygote,* or fertilized egg. As a result of repeated cell division of the zygote, there arises a group of undifferentiated cells which collectively constitute embryonic (or meristematic) tissue. In the early embryonic development of the sporophyte, mitotic cell division occurs throughout the young organism; but as the embryo enlarges, the process of growth becomes restricted to certain parts of the plant body. Hence the adult plant is composed of embryonic and mature or permanent tissues. The mature tissues are derivatives of the meristems which have undergone differentiation. Some mature tissues reacquire meristematic potentialities.

The tissues of vascular plants are:

A. Meristematic or Embryonic Tissue. Meristematic cells are usually small, thin-walled, approximately isodiametric, rapidly dividing cells, with large nuclei and lack of conspicuous vacuolation. Intercellular spaces are generally absent.

Apical or terminal meristem, responsible for growth in plant length, occurs at the apices of roots and stems and through cell division gives rise to the three primary meristems, from which the primary permanent tissues are derived. Lateral meristems, such as the vascular cambium and the cork cambium, are arranged parallel with the sides of the stem or root in which they occur and are responsible for increase in the diameter of these plant organs. Tissues derived from lateral or secondary meristems are termed *secondary permanent tissues.*

The alterations which commonly occur in cellular differentiation are: change in shape and size of cell; change in wall structure and its chemistry, increased degree of vacuolation; accumulation of non-

protoplasmic substances in the cytoplasm; and in many instances the development of plastids.

B. Epidermis. The epidermis (Fig. 5.1) is the superficial or outermost living layer of cells of all organs of the primary plant body. In

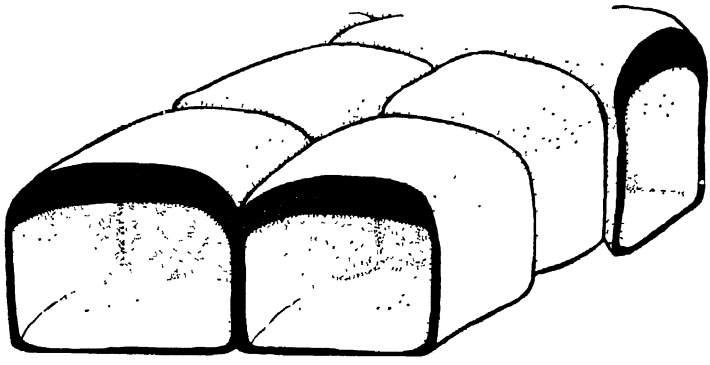


FIG. 5.1 Stereoscopic view of epidermis. Note that the outer walls of the cells are generally thickened and convex.

the stems and roots of many plants, where a cork cambium develops and cork is formed, the epidermis is destroyed. In leaves and young green stems, apertures, termed *stomata*, occur in the epidermis. They are surrounded by specialized epidermal cells called *guard cells*. The guard cells contain chloroplastids.

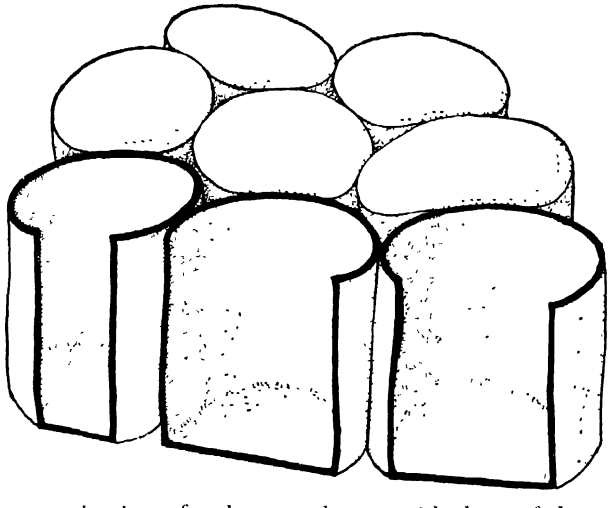


FIG. 5.2 Stereoscopic view of pith parenchyma, with three of the cells in tangential aspect.

The epidermal cell proper varies in shape and size in different plants and in some cases with position upon a plant organ in the same plant. The outer wall of the cell is frequently thickened and is in most cases impregnated and covered on its outer surface by a fatty substance called *cutin*. The cutin on the outer surface of the cell is termed the *cuticle*. Chloroplastids are absent, but pigments may be present in the cell sap. Unicellular or multicellular epidermal appendages, *trichomes* or epidermal hairs, of diverse shape and function may be present. Functions performed by the epidermis are mechanical protection, restriction of water loss, gaseous exchange through the stomata, absorption of water and mineral salts (by root epidermis), and photosynthesis (by guard cells).

C. Parenchyma. This fundamental or ground tissue, in which the other tissues are imbedded, is composed of relatively undifferentiated living cells. The cells are thin-walled and polyhedral in shape and have a large central vacuole in most instances. Intercellular air spaces are generally present. Parenchyma (Fig. 5.2) is the principal site of food and water storage, food manufacture (by photosynthetic parenchyma, or *chlorenchyma*), excretion, secretion, and assimilation. The parenchyma cells in vascular or conductive tissue assist in the transportation of water and food.

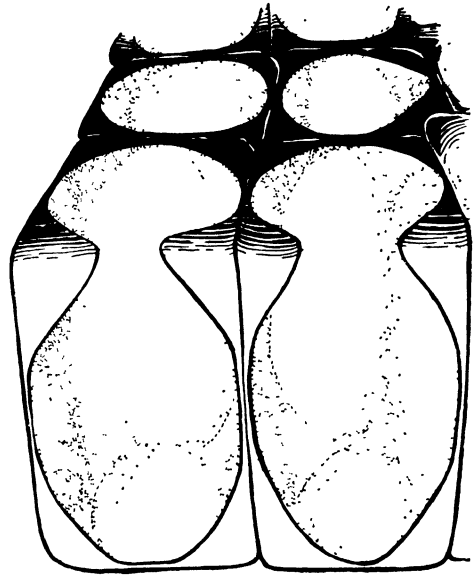


FIG. 5.3 Stereoscopic view of collenchyma, with two cells tangentially sectioned.

D. Collenchyma. The first mechanical or supporting tissue to appear in stems, leaves, and flower parts is collenchyma (Fig. 5.3). It is usually present immediately beneath the epidermis. The cells are living, closely packed, and of varying length, but in all cases polygonal in transection, and have a characteristic cellulose thickening of the cell walls at the cell corners or angles.

E. Sclerenchyma. This is a generic term for sclerenchyma fibers

and stone cells. Sclerenchyma is a supporting and strengthening tissue whose lignified, thick-walled cells protect the softer tissues from injury. At maturity the cells are without protoplasmic content.

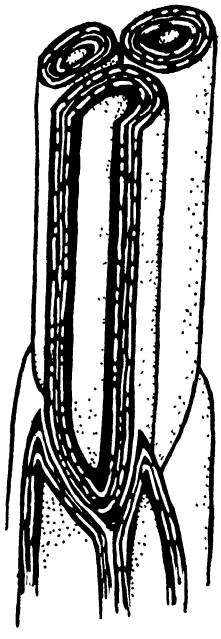


FIG. 5.4 Sclerenchymatous fibers in stereoscopic view.

(1) *Sclerenchyma fibers* (Fig. 5.4) are elongated spindle-shaped cells, usually with tapering ends. In transverse section, they are rounded, polygonal, or rectangular and have a small lumen. They occur in various parts of plant organs and are classified, according to the region of the organ where they occur, into xylem fibers (in wood or xylem), phloem fibers (in the bast or phloem), pericycle fibers (in the pericycle), and cortical fibers (in the cortex). Fibers are of economic importance, since they are used in the manufacture of rope, twine, and various textiles such as linen.

(2) *Stone cells* (Fig. 5.5) are more or less isodiametric, with thickened walls about a central lumen. Radial pore canals lead outward from the lumen to the middle lamella of the cell wall. Stone cells are found especially in fruits, seeds, and the bark of trees. The gritty particles in the fruit of the pear are aggregations of stone cells.

F. Xylem. The xylem or wood is a type of vascular tissue which is principally concerned with the upward conduction of water and inorganic salts. It is not a tissue in the structural sense, since as many as four elements may be present. They are xylem fibers, xylem parenchyma, tracheids, and tracheal tubes or vessels. Only the latter two need be described.

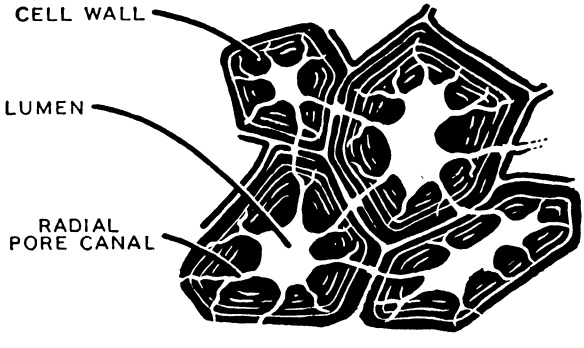


FIG. 5.5 Stone cells.

Tracheids (Fig. 5.6) are elongated cells with tapering ends, without protoplasmic contents when mature, and with lignified cell walls. The walls of tracheids exhibit various strength-giving, thickening patterns and on this basis are divided into the following types: spiral, with spiral thickenings; annular, with ring-like thickenings; scalariform, with ladder-like thickenings; reticulate, with net-like thickening; pitted, with thin areas in the wall; and bordered pitted, with areas of thickening about the pits.

Tracheal tubes are long, nonliving cylindrical tubes with lignified walls formed by the digestion of the transverse walls between elongated cells placed vertically end to end. They exhibit the various thickening patterns shown by tracheids.

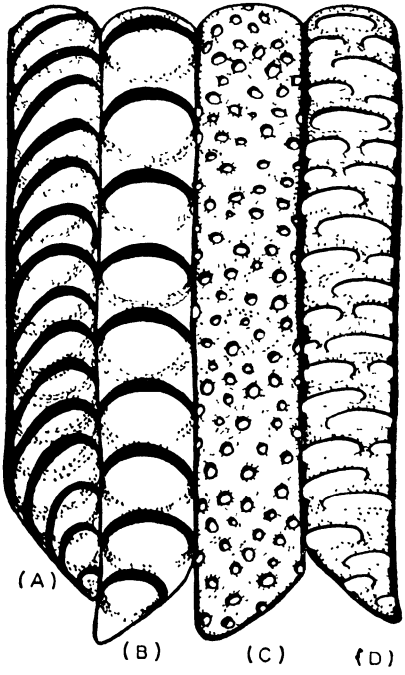


FIG. 5.6 Tracheids in longitudinal aspect. (A) spiral, (B) annular; (C) pitted, (D) scalariform.

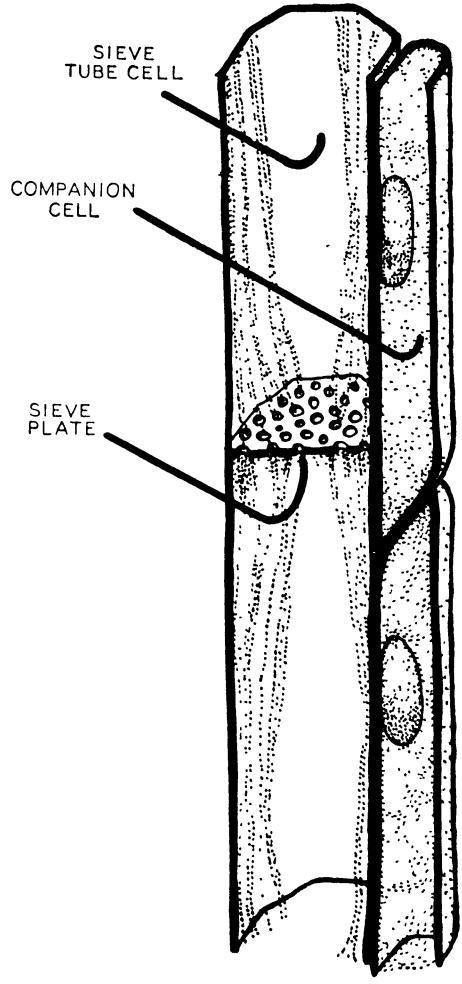


FIG. 5.7 Stereoscopic view of sieve-tube and companion cells in tangential aspect.

Tracheids and tracheal tubes function in conduction and in support.

G. Phloem. The principal food-conducting tissue of the vascular plants is the phloem. Like the xylem, it is not a tissue in the structural sense, since as many as four different kinds of cells may be present. They are phloem parenchyma, phloem fibers, sieve tube cells, and companion cells.

Sieve-tube cells (Fig. 5.7) are elongated and cylindrical and while living at maturity lack a nucleus. They are generally placed vertically end to end, and the end walls are perforated to form the sieve plates. The sieve tubes thus formed contain cytoplasm which is continuous from one sieve-tube cell to the adjacent ones in the tube through perforations in the sieve plates.

Companion cells (Fig. 5.7) border the sieve-tube cells. The number associated with a given sieve-tube cell may vary from one to several. They may be as long as or shorter than the sieve-tube cells which they border. Cytoplasm and nucleus are present at maturity, and the cytoplasm is generally continuous with that of the sieve-tube cell through pores occurring in the lateral walls of both elements.

H. Cork or Phellem. In the stems and roots of many vascular plants, the epidermis is replaced by a complex protective tissue termed the *periderm*. The periderm consists of three tissues: an intermediate meristematic tissue, the cork cambium or phellogen; an inner parenchyma or phelloderm; and an outer tissue termed the cork or phellem.

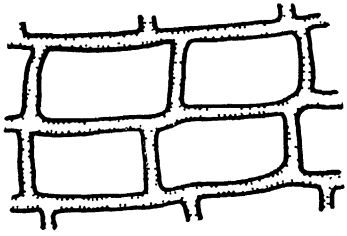


FIG. 5.8 Cork tissue in cross section. Suberin is stippled.

Cork (Fig. 5.8) is a protective tissue composed of compactly arranged cells approximately prismatic in shape, devoid of protoplasm when mature, and arranged in radial rows. Intercellular spaces are absent. The cell walls contain a waterproof substance called *suberin*. Cork protects the underlying tissues against mechanical injury and against excessive loss of water.

STEMS

Types of Stems. Stems which grow above the soil are called aerial stems while those which grow underground are termed subterranean stems.

Aerial stems may be classified as erect, climbing, and creeping or prostrate. The stems of most plants are erect, but the stems of such plants as the strawberry (*Fragaria*) and the cucumber (*Cucumis*) grow horizontally over the surface of the soil. A climbing stem grows upward by attaching itself to some support. Plants with climbing stems are termed lianas. Examples are the grape (*Vitis*) and the English ivy (*Hedera helix*).

There are various types of underground stems, the elongated underground stem of the fern being termed a *rhizome*. The enlarged fleshy end of a rhizome is called a *tuber* and is represented in the common potato. The short underground stems are either *bulbs*, as exemplified in the onion and tulip; or *corms*, as illustrated in gladiolus or crocus. The subterranean stems will be considered in some detail in the latter part of this chapter.

Herbs, Shrubs, and Trees. These terms are frequently employed in reference to plants. Some distinction may be made here as to these common terms of classification.

An herb is a plant whose stem does not develop much woody tissue and, therefore, remains soft and succulent. The plant usually dies, at least down to the soil, after flowering. Herbs may be either annual, biennial, or perennial

A shrub is a woody perennial plant, usually smaller in height than a tree, in which several aerial stems of nearly the same size arise from the root system.

A tree is a woody perennial plant with a single main stem or trunk which attains a considerable height above the soil before it branches. In trees there are two types of branching, excurrent and deliquescent. When the trunk extends vertically upward to the top of the tree, as in pines, the branching is said to be excurrent; when the main stem does not continue to the top but divides into several more or less equal branches, as in oak, it is said to be deliquescent.

Aerial stems on the basis of structure may be divided into two types, herbaceous and woody. Herbaceous stems are green and are relatively soft in texture; are readily broken, have little woody tissue; and, for the most part, have a life span of one season of growth. Examples are the monocotyledonous corn stem (*Zea mays*) and the dicotyledonous sunflower stem (*Helianthus annuus*). Woody stems, especially when they are older, are harder, thicker, rougher in surface appearance, and larger in diameter than herbaceous stems. Most

stems of this type are perennial and are composed largely of wood. They are illustrated by the American linden (*Tilia americana*) and the pine (*Pinus*).

Sectioning a Stem for Study. Before entering into a study of the development and microscopic anatomy of aerial stems, it would seem desirable to consider the various ways in which a stem may be cut for microscopic examination. A stem may be sectioned for study in three planes: transverse, tangential, and radial.

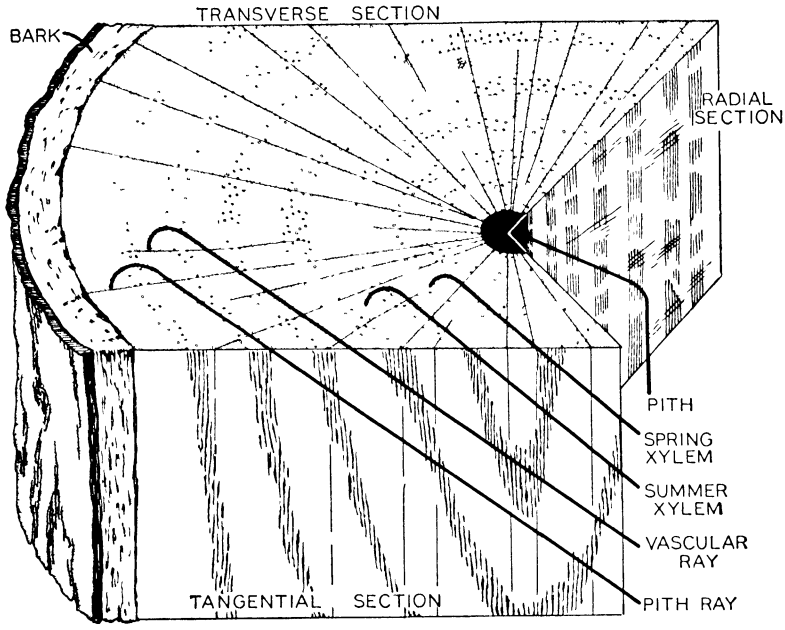


FIG 5.9 Various sections of stem. Macroscopically discernible areas have been labeled.

A transverse section (Fig. 5.9), commonly referred to as a cross section, is cut at right angles to the longitudinal axis of the stem.

A tangential section (Fig. 5.9) is actually a longitudinal section. It is cut parallel to the longitudinal axis of the stem and at right angles to the radius passing through the plane of section. Such a tangential section is often referred to in the lumberman's vernacular as a "plain-sawed section."

A radial section (Fig. 5.9) is also a longitudinal section. It is parallel to the longitudinal axis of the stem and parallel to the radius

passing through the plane of section. In the lumber mill it is generally called a "quarter-sawed section."

Obviously the tangential section is at right angles to a radial section.

Development of the Dicot Stem. For a clear understanding of development in a dicotyledonous stem, some recourse must be had to the structure of the embryo of a seed plant. The embryo (Fig. 5.10) may be briefly considered here as comprising four parts: the hypocotyl, the cotyledons, the plumule, and the radicle. The hypocotyl is that part of the longitudinal axis of the embryo below the point of

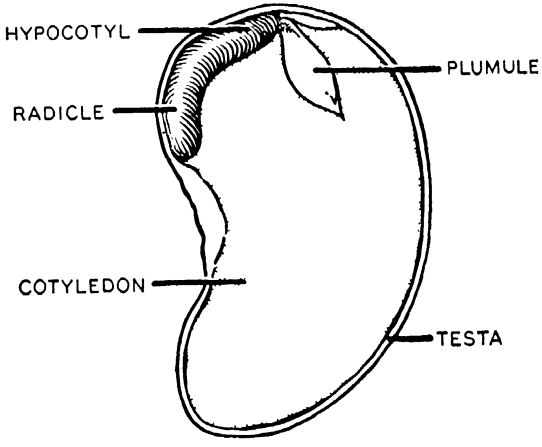


FIG. 5.10 Seed of the common bean (*Phaseolus vulgaris*) dissected to show parts of the embryo.

attachment of the cotyledons. The cotyledons are the seed leaves and function either as food-storage organs or as food-absorbing organs. These cotyledons are quite different morphologically from the ordinary leaves of the plant. The plumule, sometimes called the rudimentary stem, is that part of the embryo above the point of attachment of the cotyledons. The radicle, or rudimentary root, is that part of the embryo which develops from the lower end of the hypocotyl and extends beyond the peripheral margins of the enclosing cotyledons.

The stem begins its development in the plumule. The plumule is a mass of undifferentiated meristematic tissue, which we shall call the *promeristem* (apical meristem). However, this same mass (Fig. 5.11) of meristematic tissue may be found in the terminal bud (Fig. 5.11)

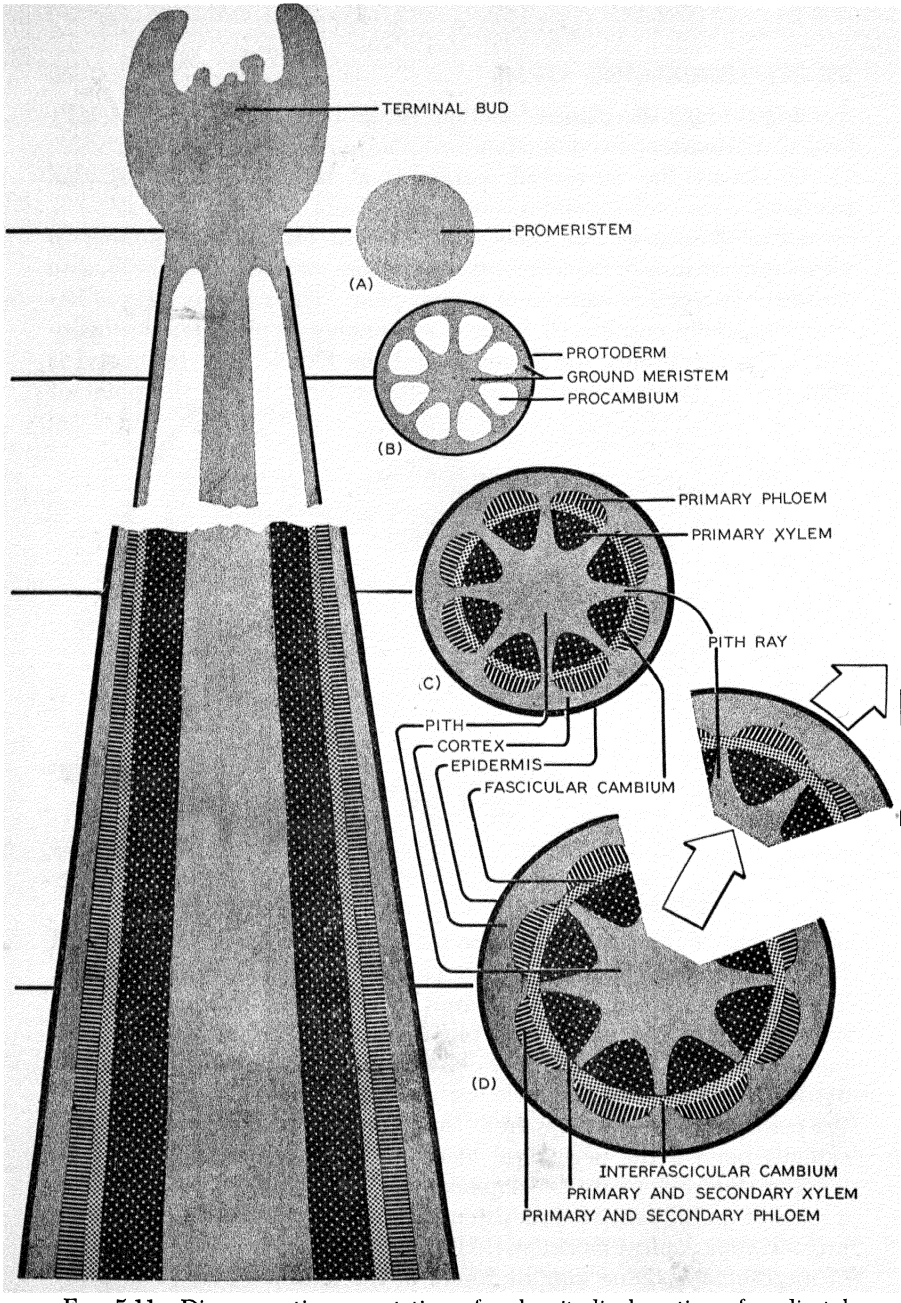


FIG. 5.11 Diagrammatic presentation of a longitudinal section of a dicotyledonous stem, with cross sections through the various developmental areas: (A) cross section through the promeristem, (B) cross section through the zone of elongation showing the elaboration of the three primary meristems; (C) cross section through the zone of primary development; (D) cross section through region of secondary development or lateral growth.

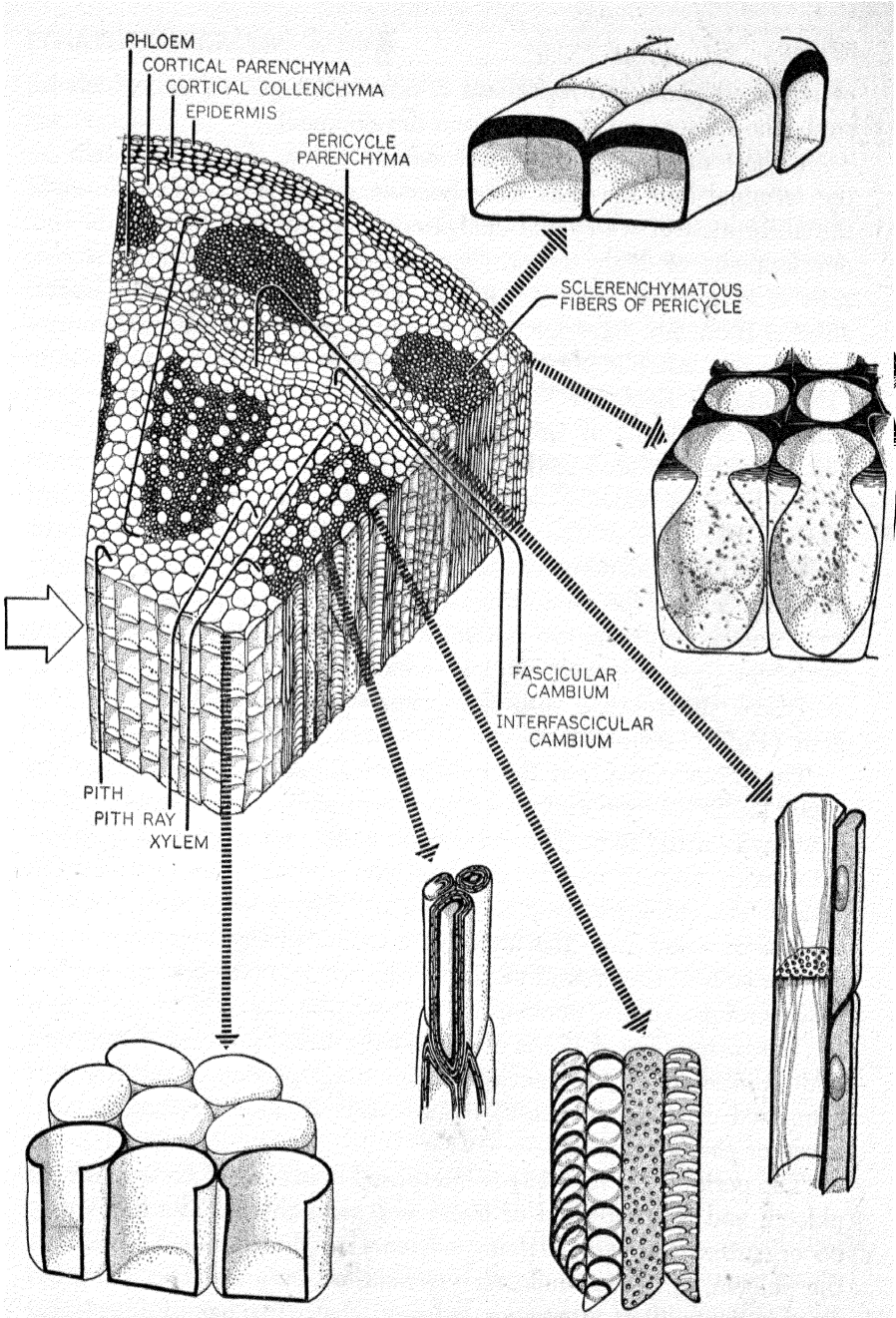


FIG. 5.12 Stereoscopic view of a dicotyledonous stem, herbaceous type, with various types of plant tissues indicated for proper orientation.

of any seed plant and represents a convenient point from which to study the subsequent stages in stem development.

A short distance (a few millimeters) below the promeristem in the terminal bud the cells have become greatly vacuolated through the absorption of water and elongated longitudinally because of the development of high turgor. This region is generally termed the *zone of elongation* (Fig. 5.11). The cells in this zone are no longer alike in form, but have become differentiated into three readily discernible regions. The outermost layer of cells is called the *protoderm* (Fig. 5.11B). Enclosed by the protoderm is the *ground meristem* which is composed of thin-walled isodiametric cells (Fig. 5.11B). Circularly intercalated in the ground meristem are groups or strands of smaller cells which collectively constitute the *procambium* (Fig. 5.11B). The cells of the procambium, while smaller in transverse section, are considerably longer in longitudinal aspect than the surrounding cells of the ground meristem. The protoderm, ground meristem, and procambium are generally referred to as the *primary apical meristems.* Just below the region of elongation, these primary apical meristems differentiate into the primary permanent tissues of the stem (Fig. 5.11C).

The protoderm forms the epidermis (Fig. 5.12) of the stem. In young stems the epidermis is a single layer of cells forming the outermost layer of the stem. The outer walls of these cells may be impregnated with cutin or may be overlaid with a layer of cutin called the cuticle. The cutin is a waxy substance and decreases to a great extent the loss of water from the underlying tissues of the stem.

The cells of the ground meristem differentiate into four permanent tissue groups: cortex, pericycle, pith, and pith rays.

The cortex (Fig. 5.12) is enclosed externally by the epidermis and limited internally by the pericycle. The outer portion of the cortex is composed of collenchymatous tissue, while its inner portion is composed of parenchyma.

The pericycle (Fig. 5.12) is interposed between the cortex and the phloem and is constituted of fibers and parenchyma. The fibers may be organized into groups lying adjacent to the peripheral limits of the phloem, as in the sunflower (*Helianthus annuus*). The parenchymatous tissue then intervenes between these patches of fibers that lie externally adjacent to the phloem. However, in stems like Dutchman's-pipe (*Aristolochia sipho*), the pericycle fibers may be formed

into a continuous ring circumjacent to the parenchymatous tissue of the region.

The pith (Fig. 5.12) is the central area of parenchymatous tissue in the stem. The cells are characteristically large.

Pith rays (Fig. 5.12) are actually radial ramifications of the pith parenchyma that extend outward to the pericycle in those dicot stems in which the procambial strands have developed into separate vascular bundles. Pith rays are commonly seen in young *Helianthus* stems and are extended during secondary growth in *Aristolochia*.

The procambial strands may become differentiated into a continuous cylinder of vascular tissue (Fig. 5.13) or into separate aggregations of vascular tissue called vascular bundles. Between the vascular bundles intervene the pith rays (Fig. 5.12). This vascular tissue, whether it is disposed in the form of a cylinder or broken up into separate vascular bundles, is composed of two major areas of vascular tissue, the phloem, derived from the outer procambial cells; and the xylem, derived from the inner procambial cells. The phloem lies immediately subjacent to the pericycle and is functionally concerned with the translocation (chiefly downward) of food through the stem. The xylem is functionally involved in the upward conduction of water and inorganic salts through the stem.

The phloem (Fig. 5.12), also called *bast*, comprises sieve tubes, companion cells, some parenchyma, and phloem fibers (in woody dicots).

The xylem (Fig. 5.12), also called *wood*, is composed of tracheal tubes, tracheids, xylem fibers, and parenchyma.

Between the phloem and the xylem there occurs a single layer of cells that retains the meristematic capacities of the procambium. This single layer of meristematic tissue, since it is intercurrent between the major areas of vascular tissue, is called the vascular cambium (Fig. 5.12) and is regarded as a secondary (lateral) meristem since it will subsequently be concerned in secondary growth or increase in thickness. When this vascular cambium is limited to individual vascular bundles, it is called fascicular cambium.

All of the developmental modifications that have eventuated from the promeristem to the elaboration of the primary permanent tissues constitute primary growth (Fig. 3.11C). Increase in the length of the stem, or apical growth, is restricted to that part of the stem where primary growth occurs. Primary growth generally reaches its comple-

tion in a matter of months, while secondary growth may extend over a broad expanse of years or even centuries.

Secondary Growth of the Dicot Stem. In those stems in which the vascular tissue is broken up into distinct vascular bundles, as in *Helianthus* or *Aristolochia,* the cambium is not in the form of a continuous ring. For secondary development to take place in such stems, the cambium is generally formed into a continuous ring by the production of an interfascicular cambium (Figs. 5.11D and 5.12). In the formation of the interfascicular cambium, certain cells in the parenchyma of the pith ray between the vascular bundles become meristematic and form an interconnecting layer of cambium.

The cambium by tangential division (i.e., the cell divides at right angles to the radius) adds new xylem (secondary xylem) to the outside of the primary xylem and new phloem (secondary phloem) to the inner part of the primary phloem. In this tangential division of the cambium a cambial cell divides along its tangential axis, the inner daughter cell becomes differentiated into a xylem element while the outer daughter cell remains a cambial cell. Relatively less frequently the outer daughter cell becomes a phloem element, the inner daughter cell retaining meristematic potential. Consequently, considerably more secondary xylem results in this manner than secondary phloem. To adapt itself to the greater increase of xylem tissue on its inner side and to preserve its own continuity of structure, the cambium must increase its own circumferential dimensions. The cambium accomplishes an increment in its own circumference by a radial division of its cells; that is to say, some of the cambial cells undergo an oblique division, with the ends of the daughter cells slipping by each other. On the other hand, the interfascicular cambium contributes to secondary growth in two ways: it may divide tangentially, as in *Aristolochia,* to form radially elongated parenchymatous cells which are added to those of the pith ray, thus preserving the radial continuity of the tissue of the pith rays and insuring transverse conduction between the pith and the pericycle; or by tangential division, as in the older part of a *Helianthus* stem, it may produce between the original vascular bundles secondary vascular bundles, so that the entire vascular tissue eventually becomes consolidated into a ring or cylinder surrounding the pith.

With the production of secondary phloem and xylem, the inner-

most area of the xylem becomes further removed from the outermost parts of the phloem. To insure proper radial conduction between these areas of the vascular tissue, the cambium, after its production of secondary phloem and xylem, undertakes by tangential division the production of radially elongated parenchymatous cells which extend as narrow radial bands of tissue into both phloem and xylem. These ribbon-like extensions of parenchyma into the phloem (phloem rays) and into the xylem (xylem rays) are collectively called vascular rays. These vascular rays are not to be confused with the pith rays. Some distinctions between the pith rays and the vascular rays would seem warranted at this time. First, a pith ray is differentiated during primary growth, while a vascular ray is developed during secondary growth. Secondly, a pith ray extends longitudinally from node to node, while a vascular ray extends longitudinally for only the depth of a few cells. Thirdly, the pith rays extend radially from pith to pericycle, while the vascular ray is limited to the confines of the vascular tissue.

Periderm Formation. Coincidental with, or sometimes subsequent to, the activity of the vascular cambium, periderm (Fig. 5.13) formation occurs in the peripheral area of the stem. It consists of three layers of tissue: the cork (phellem), the cork cambium (phellogen), and the phelloderm. These tissues are formed in the following way. The cells of the cortical collenchyma, generally those just below the epidermis, become meristematic and form a cork cambium (Fig. 5.13). This cork cambium by tangential division of its cells produces daughter cells, the outer daughter cells ultimately differentiating into cork tissue (Fig. 5.13) by suberization and the inner ones retaining their meristematic capacity to perpetuate the cork cambium. Rather less frequently the inner daughter cells will become differentiated into parenchymatous cells that are added to the cortical collenchyma, while the outer daughter cells remain cambial. The parenchymatous cells which become part of the cortex compose the phelloderm (Fig. 5.13).

Lenticels. You will recall from the discussion on tissues that the epidermis of the young stem possessed stomata through which oxygen entered to attain the tissues subjacent to the epidermis. Were the stem, as a result of secondary growth, to become encompassed completely by cork, interchange of gases between the tissues of the stem and the atmosphere would be impossible. Consequently beneath those

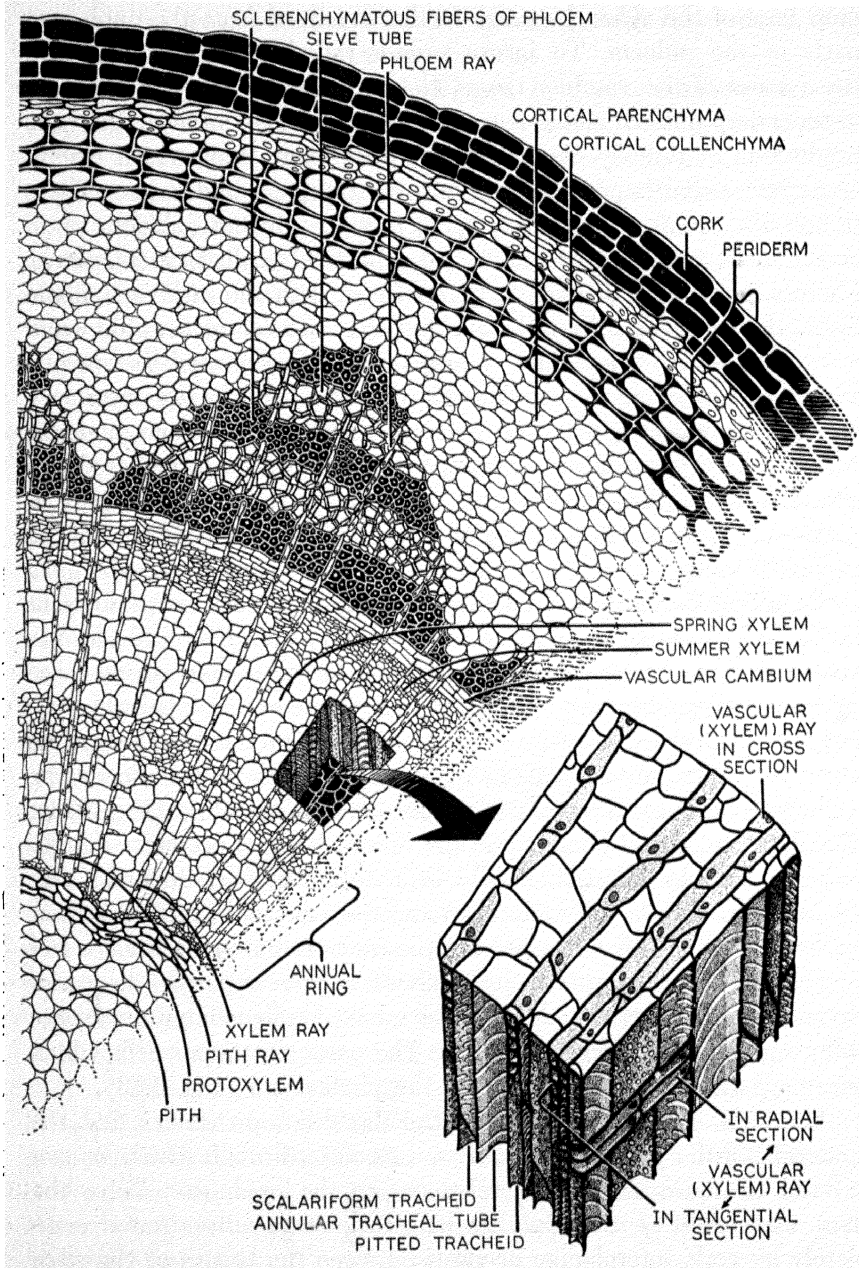


FIG. 5.13 Cross section of a two-year-old woody dicotyledonous stem, linden (*Tilia americana*), with stereoscopic section of the spring xylem in the second annual ring.

areas where epidermal stomata occur, the cork cambium, instead of producing cork cells externally, elaborates loose masses of parenchymatous tissue (lenticels) with rather large intercellular spaces. These lenticels readily facilitate gaseous interchange. Where such lenticels appear in microscopic section, the cork has the aspect of being torn or evulsed.

Comparative Aspects. The previous discourse on primary and secondary growth applies to dicot angiosperms (both herbaceous and woody) and to gymnosperms. However, there are certain modifications in growth; these are not many but are important enough to be worthy of some note. The vascular cambium of the herbaceous dicots is not as active as in the woody dicot. As a result, with some few exceptions, a continuous cylinder of vascular tissue is not of frequent occurrence in secondary growth. Further, the tissue of the pith and the cortex in the herbaceous dicot is quantitatively greater than the vascular tissue. In general, herbaceous dicots, being annuals, show little secondary growth in the comparative sense and generally remain soft. However, if the secondary growth of an herbaceous dicot is protracted in a greenhouse, the stem will become rather woody. On the other hand, secondary growth in the woody dicot is extensive, with the vascular tissue preponderant quantitatively over the tissue in its pith and cortex, even during the first year of growth. Finally, the primary tissue of a woody dicot and a gymnosperm are similar except for the fact that there are no tracheal tubes or vessels in the xylem of most gymnosperms. In contrast to the woody dicot also, the sieve tubes in the phloem of the gymnosperms lack true companion cells.

Annual Rings. On microscopic examination of a transverse section of a woody dicot, such as *Tilia americana* (Fig. 5.13) it will be noted that the yearly formation of secondary xylem occurs in the form of concentric bands called annual rings. Since each additional growth for the year takes place, in cold or temperate climates, during the spring and summer seasons of the year, the xylem in each annual ring may be microscopically distinguished on a morphological basis into two component areas (Fig. 5.13), spring xylem and summer xylem. The spring xylem possesses larger xylem elements: the tracheids and the tracheal tubes have larger luminal calibers and are thinner-walled. On the other hand, the summer xylem elements are much smaller in luminal caliber, compacted, and generally thicker-walled. In the gymnosperm, which possesses no tracheal tubes, the tracheids of the spring

xylem have a greater luminal caliber and are thinner-walled, while the summer xylem is composed of tracheids with much smaller luminal caliber and thicker walls.

In many woody stems, as they increase in diameter, the wood parenchyma cells in the oldest annual rings enlarge and send protrusions (tyloses) into the conducting elements which occlude their lumina. The tyloses stop water conduction in this part of the wood, and it is changed from sapwood to heartwood. Since all the wood parenchyma cells die in the transformation, the heartwood contains no living elements and serves merely for support. The heartwood, because of the presence of pigments, is often darker in color than the sapwood which encircles it. It is also more durable for building purposes.

By counting the number of annual rings in the base of a woody dicot or gymnosperm stem, it is possible to make a fairly accurate estimate of the age of the stem. Further, an examination of each annual ring may present to the professional botanist significant information as to the amount of rainfall and other climatic factors. Of course the formation of false annual rings because of droughts and other abnormal climatic factors is a possibility.

Bark. Bark (Fig. 5.9) is a term applied to the tissues that lie external to the vascular cambium and thus includes the following regions in the stem: phloem, pericycle and cortex (in young twigs), and periderm. The furrowing of the bark, so commonly observed in oak (*Quercus*) and in the elm (*Ulmus*) is really due to successive depositions of cork tissue by the progressive formation of cork cambia, which may extend as deeply inward as the phloem. Because of the production of cork tissue by each of these successive cambia and concurrent elaboration of more vascular tissue (xylem) internally, the original and more externally placed cork tissue undergoes great distention that eventuates ultimately in the partial furrowing of the bark itself.

Functionally the cork in the bark is effective in preventing water loss from the underlying tissues. Cork also buffers the subjacent tissues against mechanical injury and against heat and cold, and presents a fairly good barrier to the entry of parasitic insects and fungal organisms.

Steles. Stele is a term employed to indicate the pericycle and the tissues that it encloses. A few of the more important types of steles

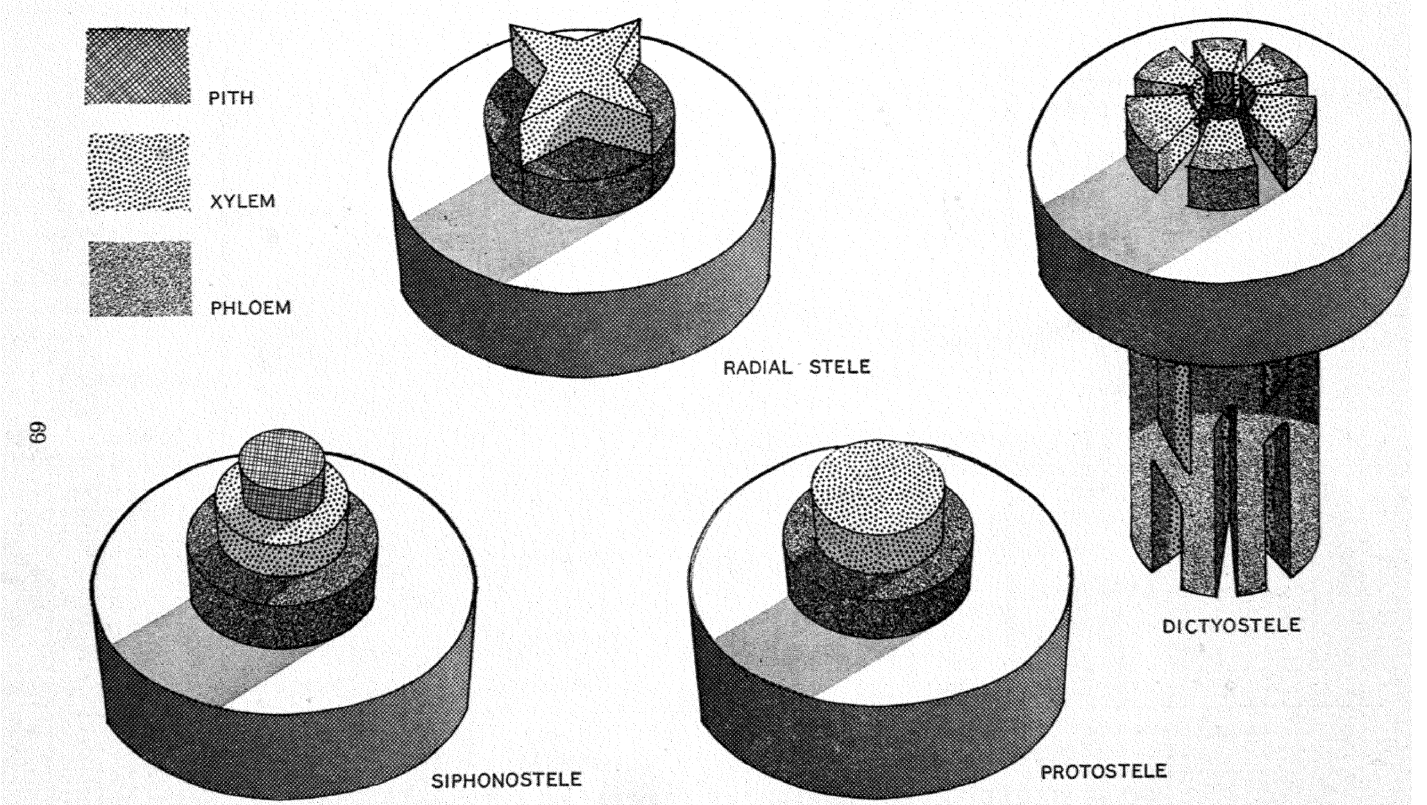


FIG. 5.14 Types of steles.

Table 1 SUMMARY OF PRIMARY AND SECONDARY GROWTH OF STEM

Primary Meristems	Regions	Primary Tissues	Lateral Meristems	Secondary Tissues
Promeristem → Protoderm		Epidermis	Cork cambium +	Tangential division → Cork with lenticels; Phelloderm
Promeristem → Ground meristem	Cortex	Collenchyma, Parenchyma, Endodermis if present	Radial division ↓	
Promeristem → Ground meristem	Pericycle	Fibers, Parenchyma	Circumferential increase in cork cambium	
Promeristem → Ground meristem	Pith rays	Parenchyma		
Promeristem → Ground meristem	Pith	Parenchyma	Circumferential increase in cambium ring ↑	
Promeristem → Procambium	Phloem	Sieve tubes, Companion cells, Fibers, Parenchyma	Radial division +	
Promeristem → Procambium	(Vascular bundle)	Cambium	Cambial ring (Fascicular cambium + interfascicular cambium) +	Tangential division → Secondary phloem; Vascular rays (Parenchyma); Secondary xylem (Spring, Summer) → Annual ring
Promeristem → Procambium	Xylem	Tracheal tubes, Tracheids, Parenchyma, Fibers		

Stele

may be considered at this point. The siphonostele (Fig. 5.14) is a stele in which the vascular tissue forms a cylinder enclosing the pith in the center. The dictyostele (Fig. 5.14), on the other hand, is regarded as a modified siphonostele in which the cylinder of vascular tissue is interrupted to such an extent in its circular continuity that the vascular tissue will appear to be broken up into vascular bundles at practically any transverse plane of section. The radial stele (Fig. 5.14), which occurs characteristically in roots and not in stems, with the exception of some of the primitive vascular stems, presents a central core of xylem with radiating arms directed toward the enclosing pericycle. In the radial stele, the phloem occupies the regions between the radiating arms of xylem.

Aspect of Xylem in Various Sections. In a microscopic cross section (Fig. 5.13), the xylem is disposed into concentric bands, the annual rings. Vascular rays extend through the annual rings eccentrically. The spring and summer xylems in each annual ring are clearly evident. In the macroscopic aspect of the "cross cut" of a log, the annual rings appear as concentric circles and the xylem rays present themselves as narrow lines running radially across the concentric circles.

In a microscopic radial section (Fig. 5.13) the vascular rays, since they are radially disposed through the xylem tissue, are cut along their longitudinal axes and therefore present themselves in the form of parallel bands crossing the tracheal tubes and tracheids at right angles. Macroscopically, in a quarter-sawed section of a log the annual rings show forth as vertical lines and the xylem rays as cross markings.

In a microscopic tangential section (Fig. 5.13), the vascular rays will themselves be cut at right angles and will appear as either lenticular or fusiform groups of cells paralleling the longitudinal axes of the neighboring xylem elements. Macroscopically, in a plain-sawed section of a log the annual rings appear as somewhat irregularly interspaced and vertically disposed wavy lines. The xylem rays are not discernible.

The Monocot Stem. In our consideration of the monocotyledonous stem (Fig 5.15) we shall limit our discussion to corn (*Zea mays*), a practical representative of this subclass of angiosperms.

The promeristem, as in the dicot stem, differentiates into the protoderm, ground meristem, and procambium. The protoderm, from

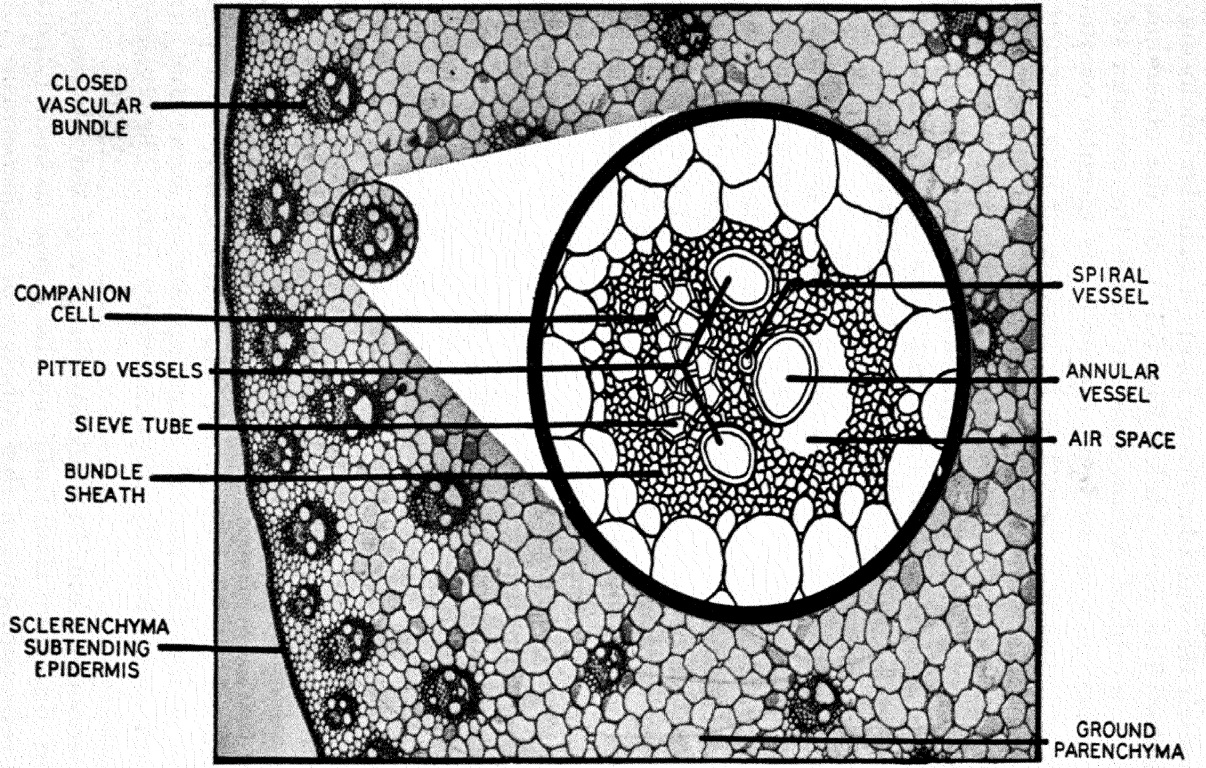


FIG. 5.15 Transverse section of the corn stem (*Zea mays*).

which is elaborated the epidermis, encloses the ground meristem, throughout which are irregularly dispersed the procambial strands. The ground meristem becomes differentiated into parenchyma, the ground tissue of the stem, with the exception of a few layers of sclerenchyma fibers lying subjacent to the epidermis. From the procambial strands are formed the vascular bundles, which, unlike those of the dicot stem, retain no cambial tissue. Consequently the vascular bundles of the monocot stems are termed *closed bundles* because they do not possess any potential for secondary growth.

The closed vascular bundles, as seen in transverse sections of the corn stem (Fig. 5.15), are distributed rather irregularly through the parenchymatous ground tissue. Each vascular bundle is seen to be enclosed by several layers of sclerenchyma fibers collectively called the bundle sheath. The phloem comprises sieve tubes and companion cells and is generally located in that portion of the vascular bundle directed toward the periphery of the stem. The xylem, directed toward the center of the stem, consists of four tracheal tubes or vessels. Two of these vessels are relatively large, pitted in form, and laterally located. The other two vessels are comparatively smaller, annular or spiral in form, and interposed between the larger vessels. These vessels may be surrounded by a large intercellular space, sometimes referred to as the air space. Interspersed between the vessels are rather thick-walled and angular tracheids, together with some sclerenchyma fibers. Because of the manner in which the ground tissue is traversed by the vascular bundles, clearly defined areas like cortex, pericycle, and pith are not present.

Secondary Growth of the Monocot Stem. Although there is no secondary growth in most monocots, nevertheless in a very limited number, notably in *Yucca* and *Aloe*, secondary growth does occur. In these monocot stems certain parenchymatous cells in the more peripheral area of the stem form a cambium which tangentially divides to form a small increment of secondary parenchyma on its outer side and both parenchyma and closed vascular bundles on its inner aspect. Periderm formation, as exemplified in *Yucca* and *Cordyline*, is rather different from that discussed in reference to the dicots. In these monocot stems, the peripherally situated parenchyma undergoes repeated division and suberinization to form several layers of cork tissue. There is no initially formed phellogen. However, in some species of *Aloe*

and in certain palms the periderm is somewhat similar to the dicot periderm.

Functional Aspects of the Stem. The functions of the stem may be treated in two aspects: the physiological significances of the various tissues in the stem and the chief functions of the stem as a whole.

(*a*) PHYSIOLOGICAL SIGNIFICANCES OF THE VARIOUS TISSUES The epidermis, and especially the cork, are protective in function. Further, the cork, because of its suberinized walls, prevents water loss from the subjacent tissues and at the same time buffers the underlying tissues against attacks of parasitic insects and fungal organisms. Also, because of its suberinization the cork protects the underlying tissues against severe climatic changes that would otherwise be incompatible with the continued viability of the subjacent tissues. The collenchyma of the cortex and the widely distributed sclerenchymatous fibers are the pillars that buttress the stem in its support of the heavy burden of leaves and fruits. The flow of raw material and the conduction of foods rest on the vascular tissue, the upward conduction of water and inorganic salts being the function of the vessels and tracheids in the xylem, while the phloem is the conductor of foods. Radial conduction of water, inorganic salts, and foods between the pith and the pericycle in the dicot stem is executed by the pith rays The vascular rays serve the same function between the phloem and xylem. The cortical collenchyma and chlorenchyma are, in herbaceous dicots, important photosynthetic centers. The storage of food is principally the work of the pith, with the cortical parenchyma a close second.

(*b*) CHIEF FUNCTIONS OF THE STEM AS A WHOLE. From our consideration of the physiological aspects of the stem tissues may be quickly derived the chief functions of the stem. The first and most obvious function is the support of leaves, flowers, and fruits. The stem distributes and supports the leaves, the photosynthetic centers of the plant, over an extensive area in such a way that the leaves have ready access to light. Secondly, the stem is functionally concerned with conduction. The ascent of water and inorganic salts may be demonstrated by the use of radioactive phosphates. On the other hand, foods are conducted, chiefly downward, by the phloem. The translocation of food through the phloem is easily demonstrated by girdling or ringing the stem. By the ringing of a stem is meant the circumferential removal of bark from a small part of the stem. When a stem is so girdled, the roots die for lack of food. The physiological

mechanisms involved in the ascent of water and mineral salts and in the movement of food through the phloem will be discussed fully in the chapter on leaf functions. A secondary function of aerial stems is food and water storage. The principal foods accumulated in the stem for future use, as for example in asparagus (*Asparagus officinalis*), are starch, fats, and proteins. The storage of water is commonly observed in the cactus stem. As will be indicated subsequently, the subterranean stems are especially modified for the storage of both water and food.

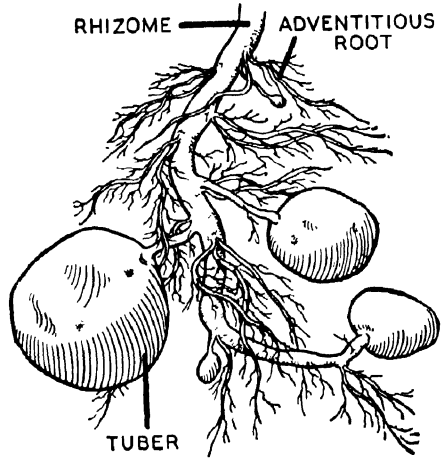


FIG. 5.16 Rhizome and tuber of the Irish potato (*Solanum tuberosum*).

Subterranean Stems. These stems, as indicated previously, are classified as rhizomes, tubers, corms, and bulbs. A rhizome (Fig. 5.16) is a more or less elongated underground stem with leaves and buds occurring at its nodes and with adventitious roots which usually grow out from its undersurface. Physiologically, such stems are organs

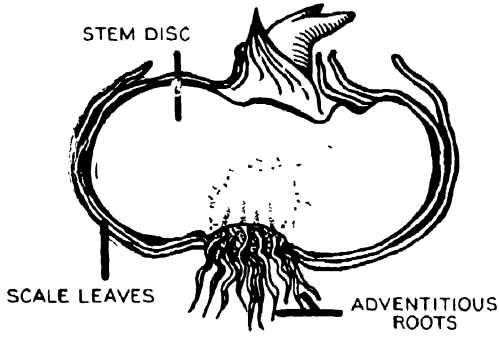


FIG. 5.17 Section of a corm (*Gladiolus*) showing the massive stem disc and associated structures.

for food storage and a means of vegetative propagation. In *Solanum tuberosum*, the white potato, the growing tips of the rhizomes, as a result of food storage, thicken to become tubers. A tuber (Fig. 5.16)

is a true stem and has buds (eyes) in the axils of small scale-like leaves. Functionally, such a stem is a food-storage organ and a means of asexual reproduction. A tuber segment with an eye, on being planted, develops into a mature plant.

Subterranean stems which are short, solid, vertically thickened, often globose and bulb-like, are called *corms* (Fig. 5.17). The stem tissue in the corm itself generally takes the form of a massive disc-like structure enclosed with relatively few scale-like leaves. From its upper surface arises a tuft of aerial leaves and from its undersurface develops a mass of fibrous adventitious roots. Food storage and reproduction are the primary functions of the corm.

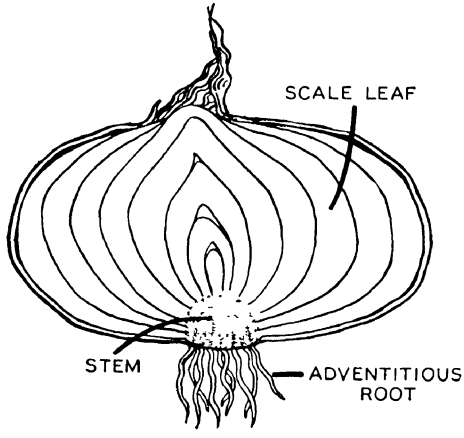


FIG 5.18 Section of a bulb of the onion (*Allium cepa*) showing numerous scale-like leaves and reduced stem tissue

In some plants, such as the onion (*Allium cepa*) and the lily (*Lilium*), the underground stem does not elongate greatly during its early development. The bulb (Fig. 5.18) is actually a miniature stem from the base of which develop numerous adventitious roots and on the top of which occurs a small terminal bud. The stem itself is obscured from view since it is enclosed by numerous scale-like leaves, and herein it differs greatly from the corm, already described. Functionally, a bulb is concerned, to a very great extent, with food storage and reproduction.

Chapter 6

THE ROOT

Definition and Classification. The root is that primary organ of the vascular plant which is typically subterranean and whose principal functions are anchorage and the absorption of water and mineral salts in solution from the soil. In contrast to the stem, the root is not divided into nodes and internodes, does not bear leaves or leaf modifications, does not branch in a regular fashion, and has an internal structure which differs from that of the stem.

The primary or first root originates from the radicle when the seed germinates. The branches of primary roots are known as *secondary* roots. They arise internally from the pericycle tissue of primary roots. Roots which arise from any part of the plant other than the primary root or its branches are called *adventitious* roots. The prop roots of corn which grow out from the base of the stem just above the soil and turn obliquely into the soil are adventitious roots. They give additional support to the shoot system.

Types of Root Systems. *Root system* is an aggregate term for the mass of roots of a plant. When the primary root continues to enlarge and becomes a conspicuous structure from which many lateral branches diverge, it is known as the taproot. The taproot with its branches constitutes a taproot system (Fig 6.0). Examples of plants with taproot systems are the carrot (*Daucus*), the beet (*Beta*), the radish (*Raphanus*), and the dandelion (*Taraxacum*). When equally prominent adventitious roots develop from the base of the stem, as in common wheat (*Triticum vulgare*) and corn (*Zea mays*), the root system is termed *fibrous* or *diffuse* (Fig. 6.0). Intermediate forms exist between the two types described. A plant may possess a taproot together with a mass of fibrous lateral branches. In a plant such as the sweet potato (*Ipomoea batatas*), diffuse roots may become enlarged as a result of food storage. Although each species of plant usually has a characteristic

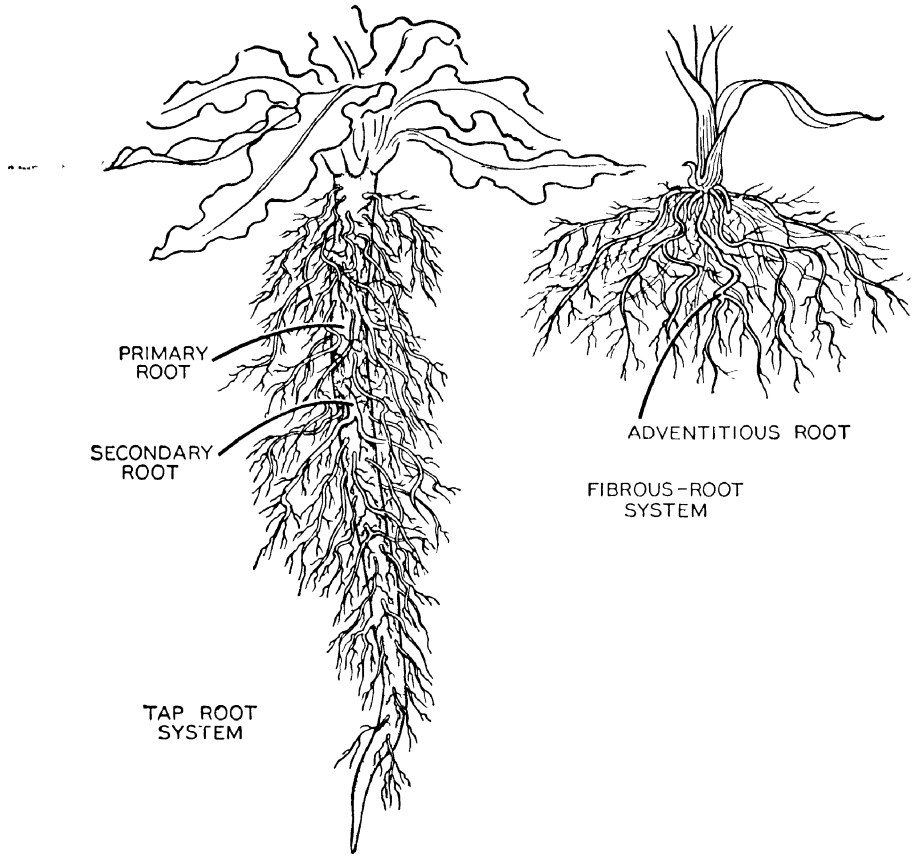


FIG. 6.0 Root systems. Taproot system in the dandelion (*Taraxacum* sp.), fibrous-root system in corn (*Zea mays*).

type of root system, such factors as soil texture and water content may modify its configuration.

An important environmental factor in determining the depth of penetration and horizontal spread of roots is the moisture content of the soil. In general, the less rainfall, the less is the depth of penetration and the greater is the horizontal spread. When much rain penetrates deeper into the soil, the depth of penetration is usually increased. In many instances the root system of a plant is more extensive and longer than the shoot system.

Root Development. The primary root begins its development in the radicle (Fig. 5.10). At this stage the radicle is a mass of undifferentiated meristematic tissue and is commonly referred to as *promeri-*

stem. However, this same mass of undifferentiated meristematic tissue may be observed to occur in a longitudinal section of a root tip. This area of the root tip is conventionally referred to as the *growing point,* more properly, it is the actual promeristem in the same sense that the undifferentiated meristematic tissue of the radicle is. An examination of the longitudinal section (Fig. 6.1A) of a root tip will indicate that this growing point or promeristem is composed of cells in which the nuclei occupy the greater portion of the protoplast in the cytoplasm of which there is very little vacuolation. Directly beyond the growing point or promeristem, there is a mass of parenchymatous tissue which in its collective aspect is thimble-shaped. This thimble-shaped parenchymatous mass, called the *root cap,* is obviously protective in function From the various chemical changes that occur in the tissue, it is assumed that it has other functions, but these functions, at this time, are not clearly evident. Directly above the growing point (Fig. 6 1A) meristematic tissue will be observed to have differentiated into three definite regions: protoderm, ground meristem, and procambium. The *protoderm* is the outermost layer and the central area of tissue is termed the *procambium.* Between procambium and the protoderm occurs the *ground meristem.* In general, the cells of this area, which is called the *zone of elongation,* will present definite vacuolation, and the cells will have increased along their longitudinal axes. Above the zone of elongation, the three primary meristematic areas aforementioned have differentiated into the primary permanent tissues (Fig. 6.1B). This area of the root tip, where the primary permanent tissues have been elaborated, is called the *zone of maturation* or the *zone of root hairs.*

From the protoderm is differentiated the epidermis. The epidermis, just as in the stem, is the outermost layer and consists of one layer of typically brick-shaped cells. A great number of these epidermal cells have evaginated their outer walls to form root hairs (Fig. 6.1B). These root hairs obviously increase the surface area of the root and therefore increase the surface area for absorption.

From the ground meristem there will develop in the zone of maturation the cortex, the endodermis, and the pericycle (Fig. 6.1B).

The cortex is in most roots composed of parenchyma, and in these cells may occur starch granules. The cortex, in comparison with a similar area of the young stem, is rather extensive.

The endodermis is generally considered to be the innermost layer

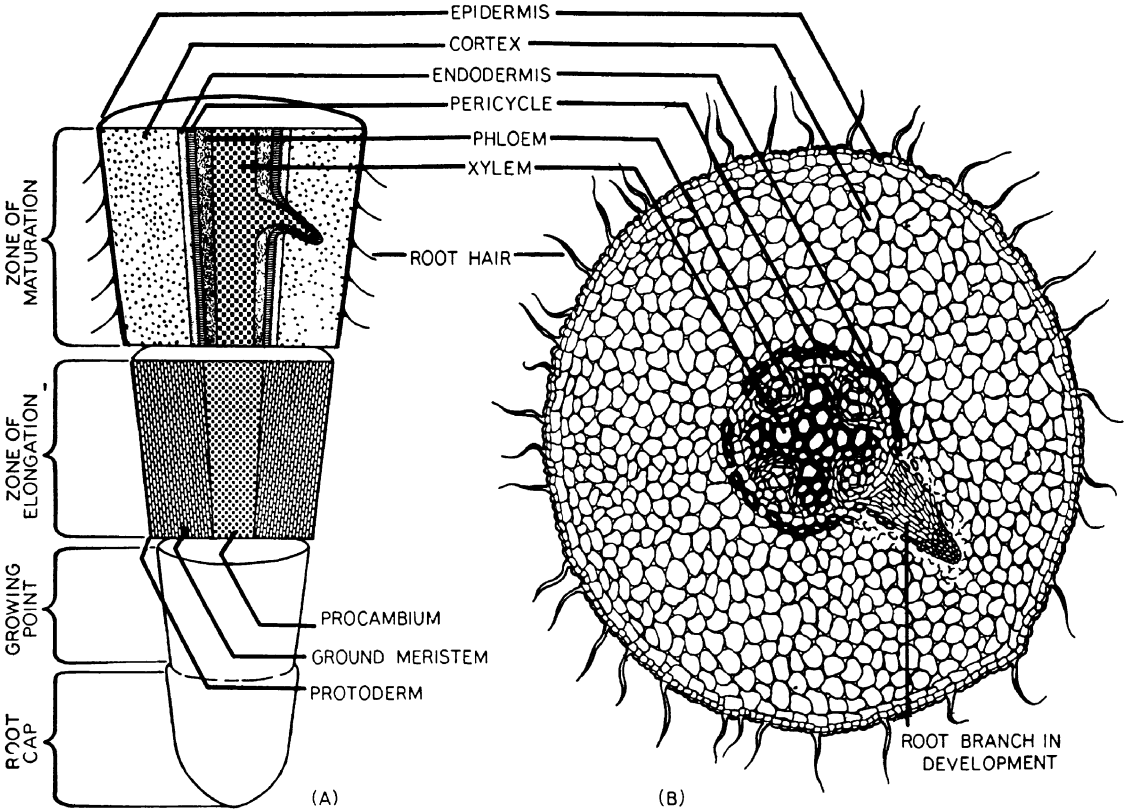


FIG 6.1 (A) Diagrammatic presentation of a longitudinal section of a root tip, showing zones of elongation and maturation, (B) transverse section of a root through the zone of maturation, showing also the development of a root branch.

of the cortex. However, the cells are modified to some extent; that is to say, the inner and radial walls are partially suberinized.

The pericycle is generally a single layer of parenchymatous tissue which lies immediately subjacent to the endodermis. It is the outermost tissue of the stele.

Vascular Tissue. From the procambium are differentiated the phloem and the xylem. The xylem in dicots generally consists of a central core of vessels and tracheids, and from this central core, arms of xylem radiate toward the pericycle. The number of these radiating arms of xylem varies with the species of plant under consideration. A xylem which is characterized by two arms is generally referred to as a *diarch*, one with three as a *triarch;* one with four as a *tetrarch;* and those with many more simply as *polyarch*. Typical dicots have open, radial, tetrarch bundles, typical monocots have closed, radial, polyarch bundles. Alternating with these arms of xylem are patches of phloem tissue. The phloem is here composed of sieve tubes and companion cells. Between the patches of phloem and the adjacent arms of xylem, there is generally interspersed a small amount of parenchyma. It is important to note here that there has been produced no cambium. The activity of a vascular cambium, which will be described later, heralds the beginning of secondary growth.

All of the developmental modifications that have taken place from the promeristem to the elaboration of the primary permanent tissues constitute primary growth in the root of dicots and gymnosperms. In monocots, the central area of the root, in contrast to the same area of the dicot root, is parenchymatous and may be regarded as having a definite pith. The pith is enclosed by xylem, between the short radiating arms of which alternate patches of phloem. The outermost tissue of the stele is the pericycle. The rest of the morphology of the monocot root is quite similar to that of the dicot root.

Lateral Root Branches. Lateral branches (Fig. 6.1B) begin their development in a small area of the pericycle lying vicinal to one of the radiating arms of the xylem. Here several adjacent cells of the pericycle parenchyma dedifferentiate (become meristematic) and produce by tangential mitosis a small root tip which consists initially of a root cap and growing point. This small root tip then grows out through the enclosing tissues of the cortex. It has been assumed that this small root tip, by virtue of secreting cytolytic enzymes, is able to digest the cells which lie in its path. It is also claimed, on the

other hand, that the root tip, as it grows radially, mechanically disperses the tissue in its path.

The vascular tissue of the lateral root is generally rendered confluent to the similar tissue in the xylem of the main stem by the activity of the pericycle. The pericycle is believed to form cells which differentiate into the vascular tissue that serves to connect eventually the vascular tissue of the root and its branches.

Secondary Development. No secondary development occurs in monocots. Whatever increase in diameter the monocots show is due primarily to the enlargement of the cells which already exist. Secondary growth is limited to dicots and gymnosperms.

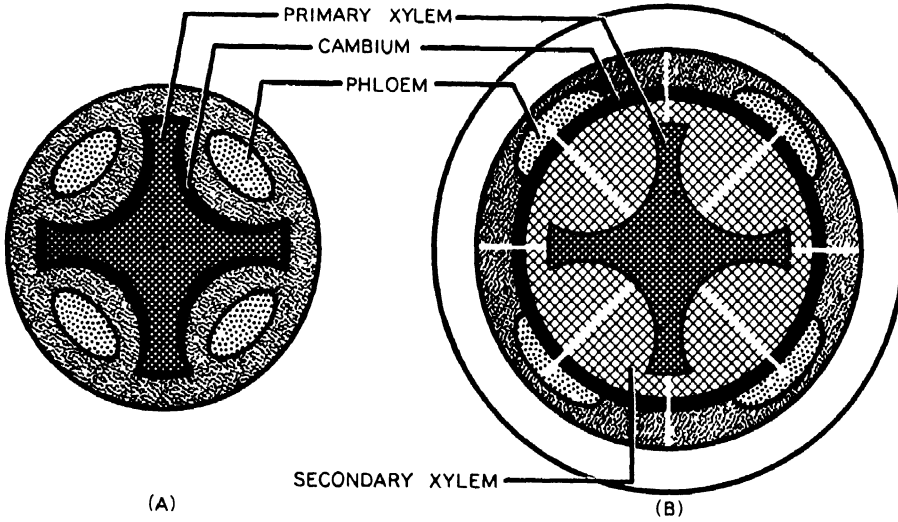


FIG 6.2 (A) Diagrammatic cross section of a dicot root showing the cambium, (B) a similar section showing secondary phloem and xylem, with vascular rays indicated in white lines.

Secondary growth is initiated by the formation of a vascular cambium (Fig. 6.2A). This cambium is formed by virtue of the fact that certain cells of the parenchyma between the phloem and the xylem become meristematic, and there is thus effectuated a cambium which has a wavy aspect because of the relative disposition of the vascular tissues between which it is formed. This cambium by division produces internally new xylem (secondary xylem) which is added to the primary xylem at a far more rapid rate than new phloem is proliferated. Consequently, the original wavy aspect of the vascular cambium,

because of the outward pressure of the progressively increasing xylem, is ultimately disposed into a definite ring. At this time, therefore, there is a central core of xylem surrounded by a ring of cambium outside of which will occur the phloem (Fig. 6.2B). In order to assure proper radial conduction between the xylem and the outlying pericycle, that part of the cambium which was originally vicinal to one of the xylem arms produces there radially elongated parenchymatous tissue extending outward in the form of narrow bands to the pericycle. Similarly, because of the secondary growth of both the xylem and the phloem, the innermost portion of the xylem becomes further removed from the outermost portion of the phloem, and here the cambium, after having produced secondary phloem and xylem, produces the radially elongated parenchymatous tissue which extends in ribbon-like fashion into both the phloem and the xylem. These narrow bands, which serve to effect radial conduction between the xylem and the pericycle and between the component areas of the vascular tissue, are vascular rays.

Generally concurrent with the activity of the vascular cambium is the formation of a cork cambium. This cork cambium arises in the cells of the pericycle. Here the cork cambium produces, by tangential division, cork cells externally and parenchymatous cells (phelloderm) internally. In contrast to the stem, more phelloderm is formed than cork.

SOIL

Since soil constitutes the environment whence the roots of most vascular plants obtain their water and inorganic salts, some consideration of it must of necessity preface any discussion of root functions.

Soils. Though soil profiles, because of differences in rainfall and temperature, may vary to some extent from one region to another, it is possible to embody in a generalized profile the essential characteristics common to most soil profiles.

The soil presents in its vertical profile three more or less distinct strata, which from soil surface downward are: topsoil, subsoil, and parent materials. The *topsoil*, also called *horizon A* by the soil investigators, is the soil layer in which occur the bacterial decomposition of organic matter and its ultimate mineralization, the chemical weathering of rock particles, the breakdown of insoluble mineral salts, and

the formation of the soil colloid, or clay. Here also takes place cation exchange between cations given off by the roots and those adsorbed[1] on colloidal soil particles (clay particles). In short, this is the layer where the physical and biological phases of weathering eventuate in the production of nutrients which may be taken up by the root. The *subsoil*, or *horizon B*, is characterized by less weathered mineral matter. Its degree of friability decreases from above downward. In this layer also are accumulations of clay which have been leached down from the topsoil. In the lowermost stratum of soil are the rocks which are transformed by weathering into the overlying strata.

Soil is therefore a heterogeneous mixture of rock particles, mineral salts, decaying organic matter, microorganisms, and a labyrinth of spaces in which are contained both water and oxygen.

Soil Particles. Soil is formed in the weathering of rock by rain, frost, snow, and air. This disintegration of rock ultimately results in the formation of particles which range in size from the coarseness of gravel (about 1 millimeter in diameter) to the submicroscopic fineness of the soil colloid, clay. The particles of intermediate size between gravel and clay are the sand particles and the still smaller silt particles. The nomenclature of various soil types is based on the particular particle which preponderates over the other particles in the soil make-up. Thus a soil which is composed mainly of silt particles is termed a *loam*, a soil in which the preponderate particle is clay is called a *clay soil*, and so on.

Since the fertility of soil depends in no small measure on clay content, some discussion of the formation and properties of clay seems relevant at this point. The coarser particles, such as gravel and sand, are in the main the unmodified fractions of such minerals as mica, feldspar, and quartz. On the other hand, clay, since it results from the action of carbonic acid (rain and CO_2) on feldspar, differs chemically from the parent rock mineral. Further, because of its colloidal character, clay is capable of imbibition. Imbibition is the capacity of a gel (a colloidal system in fairly rigid state: clay here) to take up relatively great quantities of water without the gel itself going into solution. The phenomenon of imbibition appears to be due to two factors: diffusion and capillary attraction. The constitution of the clay particle with its paralleling sheets of atoms renders it es-

[1] *Adsorption* Adhesion to the surface area of another substance (here the clay particle)

pecially adaptable to imbibition. Water enters between the paralleling layers of atoms, causing the clay particle to increase in volume. Thus clay tends to retain water within its framework, while the coarser soil particles retain water only on their surfaces. Therefore, the greater the quantity of the clay portion of the soil, the greater will be its water-holding capacity. In addition, the colloidal clay particles, because some of their atoms possess an excess of electrons, are negatively charged and are capable of adsorbing cations from the soil. Not only can these clay particles take up one cation, like hydrogen, from an acid soil solution, but they can exchange the hydrogen cation for other ions like calcium, potassium, or magnesium. This capacity of negatively charged clay particles to exchange one cation for another is referred to as *cation exchange*. By virtue of the faculty of cation exchange, clay particles are able to bind to themselves important soil cations such as calcium, magnesium, and potassium. Since the union of the latter cations with the colloidal clay particles is strong enough to resist any leaching effect in the soil, these clay particles, with their bound cations, constitute a mineral reserve available to the root.

Organic Matter of the Soil. Thus far we have discussed to some extent the mineral composition of the soil; but soil is more than just mineral particles—it also possesses organic matter. The organic matter is derived from the bacterial decomposition of dead plant and animal matter returned to the soil. A good part of this organic matter, principally the carbohydrate and protein, is easily broken down by the enzymatic action of the soil microorganisms, but the more resistant materials, such as cellulose and lignin, undergo a very slow process of decay. With further decomposition of organic matter, the more resistant lignin and cellulose increase in quantity. The degradation products of the lignin and cellulose impart to the soil its blackish or brown aspect and are collectively referred to as *humus*. Humus is colloidal, with imbibitional capacities equal to, or better than, the clay particles. Humus promotes looser soil structure and consequently effects better soil aeration.

Though organic matter is not necessary for the growth of any vascular plant, nevertheless its presence in the soil is required for the respiration and the growth of the soil microorganisms. The soil microorganisms, in turn, play a very important role in the mineralization of organic matter, which we shall discuss later. In addition, soil micro-

organisms are involved in the cementation of soil aggregates, to be considered below.

Soil Granulation. The flocculation of small soil particles into larger compound particles or granules in which the microorganisms of the soil directly or indirectly effectuate cementation constitutes soil granulation. In the development of granulated soil the positively charged calcium ions coagulate the small, negatively charged, colloidal clay particles so that the clay particles are flocculated into larger soil units, sometimes referred to as *soil crumbs*. In the main, the particles of the soil crumbs are held together by a mesh of fungal mycelia. On the other hand, some soil bacteria are capable of secreting a gum-like substance which may also serve as a cohesive in this process of soil granulation. Through the formation of such soil granules, the faculty of cation exchange and the imbibitional capacity of the individual clay particles is retained in the compound particle, which in turn creates with other similarly formed granules a greater soil porosity. A porous soil culminates in better aeration of the roots and also insures the drainage of excess water.

Earthworms may also implement granulation of the soil through their vermiform castings, for such castings simply represent soil particles that have become compacted together during their passage through the alimentary tracts of these animals. Grass roots may also exert a granulating effect through their mechanical coalescence with soil particles.

Soil Solution. The soil water, chiefly derived from rain, is the solvent in which are dissolved soluble mineral salts; that is to say, the soil solvent contains variable concentrations of cations and anions.

The cations of these mineral salts are formed through the chemical weathering of the rock particles. H_2O and CO_2 play a major role in the decomposition of these rock particles. For example, the action of carbonic acid on the various types of feldspar may be considered profitably at this point. There are three types of feldspar: potassium feldspar, calcium feldspar, and sodium feldspar. Carbonic acid decomposes potassium feldspar into clay, sand, and potassium carbonate. The potassium carbonate is soluble in soil solvent and disassociates into its ions, $2K^+$ and CO_3 . Similarly, sodium feldspar gives up sodium carbonate, which ionizes in the soil solvent to form $2Na^+$ and CO_3 ions. On the other hand, calcium feldspar forms an insoluble salt, calcium carbonate; the latter, however, in the presence

of carbonic acid, becomes calcium bicarbonate, a soluble salt, whence upon ionization there result Ca^{++} and $2HCO_3^-$ ions. The equations for the latter reactions are shown in Table 2.

Table 2. DECOMPOSITION OF VARIOUS FELDSPARS

(a) $K_2O\ Al_2O_3\ 6SiO_2 + H_2CO_3 + H_2O \rightarrow K_2CO_3 + 4SiO_2 + Al_2O_3 \cdot 2SiO_2 \cdot 2H_2O$

Potassium feldspar; Carbonic acid; Water; Potassium carbonate; Sand; Pure clay or kaolin

$$K_2CO_3 \rightleftharpoons 2K^+ + CO_3^{=}$$

Potassium carbonate; Potassium ions; Carbonate ion

(b) $Na_2O\ Al_2O_3\ 6SiO_2 + H_2CO_3 + H_2O \rightarrow Na_2CO_3 + 4SiO_2 + Al_2O_3 \cdot 2SiO_2 \cdot 2H_2O$

Sodium feldspar; Carbonic acid; Water; Sodium carbonate; Sand; Pure clay or kaolin

$$Na_2CO_3 \rightleftharpoons 2Na^+ + CO_3^{=}$$

Sodium carbonate; Sodium ions; Carbonate ion

(c) $CaO\ Al_2O_3 \cdot 6SiO_2 + H_2CO_3 + H_2O \rightarrow CaCO_3 + 4SiO_2 + Al_2O_3 \cdot 2SiO_2 \cdot 2H_2O$

Calcium feldspar; Carbonic acid; Water; Calcium carbonate; Sand; Pure clay or kaolin

$$CaCO_3 + H_2CO_3 \rightarrow Ca(HCO_3)_2$$

Calcium carbonate; Carbonic acid; Calcium bicarbonate

$$Ca(HCO_3)_2 \rightleftharpoons Ca^{++} + 2HCO_3^-$$

Calcium bicarbonate; Calcium ion; Bicarbonate ions

Even the clay itself from the latter reactions will react with the sulfuric acid formed by the autotrophic (capable of their own food synthesis) soil bacteria, to yield silicic acid, water, and soluble aluminum sulfate; the latter ionizes in water to two aluminum ions ($2Al^{+++}$) and three sulfate ions ($3SO_4^{=}$). This reaction may be visualized in the following equation:

$$H_2Al_2(SiO_3)_2\ H_2O + 3H_2SO_4 \rightarrow Al_2(SO_4)_3 + 2H_2SiO_3 + 3H_2O$$

Clay; Sulfuric acid; Aluminum sulfate; Silicic acid; Water

$$Al_2(SO_4)_3 \rightleftharpoons 2Al^{+++} + 3SO_4^{=}$$

Aluminum sulfate; Aluminum ions; Sulfate ions

From the action of carbonic acid on magnesite, a soil mineral, calcium bicarbonate, a soluble salt, may be obtained; from another soil mineral, such as dolomite, after chemical weathering with carbonic acid, are produced the soluble salts, calcium bicarbonate and magnesium bicarbonate. These reactions may be indicated as follows:

$$\underset{\text{Calcium carbonate}}{CaCO_3} + \underset{\text{Carbonic acid}}{H_2CO_3} \rightarrow \underset{\text{Calcium bicarbonate}}{Ca(HCO_3)_2}$$

$$\underset{\text{Calcium bicarbonate}}{Ca(HCO_3)_2} \rightleftharpoons \underset{\text{Calcium ion}}{Ca^{++}} + \underset{\text{Bicarbonate ions}}{2HCO_3^-}$$

$$\underset{\text{Magnesium carbonate}}{MgCO_3} + \underset{\text{Carbonic acid}}{H_2CO_3} \rightarrow \underset{\text{Magnesium bicarbonate}}{Mg(HCO_3)_2}$$

$$\underset{\text{Magnesium bicarbonate}}{Mg(HCO_3)_2} \rightleftharpoons \underset{\text{Magnesium ion}}{Mg^{++}} + \underset{\text{Bicarbonate ions}}{2HCO_3^-}$$

However, calcium phosphate, a mineral salt in the soil, is not soluble and in this form is unavailable to the plant for absorption. Here again the sulfuric acid, formed during the metabolic activity of the autotrophic sulfur bacteria, reacts with the calcium phosphate to form insoluble calcium sulfate and primary calcium phosphate, a soluble salt which ionizes to form Ca^{++} and $2H_2PO_4$ ions. The reaction may be more easily grasped if we study the following equations:

$$\underset{\text{Calcium phosphate}}{Ca_3(PO_4)_2} + \underset{\text{Sulfuric acid}}{2H_2SO_4} \rightarrow \underset{\text{Calcium sulfate}}{2CaSO_4} + \underset{\text{Primary calcium phosphate}}{Ca(H_2PO_4)_2}$$

$$\underset{\text{Primary calcium phosphate}}{Ca(H_2PO_4)_2} \rightleftharpoons \underset{\text{Calcium ion}}{Ca^{++}} + \underset{\text{Phosphate ions}}{2H_2PO_4^-}$$

Finally, the insoluble sulfate salts of calcium may be changed into soluble nitrate salt by the nitric acid produced by the nitrifying bacteria in the soil. The equation for the reaction could be written as follows:

$$\underset{\text{Calcium sulfate}}{CaSO_4} + \underset{\text{Nitric acid}}{2HNO_3} \rightleftharpoons \underset{\text{Calcium ion}}{Ca^{++}} + \underset{\text{Nitrate ions}}{2NO_3^-} + \underset{\text{Hydrogen ions}}{2H^+} + \underset{\text{Sulfate ion}}{SO_4^=}$$

So from our discussion thus far some insight may be gained into the process of chemical weathering. Of course, soil chemistry is not as simple as it may be made to appear in the study above: it actually involves many other interrelated factors in dynamic equilibrium with the chemical setup in the soil.

It might be well to emphasize at this point that the cations, or at least many of them, are adsorbed on the colloidal clay particles, and therefore are not easily leached out of the topsoil. In fact, the quantity of potassium, calcium, and magnesium available for root absorption depends primarily on the amount of these cations that has been adsorbed on the clay particles.

Release of Adsorbed Cations. When the cells of a root in the region of maturation give off carbon dioxide (CO_2) as a result of their metabolic activity, the CO_2 combines with water (H_2O) to form carbonic acid (H_2CO_3). Thus the pH of the soil solution is decreased by the slight ionization of H_2CO_3, and the dynamic equilibrium that originally existed between the clay-bound cations and the soil solution is disturbed. According to the principle of Le Châtelier, there will take place an adjustment in the direction of that action which tends to restore the original state of dynamic equilibrium that had existed between the soil solution and the adsorbed cations. So, to restore the state of dynamic equilibrium, some of the adsorbed cations are released into the soil solution, the excess hydrogen ions in the soil solution being adsorbed on the clay particles and thus replacing the released cations. Thus the pH of the soil solution is increased; the original state of dynamic equilibrium between the clay particles and the soil solution is restored, but more cations are now present in the soil solution for root absorption. On the other hand, the root may accomplish a direct transfer of nutrient cations from the clay particle, without the cations becoming dissolved in the intervening soil solution. This direct transfer of cations is termed *contact exchange*. In such contact exchange, the root exchanges the hydrogen ions adsorbed on its surface for the clay-bound nutrient cations.

Mineralization. The breakdown of complex mineral-containing organic compounds with the ultimate formation of soluble mineral salts is called mineralization. The organic matter is contributed to the soil by dead plant and animal matter. Organic nitrogenous compounds by deamination result in the production of ammonia. The ammonia is then oxidized by autotrophic bacteria to form soluble

nitrate (nitric acid). This oxidation of ammonia involves two distinct steps: the oxidation of ammonia to nitrous acid by the autotrophic soil bacterium, *Nitrosococcus;* the oxidation of the nitrous acid (nitrite ion) to nitric acid (free soluble nitrate) by another soil bacterium, *Nitrobacter.* This oxidation of ammonia to free soluble nitrate is called *nitrification.* This nitric acid, as has been already indicated, can convert the insoluble sulfates of calcium into soluble nitrate salts. The bacterial decomposition of organic sulfur compounds eventuates in the formation of hydrogen sulfide (H_2S). The hydrogen sulfide is then oxidized by autotrophic sulfur bacteria to sulfur and finally to sulfuric acid (sulfates). As has been previously explained, this sulfuric acid can convert insoluble calcium phosphate to a primary calcium phosphate, which is soluble and available for root absorption. Free phosphate (phosphoric acid) results from the interaction of calcium phosphate and sulfuric acid. Thus, the origin of such important anions as nitrate, phosphate, and sulfate becomes evident, and, more importantly, their role in the conversion of insoluble mineral salts becomes clear.

Soil Ions. The solvent of the soil solution is water, and the solutes which it contains are represented in variable concentrations of cations and anions. Those cations or anions which the roots absorb in relatively great quantity are termed *macronutrient* cations or anions, as the case may be; those which are taken in rather small quantities are called *micronutrient* cations or anions.

Though the greater number of the soil cations are adsorbed on the clay particles, these cations at one time or another, according to the adjustment necessary to maintain dynamic equilibrium in the chemical composition of the soil, will come to be contained in the soil solution. The essential (requisite for proper plant nutrition) macronutrient cations are: calcium (Ca^{++}), magnesium (Mg^{++}), and potassium (K^+); the necessary micronutrient cations are ferric iron (Fe^{+++}), manganese (Mn^{++}), zinc (Zn^{++}), and copper (Cu^{++}).

The essential macronutrient anions include: sulfates ($SO_4^{=}$), primary phosphate ($H_2PO_4^-$), and nitrate (NO_3^-). The required micronutrient anions are tetraborate ($B_4O_7^{=}$) and molybdate ($MoO_4^{=}$).

Essential Elements. Basically fifteen elements are at present known to be required for proper plant nutrition. With the exception of carbon (C), these elements are taken up by the root. Seven of the fifteen elements have already been indicated as either macronutrient or micro-

nutrient cations. Of the remaining seven, five are absorbed as anions by the root: sulfur (S) as sulfate (SO_4); phosphorus (P) in primary phosphate ($H_2PO_4^-$); nitrogen (N) as either nitrate (NO_3^-) or as the ammonium ion (NH_4^+); boron (B) as tetraborate ($B_4O_7^-$); and molybdenum (Mo) as molybdate (MoO_4). Oxygen (O) is taken up as such from the soil atmosphere. Hydrogen (H), and for that matter oxygen, is obtained in part from the water (H_2O) absorbed by the root. In the leaf, as shall be seen subsequently, the water molecule undergoes cleavage, as a result of which there are obtained two hydrogen atoms and one atom of oxygen. Carbon is secured as carbon dioxide (CO_2). Carbon dioxide is taken into the leaf by way of the stomata (see Chapter 8, Functions of the Leaf) and is utilized in the process of photosynthesis.

Since there generally exists only a limited reserve of nitrogen, phosphorus, and potassium in the soil, these nutrients are added in various types of fertilizers to soils under cultivation. In general, a soil devoid of one essential element is considered to be barren, notwithstanding the fact that all the other essential elements are present. The functional significance of the essential elements, as well as the effects of their deficiencies insofar as the plant as a whole is concerned, have been tabulated (see Table 3).

Water Relations in Soil. Soil water is obtained from rain and snow. A portion of the water may percolate through the soil particles in response to the force of gravity. This water is termed *gravitational.* Gravitational water will sink down through the soil until it ultimately attains a depth where it accumulates or stands, and is then referred to as *hydrostatic* water. The zone where the hydrostatic water finally collects is called the *water table.* In the area of this water table, which occurs at variable depths in different places, the soil spaces are completely saturated with water. One harmful effect of the gravitational water as it passes down through the topsoil is that it may carry with it important soil nutrients and thus seriously affect soil fertility. On the other hand, the forces of adhesion with which water is held on soil particles and in the vicinal capillary spaces exceed gravitational pull. Water so retained is called capillary water and is the only type of soil water that is generally available for absorption by the root. The amount of capillary water in the soil depends to a considerable extent upon the size of the soil particles. In general, the smaller the soil particles, the greater will be the exposed surface which they

Table 3 ELEMENTS ESSENTIAL TO PLANT LIFE

Element	Function	Deficiency
1 Potassium (K)	Basically catalytic or regulatory, involved in syntheses of proteins from amino acids, normal photosynthetic rate, starch deposition, involved in cell division and growth	Decreased protein synthesis, increased respiration *External symptoms* yellow mottling of leaf, eventuating in necrotic tissue at apex and leaf margins
2 Magnesium (Mg)	The only mineral constituent of chlorophyll and necessary for chlorophyll formation, involved in phosphate metabolism, specific activators for some enzymes inclusive of carboxylases, dehydrogenases, and transphosphorylases	Chlorosis or yellowing of leaves, partial or complete necrosis of leaves
3 Calcium (Ca)	Calcium ions tend to decrease permeability of plasma membrane Antagonizes permeability-increasing effect of Na^+, necessary for growth of apical meristems, absence of Ca^+ suppresses mitosis, concerned in reduction of nitrates in plant tissues, necessary as calcium pectate in cell wall formation, coagulating agent in the promotion of crumb structure, increases pH of soil and thus controls availability of manganese, phosphorus, iron, etc	Distortion in shape of young leaves, necrosis of stem at terminal bud
4 Sulfur (S)	Constituent of sulfhydril (—SH) in formation of amino acids (cystine, cysteine, methionine) and therefore enters into chemical framework of protoplasm, involved in cell division and fruit development	Not common Yellowing of young leaves, green of older leaves pales characteristically, rate of protein synthesis slowed
5 Phosphorus (P)	Occurs in composition of phospholipids and nucleic acids, required for phosphorylation of ADP to ATP, and therefore a necessary component of *oxidative system* (see Chapter 9, Plant Metabolism)	Abnormally dark leaves
6 Carbon (C)	The *sine qua non* of plant metabolism, basic element in all organic compounds in plants and animals	Limited growth
7 Oxygen (O)	Constituent of CO_2, through photosynthesis present in all foods and protoplasm, biological combustion (oxidation) and liberator of energy (see Chapter 9, Plant Metabolism)	Limited growth
8 Nitrogen (N)	Essential and characteristic constituent of protein	Limited growth
9 Hydrogen (H)	Involved in the oxidations, constituent of protoplasm	Limited growth
10 Zinc (Zn)	Constituent of enzyme carbonic anhydrase, involved in synthesis of indoleacetic acid, growth hormone in plants	Yellowing of lower leaves apically and marginally, malformation of leaves, stunted growth of young leaves, which cluster characteristically, "little leaf" disease
11 Copper (Cu)	Constituent of oxidizing-reducing enzymes, tyrosinase and ascorbic acid oxidase	Leaves wither at tips, with eventual loss of leaves, plant wilting notwithstanding good water supply
12 Molybdenum (Mo)	Involved in reduction of nitrates	Interference with normal growth
13 Boron (B)	Not known	Death of growing areas of root and stem
14 Iron (Fe)	Required for synthesis of chlorophyll though not entering into constitution of the chlorophyll molecule, involved as part of such enzymes as catalase, peroxidase, cytochromes, etc	Chlorosis of interveinal areas of leaf
15 Manganese (Mn)	Activator of such enzyme systems as dehydrogenases, carboxylases, involved in oxidation of absorbed ferrous iron, has some part in chlorophyll synthesis	Chlorosis leaves have necrotic brown or gray areas Leaves are eventually lost

collectively present for the adhesion of water. Consequently less water would be retained in sandy soil than in clay soil where the soil particles approach submicroscopic dimensions and thus offer enormously more surface for water adhesion. Capillary water, of course, will move from areas where it is more abundantly contained to those regions which have become relatively dry. Such movement is especially favored in clay soils because of the minuteness of soil spaces and is slowest in sandy soils. In fact it was originally believed that as the root absorbed water from the soil, the area from which such absorption occurred was replenished by the movement of water from a region with greater capillary water content. However, when the rate of transpiration (water outgo from the leaf) increases, the root absorbs water from the soil at a rate faster than it can be replaced in a given soil area by capillary action. It has also been demonstrated, contrary to past beliefs, that capillary movement of water in the soil is fairly slow. Then again, there are barriers that may interpose themselves against the movements of capillary water: air pockets and the cloture of spaces due to the imbibitional swelling of soil particles. How, then, do the roots get water? Roots obtain their water by growing into those areas of the soil where capillary water is available.

Soil particles which have given up their capillary water still retain on their surface a molecular film of water. This water is held so tenaciously by imbibitional forces in the particles that it is unavailable for root absorption. Water so retained is termed *hygroscopic* water.

Thus, from our consideration, the soil may be regarded as a sort of reservoir, the gauge of which possesses two significant levels. One is called *field capacity;* the other, *wilting point coefficient.* The water retained in soil after gravitational drainage has been accomplished represents the level of field capacity. A soil at field capacity contains the optimal amount of capillary water for root absorption. As far as the plant is concerned, the reservoir is full. The water is absorbed by the root and is lost chiefly to the atmosphere in transpiration from the leaf. In the absence of additional water, the reservoir is depleted to the point where the roots cannot take up enough to keep pace with that being expended in transpiration from the leaf. Turgor in the plant decreases; the plant wilts. The residual water content of the soil at the time of wilting represents the lowermost level of our gauge and is termed the wilting point or the wilting coefficient of the soil.

The attainment of either field capacity or wilting point rests entirely on the length of time between successive waterings of the soil.

Soil Atmosphere. The proper atmospheric environment for roots depends on the number of large and small soil spaces that occur in a given area of soil. Large soil spaces favor adequate drainage and the subsequent containment of air whence the root obtains its oxygen. Small or minute soil spaces or pores retain water by capillary action. Thus a soil which is almost completely clayey has great water-holding capacity. After a heavy rain such soil becomes saturated with water, since little gravitational drainage has taken place. Such completely saturated soil obviously contains little if any oxygen. The root, deprived of oxygen, is unable to accomplish respiration—and literally dies of asphyxiation. On the other hand, if a soil possesses a good crumb structure, there is a fairly even distribution of large and small soil spaces, and consequently there will be a good balance among the three essential factors—proper drainage, adequate aeration, and sufficient water retention for root absorption. Conditions favoring good crumb structure in a soil eventuate in the establishment of all three necessary factors. Tillage of the soil enhances its aeration, for it facilitates gaseous exchange—the entrance of oxygen into soil and the liberation from it of carbon dioxide, which is given off by the root as a result of its metabolic activities. Too great a concentration of carbon dioxide in the soil spaces is injurious to the root and inhibits its capacity for absorption.

Soil pH. The pH is the log of the reciprocal of the concentration of hydrogen ions. Its determination is rather helpful when we wish to know whether the soil is acid or alkaline. As perhaps you know, a pH of 7 represents the neutral point. When the pH decreases below 7, that means that the hydrogen ion concentration has increased and the solution is acidic. Should the pH show an increase over 7, that would indicate that, in the solution being tested, the hydrogen ion concentration has decreased and that the solution is alkaline. Thus by determining the pH we obtain information as to the degree of acidity or alkalinity. And so, in the case of the soil solution, we can determine its pH, the index to the extent of its acidity or alkalinity, as the case may be.

The pH of the soil solution depends largely on the extent to which the clay particles are charged with hydrogen ions. If the clay particles become charged with hydrogen ions, the clay acts like a weak acid,

ionizing slightly and thus increasing the hydrogen ion concentration in the soil solution, i.e., the pH of the soil solution is decreased. On the other hand, if the clay particles are charged mineral cations, the clay acts much like a slightly ionizing salt; that is to say, few of its cations go into the soil solution in exchange for the hydrogen ions which become adsorbed on the clay particles. Thus the hydrogen ion concentration decreases slightly in the soil solution, i.e., the pH is increased.

The majority of plants attain their optimal growth with the pH of the soil between 6 and 7. There are a few plants, citrus fruit to mention one, which develop best in soil with a pH around 5.

A soil with a pH of less than 5 may be too acidic generally for most plant growth. The pH is usually brought to the normal value of 6 or 7 by treating it with lime (CaO) or limestone ($CaCO_3$). The calcium carbonate generally forms a soluble salt by reacting with the carbonic acid in the soil to form calcium bicarbonate ($Ca(HCO_3)_2$). The formation of this salt decreases the concentration of the hydrogen ions, and the pH is thus increased. Some of the calcium may be adsorbed on the clay particles. To correct the alkalinity of the soil (to reduce pH) sulfur is added. This sulfur is oxidized by soil microorganisms to sulfuric acid. The latter acid ionizes to form $2H^+ + SO_4^{--}$. Thus the hydrogen ion concentration is increased and the pH is correspondingly reduced.

FUNCTIONS OF THE ROOT

Having considered the environment of the root, we may now consider the functions of the root. These are anchorage, absorption of water and inorganic salts, conduction, and storage.

Anchorage. The root holds the plant firmly in the soil and thus supports the shoot.

Absorption of Water and Inorganic Salts. Absorption, whether it be of water or of dissolved salts, takes place through the region of maturation or root hairs. The root hairs, you will recall from the earlier part of the chapter, are lateral outgrowths from the epidermal cells in the region of maturation of the root tip. They increase the surface area of this region of the root tip and therefore increase its capacity for absorption.

The root hairs come into close approximation with the soil particles coated with films of capillary water. These root hairs possess a

higher osmotic pressure than the soil solution, in consequence of which capillary water passes osmotically into the root hairs. As endosmosis in the epidermal cell continues, its osmotic pressure decreases and finally reaches a point at which the suction pressure of the adjacent cortical cell exceeds that of the epidermal cell. Thus water passes from the epidermal cell into the adjacent cortical cell. As these cortical cells take up water, their osmotic pressures fall; again the suction pressures of the next adjoining cortical cells pull water into these cells, and so on. Thus the translocation of water from the root hairs to the xylem of the root is accomplished by a gradient of suction pressure. This gradient of suction pressure is maintained, since the translocated water is being pulled up through the xylem vessels by osmotic forces in the mesophyll tissue of the leaf. These osmotic forces, which will be discussed later in the explanation of the ascent of water and inorganic salts, stem from the transpirational expenditure of water from the leaf. This type of water absorption by the root is sometimes termed *passive absorption* since the factors really responsible for such absorption are in the leaf and not in the root itself.

On the other hand, when the rate of transpiration is reduced, it would be reasonable to expect a commensurate reduction in the gradient of suction pressure in the tissues of the root so that the rate of water absorption would also be reduced. However, it can be demonstrated at such times that water absorption by the root often exceeds the reduced water requirements for transpirational needs, as a result of which there obtains in the xylem of the root a very definite root pressure. The development of the root pressure is explained on the basis that the root can actively absorb water notwithstanding reduced transpirational needs. The energy to effect such active uptake of water is derived from respiratory metabolism in the root. In contrast to passive absorption, active absorption stems from activity in the root itself.

The solutes that are absorbed by the root are soluble salts; that is to say, the salts are in the form of their constituent cations and anions. For example, calcium nitrate is dispersed in solution as Ca^{++} and $2NO_3^-$. The origin of the soluble salts has already been discussed and need not be repeated here.

The essential anions and cations may be absorbed either actively or passively. Passive absorption is accomplished by diffusion. Through active absorption the essential ions may be accumulated against a con-

centration gradient or contrary to the law of diffusion. The mechanisms involved in such absorption of ions have been discussed in some detail in the work on the cell.

Conduction. The physiological mechanism involved in ascent of water and inorganic salts through the xylem of the root and shoot will be considered in Chapter 8, Functions of the Leaf.

Storage. Much of the food manufactured in the leaf is translocated down through the phloem for storage in the cortical parenchyma of the root. Some roots, notably the beet (*Beta*), turnip (*Brassica*), and parsnip (*Pastinaca*), become greatly enlarged as a result of such storage. The roots of some plants growing in arid regions store water.

Reproduction by Roots. Some plants are propagated by means of root cuttings. The latter develop adventitious buds from which arise aerial shoots. Roses, sweet potatoes, and raspberries are commonly propagated in this manner.

Chapter 7

THE LEAF

THE foliage leaf is that organ of the vascular plant which is borne on the stem, is typically characterized by its thin flattened expanded form and the presence of an internal framework of veinlets and veins, and whose primary functions are photosynthesis and transpiration. Leaves, whether they be typical or atypical, always arise from stems at nodes, and invariably buds are found in their axils.

The principal categories of leaves are (1) foliage leaves, which perform the photosynthetic function; (2) floral leaves, which constitute the flower; (3) cotyledons, which are the leaves of the seed plant embryo; (4) scale leaves, which may function in protection or storage; (5) bract leaves, which appear on the axes of inflorescences (flower clusters); and (6) leaves modified in form and function, such as tendrils and spines or thorns.

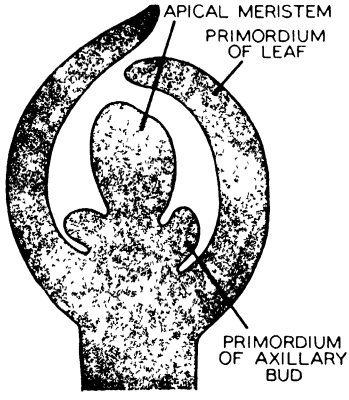


FIG. 7.0 Diagrammatic longitudinal section through the apical portion of a stem tip.

Our further discussion in this chapter will be largely limited to the external and internal morphology of the foliage leaf.

Origin and Arrangement of Leaves. Leaves arise in buds, the undeveloped growing points of stems. At regular intervals the leaf primordia (Fig. 7.0) arise as diverticula from the sides of the growing point. When the bud opens the leaf primordia enlarge and differentiate to become mature leaves. Leaves, unlike stems and roots, cease to grow when they reach maturity.

There are three principal types of leaf arrangement: (1) alternate,

where a single leaf occurs at each node; (2) opposite, where two leaves occur at each node; and (3) whorled, where there are more than two leaves at each node.

The Parts of a Foliage Leaf. A complete foliage leaf (Fig. 7.1) consists of a flattened expanded portion known as the *lamina* or blade, a stalk or *petiole* which attaches the blade to the stem and conducts materials to and from the blade, and two tiny leaf-like appendages at the base of the petiole, known as *stipules*. A leaf is

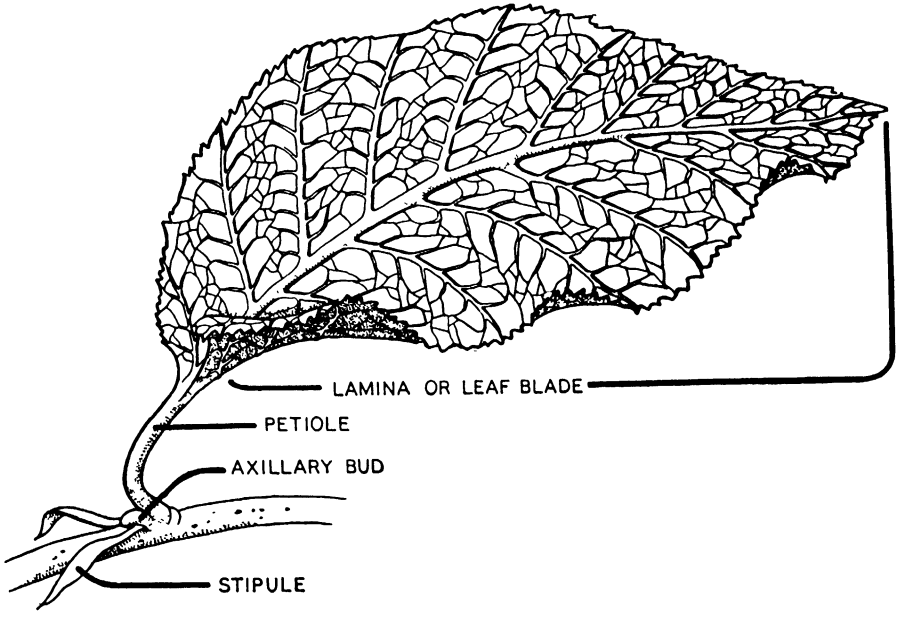


FIG. 7.1 A complete leaf.

said to be incomplete when any of these parts is lacking. Leaves from which the petiole is absent are said to be *sessile* (Fig. 7.2C). Petioles are usually slender and cylindrical in shape; but in the grass leaf they are flattened into sheaths which clasp the stem. Leaf blades exhibit differences in color, shape, texture, duration, marginal characteristics, and venation. In some instances, as in the garden pea (*Pisum sativum*), the two stipules are very prominent and perform the same functions as the blade.

Venation. The veins of a leaf are composed largely of vascular tissue which, in the case of a complete leaf, is continuous with the conducting tissue of the petiole. They are concerned with the con-

duction of water, dissolved mineral salts, and fabricated foods; and they form the structural framework of the blade.

There are two principal types of leaf venation or arrangement of veins in a leaf, namely, parallel venation and net venation. In *parallel venation* (Fig. 7.2C) the principal veins extend through the blade from base to tip in a parallel fashion, and inconspicuous anastomoses connect the principal veins. Parallel venation is charac-

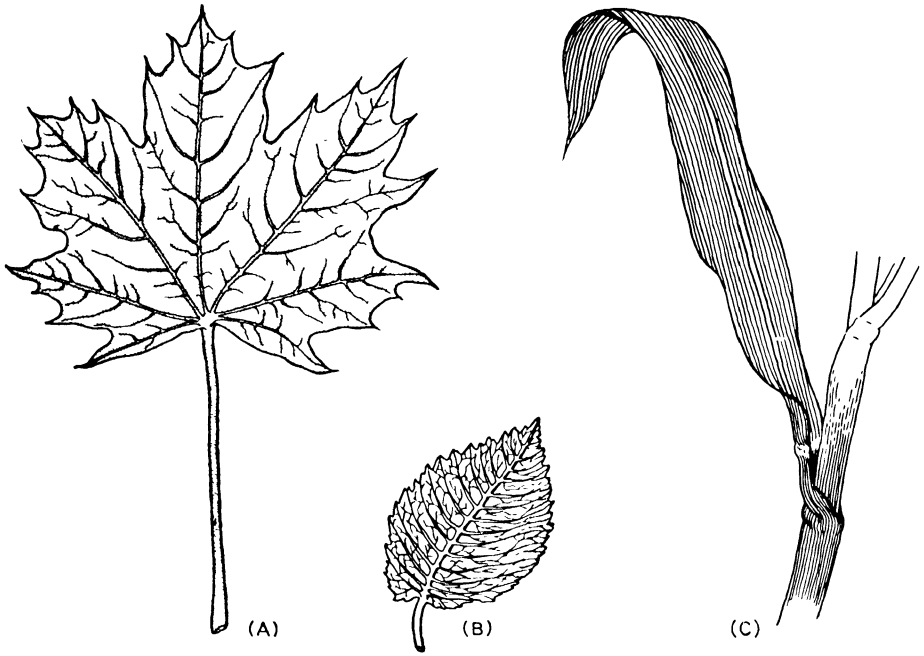


FIG. 7.2 Types of venation: (A) palmate net venation, (B) pinnate net venation; (C) parallel venation in a sessile leaf (*Zea mays*).

teristic of monocotyledonous plants such as wheat and corn. In net-veined leaves, the veins form a complicated network in the blade, and the ultimate veinlets terminate in a small area of chlorenchyma. Net venation is characteristic of such dicotyledonous plants as the maple (*Acer*) and the sycamore (*Platanus*).

In *net-veined leaves,* there are two types of venation. *Pinnately veined* leaves (Fig. 7.2B), such as those of the oak, have a midrib, or principal central vein, with other veins extending in a regular manner from the midrib to the leaf margin. *Palmately veined* (Fig. 7.2A)

leaves, such as those of the maple, have a number of veins of approximately the same size that radiate from the tip of the petiole to the leaf margin.

Simple and Compound Leaves. When the blade of a leaf is in one piece, even though the margin be deeply indented, the leaf is said to be *simple* (Figs. 7.1, 7.2A, 7.2B). Marginal modifications vary

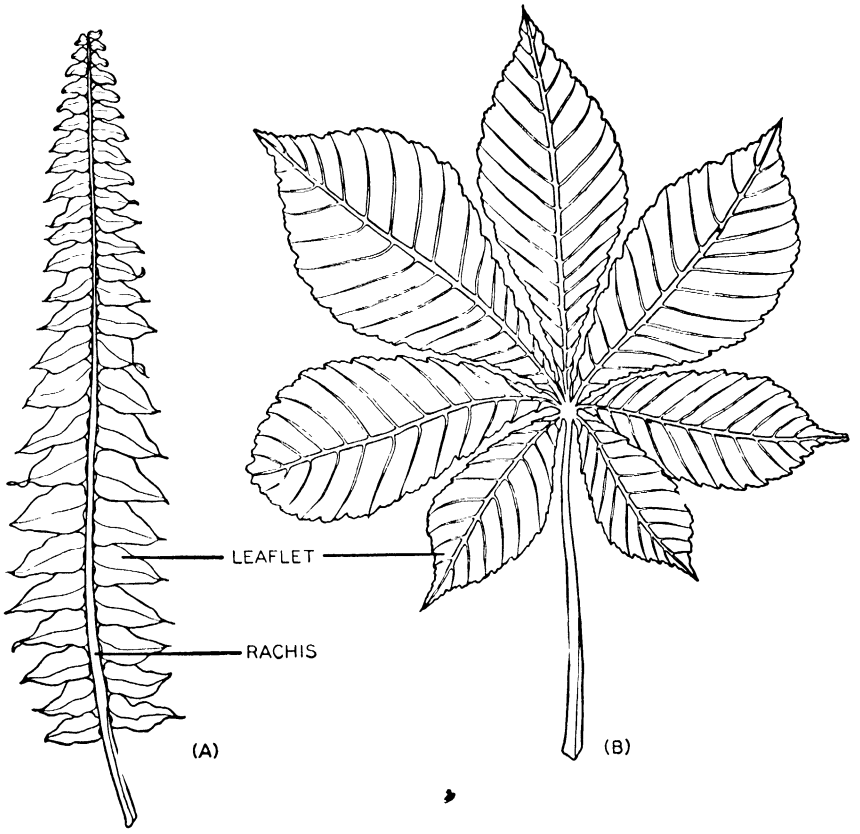


FIG. 7.3 Compound leaves: (A) pinnately compound; (B) palmately compound.

in degree from those which are smooth or entire through a series of marginal indentations that include serrate, dentate, and crenate types. Simple leaves which are lobed (marginal cutting is very pronounced) are pinnately lobed if they are pinnately veined and palmately lobed if they are palmately veined.

The leaf is said to be *compound* (Fig. 7.3) when the blade is dissected into separate leaf-like segments called leaflets. When the

leaflets arise from a continuation of the petiole (the *rachis*), as in the black walnut (*Juglans nigra*) or the bracken fern (*Pteris aquilina*), the leaf is pinnately compound (Fig. 7.3A). In palmately compound leaves, such as those of the horse chestnut (*Aesculus hippocastanum*) and red clover (*Trifolium pratense*), the leaflets arise from a common point at the tip of the petiole (Fig. 7.3B).

The presence of buds in the axils of leaves and their absence in the axils of leaflets, and the presence of stipules or stipule scars at the leaf base and their absence at the leaflet base, are features which enable the botanist to distinguish a leaflet from a leaf.

Leaf Coloration. Most foliage leaves are yellowish green in color. The green color is due to the presence of chlorophyll *a* and chlorophyll *b* in chloroplastids. Present in these same plastids are two yellow carotenoid pigments, xanthophyll and carotene, but their expression is masked by the chlorophylls until the latter disintegrate. The chlorophylls and carotenoids may also occur in other plant organs such as herbaceous stems, young woody stems, and aerial roots.

The anthocyanins are plant pigments which are red, blue, purple, and lavender in color. They are always found in solution in the cell sap and are absent from plastids. Chemically, they are glycosides, that is, compounds formed by the union of a sugar with a nonsugar. The anthocyanins occur more commonly in floral leaves and fruits and less often in foliage leaves.

Autumnal coloration of foliage leaves is largely due to (1) the decomposition of the chlorophylls, resulting in the unmasking of other pigments present, and (2) the formation of new anthocyanin pigments not previously present. Anthocyanin formation necessitates the presence of sugar in the leaf.

The absence of pigments causes plant parts to appear white.

Internal Anatomy of the Foliage Leaf (Fig. 7.4). The outermost tissue of the blade is called the epidermis. It usually consists of a single layer of highly vacuolated, colorless, irregular, interlocking cells whose exterior walls are thickened by a colorless, waxy, waterproof substance called cutin. This cutinized layer is called the cuticle and it protects the underlying tissues from injury and from excessive loss of moisture. In some plants, epidermal hairs are present. They are unicellular or multicellular outgrowths of the ordinary epidermal cells and are often secretory in function.

In the dorsiventrally flattened blade, the lower epidermis and

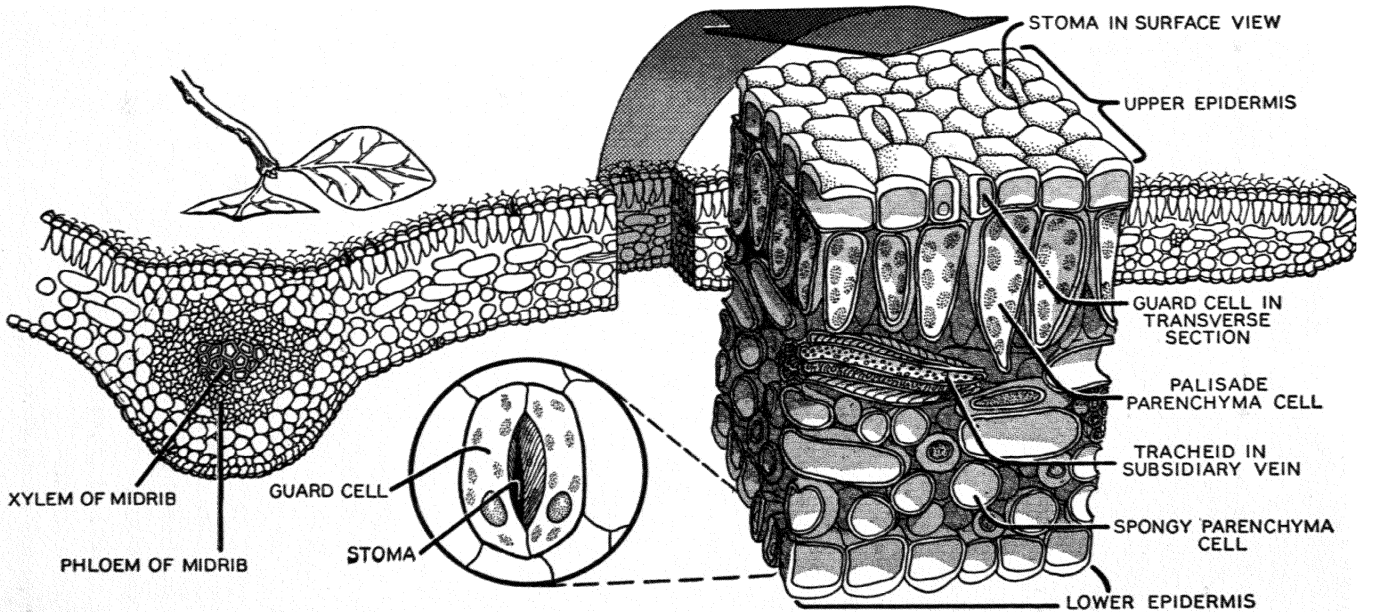


FIG. 7.4 Transverse section of the privet leaf (*Ligustrum*) showing an enlarged stereoscopic view of its microscopic anatomy together with a highly magnified surface view of a stoma and its guard cells from the lower epidermis. Each of the guard cells is phantomized to disclose its chloroplastid content.

at times the upper epidermis are perforated by many minute openings known as *stomata* (Fig. 7.4). Each stoma is surrounded by a pair of highly modified epidermal cells known as *guard cells* (Fig. 7.4). Each guard cell is crescent-shaped and possesses numerous chloroplastids and a conspicuous nucleus. The walls of the guard cells that border on the stoma are usually thickened. The opening and closing of the stomata regulate the interchange of water vapor and other gases between the interior of the leaf and the exterior atmosphere.

The photosynthetic parenchymatous tissue between the upper and lower epidermal layers is the *mesophyll.* In a typical leaf, the mesophyll is composed of palisade parenchyma and spongy parenchyma (Fig. 7.4). The palisade parenchyma is contiguous with the upper epidermis and consists of one or more layers of compactly arranged, elongated, chloroplastid-filled cells with their long axes perpendicular to the leaf surface. Between the palisade parenchyma and the lower epidermis is the spongy parenchyma. The cells of this parenchyma are approximately isodiametric and loosely arranged. Numerous large intercellular spaces are present and they form a system of air passages which are continuous with the substomatal chambers.

The cells of both the palisade and spongy parenchyma are chlorenchymatous, but the former usually contains the greater number of chloroplastids. The border parenchyma cells which form a sheath around the smaller veins in the spongy parenchyma lack chlorophyll.

The veins or vascular bundles extend throughout the spongy parenchyma of the leaf and serve to conduct water and food. The main veins (Fig. 7.4) consist of a sheath of sclerenchyma fibers surrounding xylem and phloem. The xylem lies toward the upper surface of the leaf, and the phloem lies toward the lower surface. The xylem of the main veins consists of tracheal tubes, tracheids, and parenchyma; and the phloem consists of sieve tubes, companion cells, and parenchyma. The ultimate veinlets are characterized by the absence of phloem and by the presence of two xylem elements—tracheids and xylem parenchyma. In the smaller veins the sclerenchyma sheath is replaced by a sheath of parenchymatous cells lacking plastids and is called border parenchyma.

The petiole consists of an epidermis surrounding a mass of parenchyma which is traversed by one or more vascular bundles. The bun-

dles are continuous on the one hand with the veins of the blade, and on the other hand, with the vascular tissue of the stem. A cross section through the petiole usually shows the bundles arranged in a semicircle. The cellular elements present and their disposition correspond to those which occur in a main vein.

Opening and Closure of the Stomata. The increase and decrease in stomatal caliber is controlled by changes in the turgor of the guard cells. The theory which is probably most widely accepted explains the alterations in turgor in terms of conversion of starch to sugar and sugar to starch. Since the only epidermal cells which contain chloroplastids are the guard cells, they alone can manufacture starch. Early in the morning some of the starch is converted to sugar, and since the sugar is soluble in cellular water, the osmotic pressure of the guard cells increases. Water is drawn into the guard cells from the adjacent epidermal cells and they become turgid. With this increase in turgor the thin, more elastic portion of the guard-cell wall bulges and draws with it the wall adjacent to the stoma, with the result that stomatal caliber is increased.

At night when the governing light factor is absent, the sugar of the guard cells is converted to starch. The osmotic pressure of the guard cells decreases, since the starch is insoluble in water. Water passes from the guard cells to the adjacent epidermal cells; and consequently the turgor of the guard cells becomes decreased; and the closure of the stoma is finally effectuated.

The chemical transformations described are related to cellular pH. In daylight the carbonic acid formed as a result of respiration is utilized in photosynthesis, and the acidity of the cell contents is decreased. This favors the transformation of starch to sugar. At night the increase in cell acidity due to the nonutilization of carbonic acid in photosynthesis favors the reverse process.

Abscission and Leaf Fall. Plants that retain their foliage leaves for several growing seasons are known as *evergreen* plants, while those which shed their leaves at the end of a single growing season are known as *deciduous* plants. Leaf fall in the deciduous plants is accomplished by the development of an *abscission layer*, which is usually located at the base of the petiole. The abscission layer consists of a band of thin-walled, differentiated parenchymatous cells which extends across the base of the petiole and involves all except the vascular bundles. The walls of its cells, by disintegration of the sub-

stance of their middle lamellae, become gelatinous, and this causes the cells to separate from one another until the leaf is held merely by the vascular bundles of the petiole. The swaying of the leaf caused by winds and the action of frost results in the rupture of the vascular bundles, and the leaf falls. A layer of cork cells develops to form a protective covering over the scar left by the falling leaf.

Tropistic Behavior of Plant Organs. The inherent response of a plant organ to an environmental influence acting as a stimulus is known as a *tropism*. Responses which result in the growth of an organ toward the source of the stimulus are called positive, and those in which an organ grows away from the stimulus are termed negative. Stimuli which induce growth of plant organs are gravity, light, water, contact, gases, chemicals, etc. Tropisms, since they are caused by unequal growth rates, require considerable time for completion. The differences in growth rates are caused by asymmetric distribution of auxins, or growth-regulating hormones.

The growth of a plant organ in response to the earth's gravitational force is known as a *geotropism*. Stems usually are negatively geotropic; that is, they tend to grow vertically upward. Roots of seed plants invariably grow downward and thus are positively geotropic.

The response of protoplasm to light is called *phototropism*. Stems and leaves tend to bend toward light or toward a region of higher light intensity, and this is advantageous to the plant since light is required for photosynthesis. Roots are negatively phototropic.

The response of protoplasm to sources of moisture is known as *hydrotropism*. Roots exhibit positive hydrotropism by growing toward regions of moisture in the soil.

Some other tropistic responses manifested by protoplasm are chemotropism, thermotropism, galvanotropism, and thigmotropism (response to mechanical stimulation).

Tropisms are advantageous reactions caused by the asymmetric distribution of growth-regulating hormones in response to environmental stimuli.

Chapter 8

FUNCTIONS OF THE LEAF

THE primary functions of the leaf are photosynthesis and transpiration.

PHOTOSYNTHESIS

Photosynthesis is the synthesis of energy-rich carbohydrates from water and carbon dioxide in illuminated chloroplastids. This conversion of carbon dioxide and water into carbohydrates is an energy-consuming process. The chlorophyllous cells of the plant are unique in that they are able to harness light and utilize it as a source of energy. Not only are such cells, by virtue of their chloroplastids, able to absorb light (active or kinetic energy) but they are able to transform it into chemical energy (potential energy) which is stored in energy-rich carbohydrates. These energy-rich carbohydrates, together with inorganic substances absorbed from the soil, contribute to the fabrication of more complex molecules: proteins for assimilation into protoplasm, cellulose for cell wall construction, lipids for reserve food stores and for cutinization and suberinization of tissue. Even the energy to sustain these chemical syntheses is derived from the breakdown of some of the energy-rich carbohydrates elaborated photosynthetically. Thus in the plant, the process of photosynthesis not only makes available the basic substances for chemosynthesis but supplies from its energy-rich carbohydrate the energy to drive the processes. Most of the animals, with the exception of a controversial group such as the chlorophyll-containing flagellates, are incapable of using light to accomplish the synthesis of their own nutrients and are consequently dependent directly or indirectly on plants, not only for nutrition but also for the energy to sustain their processes of assimilation, growth, and reproduction. Man is no less dependent than other animals on products made available by photosynthesis, and also owes

in no small measure his standard of living to the energy derived from coal, gas, and oil—energy absorbed and transformed eons ago in photosynthesis by chlorophyllous cells.

The water required for photosynthesis is absorbed from the soil and translocated up through the stem to the leaves. The functional aspects of transpiration will be considered later in this chapter.

The carbon dioxide, at least the greater part, is obtained from the atmosphere. It enters the leaf through the stomata and diffuses into the mesophyll tissue. Some of the carbon dioxide resulting from respiration (see Chapter 9, Plant Metabolism) may be utilized in photosynthesis.

In the initial process of photosynthesis, the decomposition or oxidation of water is driven by the light energy taken up by the chlorophyll of the chloroplastids. This light, which is absorbed by chlorophyllous cells, may be either natural or artificial Commonly, light, whether natural or artificial, is seen by the human eye as homogeneous. However, if a beam of white light is made to pass through a glass prism and thence to a screen, the light will be observed to have dispersed into a series or spectrum of colors, as in a rainbow. The colors in the visible spectrum of natural light are red, orange, yellow, green, blue, and violet. Each of these colors is due to a vibration or wave having electromagnetic properties and possessing a definite length, called a wavelength. The color having the longest wavelength is red (around 0.00008 centimeter). The other colors in the visible spectrum possess progressively shorter wavelengths in the sequence of which they have been indicated above. Wavelengths just longer than red and just shorter than violet are respectively termed infrared and ultraviolet, but infrared and ultraviolet rays are not visually perceptible. Though light travels in the form of electromagnetic waves, its energy is measured in small units called quanta. In general the shorter the wavelength, the greater is the energy contained in a light quantum.

If now we interpose between our light beam and the glass prism a solution of chlorophyll, we obtain a spectrum of orange, yellow, and green. Spectroscopically we may conclude, therefore, that chlorophyll utilizes the wavelengths of red, blue, and violet. Experimentally it has been demonstrated that photosynthesis occurs with great efficiency in red light, the wavelength with the lowest energy quanta. However, it would be profitable to point out here that the number of light quanta absorbed is not necessarily continuous upon the ...

length of the light incident upon the leaf. For example, a green plant photosynthesizing in red light would take up more light quanta in unit time than it would under blue light in order to obtain the same amount of energy. You will recall that the longer the wavelength, the less is the energy content of its light quanta. The quantum requirements for photosynthesis in natural light vary from eight to ten quanta per molecule of carbon dioxide converted to sugar.

Previous Ideas of Photosynthesis. Generally the process of photosynthesis is summed up in the following equation:

$$6H_2O + 6CO_2 \xrightarrow[\text{Illuminated chlorophyll}]{} C_6H_{12}O_6 + 6O_2$$

Yet this equation, most often cited in books on the subject, is not strictly correct even as a summary of the process. In light of the fact that the oxygen liberated comes from the water only and not from the carbon dioxide, the summary equation is more properly written as follows:

$$6CO_2 + 12H_2O \xrightarrow[\text{Illuminated chlorophyll}]{} C_6H_{12}O_6 + 6H_2O + 6O_2$$

However, neither of these over-all equations gives us any insight into the process itself. Let us, therefore, make a brief survey of the more important previous concepts so that we may appreciate the more current, and incidentally more correct, concepts of photosynthesis.

In 1870 Baeyer, the brilliant German chemist, put forth the idea that formaldehyde was the first intermediate substance elaborated in photosynthesis. He further indicated that the formaldehyde was subsequently polymerized into sugar. Baeyer's theorization on the subject may be graphically presented in the following equations:

$$\underset{\text{Carbon dioxide}}{CO_2} \rightarrow \underset{\text{Carbon monoxide}}{CO} + \underset{\text{Atomic oxygen}}{O}$$

$$\underset{\text{Water}}{H_2O} \rightarrow \underset{\text{Hydrogen}}{H_2} + \underset{\text{Atomic oxygen}}{O}$$

$$\underset{\text{Carbon monoxide}}{CO} + \underset{\text{Hydrogen}}{H_2} \rightarrow \underset{\text{Formaldehyde}}{CH_2O}$$

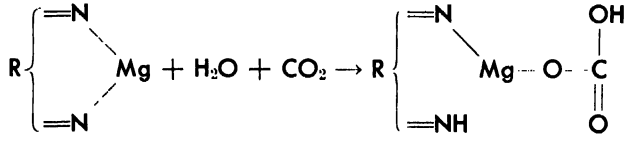
$$6CH_2O \rightarrow \underset{\text{Glucose}}{C_6H_{12}O_6}$$

As to Baeyer's work, carbon monoxide in the free state was found in only one plant; but in that plant it resulted from respiration. However, formaldehyde can be shown to exist in leaves. Thus for years formaldehyde was thought to be a true intermediate substance in the process of photosynthesis.

Wilstatter and Stoll, famous for their work on chlorophyll, put forth a more elaborate hypothesis in which formaldehyde was still regarded as the intermediate product in photosynthesis. Their ideas may be briefly presented in the following equations:

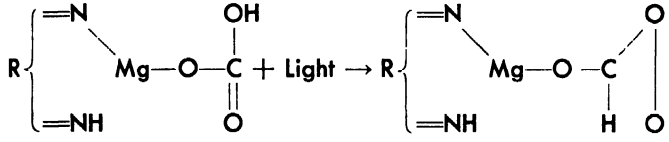
$R = C_{55}H_{72}N_2O_5$ or chlorophyll *a* minus two nitrogen atoms and magnesium
$R = C_{55}H_{70}N_2O_6$ or chlorophyll *b* minus two nitrogen atoms and magnesium

(a)



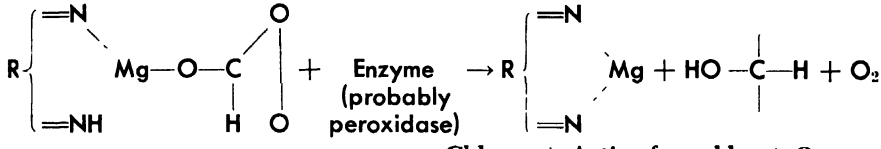
Chlorophyll — Chlorophyll bicarbonate

(b)



Chlorophyll-formaldehyde peroxide

(c)



Chloro-phyll + Active formalde-hyde + Oxygen



Hexose

The Wilstatter and Stoll hypothesis served to emphasize the possibility that formaldehyde was a true intermediate product in photosynthesis. According to this hypothesis, chlorophyll actively engages in the process forming chlorophyll bicarbonate. Further, it was maintained that the latter reaction could take place in the absence of light. In the second equation, chlorophyll functions in the absorption of light. In this photochemical reaction, the reorientation of the bicarbonate attached to the magnesium of the chlorophyll complex is ener-

gized by light and culminates in the production of a still higher energy compound, chlorophyll-formaldehyde-peroxide. In the third equation, the enzymatic cleavage of the chlorophyll-formaldehyde-peroxide results in the formation of active formaldehyde; that is to say, the formaldehyde produced does not attain its aldehydic form but quickly polymerizes to form a carbohydrate. Formaldehyde is a toxic substance, but according to this hypothesis it exists for only a very short interval of time. Then again, chlorophyll can combine with the formaldehyde, thus removing whatever toxic effect might come to pass as a result of increase in concentration.

Current Concepts of Photosynthesis. The more recent work on photosynthesis presents it as a process that may be subdivided in its over-all aspect into two component phases, one having to do with the light-energized decomposition or oxidation of water, the other concerned with the transformation of carbon dioxide to sugars.

1. In the first phase, water is oxidized by the removal of two hydrogen atoms. Since the hydrogen of the water attaches rather tenaciously to the oxygen, energy is required to bring about the cleavage. For this purpose light energy is absorbed by chlorophyll. The first phase postulates the existence of two hydrogen acceptor molecules in the chloroplastid. With *A* representing the hydrogen-acceptor molecule, the equation for the first phase of the photosynthetic process may be written as follows:

$$2H_2O + 2A \xrightarrow[\text{chlorophyll}]{\text{light}} 2AH_2 + O_2$$

The experimental work in support of the latter equation comes from two sources. In 1939 Hill demonstrated that if a suspension of chloroplastids in water together with a suitable hydrogen acceptor (here chromates or ferricyanides) were suitably illuminated, oxygen would be evolved. Essentially, in this work we have in vitro the photocatalyzed cleavage of water. In 1941 Ruben and Kamen, using the heavy isotope of oxygen (O^{18}), were able to prove rather conclusively that the oxygen which was liberated in photosynthesis came from the water and not from the carbon dioxide. Briefly, plants which photosynthesized with water containing O^{18} liberated heavy isotopic oxygen, while those plants which received heavy isotopic oxygen in the carbon dioxide molecules did not give off O^{18}. The work of Ruben and Kamen may be presented graphically in the following equations:

$$(a)\ CO_2{}^{16} + 2H_2O^{18} \rightarrow (CH_2O^{16}) + H_2O^{16} + O_2{}^{18}$$
$$(b)\ CO_2{}^{18} + 2H_2O^{16} \rightarrow (CH_2O^{18}) + H_2O^{18} + O_2{}^{16}$$

In these equations (CH_2O) represents the carbohydrate type formula.

Thus it came to pass that the first phase of photosynthesis was essentially the light-driven oxidation of water. In fact, the equation illustrating the oxidation of water in the presence of illuminated chlorophyll and hydrogen acceptors is called the Hill reaction and is now commonly held to represent one of the reactions of photosynthesis—in our discussion, the first phase of the photosynthetic process.

2. Now then, if we are correct in the assumption that the Hill reaction is representative of what occurs in the first phase of the photosynthetic process, then it follows that the second phase of photosynthesis is the reduction of the carbon dioxide to form carbohydrate. The over-all reaction for the reduction of carbon dioxide is presented as follows:

$$2AH_2 + CO_2 \rightarrow (CH_2O) + H_2O + 2A$$

In this summary equation for the second phase of photosynthesis, it will be noted that the carbon dioxide is reduced by the hydrogen atoms which resulted from the oxidation of water in our first reaction. This reaction can take place in the absence of light.

But what about the details behind our summarized equation for the second phase? What happens to the formaldehyde indicated as an intermediate photosynthate in the hypothesis of Willstatter and Stoll?

Perhaps it would be more convenient to answer the second question first. The reason for discarding the idea of formaldehyde as an intermediate photosynthate lies chiefly in the work of Ruben. In 1940 Ruben and his co-workers, using radioactive carbon dioxide, could not find any radioactive carbon in the formaldehyde which they had isolated from their test plants. In fact, they and other investigators were able to demonstrate that most of the radioactive carbon had been incorporated into organic acids, inclusive of such amino acids as alanine and aspartic acid. Concurrently they were able to show that the fixation of radioactive carbon dioxide could occur in the absence of light. Thus the hypothesis on formaldehyde as an intermediate product was ruled out.

As to our first question, on the details behind the summarized equation for the second phase of photosynthesis, much work is at

present in progress. Perhaps the most significant contribution is the work of Calvin and Benson in 1950. Calvin and Benson, employing radioactive carbon (C^{14}), found that after they shortened the photosynthetic period to two seconds, they could recover about 90 per cent of their radioactive carbon in a three-carbon acid called phosphoglyceric acid. From all experimental reports there seems to be good basis for considering phosphoglyceric acid the first stable intermediate product in photosynthesis. From the position of the radioactive carbon in the molecule of phosphoglyceric acid, it would seem that the acid was formed through the combination of carbon dioxide with some two-carbon fragment already present in the chlorophyllous cell. Though we know that radioactive carbon is utilized in the formation of phosphoglyceric acid, the exact details of its formation are yet to be worked out, notwithstanding the many controversial hypotheses that obtain in the literature. Phosphoglyceric acid, however, is a key intermediate product occurring in the anaerobic glycolysis of the hexose sugars (see Table 4 in Chapter 9). Though the available experimental data do not permit us to say that hexose sugars are synthesized by way of phosphoglyceric acid through a reversal of the reactions in anaerobic glycolysis in respiration, the probability of such a synthetic mechanism appears very likely at this writing. Such a hypothesis is not without some experimental support. If the photosynthetic period is extended to ninety seconds, the phosphoglyceric acid is quickly transformed into hexose sugars with radioactive carbon occupying the third and fourth positions in the molecule. If, as seems rather probable, the carbon dioxide reduction phase of photosynthesis is accomplished partially at least in the reversal of anaerobic glycolysis, then photosynthesis indeed is in part the antithesis of respiration.

In summary, therefore, photosynthesis involves initially the light-energized oxidation of water and the complex reduction of carbon dioxide to carbohydrate, with the reversal of anaerobic glycolysis in respiration appearing the most likely mechanism by which such reduction could be attained.

Products of Photosynthesis. At least four products are known to result from the photosynthetic process: glucose, fructose, sucrose, and starch. As to which one of these is first formed, there is a good deal of controversy. A number of investigators have indicated from their work on the leaf that these compounds are formed in the sequen-

tial order of their complexity. Chemically it would appear that the hexoses, either fructose or glucose, are the first sugars formed in photosynthesis.

Factors Affecting the Rate of Photosynthesis. The factors which affect the photosynthetic rate may be grouped into external factors and internal factors. The external factors are light, carbon dioxide, and temperature. The internal factors are chlorophyll content, anatomical structure of the leaf, a protoplasmic factor, and accumulation of photosynthetic products.

External Factors. The oxidation of water, the first phase of the photosynthetic process, is a photochemical action, the rate of which is governed by radiant energy. Obviously, low light intensity will limit the rate of this reaction. Further, it has been established that neither increase in temperature nor increase in carbon dioxide concentration will increase the rate of photosynthesis when light intensity is weak. In general, therefore, when low light intensity occurs, the photochemical reaction determines the rate of photosynthesis. On the other hand, when light intensity is high, the availability of the carbon dioxide becomes the controlling factor in the rate of photosynthesis. If the concentration of the carbon dioxide is increased above the average content (.035 per cent) of the air, the rate of photosynthesis is increased. Finally, provided that neither light intensity nor carbon dioxide becomes a limiting factor, a rise in temperature increases the rate of photosynthesis. However, it must be emphasized at this point that there is for each plant a maximum temperature beyond which the rate of photosynthesis, instead of continuing to increase, falls rather sharply. This rapid decline in photosynthetic rate is attributed chiefly to the injury of the protoplasm by higher temperatures.

Internal Factors. In fully developed leaves the chlorophyll content does not appear to have any effect on photosynthesis; in other words, there does not exist a proportional relation between the chlorophyll content and the rate of photosynthesis. The protoplasmic factor is believed to be enzymic in nature, and at present it can only be generalized that the quantity and the proportions of these enzymes in the chlorophyllous cells do have some effect on the rate of photosynthesis. The hydration of the protoplasm also enters the picture, for any reduction in the water content of the leaves will lead to a slowing down of the rate of photosynthesis. Insofar as leaf structure

is concerned, the size and distribution of the leaf stomata exert a modifying effect on the rate of entrance of the carbon dioxide; the thickness of the cuticle and epidermis will modify the penetration of light to the palisade and spongy mesophyll.

In reference to the effect of accumulation of photosynthetic products, there are two schools of thought. One group maintains, on the basis of the law of mass action, that the initial rate of photosynthetic action will be sustained only by the maintenance of original concentrations of the reactants and by removal of the products formed. Consequently, if the products of photosynthesis are not efficiently translocated from the leaf mesophyll, the effect would be retardation of the rate of photosynthesis. Further, it is claimed by this group that if the soluble sugars are converted to starch, the starch accumulation will in turn reduce the effective surface of the chloroplastids. The second group contends that no consistent relationship exists between accumulated carbohydrates in the mesophyll cells and the photosynthetic rate.

TRANSPIRATION

Transpiration is the evaporation of water from the tissue of the leaf and its diffusion through the stomata. There are two types of transpiration: cuticular and stomatal. Cuticular transpiration is that which occurs through the cuticle. It has been established that some water outgo takes place through the cuticle notwithstanding its degree of thickness. Generally, about 10 per cent of water loss from the leaf may come about in this manner. Water outgo through the stomata is referred to as *stomatal transpiration* and in most cases accounts for about 90 per cent of water loss from the tissues of the leaf.

Rate of Transpiration. The rate of transpiration is modified by both external and internal factors. The important external factors are light, air currents, atmospheric humidity, atmospheric pressure, and temperature. The chief internal factors are stomata and leaf structure.

EXTERNAL FACTORS. The major external factor which influences the rate of transpiration is light or radiant energy. Only about a fourth of the radiant energy absorbed by the leaf is finally represented as chemical energy in the photosynthetic products. The major portion of the absorbed radiant energy is converted into heat, as a result of

which there is effected a general heating of the leaf. Warming of the leaf in turn increases the vapor pressure of water in the intercellular spaces of the mesophyll tissues; the vapor pressure in the intercellular spaces finally exceeds the atmospheric vapor pressure. As the difference between the latter two vapor pressures increases, the diffusion rate of vapor from the leaf is commensurately accelerated, or the rate of transpiration is increased. Light, you will recall from the previous chapter, is involved in the opening of the stomata and thus by its occurrence or nonoccurrence indirectly exerts a regulatory effect on transpiration.

Air currents, in removing the moisture-laden atmosphere from around the leaf, will steepen the diffusion gradient between intercellular spaces of the leaf and the outside atmosphere. The transpiration rate is, therefore, increased by air currents.

On a very humid day the atmosphere is saturated or nearly saturated with moisture. Since the loss of water from the intercellular spaces is a process of diffusion in which water passes from an area of relatively greater abundance to a region where it is less abundant, the rate of diffusion of water vapor from the leaf will depend on the concentration differential between the intercellular spaces and the outside atmosphere. Obviously, on a very humid day the moisture content of the atmosphere is greatly increased, the concentration differential is reduced, and the rate of transpiration is decreased. In general, the greater the humidity, the slower will be the rate of transpiration.

With temperature constant the vapor pressure in the intercellular spaces will vary inversely as the barometric pressure. In other words, the lower the barometric pressure, the greater will be the rate of transpiration. Ordinarily, the effect of barometric pressure on transpiration is insignificant except on plants grown at high altitudes. The greater the altitude, the less the barometric pressure; thus plants grown at high altitudes will transpire much more rapidly than those grown at ordinary elevations.

Atmospheric temperature plays an indirect role in influencing the rate of transpiration. Increase in atmospheric temperatures will increase the volume of atmospheric water vapor and therefore decrease the concentration of the water vapor around the leaf. Thus, under such conditions, there is established a steeper diffusion gradient, which eventuates in increasing the rate of transpiration. In general,

therefore, the higher the temperature of the atmosphere, the greater will be the rate of transpiration.

INTERNAL FACTORS. As already indicated, the two important internal factors modifying the rate of transpiration are the stomata and the leaf structure.

Several smaller stomata with considerable interstomatal surface between them are more effective in the diffusion of water vapor than one large stoma with a luminal area equivalent to the combined luminal areas of the smaller stomata. The reason for the effectiveness of the smaller stomata lies in the fact that the interstomatal surface between them serves as a reservoir for the water-vapor molecules. Thus the water vapor is in effect exposed to a larger volume of outside air than it would be in the case of the large stoma. In other words, because of the involvement of the interstomatal surface as a water-vapor reservoir, the rate of water loss is proportional to the perimeter of the stoma rather than to its luminal area. Consequently, the rate of transpiration is determined to some extent by the size and distribution of the stomata. Recessed stomata, or stomata contained in cavities formed by invaginations of the leaf surface, are likely to slow the rate of transpiration, since these cavities generally favor retention of saturated air. The location of stomata has some bearing on the rate of transpiration. Stomata confined to the lower epidermis would tend to reduce the rate of transpiration since they would thus be shielded from the direct effect of the sun. Obviously, the number of stomata which a leaf possesses may modify its rate of transpiration.

Leaf structure may affect the transpirational rate in many ways. A heavily cutinized epidermis will reduce cuticular transpiration. Reduction of the intercellular spaces in turn decreases the evaporating surface of the mesophyll cells, with a resulting fall in the rates of transpiration. Some leaves, for example, those of corn, may roll up when the transpirational rate becomes very high. The water-retaining capacity of the mesophyll tissue is a rather potent factor in limiting the rate of transpiration. In general the water-retaining ability of the leaf will depend on its hydrophilic colloidal content. Hydrophilic colloids take up water and retain it by imbibitional force. It is not surprising, therefore, to discover that desert plants possess a high hydrophilic colloidal content. Thus, the higher the hydrophilic colloidal content of the leaf, the greater will be its effect on the reduction of the transpirational rate.

SECONDARY FUNCTIONS OF LEAVES

Flowers are actually leaves adapted for the process of sexual reproduction. The leaves of the bulb—the onion for example—serve in food storage. Some leaves, like those of the succulent plants, contain a chlorophyllic parenchyma which stores water. Bud scales are really leaves modified to protect the terminal bud of the stem. The leaves of the cactus plant are its spines, obviously protective in function. The leaves of the insectivorous plants are morphologically and physiologically modified for the capture and digestion of insects.

FUNCTIONS OF THE STEM INCIDENTAL TO FORCES OPERATIVE IN THE LEAF

Ascent of Sap. The explanation of the upward transport through the xylem has presented itself as a real challenge to the plant physiologist. In the past, such forces as imbibition, capillary action, and atmospheric pressure have been put forward in one form or another to explain the mechanism involved in the upward conduction of water through the xylem, but all of these hypotheses have proved unsatisfactory. Perhaps the best explanation as to the mechanisms involved in the ascent of sap is the transpiration-pull-and-water-cohesion theory formulated long ago by Dixon and Joly. The idea of Dixon and Joly rests on a repeatedly demonstrated property of water: its strong cohesive force.

According to this hypothesis the evaporation of water from the intercellular spaces during transpiration results in the establishment of suction pressures in the mesophyll cells. As a result there is set up, from the area of xylem across the mesophyll tissue, a gradient of suction pressure. Consequently there is exerted on the cohering water in the xylem a pull or tension. The latter tension is transmitted down through the xylem of stem and finally into the root. Thus the water is actually pulled up through the vascular tissues by forces operative in the leaf itself: evaporation (transpiration) and the suction-pressure gradients.

Some idea of the tensile strength of the fine water columns that hang in the xylem of the plant by virtue of adhesion and cohesion may be gained from the fact that these fine water columns can withstand a tension of at least 200 atmospheres of pressure.

Dissolved inorganic (mineral) salts, and even organic solutes

whenever they occur, are borne along in the water columns that are being pulled up through the conductive elements of the xylem. The dissolved solutes pass into the mesophyll tissue upon reaching the leaf. The rate of upward conduction of solutes and that of upward movement of water correspond.

Should the transpiration rate be reduced to the zero point, what then? Under these circumstances, water is actively absorbed by the root. There is thus effected a root pressure, as a result of which water and dissolved solutes may be slowly forced up from below.

Translocation in Phloem. The translocation of organic solutes (soluble sugars, mostly) and even of inorganic solutes from the leaves and downward through the stem takes place by way of the phloem. Many hypotheses have been put forward as to the mechanism of solute transport through the phloem. It was once thought that the physical process of diffusion was involved in the transportation of solutes through the phloem, but it has been demonstrated that diffusion is too slow a process to account for the speed of movement in the phloem. Then it was thought that protoplasmic streaming might account for the rapid movement of solutes through the phloem, but this idea was discarded, since no protoplasmic streaming has ever been observed to occur in mature sieve tubes. Finally, the idea of a pressure-flow mechanism was formulated by Munch in 1930. Perhaps the best support for this hypothesis reposes in the fact that the solution in a sieve tube can be easily demonstrated to be under pressure.

Munch's hypothesis is based on the assumption that the higher turgor pressure of the leaf can be the driving force for a mass flow of solution down through the phloem of the plant. The mechanism of this pressure flow may now be considered in some detail. First, the sugars resulting from photosynthesis in the mesophyll effectuate in the cells there a rather high osmotic pressure. Endosmosis follows, and the turgor pressure in the mesophyll cell is greatly increased. Because of these high turgor pressures, sugars and other solutes are believed to be pressed out of these cells through their plasmodesmata.[1] Through the plasmodesmata the movement of the solution from cell to cell is effected, the solution finally attaining a sieve tube. The turgor pressure of the mesophyll still supplies the force to drive the solution through the sieve tubes into the protoplasts of receiving cells which utilize the sugar and other solutes in their processes of respiration

[1] Plasmodesmata are cytoplasmic connections between adjacent cells.

and growth. Of course this pressure flow will occur only when there exists a gradient of turgor pressure between the mesophyll cells and the receiving cells. In other words, the turgor pressure of the supplying mesophyll cells must be maintained at high level, and even among these there must exist a turgor pressure gradient to effect movement from cell to cell through their connecting plasmodesmata. On the other hand, the turgor pressure of the receiving protoplasts must be kept at a low level. The maintenance of low turgor pressure in the receiving protoplasts is accomplished by the utilization of the sugars and other solutes in respiration and growth, or through storage. Basically, therefore, this hypothesis postulates a gradient of turgor pressure from the supplying mesophyll cells to the protoplasts of the receptive tissues. The tissue of the phloem is assumed to be passive between the supplying end and the receiving end.

Chapter 9

PLANT METABOLISM

PLANT METABOLISM is the sum total of all the chemical syntheses and degradations which occur within the cells of plants. Through the process of photosynthesis (see Chapter 8) sugars are formed in the cells which contain chloroplastids, and from them the plant body is capable of manufacturing a host of other organic compounds. In the degradative processes more complex substances are converted to simpler ones and energy is evolved. The energy released is utilized by the plant to drive the synthetic reactions essential to cellular life.

ENZYMES

The rate at which the myriad of intracellular chemical transformations occur is hastened by specific catalysts known as enzymes. Catalysts are substances which influence the velocity of chemical reaction in the direction of either acceleration or inhibition, without being used up in the reaction. Enzymes are thermolabile (easily decomposed by heat) catalysts, protein in nature and of high molecular weight, which are elaborated by cells and have a specific action on substances called substrates. Frequently the enzymatic protein has associated with it as an active functional group a nonprotein prosthetic group. In many instances, heavy metals such as iron, zinc, manganese, and copper constitute the prosthetic group. Enzymes are capable of exerting their effects independently of the cells which produce them. Endoenzymes act within cells and exoenzymes exert their effects outside cells.

The various groups of intracellular enzymes which make life possible are the oxidases, dehydrogenases, hydrolyases, hydrases, decarboxylases, deaminases, transaminases, transmethylases, etc. The number of enzymes in an individual cell totals perhaps a thousand or more. Each enzyme in each group is usually specific to one chemical

reaction. Some factors which affect enzymatic action are (1) the concentration of the substrate (substance on which an enzyme acts), (2) the concentration of the enzyme, (3) the hydrogen ion concentration of the solution, (4) temperature, (5) the concentration of coenzymes if they are required, and (6) the concentration of various inhibitors and accelerators.

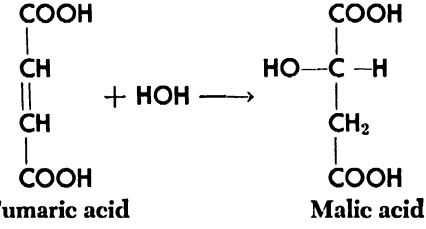
REACTIONS CATALYZED BY ENZYMES

Some of the various types of chemical reactions which are catalyzed by enzymes are hydrolysis, hydration, decarboxylation, deamination, transamination, transmethylation, phosphorylation, oxidation, and reduction.

Hydrolysis is a type of decomposition in which one of the products of the reaction takes up the hydroxyl group of water and the other takes up the hydrogen of water. For example, sucrose on hydrolysis yields glucose and fructose.

$$\underset{\text{Sucrose}}{C_{12}H_{22}O_{11}} + H_2O \rightarrow \underset{\text{Glucose (an aldohexose)}}{C_6H_{12}O_6} + \underset{\text{Fructose (a ketohexose)}}{C_6H_{12}O_6}$$

In *hydration,* water is added to a substance without hydrolyzing it. For example, fumaric acid + water yields malic acid.



Fumaric acid Malic acid

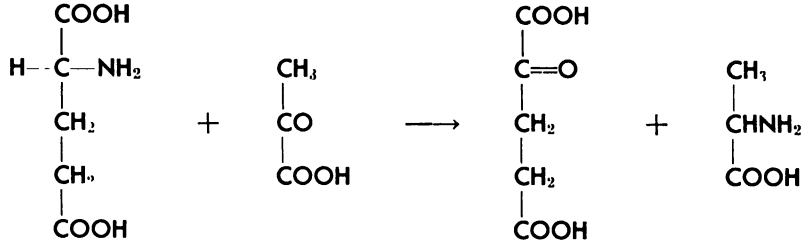
In *decarboxylation,* carbon dioxide is eliminated from the carboxyl group of an organic acid molecule or related compound. For example, the amino acid, alanine, on decarboxylation, yields ethyl amine and carbon dioxide.

$$\underset{\text{Alanine}}{CH_3CHNH_2COOH} \rightarrow CO_2 + \underset{\text{Ethyl amine}}{C_2H_5NH_2}$$

Deamination is any reaction whereby an amino (NH_2) group is removed from a compound. For example, alanine by oxidative deamination forms pyruvic acid + ammonia.

$$\underset{\text{Alanine}}{CH_3CHNH_2COOH} \xrightarrow{O} \underset{\text{Ammonia}}{NH_3} + \underset{\text{Pyruvic acid}}{CH_3COCOOH}$$

Transamination is the transfer of amino groups from one compound to another. For example, glutamic acid plus pyruvic acid yields α-ketoglutaric acid + alanine.



In this reaction we see how pyruvic acid, an intermediate in carbohydrate metabolism, can be converted to alanine, which is an amino acid. The reverse reaction also occurs.

The transfer of methyl (CH_3) groups from one compound to another is called *transmethylation*. The amino acid, methionine, can furnish methyl groups for the synthesis of choline, which is an organic base.

Phosphorylation is the esterification of an organic compound with phosphoric acid. (An ester is a compound formed from an alcohol and an organic or inorganic acid by the elimination of water.)

$$\text{Glucose} + \text{adenosine triphosphate} \xrightarrow{\text{hexokinase}} \text{glucose-6-phosphate} + \text{adenosine diphosphate}$$

This latter reaction appears to be the first step in many of the metabolic transformations to which the sugars are subject.

Oxidation and reduction are defined in the next section.

BIOLOGICAL OXIDATIONS

The biochemical reactions which are oxidative in nature involve combination with oxygen or loss of hydrogen—in any case, electron loss, or *deelectronation*. Most biological oxidations involve the transfer of hydrogen (hydrogen ion plus electron) from one compound to another until the cytochrome–cytochrome oxidase system is reached, and

then only electron transfer is involved. Ultimately, water is formed by the combination of hydrogen and oxygen ions in this type of oxidation. Electron transfer is always involved in oxidation *in toto*. Every oxidation is accompanied by a reduction.

$$\underset{\text{Ferrous iron}}{Fe^{++}} \xrightarrow{\text{oxidation}} \underset{\text{Ferric iron}}{Fe^{+++}} + e\ (\text{electron}) \rightarrow \text{to an electron acceptor (which is thus reduced)}$$

$$\underset{\text{Lactic acid}}{CH_3CHOHCOOH} \xrightarrow{\text{oxidation}} \underset{\text{Pyruvic acid}}{CH_3COCOOH} + 2H(2H^+ + 2e) \rightarrow \text{to hydrogen acceptor}$$

$$\underset{\text{Acetaldehyde}}{CH_3CHO} \xrightarrow[O]{\text{oxidation}} \underset{\text{Acetic acid}}{CH_3COOH}$$

The enzymes involved in biological oxidations and reductions, or the enzymes concerned with the oxidation of metabolites or substrates in protoplasm, are termed *respiratory enzymes*. Most enzymatic reactions require another agent in addition to substrate and enzyme. This agent is called a *coenzyme*. Coenzymes are thermostabile (not easily decomposed by heat), dialyzable (capable of passing through a membrane) organic compounds which are necessary for the action of their respective enzymes. The coenzymes associated with the respiratory enzymes are termed *respiratory coenzymes*. The respiratory coenzymes which are best known are those associated with the dehydrogenases, with which they act as hydrogen acceptors. They can be alternately reduced and oxidized.

Respiratory Enzymes. The respiratory enzymes are the dehydrogenases, the oxidases, the peroxidases, and catalase.

1. *Dehydrogenases* are respiratory enzymes which characteristically remove pairs of hydrogen atoms from a metabolite (substance to be oxidized) so that they can be shifted from the metabolite to a hydrogen acceptor. The dehydrogenases are divided into two main groups: (1) aerobic dehydrogenases, or those enzymes which remove hydrogen atoms from the metabolite, the hydrogen atoms subsequently reacting with oxygen; and (2) the anaerobic dehydrogenases or those enzymes which remove hydrogen atoms from a metabolite, the hydrogen atoms subsequently reacting with a respiratory coenzyme. The latter is the larger group.

Reactions involving the anaerobic dehydrogenases are most complicated because, in addition to the activating dehydrogenase, carriers

and other enzymes take part. In oxidation by dehydrogenation, electrons are removed from the substrate together with protons—in effect, hydrogen atoms. These hydrogen atoms, ordinarily removed two at a time, in most instances are taken by an anaerobic dehydrogenase which in the process becomes reduced. The reduced anaerobic dehydrogenase is reoxidized when the hydrogen atoms which it had received are transferred to a coenzyme of the pyridine nucleotide group, such as DPN and TPN (see the next section, Respiratory Coenzymes). In this reaction the pyridine nucleotide coenzyme is reduced, only to be reoxidized by the transfer of the hydrogen atoms that it has received to a coenzyme of the flavoprotein group, which in the process becomes reduced. The electrons of the accepted hydrogen atoms pass from reduced flavoprotein to cytochrome, and in this step the protons are liberated as hydrogen ions, the cytochrome is reduced, and the flavoprotein is reoxidized. The electrons taken up by cytochrome are then shifted to cytochrome oxidase, as a result of which the cytochrome is reoxidized and the cytochrome oxidase is reduced. The electrons are then shifted from reduced cytochrome oxidase to atoms of molecular oxygen; the atoms of molecular oxygen become oxygen ions; in the process the cytochrome oxidase is reoxidized. The protons liberated as hydrogen ions from reduced flavoprotein then react with the oxygen ions to form water.

These reactions are shown in the form of equations:

(1) MH_2 (substrate) + specific dehydrogenase
= M (oxidized substrate) + reduced dehydrogenase
(dehydrogenase-H_2)

(2) Dehydrogenase-H_2 + oxidized phosphopyridine nucleotide
= oxidized dehydrogenase + reduced phosphopyridine nucleotide
(phosphopyridine nucleotide-H_2)

(3) Phosphopyridine nucleotide-H_2 + oxidized flavoprotein
= oxidized phosphopyridine nucleotide
+ reduced flavoprotein (flavoprotein-H_2)

(4) Flavoprotein-H_2 + 2 oxidized cytochrome
= oxidized flavoprotein + 2 reduced cytochrome
+ $2H^+$ (hydrogen ions)

(5) 2 reduced cytochrome + 2 oxidized cytochrome oxidase
= 2 oxidized cytochrome + 2 reduced cytochrome oxidase

Reaction (5) involves only the shifting of electrons.

(6) 2 reduced cytochrome oxidase + $\frac{1}{2}O_2$ = 2 oxidized cytochrome oxidase + $O^{=}$ (active oxygen or oxygen ion)

Reaction (6) involves only the transfer of electrons.

(7) $2H^{+}$ (from equation 4) + $O^{\cdot}$ = H_2O (water)

2. *Oxidases* are metalloprotein (catalytic activity is dependent on the presence of an iron or copper complex bound to their protein) enzymes which activate molecular oxygen and bring about oxidation by the addition of oxygen. The most widely distributed member of this category of enzymes appears to be cytochrome oxidase (indophenol oxidase) and it is needed for the oxidation of reduced cytochrome.

$$\underset{\text{Reduced cytochrome}}{2\text{Cyt-Fe}^{++}} + \underset{\text{Oxidized cytochrome oxidase}}{2\text{Cyt-Ox-Fe}^{+++}} \rightarrow \underset{\text{Oxidized cytochrome}}{2\text{Cyt-Fe}^{+++}} + \underset{\text{Reduced cytochrome oxidase}}{2\text{Cyt-Ox-Fe}^{++}}$$

$$2\text{Cyt-Ox-Fe}^{++} + \tfrac{1}{2}O_2 \rightarrow 2\text{Cyt-Ox-Fe}^{+++} + O^{=}$$

Cytochrome and cytochrome oxidase play a role in many biological oxidations.

3. *Peroxidases* are metalloprotein enzymes which catalyze the oxidation of many aromatic amines and other compounds in the presence of hydrogen peroxide. The hydrogen peroxide is split into water and active oxygen, and the latter oxidizes the metabolite.

$$\underset{\text{Hydrogen peroxide}}{H_2O_2} \rightarrow \underset{\text{Water}}{H_2O} + \underset{\text{Active oxygen}}{O\bullet}$$

4. *Catalase* is a metalloprotein enzyme with iron in its prosthetic group. It catalyzes the decomposition of hydrogen peroxide into molecular oxygen and water.

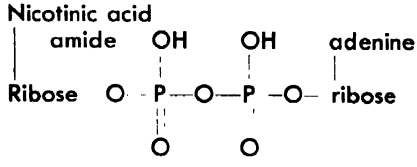
$$\underset{\text{Hydrogen peroxide}}{2H_2O_2} \xrightarrow{\text{catalase}} \underset{\text{Water}}{2H_2O} + \underset{\text{Molecular oxygen}}{O_2}$$

A function of the enzyme is to protect protoplasm from the toxic effect of hydrogen peroxide, which is probably formed during many oxidations.

Respiratory Coenzymes. Some of the principal respiratory coenzymes will now be considered. It should be noted at this time that the functions of some of the vitamins, such as nicotinic acid, thiamine,

and riboflavin, can be described in terms of their places in the chemical structure of coenzymes. These vitamins of the B complex are needed for the molecular fabrication of certain respiratory coenzymes. If one is present in inadequate amount, there will be a deficiency of one or more specific coenzymes. The manifestations of a vitamin deficiency then are due to the inadequacy of the amount of a particular coenzyme present.

1. *Coenzyme I* or *cozymase* is diphosphopyridine nucleotide (DPN). A mononucleotide is a compound composed of a purine (or pyrimidine base), a sugar, and one molecule of phosphoric acid. DPN is a dinucleotide of ribose and the two bases adenine (a purine base) and nicotinic acid amide (a pyrimidine base). It functions as a coenzyme in several dehydrogenation reactions in cellular respiration.



Diphosphopyridine nucleotide

2. *Coenzyme II* is called triphosphopyridine nucleotide (TPN) and it functions as a coenzyme in several dehydrogenation reactions in cellular respiration.

3. *Thiamine pyrophosphate or cocarboxylase* is a coenzyme that functions with the enzyme carboxylase which splits carbon dioxide from the carboxyl group of the α-ketonic acids.

$$\underset{\text{Pyruvic acid}}{CH_3COCOOH} \rightarrow CO_2 + \underset{\text{Acetaldehyde}}{CH_3CHO}$$

4. *Cytochrome* is a generic term used to designate cytochromes A, B, and C. They are metalloprotein coenzymes in which the prosthetic group is the iron-containing hematin, and it is believed that they are the last members of a chain of carriers functioning in cellular oxidation.

$$\text{Reduced flavoprotein (flavoprotein-}H_2\text{)} \rightarrow \text{oxidized flavoprotein} + 2H^+ + 2e$$

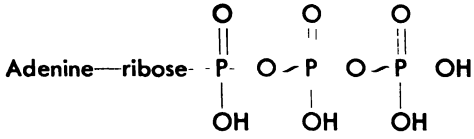
$$\underset{\substack{\text{Oxidized}\\\text{cytochrome}}}{2\text{Cyt-Fe}^{+++}} + 2e \rightarrow \underset{\substack{\text{Reduced}\\\text{cytochrome}}}{2\text{Cyt-Fe}^{++}}$$

5. *Flavin nucleotides*, some biochemists maintain, are attached to a molecule of protein, and hence these coenzymes should be called

flavoproteins. Thus far, at least nine such coenzymes have been described. They contain in their molecule riboflavin (vitamin B_2) and act as hydrogen carriers.

Reduced coenzyme I (DPN-H_2) + oxidized flavoprotein
= oxidized coenzyme I (DPN) + reduced flavoprotein (flavoprotein-H_2)

6. *Adenosine phosphates* form a group including three compounds, adenosine triphosphate (ATP), adenosine diphosphate (ADP), and adenylic acid or adenosine monophosphate (AMP). They act as coenzymes in phosphate transfer in the cell and in particular in the transfer of high-energy phosphate bonds. The chemical bonds of the second and third phosphate groups of ATP and of the second phosphate group of ADP are high-energy bonds. The term *high-energy* phosphate bonds indicates that when such bonds are disrupted in a chemical reaction, relatively large amounts of energy are released. The best-known and probably the most important cellular compounds in which high-energy phosphate bonds are present are ATP and ADP.



Adenosine triphosphate
[~ = High-energy bond]

Examples of the functions of the adenosine phosphates are:

ATP + glucose → glucose-6-phosphate + ADP
Phosphopyruvic acid + ADP → ATP + pyruvic acid

In the first reaction ATP acts as a phosphate donor. In the second reaction ADP acts as a phosphate acceptor.

7. *Ascorbic acid* or *vitamin C*, it has been suggested, functions as a hydrogen carrier.

SYNTHESIS OF CHEMICAL COMPOUNDS IN HIGHER PLANTS

Carbohydrates. It has so far been impossible to determine the first free carbohydrate formed in the leaf cells as a result of photosynthesis. Glucose, fructose, sucrose, and starch appear during and immediately after photosynthesis. It has been generally considered that glucose or, in at least some cases, fructose is the direct product. However, more recent investigation suggests that sucrose is the first sugar

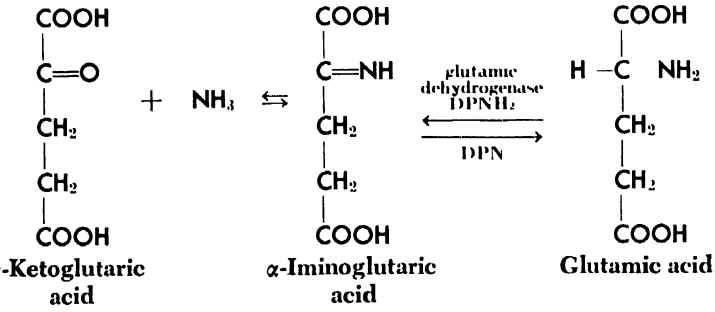
to be formed and that the hexoses, such as glucose and fructose, arise from the digestion of sucrose. In addition, it is known that in plant cells glucose and fructose are intraconvertible and that sucrose can be synthesized from these two simple sugars. Whatever the direct product or products of photosynthesis be, sugar serves as the principal food of all plant organisms and is the basis of other food synthesis.

The chief temporary storage carbohydrates are sucrose and starch. Sucrose is very soluble in water and is readily translocated as such to the regions of the plant where it can be stored or where it can serve as a substrate for growth and respiration. In most plants, however, the chief reserve carbohydrate is starch. Starch is stored in large amounts in tubers and roots, where it provides a source of nutriment for the fabrication of new cells when growth is resumed after a period of dormancy. Starch is also stored in large amounts in some seeds, where it provides a source of food for the developing embryo at the time of germination. Storage of starch occurs in the form of microscopic granules or grains which are characteristically laminated into denser and less dense regions. Digestion of starch must occur before translocation. Chemically, starch is made up of two components, amylose and amylopectin. Both are condensation products of glucose and can be degradated by hydrolytic cleavage by the amylases or by phosphorolytic cleavage by starch phosphorylase.

A variety of other carbohydrates and carbohydrate derivatives are present in plant cells. In the Jerusalem artichoke (*Helianthus tuberosus*) the reserve carbohydrate is the polysaccharide inulin, a condensation product of fructose. Cellulose, hemicelluloses, pectic materials, plant mucilages, plant gums, and glycosides are other carbohydrates found in plants.

Proteins. In the higher plants, the sources of nitrogen for protein construction are nitrate (NO_3^-) and ammonium (NH_4^+) ions in the soil. The nitrate is deposited in the soil by the biological processes of nitrogen fixation and nitrification. The nitrate ion, before it can be utilized for amino acid synthesis, must be reduced in the plant to the ammonium level. The ammonia thus produced is taken up into organic combination to form amino acids, which then are linked together to form proteins. The principal way in which ammonia is introduced into the organic combination appears to be through the reaction between α-ketoglutaric acid and ammonia to form glutamic acid (an amino acid). α-Ketoglutaric acid is an intermediate compound produced in

cellular respiration. The amino group of glutamic acid can be transferred to other α-ketonic acids to form other amino acids.



α-Ketoglutaric acid — α-Iminoglutaric acid — Glutamic acid

Amino acids synthesized by plant cells can be used in the fabrication of cytoplasmic and nuclear proteins. Some of these proteins possess enzymatic properties and play a role in cellular metabolism. The amino acids may also be used in the manufacture of nonenzymatic reserve protein. Much of the protein of the seed is of the latter type. On germination of the seed, this protein is hydrolyzed to amino acids which are translocated to the developing embryo. The specialized nucleoproteins of the nucleus which constitute the chromosomes determine the genetic characteristics of living organisms. Amino acids can also be converted to sugar, and in small amount they may be broken down into such simple compounds as carbon dioxide, water, etc.

Lipids. Neutral fats and neutral oils, esters of fatty acids and glycerol, are deposited as reserve material in the cytoplasm of plant cells in the form of small globules and are found characteristically in seeds, where they accumulate during seed ripening. The lipids which are stored in the cotyledons of the embryo or in the endosperm of the seed are used as a source of energy for the seedling at the time of germination.

Present in plant cells is the lipolytic enzyme, lipase, which catalyzes the hydrolysis of fats to fatty acids and glycerol. Under appropriate conditions it can catalyze the synthesis of fats from the latter substances. In the higher plants the exact mechanism of respiratory oxidation of fatty acids to carbon dioxide and water and of fatty acid synthesis is not known. The mitochondria are the site of fatty acid oxidation in animal cells. Here fatty acids are oxidized, beginning at the carboxyl end, by the successive removal of the 2-carbon fragments. The 2-carbon fragments are liberated as acetyl

derivatives of coenzyme A.[1] Acetyl coenzyme A (CH_3COCoA) may be oxidized through the Krebs cycle to carbon dioxide and water, or utilized in the synthesis of sugars and fatty acids.

According to recent studies, the oxidation of palmitic acid (a saturated higher fatty acid) by a microsomal fraction isolated from homogenates of germinating peanut cotyledons appears to be of a type radically different from that found in animal and microbial systems. Essential cofactors in the animal fatty acid oxidase system are CoA, ATP, Mg^{++}, and DPN. In the higher plant fatty acid oxidase system studied, only DPN was specifically required for the internal oxidation of palmitic acid. Furthermore, the patterns of $C^{14}O_2$ production in animal and higher plant systems differ greatly when palmitic acid labeled in different positions by C^{14} is oxidized.

The phospholipids, such as the lecithins and the cephalins, are believed to enter into the structure of protoplasm and not to serve primarily as storage materials. Waxes, which are also lipids, are found principally in cell walls.

Plant Hormones and Vitamins. Phytohormones or plant hormones are organic substances which regulate and integrate physiological processes locally or at a distance from where they are produced. The most widely known phytohormones are the *auxins*. They are a group of compounds which promote cell elongation or growth along the horizontal axis of the cell. The best known of the naturally occurring auxins is indoleacetic acid. It is produced primarily in terminal buds and young leaves. The auxin formed by the terminal bud is responsible for stem elongation and other plant activities.

Other phytohormones are the wound hormones which promote cell division and growth in mature plant tissue. They result in callus formation and hence healing after wounding. The best-known of the wound hormones is traumatic acid. Ethylene, a hydrocarbon, acts as a fruit-ripening hormone, and the carotenoids serve as algal sex hormones.

Certain vitamins of the B complex, such as thiamine, pyridoxine, and nicotinic acid, are synthesized in foliage leaves and are translocated in small amounts to roots, where they are required as factors for growth. They must be considered plant hormones, since they are chemical regulators of plant growth produced in one organ of the

[1] Panthothenic acid, a vitamin of the B complex, forms a part of the coenzyme-A molecule and no metabolic function has been described for this vitamin other than its relation to coenzyme A production.

plant and transported to another where they are utilized. Earlier in this chapter we have seen that the vitamins here mentioned form prosthetic groups of coenzymes which function in cellular respiration. In conclusion it can be stated that the growth of a plant is dependent not only on the end products of photosynthesis, on mineral nutrients derived from the soil, and on environmental factors but also on specific organic chemical regulators which it produces. The latter integrate the physiological processes of plants.

AEROBIC AND ANAEROBIC RESPIRATION

Every cell, to maintain its living state, must be constantly supplied with energy to enable it to carry on its vital activities. The energy is made available by the process of respiration. Respiration is a continuous process in which, for the most part, sugars are oxidized to carbon dioxide and water by the living cell. The summary equation for the process of respiration (oxidation of a six-carbon sugar) is as follows:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 673 \text{ kilogram calories}$$

The intermediate steps in this oxidation are described in the latter part of this chapter.

Under special conditions other materials, such as amino acids, fats, and other organic compounds, may be oxidized. The energy derived from respiration is utilized by the plant to do various types of work, such as the active absorption of ions, the building of energy-rich organic compounds for assimilation and storage, and the growth of plant organs. In contrast to photosynthesis, which is an energy-storing process, respiration is an energy-producing process. It is not totally efficient, since a part of the respiratory energy is liberated as heat.

There are two types of respiration (depending upon whether free oxygen is used): aerobic and anaerobic respiration. In *aerobic respiration*, free oxygen is utilized at least in the terminal stages of the process and complete oxidation results in the formation of carbon dioxide and water. Respiration in the absence of free oxygen is termed *anaerobic respiration* or fermentation. In this type of respiration, which is characteristic of many fungal organisms, oxidation is incomplete and there are produced compounds such as alcohols and organic acids which are capable of further oxidation. Fermentation utilizes the same

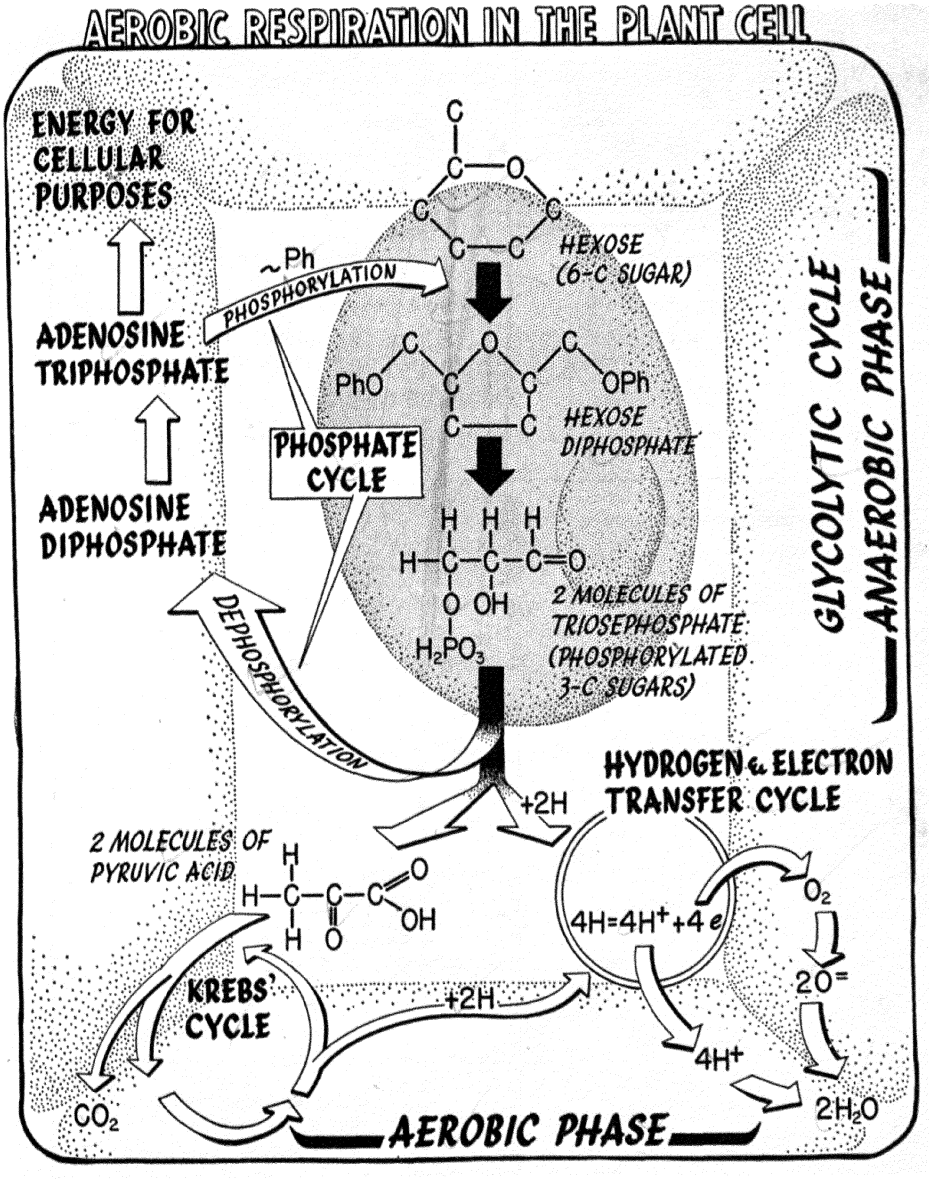
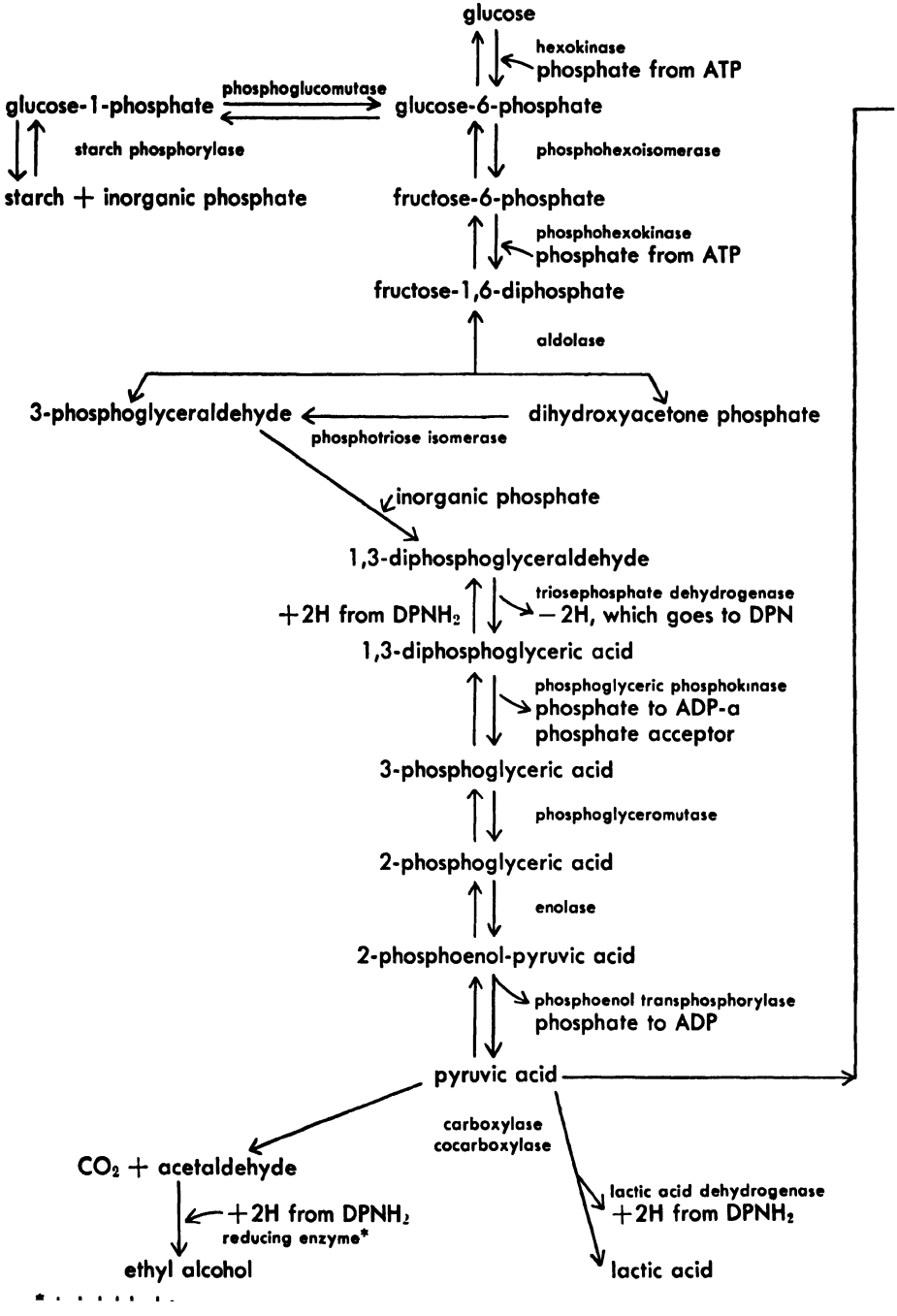
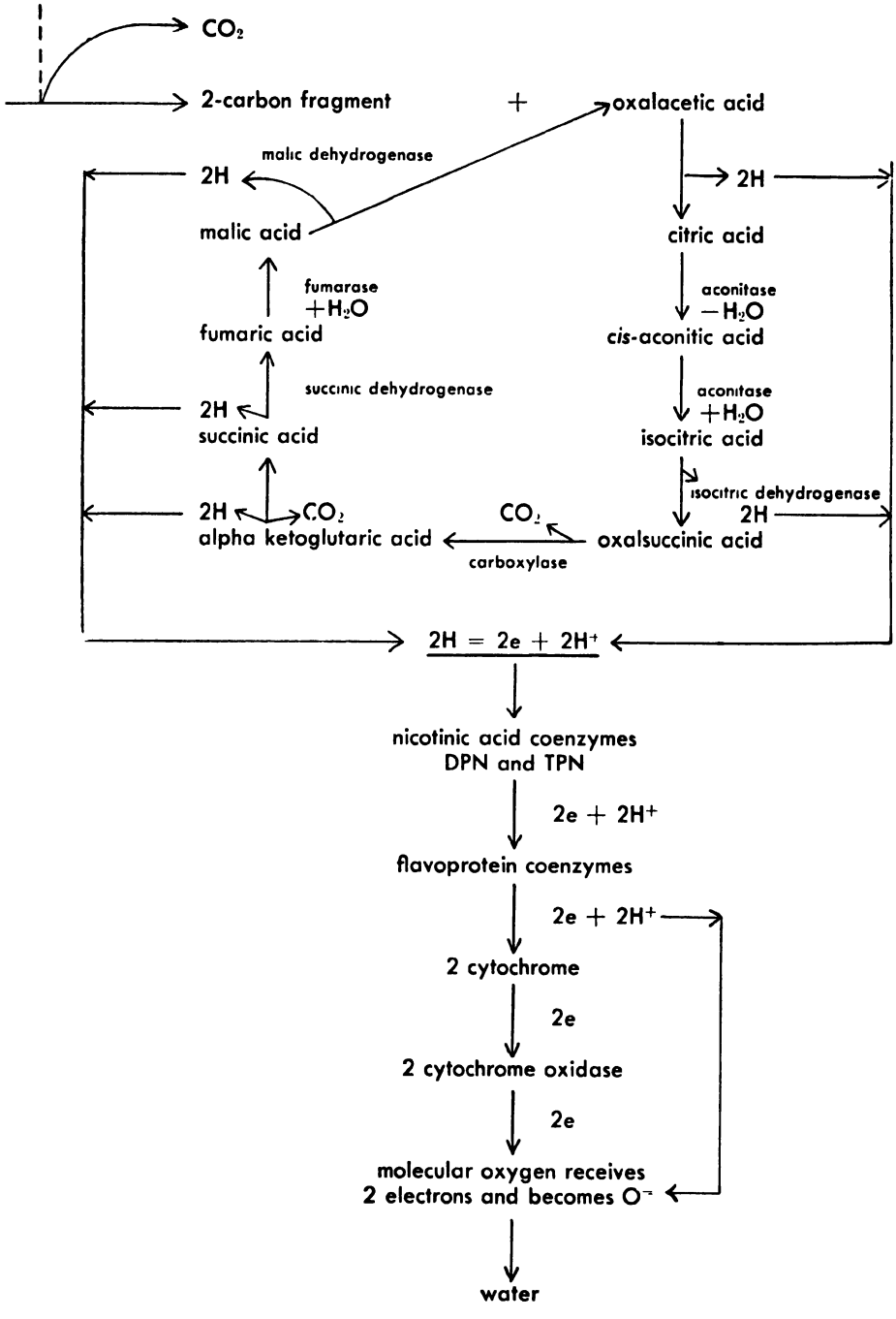


FIG. 9.0

foods (especially sugars) as aerobic respiration, and the energy release is accomplished through molecular rearrangement. One of the most familiar types of anaerobic respiration is the alcoholic fermentation of sugars by yeasts, in which the end products are carbon dioxide, ethyl alcohol, and energy. The latter is used by the yeast plant to carry on its vital activities. The respiratory enzymes involved in the above

Table 4 SUMMARY OF ANAEROBIC AND AEROBIC RESPIRATION




CO_2
2-carbon fragment
+
oxalacetic acid
malic dehydrogenase
2H
2H
malic acid
citric acid
fumarase
$+H_2O$
aconitase
$-H_2O$
fumaric acid
cis-aconitic acid
succinic dehydrogenase
aconitase
2H
$+H_2O$
succinic acid
isocitric acid
isocitric dehydrogenase
2H
CO_2
2H
CO_2
2H
alpha ketoglutaric acid
oxalsuccinic acid
carboxylase
$2H = 2e + 2H^+$
nicotinic acid coenzymes
DPN and TPN
$2e + 2H^+$
flavoprotein coenzymes
$2e + 2H^+$
2 cytochrome
2e
2 cytochrome oxidase
2e
molecular oxygen receives
2 electrons and becomes $O^=$
water

process are collectively called *zymase*. Alcoholic fermentation may be summarized in the following equation:

$$C_6H_{12}O_6 \xrightarrow{(zymase)} 2C_2H_5OH + 2CO_2 + 21 \text{ kilogram calories}$$

In higher plants, respiration (Fig. 9.0), which is largely the degradative phase of carbohydrate metabolism, occurs in two stages. The first is an anaerobic stage. In this stage, pyruvic acid is formed. The second is an aerobic stage in which oxygen is utilized and pyruvic acid is oxidized to carbon dioxide and water. The initial stages in aerobic respiration are similar to those of fermentation, but the higher plants could not survive indefinitely in the absence of free oxygen because of the inadequate amount of energy liberated and the toxic nature of the end products of anaerobic respiration.

The initial anaerobic stage (Fig. 9.0) in aerobic respiration is termed *glycolysis*. It involves the production of pyruvic acid from sugar through a series of complex enzymatically catalyzed reactions (Table 4). The six-carbon sugar or hexose is converted to fructose diphosphate. ATP acts in this stage of phosphorylation as a donor of energy-rich phosphate. The phosphorylated six-carbon sugar is then cleaved into two molecules of phosphorylated three-carbon sugars, or trioses. These are 3-phosphoglyceraldehyde and dihydroxyacetone phosphate. The latter is converted into the former by the action of phosphotrioseisomerase. Hence, from one molecule of fructose diphosphate we get two molecules of 3-phosphoglyceraldehyde. This compound is phosphorylated with inorganic phosphate to form 1,3-diphosphoglyceraldehyde. In a series of reactions, shown for reference in Table 4, this compound is converted to pyruvic acid, and four molecules of ATP are formed. Hence a surplus of two ATP molecules, whose energy is available for cellular activity, is formed in glycolysis for every hexose molecule utilized.

In conversion of glucose to pyruvic acid, the reaction entailing the change of 1,3-diphosphoglyceraldehyde to 1,3-diphosphoglyceric acid is a dehydrogenation or oxidation. DPN receives the hydrogen and becomes $DPNH_2$ or reduced DPN. It must be oxidized before it can accept more hydrogen. This occurs by transferral of the hydrogen to the flavoprotein coenzymes. The terminal stage in aerobic respiration involves the oxidation of pyruvic acid to carbon dioxide and water. This occurs in a cyclic series of steps termed the *Krebs cycle*, which is set forth for reference in Fig. 9.0 and Table 4. In each

oxidative step of the cycle, two hydrogen atoms are removed from the substrate acid, and they enter the hydrogen and electron transfer cycle to be oxidized by oxygen to water. Certain steps in the Krebs cycle are associated with energy-rich phosphate production. The energy-rich phosphate provides a source of energy to carry on various types of cellular work.

Fermentation differs from aerobic respiration in that the pyruvic acid formed in glycolysis is reduced. In the alcoholic fermentation (Fig. 9.0) of sugars by yeast, the pyruvic acid formed undergoes decarboxylation to become acetaldehyde, and the latter compound is reduced to ethyl alcohol. In some fungi, if sufficient oxygen is available, alcohol is oxidized to carbon dioxide and water. In lactic acid fermentation (Fig. 9.0), such as occurs in the souring of milk, pyruvic acid is reduced to lactic acid by the action of lactic acid dehydrogenase of bacterial origin. Reduced DPN provides the hydrogen for the reduction, and in the process it becomes oxidized.

In the process of respiration, energy is liberated and made available to carry on the multitude of cellular energy-utilizing processes. The energy transfer in many instances occurs through the mediation of labile energy-rich phosphate. Knowledge of the steps in carbohydrate degradation are found useful in understanding the possible mechanism of photosynthesis, the antithesis of respiration.

Chapter 10

THE FLOWER

A FLOWER is a specialized stem of limited growth, generally a branch stem, which bears floral leaves specially adapted to carry on reproduction. The floral leaves differ from foliage leaves in a number of respects. They are crowded together instead of being arranged at intervals along the stem, and normally there are no buds in their axils.

The first visible evidence of flower formation is the occurrence of flower primordia in buds. The initiation of flower buds sometimes occurs during the preceding growing season and sometimes during the same growing season. Flower primordia may develop from the stem tip in the terminal buds of main or branch stems or from the stem tips of axillary buds. The opening of flower buds is largely the result of cell enlargement accompanied by the osmotic absorption of water. Most of the cell division and a great deal of the cellular differentiation, including the early differentiation of the reproductive cells, occurs before the flower bud opens.

Sexual reproduction in the flowering plants, through the medium of the essential flower parts, that is, the pistils and the stamens, results in fruit and seed production. Within the seeds are the embryos of a new generation of plants. The environmental factors commonly concerned in the control of reproduction are length of the daily photoperiod and temperature. Short-day plants, such as the violet and poinsettia, blossom when exposed each day to illumination for relatively short periods. Long-day plants, beets (annual) and radishes for example, require long-day photoperiods. In day-neutral plants, floral initiation occurs during either short or long photoperiods. The effect of temperature on flowering is dependent upon so many variable factors that a concise treatment in a book of this type is not feasible.

The floral initiation stimulus is produced by leaves and is translocated through the vascular tissue to the bud. This is evident since total defoliation of a plant renders it insensitive to photoperiodic stimulation.

Parts of a Typical Flower (Fig. 10.0). The parts of a typical flower are divided into two groups, the essential flower parts and the accessory flower parts. The essential parts are those which are

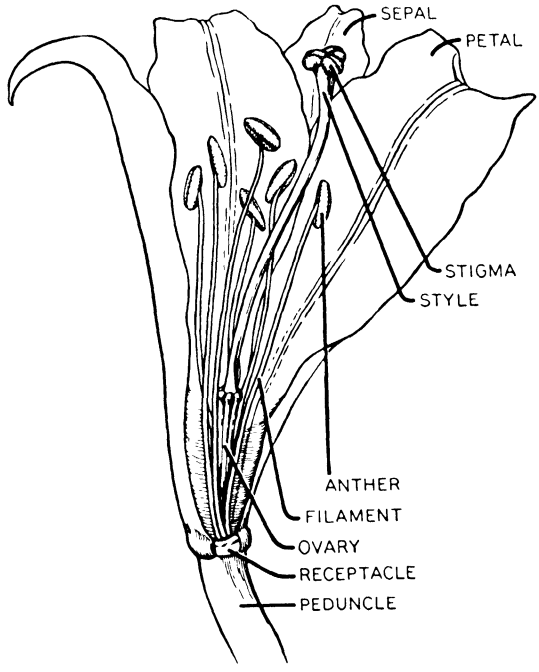


FIG. 10.0 Easter lily (*Lilium longiflorum*) dissected to show the stamens and the pistil. Only one sepal of the calyx is shown.

necessary for sexual reproduction and seed formation. The accessory parts attract insects and protect the essential parts before the flower bud has opened.

The essential floral parts are the pistils and the stamens. The *pistil* is a flask-shaped structure made up of a modified leaf or leaves (carpel or carpels). A *carpel* is an ovule-bearing leaf. If the pistil is derived from one carpel, as in the garden pea (*Pisum sativum*), it is said to be a simple pistil. If it arises from the fusion of a number of carpels, as in the Easter lily (*Lilium longiflorum*), it is a compound

pistil. In either case, the pistil is composed of three parts: ovary, style, and stigma. The *ovary* is the basally expanded hollow part of the pistil which encloses the *ovules* or incipient seeds. The neck-like column of tissue which arises from the top of the ovary and through which the pollen tubes grow is the *style*. The expanded tip of the style, to which the pollen grains adhere, is the *stigma*. The *stamen* is composed of a stalk or filament which supports a terminal *anther* from which numerous pollen grains are liberated when it is ripe.

The accessory floral parts are: the peduncle, the receptacle, and the sepals and petals. The *peduncle* is the stalk of a flower. Its upper broadened end to which the other floral parts are attached is the *receptacle*. The outermost tier of leaf-like structures is the *calyx*. It is composed of the *sepals*. The sepals may remain green or become variously colored as the flower matures. Their function is to enclose and to protect the other floral parts which are attached to the peduncle. Within the whorl of sepals is a whorl of leaf-like structures called the *petals*. Collectively the petals constitute the *corolla*. The corolla and calyx together constitute the floral envelope or *perianth*.

In a flower such as the Easter lily (*Lilium longiflorum*), the center is occupied by a tricarpellate pistil. Arranged in a circle around this compound pistil are six stamens. Outside these is a whorl of three petals. Surrounding the petals is a whorl of three sepals whose margins, for about two thirds of their length, are inserted into the midrib of the petals. The arrangement of sepals and petals in cycles of three is characteristic of monocotyledonous plants. In dicotyledonous plants these parts are generally arranged in cycles of five.

The flower of the Easter lily plant exhibits radial symmetry and is said to be *regular* or *actinomorphic*. A flower of this type can be cut vertically in any plane through the center, and the resulting halves will be somewhat like mirror images of each other. The flower (Fig. 10.1) of the sweet pea (*Lathyrus odoratus*) can be cut in only one vertical plane to attain halves that are mirror images of each other. Such a flower is said to be *irregular* or *zygomorphic* and has bilateral symmetry. The corolla of the pea flower is composed of five petals to which special terms have been applied. The *standard* is a broad petal and encloses the others in the bud; the two lateral petals are the *wings;* and the remaining two are ventrally fused to form the *keel*. The latter encloses the simple pistil and the stamens.

A complete flower is one which has both essential and accessory

parts. If it lacks any of these parts, it is said to be incomplete. Flowers in which the perianth is absent are said to be *naked* and those in which the petals are lacking are termed *apetalous*. While most flowers have both essential parts, in some plants two kinds of flowers are produced: one bearing stamens (staminate flowers) and the other bearing pistils (pistillate flowers). Such flowers are said to be imperfect, to distinguish them from perfect or hermaphroditic flowers which possess both essential parts (Figs. 10.0 and 10.1). In some cases both staminate and pistillate flowers occur on the same plant and the species is said to be *monoecious*. The tassel of the corn plant is a group of

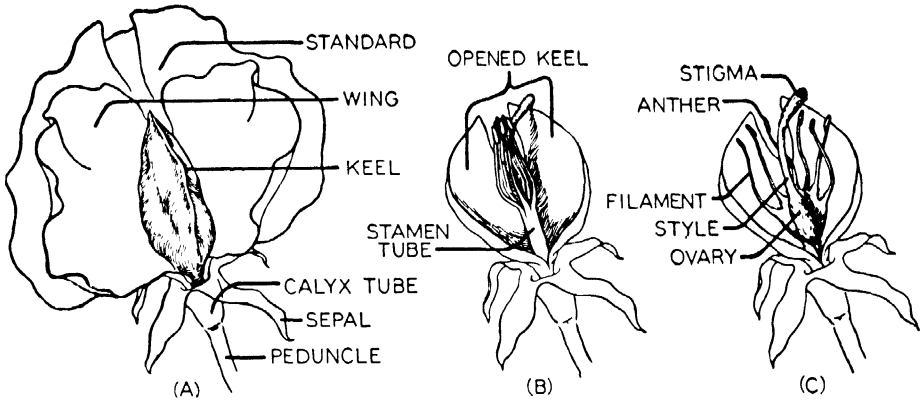


FIG. 10.1 (A) Face view of the sweet pea (*Lathyrus odoratus*), (B) keel dissected to show the stamen tube; (C) stamen tube opened to disclose more fully the external morphology of the pistil.

staminate flowers, and the young ear is a group of pistillate flowers. In other cases staminate flowers are produced by one individual plant and pistillate flowers by another. The latter condition is described as *dioecious*.

Fusion of Flower Parts. In some flowers there are separate stamens, separate pistils, separate petals (polypetaly) and separate sepals (polysepaly). In others there may be fusion or growing together of parts. Union may involve stamens (synandry), pistils (syncarpy, Fig. 10.0), petals (sympetaly, Fig. 10.0), or sepals (synsepaly). In sympetalous flowers, the basal portions of the petals are joined to form a corolla tube. In synsepalous flowers, a calyx tube is similarly formed. Sepals, petals, and stamens may be basally united to form a floral tube or *hypanthium*.

Structure of a Mature Pistil. In the formation of a simple pistil, the margins of the ovule-bearing leaf or carpel have been inrolled longitudinally and united to form a suture, the ventral side of the leaf being on the outside. On the side of the carpel opposite the suture, there is usually a ridge which represents the midrib of the carpellary leaf. Within the enclosed cavity or *locule* of the pistil or ovary are borne the ovules. The part of the ovary wall to which the ovules are attached is the *placenta* and the manner of their distribution is termed *placentation.* In the unilocular ovary of the simple pistil, placentation

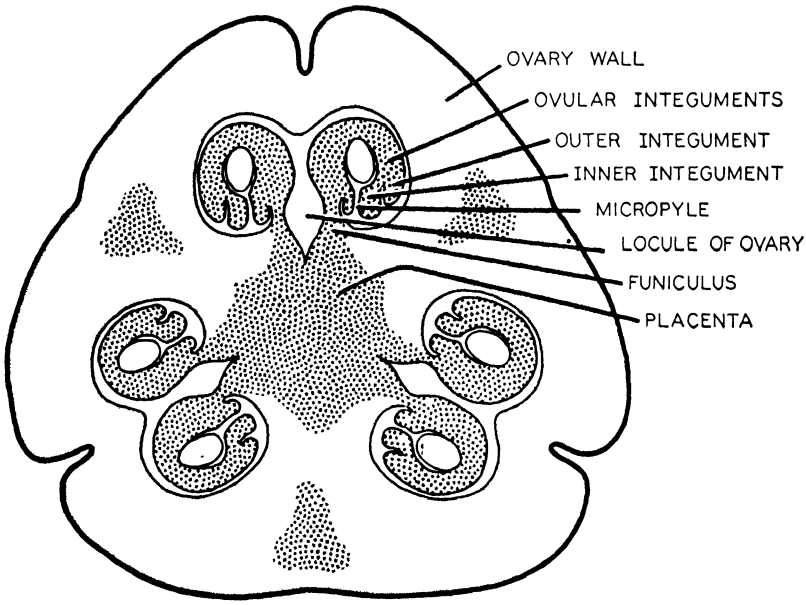


FIG. 10.2 Transverse section of the lily ovary, showing six ovules and the manner of placentation.

is parietal. The ovules are usually attached to the fused edges of the carpellary leaf. In the garden pea, where the ovary is derived from a single carpel and the placentation is parietal, the ovules are arranged in an alternate fashion in a single row, every other one being attached to the same carpellary margin.

When two or more carpels form one structure (Figs. 10.0 and 10.2), the structure is a *compound pistil.* The carpels of a compound pistil may be fused to form a unilocular or multilocular ovary, and hence the number of the locules may or may not be the same as the

number of carpels. In addition, pseudosepta may develop which do not correspond with the carpellary walls. In a multicarpellate ovary, the placentation may be parietal, axile, or free central. When, as in the Easter lily, the placentae occur on the central axis of the ovary, the placentation is said to be *axile* (Fig. 10.2). In pinks and in primroses the ovules are attached to a central axis which is only connected with the ovary wall basally, and the placentation is termed *free central.* The free central axis may arise as an upgrowth from the ovarian floor, or it may result from the dissolution of septa previously present.

For a proper understanding of fruits, the position of the ovary with reference to the other floral parts must be considered. A flower in which the sepals, petals, and stamens are attached to the receptacle below and free from the ovary or ovaries is said to be *hypogynous,* and the ovary or ovaries are said to be *superior.* When a floral tube is present and is fused with the wall of the ovary, the flower is *epigynous* and the ovary is *inferior.* In this type of flower the other floral parts appear to arise from the top of the ovary.

The ovary wall consists largely of parenchyma and vascular tissue. It has both an outer and an inner epidermis. The outer epidermis bears a cuticle.

The styles of a compound pistil may be separate or they may have undergone concrescence to form a single stylar column (Fig. 10.0). In most angiosperms the style is solid (no canals present) and is composed of a core of elongated cells surrounded by an epidermis.

The stigma of the pistil (Fig. 10.0) consists of a cuticularized glandular epidermis which may secrete a viscous sugary solution. Beneath the epidermis is a glandular parenchyma whose cells are rich in cytoplasm. In some plants the stigmatic epidermal cells develop minute hairs (Fig. 10.1C). Both the stigmatic fluid and the hairs facilitate the adherence of pollen.

An ovary contains one or more bodies called ovules (Fig. 10.2). The mature ovule (Fig. 10.3) is differentiated into the following parts: a single, large, centrally located cell with eight nuclei called the *eight-nucleate embryo sac* or mature female gametophyte; the *nucellus,* usually a single layer of cuboidal cells surrounding the embryo sac; one or two *integuments,* each only a few cells in thickness, enclosing the nucellus; and a *funiculus* or stalk which attaches the

ovule to the placenta. The integuments do not quite enclose the nucellus at one end and hence leave a small tubular passageway, the *micropyle,* for passage of the pollen tube.

In the eight-nucleate embryo sac, the two nuclei in the center are the *polar nuclei.* The three nuclei at the end of the embryo sac opposite the micropyle are the *antipodals.* Of the three nuclei at the micropylar end of the sac, one is the female gamete or *egg,* and the

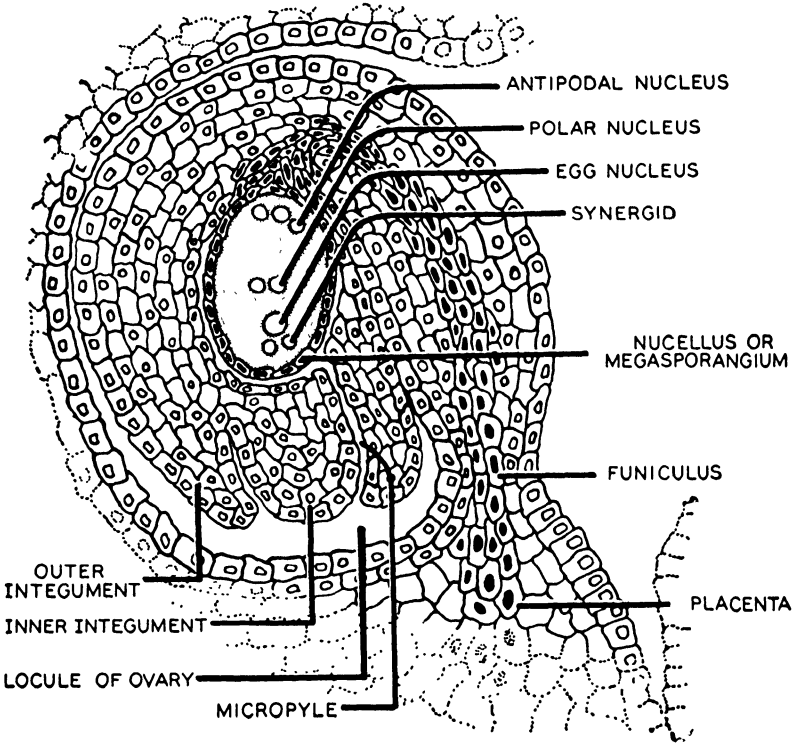


FIG. 10.3 Longitudinal section of the lily ovule.

remaining two are the *synergids.* The synergids, the antipodals, and in some species the egg nucleus may be surrounded by cytoplasm and separate cell walls.

The relationship of the funiculus to the ovule is of taxonomic importance. An *orthotropous* ovule is one which forms a straight line with its stalk. An *anatropous* ovule is one whose micropyle is turned toward the funiculus (Fig. 10.2). Between these two forms of ovules there are various intermediate types with various degrees of curvature.

Structure of a Mature Stamen. The mature stamen usually consists of a stalk or filament bearing at its upper end a two-lobed, two-chambered anther.

The filament has a central strand of vascular tissue which may or may not be prolonged into the tissue between the anther lobe—the so-called *connective*. Enclosing this strand is a ground tissue of vacuolated parenchyma, and about the latter is a cutinized epidermis. The filament is attached to the base of the connective of the anther or to its center.

In each lobe of the mature anther (Fig. 10.4) is an elongated cavity or pollen sac in which are pollen grains. The external cell layer of the wall of the pollen sac is the epidermis. Beneath the

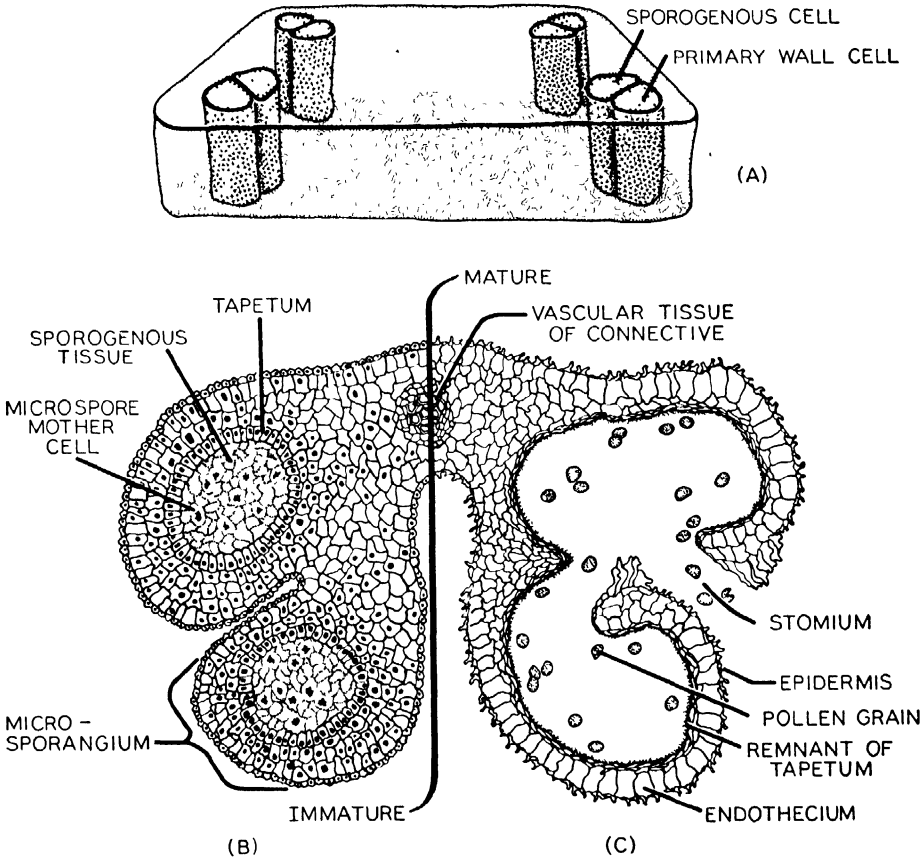


FIG. 10.4 Development of the anther: (A) primordial anther; (B) immature anther; (C) mature anther.

epidermis is the *endothecium*, a layer of large columnar-shaped cells containing hygroscopic rods which play a role in the splitting open or *dehiscence* of the anther to release the pollen. The opening through which the pollen grains are discharged from the pollen sac is termed the *stomium*. The specialized cells about the stomial margin are the lip cells.

The pollen grain (Fig. 10.5), at the time it is shed, is a spherical or ovoid cell with two membranes: a rough outer wall of cutin called

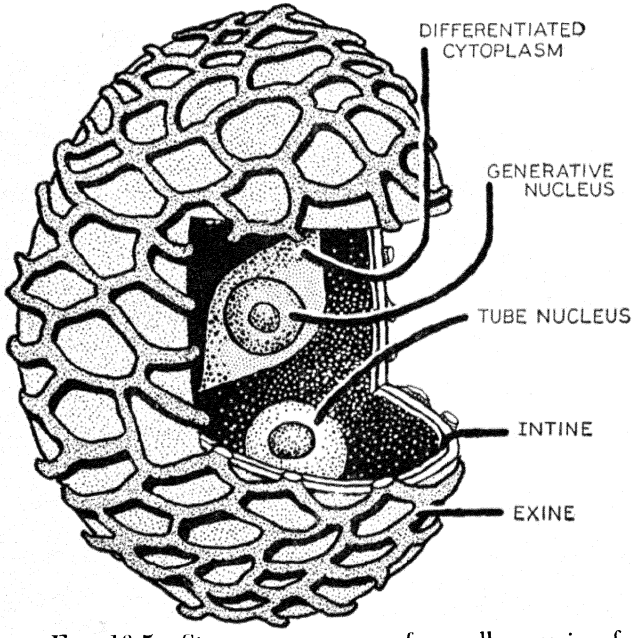


FIG. 10.5 Stereoscopic view of a pollen grain of the lily.

the *exine* and an inner thin wall of cellulose and pectin substances called the *intine*. About the time the anther dehisces, the single nucleus of each young pollen grain (microspore) divides mitotically to form a generative nucleus and a tube nucleus. The generative nucleus can sometimes be distinguished from the tube nucleus by the spindle-shaped area of differentiated cytoplasm which surrounds it.

Inflorescences. Flowers may occur singly or in clusters. A cluster of flowers is termed an inflorescence. The sunflower, daisy, aster gladiolus, and hyacinth are examples of inflorescences. The morphological parts of inflorescences are peduncle, rachis, pedicel, bract,

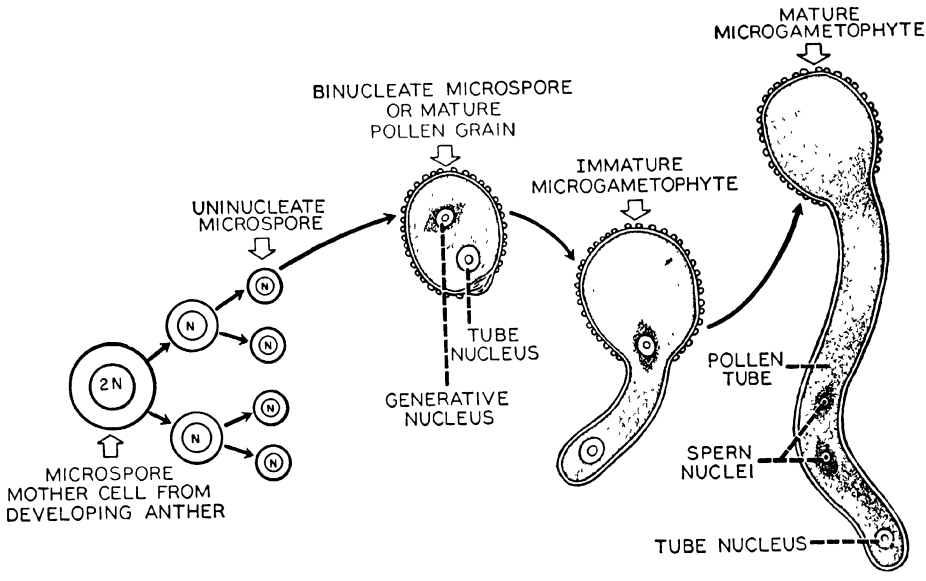


FIG 10.6 Diagrammatic presentation of microsporogenesis; binucleate microspore or mature pollen grain (see Fig. 10.4B), germinating pollen grains as immature and mature microgametophytes

bracteole, and flower. Not all inflorescences possess all these parts. The peduncle is the stalk of a flower cluster. The axis of a prolonged inflorescence is called a *rachis*. A *pedicel* is the flower stalk of a single flower. If the flower is attached directly to the rachis, it is said to be *sessile*. A modified leaf appearing on the rachis is known as a *bract*.

There are two principle types of inflorescences, indeterminate and determinate. When axillary flowers and a terminal flower occur in the same cluster and the opening of the terminal bud as a flower completes the growth of the stem of the flower cluster, the inflorescence is *determinate*. When all the flowers arise from axillary buds and the teminal bud of the flower cluster continues to grow and to increase the length of the stem indefinitely, the inflorescence is *indeterminate*.

Germination of Pollen Grains (Figs. 10.6 and 10.8). After deposition of the pollen grain upon the stigma it is held there generally by stigmatic fluid, secreted by the cells of the stigma. The stigma may also be ridged, and this ridging of the stigma may contribute in some degree to the adherence of the pollen grain. As the pollen grain lies upon the stigma, it absorbs water, as a result of which the turgor pressure of the pollen grain necessarily becomes greatly increased. The first sign of the germination of a pollen grain is usually given

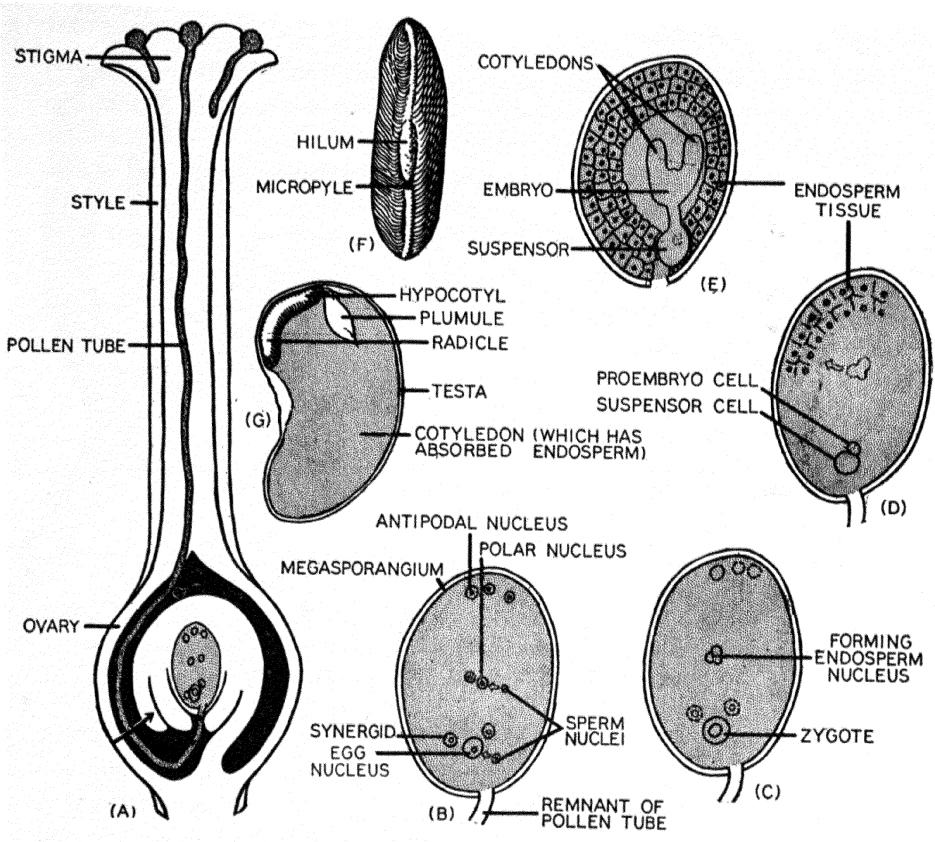


FIG. 10.7 Fertilization, and development of the seed.

by the vacuolation of its cytoplasm. In due time the exine is ruptured, and through the ruptured exine there evaginates the intine, into which now flow the nuclei and some of the cytoplasm of the pollen grain (Fig. 10.6). The evaginated intine and its contents constitute the beginning of the formation of the pollen tube. This pollen tube (Fig. 10.6) now grows down through the tissue of the style. Some plant physiologists believe that the pollen tube secretes an enzyme which serves to digest the tissue of the style before the growing pollen tube. As the pollen tube (Fig. 10.7A) grows down into the tissue of the style, the generative nucleus divides mitotically to form two sperm nuclei. At this time there are now present in the pollen tube two sperm nuclei and one tube nucleus. The pollen tube finally makes its way through the micropyle and subsequently perforates the nucellus to attain the embryo sac. The tip of the pollen tube then ruptures and discharges into the embryo sac the two sperm nuclei and the one tube nucleus.

Fertilization (Fig. 10.7). One of the sperm nuclei fuses with the

egg nucleus and the resulting fusion nucleus becomes surrounded with a cell wall to form a zygote. The fusion of the sperm nucleus with the egg nucleus is commonly referred to as fertilization (Figs. 10.7B and C). Fertilization may be briefly defined here as the fusion of two heterogametes, one a microgamete (sperm nucleus here) and the other a macrogamete (egg nucleus here), to form a single cell termed a zygote. The other sperm nucleus fuses with the two polar nuclei to form the endosperm nucleus. This endosperm nucleus multiplies at quite a rapid rate to form a number of endosperm nuclei (Fig. 10.7D). The cytoplasm around these endosperm nuclei becomes simultaneously septated to form the endosperm tissue, the functional significance of which will be considered below. The zygote (Fig. 10.7D), in the meantime has divided by an unequal cleavage of its cytoplasm to form a small cell called the *proembryo* and a large cell called the *suspensor cell.* The proembryo (Figs. 10.7D and E) differentiates into the embryo and subsequently will be observed to possess one or two cotyledons, a hypocotyl, and a developing plumule. Attached to one end of this developing embryo will be the suspensor, which has actually differentiated by cell division from the original suspensor cell. The suspensor (Fig. 10.7E) serves to anchor the embryo in the embryo sac. In the meantime the endosperm tissue (Fig. 10.7E) has proliferated to such an extent that it practically fills the embryo sac with the exception of the space occupied by the developing embryo. The endosperm tissue constitutes a food reserve for the developing embryo. In some seeds, for example the common bean (*Phaseolus vulgaris*), this endosperm tissue is absorbed completely by the cotyledons of the embryo (Figs. 10.7F and G). Such seeds will be referred to subsequently as exalbuminous seeds. The tube nucleus, the synergids, and the antipodal nuclei in most cases ultimately become disorganized into the cytoplasm of the embryo sac.

Development of the Seed. The process of fertilization is accompanied by many changes that occur both in the ovule and the ovary itself. The ovule becomes much larger and generally attains a point in maturation where its volume is sometimes one hundred times that of the original ovule. The integuments expand, undergo a dehydration, and finally harden to form the seed coats, the outer one being called the *testa* and the inner one the *tegmen.* The soluble foods which have been translocated into the ovary are generally now transformed into insoluble storage products: the sugars are generally con-

densed to form starch and may even be converted into the hemicelluloses; the amino acids are transformed into proteins; the glycerin and the fatty acids are converted into fats. The whole ovule now seems to undergo a general dehydration and becomes a relatively hard body in contrast to its originally succulent nature. The ovule is now said to have matured, and such a matured ovule is botanically known as a seed (Fig. 10.7F). The physiological activity in the seed now becomes reduced to a minimum, and the seed is said to enter a period of dormancy.

Fruit Formation. While the ovule is undergoing its maturation into a seed, the ovary wall is being differentiated into several layers of tissue which will collectively constitute the pericarp. Such a matured ovary is botanically referred to as a fruit, the morphology of which will be considered in the chapter on fruit. The other flower parts, such as the petals, the style, and the stigma, excepting perhaps the sepals, wither and die.

MEIOSIS

Introductory Data on Meiosis. If you will recall our discussion on somatic cell division, you will remember that each of the daughter cells resulting from the division of the parent cell possessed the same number of chromosomes. This was due to the equational disjunction of the sister chromatids, each of which became in the telophase a chromosome. Thus if we began with a parent cell having thirty chromosomes, there would be in the nucleus of each daughter cell after somatic division thirty chromosomes. By way of contrast, in meiosis, which comprises two divisions, there will obtain in each of the four daughter cells one half the number of the chromosomes that there were originally in the nucleus of the parent cell. The reason for the reduction in the number of chromosomes lies in the fact that there were two divisions of the nucleus, but only one division of its chromosomes. In other words, as we shall observe in our detailed analysis of the process, there will take place in one metaphase the separation of whole chromosomes; the centromere of each chromosome at the time does not become divided into two daughter centromeres.

Some Basic Concepts of Genetics. Before going into a detailed discussion of meiosis, several fundamental concepts present themselves for examination, for in our comprehension of these concepts

will ultimately repose the reasons for meiosis. Further, any knowledge which we may wish to attain concerning either plant or animal genetics will have its real basis here in our grasp of these fundamental principles.

Take yourself as an example. In each of your body or somatic cells there are 48 chromosomes or 24 pairs of homologous chromosomes. This number of chromosomes is called the *diploid* or normal somatic number, sometimes referred to as the $2n$ number. However, in each of your mature germinal or reproductive cells (the spermatozoa in the male and the ova in the female) only one half of the normal somatic number occur. Thus in each mature reproductive cell there are the 24 chromosomes or the *haploid* number, sometimes referred to as the n number. The type of cell division concerned in accomplishing a reduction from the diploid or $2n$ number to the haploid or n number is called *meiosis* or *reductional cell division.*

Genes and Homologous Chromosomes. Homologous chromosomes are chromosomes which bear the same genes in the same linear sequence; that is, each of a pair of homologous chromosomes corresponds gene for gene with the other. A *gene* may be concisely defined here as that which is responsible for the production of an hereditary characteristic, such as height, eye color, and so on. Human subjects, even in the same family, are obviously genetically different for a great many hereditary characters. These genetic differences as reflected in hereditary characters indicate very clearly that the homologous genes situated at corresponding positions or loci on homologous chromosomes very often differ from each other. Such genes which differ from each other at the same loci on homologous chromosomes are termed *alleles,* one of which is a mutation of the other. A mutation is a genic change or an altered gene. Mutations may be artificially produced in the laboratory by the use of X rays or radioactive substances, but in nature these mutations arise over long periods. (All of these phenomena will be discussed somewhat further in Chapter 31, Plant Genetics.) It might be profitable to add here that some genes undergo a number of different mutational changes, but any one plant or animal organism can carry only two allelic forms for the original genes. The gene which expresses itself in the hereditary character of the individual is said to be *dominant* while the gene which remains hidden is termed a *recessive.* (For more about genic dominance, see Chapter 31, Plant Genetics.)

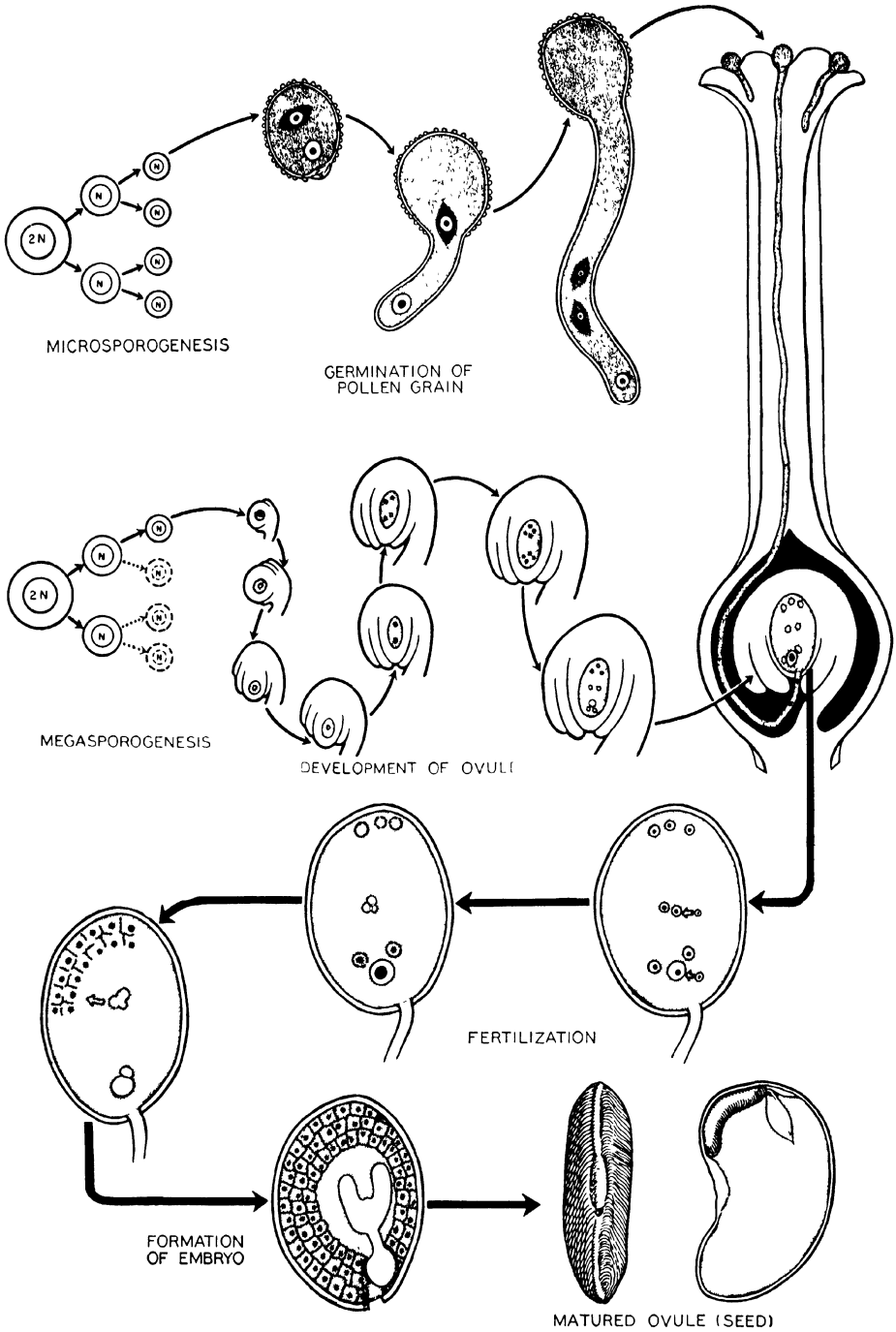


FIG. 10.8 Microsporogenesis, megasporogenesis, fertilization, and the development of the seed.

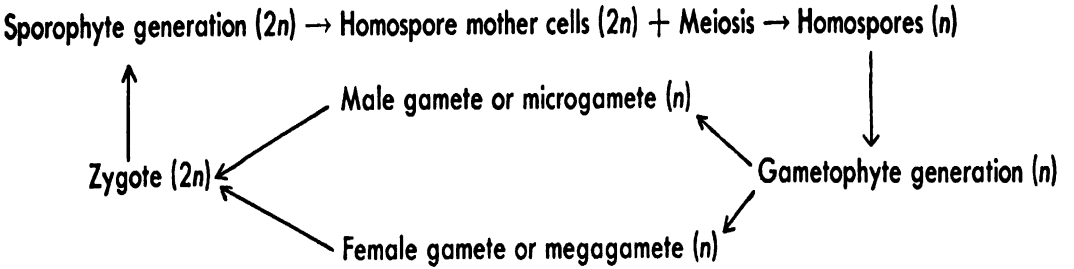
Types of Life Cycles. In human fertilization two haploid gametes or sex cells, spermatozoon and ovum, unite in the formation of a diploid zygote, whence a human individual develops, in each of whose somatic cells obtains the $2n$ or diploid number of chromosomes. Such a developmental cycle is often termed a *gametic* or *terminal cycle,* in which the diploid generation, by meiosis, gives rise to the haploid generation. In other words, in the case of a human subject, the individual himself represents the diploid generation, and his gametes or sex cells the haploid generation.

In most plants there is an alternation of generations; that is, the alternation of a sporophyte generation with a gametophyte generation. The sporophyte generation, as represented in the root, the stem, the leaf, and so on, contains in each of its cells the diploid number of chromosomes; while the gametophyte generation, generally inconspicuous in vascular plants, possesses in each of its cells the haploid number of chromosomes. In this developmental cycle, often referred to as a *sporic* or *intermediate cycle,* the spore mother cells of the sporophyte generation undergo meiosis to form haploid spores, whence in turn the mature gametophytes develop in which the gametes are produced. In the angiospermal plants, for example the lily, we have two types of spore mother cells (Fig. 10.8): the smaller or microspore mother cells and the larger or megaspore mother cells. The two types give rise meiotically to, respectively, microspores (immature microgametophytes or immature male gametophytes) and megaspores (immature megagametophytes or immature female gametophytes). The immature microgametophyte (uninucleate pollen grain) develops into a mature male gametophyte (germinated three-nucleate pollen grain) in which the sperm nuclei are representative of the microgametes or male gametes. On the other hand, the immature female gametophyte (megaspore or uninucleate embryo sac) develops into a mature female gametophyte (in the lily, eight-nucleate embryo sac) in which the egg nucleus is representative of the megagamete or female gamete. The fusion of the male and female gametes in fertilization culminates in the zygote, which marks the beginning of the sporophyte generation.

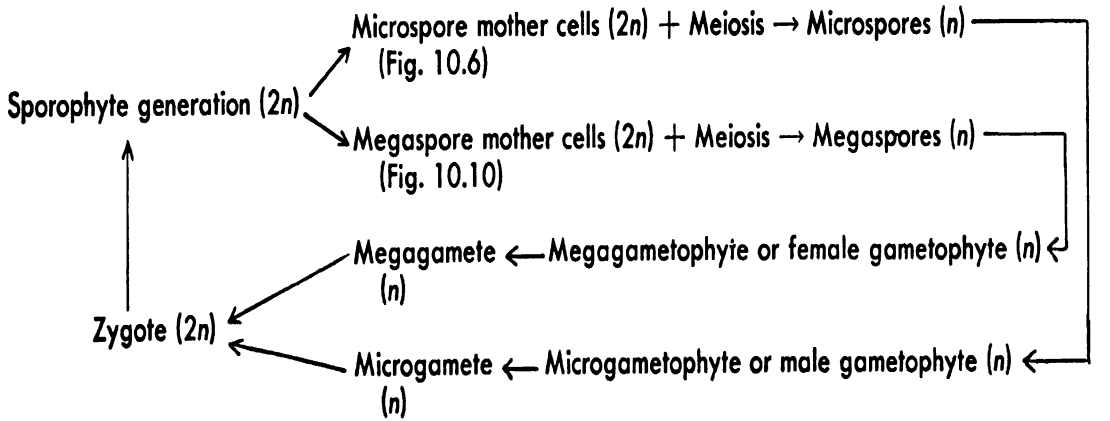
The intermediate or sporic cycle, applicable to both homosporous and heterosporous cycles, may be visualized in the accompanying diagrams.

Phases of Meiosis. It is theorized from some experimental investi-

(a) CYCLE WITH HOMOSPORES (MORPHOLOGICALLY SIMILAR SPORES)



(b) CYCLE WITH HETEROSPORES (MORPHOLOGICALLY DISSIMILAR SPORES)



gations that the suppression of the duplication of the sister chromonemata in the prometaphase of the last mitotic division is actually a factor in initiating the process of meiosis.

Meiosis itself is generally considered in two divisions known as the first meiotic division and the second meiotic division.

FIRST MEIOTIC DIVISION. The prophase of the first meiotic division is so protracted that it itself is divisible into the following phases in the order of their sequential occurrence: leptotene, zygotene, pachytene, diplotene, and diakinesis.

PROPHASE OF THE FIRST MEIOTIC DIVISION. *A. Leptotene* (*Fig.* 10.9A). This stage involves the dehydration of the nucleus and the appearance of the chromonemata. Each chromonema is characterized at definite intervals by bead-like enlargements commonly referred to as *chromomeres*. There is some speculation that these chromomeres may represent the loci of the genes. The genes, as has been already indicated, are actually the entities concerned in the determination of hereditary characteristics. The leptotene is of very short duration. For the purpose of simplification, we shall henceforth refer to the chromonemata as chromosomes. However, it should be borne in mind that in the strict sense these chromonemata will not actually become chromosomes until the stage of diakinesis is finally attained.

B. Zygotene (*Fig.* 10.9B). The zygotene involves a regionally specific pairing of homologous chromosomes, one half of which are to be regarded as being paternal in origin and the other half as maternal. This regionally specific conjugation of homologous chromosomes postulates some sort of attraction. What is causative of this attraction is not known definitely at this time.

C. Pachytene (*Fig* 10.9C). In this phase the homologous chromosomes become longitudinally divided except at a certain specialized region where they remain single or unstainable. The latter specialized region is called the centromere. Thus each chromosome is now observed to be constituted of two chromatids which in turn are attached subterminally to each other by a centromere. The mutual attraction which originally existed between the homologous chromosomes in the zygotene now seems to be replaced by a tendency to repulsion, and consequently in this stage the homologous chromosomes appear to diverge from one another.

D. Diplotene (*Figs.* 10.9D *and* E). The complete divergence of the homologous chromosomes is prevented in this stage by what is

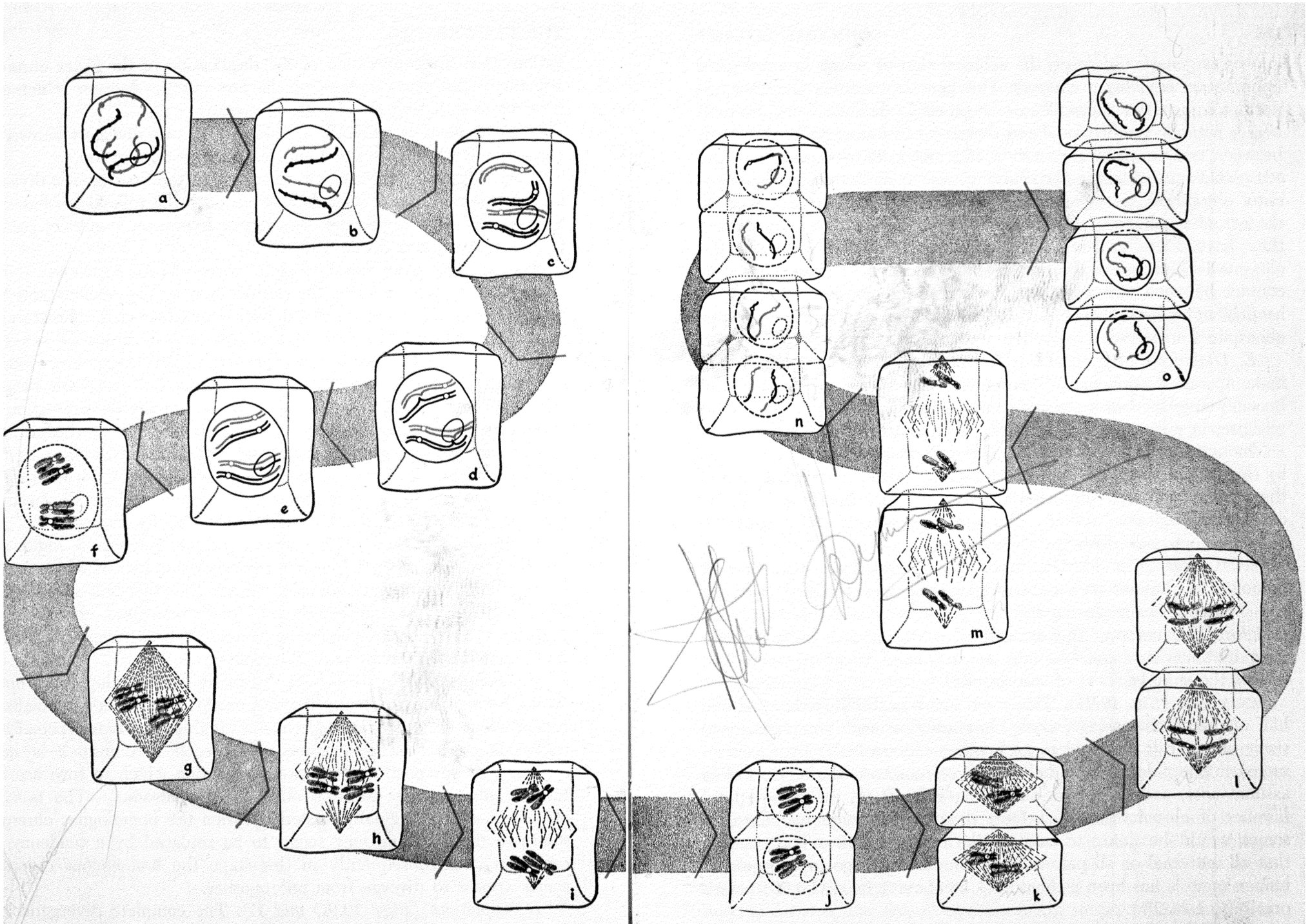


FIG. 10.9 Meiosis: $2n = 4$ chromosomes. Maternal chromosomes are shown in red, paternal chromosomes in black. See the text for details.

known as genetic crossover, the external sign of which in cytological examination is called a *chiasma*. This genetic crossover is rather important in genetics and will now be precisely defined. Genetic crossover is actually the breakage and reciprocal fusion at point of contact between two nonsister chromatids. It is not a literal crossover in the sense that one nonsister chromatid comes to lie across another nonsister chromatid. In such a case the chiasma would actually precede the actual breakage of the nonsister chromatids at the point where they have literally traversed each other. Actually, however, the chiasma is the result of the breakage and reciprocal fusion at point of contact between two nonsister chromatids. The important thing to keep in mind here is that in this genetic crossover, whole blocks of genes are transferred from one nonsister chromatid to the other.

E. Diakinesis (*Fig.* 10.9 F). In diakinesis the chromatids which make up each homologous chromosome shorten by a spiralization and become enveloped in a stainable matrix. It is here that we can actually use, in a strict sense, the term chromosome.

PROMETAPHASE (Fig. 10.9G). The prometaphase is characterized by the disappearance of the nucleoli and the nuclear membrane. From the karyolymph the spindle is organized. These fibers, as was the case in karyokinesis, actually represent a gelification of the karyolymph, the ground substance of the nucleus.

METAPHASE (Fig. 10.9H). In the metaphase the centromeres of homologous chromosomes are arranged at the equatorial plate of the cell. *The centromere does not in this phase become divided into two daughter centromeres.* The unmodified centromere of each homologous chromosome now becomes approximated to or connected to one of the spindle fibers of the spindle.

ANAPHASE (Fig. 10.9I). This stage involves the movement of one half of the chromosomes (whole chromosomes: each comprising two sister chromatids attached to each other subterminally by a centromere) to one pole, and one half the chromosomes to the other. Let us assume now, as has been indicated in Fig. 10.9A, that the diploid number of chromosomes was four; then at this stage two chromosomes would be going to each of the opposite poles. The chances that all maternal or all paternal chromosomes will go to one pole in human meiosis has been estimated to be about 1 in 17,000,000 (more precisely, 1 in 2^{24}).

TELOPHASE (Fig. 10.9J). Generally in the telophase of the first

meiotic division the chromosomes at each pole do not undergo any despiralization, but simply remain as they are and become surrounded by a nuclear membrane. The cell then undergoes cytokinesis and the daughter cells separate. In each of the daughter cells there are now two chromosomes—i.e., the haploid number.

SECOND MEIOTIC DIVISION. In the greater number of cases, the second meiotic division begins with the prometaphase. There is no need for a prophase since the chromosomes in the original telophase did not undergo despiralization to form chromonemata which would subsequently anastomose in their characteristic manner to form the nuclear reticulum of the metabolic nucleus.

PROMETAPHASE (Fig. 10.9K). This simply involves the disappearance of the nuclear membrane and the formation of the spindle in the usual manner.

METAPHASE (Fig. 10.9L). The chromosomes in each daughter cell now line up at the equatorial plate. The centromere of each chromosome divides to form two daughter centromeres. Each daughter centromere now becomes the centromere of the chromatid to which it is attached. Finally, each chromatid becomes approximated to or connected with one of the spindle fibers of the spindle by means of its centromere.

ANAPHASE (Fig. 10.9M). This stage involves the movement of one half of the chromatids to one pole and the movement of one half of the chromatids to the other pole.

TELOPHASE (Fig. 10.9N). The telophase chromatids, now properly referred to as daughter chromosomes, despiralize and lose their matrices to become chromonemata. The chromonemata at each pole now anastomose by small lateral filaments to form the nuclear reticulum in much the same manner as has already been indicated in the discussion of karyokinesis (see Chapter 3, Plant Cells).

Cytokinesis follows. Thus there are formed finally four daughter cells each of which is now characterized by the reduced number (Fig. 10.9O), i.e., the haploid number of chromosomes.

From a consideration of the preceding analysis of meiosis, it would appear that meiosis simply involves the disjunction of homologous chromosomes. In the previous discussion of this process, the separation of the homologous chromosomes really occurred in the first meiotic division, the second division being simply equational. Consequently it would seem that the process of meiosis can be made to fall

within well-defined lines. However, in nature it often happens that both a meiotic and a mitotic division can occur simultaneously in the same cell. For example, in the first meiotic division it is quite possible to have a disjunction of some of the homologous chromosomes and at the same time a separation of sister chromatids of some of the other homologous chromosomes; but, as has already been indicated, the separation of sister chromatids is by definition karyokinetic (mitotic) rather than meiotic. When such a phenomenon has happened in the first meiotic division, there will necessarily occur in the second meiotic division the separation of the sister chromatids of the homologous chromosomes that originally underwent disjunction to the opposite poles in the preceding division. At the same time there must take place the separation of nonsister chromatids. The latter nonsister chromatids, it should be emphasized here, are actually the chromatids that resulted from the equational or mitotic division of the homologous chromosomes in the preceding division. Thus meiosis may be defined more precisely as either the disjunction of homologous chromosomes or the separation of nonsister chromatids derived from the previous equational division of homologous chromosomes.

HISTOGENESIS OF THE ANTHER AND MICROSPOROGENESIS

The anther begins its development (Fig. 10.4) as a mass of meristematic tissue surrounded by an epidermis. Initially the cells of this primordial mass, with the exception of the epidermis, are morphologically similar. However, within a very short time the centrally situated cells develop a rather dense cytoplasm and constitute the provascular strand whence develops the vascular tissue of the anther connective. Concurrently in each of the opposite peripheral angles of the primordial mass a single longitudinal row of cells becomes cytologically modified in the same way as the centrally placed cells aforementioned. The cells in each longitudinal row are commonly referred to as *archesporial cells*. Subsequently these archesporial cells mitotically divide, parallel to the anther surface (periclinally or tangentially), to form outer primary wall cells and inner sporogenous cells (Fig. 10.4A). The outer primary wall cells, by further mitotic differentiation, form an outer layer of column-shaped cells, or the *endothecium* (Fig. 10.4), and an inner layer of nutritive cells, the *tapetum*. The tapetum (Fig. 10.4) functions as a source of nutriment

for both the microspore mother cells and microspores. The epidermis and endothecium form the walls of the four *microsporangia* (spore containers, Fig. 10.4) that come about in the development of the anther. In the meanwhile the inner sporogenous cells multiply mitotically to form microspore mother cells (Figs. 10.4 and 10.6). These microspore mother cells undergo meiosis to form haploid microspores (also called uninucleate pollen grains or immature microgametophytes). At the same time the tapetum undergoes digestion during the development of microspores, so that there are thus produced the four locules of the microsporangia. At maturity the intervening cellular partitions between adjacent microsporangia disintegrate to form a two-chambered anther. The two-chambered anther is generally referred to as the mature anther.

As you will recall from previous discussion, the nucleus of the uninucleate microspore or young pollen grain (Fig. 10.6), at the time that it is shed from the dehiscent anther, divides to form a tube nucleus and a generative nucleus. Upon germination the generative nucleus in the pollen tube divides to form two sperm nuclei (Fig. 10.6). The germinated pollen grain (pollen grain with pollen tube) possesses three nuclei and constitutes the mature microgametophyte or male gametophyte.

HISTOGENESIS OF THE OVULE AND MACROSPOROGENESIS

The ovule makes its appearance (Fig. 10.10) as a knob of meristematic tissue at the placenta of the ovary. This knob of tissue develops into the nucellus or megasporangium. Almost concurrently two rings

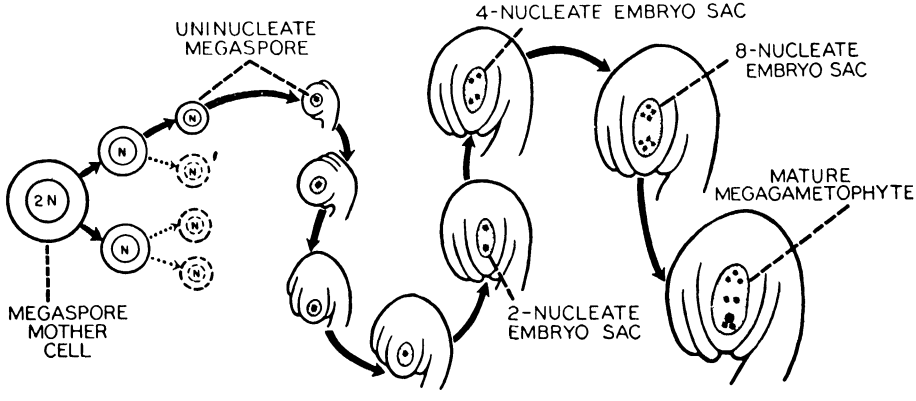


FIG. 10.10 Megasporogenesis (macrosporogenesis) and development of the ovule.

of tissue are formed around the base of the developing nucellus and ultimately enclose the nucellus except for a small passageway, the micropyle. In the meantime, one of the hypodermal cells of the developing nucellus becomes larger and cytologically distinguishable from the vicinal cells. This cell is called the *megaspore mother cell.* It undergoes meiosis to form a linear tetrad of haploid megaspores. Three of these megaspores degenerate or abort. The remaining megaspore enlarges considerably to form the uninucleate embryo sac or immature megagametophyte, while the surrounding nucellar tissues constitute the megasporangial wall enclosing the embryo sac. The nucleus of the uninucleate embryo sac now undergoes three successive equational divisions to form the eight nuclei (three antipodals, two polars, two synergids, and one egg nucleus) characteristic of the mature embryo sac or mature megagametophyte. Incidentally, in some plants the megaspore nucleus will divide mitotically only twice, to form a four-nucleate embryo sac.

Chapter 11

FRUIT, SEED, AND SEEDLING

THE FRUIT

A FRUIT is a structure composed of one or more matured ovaries with or without seeds, together with any other accessory flower parts which may be vicinal to the ovaries. The botanical definition of a fruit includes many structures which, in familiar usage, are not called fruits. Thus pea pods, grains of wheat and corn, and tomatoes are fruits. Noncarpellary parts such as receptacle tissue, the enlarged basal portions of sepals, petals, and stamens may become a part of the fruit.

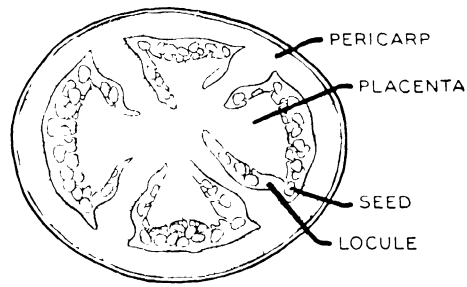


FIG. 11.0 A berry (tomato).

The stimulus which commonly induces the development of a fruit from the ovary and of a seed from the ovule is pollination and the subsequent fertilization of the egg. In the absence of fertilization, the flower usually dies. In some instances, however, fruit development can occur in the absence of fertilization. The condition is termed *parthenocarpy*. Examples of parthenocarpic fruits are seedless grapes and navel oranges. Parthenocarpic fruits are usually seedless. However, seeds may develop parthenogenetically, that is, without fertilization. It should be noted that not all seedless fruits are parthenocarpic. The absence of seeds may be due to abortion of embryos after fertilization.

Fruit development may also be induced by the artificial application of auxin to the unpollinated ovary, and it is highly probable that auxin supplied by the developing ovules is necessary for natural fruit development.

The Fruit Wall. When the ovary develops into a fruit, the wall of the ovary becomes the pericarp. No term exists to designate the merged structure consisting of pericarp and noncarpellary parts when the fruit is derived from a syncarpous epigynous flower. The pericarp is usually differentiated into the three morphologically distinct layers: the exocarp or outer layer, the mesocarp or middle layer, and the endocarp or inner layer.

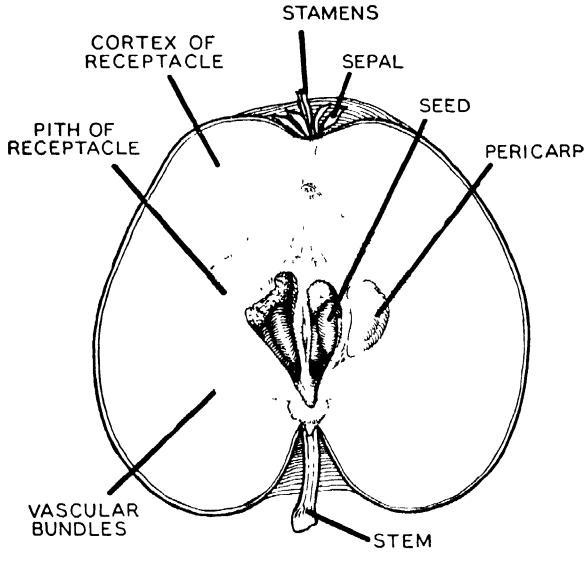


FIG. 11.1 A pome (apple).

The *exocarp* is often a single layer of cells which constitutes the epidermis. Epidermal hairs and stomata may be present. The *mesocarp* is variable in thickness and is generally composed of parenchyma and vascular tissue. The tissue of the *endocarp* varies according to the species of fruit under consideration. It may consist of a single layer or of many layers of cells. In such fruits as the cherry and the olive the endocarp is stony and encloses a seed. The pit of such fruits is not merely the seed.

Classification of Fruits. Fruits may be classified into three main groups: simple, aggregate, and multiple. Simple fruits (Figs. 11.0, 11.1, and 11.2) develop from a single ripened ovary, together with any closely associated parts. Aggregate fruits (Fig. 11.3) develop from a number of ripened ovaries belonging to a single flower. Multiple fruits arise from the matured ovaries of the flowers of an inflorescence.

Simple fruits are further classified into fleshy fruits, in which the fruit wall is fleshy at maturity, and dry fruits, in which the fruit wall is dry at maturity. Dry fruits may be further subdivided into dehiscent fruits, which split open when ripe, and indehiscent fruits which do not split open when ripe. A tabular classification of fruits is shown in Table 5.

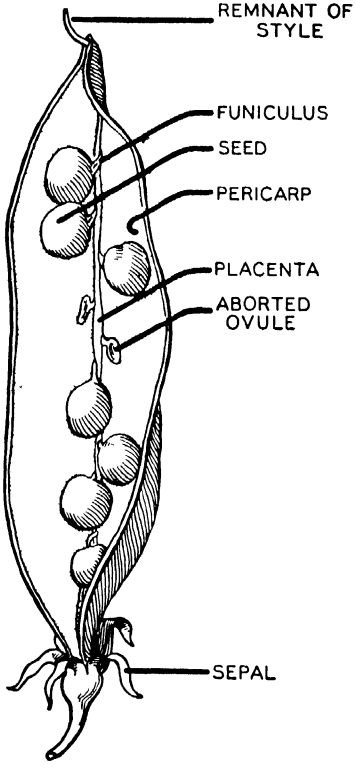


FIG. 11.2 A legume (garden pea).

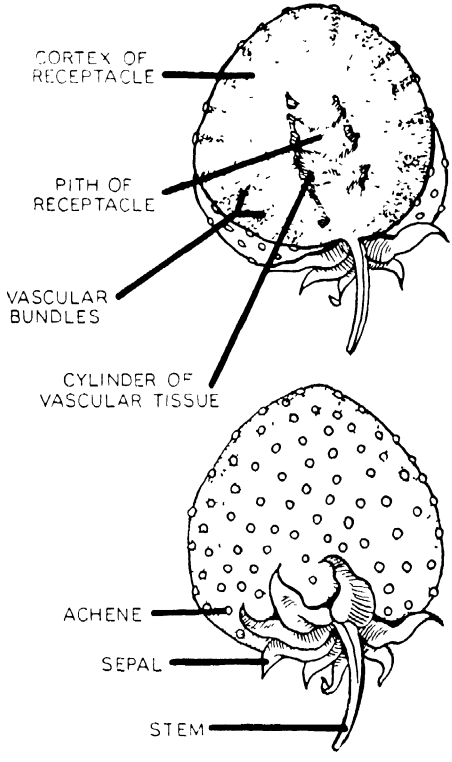


FIG. 11.3 An aggregate fruit (strawberry).

THE SEED

General Morphology of Dicot Seeds (Figs. 11.4, 11.5, and 11.6). Seeds are ripened ovules which serve to disseminate and reproduce the species. They are variable in size, shape, color, and other characteristics. The mature seed consists of an embryo, food stored in the embryo or in the endosperm, and one or two protective seed coats.

The outer, thicker seed coat is the *testa* and the inner usually thinner one, when present, is the *tegmen*. Various external markings

Table 5 CLASSIFICATION OF FRUITS

Chief Types	Subtypes	Description	Examples
Simple fleshy	Berry (Fig 11.0)	Matured ovary wall fleshy and enclosing one or more seeds	Tomato, grape, and orange
	Pome (Fig 11 1)	Outer portion of fruit wall fleshy, inner part papery and forming the core	Apple and pear
	Drupe	One-seeded, endocarp stony, mesocarp fleshy, exocarp thin and forming the skin	Olive and cherry
Simple dry dehiscent	Legume (Fig 11.2)	Fruit a pod developed from the ovary of a unicarpellate pistil, two lines of dehiscence	Garden pea
	Follicle	Similar to legume except that there is only one line of dehiscence	Milkweed
	Capsule	Develops from a compound pistil	Iris, lily, and poppy
Simple dry indehiscent	Achene	Small, one-seeded, pericarp attached to seed at only one point	Buckwheat
	Grain or caryopsis (Fig 11 7)	One-seeded with pericarp completely fused to seed coat	Corn and wheat
	Samara or key fruit	A winged achene	Maple and ash
	Schizocarp	Consists of two or more carpels, each an indehiscent mericarp (one of the carpels of the schizocarp) containing a single seed, the carpels separate at maturity	Celery
	Nut	Pericarp becomes thick and hard	Acorn and chestnut
Aggregate	Fig 11 3	Derived from several ovaries of a single flower	Strawberry
Multiple		Develops from the flowers of an inflorescence	Pineapple

on a seed can be traced to anatomical details of the ovule. Where the seed breaks off from the seed stalk, there remains a scar called the *hilum*. Below the hilum is a small pore, the *micropyle*. In seeds derived from anatropous ovules, because seed abscission occurs near the placenta, a ridge called the *raphe* appears above the hilum. This ridge represents the point where the funicular tissue is continuous with the ovulary tissue. At the base of the castor bean seed is the *caruncle*, a structure not ordinarily present on seeds. It is a spongy outgrowth from the testa which hides the micropyle.

The embryo, in the mature angiosperm seed, consists of the hypocotyl, the plumule, the cotyledon or cotyledons, and the radicle. The

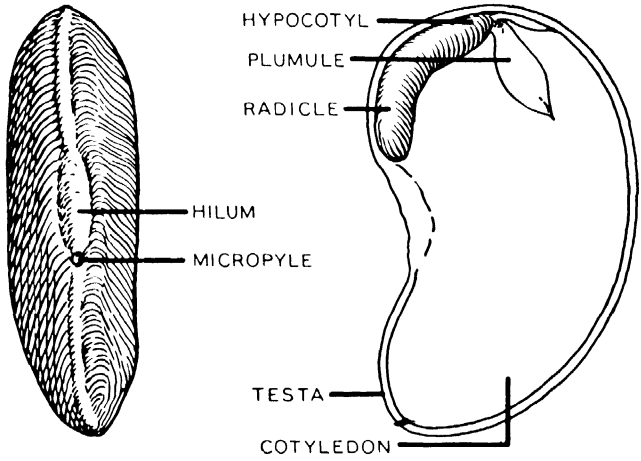


FIG. 11.4 Seed of the bean (*Phaseolus vulgaris*) in face view, and dissected to show the embryo.

embryonic shoot includes the plumule and hypocotyl. The plumule is that part of the embryonic shoot above the point of attachment of the cotyledons, while the hypocotyl is that part of the embryonic shoot to which the cotyledons are attached together with the part below it. Cotyledons are seed leaves and are attached to the uppermost limits of the hypocotyl. They function in some cases as food-storage organs and in other cases as food-absorbing organs. Cotyledons of some plants become photosynthetic organs after germination. The radicle is the embryonic root, and it arises from the lower end of the hypocotyl.

The endosperm is a nutritive tissue containing stored food. It surrounds the embryo. The endo-

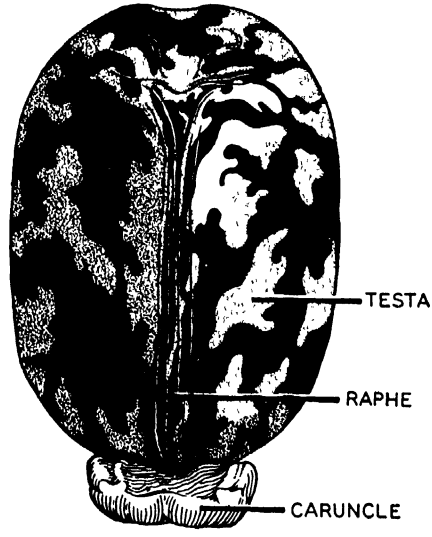


FIG. 11.5 Castor-oil plant seed (*Ricinus communis*).

sperm may be completely absorbed by the cotyledon or cotyledons and the developing embryo before the seed ripens, or it may remain until the seed matures and not be utilized until germination takes place.

The seed of the common bean (*Phaseolus vulgaris*) is an example of a typical dicotyledonous exalbuminous seed, which when mature lacks endosperm. The castor bean (*Ricinus communis*) seed, except for the presence of the caruncle, is typical of dicotyledonous albuminous seeds which when mature have endosperm.

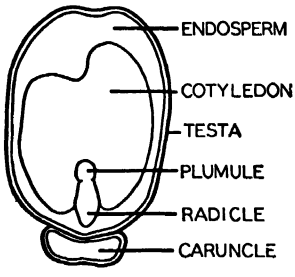


FIG. 11.6 Castor-oil plant seed in longitudinal section parallel to the cotyledons.

Morphology of a Monocot Seed (Fig. 11.7). The corn grain is a fruit consisting of a mature ovary and a single monocotyledonous seed. The hull of the mature grain is made up of the pericarp fused to the remains of the inner seed coat. The outer integument of the ovule is resorbed early in development, but the inner integument persists. Immediately inside the hull is the nucellar membrane, which consists of the disintegrated noncellular remains of the nucellus.

The embryo lies embedded in a large mass of endosperm at the concave side and next to the base of the grain. The base of the grain is stalk-like and is derived from the pedicel of the flower. The outermost part of the endosperm is a single layer of thick-walled cuboidal cells known as the *aleurone layer*. The cells of this layer are filled with aleurone grains, which are mainly protein in composition. Abutting the aleurone layer is the horny endosperm, whose cells contain more protein than those of the inner starchy endosperm.

The embryo enclosed by the starchy endosperm consists of a radicle, a diminutive hypocotyl, a single cotyledon which in grains is called the *scutellum*, a plumule or shoot apex, and young leaves. The plumule is enclosed by a hollow conical cellular sheath called the *coleoptile*. The *coleorhiza* is a cellular sheath which encloses the radicle.

Seed Dissemination. Since the higher plants have no locomotion, the dispersal of their fruits and seeds serves as the mechanism by which they can be spread from place to place. The chief agencies of seed dispersal are wind, water, and animals.

Many seeds and some fruits are light in weight and possess devices such as wings or tufts of hairs which make it possible for them to be carried great distances by the wind. The seeds and fruits of aquatic and of many land plants are dispersed by floating on water. Animals disseminate seeds in several ways. The fruit may be eaten

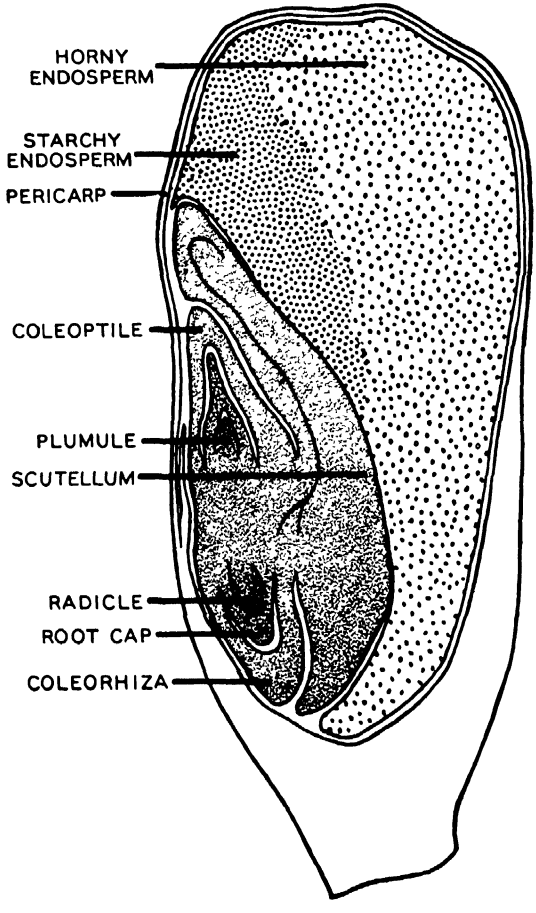


FIG. 11.7 Corn grain in longitudinal section.

and the enclosed seeds may survive the action of the animal's digestive juices. Some fruits and seeds possess spines, hooks, or a sticky secretion which enable them to adhere to the fur of mammals and to the feet of birds and other animals. Finally, man himself is an agent in the dispersal of seeds, especially those of useful species.

Conditions Required for Seed Germination. When a seed germinates a new plant is not produced. Seed germination is the resumption of the growth of the embryo after a period of dormancy. The seeds of most species of plants require a period of dormancy before they are able to germinate. The external conditions required for germination are an adequate supply of water and free oxygen and a favorable temperature.

The water content of most mature seeds is low, and as a result physiological activities occur at a very slow rate. Before resumption of embryonic growth can proceed, water must be absorbed. The absorption of water results in an increase in seed volume and in a softening and weakening of the seed coats; as a result the developing embryo breaks through more easily. Water absorption also results in the activation of digestion and translocation of stored food reserves, resumption of growth, and an increase in the rate of respiration. Before most stored food reserves can be translocated, they must undergo digestion, and since digestion is a hydrolytic process, an adequate supply of water is needed.

The dormant seed respires, but at an almost imperceptible rate. To provide the extra energy for the resumption of growth, the rate of food oxidation or of respiration must be markedly increased. The latter necessitates an increased supply of oxygen. The entrance of oxygen into the seed is promoted by the absorption of water.

For each species of plant there is a temperature range within which seed germination occurs. The most favorable temperature of this range is called the optimum temperature; the lowest, the minimum; and the highest, the maximum. The optimum temperature for many seeds is 25° to 30°C. Temperature exerts its action on seed germination by virtue of the effect it exerts on physicochemical changes within the seed.

Changes Occurring during Germination. After the absorption of water by seeds, the digestion of stored food reserves is initiated, and the rate of respiration is greatly increased. Digestion of those substances which are insoluble renders them soluble and diffusible so that they can be translocated and utilized in respiration and assimilation. In albuminous seeds these substances in the endosperm are digested and translocated to the cotyledons of the embryo, and from there to the meristematic regions of the radicle and the plumule. In exalbuminous seeds the stored food in the cotyledons is digested and

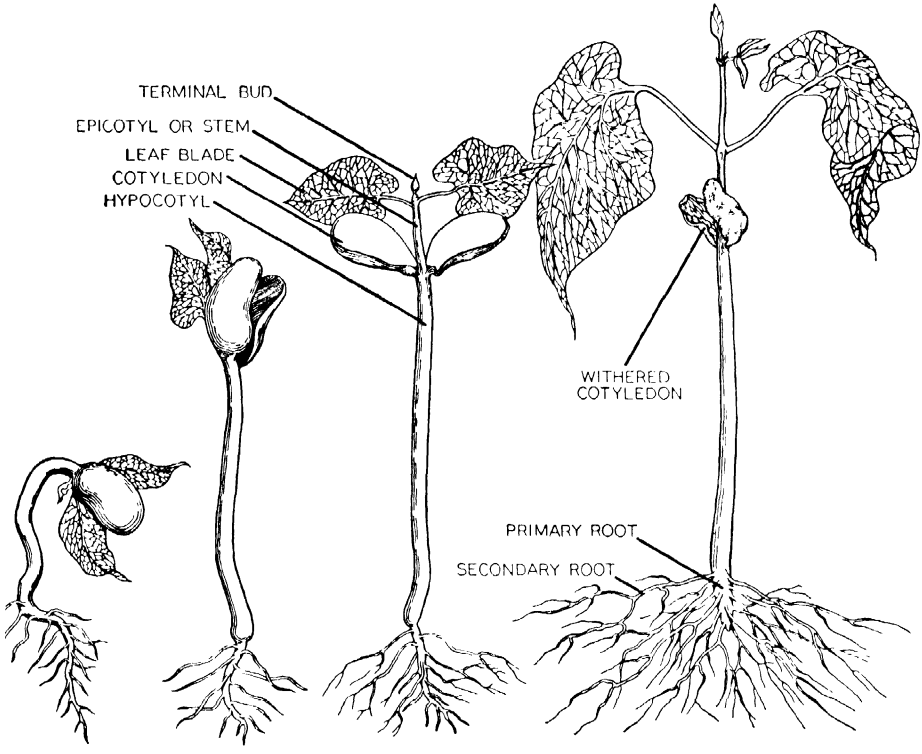


FIG. 11.8 Stages in the development of the lima-bean seedling.

transferred to the hypocotyl and to the meristematic regions of the embryo.

The first part of the embryo to emerge from the seed is the radicle. The hypocotyl in the garden bean elongates and emerges from the seed and carries with it the cotyledons and plumule. In corn and the garden pea, the hypocotyl does not elongate and the cotyledons remain in the soil; only the plumule and radicle elongate.

The growth of the embryo is due in part to the cell enlargement which results from the uptake of water and in part to the division of cells in the meristematic regions of the plumule and the radicle.

THE SEEDLING

A plant is a seedling (Fig. 11.8) from the time that its radicle emerges from the seed to the time that it can carry on an existence independent of the food reserves stored in the seed. On the basis of cotyledonary function during germination, there are several varieties of seedlings.

In the germination of corn, the cotyledon or scutellum absorbs digested food from the endosperm and transfers it to the growing

regions. The emergence of the radicle from the corn seed is quickly followed by the emergence of the plumule. The hypocotyl does not elongate but remains with the cotyledon in the soil. The radicle becomes the primary root and persists for a short time until adventitious roots develop. The plumule gives rise to a vegetative shoot which pushes its way upward through the soil.

In the germination of the lima bean, the radicle emerges first. The hypocotyl elongates and ultimately grows above the soil. The early growth of the cells of the bean hypocotyl is unequal, resulting in the formation of an hypocotyl arch. The arched hypocotyl then straightens and pulls the cotyledons out of the seed coats and above the soil. The plumule at this time rapidly develops into a leafy shoot. When the food in the cotyledons has been consumed, they wither and fall off. In the common bean the lowermost part of the stem is the hypocotyl.

Chapter 12

THE THALLOPHYTES

Introduction. The phylum Thallophyta consists of a vast diverse group of the most primitive types of plant life. These plants range in size from microscopic forms to the giant seaweeds which are several hundred feet in length. The plant body, a thallus, is unicellular or multicellular. In the multicellular forms there may be some differentiation of tissues, but the vascular tissues characteristic of the higher plants are absent. The thallophytes lack true roots, true stems, and true leaves. The gametangia or gamete-producing structures and the sporangia or spore-producing structures are typically unicellular.

There are two great subdivisions of the phylum Thallophyta, the subphylum Algae and the subphylum Fungi. *Algae* are thallophytes which possess chlorophyll and hence can carry on photosynthesis. All plants which fabricate their own foods from simpler substances are said to be *autotrophic,* and hence all green plants, including the algae, are autotrophic. *Fungi* are thallophytic organisms which lack chlorophyll. They are, for the most part, *heterotrophic,* which means that they cannot manufacture their own foods from simple substances. While the majority of the fungi derive their food from nonliving matter and are thus saprophytic in nutrition, many species obtain their food from the living tissues of plants and animals and are termed *parasites.* The organism upon which a parasite feeds is called a *host.* A saprophytic organism which can also exist as a parasite is called a *facultative parasite;* also a parasite which is capable of subsisting saprophytically is known as a *facultative saprophyte.* However, an organism which must live strictly as a parasite is referred to as an *obligate parasite.* Similarly, one which is restricted to saprophytic existence is an *obligate saprophyte.*

Methods of Reproduction. Thallophytes exhibit two types of reproduction, asexual and sexual. In *asexual reproduction* offspring are pro-

duced without cellular fusion. The three types of asexual reproduction are fission, budding, and spore formation. *Fission* is the division of an unicellular organism into two new organisms of equal size. In fission the nucleus divides mitotically, and cytokinesis occurs either by the formation of a middle lamella (in which case the daughter cells remain associated) or by cytoplasmic constriction (in which case the daughter cells may become separated). In *cellular budding* a portion of a cell evaginates to form a projection or bud. The bud gradually increases in size, and one of the daughter nuclei produced by division of the nucleus of the parent cell passes into it. Cytoplasmic constriction occurs, and two daughter cells of unequal size result. Asexual *spore formation* is a method of reproduction in which by various means small cells are produced differing from the other cells of the species in that when they germinate, they give rise to the mature form of the species. In many instances, spores are produced in structures called *sporangia*, but the latter are not essential to all spore formation. Asexual spores may be motile, in which case they are called *zoospores;* or they may be nonmotile. The structures in which zoospores are produced are called *zoosporangia.* Zoospores are naked protoplasts which are locomotive by means of ciliary or flagellate movement. Nonmotile spores are vegetative protoplasts surrounded by a thick cell wall. Lacking a locomotor mechanism, they depend upon an external agent for their dissemination.

Sexual reproduction involves the fusion of pairs of gametes. A *gamete* is a sex cell. Gametes which are structurally similar are said to be *isogametes.* The process of their fusion is called *conjugation* and the fusion cell is known as a *zygospore.* The structure in which isogametes are produced is termed an *isogametangium. Heterogametes* are sex cells which are dissimilar in structure and size. The fusion of heterogametes is called *fertilization,* and the fusion cell is a *zygote* or *oospore.* The male gamete is known as a sperm or microgamete, and the female gamete is termed an egg (ovum) or megagamete. The male gametangium or the structure in which the sperms are produced is the *antheridium.* The female gametangium in the thallophytes is usually unicellular and is known as the *oogonium.* In higher plants the homologous structure is always multicellular and is called the *archegonium.*

THE ALGAE

The algae are a large heterogeneous group of thallophytes which contain chlorophyll and are universal in their occurrence. They are primarily aquatic and are found in the fresh water of lakes, ponds, streams, reservoirs, ditches, and pools, and in the salt water of the oceans. They are also found growing on damp soil, on rocks and trees, on snow and ice, and in hot springs. Some aquatic species grow attached to rocks, logs, and other submerged objects, while others are unattached. The minute free-floating algae are referred to as *phytoplankton*. Together with similar animals they constitute plankton. (Animal plankton is called *zooplankton*.)

Critical studies of the algae based on the architecture of the vegetative cells, the type of reserve food stored as the result of photosynthesis, the reproductive structures, the nature of the motile cells, and the types of pigment present have led students of the algae to divide them into numerous groups.

Since only a general consideration is to be presented here, we shall limit our discussion to the following five classes of the algae:

Class Cyanophyceae, the blue-green algae
Class Chlorophyceae, the green algae
Class Bacillariophyceae, the diatoms
Class Phaeophyceae, the brown algae
Class Rhodophyceae, the red algae

THE FUNGI

The fungi are a large heterogeneous group of thallophytes which are devoid of chlorophyll. Whereas the algae are typically aquatic forms, the fungi are largely terrestrial in habitat. Some species are parasitic on plants and on animals, but the majority are saprophytic in nutrition.

The plant body of a typical fungal organism consists of a mass of thread-like structures, the *hyphae*, which collectively constitute the *mycelium*. Some hyphae are *septate*, while others lack cross walls and are said to be *nonseptate* or *coenocytic*. The septate hyphae are composed of cells which may be uninucleate or multinucleate. In older hyphae, vacuoles and accumulations of reserve food materials may be seen in the cytoplasm. The mycelium in many instances is differen-

tiated into two types of hyphae: vegetative hyphae, which penetrate the substrate or medium upon which the fungus grows in order to obtain food material; and fertile or reproductive hyphae, upon which spores are borne.

The characteristic method of reproduction in the fungi, considered as a group, is by means of asexual spores. When produced within a cell, these spores are said to be *endogenous spores.* A hypha called a *sporangiophore* becomes differentiated from the rest of the mycelium to form a sporangium. The multinucleate mass of protoplasm within the sporangium becomes organized into a number of spores termed *sporangiospores. Exogenous spores* are produced externally in a variety of ways at the tips of fertile hyphae. The spores of terrestrial species of fungi are nonmotile and are largely wind-disseminated. In aquatic fungi the asexual spores are generally zoospores.

The subphylum Fungi is divided into the following classes:

Class Schizomycetes, the bacteria
Class Myxomycetes, the slime fungi
Class Phycomycetes, the alga-like fungi
Class Ascomycetes, the sac fungi
Class Basidiomycetes, the club fungi
Class Deuteromycetes, the fungi imperfecti

Chapter 13

THE BLUE-GREEN ALGAE

General Characteristics of the Class Cyanophyceae (Myxophyceae). These are the blue-green algae. They are found largely in fresh water, although species occur in salt water, in soil, and in other situations. The plant body is a single cell or a colony. A *colony* is an assemblage of similar unicellular organisms of the same species which live together and in which each cell has little or no dependence on the others. Each cell is surrounded by a gelatinous sheath. The clear central portion of the cell is called the central body and is considered to be an incipient nucleus (scattered nuclear material not surrounded by a nuclear membrane). The peripheral portion of the cell which surrounds the central body is considered to be cytoplasm. Plastids are absent. The pigments present are for the most part in granular form and are scattered throughout the cytoplasm. For this reason the peripheral portion of the cell is sometimes called *chromoplasm*. The pigments usually present are chlorophyll, carotene, xanthophyll, and the water-soluble blue pigment phycocyanin. In addition to the pigments enumerated, a red pigment is present in some salt-water species. The cell wall is composed of cellulose. The storage materials resulting from photosynthesis are glycogen or glycoprotein. Reproduction is by fission.

Organization in the Cyanophyceae. In a few members of this class the daughter cells may remain separate and thus may be regarded as solitary or unicellular plants. However, the mode of organization among the species of the class usually involves colony formation, either filamentous or nonfilamentous in final disposition. A *filament* may be defined as a single row of joined algal cells. In this class, the filament is enclosed in a gelatinous sheath. Obviously, the formation of a filament involves fission in one plane. On the other hand, the formation of nonfilamentous colonies is due to the con-

fluence of the gelatinous sheaths enclosing individual cells. This fusion of the individual gelatinous sheaths is considered to be complete when all of the individual gelatinous sheaths have coalesced into the composition of a homogenous gelatinous matrix, in which the cells of the colony lie embedded. The confluence of the individual gelatinous sheaths is looked upon as being incomplete when evidence of the individual sheaths is still to be found in the colony. The shape of any nonfilamentous colony is determined by the number of planes in which fission of the cells occurs. Thus a spherical colony results from fission in three planes; a flat rectangular colony one cell in thickness is effected by the alternate division of cells in two directions in one plane.

Representative Members of the Cyanophyceae. One of the simplest forms in the class is *Synechococcus*. The *Synechococci* occur as solitary spherical cells, each cell being enveloped in its own gelatinous sheath.

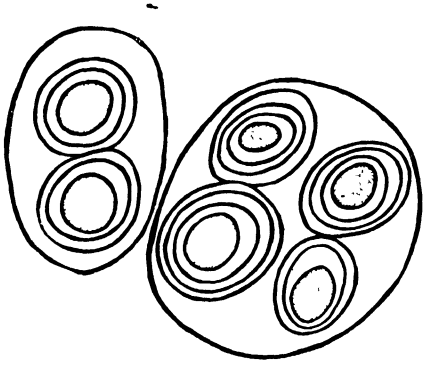


FIG. 13.0 *Gloeocapsa*

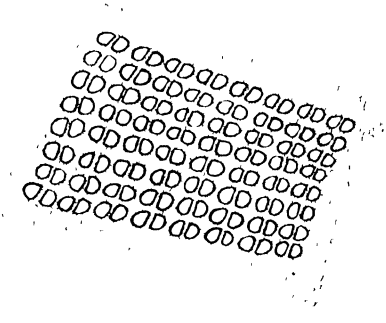


FIG. 13.1 *Merismopedia*

In *Gloeocapsa* (Fig. 13.0) the cells are generally aggregated into spherical colonies. The confluence of the individual gelatinous sheaths, however, is incomplete. The individual gelatinous sheath generally presents a characteristic lamellation. *Gloeocapsa* occurs in the bluish slime on the glass enclosures of old aquaria and in jelly-like masses on wet rocks.

Merismopedia (Fig. 13.1) is a classical example of a flat rectangular colony one cell in thickness. The cells are embedded in a homogeneous gelatinous matrix. *Merismopedia* is abundant in lakes, ponds, and ditches.

The filamentous colonies of the class are exemplified in *Nostoc* and *Oscillatoria*.

Nostoc (Fig. 13.2) is a bead-like filament of globose cells in a gelatinous sheath. Here and there along such a filament occur relatively larger spherical cells called *heterocysts*. Each heterocyst possesses, when it is first formed, two polar pores through which cytoplasmic connections are effectuated with the adjoining vegetative cells. As the heterocysts mature, these polar pores become occluded

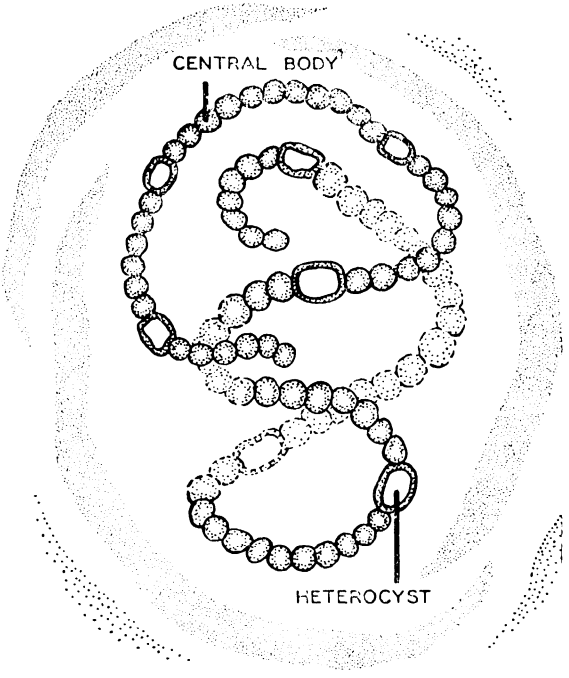


FIG. 13.2 *Nostoc*.

through the deposition of wall material and are termed *polar nodules*. With the formation of these polar nodules, the protoplasts of the heterocysts become modified into a homogeneous viscous material. These heterocysts apparently represent a mechanism for the fragmentation of the filament into two shorter filaments or *hormogonia*. The break of the filament occurs at the junction of the heterocyst and a vegetative cell. The hormogonia generally become longer filaments by fission in one plane. Characteristically the filaments of *Nostoc* are aggregated into spherical masses of jelly or compound colonies. Along

some filaments of *Nostoc,* spores are formed. The spores are simply enlarged vegetative cells containing a rich store of reserve food and surrounded by a thickened wall. These spores are capable of maintaining viability over long periods of desiccation. Each spore, upon attainment of favorable environmental conditions, will germinate to form a filament of *Nostoc.* Formation of spores constitutes a mechanism for resisting unfavorable environmental conditions as well as a means of reproduction.

Nostoc grows abundantly on damp soil and in shallow water. Further, it is believed that *Nostoc* is able to fix nitrogen. The latter action would tend to explain the continuous fertility of the rice paddies in which it is a regularly occurring algal organism.

Oscillatoria (Fig. 13.3) is a filamentous colony of cylindrical cells which in different filaments appear either as slender and long or as short and broad. The terminal cell may be rounded or even capitated (modified into a head). In many species of *Oscillatoria* the pigment granules are disposed along each side of the common wall between the cells of the filament. Along such a filament there may occur a concave cell or dead cell. The concave cell represents the area at which a filament may fragment into two shorter filaments or hormogonia. Each hormogonium, by fission in one plane, can become a longer filament. The vegetative cells of *Oscillatoria* do not form spores as in *Nostoc.*

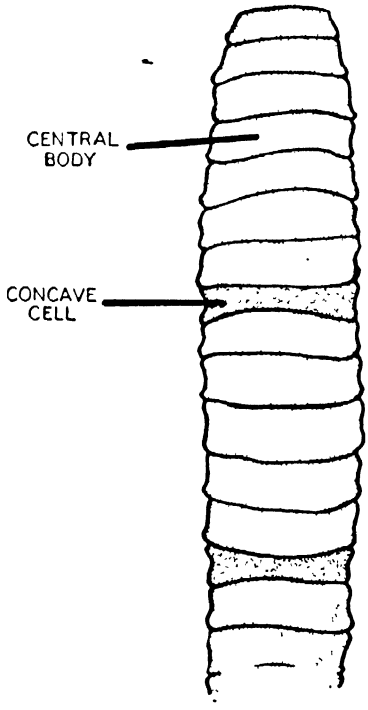


FIG. 13.3 *Oscillatoria.*

Perhaps the most interesting feature of the plant is its ability to vibrate or oscillate or to pass through the water with a sort of gliding movement. Though the real mechanism responsible for the production of such motion is not known, some investigators have put forth the hypothesis that movement is accomplished peristaltically; other workers believe the movement to be ascribable to a secretion of gelatinous material.

Oscillatoria occurs in damp soil and grows abundantly on rocks in shallow water. It seems to be rather common in contaminated water. Paradoxical as it may seem, a blue-green alga, *Oscillatoria erythraea,* is the reason for the name of the Red Sea. Since these algal organisms sometimes float along the water surface, the water often presents a reddish aspect. This red aspect, incidentally, is due to an accessory red pigment in the protoplasts of *Oscillatoria erythraea.* The pigment is somewhat comparable to phycoerythrin, the accessory red pigment in the protoplasts of red algae. Because the pigment has been shown spectroscopically to be slightly different from phycoerythrin, it has been termed schizophycean phycoerythrin.

Economic Aspects of the Cyanophyceae. These algae, together with other algae, are ingested by fish. Those blue-green algae that live and die in the soil serve ultimately to enrich the organic component of soil and thus to increase soil fertility. On the other hand, the peculiar taste of reservoir water may be sometimes ascribed to the contamination of the water with these algal organisms.

Chapter 14

THE GREEN ALGAE

General Characteristics of the Class Chlorophyceae. These are the green algae. The majority are widely distributed in fresh water and live attached to rocks, other plants, and submerged debris; or they live unattached and constitute much of the phytoplankton of these waters. Others live in salt water, in and on the surface of soil, on trees and rocks, and in snow and ice. A few live in symbiotic relationship with lower animal forms such as *Hydra.* (Symbiosis is the living together of two unlike organisms as a result of which both are benefited.)

Plant bodies of the green algae are either single cells or colonies. Most colonies are long filamentous structures. The cells of the green algae have well-defined nuclei, cytoplasm, and distinct chloroplastids containing chlorophyll, carotene, and xanthophyll. Small, rounded bodies known as *pyrenoids* are usually located in the chloroplastids and are probably centers of starch formation. The cell walls are constituted of cellulose. The storage product of photosynthesis is generally starch. Asexual reproduction may occur by fission and spore formation, while sexual reproduction takes place by conjugation and fertilization. The gametangia are unicellular. Many species of green algae exhibit alternation of generations.

Representative Forms of the Chlorophyceae. The members of the Chlorophyceae that will be discussed on the following pages have been selected with the thought of giving a broad picture of the morphological and reproductive features of the class. The reproductive mechanisms may be grouped into several categories. Reproduction is generally accomplished by fission in the more primitive types. Sexual reproduction in the form of conjugation is encountered for the first time in *Ulothrix.* While the latter organism is isogamous, it also reproduces by zoospores. *Spirogyra,* another organism which we shall dis-

cuss in some detail, is entirely isogamous. In *Oedogonium* and *Vaucheria*, sexual reproduction is by fertilization, and asexual reproduction is accomplished in the production of zoospores.

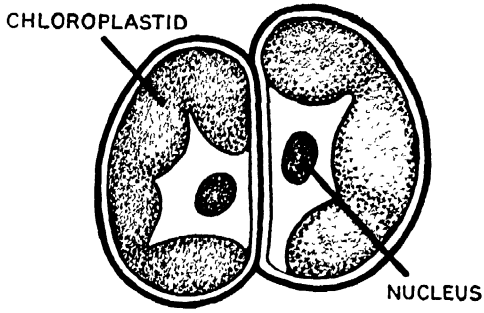


FIG 14.0 *Protococcus viridis.*

Protococcus viridis (Fig. 14.0). This algal organism, perhaps the most common of the green algae and at the same time comparatively primitive, forms the green incrustation that is so often observed to occur on the shaded sides of tree trunks, stone walls, and wooden fences in the temperate zone.

The individual cells are typically spherical and uninucleate; the cell walls are rather thickened. Situated parietally is a laminate chloroplastid that is marginally lobed. Frequently the lobulations of the single chloroplastid may be so extensive as to suggest the presence of more than one chloroplastid. Pyrenoids, rather common in their occurrence in the chloroplastids of other members of the green algae, are missing from the chloroplastid of *Protococcus.*

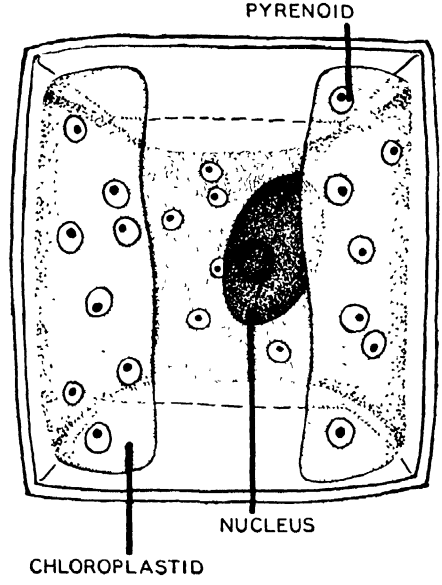


FIG 14.1 Vegetative cell from a filament of *Ulothrix.*

Each cell reproduces by fission. However, the daughter cells tend to remain associated in groups of two and four. The mutually apposed

surfaces of such daughter cells are flattened, each cell assuming its characteristically spheroidal character upon separation from the group.

Ulothrix. Ulothrix occurs rather abundantly in cold flowing water and thus abounds in such water during the early spring and late fall. The cells of *Ulothrix* are cylindrical and are formed into unbranched filaments. The basal cell, generally colorless, is elongated into a narrow holdfast cell which serves to attach the filament to some substrate.

Each vegetative cell (Fig. 14.1) of the filament is uninucleate and contains a girdle-shaped chloroplastid that may totally or incompletely encompass the protoplast. The chloroplastid, which sometimes extends through the full length of the cell, generally bears several sparsely allocated pyrenoids.

Ulothrix reproduces asexually by means of zoospores (Fig. 14.2A). In the formation of these zoospores, the protoplast of a vegetative cell divides initially along a plane at right angles to the longitudinal axis of the filament to form two daughter protoplasts. Division of the latter daughter protoplasts subsequently occurs perpendicular to the original plane of division. There may be thus formed from two to thirty-two naked, more or less pear-shaped protoplasts. Finally, each of these protoplasts develops a red pigment spot and four cilia to form a quadriciliate zoospore. The zoospores, usually gathered into a thin vesicle, escape through a small opening in the lateral wall of the parent cell. Upon being discharged into the water, the zoospores become quickly dissociated from the vesicle and remain actively motile for several days. Ultimately many of the zoospores become attached to some substrate; the cilia are lost; each zoospore encloses itself within a wall. Subsequently each zoospore germinates, forming a new filament of cylindrical cells by fission in one plane. Occasionally, especially during adverse environmental conditions, the protoplast of a vegetative cell may contract and secrete around itself a cell wall to form a resting spore. On the attainment of favorable environmental conditions, such a spore may form, on germination, several zoospores.

Sexually *Ulothrix* reproduces by conjugation. The isogametes (Fig. 14.2B) result from the division of a protoplast of a vegetative cell. Like the zoospore, each isogamete is pyriform and possesses a red pigment spot. Unlike the zoospore, the isogamete is smaller and has only two cilia. Again, the number of isogametes formed in a vegetative cell varies from eight to sixty-four. The isogametes escape in the same

way as the zoospores. After a period of motility the isogametes from different filaments fuse to form zygospores. These zygospores are diploid and represent the sporophyte generation in the life cycle of *Ulothrix*. The zygospore forms a thick wall around itself, and after a period of dormancy the protoplast divides to produce four to sixteen zoospores, or nonmotile spores. Each of the spores, whether motile or nonmotile, develops into a filament of *Ulothrix*. Since the nucleus of a zygospore divides initially by meiosis, the filament of *Ulothrix* is haploid and therefore represents the gametophyte generation in the life cycle of *Ulothrix*.

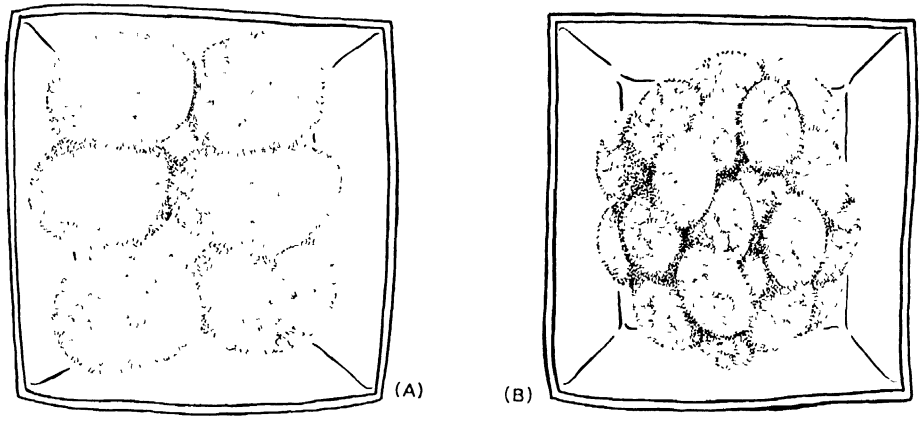


FIG. 14.2 *Ulothrix* (A) zoospores, (B) isogametes.

Spirogyra. *Spirogyra*, commonly known as "pond scum" or "water silk," is widely distributed. Though some species are found in flowing water and in the littoral zones of lakes, the majority of them favor stagnant water. Individual *Spirogyra* plants are generally aggregated into bright green masses that are characteristically smooth and mucilaginous to touch.

Microscopically, the individual *Spirogyra* is observed to be a single, unbranched, cylindrical filament, the cells of which are longer than broad. Each vegetative cell (Fig. 14.3) in the filament has a two-layered wall, the inner layer of which completely encloses a single vegetative protoplast. The cytoplasm of the protoplast is largely restricted to the periphery of the cell because of the presence of a large central vacuole. The nucleus, encased in a barely discernible cytoplasmic envelope, is generally suspended in the central vacuole

by cytoplasmic strands that radiate from the parietally restricted cytoplasm. The most striking feature of the protoplast, however, is the ribbon-like chloroplastid that spiralizes itself through the peripheral cytoplasm. The chloroplastid bears conspicuous pyrenoids.

Spirogyra reproduces by conjugation, of which there are two types: scalariform and lateral. Scalariform conjugation, the more frequently occurring of the two, involves fusion of the isogametes of two different filaments, while lateral conjugation entails the fusion of isogametes of the adjoining cells of the same filament.

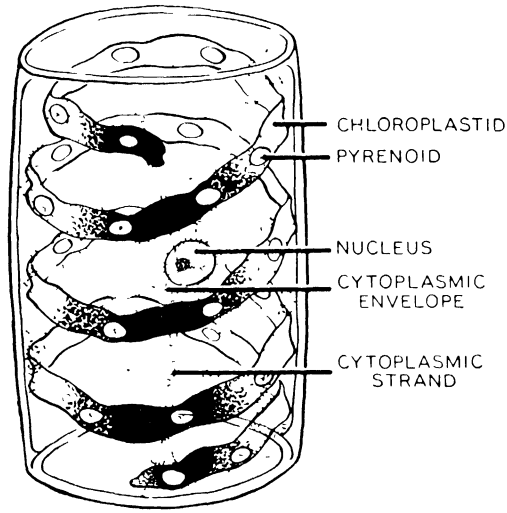


FIG 14.3 Vegetative cell from a filament of *Spirogyra*

In scalariform conjugation (Fig. 14.4) two filaments become approximated to each other. The neighboring cells of these two filaments soon put forth protuberances, or papillae. Initially the free ends of adjoining protuberances become contiguous and finally attached to each other. Through a resorption or digestion of the walls at their mutual area of attachment, the protuberances become luminally continuous so as to form a conjugation tube. In the meantime the protoplasts of the cells connected by such conjugation tubes have condensed to form isogametes. Though these isogametes are morphologically similar, there is a physiological difference in that one isogamete is active and moves by way of the conjugation tube into the cell containing the other isogamete. The actively amoeboid isogamete

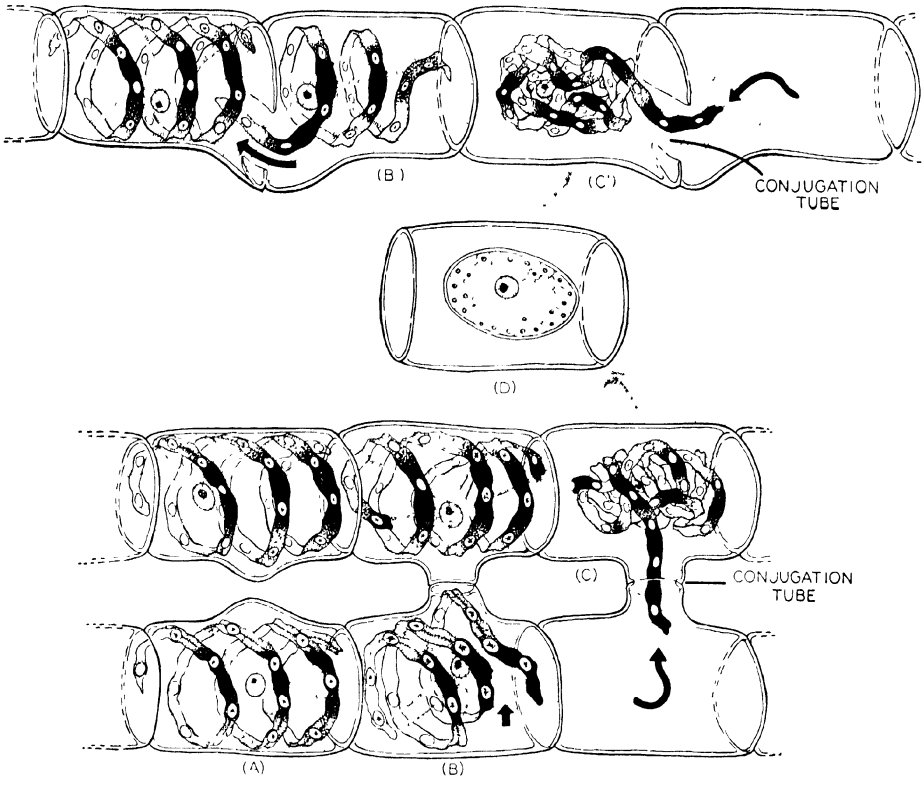


FIG. 14.4 SCALARIFORM CONJUGATION in *Spirogyra*. (A) potential conjugants forming protuberances; (B) male protoplast in process of migration through the conjugation tube, (C) fusion of the male protoplast with the female protoplast, (D) zygospore LATERAL CONJUGATION (B') male protoplast beginning its passage through the conjugation tube, (C') migration almost complete.

is frequently referred to as the male isogamete and the passive isogamete as the female isogamete. The zygospore resulting from the fusion of the male isogamete with the female isogamete forms around itself a wall which subsequently becomes differentiated into a three-layered wall. Eventually the gametangial walls enclosing the zygospore deteriorate, the zygospore is released and settles to the bottom of the pond or lake in which it was formed. Generally in the spring of the following year the zygospore germinates. Just prior to germination, however, the diploid nucleus of the zygospore (Fig. 14.5) divides meiotically to form four haploid nuclei, three of which abort. On germination the protoplast enlarges to such an extent that the outer and middle layers of the wall rupture at one end. The protoplast, still surrounded by the inner layer, emerges through the ruptured end as a short cylindrical tube. The haploid nucleus of the protoplast

divides; transverse septation follows. Generally the basal or lower daughter cell remains somewhat undeveloped, while the upper daughter, by fission in one plane, develops into a characteristic filament of *Spirogyra*.

In lateral conjugation (Fig. 14.4) the area of the longitudinal wall vicinal to the transverse septum of two adjoining isogametangia of the same filament swells or protrudes unilaterally. The transverse wall in the area of this lateral protrusion ruptures, and thus there is effectuated a perforation for the passage of the male isogamete. The zygospore is formed and undergoes the same modifications as just described under scalariform conjugation.

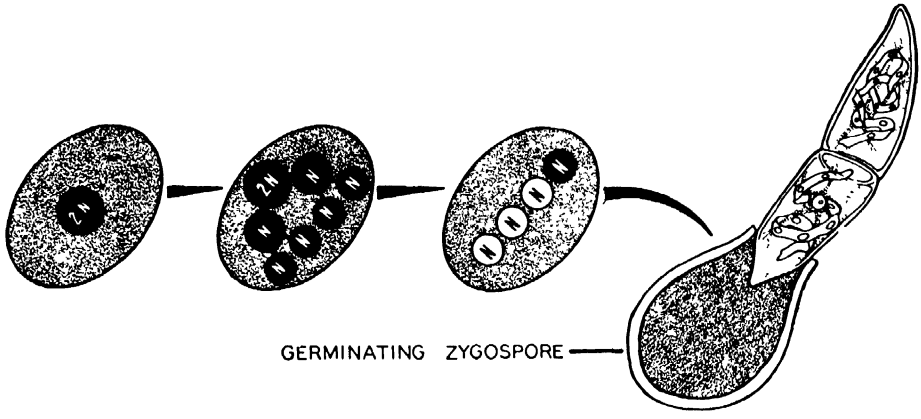


FIG. 14.5 Meiosis in the zygospore of *Spirogyra* before germination, the short cylindrical tube emerging from the zygospore.

Occasionally an isogamete, generally before the conjugation tube becomes luminally patent, contracts and secretes around itself a thick wall. An isogamete so modified is called a *parthenospore*, which under favorable conditions will germinate to form a filament of *Spirogyra*. On the other hand, in some species of *Spirogyra* fragmentation of a filament into two shorter filaments is somewhat common. Such a filamentous dissociation generally results from a weakening of the middle lamella of the cross wall at the imminent point of breakage. This is followed by the imposition of a cleavage strain on the vicinal portion of the longitudinal wall common to the two cells at the point of rupture.

Desmids (Fig. 14.6). The desmids, notable for their diversity of morphology and sharpness of symmetry, are generally unicellular

plants. A limited number of species, however, may form long twisted filaments, since the cells remain united end to end after division. Desmids occur in ponds and along the quiet shore lines of lakes, being rather abundant in fresh water with a pH between 5 and 6.

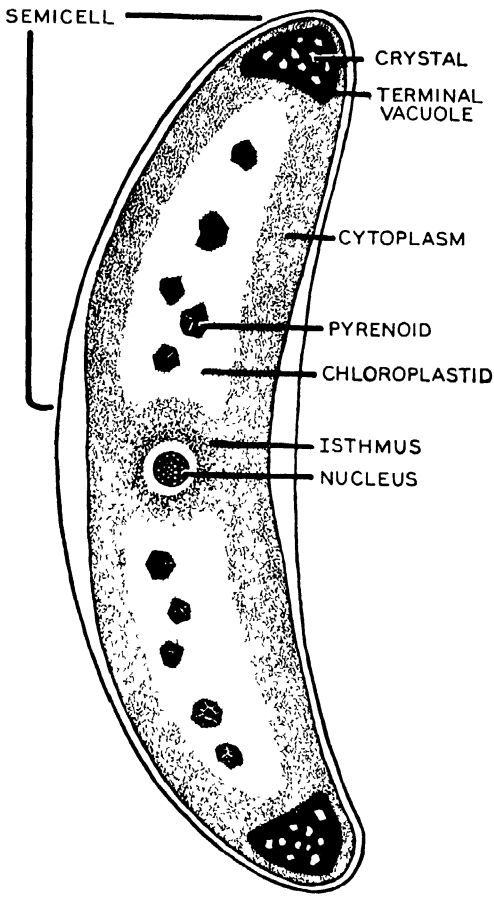


FIG. 14.6 A desmid (*Closterium*).

With the exception of a few species, a desmid is composed of two symmetrical halves, called *semicells*, united at a relatively narrower constricted area termed the *isthmus*. Each desmid possesses a single nucleus that is invariably situated in the cytoplasm of the isthmus. In most of the desmids, there occurs in each semicell at least one chloroplastid that is axile in position. Pyrenoids occur in the chloroplastids. The wall of a desmid is three-layered. The outer layer

of the wall is enveloped in a thin, mucilaginous coat by virtue of which the desmid may adhere to other aquatic plants. The mucilage is excreted through pores in the cell wall. Some desmids are capable of a slow movement over a substrate because of the localized exudation of mucilage at one pole of the cell. Reproduction is generally accomplished by the transverse fission of a desmid into two semicells. Each of the latter daughter semicells forms another semicell, and so there result two whole desmids.

Closterium (Fig. 14.6). This common genus of desmids presents two morphological features worthy of some further consideration. The species of this genus are shaped like crescents, and like other desmids, each consists of two semicells; but unlike other desmids, there is no constriction between the semicells. Further, in contrast to other desmids there is situated at the apex of each semicell of *Closterium* a small vacuole containing rather small crystals of calcium sulfate which are in a continuous state of vibration and exemplify classically the phenomenon of Brownian movement.

Oedogonium. The various species of *Oedogonium*, which number about 285, are found submerged in smaller bodies of fresh water. They may be epiphytic on submerged vascular plants or upon larger algal organisms. When young, the filaments of *Oedogonium* are generally attached; the mature forms are usually free-floating.

All of the species of *Oedogonium* consist of unbranched filaments of cells. The basal cell of each filament is generally modified into a holdfast mechanism. Each vegetative cell (Fig. 14.7) in the filament is cylindrical. The wall, while appearing to be structurally homogeneous, is constituted of at least two layers. The inner layer is mainly chitinous in composition. The chloroplast of each vegetative cell is characteristically a reticulated cylindrical structure within the protoplast. Pyrenoids generally occur at the anastomosing points of the net-like plastid. The nucleus is generally restricted to the periphery, lying just beneath the chloroplast and possessing one or two nucleoli. There is generally a large central vacuole.

Growth in the length of a filament results from division in one plane (Fig. 14.8). However, this cellular reproduction presents a few interesting peculiarities that may be conveniently considered here. The nucleus of the cell about to divide moves into the upper portion of the protoplast. The nucleus divides mitotically. Just at the beginning of the latter nuclear division, the inner layer of the uppermost

portion of the lateral wall invaginates to form a ring of wall thickening. Simultaneously, what remains of the lateral wall in this area undergoes a transverse splitting. In the meantime cytokinesis has eventuated in the formation of a cross wall between the two daughter protoplasts. These daughter protoplasts now begin to elongate. The lower daughter protoplast increases its length. At the same time the upper end of

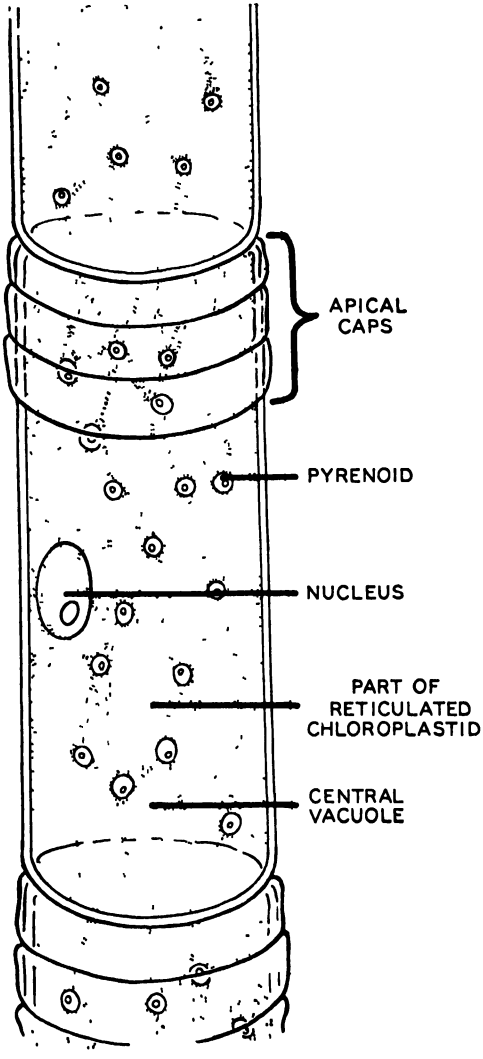


FIG. 14.7 Vegetative cell of *Oedogonium*, with other cells of the filament partially shown.

the lower daughter protoplast pushes upward the recently formed cross wall. The lower daughter protoplast thus remains encased in what was originally the lateral wall of the parent cell. At the same time the upper daughter protoplast elongates, but the ring of wall thickening stretches concurrently to form its lateral wall. However, a small part of the original wall of the parent cell (the part above the transverse splitting vicinal to the ring of wall thickening) remains to project itself over the upper end of the daughter cell and is termed the apical cap. These apical caps, therefore, will occur characteristically on alternate cells of the filament.

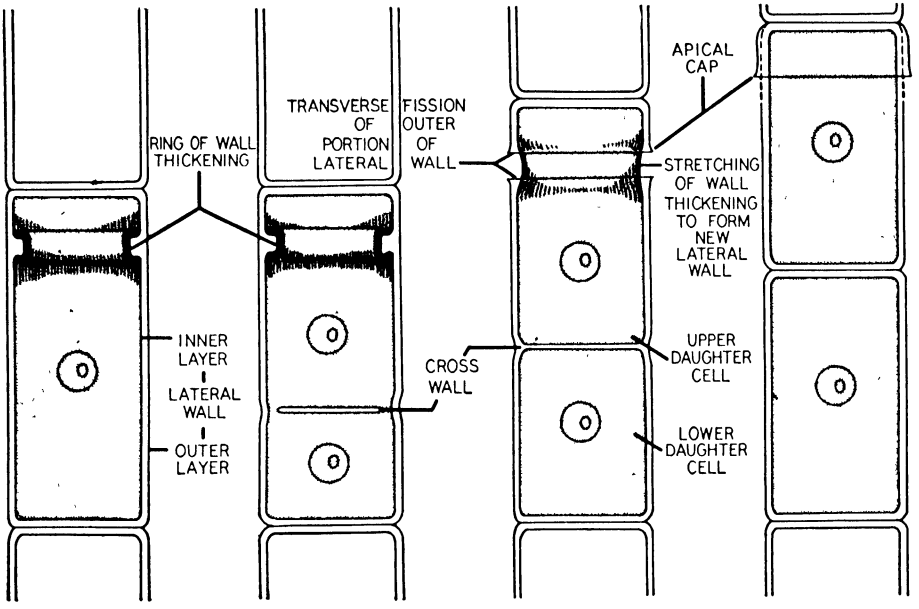


FIG. 14.8 Growth in the length of a filament of *Oedogonium*.

Reproduction among the many species of *Oedogonium* is both asexual and sexual. Asexual reproduction involves the formation of multiciliate zoospores and sexual reproduction is by fertilization.

In zoospore formation (Fig. 14.9) the contents of a vegetative cell undergo a slight contraction, the nucleus withdrawing to some degree from its originally close relation with the chloroplast. Ultimately a hyaline area develops in the part of the protoplast between the nucleus and the cell wall. The cell wall now splits transversely in the region of the apical cap. A collar of cilia springs from the

margin of the hyaline area aforementioned and thus there is formed a single zoospore with the characteristic disposition of cilia. The cell now unhinges at the point of transverse splitting, and the sphere-shaped zoospore is discharged in a delicate mucilaginous vesicle. The zoospore quickly becomes dissociated from its vesicle, and after a rather short period of swimming about in the water settles down at its hyaline end. Retraction of the cilia follows; the zoospore forms

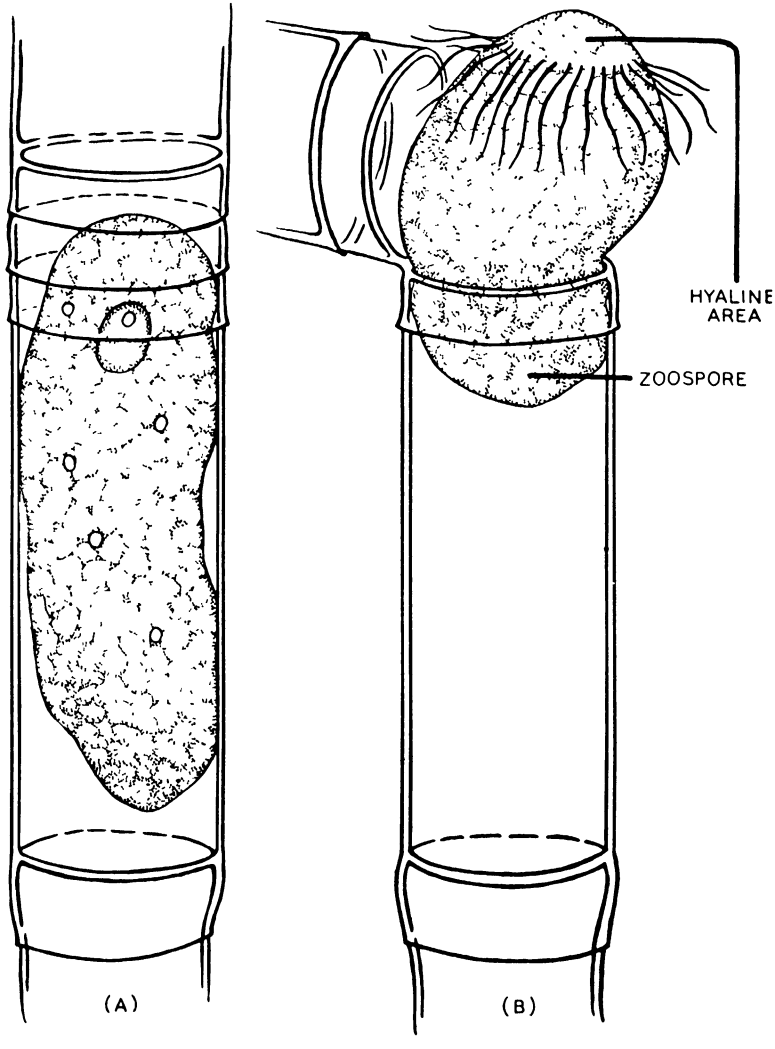


FIG. 14.9 *Oedogonium*: (A) zoospore formation, (B) escape of zoospore.

into a holdfast cell whence arises a new filament by division in one plane. In some species of *Oedogonium*, the zoospore forms a hemispherical cell from the convex surface of which there is formed a new filament.

Insofar as sexual reproduction is concerned, the various species of *Oedogonium* may be allocated to three groups: first, the monoecious (homothallic) type, in which the same filament possesses both antheridia and oogonia; second, the dioecious (heterothallic) type, in which the antheridia and oogonia are born on different filaments approximately equal or normal in size, third, the dioecious or heterothallic type, in which the antheridia are borne on very short filaments, generally referred to as *dwarf males*. Further, those species which bear antheridia in filaments of normal size are sometimes called *macroandrous* while those species in which the dwarf male gametophytes develop are termed *nannandrous*.

In the macroandrous species, either the homothallic or heterothallic type, a vegetative cell, often termed the *antheridial mother cell*, divides to form an upper shorter daughter cell and a lower longer daughter cell. The shorter daughter cell becomes a single antheridium. Generally the lower daughter cell continues to undergo division which eventuates in the formation of from two to forty successive antheridial cells (Fig. 14.10A). The latter aggregation of antheridia is called a *compound antheridium*. Whether a single or compound antheridium is formed, the protoplast of each individual antheridium divides either vertically or transversely to form two microgametes (Fig. 14.10A), or sperm, each bearing a hyaline crown from the peripheral margin of which develops a collar of long cilia. These sperm are discharged in a thin, mucilaginous vesicle upon rupture of the antheridium near its apical cap.

On the other hand, a vegetative cell, called an *oogonial mother cell*, divides into two daughter cells. The upper daughter cell develops into an oogonium, while the lower daughter cell becomes a supporting cell. The upper daughter cell destined to form an oogonium becomes spheroidal and at the same time wider than a vegetative cell. The protoplast of the oogonium metamorphoses into a megagamete or egg (Fig. 14.10B). Generally the upper end of the lateral wall of the oogonium becomes papillated. The apex of the papilla soon undergoes gelatinization to form a pore through which the sperm may enter the oogonium. The egg within the oogonium now contracts to

some degree and becomes rather rounded. A hyaline spot makes its appearance on the egg near the eccentrically situated nucleus of the egg, which is now ready to receive sperm.

With the fusion of a sperm with the egg, there is formed an oospore (Fig. 14.10C). The oospore forms a three-layered wall around itself. The oospore, incidentally, possesses the diploid number of chromosomes and represents the sporophyte generation in the life cycle of *Oedogonium*. With the advent of winter, the oogonial wall deterio-

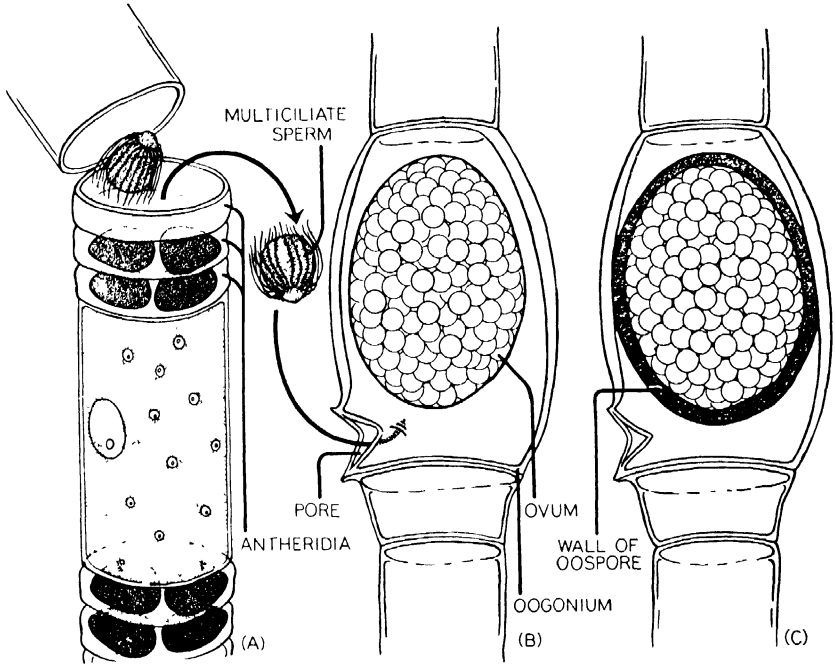


FIG. 14.10 Sexual reproduction in *Oedogonium* (heterothallic species).

rates, the oospore is released and sinks to the bottom of the pond or lake as the case may be. The oospore remains dormant over the winter period. In the spring, the nucleus of the oospore divides meiotically to form four naked haploid masses of protoplasm. Each of the latter develops a characteristic crown of cilia to become a zoospore. The wall of the oospore swells and finally ruptures to liberate the haploid zoospores, which are generally contained in a thin-walled vesicle. The zoospore quickly becomes free of the vesicle and after a short period of swimming about settles down at its ciliated end.

The cilia are soon withdrawn, and each zoospore ultimately forms a new haploid filament of *Oedogonium*.

In nannandrous species, the dwarf male filament eventuates on the germination of a special type of zoospore called an androspore. Each androspore is elaborated in a flat discoid androsporangium, which structurally resembles an antheridium. Each androspore is discharged in a vesicle, from which it becomes quickly disengaged. Thereafter the androspore attaches itself to an oogonium. The androspore germinates to form a short filament consisting of an elongated basal cell, which attaches to the oogonial wall, and several flat discoid antheridial cells. Each antheridial cell forms two microgametes, each of which possesses a typical crown of long cilia.

The development of oogonia in nannandrous species is similar to that already described for the macroandrous species. The oospore in nannandrous species undergoes all the modifications discussed with reference to the oospore in the macroandrous species.

Vaucheria (Fig. 14.11). The various species of *Vaucheria* may be grouped into either aquatic or terrestrial forms. The aquatic *Vaucheria* generally occur in aerated water and consequently abound on rocks over which water is continuously trickling or flowing. The terrestrial forms are found in muddy areas or on damp soil.

Each species of *Vaucheria* generally consists of branched tubular filaments in which the cytoplasm is not septated into definite cells. Such a filament in which the cytoplasm is continuous and multinucleate is generally referred to as a *coenocyte*. Throughout the tubular filament there extends a central vacuole. In consequence the cytoplasm is restricted to the periphery of the tubular filament. The chloroplastids, minute in size and either spherical or elliptical in shape, are distributed in that portion of cytoplasm vicinal to the wall of the filament. Pyrenoids are absent from the chloroplastids. Droplets of oil, representing stored food reserve, abound in this cytoplasm; no starch is generally formed in this organism unless it has been exposed to continuous illumination. The nuclei are generally restricted to the inner aspect of the cytoplasm or that part of the cytoplasm which encompasses the centrally running vacuole already mentioned. The relative thinness of the tubular walls, coupled with the lack of cross walls, suggests that the filaments of *Vaucheria* are fragile and readily susceptible of injury by compression.

The aquatic species of *Vaucheria* reproduce asexually by means

of large multiciliate zoospores. In the formation of a zoospore the free end of a filament swells to form a club-shaped zoosporangium, which becomes demarcated from the rest of the filament by a cross wall. In the meantime the protoplasmic contents of the sporangium undergo several modifications. The nuclei and chloroplastids are transposed from their original positions, the nuclei being finally situated in the peripheral area of the protoplasm. The protoplasm contracts into a rounded or oval shape, with the original vacuole much reduced in size and traversed here and there by cytoplasmic strands. Finally

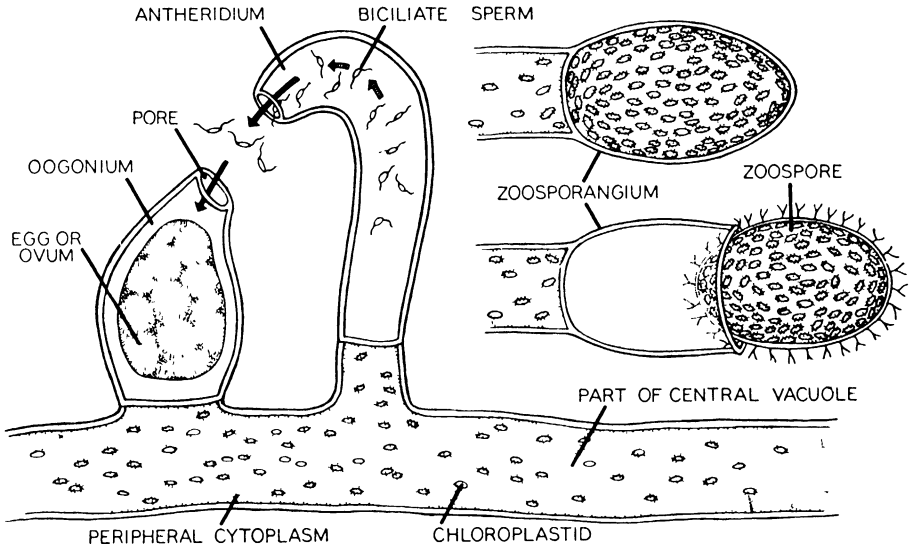


FIG. 14.11 *Vaucheria sessilis* showing asexual and sexual reproduction.

from the area closely vicinal to each peripherally situated nucleus there emanates a pair of short cilia to complete the formation of the mature zoospore. The apex of the zoosporangium now gelatinizes to form a narrow aperture through which the zoospore finally squeezes out. The zoospore swims about for a rather limited time. It finally settles down and after withdrawing its cilia forms around itself a wall. This zoospore does not enter a period of dormancy but germinates almost at once to form a branched tubular filament of *Vaucheria*. Generally one of the filaments puts forth colorless root-like branches, termed *rhizoids*, by which the organism attaches itself to some substrate.

The terrestrial forms, if they do not become covered with water, form sporangia at their ends. The protoplasmic contents of each sporangium become embodied within a thick wall to form a nonmotile spore, sometimes called an *aplanospore*. Liberation of the latter spore occurs upon rupture of the sporangial wall. The aplanospore germinates directly to form a new branched filament of *Vaucheria;* or the protoplast of the aplanospore may divide to form several cyst-like structures. Each cyst, on rupture, discharges an amoeboid protoplast. Subsequently each amoeboid protoplast secretes a wall around itself and thereafter germinates to form a filament of *Vaucheria.*

Sexual reproduction is by fertilization and occurs frequently among the terrestrial species and among the aquatic species that occur in still water. Most of the species of *Vaucheria* are monoecious. Both gametangia, always formed in close approximation to each other, are either sessile or are borne on short lateral stalks. The antheridia arise as sharply curved cylindrical tubes, the protoplasmic content of each being separated from that of the parent filament by a cross wall. The nuclei in the antheridium divide, each of the daughter nuclei ultimately being embodied within a small mass of cytoplasm. These uninucleate masses of protoplasm assume an oval or pear-shaped form and develop two laterally placed cilia to become mature microgametes or sperm. The terminal wall of the antheridium ruptures and the extrusion of the laterally biciliate sperm follows. On the other hand, in the formation of the oogonium, the lateral wall of filament near the concurrently developing antheridium evaginates to form a blunt lateral outgrowth. In the meantime there has accumulated in this area of the parent filament a large mass of multinucleate protoplasm, which now begins to migrate into the evaginated area of the parent filament. The lateral protrusion of the parent filament finally develops into a papillated rounded structure, or oogonium. The base of the oogonium is at this time sharply defined by the development of a cross wall. The mature oogonium encompasses a single uninucleate megagamete. With the exception of one nucleus, the rest of the nuclei, originally contained in the developing oogonium, either return to the parent filament before the formation of the cross wall at the base of the oogonium, or simply degenerate if caught by wall formation. At maturity the papillated beak of the oogonium gelatinizes to form an aperture, directly adjacent to which lies the receptive area of the megagamete. Fertilization ensues in a somewhat peculiar manner.

A single sperm nucleus penetrates the ovum, but does not at this time unite with the nucleus of the ovum. Rather, it first enlarges considerably and then fuses with the nucleus of the ovum. The latter fusion nucleus then becomes centrally placed in the zygote, which now forms a multilayered wall around itself. This zygote then generally remains in a period of dormancy for several months before germination. On the basis of extant experimental data it is considered rather probable that the initial divisions of the zygote nucleus are meiotic and that the branched tubular filament that eventuates after germination of the zygote represents the gametophytic phase in the life cycle of *Vaucheria*.

Economic Importance. The green algae constitute the ultimate source of food for both fresh-water and marine animal life. They serve to keep the water saturated with oxygen, which in turn plays so important a part in respiration of aquatic animal life.

Chapter 15

THE DIATOMS

General Features. This class comprises the diatoms. The individual diatom is unicellular (Fig. 15.0). Rather commonly diatoms of the same species will join together in the formation of a colony, the individual cells being held together by mucilage secreted through pores in the walls. The wall of the diatom is constituted of pectin impregnated with silica and consists always of two halves, called *valves,* which overlap each other like the parts of a pillbox. The valves are as a rule highly detailed by characteristic striae. The diatoms, on the basis of structural symmetry, may be divided into two large groups: the centric diatoms which are radially symmetrical (Fig. 15.1); and the pennate diatoms (Fig. 15.0) which are bilaterally symmetrical. The plastids of the diatoms vary in color, being yellow or golden brown. The presence of an accessory brown pigment, called *diatomin* and considered to be somewhat similar to the accessory brown pigment of the class Phaeophyceae, still remains a controversial matter among investigators. A few investigators maintain that the brown pigment is simply a modification of chlorophyll, called *phaeophyll.* The customary method of reproduction is by cell division, one daughter cell being slightly smaller than the other. Obviously with continued division of the smaller daughter cells, diatoms in succeeding generations will tend to become progressively smaller. Compensation—frequently referred to as rejuvenescence—for this reduction in the size of the members of diatom populations is effectuated through the formation of *auxospores.* Auxospores are spores which result from excessive growth of a protoplast or from fusion of two diatoms. Fats, strangely enough, represent the products of photosynthetic activity.

Occurrence. Diatoms enjoy a wide distribution in both fresh-water and marine plankton.

The fresh-water diatoms, either sessile or floating, are rather more

abundant during the spring when the water is cool. In the summer they are relatively scarce, but appear again in some number during the fall.

In the marine plankton, centric diatoms, primarily because their morphology renders them more adaptable for a free-floating existence,

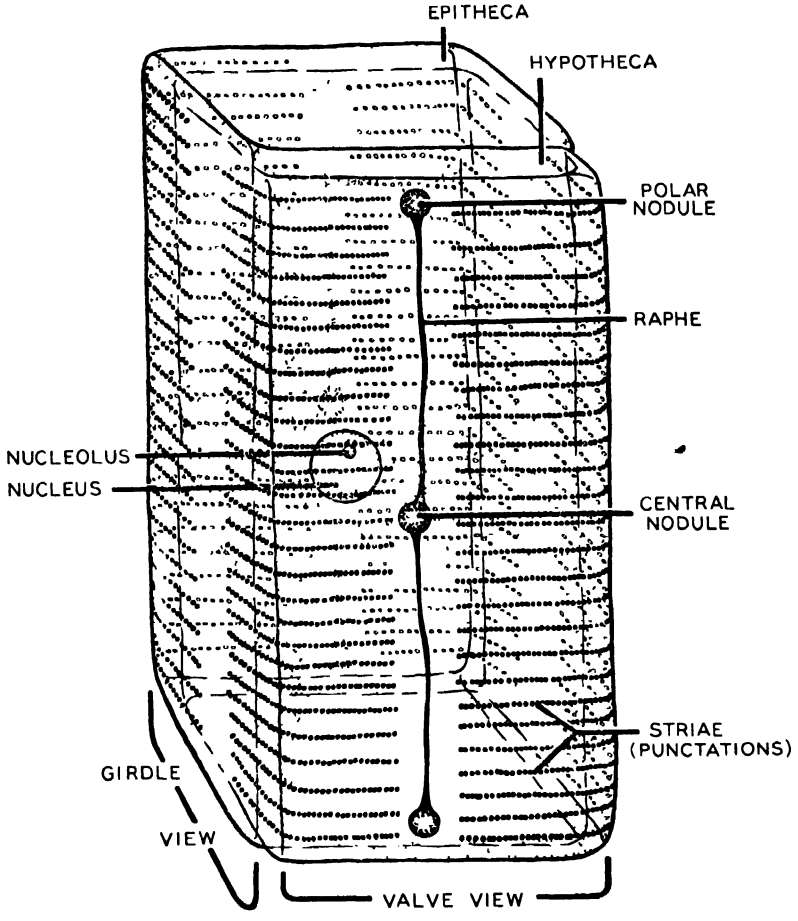


FIG 15.0 A pennate diatom in three-dimensional aspect. The cytoplasm is indicated in fine stippling.

preponderate over the pennate forms. Further, diatoms in the oceanic plankton are relatively less numerous but more diverse in species than those in the neritic (coast) plankton. In general, pelagic diatoms appear to favor the colder regions of the oceans in which they occur. In the bottom-dwelling flora of the photic regions of both fresh water

and salt water, diatoms probably constitute the most abundant type of vegetation.

Diatoms are also epiphytic on filamentous algae. The common brown coating so often seen on submerged rocks and plants represents tremendous aggregations of diatoms of the same species. Diatoms are also found in the soil and have been reported to be rather abundant on sandstone surfaces.

Cell Wall of the Diatoms (Fig. 15.0). The cell wall, as was indicated previously, consists of two halves called valves. The outer valve is called the *epitheca* while the inner valve is termed the *hypotheca*. Each valve is convex in shape and is incurved peripherally to form a connecting band. The connecting bands represent the area where the valves overlap each other and constitute the girdle of the diatom.

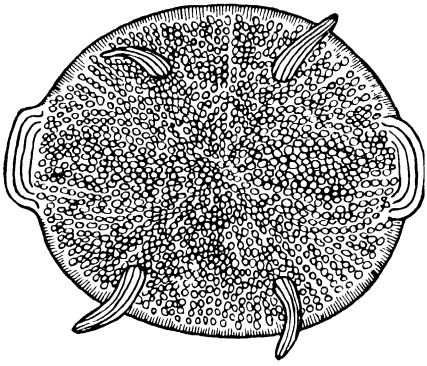


FIG. 15.1 A centric diatom.

Since the deposition of silica in each valve is not uniform, the valve reflects, in a definite pattern of ornamentation, the thinner areas. These thin places, called punctuations, are indicative of minute cavitations (areolae) in the siliceous composition of the valve. In the pennate diatoms, the striae of the valves are actually due to a lineal disposition of these areolae. The areolae are insinuated between interlinear ridgings of the wall. In the centric diatoms, on the other hand, the ridges of the wall interconnect to form a network which circumscribes the areolae. These areolae may be perforated by minute canals called pores.

Locomotion in Pennate Diatoms (Fig. 15.2). In pennate diatoms

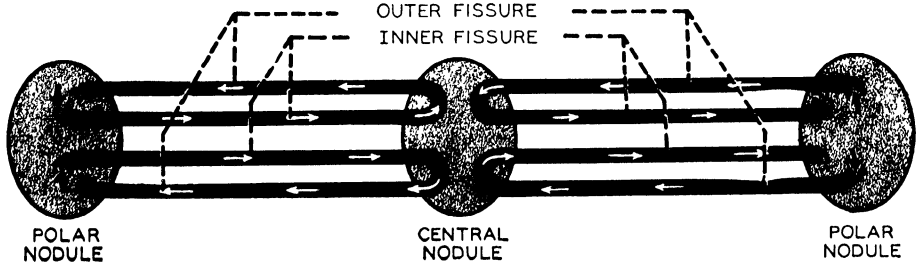


FIG. 15.2 Diagrammatic presentation of locomotion in a pennate diatom.

the striae are directed toward a longitudinal axial line which generally coincides with the location of a longitudinal cleft called the *raphe*. This raphe is concerned with the capacity of pennate diatoms to accomplish locomotion. The raphe is actually a V-shaped cleft. At the halfway mark between the opposite ends of the valve the continuity of this raphe is broken by an internal thickening of the wall, called the *central nodule*. At each end of the raphe there is a shallow thickening of the wall, called the *polar nodule*. The central nodule divides the raphe into two halves. Each half of the raphe contains an outer and inner fissure connected by a minute, loop-like canal in the central nodule and terminating in their respective polar nodules, whence they communicate by separate clefts with the protoplast. A cyclosis of cytoplasm is maintained through the outer and inner fissures of each half of the raphe, the direction of cytoplasmic movement in the outer fissure being opposite to that in the inner fissure. The cyclosis of the cytoplasm in each half of the raphe (Fig. 15.2) coincides with that in the other, however, and may be compared to separate wheels or threads rotating in the same direction. The movement of the cytoplasm in the outer fissures eventuates in the establishment of frictional water currents, and thus the diatom is propelled in a direction opposite to the movement of the cytoplasm in the respective outer fissures of the raphe.

Protoplast of Diatoms (Fig. 15.0). The cytoplasm in both pennate and centric diatoms is usually restricted to the periphery of the cell and thus generally surrounds a large central vacuole. However, in the pennate diatoms there is invariably found a relative thickening of the parietal cytoplasm at each pole of the cell, for here are located the clefts of communication for both the inner and outer fissures of each respective half of the raphe. The nucleus of the pennate diatom is centrally placed, occupying a conspicuous band of cytoplasm that crosses the central vacuole midway between the two poles of the cell. The plastids of both the pennate and centric diatoms are situated in the parietal cytoplasm. The plastids of the centric diatoms are numerous and vary in shape from granules to lobulated discs. The pennate diatoms generally possess two plastids, which are generally laminate in form and oppositely placed in the protoplast. If only one plastid occurs, it is generally lobulated. Pyrenoids may occur in the plastids or they may be absent. Droplets of fat, representing the product of photosynthesis, frequently present themselves either in the cytoplasm or plastids.

Reproduction. The usual method of reproduction among the diatoms is by cell division. The actual division of the cell is preceded by an increase in the volume of the protoplast as a result of which there is placed upon the internal surfaces of the enclosing valves a stress which eventuates in the slight dissociation of the epitheca from the hypotheca. Karyokinesis follows, the spindle being formed at right angles to the longitudinal axis of the cell. The rest of the protoplast divides parallel to the longitudinal axis. Each daughter protoplast receives one of the original valves and subsequently secretes another valve. Thus there are produced two daughter cells, one of which is smaller than the other. The smaller daughter cell is the one which received the hypotheca from the parent cell. Naturally as this daughter cell continues to undergo division, there will be a progressive reduction in the size of the diatoms in succeeding generations. These diatoms apparently attain a certain threshold of diminution and then undergo rejuvenescence (auxospore formation) as described below. In some centric diatoms spore formation is known to occur, but very little is known as to the mechanism of sporogenesis.

Auxospore Formation. In the centric diatoms auxospore formation involves a single protoplast. The rigid valves of the small diatoms are forced apart by the protoplast. The protoplast then becomes enclosed within a delicate membrane called the *perizonium*. Within the perizonium the protoplast undergoes considerable enlargement and actually constitutes the auxospore. Still within the confines of the perizonium, the enlarged protoplast secretes successively the new valves that are to compose its wall. Finally there emerges a diatom which is considerably larger than the original cell.

In the pennate diatoms the actual formation of the auxospore is preceded by conjugation. Two diatoms generally approximate each other along their girdle aspects and are held thus together by mucilage secreted at the poles of the fusing cells. The protoplast in each diatom contracts. The contraction of each protoplast is attended by the formation of mucilage in each cell. This mucilage produces a divergence of the valves of each cell and serves to form a mucilaginous connection between the two contiguous diatoms. The nucleus of each contracted protoplast now divides meiotically, two of the four haploid nuclei in each protoplast degenerating. Each protoplast now undergoes a transverse cleavage to form two gametes, each of which has received one of the original haploid nuclei. One gamete in each cell becomes amoeboid and is known as the male gamete, while the other

gamete remains passive and is termed the female gamete. The male gametes migrate into opposite cells through the mucilaginous bridge and there fuse with the female gametes. Thus there are produced two diploid zygotes. Each zygote subsequently undergoes considerable elongation to form an auxospore. Each auxospore, now definitely much longer than the original parent cell, forms two valves to become a diatom. As a result of the process just described there are formed two larger diatoms. However, it often happens that only one auxospore is ultimately formed when two diatoms conjugate. In such cases the nucleus of each protoplast undergoes the usual meiosis, but three of the haploid nuclei in each protoplast degenerate. Each protoplast with its haploid nucleus constitutes a gamete. The gametes fuse between the apposed cells to form a single diploid zygote, which subsequently enlarges to form a single auxospore. This auxospore, also relatively much larger than either of the parent cells, forms its enclosing valves to become a diatom. From the previous description of auxospore formation it is obvious that the diatom's nucleus is diploid.

Economic Importance. Diatoms are perhaps the most important phytosynthetic mechanisms in the floating plankton of the sea and thus contribute in very great measure to the pelagic pasture on which feeds marine life, large and small. Similarly the diatoms in the neritic plankton sustain the breeding of fish in the shallower waters along the coast. The vitamin A that occurs in cod-liver oil and other fish-liver oils is really synthesized in the protoplast of the lowly diatom. When diatoms die, their siliceous valves sink to the bottom of the body of water in which they are contained. Here over long periods of time these siliceous skeletons of the diatoms accumulate to form extensive deposits of diatomaceous earth. In Lompoc Valley in California and in some lakes of Florida there occur great quantities of diatomaceous earth, the use of which in industry seems to be ever increasing. Diatomaceous earth is regularly used as an absorbent for nitroglycerin in the preparation of certain types of dynamite. It has long been used for its abrasive quality in certain dentrifices and also in the manufacture of many metal polishes. It is also employed in the filtration of oil, and in many sugar refineries it is utilized in the filtering of the sugar syrup. Diatomaceous earth has been found to be more resistant to very high temperatures than asbestos and consequently finds wide use in the insulation of boilers and blast furnaces.

Chapter 16

THE BROWN ALGAE

General Characteristics. The brown algae are, except for a few species, cold-water marine plants which characteristically grow attached to rocks at the coast line. The presence of the photosynthetic pigments is masked to a varying degree by fucoxanthin, a golden-brown pigment present in the plastids. The multicellular thalli are diverse in size and form, and range from the small microscopic filamentous types to the giant kelps, which may be over a hundred feet in length. All motile reproductive cells are pyriform and are characterized by the presence of two laterally attached cilia of unequal length. Alternation of generations is exhibited by all members of the Phaeophyceae.

Most familiar of the brown algae are the rockweeds and kelps. The rockweeds, which are usually restricted to the upper littoral zone, range in size from a few inches to a few feet and have a plant body which consists of a ribbon-like thallus with holdfasts. The kelps are generally limited to the lowermost portion of the littoral zone and have a sporophytic plant body which consists of a root-like holdfast for anchorage, a long so-called stem (stipe), and one or more expanded blades that float on the surface of the water. Club-shaped zoosporangia are borne on the surfaces of the blades. Air bladders are often borne by the plant body to give it buoyancy.

The kelps show considerable cellular differentiation in comparison to algal organisms previously considered. The so-called stem has a surface layer of epidermal cells. The epidermis encloses the cortex, a region of cells containing chromoplastids. The central region or medulla contains sieve-tube-like cells which probably function in conduction. The gametophytes of all kelps are small, filamentous, and inconspicuous. They arise from germinating zoospores.

In the class Phaeophyceae we shall consider *Ectocarpus,* a rather simple form, and *Fucus,* a more complex organism.

Ectocarpus. Ectocarpus generally occurs as a small brown tuft of filaments attached to other algae or stones around the tide level. The attached part of the plant consists of branched, creeping filaments whence rhizoids arise to penetrate the substrate. The erect portion of the plant is simply a tufted mass of branching filaments.

Each vegetative cell (Fig. 16.0) usually possesses a large central vacuole in which the nucleus is suspended by cytoplasmic strands from the peripherally situated cytoplasm. In the parietal cytoplasm there generally occur several plastids which are either discoidal or irregularly banded in shape. The band-shaped plastids are frequently elongated and somewhat spirally disposed in fairly close approximation to the cell wall.

Ectocarpus reproduces asexually by zoospores (Fig. 16.0). The latter are contained in zoosporangia which are generally borne on short lateral branchlets of a filament. However, the zoospores may be either haploid or diploid, according to the type of sporangium in which they are formed. One type of sporangium is unilocular. A *unilocular* sporangium represents the much enlarged terminal cell of a lateral branchlet. The nucleus of this cell undergoes meiosis to form four haploid nuclei, which subsequently divide mitotically to form nuclei in multiples of thirty-two. Ultimately the cytoplasm undergoes cleavage, as a result of which there are formed numerous uninucleate protoplasts. The latter metamorphose into laterally biciliate zoospores, which are characteristically pyriform in shape. The fully formed unilocular sporangium, spherical in shape and relatively smaller than the plurilocular sporangium, finally ruptures at its free end. The haploid zoospores are thus liberated and upon germination give rise to haploid filaments which will bear isogametangia. The other type of sporangium, called *plurilocular*, is a tapering, elongated multicellular structure formed as a result of repeated equational divisions of the terminal cell of the branchlet of a diploid filament. This plurilocular sporangium in its finally developed form is composed of numerous cubical cells, the protoplasts of each of which finally metamorphose into pear-shaped, laterally biciliate zoospores. Finally the cell walls begin to break down progressively, and the diploid zoospores are discharged through a terminal rupture of the sporangium. Each diploid zoospore upon germination develops into a diploid filament bearing both unilocular and plurilocular sporangia.

Sexual reproduction involves conjugation (Fig. 16.0). The iso-

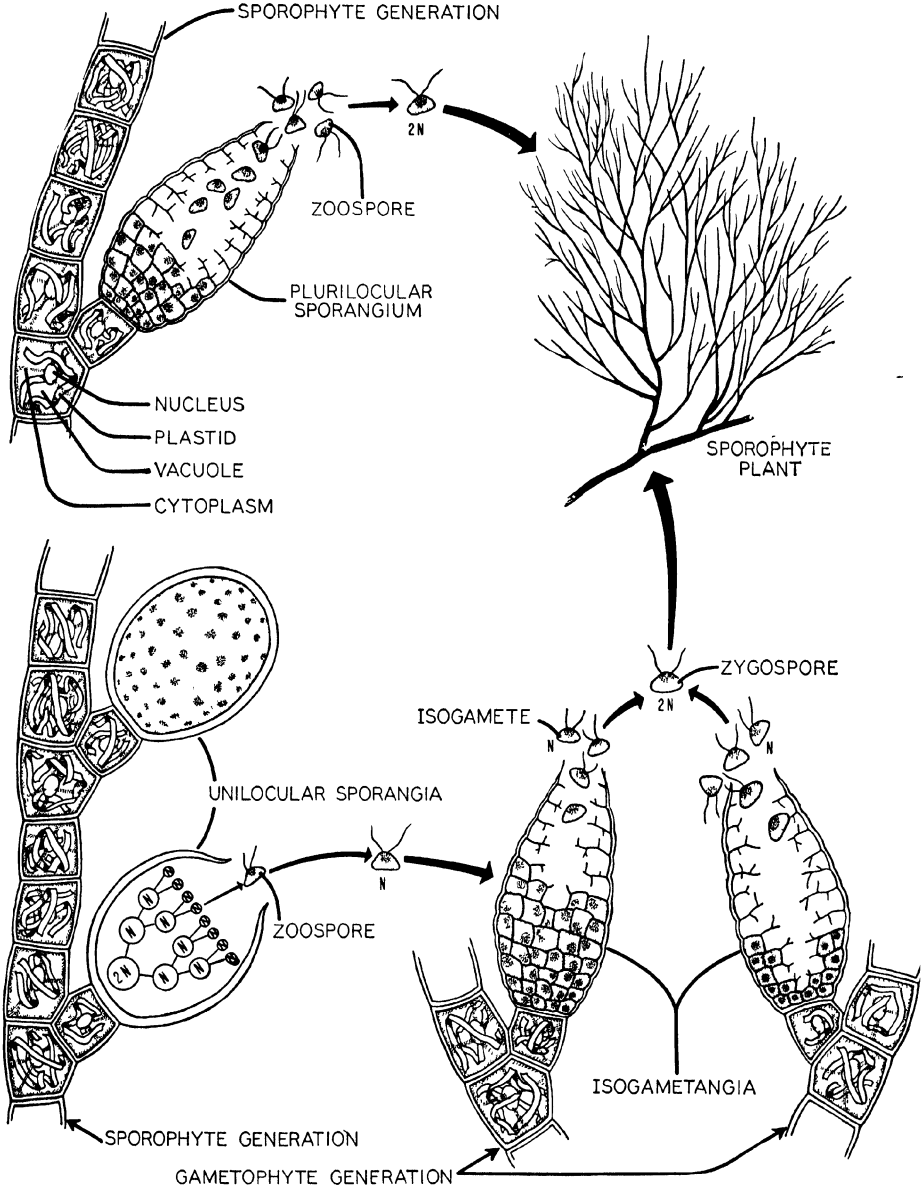
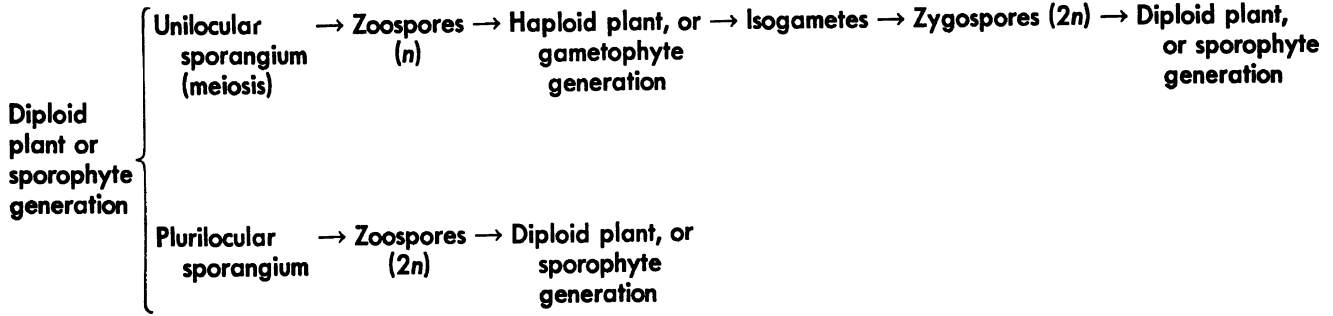


FIG. 16.0 *Ectocarpus*, showing the life cycle and illustrating asexual and sexual reproduction.

gametangium is a tapering, ellipse-shaped structure when fully developed and shows no discernible microscopic difference from that of the plurilocular sporangium. However, it might be well to point out here that this isogametangium is a haploid structure. The cubical cells of this isogametangium contain uninucleate protoplasts, each of which


Diploid plant or sporophyte generation
Unilocular sporangium (meiosis)
→ Zoospores (n)
→ Haploid plant, or gametophyte generation
→ Isogametes
→ Zygospores (2n)
→ Diploid plant, or sporophyte generation
Plurilocular sporangium
→ Zoospores (2n)
→ Diploid plant, or sporophyte generation

becomes transformed into a laterally biciliate isogamete. The walls of the cells break down, and the isogametes are discharged through a terminal rupture of the isogametangium. The isogametes fuse in the water to form a zygospore, whence develops upon germination a diploid plant. Because of the meiosis that occurs in the unilocular sporangium, there is a definite alternation of generations in the life cycle of *Ectocarpus*. This will be evident from the summary of the cycle on the preceding page.

Fucus (Fig. 16.1A). The thallus is flattened and dichotomously branched. The forked part of the thallus, commonly referred to as the *frond*, tapers into a stalk called the *stipe*, the end of which is modified into a disc-like holdfast mechanism for attachment to the substrate. Each branch of the frond is characterized by a midrib and generally at some distance from its free end presents a pair of small bladder-like elevations termed *air vesicles*. These air vesicles, owing to accumulation of carbon dioxide and oxygen from the tissue below where they occur, serve to buoy the thallus up on its being submerged at high tide. At low tide the thalli of *Fucus* lie limply on the rocks in the intertidal zone.

At the time of reproduction the tips of the frond branches swell because of the accumulation of mucilage and are now referred to as *receptacles*. The receptacles are covered by small wart-like protuberances in the center of each of which there is a minute opening or *ostiole*. The ostioles communicate below with the spherical cavities or *conceptacles* (Figs. 16.1C and C′). In dioecious species of *Fucus*, common on the rocks along our Atlantic coast, either microsporangia or macrosporangia are developed within the conceptacle. In the monoecious species of *Fucus*, common along our Pacific coast, both microsporangia and macrosporangia occur in the same conceptacle.

The microsporangia are oval in shape and are borne on branched filaments. Initially the single diploid nucleus of the microsporangium divides meiotically to form four haploid microspores, each of which subsequently undergoes four mitotic divisions to form sixteen laterally biciliate microgametes or sperm. The microsporangium housing these sperm may now be regarded as an "antheridium" (Fig. 16.1C′). In addition to the fertile filaments which bear the microsporangia, there are numerous sterile filaments which practically obscure the microsporangia. These sterile filaments, called *paraphyses*, arise from the floor of the conceptacle and secrete a gelatinous or mucilaginous

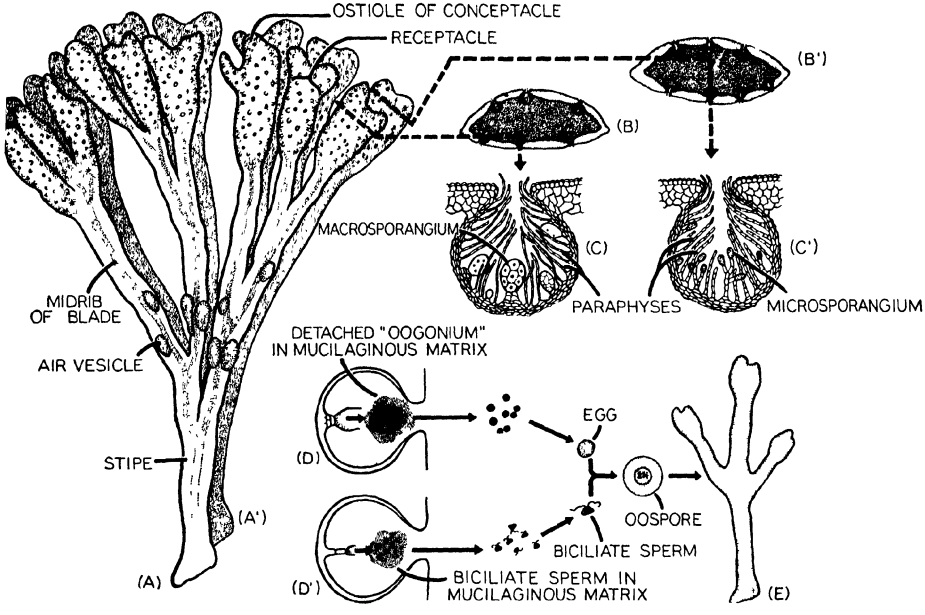


FIG. 16.1 Life cycle of *Fucus* (dioecious species): (A) macrosporangial plant; (A') microsporangial plant.

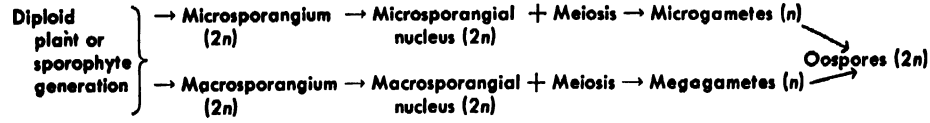
material. The wall of the "antheridium" ruptures and the sperm become engulfed in the mucilaginous material. At low tide the mucilaginous material is compressed out of the conceptacle through the ostiole, presumably because of the tissue shrinkage of the conceptacle. At high tide the water carries away the effused mucilage and disengages the sperm so that they are free to seek out an egg or megagamete.

On the other hand, the macrosporangium is a spherical structure borne on a single stalk cell. Initially the diploid nucleus of the macrosporangium divides meiotically to form four haploid nuclei, each of which divides mitotically once to form eight haploid nuclei. Cleavage of the cytoplasm follows and there result eight uninucleate rounded masses or megagametes. The macrosporangium may be considered at this time to have become an "oogonium" (Fig. 16.1C). The wall of the "oogonium" is composed of three layers. Upon the attainment of maturity the outer wall ruptures and the two-walled "oogonium" (Fig. 16.1D) becomes detached from the stalk cell and subsequently is entrapped by the mucilage secreted by the paraphyses. Effusion of the mucilage with the two-walled "oogonium" from the conceptacle occurs at high tide. The two-walled "oogonium" ruptures, and its megagametes or eggs are set free in the water.

Fusion of the sperm and eggs takes place in the water. The

oospore, representing the beginning of the sporophyte generation, sinks to the bottom and forms a wall around itself. Within a couple of days it germinates to form a pear-shaped multicellular mass which subsequently develops into the flat, dichotomously branched thalloid body (Fig. 16.1E) characteristic of *Fucus*.

From the following summary it becomes evident that the plant body of *Fucus* represents the sporophyte generation, while the gametophyte generation is reduced to the gametes. It might be noted in passing that the cycle of *Fucus* resembles the terminal or gametic cycle characteristic of animals, to which reference has already been made in the discussion of meiosis, Chapter 10.



Economic Importance. *Kombu,* an important element in the diet of Japan, is derived from nine or ten species of *Laminaria.* In Japan the various preparations of *kombu* are used as vegetables and as flavoring agents for soups. It has been reported that at least five or six types of seaweed are employed in the preparation of a single Japanese meal. Rather significant is the fact that goiter is practically unknown in Japan. The absence of goiter is ascribed to the high commercial iodine content of the kelp. In fact iodine is obtained from *Fucus* and *Laminaria,* while *Nereocystis* and *Macrocystis,* the giant kelps, yield appreciable quantities of potassium. In various sections of Japan various species of kelp are used as soil fertilizer, while the farmers of Scotland and Ireland utilize *Sargassum* and other seaweeds as cattle feed. Some time ago the fronds of *Macrocystis pyrifera* were subjected to a thorough chemical analysis and found to contain iodine, sulfur, sodium, magnesium, phosphorus, and calcium—to mention just a few of the elements. This plant was also discovered to be a good source of D and B vitamins and to contain in even greater quantities the vitamins A and E. Even in the United States various kelp preparations are on the market for human consumption, while other kelp products are regularly used to supplement cattle feeds. So the brown algae are not just items in the dietary regimens of the marine animals.

Chapter 17

THE RED ALGAE

General Characteristics. The class Rhodophyceae is the red algae. In these plants the red color is due to the presence of plastids which contain the red pigment *phycoerythrin.* Most species are marine, and they usually grow attached to rocks near the shore. They are most plentiful in the warm seas. All members of this class have multicellular thalli, the largest of which are only several feet in length.

The thalli are diverse in form. In some species the thallus is a much-branched, filamentous structure, while in others it is like a ribbon, a leaf, or a forking cylinder. The cells have a single nucleus embedded in the peripherally located cytoplasm. One or more plastids are present in most vegetative cells, and some of them possess pyrenoids. A distinguishing cellular feature of the red algae is the presence of cytoplasmic connections between cells. These connections pass through openings in the cell walls. Another distinguishing feature is the absence of any motile reproductive cells. The food reserve is a carbohydrate, called *floridean starch,* which chemically is an intermediate between true starch and dextrin.

Plants which are often studied as representative of the red algae are *Batrachospermum, Nemalion,* and *Polysiphonia.*

Polysiphonia (Fig. 17.0). As a representative of the red algae, we have selected *Polysiphonia,* a form commonly studied in the laboratory. The life cycle of *Polysiphonia* is unique in that it presents three phases instead of the usual two.

The thallus of *Polysiphonia,* attached at its base by rhizoids, possesses a main axis bearing alternate lateral branches. The main axis, as well as its lateral branches, consists of a seriated alignment of central cells, the contiguous ends of which are annexed by a cytoplasmic connection. These central cells are typically elongate and cylindrical, and because they give the impression of being tubular in arrange-

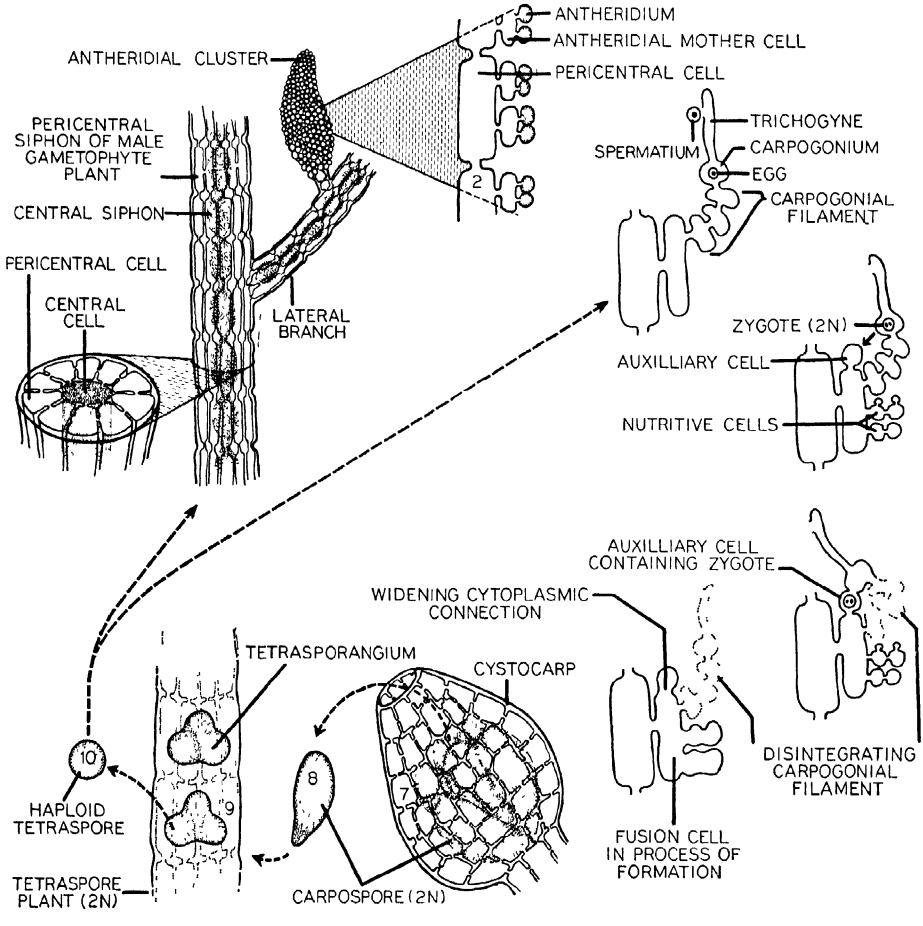


FIG. 17.0 Life cycle of *Polysiphonia* (see text).

ment, they are collectively referred to as the *central siphon.* Enclosing the central siphon is a tube of elongated pericentral cells, each of which bears on its inner aspect a cytoplasmic connection with the central cell at the same level. The pericentral cells constitute collectively the *pericentral siphon.*

The individual cells are generally centrally vacuolated, the nucleus and plastids occupying the peripherally restricted cytoplasm. The red plastids, small and disciform, are more numerous in the pericentral siphon than in the central siphon. The cytoplasmic continuity of both the central and pericentral cells has already been indicated.

Reproduction in *Polysiphonia* is somewhat complex. Briefly, the union of its gametes eventuates in the formation of diploid carpospores, whence in turn are developed tetrasporic plants. These produce haploid tetraspores from which arise the gametophyte plants.

We shall consider in some detail below the reproductive mechanisms of *Polysiphonia* according to the sequence just outlined.

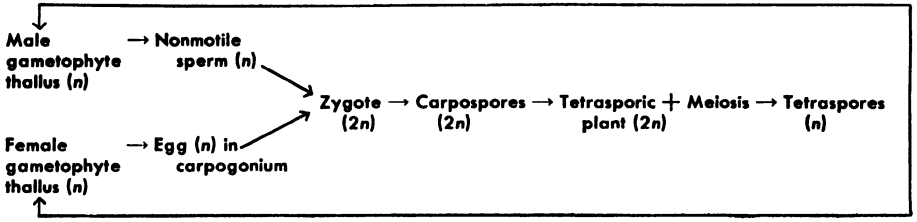
Polysiphonia is heterothallic; that is to say, the male and female gametangia occur on separate plants. The antheridia, which are unicellular, are formed in clusters on the lateral branches. Since the antheridial clusters are light yellow in color, the male gametophyte may readily be distinguished from the female gametophyte. In the formation of antheridia there arise from the lateral aspect of each pericentral cell of the lateral branch several flat-topped antheridial mother cells which retain continuity with the pericentral cell by a cytoplasmic connection. Each antheridial mother cell then evaginates to form one or two unicellular antheridia. As the antheridia mature, they become definitely spherical and are still connected to the antheridial mother cell by cytoplasmic connections. Finally each antheridium swells and ruptures to discharge a single nonmotile sperm called a *spermatium*. Each spermatium has a central vacuole in which the nucleus is suspended from the parietal cytoplasm, immediately circumjacent to which is a rather delicate wall. The spermatia are discharged in great number and are borne along by the water currents. In this manner some of the spermatia inevitably come into contact with the slender filament (trichogyne) that projects from the female gametangium.

On the other hand, the female gametangium in *Polysiphonia* is called a *carpogonium*. This carpogonium is actually the metamorphosed terminal cell of a small carpogonial filament (generally four-celled) that originated from a fertile pericentral cell of a lateral branch. The upper surface of the carpogonium is protracted into a slender tubular upgrowth called the *trichogyne*. The latter represents a receptive mechanism for the sperm. The carpogonium contains one haploid egg. Water currents bring the spermatia into contact with this trichogyne. There then follows a mutual dissolution of the contacting walls of both the spermatium and the trichogyne. The spermatium moves down the trichogyne and fuses with the egg in the carpogonium to form a zygote. Thereupon the fertile pericentral cell forms on its upper apical aspect an auxiliary cell. The carpogonial filament now turns inward toward the auxiliary cell in such a manner as to bring the carpogonium into contact with the recently formed auxiliary cell. In the meantime the nucleus of the zygote undergoes mitosis to form two diploid nuclei. The approximated walls of both the carpogonium and auxiliary cell break down at the point of con-

tiguity, and the two diploid nuclei move into the auxiliary cell. The carpogonium now degenerates. The cytoplasmic connections between the pericentral and the auxiliary cells, as well as those between adjacent nutritive cells developed from the fertile pericentral cell at fertilization, widen in such a way that nuclei and cytoplasm become conjoined into an irregular-shaped, multinucleate fusion cell. The diploid nuclei, which had been previously formed as a result of mitosis of the zygote, move to the periphery of the fusion cell and there divide mitotically to form a number of diploid nuclei. The peripheral area of the large fusion cell now evaginates to form a number of bud-like outgrowths into which migrates one of the diploid nuclei. Each bud then becomes constricted at its base and is thus differentiated into a stalk supporting a carpospore. The diploid nucleus of the original bud in the meantime has divided mitotically to form two nuclei, one of which becomes the nucleus of the carpospore and the other the nucleus of the supporting stalk. The carpospore, when fully formed, is pyriform in shape. At this time the carpospores have come to be contained in a two-layered, urn-shaped cystocarp, which has a pore-like opening at its free end for the discharge of the carpospores. The cystocarp was formed by cells that originated from the central cell and the pericentral cell on each side of the fertile pericentral cell whence had been formed the carpogonial filament already described.

The carpospore on germination forms a tetrasporic plant. The latter, insofar as its cellular alignment is concerned, is no different morphologically from the gametophyte thallus previously described. However, it must be borne in mind that the nuclei of the tetrasporic plant are diploid. In a mature tetrasporic plant, one pericentral cell in a tier at any given level divides transversely to form a lower stalk cell and upper sporangial cell. The diploid nucleus of the sporangial cell divides meiotically to form four haploid nuclei, as the sporangial cell enlarges considerably to form a sporangium. Cleavage of the cytoplasm within the sporangium follows, each nucleus and its vicinal cytoplasm becoming a spore. Because of the tetrahedral disposition of the spores, the sporangium is commonly referred to as a *tetrasporangium.* The spores, since they occur as a quartet in each tetrasporangium, are called *tetraspores.* The haploid tetraspores on germination eventuate in the formation of gametophyte plants.

A summary is presented below to highlight the life cycle of *Polysiphonia,* with special reference to its alternation of generations:



Economic Importance. *Chondrus crispus,* or Irish moss, is a red algal organism common along the coast of Ireland and the eastern coast of the United States. Because of its gelatinous nature, it is commonly utilized in the curing of leather and as a sizing in textile manufacture. It is employed to emulsify oils and has been incorporated into shaving soaps so as to increase the quantity of the lather. In the laboratory it is used as a nutrient medium for amoebae. Another red alga, *Gelidium corneum,* and other species of *Gelidium* are the sources of agar, which has been used in medicine as a laxative and as an important constituent in the preparation of culture media for bacteriological work. In Japan and Europe agar has been found useful in sizing textiles and in the clarification of various beverages. In our own country agar has been used in the manufacture of ice cream and jellies. *Rhodymenia palmata,* or Irish dulse, is still used as a food and a relish. Of historical significance is the role which dulse played in the diet of the Irish people when their country was struck by the great famine. Even today many youngsters in Ireland and Scotland chew on dulse. It is often referred to as "sheep's weed" because sheep in Norway are wont to graze upon it at low tide. Lastly, the red algae form a very important item in the diet of fish.

Chapter 18

THE BACTERIA

General Considerations of the Class Schizomycetes. The Schizomycetes or bacteria are microscopic, unicellular, chlorophyll-free, plant organisms which commonly reproduce by simple transverse fission. They may occur singly or in aggregations to form colonies. In bacterial colonies the individual cells are functionally independent. The distribution of bacteria is almost universal.

To illustrate their minute size, let us examine a few specific bacterial organisms. *Clostridium tetani,* the causative organism of lockjaw or tetanus, is a slender rod which varies from 2 to 5 microns in length and from 0.3 to 0.8 microns in width. A micron is 1/1000 millimeter or about 1/25,000 inch. *Mycobacterium tuberculosis hominis,* the bacterium commonly responsible for tuberculosis in man, is a rod-shaped organism varying from 0.5 to 4.0 microns in length and from 0.3 to 0.6 microns in breadth.

On the basis of shape (Fig. 18.0) there are three fundamental types of bacteria: the spherical bacteria, or *cocci;* the rod-shaped bacteria, or *bacilli;* and the spiral or screw-shaped bacteria, or *spirilla.* In many species of cocci the daughter cells remain attached after cell division and the type of cell aggregation which results is determined by the number of planes of fission. Division in a single plane results in a group of two cocci (diplococcus) or a chain of cocci (streptococcus) and division in two or more planes gives rise to a cubical packet (sarcina) or to a grape-like cluster (staphylococcus). Rod-shaped bacteria occur singly, in groups of two (diplobacillus), or in chains (streptobacillus). The curved types of bacteria are the *vibrios* and the spirilla proper. Vibrios usually show a single curve, while spirilla proper are longer, rigid or relatively rigid curved forms. There exist other unicellular, filamentous, flexible, motile, spiral organisms coiled in three dimensions. They differ from the bacteria in that they

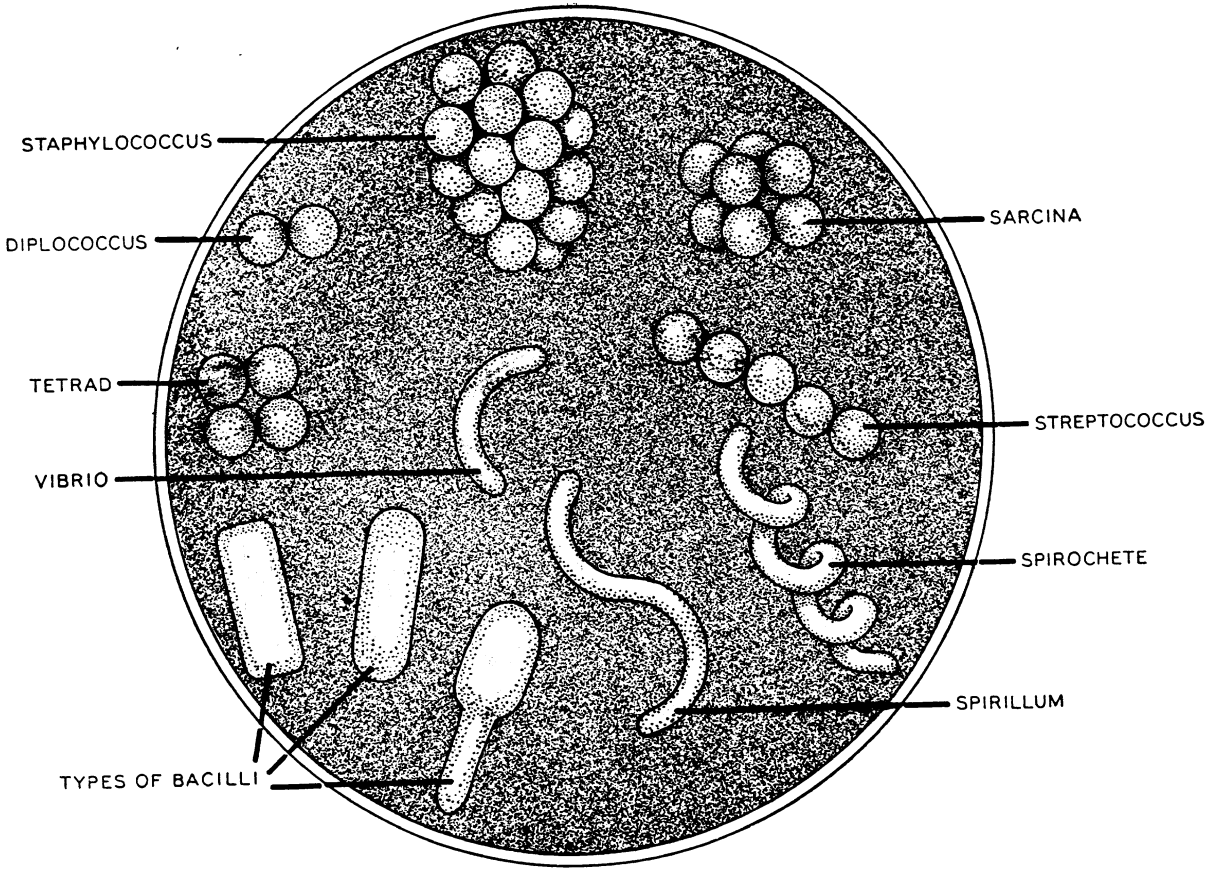


FIG. 18.0 Morphological types of bacteria.

do not possess a rigid cell wall. They are called *spirochetes*. It is not known with certainty whether they are bacteria, protozoa, or organisms intermediate between the bacteria and the protozoa. It is very probable that they are more closely allied to the bacteria than to the protozoa.

The typical bacterial cell consists of four structurally distinct parts (Fig. 18.1): cytoplasm, cytoplasmic membrane, cell wall, and slime layer or capsule. In a number of species of bacteria substances are present in the cytoplasm as free granules or in vacuoles. The granules probably constitute a store of reserve food material. The chemical architecture of the cell wall varies in different species; in many it is apparently constructed of cellulose or hemicellulose, while in others

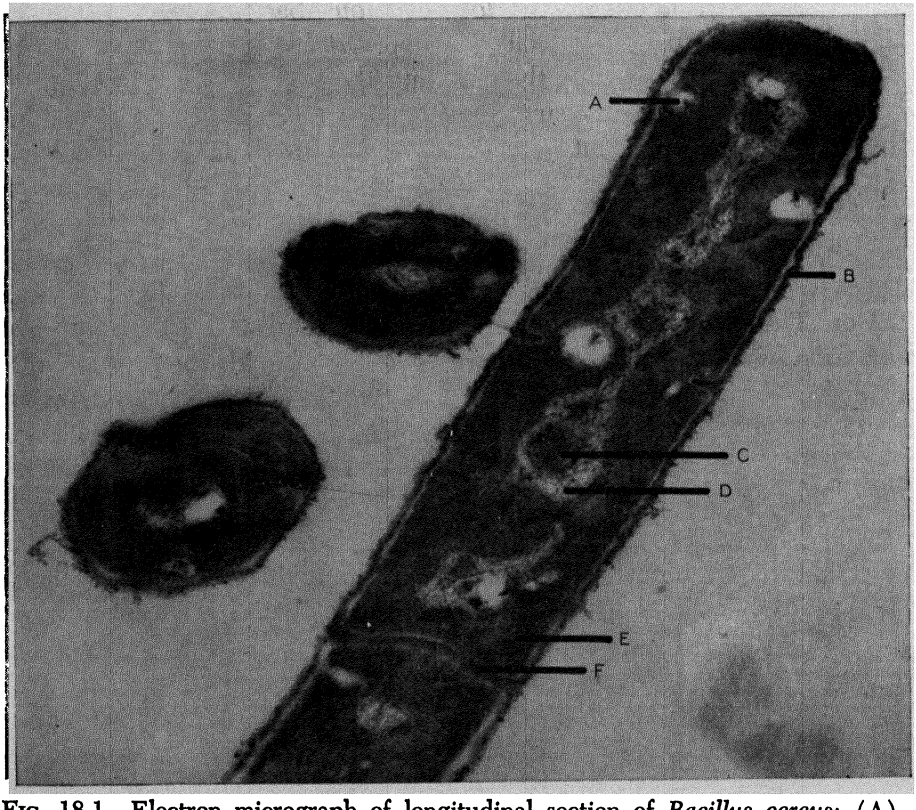


FIG. 18.1 Electron micrograph of longitudinal section of *Bacillus cereus*: (A) vacuole; (B) cell wall; (C) dense body in the nuclear apparatus; (D) fibrous component of the nuclear apparatus; (E) cytoplasm; (F) transverse wall. (Courtesy, Dr. George B. Chapman and Dr. James Hillier, Department of Biology, Princeton University, and RCA Laboratories Division, Princeton, New Jersey.)

it consists of a nitrogenous organic substance. The cell wall in certain bacteria is surrounded by a thin coating of gelatinous material called the slime layer. When this layer becomes thickened, it is called the capsule. Ordinary microscopy does not reveal any discernible nucleus. However, recent investigations with special staining techniques and the electron microscope indicate the presence of a diffuse nucleus or an organized nucleus.

The locomotor organs in the majority of the motile bacteria are flagella. A *flagellum* is a long, slender, whip-like, protoplasmic process of a cell. The nonflagellated bacteria are said to be *atrichous*. On the basis of their type of flagellation, the flagellated bacteria are divided into four groups: the *monotrichous* bacteria with a single flagellum at one end of the cell, the *lophotrichous* bacteria with a tuft of flagella at one end of the cell, the *amphitrichous* bacteria with a tuft of flagella at both ends of the cell, and the *peritrichous* bacteria with flagella about the entire surface of the cell.

The most important differential stain used in bacteriology is Gram's stain. By its use, bacteria can be subdivided into two groups: the Gram-positive and the Gram-negative. Suppose both types are present on a microscopic slide in the form of a smear. The smear is stained with crystal violet and the bacteria become dark violet in color. The excess dye is rinsed off and the smear is treated with a solution of iodine. The iodine forms a complex with the crystal violet which is bluish-black in color. The solution of iodine is poured off, and the slide is immersed in alcohol or in an alcohol-acetone mixture for a brief interval (ten to thirty seconds). The iodine-and-crystal-violet complex is more rapidly removed from Gram-negative bacteria. While the Gram-negative bacteria lose most of their stain on decolorization, the Gram-positive bacteria still retain their coloration. A dye with a color other than that of crystal violet is then used to stain the Gram-negative bacteria in order to make them readily discernible.

Bacterial Endospores. The formation of endospores is a distinguishing feature of many bacilli. An endospore is a refractile, spherical or ovoid body, formed centrally, terminally, or subterminally by the condensation of the protoplasm of a vegetative bacterial cell within the confines of the old cell wall, which then becomes a sporangium. The condensed mass of protoplasm secretes about itself a relatively thick spore wall. After a short period the sporangium undergoes dissolution, and the spore is freed.

Spores are usually more resistant than vegetative cells to nocuous conditions, such as extremes of temperature, absence of moisture, and various chemical agents. They may remain dormant for a long period of time. When exposed to suitable environments they germinate (Fig. 18.2) and each one gives rise to a single vegetative cell. Endospore formation is thus not a method of bacterial multiplication.

Spore formation occurs most commonly when environmental factors for vegetative growth become gradually unfavorable, but it may occur at times under favorable conditions. Hence the old concept that spore formation by bacteria is solely an adaptive mechanism to temporarily survive deleterious environmental conditions does not

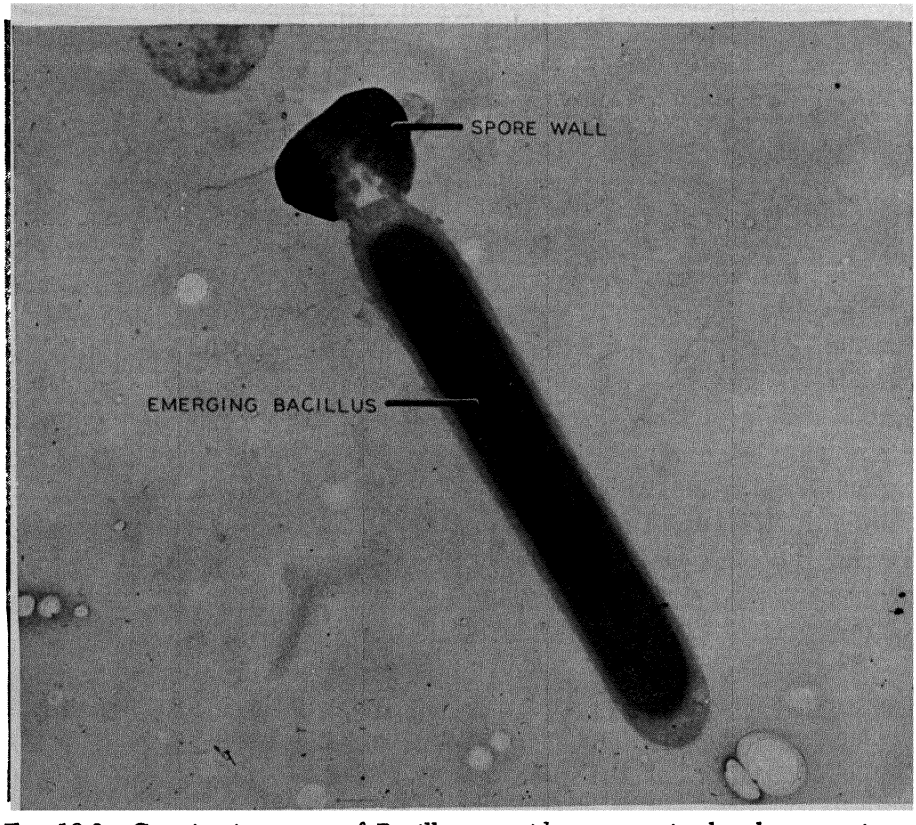


FIG. 18.2 Germinating spore of *Bacillus mycoides* as seen in the electron micrograph. (Courtesy, Dr. George B. Chapman and Dr. James Hillier, Department of Biology, Princeton University, and RCA Laboratories Division, Princeton, New Jersey.)

appear to be entirely correct. It is the opinion of some bacteriologists that the production of endospores in the bacterial life cycle has a greater significance than is indicated by the old concept and that possibly it is a means of bacterial rejuvenescence or the result of sexual reproduction. The biological function of the spore is essentially unknown.

Bacterial Reproduction. The common mode of bacterial reproduction is by fission. The two cells which result are equal or nearly equal in size. In the process, constriction of the cytoplasmic membrane and the cytoplasm occurs. When all portions of the membrane meet in the center of the plane of division, splitting of the membrane occurs. This is followed by the formation of cell walls.

Some other modes of asexual bacterial reproduction which have been described are budding, branching followed by segmentation of the branches into cells, filamentous growth followed by segmentation, conidiospore formation by abstriction of the terminal portion of a bacillus, and so on. The evidence for bacterial reproduction by the sexual method of conjugation is not very convincing.

Bacterial Nutrition and Metabolism. The term *nutrition* with respect to bacteria has reference to their requirements of food which, when taken in, is utilized as building material and as a source of energy. On the basis of their mode of nutrition, bacteria may be divided into two major groups, the autotrophs and the heterotrophs.

The *autotrophic bacteria,* a minority of the bacterial species in number, can synthesize their essential foodstuffs from an inorganic medium containing water, carbon dioxide (or bicarbonates), and inorganic salts. The fixation of carbon dioxide in these organisms is a source of all the organic compounds which they synthesize. The autotrophic bacteria are divided into two major groups: the chemosynthetic autotrophs and the photosynthetic autotrophs. The *chemosynthetic* species obtain the energy for foodstuff synthesis from the oxidation of inorganic compounds such as hydrogen sulfide, ferrous compounds, molecular hydrogen, ammonia, and nitrites. Examples of chemosynthetic autotrophic bacteria are *Nitrosomonas europaea* and *Thiobacillus denitrificans. Nitrosomonas europaea* obtains its energy from the oxidation of ammonia.

$$\underset{\text{Ammonia}}{NH_3} + 1\tfrac{1}{2}O_2 \rightarrow H_2O + \underset{\text{Nitrous acid}}{HNO_2} + \text{energy}$$

Thiobacillus denitrificans obtains its energy solely by anaerobically oxidizing sulfur or sulfur compounds. Nitrate must be present as the oxidizing agent. In the process nitrate is reduced to gaseous nitrogen.

$$\underset{\text{Sulfur}}{5S} + \underset{\substack{\text{Potassium}\\\text{nitrate}}}{6KNO_3} + 2H_2O \rightarrow \underset{\substack{\text{Potassium}\\\text{acid}\\\text{sulfate}}}{4KHSO_4} + \underset{\text{Nitrogen}}{3N_2} + \underset{\substack{\text{Potassium}\\\text{sulfate}}}{K_2SO_4} + \text{energy}$$

Most *photosynthetic* species, such as the green and purple sulfur bacteria, can multiply in an inorganic medium. The energy for the reduction of CO_2 to organic cellular constituents is obtained from light. The photosynthetic pigments of the photosynthetic bacteria are related to, but not identical with, the chlorophylls of the green plants. An example of a photosynthetic autotroph is *Chlorobium limicola,* a green sulfur bacterium. It couples the reduction of carbon dioxide by light with the oxidation of hydrogen sulfide to sulfur.

$$\underset{\substack{\text{Hydrogen}\\\text{sulfide}}}{2H_2S} + CO_2 \xrightarrow{\text{light}} \underset{\substack{\text{Carbo-}\\\text{hydrate}}}{(CH_2O)} + 2S + H_2O$$

Photosynthesis in this organism differs from photosynthesis occurring in green plants in that hydrogen sulfide, not water, is the hydrogen donor, and sulfur, not oxygen, is the by-product.

The *heterotrophic bacteria,* which constitute a majority of the bacterial species, are unable to synthesize organic substances from carbon dioxide and depend on other organisms for the production of their essential organic foodstuffs. They can, however, fix carbon dioxide into organic linkage. Carbon dioxide fixation usually consists of the combination of carbon dioxide with an organic acid to form an organic acid with one more carboxyl group; from the latter in further metabolic reactions other compounds may be produced. The heterotrophic bacteria live either saprophytically or parasitically. The nutritional requirements of these bacteria vary among different species. Some can live largely on carbohydrates, while others require fats, proteins, and other organic compounds. Specific vitamins are essential growth factors in some species. To obtain foodstuffs in diffusible form they liberate into the surrounding medium enzymes which are largely concerned with the hydrolytic splitting of complex foodstuffs to render them diffusible and capable of being absorbed. These enzymes are

called *extracellular enzymes* or *exoenzymes,* to distinguish them from the *intracellular enzymes* or *endoenzymes* whose sole site of action is in the cell. The endoenzymes are liberated from the cell only when the latter disintegrates.

Some of the hydrolytic exoenzymes secreted by bacteria and the substrates upon which they act are shown in Table 6.

Table 6. HYDROLYTIC EXOENZYMES OF BACTERIA

Substrate	Enzyme	End Products
Starch	Amylase	Maltose
Sucrose	Sucrase	Glucose and fructose
Maltose	Maltase	Glucose
Cellulose	Cellulase	Cellobiose
Cellobiose	Cellobiase	Glucose
Fats	Lipase	Fatty acids and glycerol
Proteins	Various proteinases	Mainly peptides
Peptides	Peptidases (appear to be chiefly intracellular)	Amino acids

Respiration in Heterotrophic Bacteria. Because of the varied metabolic groups of bacteria, a coherent picture of all the chemical changes which occur in bacterial cultures is not possible. Hence we shall limit our account of bacterial metabolism to the oxidation-reduction reactions involving organic compounds which yield energy for the life and growth of heterotrophic bacteria and provide substances which are assimilated and synthesized into cellular material. These activities are grouped under the term respiration.

Respiration does not necessarily imply the use of molecular oxygen. Bacteria that require molecular oxygen in their metabolism are said to be *obligate aerobes;* those to which it is toxic or which require its absence are said to be *obligate anaerobes;* and those aerobes which can live in the absence of molecular oxygen are termed *facultative anaerobes.*

Respiration in the heterotrophic bacteria is a process in which, for the most part, carbohydrates are broken down. A wide variety of other organic substances such as fatty acids, lactic acid, succinic acid, and monohydroxy alcohols may be oxidized. In aerobic respiration free oxygen is utilized, at least in the terminal stages of the process (Krebs cycle, or a modified form of it) and complete oxidation results in the formation of carbon dioxide and water. In anaerobic respiration, or fermentation, a substance other than oxygen serves as a hydrogen

acceptor and oxidation is incomplete. The pathway of fermentation varies with the bacterial species, with the type of foodstuff, and in some instances with different environmental conditions. Some products of bacterial fermentation are gases such as hydrogen, carbon dioxide, and methane; acids such as lactic acid, pyruvic acid, succinic acid, acetic acid, formic acid, propionic acid, and butyric acid; alcohols such as ethyl alcohol, propyl alcohol, isopropyl alcohol, and butyl alcohol; and amines and other amino acid residues.

The heterotrophic bacteria do not obtain energy in a single step from the substrate oxidized, but from many consecutive oxidation-reduction reactions, each of which is catalyzed by a specific respiratory enzyme. The respiratory enzymes in bacteria are of the same types as those found in the higher plants. Oxidations of all types generate adenosine triphosphate, and the energy stored in this highly labile high-energy compound is utilized in almost every type of biological work.

IMPORTANCE OF BACTERIA TO MANKIND

Bacteria are of prime importance to mankind since they exert both deleterious and beneficial effects upon human life. Some of these effects are direct, others are indirect. The relations of bacteria to man may be described as follows.

1. Putrefaction and Decay. Putrefaction is the anaerobic decomposition of proteins. It results in the production of such substances as hydrogen sulfide, ammonia, carbon dioxide, hydrogen, and organic acids. Decay is the aerobic decomposition of any organic material into simpler substances (H_2O, CO_2, NH_3, etc.) by the action of bacteria and other fungi without the concomitant production of malodorous compounds. The result of these processes is the return, to the air and soil, of chemical substances in a form available to plants. The organic matter of the dead bodies of plants and animals would accumulate and encumber the earth in the absence of putrefaction and decay.

2. Fermentation. The anaerobic decomposition of carbohydrates is termed fermentation. Bacterial fermentations are of economic importance because many of the products are of industrial value. Examples of such products are acetone, butyl alcohol, lactic acid, and ethyl alcohol.

The commercial production of vinegar involves bacterial action. In the first step carbohydrates undergo fermentation to ethyl alcohol through the action of yeasts. In the second step aerobic bacteria oxidize the alcohol to acetic acid.

The production of silage, a food of high nutritive value for cattle when green plants are not available, involves bacterial metabolism. Organs of green plants, especially the stems and leaves of corn, are cut and packed into a silo. The aerobic respiration of these green plants soon consumes the oxygen present. Certain bacteria then ferment the carbohydrates which are present in the stems and leaves. Lactic acid and other organic acids are elaborated, and they prevent the spoiling of the fodder by putrefactive bacteria. They also prevent undesirable fermentations and inhibit the growth of molds.

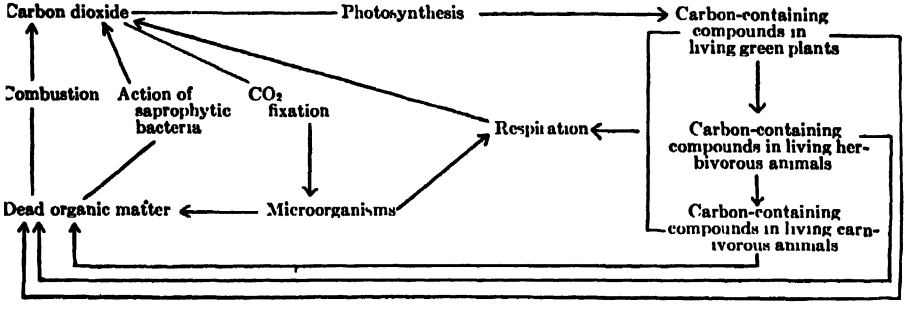
3. The Nitrogen and Carbon Cycles. Since the marine cycles of these elements are not fully known, only their terrestrial cycles will be considered. These cycles are the pathways by which carbon dioxide and nitrate are utilized by green plants to synthesize organic materials necessary for the nutrition of heterotrophic organisms and by which these organic materials are decomposed to yield carbon dioxide and nitrate. Both cycles begin with the manufacture of organic compounds by autotrophic organisms. Many of these compounds are synthesized by green plants and are used for the nutrition of heterotrophic organisms. From atmospheric carbon dioxide and from water, nitrates, and other inorganic ions of the soil, green plants are able to synthesize the organic compounds found in protoplasm.

The quantities of carbon dioxide in the air and of nitrate in the soil are limited. Were it not for the action of bacteria and other fungi, these compounds would be locked up in organic combination and thus become unavailable for succeeding generations of plants. The decomposition of dead plant and animal bodies largely by bacterial action returns carbon dioxide to the atmosphere and nitrate to the soil.

The carbon cycle (Cycle 1, Table 7) is quite simple. It begins with the synthesis of organic compounds by green plants. Carbon dioxide is thus locked into organic combination. The green plants are ingested by herbivorous animals, and they in turn are eaten by carnivorous animals. Ultimately the green plants unconsumed by animals and the animals themselves die. Through the action of sapro-

phytic bacteria on these dead organisms, carbon dioxide is returned to the atmosphere. In addition, aerobic respiration by plants and animals contributes to the quantity of carbon dioxide in the air.

Table 7. CYCLE 1: THE CARBON CYCLE



The nitrogen cycle (Cycle 2, Table 8) will be considered only in its broad biological applications. The nitrogen which is to enter into the composition of proteins and other nitrogenous compounds in the green plant is absorbed from the soil mainly in the form of nitrates in solution. The decay of plant and animal proteins effected by saprophytic soil bacteria returns nitrogen to the soil in the form of ammonia. The process is termed *ammonification*. The ammonia is not readily utilized by plants. Ammonia reacts with soil water to form ammonium hydroxide, which in turn reacts with various chemical substances in the soil to form ammonium salts.

Table 8. CYCLE 2: THE NITROGEN CYCLE

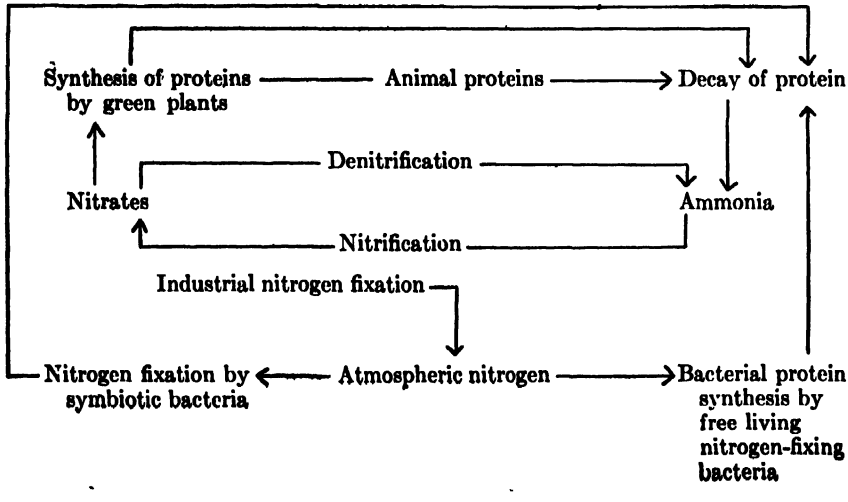


TABLE 10. CHEMICAL AGENTS IN DESTRUCTION OF BACTERIA

Inorganic compounds of heavy metals:	
(*a*) Bichloride of mercury	For disinfection of arms and hands, catheters, clinical thermometers, etc.
(*b*) Silver nitrate	For installation into the conjunctival sac as a prophylactic against gonococcal infection of the conjunctiva in the newborn
(*c*) Copper sulfate	To control the growth of algae in water supplies
Halogens and halogen compounds:	
(*a*) Chloride of lime (calcium hypochlorite)	For the disinfection of inanimate objects and excreta
(*b*) Chlorine gas	As a disinfectant in the treatment of drinking water, water in swimming pools, and sewage
(*c*) Chloramines	As antiseptics in the treatment of infected wounds
(*d*) Tincture of iodine	As an antiseptic in the home for the treatment of minor wounds and for preoperative sterilization of the skin
Dyes	In medicine as antiseptics and in bacteriology to separate bacteria
Phenol (carbolic acid)	For disinfection of excreta
Ethyl (grain) alcohol	To disinfect clinical instruments or the site of injection or surgery
Hydrogen peroxide	Preoperative skin disinfection
Detergents or wetting agents (e.g. Zephiran chloride)	Treatment of infected wounds, to preserve the sterility of surgical instruments, and disinfection of skin and mucous membranes
Organic mercurials (Mercurochrome, Merthiolate, etc.)	As antiseptics and for the preservation of serums and vaccines
Formaldehyde	
(*a*) In aqueous solution	As a germicide and for the preservation of animal tissues
(*b*) As a gas	As a fumigant

organisms on the skin and mucous membranes and in superficial wounds. A *chemotherapeutic* agent is a substance most generally employed to exert antimicrobial action after entrance into the circulating fluids of the animal body. All the terms defined, except sterilization, are relative, since an agent that is bactericidal or germicidal in one concentration may be only bacteriostatic (inhibitory) in another concentration.

Table 11. CHEMOTHERAPEUTIC DRUGS (SYSTEMIC ANTI-INFECTIVES)

Isoniazid	Used clinically in the treatment of tuberculosis
Sulfonamides	Most effective in the treatment of infections caused by Gram-positive and Gram-intermediate cocci
Antibiotics	See text of this chapter

The more prominent physical methods (Table 9), chemical agencies (Table 10), and chemotherapeutic drugs (Table 11) employed to destroy bacteria or reduce their number and their application are shown in tabular form on the preceding pages.

Bacteriophages. The bacteriophages or phages (Fig. 18.3) are a group of viruses parasitic on bacterial organisms. Their range of effect on the bacteria cell varies from entrance into the cell and multiplication therein, with subsequent complete dissolution of the cell, to entrance into the cell and multiplication therein, with no perceptible

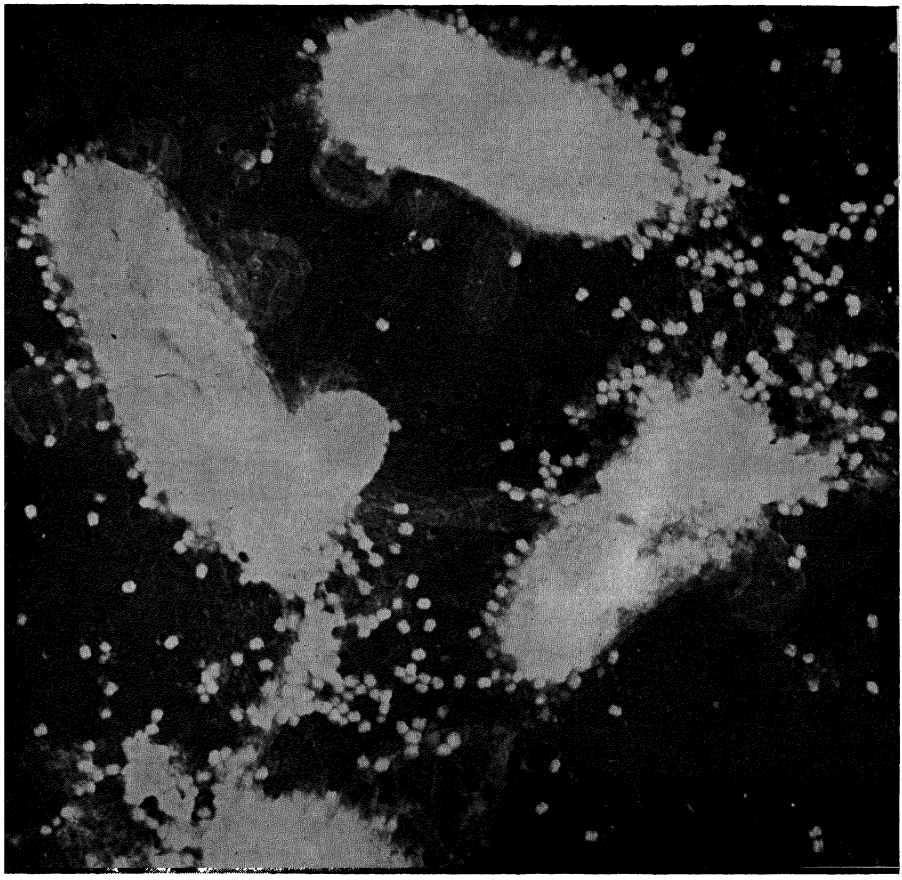


FIG. 18.3 Electron micrograph of *Escherichia coli* after infection with phage. There are three bacilli in the this micrograph and each of them is undergoing lysis. The phage appear as small spherules. (Courtesy, Dr. George B. Chapman and Dr. James Hillier, Department of Biology, Princeton University, and RCA Laboratories Division, Princeton, New Jersey.)

damage to the cell. Phages exhibit a high degree of specificity, often acting on a single strain of bacteria within a species.

Ultrafiltration, electron microscopy, and other studies show that some phages are more or less spherical in shape. Others are rod-shaped particles, and a few are spermatozoon-like in shape, with a large head-like part and an elongated tail-like part. Phages range in size from approximately 8 to approximately 215 millimicrons. Their number is enormous and their distribution parallels that of their hosts. They occur in feces, sewage, insects, soil, and decaying plant material. Chemical analysis reveals that they contain protein and desoxyribonucleic acid.

The in vitro destruction of host bacteria by phages led to the notion that phages could be used as therapeutic agents in the treatment of bacterial infections. Up to the present day their use to combat infectious diseases has not met with success. Nevertheless, they are of practical value in the typing of certain species of bacteria.

Chapter 19

VIRUSES AND RICKETTSIAE

VIRUSES

We can define viruses (formerly called "filterable viruses") as submicroscopic, particulate, antigenic, amphoteric, obligately parasitic, infectious entities endowed with genetic continuity and mutability and capable of entering into, and multiplying only in, specific living plant or animal cells. This definition is not correct in its entirety since the largest viruses can be observed with the light microscope. Although general agreement does not exist as to whether any or all of the viruses are chemical or biological entities, many biologists consider them to be microorganismal in nature. However, the question as to whether they are animate or inanimate is still a biological enigma. Submicroscopic microorganisms, such as the pleuropneumonia organisms do exist, but they differ from the viruses in that they they are free living and have well-defined nutrient requirements for growth. Viruses in the free state seem to be metabolically inert.

With reference to size, tobacco necrosis virus, one of the smallest, is a sphere approximately 17 millimicrons in diameter. Psittacosis (parrot fever) virus, one of the largest, is spherical in shape and has a diameter of over 400 millimicrons. Chemical analysis of one of the larger viruses, such as vaccinia or cowpox virus, reveals the presence of water, nucleoprotein and other proteins, phospholipids, cholesterol, neutral fat, carbohydrate, copper, biotin, riboflavin, catalase, lipase, ribonuclease, desoxyribonuclease, phosphomonesterase, and phosphodiesterase. The enzymes enumerated are probably compounds of host origin adsorbed onto the virus. The host cell apparently provides essential enzyme systems for the viral metabolic mechanism. A small virus, such as the tobacco mosaic virus, does not possess the chemical complexity of the vaccinia virus. A complex nucleoprotein can be crystallized from the juice of plants infected with tobacco mosaic

virus which, from all evidence, appears to have some identity with the virus itself.

The viruses are commonly divided into three groups, the bacterial viruses (phages Fig. 18.3), the plant viruses (Fig. 19.0), and the animal viruses (Fig. 19.1). Animal viruses may be classified according to the tissue which they most specifically affect. The viruses such as those which cause poliomyelitis and rabies affect the nervous system and are said to be *neurotropic*. The viruses which are the causative agents of measles and chickenpox affect the skin and are termed

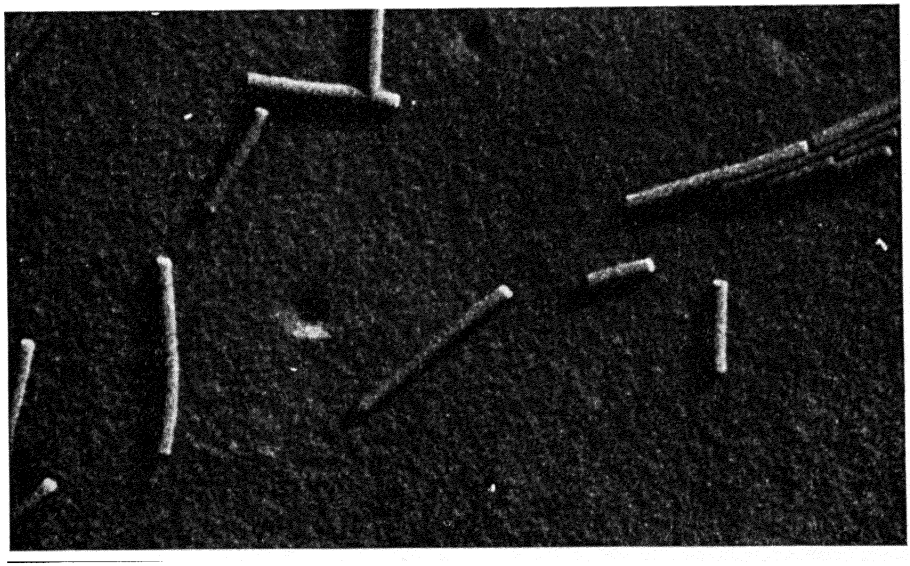


FIG. 19.0 Electron micrograph of tobacco-mosaic virus. (Courtesy, Dr. C. A. Knight and Dr. Robley C. Williams, Virus Laboratory, University of California, Berkeley, California.)

dermotropic. The *viscerotropic* viruses, such as the hog cholera virus, are so called because they affect the internal organs or viscera. *Pneumotropic* viruses attack the lungs. The *pantropic* viruses are those which affect several types of tissue. Bacterial viruses are known to exist for almost all bacteria. The only invertebrate animals in which virus diseases have been demonstrated are the insects. In inframammalian vertebrates, virus diseases have been observed in fish, in amphibia, and in birds. Among mammals they have been observed in man and most domestic animals.

In the plant kingdom, virus diseases have been recognized only

in the flowering plants. Some of the plants of economic importance affected by virus diseases are potato, tobacco, sugar beet, sugar cane, bean, cucumber, and peach. Practically all of the plant viruses and many of the animal viruses are transmitted by arthropod vectors.

Often plant and animal cells continue to divide after virus infection, and this abnormal proliferation of host cells may lead to the formation of abnormal growths called *tumors* or *neoplasms*. There is good reason to implicate viruses as the etiological agents of such tumors. In man, skin, laryngeal, and genital papillomas (warts) are caused by viruses.



FIG. 19.1 Electron micrograph of influenza virus (strain PR8). (Courtesy, Dr. C. A. Knight and Dr. Robley C. Williams, Virus Laboratory, University of California, Berkeley, California.)

Some of the familiar virus diseases of man are: influenza, common cold, mumps, poliomyelitis, infectious hepatitis, rubella (German measles), herpes simplex (cold sore), herpes zoster (shingles), and verrucae (warts). With the exception of herpes zoster, transmission of the virus diseases enumerated is by contact. With respect to herpes zoster, the mode of transmission is in doubt.

RICKETTSIAE

The rickettsiae are a group of small, pleomorphic, obligate parasitic, bacteria-like microorganisms widely distributed among the members of the class Insecta and the class Arachnoidea of the phylum Arthropoda. They occupy a position between the bacteria and the viruses and in their morphological characteristics resemble the bacteria more than they do the viruses. The rickettsiae differ from the bacteria in their inability to grow on inanimate media, in their resistance to staining with aniline dyes, and in their intimate association with arthropod life. They differ from the viruses in their larger size and microscopic visibility, in their possession of metabolic systems (e.g., oxidation and transamination of glutamic acid) not as yet demonstrated in viruses, and in their inability, with one exception, to pass through bacteria-retaining filters. They resemble the viruses in their growth requirements, since they grow only in the presence of living cells, with the exception of *Rickettsia melophagi*, a nonpathogenic form found in the sheep tick (*Melophagus ovinus*). The pathogenic rickettsiae proliferate within cells.

The rickettsiae exhibit a wide range in size and shape. Some are spherical, while others are coccobacillary, bacillary, diplobacillary, streptobacillary, or filamentous microorganisms. All are Gram-negative in stainability, but they can be stained with Giemsa's or Machiavello's stain.

The diseases of man (Table 12) caused by the rickettsiae are transmitted to man by various arthropod vectors. The cells lining the intestinal tracts of these vectors are parasitized by the rickettsiae, but in most cases the microorganisms are not pathogenic to the arthropod host. The diseases are transmitted to man either in the feces or the saliva of the vector. Some of the rickettsial diseases of man are shown in Table 12.

Vaccines appear to be of value in the immunization of humans exposed to rickettsial infection. Para-aminobenzoic acid and such

Table 12. SOME RICKETTSIAL DISEASES OF MAN

Disease	Pathogen	Vertebrate Reservoir	Vectors
Epidemic typhus fever	*Rickettsia prowazeki* var *prowazeki*	Man	*Pediculus humanus* (human louse)
Endemic or murine typhus fever	*Rickettsia prowazeki* var *mooseri*	Rat	*Xenopsylla cheopis* (rat flea) *Polyplax spinulosa* (rat louse)
Scrub typhus fever (Tsutsugamushi disease)	*Rickettsia orientalis*	Field mouse and rat	*Trombicula akamushi* (mite) in Japan *Trombicula deliensis* (mite) in Malay and Sumatra
Rocky Mountain spotted fever	*Rickettsia rickettsi* (*Dermacentroxenus rickettsi*)	Wild rodents	*Dermacentor andersoni* (wood tick) in the western United States *Dermacentor variabilis* (dog tick) in the Atlantic region
Q fever	*Rickettsia burneti* (*Coxiella burneti*)	Bandicoot and possibly a number of other rodents	*Hemaphysalis humerosa* (tick) Infection in man occurs by inhalation of infected dried tick feces

antibiotics as Aureomycin, Chloromycetin, and Terramycin are of therapeutic value in the treatment of rickettsial diseases. The most important control measure to prevent the spread of these diseases are those which result in the eradication of the specific vectors.

Chapter 20

THE SLIME MOLDS

THE organisms in the class Myxomycetes are commonly referred to as the slime fungi or slime molds, since in the vegetative form they are constituted of slimy, naked masses of multinucleate cytoplasm, generally referred to as *plasmodia.* They are practically world-wide in their occurrence and for the most part are saprophytic on decaying wood and bark, on dead leaves, and on nonliving organic matter in damp soil. There are a few forms which are parasitic on lettuce, cabbage, and potatoes.

The taxonomic position of the slime molds, however, is still controversial. Because of certain cytological aspects of the plasmodium, their amoeboid mechanism of locomotion, and their mechanism of feeding, they were frequently classified as primitive animal forms and were originally considered to be members of the order Mycetozoa of the class Sarcodina in the phylum Protozoa. However, because of their manner of reproduction, they are now generally looked upon as more plant-like in nature. Further, because of the absence of photosynthetic pigments, they are considered to be fungal organisms.

As a representative of this class we have selected *Stemonitis* because of its common use in the laboratory study of the Myxomycetes.

Stemonitis. In the vegetative form this slime mold consists of a naked, irregular-shaped mass of protoplasm called the plasmodium. The nuclei are small and numerous, and are distributed through the cytoplasm without cellular demarcation. There is no cell wall circumjacent to the peripheral limits of the plasmodium itself. In brief, the plasmodium may be regarded as a single, multinucleate protoplast. However, the cytoplasm is differentiated into a clear, narrow, outer portion called the *ectoplasm* and a granular inner portion termed the *endoplasm.* The endoplasm is not static, but flows through the central part of the plasmodium owing to the unique manner in which

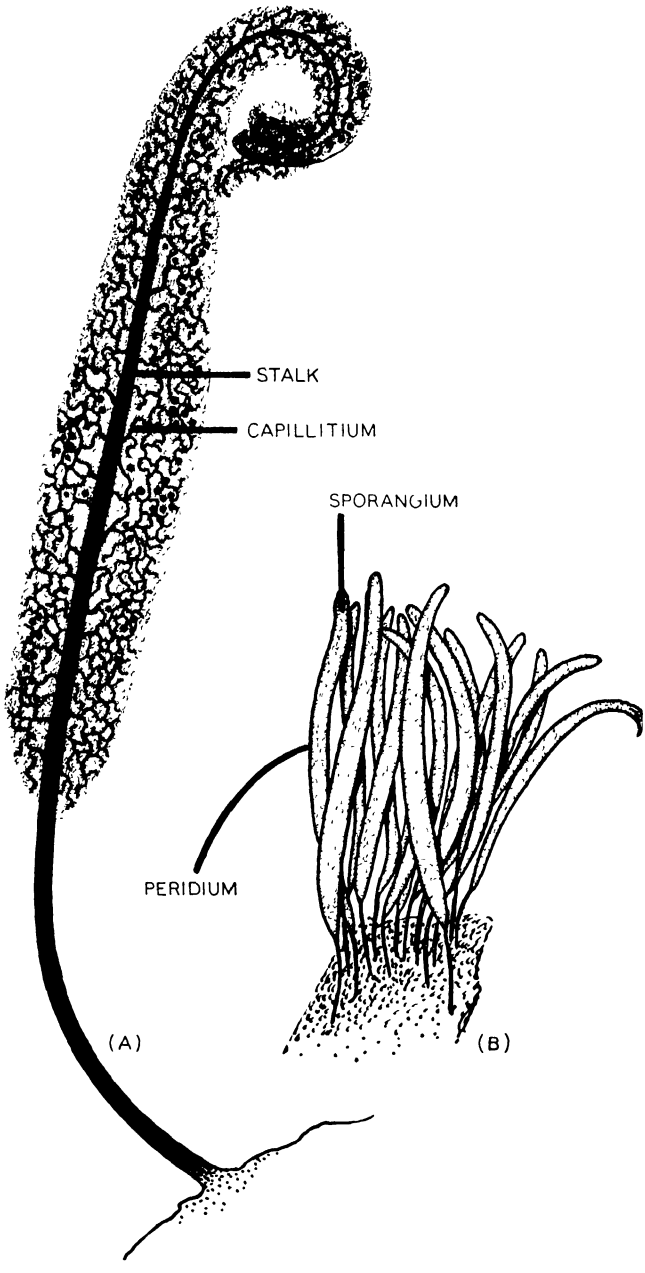


FIG. 20.0 (A) Magnified view of the capillitium within the sporangium of *Stemonitis*. The spores appear as small black dots within the meshes of the capillitium. (B) Group of sporangia of *Stemonitis*.

it solates and gelates in different areas of the plasmodium. The flow of endoplasm, by means of its propulsive force, eventuates in the projection from the plasmodium of successive protoplasmic processes or pseudopodia. The plasmodium thus creeps along over the substrate by virtue of its progressively advancing pseudopodia. Again, the plasmodium engulfs very small particles of wood or dead leaves between any two pseudopodia, which subsequently become continuous with one another at the mutual point of contiguity between their free ends. The particle of dead wood or leaf thus comes to be contained within a vacuole wherein the cellulose and hemicellulose of the particle are digested into simple and diffusible sugars. The latter are absorbed from the vacuole and utilized by the plasmodium either in synthesis or in its respiration. The undigested part of the particle is ejected through the plasma membrane of the plasmodium, the ruptured part of the membrane being quickly reformed after the discharge of the undigested remnants of the particle. Up to this point the plasmodium of *Stemonitis* has behaved in much the same manner as the amoeba; but here the similarity ends, for its mechanisms of reproduction are very definitely plant-like.

In its vegetative form the plasmodium of *Stemonitis* avoids light and is consequently found on the shaded side of its substrate. At the time of reproduction, however, the plasmodium moves to a well-lighted and drier area of its substrate. Here the plasmodium generally fragments. From each fragment there develops a stalked sporangium. The stalk extends through the central portion of the sporangium (Fig. 20.0A). The sporangial wall, formed by waste material from the protoplasm and called the *peridium,* initially encloses a multinucleate mass of protoplasm. This mass of protoplasm undergoes cleavage as a result of which there are formed numerous uninucleate spores, each with a definite cellulose wall. These spores are generally entangled in a network of interbranching threads called the *capillitium* (Fig. 20.0B). The peridium finally ruptures upon drying, and the spores are dispersed by the wind. Water is necessary for the germination of the spores. On germination the wall of each of the spores discharges an amoeboid protoplast which subsequently develops a cilium to become a zoospore. The zoospores, subsequently acting as gametes, fuse in pairs to form zygotes. The fusion nucleus of the zygote, by a series of successive mitotic divisions, gives rise to numerous small nuclei as the zygote grows into a plasmodium.

It has been asserted that the nucleus of each spore divides meiotically, three of the haploid nuclei degenerating. The spore, then, as it leaves the sporangium, would be haploid. The zygote resulting from the fusion of the haploid uniciliate zoospores (functioning as gametes) would mark the beginning of the diploid or sporophyte generation, and thus the plasmodium would also be diploid.

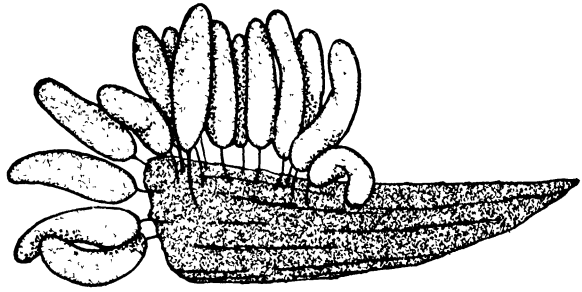


FIG. 20.1 Sporangia of *Arcyria*, a slime mold.

Plasmodiophora brassicae. Perhaps the most widely known parasitic slime mold is *Plasmodiophora brassicae*, the causative organism of the club-root disease in cabbage and other cruciferous plants (cauliflower, turnip, radish, and rutabaga). This disease is characterized by a hypertrophy of the root in the form of small and large tuberculose swellings. A summary of the life cycle of this organism is presented below.

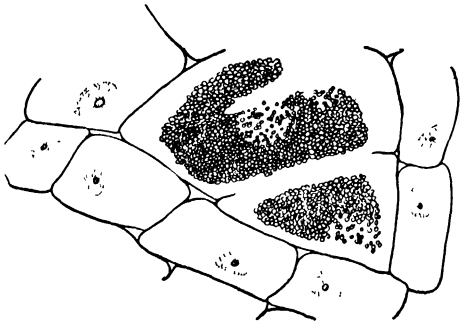


FIG. 20.2 Spore masses of *Plasmodiophora brassicae* in the cortical parenchyma of the root. These are the infective spores formed at the end of the cycle in the infected root.

The cabbage root becomes infected during the seedling state of the plant. The uniciliate zoospore, resulting from the germination of the spore in the contaminated soil, sheds its cilium and becomes an amoeboid protoplast. The latter penetrates a root hair of an epidermal cell and therein develops into a small multinucleate plasmodium. The plasmodium fragments into uninucleate protoplasts, each of which secretes a wall around itself. Each of these cells eventually divides to form an eight-nucleate mass which

subsequently undergoes cleavage to form uniciliate gametes. Fusion of the gametes follows, with the zygotes developing eventually into multinucleate plasmodia. The plasmodia pass through the cortical area of the root and thus attain its cambial layer, wherein they migrate vertically throughout the root. Finally these plasmodia leave the cambial layer and return to those cortical cells rich in food reserve. Here the plasmodia apparently provide a sort of stimulation to the cortical cells, as a result of which the cortical cells divide rather rapidly or become greatly enlarged. Both the division of the cortical cells and their enlargement ultimately effectuate tuberculated swellings of the root. The nuclei of each plasmodium undergo meiosis, after which the plasmodium becomes greatly vacuolated. Fusion of the vacuoles results in the fragmentation of the plasmodium into a number of uninucleate masses, each of which becomes rounded by a distinct wall to form an infective spore (Fig. 20.2).

Economic Aspects. Club-root disease has spread to some thirty-six states of this country. Primarily because of methods of control it is no longer the scourge that it was originally. When measures of control are not successful, however, the farmer is faced with a twofold loss: the loss of his crop of cabbage or turnips, as the case may be, is compounded by the fact that he cannot use for several years the contaminated soil for the replanting of any susceptible cruciferous plants.

Chapter 21

THE ALGAL FUNGI

THE Phycomycetes are the algal fungi, so-called because of their resemblance in both morphology and reproduction to certain green algae, principally *Vaucheria.* For the most part the hyphae are multinucleate, tubular, and nonseptate, with the exception of those parts of the hyphae on which are developed reproductive structures.

The Phycomycetes are generally grouped on the basis of their characteristic reproductive mechanisms into two subclasses, Oomycetes and Zygomycetes. The Oomycetes are heterogamous and reproduce asexually by zoospores. This subclass includes the *Saprolegnia,* or water molds; *Albugo,* or the white rusts that parasitize many of our flowering plants; and the downy mildews that are so destructively parasitic to the grape, the potato, the onion, and the cucumber. The Zygomycetes, on the other hand, are isogamous and reproduce asexually by nonmotile spores. This subclass is composed of the black molds, saprophytic on dead organic matter rich in carbohydrates and classically represented in common bread mold, *Rhizopus nigricans.* Also placed in this subclass are the fungal organisms that parasitize flies, plant lice, and the larvae of butterflies and beetles.

Saprolegnia. The greater number of the species in this genus are saprophytic on the plant and animal debris that occurs in fresh water. A rather limited number have been reported as being parasitic on algal organisms, notably the diatoms. Perhaps the best-known parasitic form is *Saprolegnia parasitica,* which attacks fish and is a matter of no small concern in fish hatcheries. Some species of *Saprolegnia* have been found in the soil. However, the morphology of these plant organisms and the fact that zoospores are produced in their life cycle would seem to favor the idea that most species of *Saprolegnia* are aquatic in their occurrence. In the laboratory pure cultures of *Saprolegnia* are grown in water on hemp seed. The coenocytic

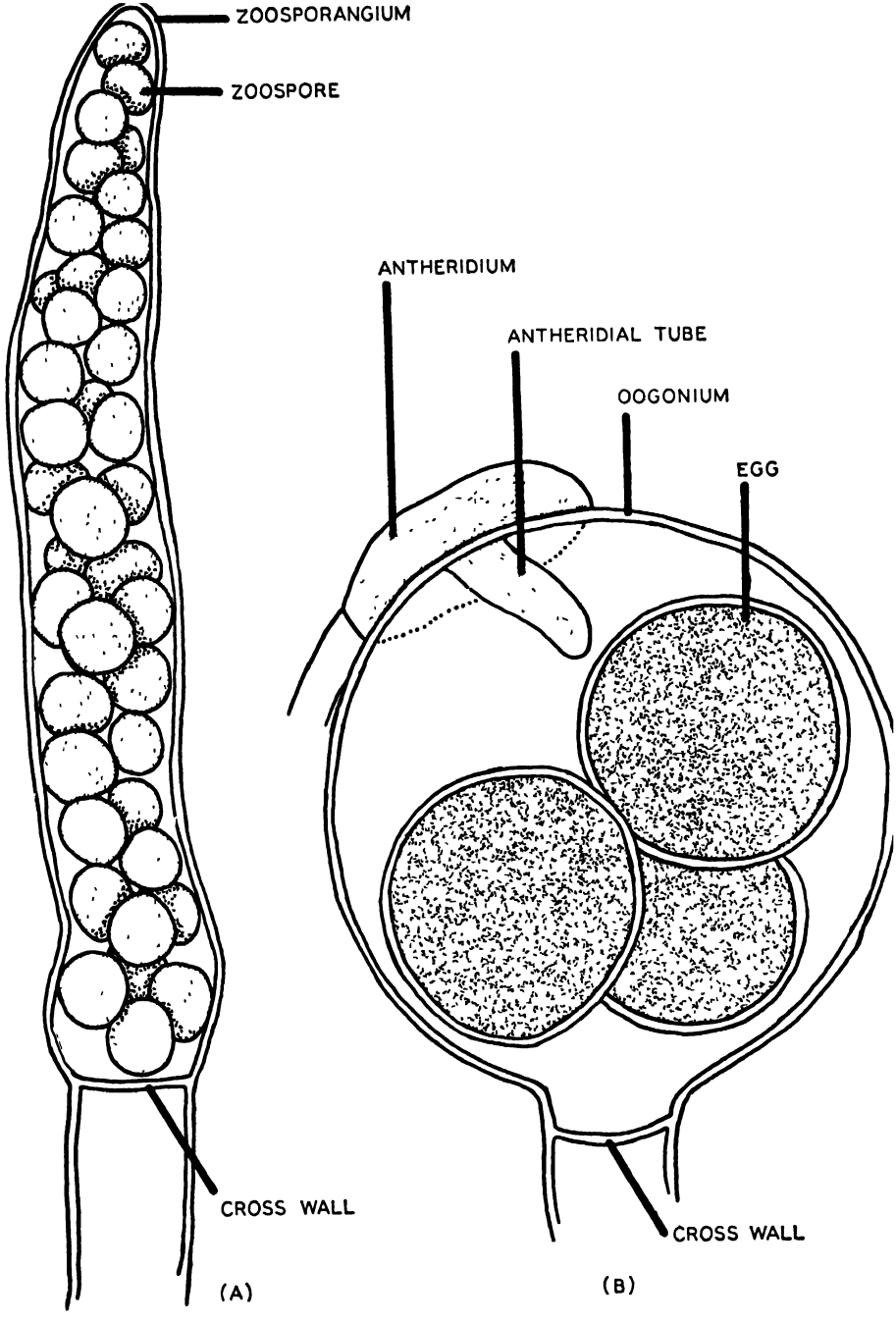


FIG. 21.0 *Saprolegnia:* (A) asexual reproduction; (B) sexual reproduction.

hyphae intertwine themselves into a fairly close reticle so that the mycelium in macroscopic aspect presents itself as a sort of white mat on the hemp seed.

Asexually *Saprolegnia* reproduces by means of zoospores (Fig. 21.0A). Generally the terminal part of a hypha, after having enlarged slightly, becomes demarcated from the rest of the hypha by a transverse septum to form a zoosporangium. Subsequently the multinucleate cytoplasm undergoes cleavage to form uninucleate protoplasts. Each uninucleate protoplast metamorphoses into a biciliate zoospore. The zoosporangium, which is at this time either fusiform or cylindrical, develops an aperture at its free end for the discharge of the biciliate zoospores. These zoospores, pyriform in shape and biciliate at their apical ends, swarm about for a while in the water. Finally they come to rest and withdraw their cilia. Each zoospore then encysts itself by the secretion of a wall. Ultimately through an opening in the latter cyst there is liberated a secondary zoospore. This secondary zoospore is reniform and bears two cilia on its concave side. The successive production of two different types of zoospores by a single fungal organism is termed *diplanetism*. The functional significance of diplanetism in the life cycles of the *Saprolegnia* is not known. In any event the secondary zoospores, upon the attainment of suitable substrate, germinate to form a mycelium. While part of this mycelium is contained within the substrate itself, a good portion of the mycelium is readily discernible as a white matted overgrowth investing the substrate.

Sexual reproduction (Fig. 21.0B) entails the formation of oogonia and antheridia. The oogonium generally is initially formed as a globular expansion of the terminal portion of a lateral branch of a main hypha. Shortly thereafter a cross wall separates the cytoplasm of the oogonium from that of the hypha. At this stage central vacuolation of the oogonium restricts its multinucleate cytoplasm to the periphery. Centrifugal cleavage of the oogonial cytoplasm results in the formation of a variable number of sphere-shaped multinucleate eggs. Each egg finally becomes uninucleate through the degeneration of all except one of its nuclei. The mature oogonium is now a definitely spherical structure containing several rounded uninucleate eggs. In the meantime, generally in close approximation to the already developed oogonium, the end of another hyphal branch becomes slightly enlarged to form an antheridium, the multinucleate cytoplasm of

hyphae, or *sporangiophores;* and the horizontally disposed hyphae, or *stolons.* The rhizoidal hyphae penetrate the substrate and are functionally concerned in the secretion of carbohydrases and in absorption. The carbohydrases are amylase and maltase. Amylase accomplishes the enzymatic hydrolysis of starch to maltose; the hydrolysis of maltose to glucose is catalyzed by maltase. The glucose, after being absorbed by the rhizoids, may be utilized in the growth of the mycelium or it may be oxidized for its energy content. From the base of the rhizoidal hyphae grow several erect hyphae which, since they become terminally modified into sporangia, are called sporangiophores. Originating also from the base of the rhizoidal hyphae are the horizontal hyphae, or stolons. Each stolon traverses the surface of the substrate for some distance, abruptly turning to invade the substrate where it forms rhizoids, from the base of which, as already described, arise sporangiophores.

For asexual reproduction (Fig. 21.3) a sporangiophore, after having attained a certain height, expands terminally into a globular sporangium. Initially the protoplasmic content of the sporangium is differentiated in such a manner that a relatively nonvacuolated but heavily nucleated mass of protoplasm becomes restricted to the area just beneath the sporangial wall, while a vacuolated protoplasm with considerably fewer nuclei constitutes the central portion of the sporangium. Subsequently the dense, peripherally situated protoplasm is delimited from the vacuolated protoplasm by the development of a cell wall. The peripheral protoplasm represents the fertile area of the sporangium and undergoes cleavage to form numerous multinucleate masses of protoplasm. Each of these protoplasmic masses becomes rounded off and invested by a cell wall to form a multinucleate spore. The central and now dome-shaped area of vacuolated protoplasm remains unmodified and is referred to as the *columella.* As the spores attain maturity, the sporangial wall dries to the point of being very friable, so that very little environmental agitation is required to bring about its rupture. The spores, once liberated, are dispersed by air currents and on coming to rest on suitable substrate germinate to form a mycelium having the characteristics previously described.

The sexual reproduction (Fig. 21.3) of *Rhizopus nigricans* is by conjugation. However, conjugation will not occur unless two different strains of mycelia, referred to as *plus* and *minus,* are grown in the same culture. The plus strain of the mycelium appears to be capable

of a relatively more vigorous growth than the minus strain. If, then, there are a plus and a minus mycelium in the same culture, the erect hyphae of the different strains are observed to form lateral club-shaped protuberances called *progametangia.* These progametangia approximate each other. Subsequently each progametangium is septated by a cross wall. The distal portion of the septated progametangium contains a rather dense protoplasm and is termed the *isogametangium;* the proximal portion embodies a rather vacuolated protoplasm and is called the *suspensor.* The isogametangial walls dissolve at the point of contact and the contents of each isogametangium, sometimes referred to as a *coenogamete,* fuse to form a zygospore. The zygospore is characterized by a spiny, highly resistant wall. After a fairly long period of dormancy, the zygospore germinates by sending forth a short hypha (sporangiophore) at the end of which there is developed, in a manner previously described, a sporangium whence multinucleate spores will be ultimately discharged.

Conjugation between hyphae of different strains, as exemplified in *Rhizopus nigricans* above, is called *heterothallic* conjugation. However, there are species of black mold, such as *Rhizopus sexualis* and *Sporodinia grandis,* in which conjugation is *homothallic;* that is, hyphae of the same strain may be involved in the formation of a zygospore.

Economic Aspects. *Rhizopus oryzae* and *Mucor javanicus* are used commercially in the saccharification of starch to fermentable sugars from which, by virtue of zymase of yeast, ethyl alcohol is produced. *Rhizopus nigricans* can bring about the soft rot of sweet potatoes, traumatic injury and humidity being the predisposing factors. *Rhizopus nigricans* is very frequently involved in the spoilage of fruit. Perhaps the most common example is the infection of strawberries. The strawberries "leak"; that is, they soften and become drippy. *Rhizopus nigricans* often confronts the bacteriologist by contaminating and overgrowing his cultures. Other black molds, *Absidia corymbifera* and *Absidia cornealis,* are capable of pathogenicity in the human subject, the former being involved in a type of bronchomycosis and the latter being associated with corneal lesions.

Chapter 22

THE SAC FUNGI

General Characteristics of the Class Ascomycetes. This class, the largest group of fungal organisms, possesses a septate mycelium. The cross walls of the hyphae are centrally perforated so that protoplasm may stream from cell to cell. Generally the cells of the hyphae which ramify through the tissues of the host are haploid and uninucleate. Gametangia develop on the haploid hyphae. In the life cycle of the Ascomycetes there invariably occurs a sac-shaped sporangium, called an *ascus,* in which are contained four or, more commonly, eight ascospores (Fig. 22.0). The ascus generally represents the enlarged penultimate cell of a binucleate ascogenous hypha that has developed from a fertilized *ascogonium*—the term applied to the female gametangium in Ascomycetes. The ascogenous hyphae are sometimes referred to as the *diploid mycelium.* The ascus when young is binucleate, but the two nuclei soon fuse to form a single diploid nucleus. The latter nucleus, as we shall see below, undergoes meiosis, and the resulting haploid nuclei divide once mitotically; as a result there are produced eight haploid nuclei. Each haploid nucleus ultimately becomes the nucleus of a haploid ascospore.

Reproduction. Asexually the Ascomycetes reproduce by *conidiospores.* A conidiospore is a spore produced by the abstriction of a hypha. The hypha whence such conidiospores are cut off is termed a *conidiophore.* These conidiospores, according to the species of Ascomycete, may be grouped into characteristic morphological patterns.

The sexual processes (Fig. 22.0) of reproduction among most of the Ascomycetes, with the exception of the yeasts, may be presented in a generalized way. The gametangia, as has already been indicated, are produced on the haploid mycelium that ramifies through the tissue of the host. The female gametangium, called an ascogonium, is generally a single cell at the end of a lateral hyphal branch. This

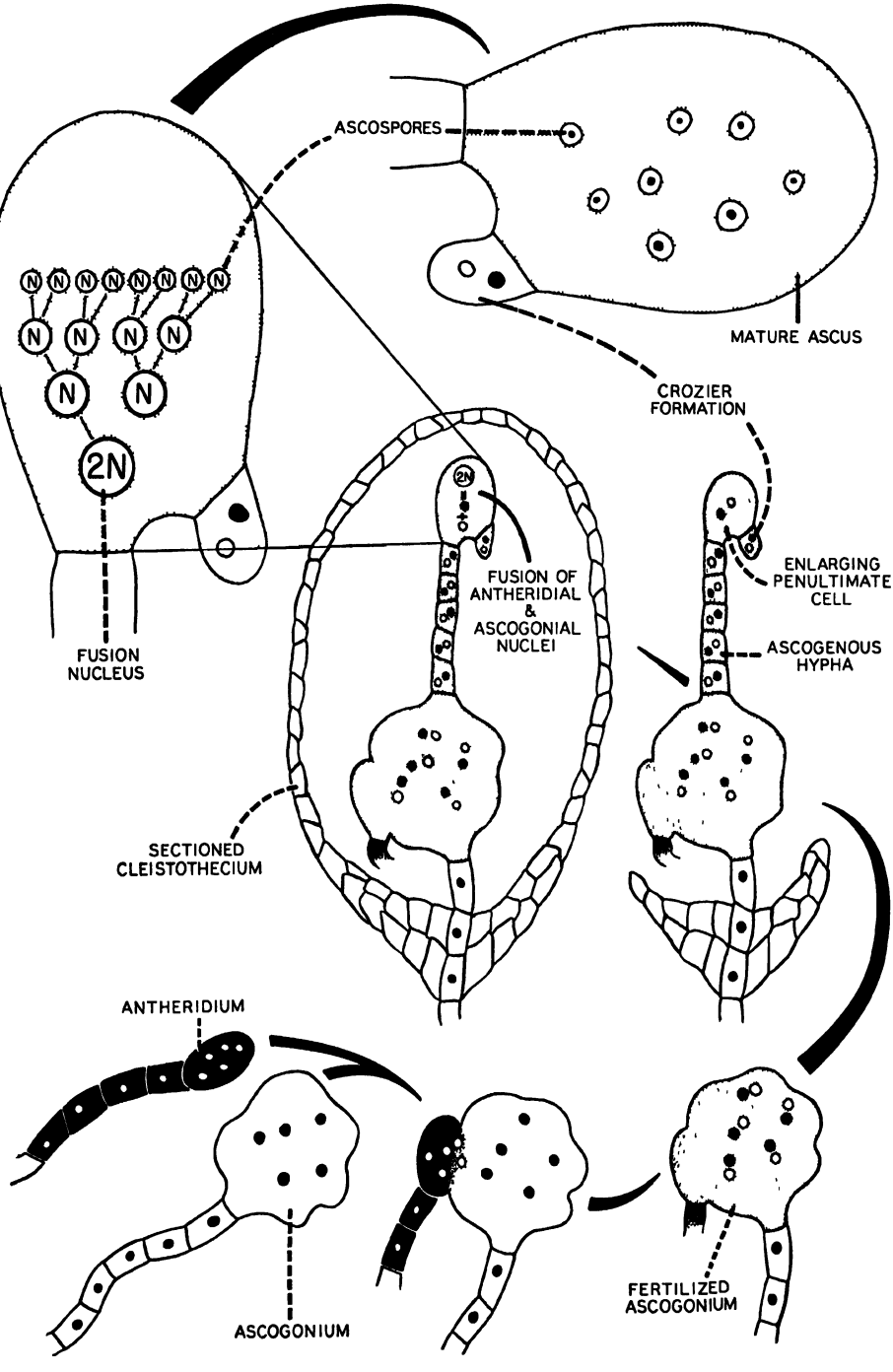


FIG. 22.0 Generalized scheme of sexual reproduction in ascomycetes.

single cell may be uninucleate or it may be enlarged considerably and contain numerous nuclei. Sometimes there may arise from the ascogonium a slender stalk or *trichogyne.* On the other hand, the antheridium, generally elongate in form, develops at the end of another short lateral hypha. Like the ascogonium, it is a single terminal cell, either uninucleate or multinucleate. The antheridia and ascogonia may develop on hyphae of the same mycelium or of different mycelia; that is, a mycelium may be homothallic or heterothallic. In any event, the antheridia come to lie in close apposition to the ascogonia. Assuming that such an apposition of the sex organs has occurred, there is a dissolution of the contacting surfaces of the approximated sex organs. The nucleus or nuclei of the antheridium pass into the ascogonium. The male and female nucleus or nuclei, as the case may be, do not fuse but become aligned in pairs—a male nucleus with a female nucleus. From the fertilized ascogonium there now develop binucleate ascogenous hyphae. The ascogenous hyphae may recurve terminally into characteristic crozier formations, with the penultimate cell of each ascogenous hypha enlarged into a sac-shaped ascus which contains two nuclei. These two nuclei, one antheridial in origin and the other ascogonial, fuse to form a single nucleus. This single nucleus now divides meiotically to form four haploid nuclei, each of which divides so that the ascus embodies eight haploid nuclei. Cleavage of the cytoplasm in the ascus follows. Finally, each nucleus with its vicinal cytoplasm forms into an ascospore. In the meantime the process of fertilization has stimulated the development, from the adjacent haploid mycelium, of a mass of sterile hyphae that enclose the ascogenous hyphae and their asci, either partially or completely. These enveloping hyphae with the asci contained therein are called *fruiting bodies* or *ascocarps.* There are three types of ascocarps: the closed ascocarp, or *cleistothecium;* the ascocarp with ostiolate opening, or *perithecium;* and the open saucer-shaped ascocarp, or *apothecium.*

In the yeasts asexual reproduction, according to the genus being considered, is accomplished either by fission or budding. Sexual reproduction entails conjugation between two haploid yeast cells. The fusion nucleus of the resulting zygote divides meiotically, each of the four haploid nuclei becoming the nucleus of an ascospore. The conjugating cells broaden into a single structure which serves as an ascus for the ascospores.

Classification. The class Ascomycetes is divided into two subclasses:

the Protoascomycetes and the Euascomycetes. In the Protoascomycetes ascogenous hyphae and ascocarps are lacking. The zygote develops directly into an ascus. In the Euascomycetes asci are formed by ascogenous hyphae and are finally contained in ascocarps.

The yeasts will be considered as representative of the Protoascomycetes. The Euascomycetes, a rather large subclass, may be arbitrarily subdivided according to their distinctive ascocarpial characteristics into three large groups. The types of ascocarps are as follows:

CLEISTOTHECIUM (Fig. 22.7). The closed ascocarp occurs in the powdery mildews (*Erysiphe*) and in the blue-green molds (*Aspergillus* and *Penicillium*).

PERITHECIUM (Fig. 22.8). The ostiolate ascocarp is characteristic of the ergot fungus (*Claviceps*).

APOTHECIUM (Fig. 22.9). The open ascocarp is the mark of the cup fungi (*Peziza*).

YEASTS

Occurrence. The majority of yeasts, known from ancient times for their capacity to accomplish the fermentation of sugar, flourish saprophytically on fruits and flower nectar. Yeasts also occur on vegetables, on the leaves of plants, and on the sugary exudates of trees. Yeasts have been isolated from the soil. They have been found on, and in, insects. In fact, insects play a rather important role in the dissemination of yeasts. Some yeasts are known to live a symbiotic existence in the body cavities of certain insects. In brief, yeasts are as common in their distribution as the hexose sugars which they ferment.

Cytological Aspects. Yeasts as a whole do not lend themselves to inclusive definition. For the practical purposes of this text, however, yeasts are regarded as unicellular organisms that are uninucleate and larger in size than bacteria. Mycelial formation is suppressed.

Yeast cells (Fig. 22.1A) may be oval, spherical, or even ellipsoidal in shape. The wall of the cell is composed of one or more polysaccharides. Its exact composition awaits further elucidation. The protoplast has a definite nucleus which is rendered microscopically discernible by the use of special stains. While the young cell is practically devoid of either vacuolation or granulation, the cytoplasm of the older cell is characterized by several vacuoles and two types of granules. Vicinal to the nucleus of the older cell is a fairly large

vacuole containing *volutin*. This volutin, generally in liquid form though some of it may be coagulated into granules, is actually ribose-nucleic acid, to be distinguished from the desoxyribonucleic acid of the nucleus. Volutin is at present looked upon as a reserve material which is utilized in some manner during sporulation. The other vacuoles are generally very refractile and have been demonstrated to con-

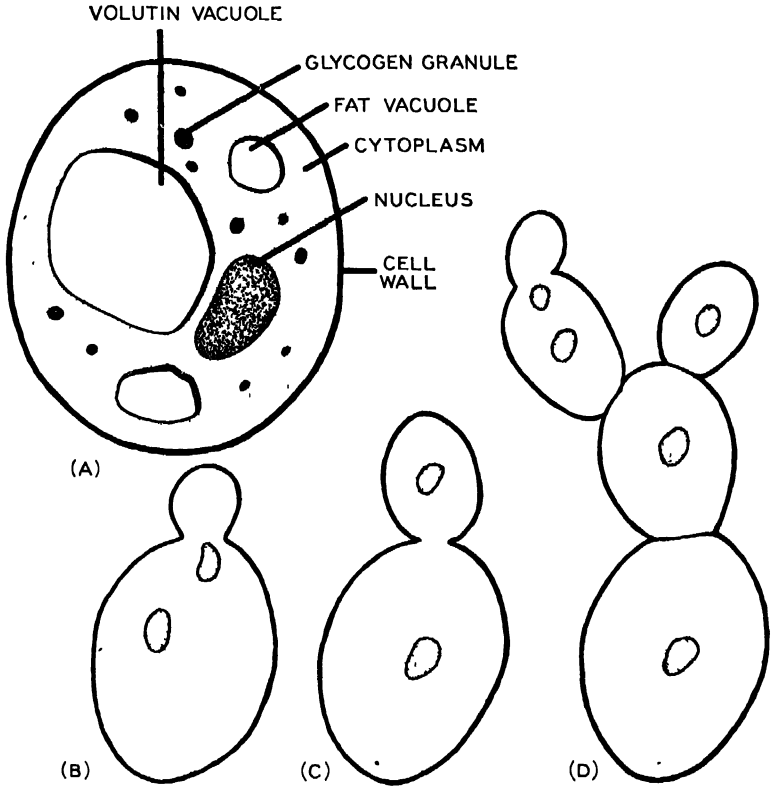


FIG 22.1 Yeast (*Saccharomyces cerevisiae*): (A) mature cell; (B–C) bud development, (D) chain-like disposition of buds.

tain fatty substances. Initially the vacuoles are rather small, but as the cell grows larger, they fuse into one large vacuole. The granules which occur in the cytoplasm are of two distinct types: the rounded granules of glycogen and the angular albuminoid granules. Obviously the fat, glycogen, and albuminoid substances represent food reserves.

Reproduction. Asexually yeasts may reproduce by binary fission as in *Schizosaccharomyces*, a type of yeast that thrives on Jamaican

and Formosan molasses. The various species of *Saccharomyces*, which include the important industrial yeasts, reproduce by budding. Budding (Fig. 22.1B) involves the evagination of the cell wall into a small outgrowth or bud. In the meantime the nucleus of the parent cell has divided mitotically. One of the daughter nuclei migrates into the bud (Figs. 22.1B and C). The bud constricts completely at its point of origin and there finally result two daughter cells of unequal

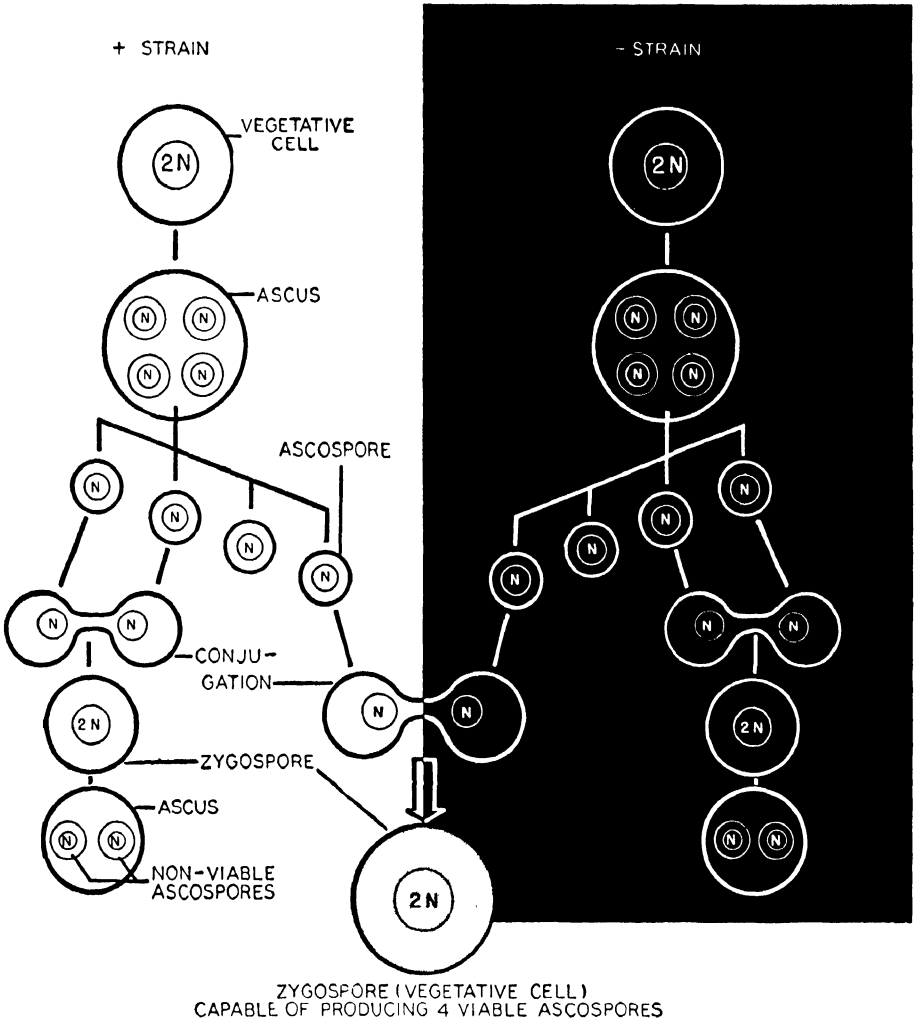


FIG. 22.2 Conjugation in yeast (*Saccharomyces cerevisiae*). The opposite strains have been visualized on different backgrounds (see text for details).

size. Generally, however, the smaller daughter cell does not become immediately detached from the parent cell, but may itself bud (Fig. 22.1D) so that budding yeast cells very often present themselves in a chain-like disposition.

Sexual reproduction (Fig. 22.2), when it occurs among yeast cells, is accomplished by conjugation. Both homothallic conjugation (between cells of the same strain) and heterothallic conjugation (between cells of different strains) occur. *Schizosaccharomyces octosporus* exemplifies homothallic conjugation. Here two haploid cells of the same strain put forth minute protuberances which fuse to form a conjugation tube. The nuclei fuse in the conjugation tube. The conjugation tube widens so that the two conjugants become resolved into a single barrel-shaped ascus. The fusion nucleus undergoes meiosis to form four haploid nuclei, each of which subsequently divides equationally. Upon cleavage of the cytoplasm in the ascus, each of the eight haploid nuclei becomes ultimately the center of an ascospore. Each ascospore germinates in the ascus by dividing into two daughter cells. The daughter cells escape to become the ordinary vegetative cells of *Schizosaccharomyces octosporus*. Finally four ascospores may develop in a cell without previous conjugation; that is, the ascospores may develop parthenogenetically. On the other hand, heterothallic conjugation (Fig. 22.2) has been demonstrated in the life cycle of *Saccharomyces cerevisiae*, commonly referred to as *brewers' yeast*. In *Saccharomyces cerevisiae* the ordinary vegetative cell is diploid and generally ellipsoidal in shape. At the time of sporulation the nucleus of this diploid cell divides meiotically, and there are delimited within the cell (now the ascus) four haploid ascospores. These ascospores generally become somewhat enlarged before their liberation from the ascus. The ascospores germinate to form relatively smaller, rounded, haploid yeast cells. These haploid cells represent two different strains, called *plus* and *minus*. When conjugation takes place between plus and minus haploid cells, the resulting zygote (Fig. 22.2) will ultimately yield on sporulation four viable ascospores. On the other hand, should conjugation between two cells (Fig. 22.2) of the same strain occur, the zygote yields only two nonviable ascospores. In other words, heterothallic conjugation must take place so that viable ascospores may be produced for the continuation of the life cycle of *Saccharomyces cerevisiae*. Among some species of *Saccharo-*

myces, the diploid cell produces four haploid ascospores. These ascospores, presumably of different genetical strains, conjugate in pairs within the ascus to form ultimately two diploid vegetative cells.

Economic Importance. The economic aspects of yeast are the outcome of the enzymatic properties of the yeast cell itself. Yeast is known to secrete at least two extracellular enzymes, invertase and maltase. Invertase catalyzes the hydrolysis of sucrose into invert sugar (glucose and fructose); maltase effects the enzymatic hydrolysis of maltose into glucose. However, the really significant feature in the enzymic make-up of yeast is its intracellular enzyme complex called *zymase.* Zymase accomplishes the fermentation of hexose sugars, either glucose or fructose. This anaerobic breakdown of hexose sugars, as visualized and tabulated in Chapter 9, Plant Metabolism, involves the anaerobic glycolysis of hexose sugar to pyruvic acid, the decarboxylation of pyruvic acid to acetaldehyde and carbon dioxide, and finally the reduction of the acetaldehyde to ethyl alcohol. From the fermentation of invert sugar, the yeast cell obtains the energy to maintain its vital activities but is not changed during the process. The by-products of this action, often referred to as alcoholic fermentation, are ethyl alcohol and carbon dioxide, both of which are commercially important. With the over-all picture of the enzymatic actions of yeast in mind, we may address ourselves to some of the practical applications of yeast.

Yeast is utilized in the manufacture of ethyl alcohol from blackstrap molasses, a by-product of the extraction of cane sugar in the refineries. This molasses, which contains sucrose as its principle sugar, is made into a mash by addition of water. To the mash are added strains of *Saccharomyces cerevisiae.* Invertase from the yeast cells catalyzes the conversion of sucrose into invert sugar. The invert sugar is fermented by zymase. The actual fermentation takes about forty-eight hours. The fermented mash at this time contains between six and twelve per cent of alcohol. The fermented mash is then distilled with steam. The distillate, however, is not pure and is termed crude alcohol. The crude alcohol is rectified by redistillation. The carbon dioxide from the fermenting mash is compressed for use in carbonation, while the residue from the distillation of the fermented mash is converted into potash for the manufacture of fertilizers.

Materials with a high starch content, such as corn or potatoes, may be utilized in the manufacture of ethyl alcohol. Essentially these

materials are made into a mash. To this mash malt is generally added. The malt, which is simply germinating barley, supplies the amylase for the hydrolysis of starch to maltose. The mash is then inoculated with yeast. Maltase from yeast brings about the hydrolysis of maltose to glucose. The glucose is in turn fermented by the zymase of the yeast to ethyl alcohol and carbon dioxide. More recently *Rhizopus oryzae* and *Aspergillus niger* have been used instead of malt. Both of these molds accomplish the saccharification of the starch to fermentable sugars. In fact when these molds are employed, the alcohol yield at the end of fermentation is greater.

In making bread, strains of *Saccharomyces cerevisiae* are employed to leaven the dough. The wheat diastase in the flour converts the starch in the dough to maltose. The maltase from the yeast hydrolyzes the maltose to glucose. Zymase ferments the glucose to ethyl alcohol and carbon dioxide. The carbon dioxide raises the dough. The alcohol is driven off during the baking process.

In the making of malt beverages, ground barley malt is mixed with water to form a mash. The amylase from the malt hydrolyzes the starch in the barley grains to maltose within a few hours. The liquor of the mash, referred to as *wort*, is transferred to copper kettles and there boiled with hops. The hops serve to give the malt beverage its characteristic flavor. After several hours of boiling, the wort is cooled and filtered. The wort is now ready to be inoculated with yeast. At this point the brewer has at his disposal two varieties of *Saccharomyces cerevisiae:* top yeasts and bottom yeasts. The top yeasts in their growth are distributed through fermenting wort, but because of the abundant evolution of carbon dioxide in the early phases of the fermentation, the yeast cells are carried up to the surface of the fermenting liquid. Bottom yeasts, on the other hand, tend to sink to the bottom of the fermenting liquid since the evolution of carbon dioxide is relatively much slower in the initial stages of fermentation. The brewer uses top yeasts in the making of ale and the bottom yeasts in the manufacture of lager beer. In any event, the maltose of the wort is hydrolyzed, by maltase from the yeast, to glucose. The glucose is then fermented to alcohol and carbon dioxide by the zymase. The malt beverage, whether it be ale or beer, is generally stored for a period of months, during which it attains its mellowness. The beer or ale is finally carbonated.

Yeasts are also employed in the manufacture of wine and distilled

spirits such as whisky, brandy, and liqueurs. The role of yeast in the making of vinegar has already been indicated in Chapter 18, Bacteria.

Yeast has other uses. It is an excellent source of the B-complex vitamins. Its ergosterol content is converted by ultraviolet irradiation to a D vitamin; hence the commercial use of irradiated yeast.

Finally on the darker side of the economic picture is the fact that yeasts can readily effect the spoilage of foodstuffs having high carbohydrate content. The fermentation of fruit juices, tomato catsup, and dilute sugar syrup are familiar examples.

POWDERY MILDEWS

The powdery mildews are obligate parasites that reflect themselves in the white, powdery blotches that speckle the leaves or stems of the affected host plants. The mycelium (Fig. 22.3), composed of

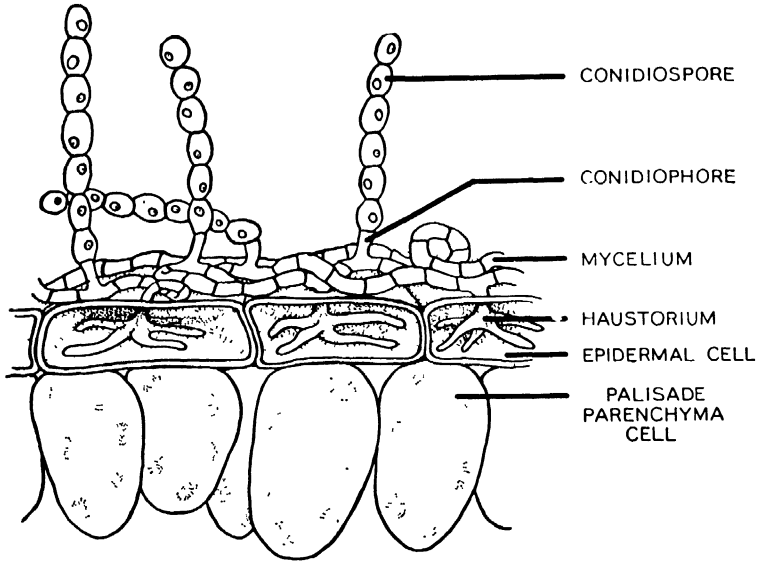


FIG. 22.3 Mycelium of *Erysiphe graminis* on the surface of the parasitized leaf. Asexual reproduction is also visualized.

uninucleate cells, ramifies in a skein-like pattern over the superficial surface of the parasitized leaf or stem. Haustoria from the hyphae invade the subjacent epidermis and in a few isolated cases penetrate beyond the epidermal layer.

Powdery mildews restrict their parasitism generally to herbaceous dicots, with the exception of *Erysiphe graminis*, the mildew of the

grasses and cereals. In distribution the powdery mildews range through the North Temperate Zone, occurring more commonly in semiarid regions than in areas where abundant rainfall obtains. In reference to the distribution of these mildews, it is interesting to note that the conidiospores of the powdery mildews require only the moisture of high humidity at the leaf surface for germination.

Reproduction. Asexual reproduction (Fig. 22.3) is accomplished by conidiospores. From the mycelium, after its establishment on the surface of the host tissue, grow forth in angulate fashion numerous short hyphae or conidiophores. From these conidiophores there are finally abstricted oval conidiospores. The conidiospores are dispersed by the wind. On the attainment of suitable substrate—the dew-moistened surface of another sensitive leaf, for example—each conidiospore germinates by sending forth a germ tube. From this a mycelium will develop, whence ultimately the wind will harvest another crop of infective conidiospores.

Sexual reproduction generally occurs near the end of the growing season of the host plants, a date that would seem to indicate that this process, while generative in every sense, is at the same time productive of a mechanism (a closed ascocarp in this case) in which the parasite hibernates through the winter, to resume physiological activity in the following spring. In sexual reproduction, two hyphae become applied to each other in twisted embrace. The terminal cell of one of these hyphae develops into an antheridium, while the terminal cell of the other becomes ellipsoidal to form an ascogonium. Subsequently through the mutually contiguous walls of the two gametangia there is formed a pore-like passage through which the protoplast of the antheridium passes into the ascogonium. Generally the antheridial and ascogonial nuclei unite to form a fusion nucleus. This fusion nucleus divides to form several nuclei; transverse septation follows and there is produced an alignment of cells, the penultimate cell of which is binucleate. From this penultimate cell arise several outgrowths, from each of which there is ultimately derived a binucleate ascogenous hypha. The terminal cell of each ascogenous hypha becomes inflated into an ascus; the two nuclei of the terminal cell combine into a fusion nucleus which shortly undergoes meiosis; the four haploid nuclei then divide mitotically to form eight nuclei for the final delimitation of the ascal contents into eight ascospores. In the meantime sterile hyphae emanate, chiefly from the cells below

the ascogonium, and become compacted around the developing ascogenous hyphae to form a cleistothecium. The asci are disposed in

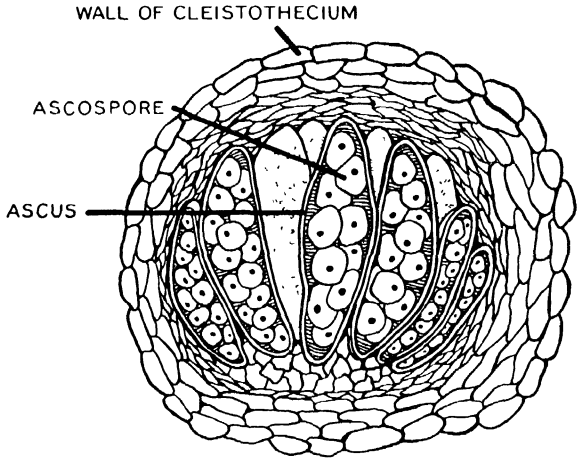


FIG 22.4 Section of the cleistothecium of *Erysiphe aggregata*

parallel fashion within this cleistothecium (Fig. 22.4). With the rupture of the cleistothecium in the following spring, the ascospores are liberated from the asci. Upon coming in contact with suitable substrate, each ascospore germinates to form a mycelium from which within a few days infective conidiospores will be produced.

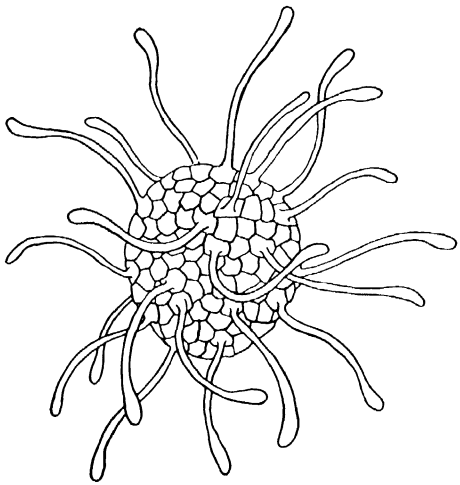


FIG. 22.5 Surface view of the cleistothecium in *Erysiphe cichoracearum.*

The cleistothecia (Fig. 22.5) are externally characterized by appendages which serve to anchor them in the mycelium. The forms of these appendages are of some taxonomic importance in distinguishing the various genera of the powdery mildews. For example, simple flexible appendages characterize the mildews in the genus *Erysiphe,* while the ends of the appendages are dichotomously branched in the genus *Microsphaera.*

Economic Aspects. *Erysiphe graminis,* the powdery mildew of the cereals, is rather destructive to wheat, barley, and oats. *Erysiphe cichoracearum,* the downy mildew of the melon, parasitizes cucumbers, melons, and squashes. In 1926 this parasite reduced the melon crop in California so considerably that the farmers took measures to counteract it by developing powdery-mildew-resistant melons. *Sphaerotheca mors-uvae,* the gooseberry mildew, is so destructive in its parasitism on the plant that it limits in many sections of the country the production of gooseberries. Other economically significant powdery mildews are the apple mildew, *Podosphaera leucotricha;* and the hop mildew, *Sphaerotheca humuli.* The lilac mildew is as familiar to gardeners as the phlox mildew.

BLUE AND GREEN MOLDS

The blue and green molds are cosmopolitan in their distribution, being for the most part saprophytic on all types of organic matter. A few are parasitic and causative of mycoses to be described later. The green mold on stale bread, cereals, and jellies, as well as the blue mold on cheese, oranges, and lemons, are rather familiar. The color of the mold, whether it be blue or green—and sometimes it may be even yellow or black—is principally attributable to the pigment present in the walls of the conidiospores. Perhaps the reason for the occurrence of these molds on such a variety of substrates lies largely in their enzyme-secreting capacities. We shall limit our considerations to two prominent genera, *Aspergillus* and *Penicillium.*

Structural Aspects. Both *Aspergillus* and *Penicillium* have septate mycelia. From the mycelium arise vertical aerial hyphae, while other hyphae penetrate into the substrate. *Aspergillus* and *Penicillium* are generally distinguished from each other according to the morphology of their conidiophores (Fig. 22.6). The conidiophore of *Aspergillus* is an erect hypha that terminally swells into a vesicle whence radiate many bottle-shaped sterigmata bearing sphere-shaped conidiospores. The conidiophore of *Penicillium,* on the other hand, divides to form several branches, called *metulae,* each of which bears from one to four bottle-shaped sterigmata surmounted by chains of conidiospores.

Reproduction (Fig. 22.6). Asexually both *Aspergillus* and *Penicillium* reproduce by conidiospores. Sexual reproduction, as observed in some species of both genera, involves the formation of ascogenous hyphae and cleistothecia. In *Aspergillus repens,* the ascogonium is

multinucleate and possesses a trichogyne; the antheridium is also multinucleate. The antheridium generally fuses with the trichogyne and there is a subsequent pairing of antheridial and ascogonial nuclei. From the fertilized ascogonium arise binucleate ascogenous hyphae on which develop asci. The ascogenous hyphae with their asci are en-

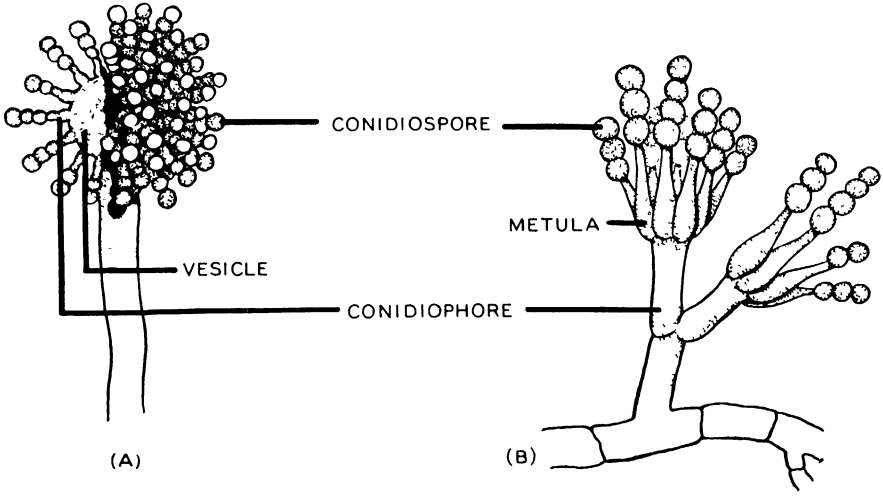


FIG. 22.6 (A) *Aspergillus;* (B) *Penicillium.*

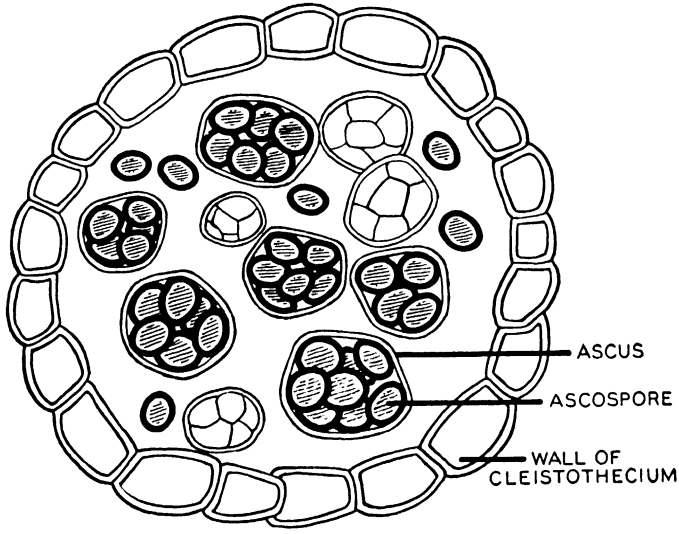


FIG. 22.7 Cleistothecium of *Aspergillus.*

veloped within a cleistothecium. In *Penicillium glaucum* two short hyphae, one an antheridium and the other an ascogonium, become twisted about each other. From the fertilized ascogonium there arise ascogenous hyphae, the cells of which enlarge to form asci so that the asci appear to be disposed in chain-like fashion. Cleistothecia are formed (Figs. 22.7 and 22.8).

It might be well to indicate at this point that sexual reproduction has not been observed to occur in all of the species of either *Aspergillus* or *Penicillium* and for that reason many of these species of either genus have been put in the class Deuteromycetes or the Fungi Imperfecti.

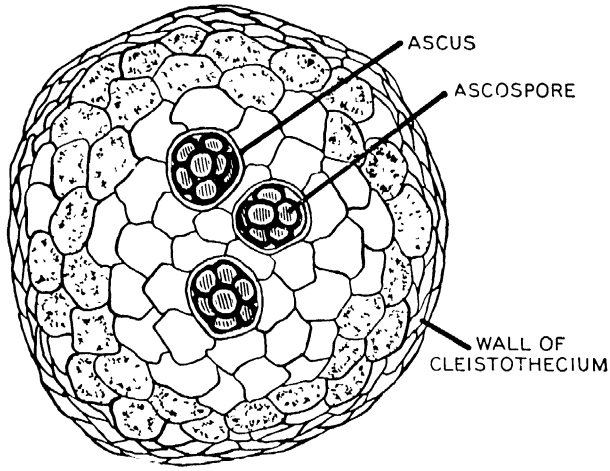


FIG. 22.8 Cleistothecium of *Penicillium*.

Economic Considerations. From *Penicillium notatum* is obtained the Gram-positive antibiotic, penicillin, the action of which has been indicated in the chapter on bacteria. *Penicillium roqueforti* by its enzymatic hydrolysis of butter fats to saturated fatty acids, such as butyric and caproic, gives Roquefort cheese its distinctive flavor. *Penicillium camemberta* by its hydrolysis of casein characterizes the taste of Camembert cheese. Various species of *Penicillium*, such as *Penicillium glaucum* and *Penicillium olivacaeum*, are used in industry for the production of citric acid. *Penicillium italicum* and *Penicillium digitatum* are responsible for the mold rot that develops on stored citrus fruits.

On the other hand, many antibiotic substances have been isolated from various species of *Aspergillus* but have been subsequently found

to be too toxic for therapeutic use in the human subject. However, one antibiotic substance, called *fumagillin* and isolated from cultures of *Aspergillus fumigatus,* is being utilized rather successfully in the treatment of intestinal amoebiasis. *Aspergillus oryzae,* because of its secretion of amylase, is employed in the saccharification of rice starch. As a matter of fact, the Japanese have made routine use of this organism for centuries in the mashing of rice for the making of sake. *Aspergillus niger* and *Aspergillus oryzae* are also commonly used in the industrial production of citric acid. *Aspergillus niger* is responsible for the storage rot of onions and apples and for the black mold rot of the peach.

In reference to their pathogenic effects on man, *Aspergillus fumigatus, Aspergillus nidulans,* and *Aspergillus niger* are causative of various types of aspergilloses. One type involves a mycosis of the external ear. In this otomycosis, the external auditory meatus may become filled with mycelium, with ulceration and suppuration of the walls of the meatus. The infection may spread into the middle ear. Aspergillosis of the ear has been reported to have frequent incidence in India. The other type of aspergillosis is a pulmonary mycosis. It is characterized by extensive cavitation of the lungs and a blood-streaked sputum—a clinical picture suggestive of pulmonary tuberculosis. In fact pulmonary aspergillosis resembles pulmonary tuberculosis to such a degree that it is often either overlooked or incorrectly diagnosed as pulmonary tuberculosis. Human aspergillosis is generally limited to those who force-feed pigeons for the market or who work as feather dressers. To make matters worse, pulmonary aspergillosis may occur coincidentally with tuberculosis.

ERGOT FUNGUS

The species of the ergot fungus (*Claviceps*) are cosmopolitan in occurrence, being parasitic on the ovaries of the grasses, particularly the cereals. The ultimate effect of this parasitism is the replacement of the ovarian tissue by a compacted hyphal mass called a *sclerotium* or *ergot grain.* Our considerations shall be limited to *Claviceps purpurea,* which ergotizes rye (*Secale cereale*).

Life Cycle. The spores, either conidiospores or ascospores, are disseminated by the wind or insects. On the attainment of an ovary in a spikelet[1] of rye, the spore germinates to form a mycelium that super-

[1] *Spikelet.* a unit of an indeterminate inflorescence, common to the grasses, a small group of sessile flowers occurring at a given point on the main elongated axis.

ficially penetrates and invests the ovary at this time. From the peripheral surface of this circumjacent mycelial mass there arise in columnar disposition numerous conidiophores bearing conidiospores. The mycelial mass with its conidiospores represents the sphacelial stage (Fig. 22.9) in the life cycle of *Claviceps purpurea*. The conidiospores, upon abstriction from the conidiophores, congregate in a sugary exudate called "honeydew." The latter secretion, said by some to originate from the flower nectary and by others from the sphacelial mycelium, is

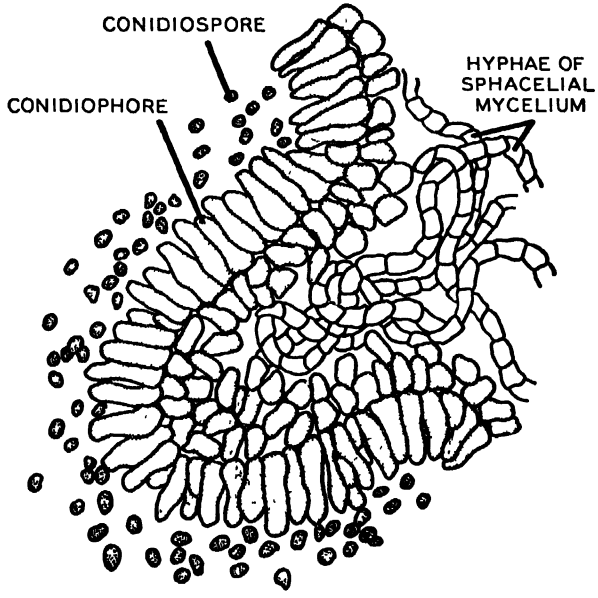


FIG. 22.9 Sphacelial stage in the life cycle of the ergot fungus (*Claviceps purpurea*).

attractive to insects. The insects feeding upon the "honeydew" pick up the conidiospores and serve as the agents of transmission of the infection to other spikes[1] of rye. In the meantime the sphacelial mycelium has accomplished the complete invasion and destruction of what remains of the ovarian tissue. Gradually, as the production of conidiospores tapers off, the hyphae of the sphacelial mycelium become compacted to form a grayish-violet and generally curved body termed the sclerotium (Fig. 22.10) or ergot grain. The ergot grains are generally greater in size than the ovaries which they have replaced

[1] *Spike:* an indeterminate inflorescence in which sessile flowers are borne on a main elongated axis.

and consequently are discernible as dark spurs (Fig. 22.10) on the rye spike.

The sclerotia mature at about the same time as the other ovaries in the various spikelets of rye ripen into rye grains. Some sclerotia fall to the ground and others become admixed with the rye grain at harvest time. Those sclerotia which have fallen to the ground are generally

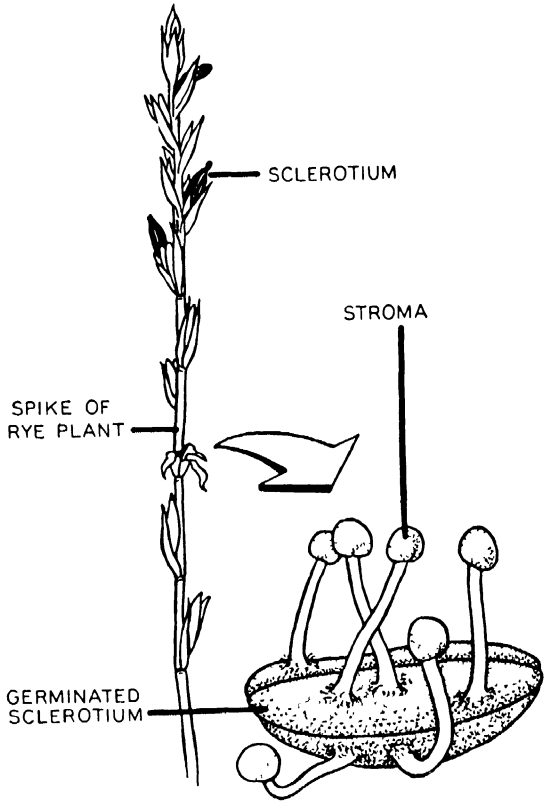


FIG. 22.10 Spike of rye plant with sclerotia of ergot (*Claviceps purpurea*) in the spikelets. BELOW RIGHT: A germinated sclerotium.

capable of hibernating until the following spring, when they germinate. On germination a sclerotium (Fig. 22.10) gives rise to a number of slender stalks, each surmounted by a spherical head commonly referred to as the *stroma* (Fig. 22.11). In the peripheral area of this stroma, the terminal cells of lateral branches of the same hyphae develop into antheridia and ascogonia. Both of the latter gametangia are

multinucleate at maturity, with the ascogonia relatively larger than the antheridia. Contact is generally effected between a vicinal antheridium and ascogonium. Dissolution of the mutually contacting walls occurs and the antheridial nuclei pass into the ascogonium. From the fertilized ascogonium issue forth ascogenous hyphae that recurve terminally to form croziers, with the penultimate cells of the ascogenous hyphae being modified into elongate asci (Fig. 22.12). In each

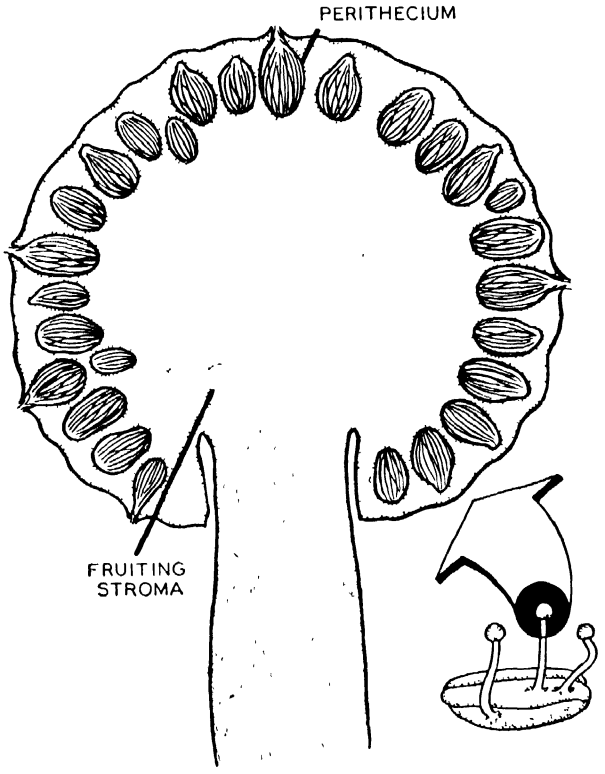


FIG. 22.11 Fruiting stroma of *Claviceps purpurea*.

ascus there are disposed in parallel fashion eight capilliform ascospores. The asci are contained in perithecia submerged in the cortical area of the stroma. Each perithecium opens out on the periphery of the stroma by a minute ostiolate opening. The ascospores are delivered from each perithecium (Fig. 22.12) rather violently and are then borne by convection air currents to flowering spikes of rye. Thus a new life cycle begins.

Economic Aspects. The sclerotium of *Claviceps purpurea* is the official drug, *ergot*. Ergot contains several alkaloids: ergonovine, ergotoxine, and ergotamine. These alkaloids have been isolated from ergot and are utilized in obstetrics as ecbolics. At present these alkaloidal principles are more extensively employed to control postpartum hemorrhage.

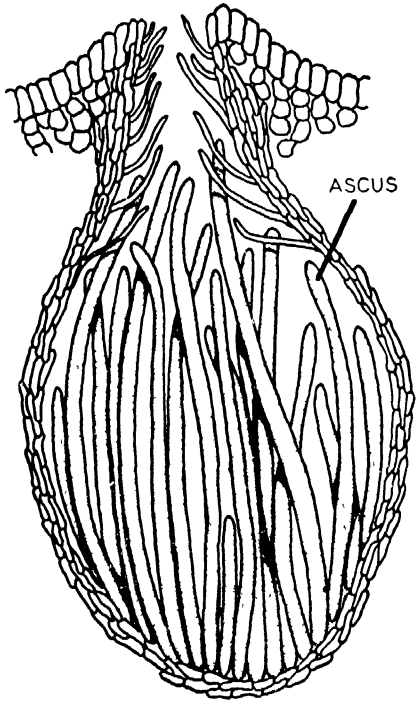


FIG. 22.12 Enlarged view of the perithecium from a fruiting stroma of the ergot fungus, *Claviceps purpurea*.

Ergotism in man, though a rare occurrence in these days, results from the ingestion of bread made with ergotized rye. The more severe form of ergotism generally eventuates in gangrene of the toes and feet because of the development of obliterative endarteritis in the legs of the victim. The "holy fire" epidemics of ancient times are believed to have been due to gangrenous ergotism.

Livestock suffer ergotism on the consumption of ergotized pasture grasses and hay. The very severe type of ergotism involves gangrene of the extremities, with necrosis and sloughing of the toes, feet, and even the tail. Cattlemen suffer considerable losses when their cows and mares abort because of the ingestion of grasses infected with ergot.

CUP FUNGI

General Characteristics. The cup fungi, a large group of more than four thousand species, are cosmopolitan in distribution, and are characterized by the development of cup-shaped ascocarps (Fig. 22.13) or apothecia. Within these apothecia are contained asci and sterile hyphae (paraphyses). Some of these apothecia are barely discernible while others attain an over-all diameter of several inches. The cup fungi in general are saprophytic and are commonly observed growing

on decaying wood or on soil rich in organic matter. Many of these cup-shaped ascocarps are brilliantly colored and often present themselves strikingly in the form of stalked cups on rotting tree stumps. The genus *Peziza* is usually considered fairly representative of this group of fungi.

Reproduction. The production of conidiospores in the genus *Peziza* is of rather limited occurrence, having been reported for such species as *Peziza rapanda* and *Peziza vesiculosa.*

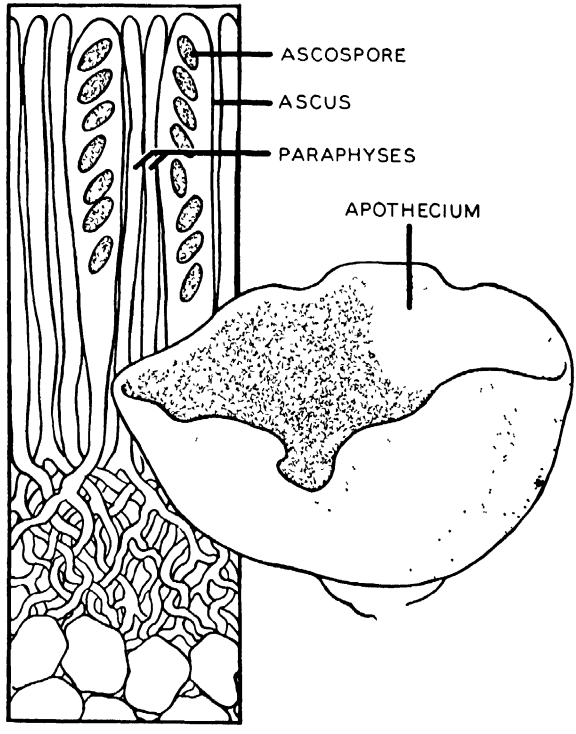


FIG. 22.13 Apothecium of *Peziza.*

On the other hand, sexual reproduction, which finally eventuates in apothecial development, is the rule. Sexual reproduction follows the general pattern outlined at the beginning of this chapter. Multinucleate antheridia are generally formed vicinal to multinucleate ascogonia, each of which possesses a trichogyne. The trichogyne usually curves into contact with a neighboring antheridium. There is a mutual dissolution at the point of contact between the antheridium and the

trichogyne. The antheridial nuclei pass through the trichogyne into the ascogonium. The antheridial and ascogonial nuclei become aligned in pairs. From the ascogonium thus fertilized there now stem binucleate ascogenous hyphae that recurve terminally in crozier formation, the penultimate cells developing into asci in the usual manner. Meantime from the cells which subtend the ascogonium originate sterile hyphae that weave themselves into an enclosing weft that eventually arcuates itself over the joined antheridium and ascogonium to form finally a cup-shaped ascocarp. Frequently the sterile hyphae of one developing apothecium become intermeshed with similar hyphae from another so that a larger compound apothecium is produced. The size of the mature ascocarp, therefore, becomes contingent upon the number of potential simple apothecia that contributed to its formation.

Chapter 23

THE FUNGI IMPERFECTI

THE Deuteromycetes represent a heterogeneous group of fungal organisms in the life cycles of which sexual mechanisms do not apparently occur. This lack may be due to the fact that the sexual stage of the life cycle has not yet been discovered or that it has disappeared in the evolution of the fungal organism. There is evidence to suggest that a number of the Fungi Imperfecti were originally Ascomycetes that have lost their capacity to produce ascospores. Many of the members in this group of fungi produce various mycoses in the human subject. Some of these pathogenic organisms will be discussed briefly below.

Blastomyces dermatitidis. This organism causes blastomycosis in the human subject. This disease is of two types: cutaneous and systemic. In the cutaneous type, the organism is thought to enter a traumatized area of the skin. It most commonly involves the skin of the face and upper and lower extremities. The cutaneous lesion begins as a pustule which spreads peripherally to form a warty plaque, the periphery of which is characterized by abscess formation. These lesions generally heal but leave much scar tissue in their wake. The systemic type generally begins with a primary lesion in the lungs whence the organism spreads by way of the blood vascular system to any organ in the body, notably the bones, joints, kidneys, and central nervous system. Its presence in these organs is attended by granulomatous lesions and suppurative abscesses. Microscopically, a culture of this organism shows itself to be composed of delicate, septate hyphae whence arise lateral branches (conidiophores) bearing conidiospores. In the tissues of the human subject no mycelium occurs. Instead, the organism appears in the form of doubly contoured, rounded, single budding cells. Cutaneous blastomycosis is generally treated more or less successfully with the intravenous administration of sodium iodide. Systemic blasto-

mycosis is rather difficult to treat. The prognosis is generally poor. While this disease is distributed throughout the United States, it seems to occur with relatively greater incidence in the Middle West.

Sporotrichum schencki. This organism occurs as a saprophyte on vegetation. However, it may enter the human skin through a wound or find its way into the alimentary tract whence it may spread by way of the blood vascular system to involve the lungs, liver, or testes. In the majority of cases, the disease is limited to the skin and subcutaneous tissue. After entering the skin, subcutaneous lesions develop. These are at first indurated but subsequently soften because of pus formation. Finally the overlying skin breaks down and ulcerates. Within a week or so, the infection spreads from the primary lesions by way of the subcutaneous lymphatic vessels. Multiple subcutaneous nodules and ulcerations of the overlying cutaneous area reflect the course of the infection as it passes along the subcutaneous lymphatic vessels. Cultures of this organism present a delicate, septate, branching hypha. Lateral hyphal branches generally support a cluster of sterigmatically borne conidiospores. In the tissues of the human subject no hyphae occur. The organism takes the form of small cigar-shaped bodies within the polymorphonuclear leucocytes. The disease, to sum up, is characterized by subcutaneous abscesses, cutaneous ulceration, and lymphangitis. It is treated rather successfully with potassium iodide. The distribution of this fungal organism includes the United States, France, and South America. In the United States it is common in the vicinity of the Mississippi Valley, where it occurs mostly in farmers.

Cryptococcus hominis (Torula histolytica). This organism is causative of cryptococcosis, a subacute or chronic disease which involves the brain and meninges but may also attack the bones, lungs, and skin. The organism probably enters the human subject by way of the respiratory tract. Cultural mounts of this organism disclose neither conidiospores nor hyphae. Yeast-like budding cells with gelatinous capsules are generally discernible in special India-ink mounts. Prognosis in cryptococcosis is poor.

Monilia albicans. This organism causes moniliasis. The disease may be localized or generalized. It affects the skin, mucous membranes, heart, lungs, and even the meninges. Cultural mounts reveal no conidiospores, but chlamydospores may be demonstrated by grow-

ing the organism on corn-meal agar. In human tissues the organism generally occurs in the form of small, budding cells.

Dermatophytes. These are a group of organisms causative of ringworm infections of the skin, nails, and hair. In culture these organisms are characterized by the production of *macroconidiospores*—rather large clavate or fusiform spores, some of them septated into several cells. In the skin and hair the dermatophytes reproduce by the production of *arthrospores;* that is, the hypha or mycelium fragments into its constituent cells (arthrospores). Consequently, for determination of the species of dermatophyte involved, cultures are necessary. Perhaps the most common dermatophyte is referred to as "athlete's foot" (*Tinea pedis*). Most of the ringworm diseases are caught by contact. Many of the diseases respond to treatment with various fungicides, while the more resistant infections require radiation therapy.

Deuteromycetes Pathogenic to Plants. Finally, some mention of those Deuteromycetes that are pathogenic to plants should be made at this time. Some of these pathogenic Deuteromycetes are seed-borne and include: *Cercospora beticola,* which causes the leaf spot of beet; *Diplodia zeae,* causative of ear rot of corn; and *Asochyta pisi,* productive of the leaf and pod blight of the pea. Other Deuteromycetes are soil-borne pathogens, one of the commonest being *Phymatotrichum omnivorum,* generally referred to as Texas root-rot fungus. The latter organism is reported to be destructive to some 1700 species of flowering plants. Certain Deuteromycetes which grow saprophytically in soil will produce wilt diseases of such plants as the tomato, the banana, and cotton.

Chapter 24

THE CLUB FUNGI

General Characteristics. The life cycle of any basidiomycete is characterized by the production of a club-shaped hypha termed a *basidium*. This basidium may be septate or nonseptate. The septate basidium is generally delimited into four cells from each of which projects a minute protrusion (*sterigma*) that supports a basidiospore. The nonseptate basidium, on the other hand, generally possesses four sterigmatically borne basidiospores at its distal (free) end.

The septate basidium, peculiar to the smut and rust fungi in this class, results from the germination of a binucleate spore (Fig. 24.5A and D). On germination the two nuclei in the spore fuse. The fusion nucleus divides meiotically to form four haploid nuclei. From the spore there emanates a short club-shaped hypha into which the nuclei migrate. Septation of the hypha follows. Each cell of the basidium then develops a sterigmatically borne basidiospore. The nonseptate basidium, characteristic of gill and bracket fungi in this class, has its origin in the binucleate terminal cell of a hypha (Fig. 24.0). The nuclei in this terminal cell are of opposite strains. They fuse. The fusion nucleus, which is diploid, divides meiotically to form four haploid nuclei. The distal end of the basidium develops four projections, into each of which moves a nucleus to become the center of a sterigmatically borne basidiospore.

In the life cycle of the basidiomycetes there generally occur two types of mycelia: one is uninucleate and is often referred to as a haploid mycelium; the other is binucleate and is frequently termed a diploid mycelium. The uninucleate mycelium stems from the germination of the haploid basidiospore. The binucleate mycelium has its origin in the conjugation or anastomosis of hyphae of different strains or in the fusion of uninucleate spores of different strains, or even in the fusion of a uninucleate spore with a vegetative cell in a haploid

hypha or mycelium. In whatever manner this fusion of two uninucleate protoplasts is attained, it must be emphasized that while the cytoplasm of the protoplasts becomes continuous, the nuclei remain separate. Thereafter in the cell division of each binucleate cell the nuclei divide synchronously or conjugately. Of more than passing interest is the formation of clamp connections (Fig. 24.1) that are associated with the division of binucleate cells. In these cases cell division is limited to the terminal cell of the hypha. About midway along its

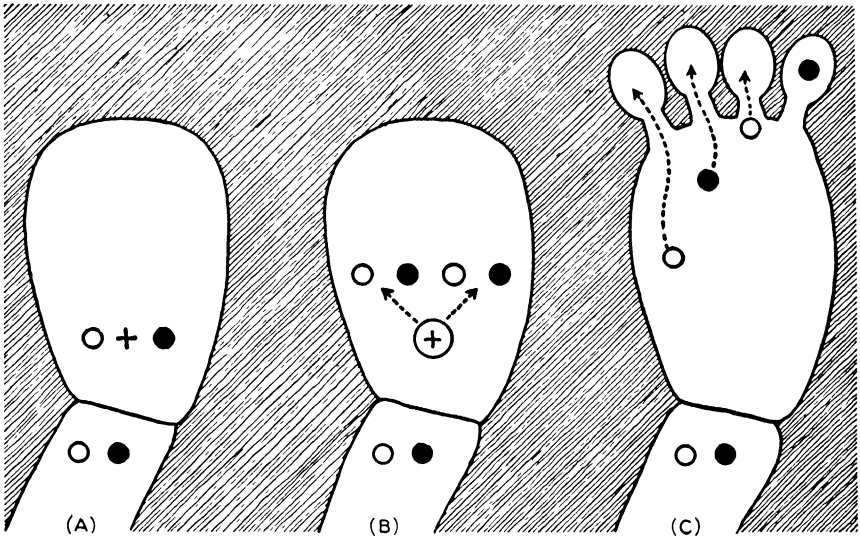


FIG. 24.0 Development of nonseptate basidium: (A) binucleate terminal cell with nuclei of opposite strains; (B) meiosis of the fusion nucleus; (C) basidium, showing migration of haploid nuclei to form basidiospores.

longitudinal axis the terminal cell evaginates into a small arcuate protrusion directed toward the base of the cell. The two nuclei of the terminal cell divide mitotically. One of the lower daughter nuclei moves into the arcuate outgrowth, which subsequently becomes delimited from the terminal cell by a cross wall. The arcuate outgrowth is now termed a clamp cell. The other lower daughter nucleus comes to lie below the point where the clamp cell had originally developed. Transverse septation follows, with two daughter nuclei in the new terminal cell and one nucleus in the penultimate cell. The clamp cell now fuses with the penultimate cell, into which the nucleus of the clamp cell migrates. The penultimate cell thus becomes binucleate. Cytologically

the presence of these clamp connections is indicative of a binucleate hypha or mycelium among the basidiomycetes.

Classification. The class Basidiomycetes is divided into two subclasses: the Homobasidiomycetes and the Heterobasidiomycetes. In the Homobasidiomycetes the basidia develop directly from a vegetative terminal cell of a hypha. This subclass includes the mushrooms, the puffballs, and the bracket fungi so common on some of our deciduous trees. In the Heterobasidiomycetes the basidium results from

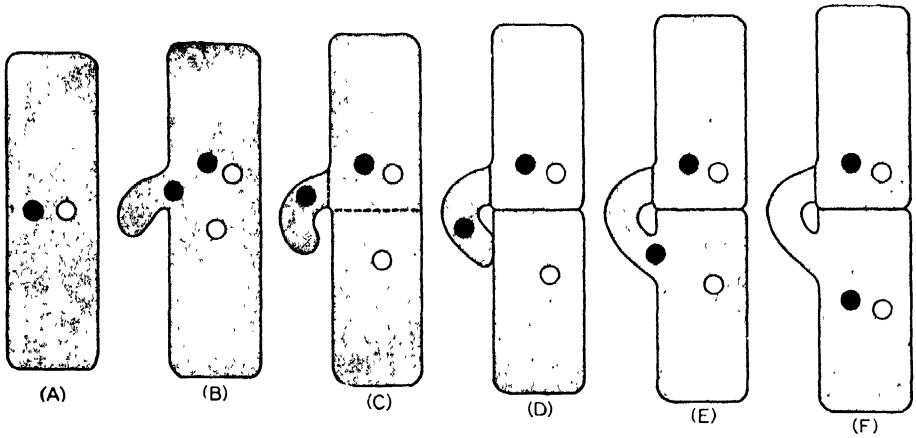


FIG. 24.1 Steps in clamp formation among the basidiomycetes. (A) terminal cell, (B) formation of an arcuate outgrowth and mitoses of the nuclei in the terminal cell; (C) movement of one of the lower daughter nuclei into the outgrowth; (D) delimitation of the uninucleate outgrowth by septation; septation of the upper and lower daughter cells; (E) clamp connection with the lower daughter cell and movement of its nucleus into the lower daughter cell; (F) two binucleate daughter cells with an empty clamp connection.

the germination of a spore. In this subclass are the smut fungi and the rust fungi—all economically important since they parasitize corn and wheat plants.

In this chapter we shall consider the edible mushroom (*Agaricus campestris*) as representative of the Homobasidiomycetes. As examples of the Heterobasidiomycetes we shall study corn smut (*Ustilago maydis*) and wheat rust (*Puccinia graminis*).

AGARICUS CAMPESTRIS

The edible mushroom, as we see it, represents a sporophore or fruiting body (Fig. 24.2A). It consists of a stalk, called a *stipe*, which

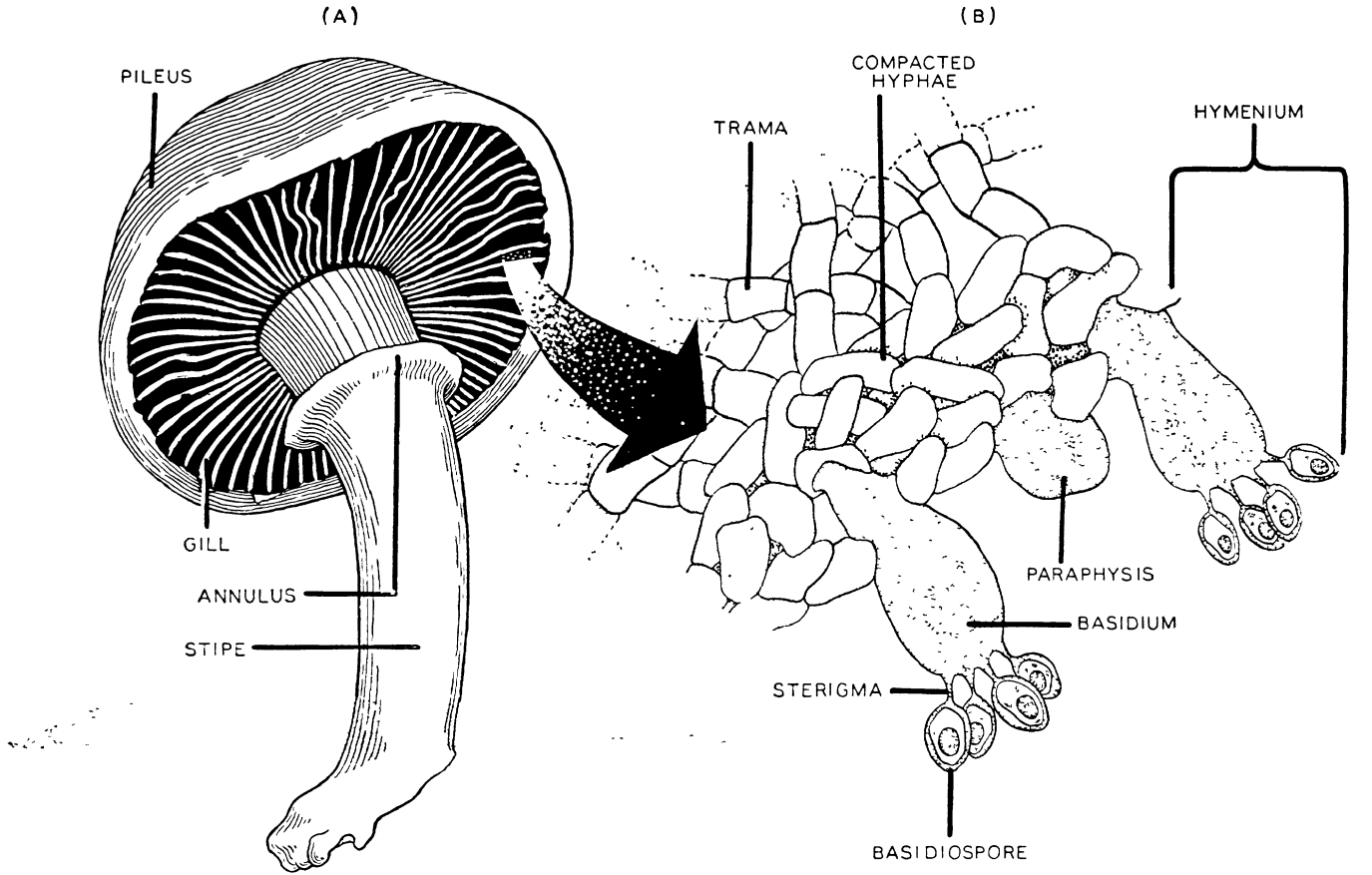


FIG 24.2 (A) Sporophore of *Agaricus campestris*, (B) trama and hymenium of a gill in same organism.

is surmounted by an umbrella-shaped cap termed a *pileus*. From the undersurface of the pileus are suspended numerous mycelial plates or gills. Each gill on microscopic examination is observed to be composed of a central area of loosely interwoven hyphae, collectively referred to as the *trama* (Fig. 24.2A). The hyphae of the trama become compacted at the surface of each gill and finally terminate there in the formation of basidia and paraphyses. The basidia bear generally four sterigmatically supported basidiospores. The basidia, basidiospores, and paraphyses constitute the hymenia portion, or *hymenium*, of the gill. After abstriction from the basidia the basidiospores are dispersed by the wind.

Life Cycle. The basidiospore on the attainment of suitable substrate, generally soil rich in organic matter, germinates to form a uninucleate mycelium which grows saprophytically below the soil surface. After a short time the uninucleate hyphae fuse or conjugate to form a binucleate mycelium, which undergoes intensive growth. The hyphae of the mycelium tend to interweave in such a manner as to form matted mycelial strands termed *rhizomorphs*. Ultimately on these rhizomorphs are produced sphere-shaped masses of compacted hyphae known as "buttons." These buttons are the primordia of the sporophore already described. The upper part of the button becomes differentiated into the pileus and gills, while the lower part develops into the stipe. As the young sporophore appears above the soil, there extends from the margin of the pileus to the stipe a membranous layer of hyphae. This hyphal membrane conceals the gills from view. As the pileus enlarges, the membrane is ruptured and part of it remains as a ring-like fragment (*annulus*) (Fig. 24.2A) around the upper portion of the stipe. As the pileus grows in diameter, it flattens out somewhat to expose the underlying gills. The composition of a gill has already been discussed. Suffice it to say at this point that the tramatic hyphae become densely aggregated at the surface of the gill. The terminal cells of the tramatic hyphae are binucleate. Some of these cells are differentiated into basidia. In each of these cells the nuclei fuse. Each fusion nucleus then divides meiotically to form four haploid nuclei. In the meantime the distal end of such a terminal cell, now termed a basidium, forms four projections or sterigmata. Each sterigma becomes terminally dilated as a haploid nucleus migrates into its inflated tip to form a basidiospore.

Other Gill Fungi. The gill fungi are generally classified into several

groups on the basis of spore color. Only a few of these groups will be discussed by way of illustration. The spore of *Agaricus campestris,* which we have considered in some detail, is purple. The shaggy-mane mushroom, *Coprinus,* which is characterized by a narrow and somewhat elongated pileus, produces black spores in droplets resulting from the progressive liquefaction of the gills. On the other hand, some of the most poisonous gill fungi belong to the genus *Amanita.* All of them produce white spores. *Amanita muscaria,* fairly common in coniferous forests, is rather toxic because the fruiting body contains a substance known as *muscarine.* The consumption of such a mushroom by man eventuates in purging, which may be brought under control by atropine.

Incidentally it might be indicated at this point that there is no set norm by which to distinguish the edible from the poisonous mushrooms. The determination as to what mushroom is edible is best left to the expert.

Other Members of the Homobasidiomycetes. The *bracket fungi* are shelf-like fructifications conspicuous on trees. The mycelium of the fungal organism generally invades a tree through an open wound and finally attains its xylem. Here by virtue of the enzymes secreted by the mycelium, the wood is gradually and progressively decomposed. For this reason the bracket fungi are often called the wood-destroying fungi. The sporophores of a bracket fungus, instead of having gills as in *Agaricus,* possesses numerous tubes each lined by a hymenial layer. These tubes open by small pores on the undersurface of the fructification. In consequence of these pore-like openings, this type of homobasidiomycete is often referred to as a *pore fungus.* Some of these bracket sporophores are fleshy in texture and survive only for a year. Others are hard and almost wood-like in consistency. The latter type of sporophore, by virtue of the fact that it is able to form each year a new layer of hymenial tubes, is able to perennate itself. The damage which these wood-destroying fungi accomplish within a year has been computed to exceed the total damage done by forest fires over a similar period of time. On the other hand there is a brighter side to the economic aspects of the bracket fungi. Some of these fungi subsist saprophytically on decaying tree stumps and other woody debris in the forest and thus play no small part in the decomposition of these dead tissues, with the subsequent release of elements so essential in the economy of the forest.

The *puffballs*, common in the pasture and woods, are generally large spherical white fructifications. The vegetative mycelium grows on rotting wood or in soil. The unique feature of the puffball is that the hymenial compartments are enclosed by a covering called the *peridium*. The basidiospores escape when the peridium either breaks open or decays. Some of these puffballs may attain a diameter of twenty or more inches. Most of the puffballs are edible before their color darkens. The color change is concurrent with the production of basidiospores within basidia-lined compartments.

USTILAGO MAYDIS

The smuts in general are pathogenic fungi which are parasitic on flowering plants, notably those of the cereals and grasses. The life cycle of a smut fungus is characterized by the production of black or brown thick-walled spores termed *chlamydospores*. Each chlamydospore represents an enlarged cell of a binucleate mycelium. The cell is densely granular and its original wall gelatinizes, to be replaced usually by a sculptured wall. These chlamydospores are resistant to adverse conditions. While the mycelium of most smuts is intercellular, that of *Ustilago maydis* is intracellular. The smuts generally parasitize one species of host. *Ustilago maydis*, or corn smut, which we will discuss as being representative of smuts, is restricted in its parasitism to corn. Corn smut may infect any part of the corn plant, but generally occurs on the ears, tassels, leaves, or stalks.

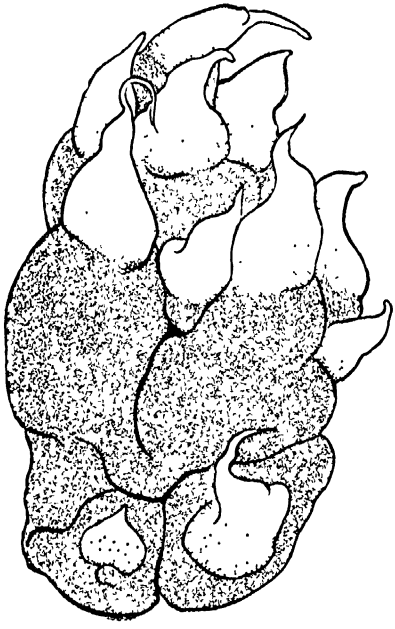


FIG. 24.3 Tumorous swellings of corn kernels due to infection with *Ustilago maydis* (advanced stage).

Life Cycle of Ustilago maydis. Infection of the corn plant begins with the germination of basidiospores. The hyphae from such basidiospores penetrate the epidermis and thereafter grow horizontally through tissue just subjacent to the epidermis. These hyphae are uninucleate. If they are from two different

strains of basidiospores (plus and minus), the uninucleate mycelia conjugate to form a diploid or binucleate mycelium. Some of the cells of this binucleate mycelium now enlarge to form chlamydospores. The original wall of the cell gelatinizes, and within this gelatinizing wall is formed the characteristically sculptured wall of the chlamydospore. With the complete gelatination of the original cell walls, the chlamydospores separate from one another. In the meantime the mycelium in some way or other stimulates the cells of the host tissue to

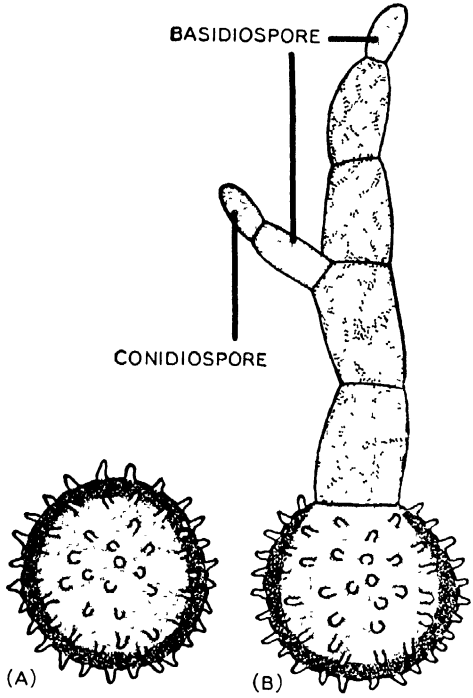


FIG. 24.4 (A) Chlamydospore of *Ustilago maydis*, (B) germinated chlamydospore with four-celled basidium.

divide and redivide. The resulting hyperplasia of the tissue in the infected area—an area generally beneath the epidermis—reflects itself in the production of tumorous swellings on the ear or tassel, as the case may be (Fig. 24.3). Finally these swellings partake of the nature of a fairly large gall. If examined at this time, a gall is found to be composed of the epidermis of the part of the infected area beneath which is a powdery accumulation of black chlamydospores commingled with what remains of the host tissue. As soon as the epidermal

layer of the gall undergoes desiccation, it ruptures to discharge mature chlamydospores.

The chlamydospores (Fig. 24.4A) are generally dispersed by air currents. Usually they hibernate and germinate in the following spring. The chlamydospore is binucleate. At germination the nuclei unite to form a fusion nucleus, and this nucleus undergoes meiosis to form four haploid nuclei. In the meantime a short tubular outgrowth is produced by the chlamydospore (Fig. 24.4B). Into this outgrowth migrate the four nuclei. Septation follows, and a four-celled basidium is thus developed. Now each cell of the basidium evaginates to form a small bud. The nucleus of the budding cell of the basidium divides mitotically, and subsequently one of these daughter nuclei enters the bud to form a basidiospore. Sometimes this basidiospore, either before or after its detachment from the basidium, may itself bud to form a conidiospore. Either the basidiospore or the conidiospore budded from it is infective to the corn plant. They are generally disseminated by the wind.

Economic Significance. Some concept as to the economic impact of these smuts may be realized from the reported observation that smuts are able to reduce grain yield by as much as fifty per cent.

PUCCINIA GRAMINIS

Rusts in general are obligate parasites. Though they are especially destructive to the cereals (wheat, rye, barley, and the like) they also parasitize fruits, vegetable crops, forage crops, and forest trees (pine especially). In fact these fungal organisms may attack any species of seed plant. In the life cycle of any rust there is invariably encountered a thick-walled spore, called a *teliospore*. This is either stalked or sessile and may be constituted of a single cell or several cells. Each cell of the spore is binucleate. On germination each cell of the teliospore puts forth a club-shaped outgrowth as the two nuclei of the cell fuse; the fusion nucleus divides meiotically. The four haploid nuclei pass into the outgrowth; septation follows; the outgrowth becomes a four-celled basidium. Each cell of the basidium ultimately forms a sterigma into the inflated tip of which the nucleus migrates to form a basidiospore.

Wheat rust (*Puccinia graminis*), the most destructive of all the rusts, usually requires two hosts in its cycle: wheat (*Triticum vulgare*) and the common barberry plant (*Berberis communis*). In the complete life cycle of this fungal parasite, five different types of spores

are produced. It is to the sequence of this spore production that we shall address ourselves.

Life Cycle of Puccinia graminis (Fig. 24.5). The first evidence that a wheat plant is infected with *Puccinia* is the appearance of reddish-brown streaks or pustules on the wheat leaf or stem. These pustules, since they are composed of uredospores, are termed *uredosori.* Microscopic examination of the pustular area reveals the uredospores to be stalked, spiny, ovoid, binucleate spores. They are easily abstricted and are dispersed by air currents to other wheat plants in the vicinity. Upon coming to rest upon a wheat leaf, the uredospore germinates within a few hours by forming a germ tube. The germ tube ultimately reaches a stoma through which it attains the intercellular spaces among the mesophyll tissues of the wheat leaf. Here the hypha develops into a greatly branched, binucleate mycelium which ramifies through the intercellular spaces, sending haustoria into the cells of the mesophyll tissue. Within several days, from the compacted hyphae just beneath the upper epidermis there is formed a row of binucleate basal cells. Each basal cell then divides to form two cells. The lower daughter cell undergoes no further division and is termed a *foot cell.* The upper daughter cell divides again. The upper daughter cell of this division becomes a uredospore, and the lower daughter cell differentiates into the elongated stalk cell, which supports the uredospore. The overlying epidermis of the wheat leaf ruptures at this time, and the uredospores are again disseminated by air currents. Throughout the summer months, the short cycle—uredospores → binucleate mycelium → uredospores—will repeat itself over and over again in the wheat field.

Near the end of the summer, however, the binucleate mycelium, instead of producing binucleate uredospores, forms stalked, bicellular, thick-walled spores called *teliospores.* Each cell of such a teliospore is at this time binucleate. These teliospores betray their presence on either wheat stem or leaf in the formation of elongated black streaks. These black pustules, since they are composed of teliospores, are sometimes referred to as *teliosori.* The teliospores remain dormant during the winter and may be found on old wheat stalks around the wheat field. In the following spring there emanates, as already described, from each cell of the teliospore a four-celled basidium. Each cell of the basidium comes to support a sterigmatically borne basidiospore. Half of these basidiospores are plus and half are minus in strain

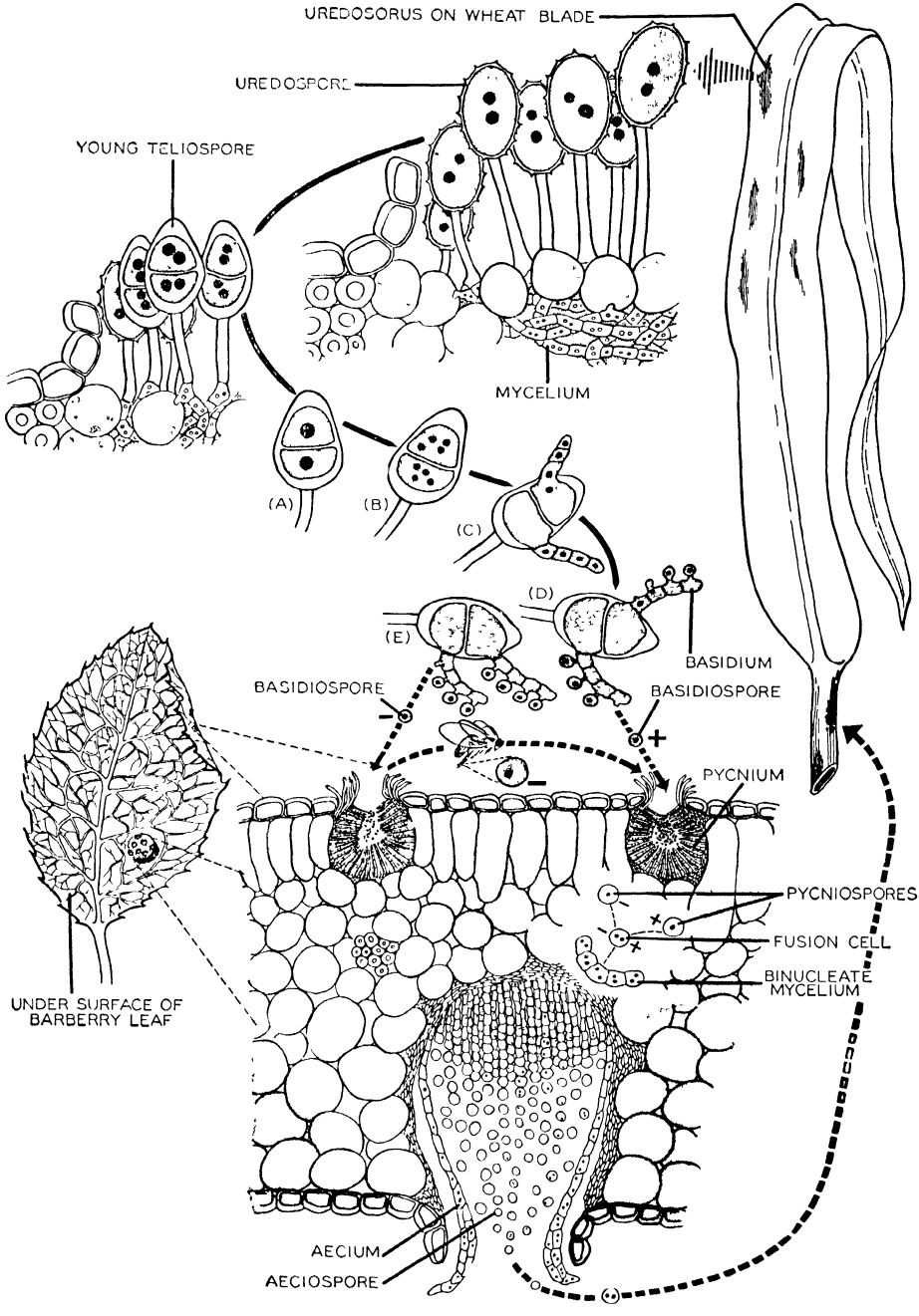


FIG. 24.5 Life cycle of *Puccinia graminis*. (A) mature teliospore, each cell possessing a fusion nucleus; (B) four haploid nuclei in each cell as a result of meiosis; (C) formation by the basidium of four sterigmatically borne basidiospores; (D) and (E) abstriction of plus and minus basidiospores.

–a fact to be remembered because, as will be evident subsequently, *'uccinia graminis* is heterothallic. In any event these basidiospores are ather violently abstricted from their sterigmata and are dispersed by vind currents.

Should the basidiospore settle upon the young leaves of a barberry ılant, the basidiospore germinates to form a germ tube which penerates the outer wall of the epidermal cell and there gives rise to a hort uninucleate hypha, from each cell of which in turn arises a ıyphal branch. These hyphal branches form a rather extensive myelium which ramifies through the intercellular spaces of the mesoıhyll tissue of the barberry leaf. Around the third or fourth day after ınfection, hyphae begin to compact themselves beneath the upper ·pidermis of the leaf. From these matted hyphae, the primordium of he pycnium or spermagonium, there originate erect hyphae that ·orradiate to a common area just beneath the overlying epidermis, vhich now is somewhat elevated. The converging erect hyphae, to-;ether with sterile hyphae (*paraphyses*) of the area, become finally ırganized into a flask-shaped structure called the *pycnium* or *spernagonium,* which erupts on the epidermis in an ostiolate opening. The uninucleate fertile hyphae of the pycnium cut off at their ends mall spherical, uninucleate spores called *pycniospores* or *spermatia.* These spores, after their abscission, congregate in the nectar-like ecretion from the paraphyses. This secretion exudes through the ıstiole of the pycnium and is attractive to insects. The pycniospores ıre either plus or minus in strain, according to the strain of basidiopore originally deposited on the leaf. Extending out of these pycnia ıre trichogynes, or flexuous hyphae.

The next step in the cycle is the transfer of pycniospores or permatia of one strain to the pycnia or spermagonia containing ›ycniospores of the opposite strain. Insects serve as vectors. Thus pyc-ıiospores of opposite strains are brought into contact, or pycniospores ›f one strain may be brought into contact with a trichogyne extending ›ut of a pycnium of the opposite strain (Fig. 24.6). In the latter case he pycniospore fuses with the receptive trichogyne and subsequently ›asses down through the trichogyne to unite with its basal cell, sometimes rather loosely referred to as an "egg" cell. In any event, whether ·ombination involves two pycniospores of opposite strains or the union ›f a pycniospore with a basal cell of a trichogyne, there is formed a ›inucleate fusion cell, sometimes called an *aeciospore mother cell.*

This binucleate fusion cell gives rise to a binucleate mycelium which in a manner as yet unexplained attains the area near the lower epidermis to form an open cup-shaped mycelial structure termed an *aecium*. This aecium contains a columnar disposition of binucleate basal cells that stem from a compacted hyphal mass at its base. From these binucleate basal cells are formed by division numerous binucleate aeciospores.

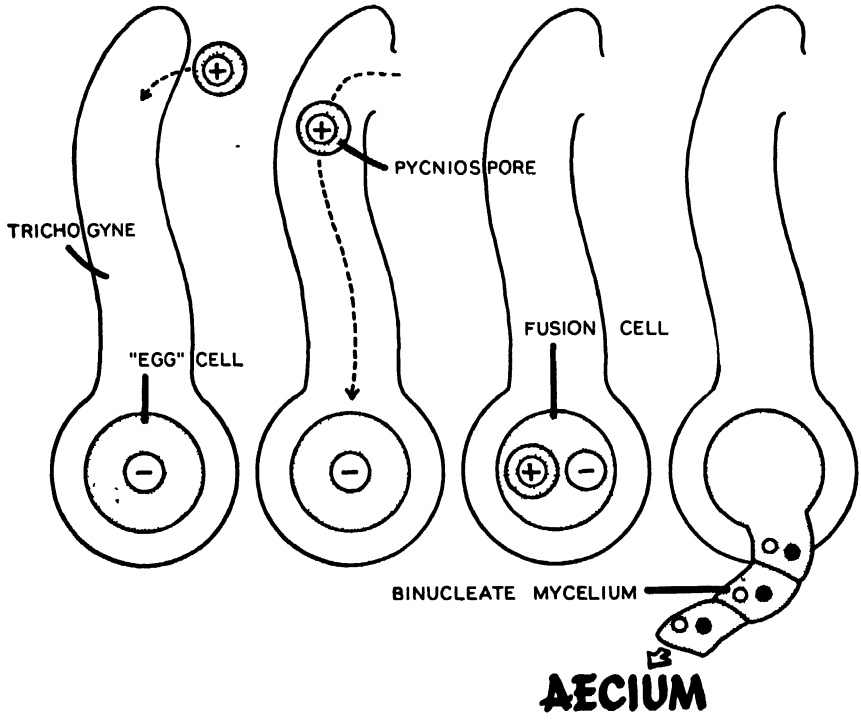


FIG. 24.6 Sexual reproduction in the life cycle of *Puccinia graminis*.

The aeciospores are produced in the late spring. If brought into contact with a wheat leaf or stem, they will germinate to form a binucleate hypha that enters the wheat leaf through a stoma. From that binucleate hypha a binucleate mycelium is produced that ramifies through the mesophyll of the wheat. Ultimately this binucleate mycelium becomes compacted beneath the upper epidermis to give rise to uredospores. Thus the cycle resumes.

As must be obvious at this point, there is in the long cycle the alternation of a sporophyte generation with a gametophyte generation.

Economic Aspects of Wheat Rust. Some concept of what *Puccinia graminis* can do to wheat crops may be realized from the fact that in the great rust epidemic of 1916 the wheat yield in the United States was reduced by some 140,000,000 bushels. Removal of barberry plants has in the interim moderated the effect of recurrent rust infestations. It has been calculated that in some ten states where the removal of the barberry plants has been made mandatory, the annual loss of wheat has been brought down from 50,000,000 bushels to 9,000,000 bushels. Even with this reduction in wheat loss, the monetary losses still remain in the million-dollar brackets so far as the farmers are concerned. Spraying the wheat crop with sulfur dust is widely practiced in California and Canada and has been reported to increase the crop yield of wheat. To make matters worse, it has also been discovered that in Mexico and Texas, where the winter climate is relatively mild, the uredospores are capable of overwintering without any impairment of their virulence. In the following spring these uredospores reinfect wheat plants. Wind currents can carry these same uredospores into the northern states, where they can infect young wheat plants—all this, mind you, without either the production of teliospores or the presence of the alternate host, the barberry plant!

The breeding of rust-resistant varieties of wheat in both the United States and Canada has resulted in a substantial increase in the crop yield—and perhaps herein lies the solution of the wheat rust problem that continues to confront us.

Chapter 25

THE LICHENS

LICHENS are variously colored, autotrophic, thallophytic, composite organisms consisting of an algal and a fungal plant living intimately together in symbiotic relationship. In this type of organismal association, termed *symbiosis*, the partners derive mutual benefit since the

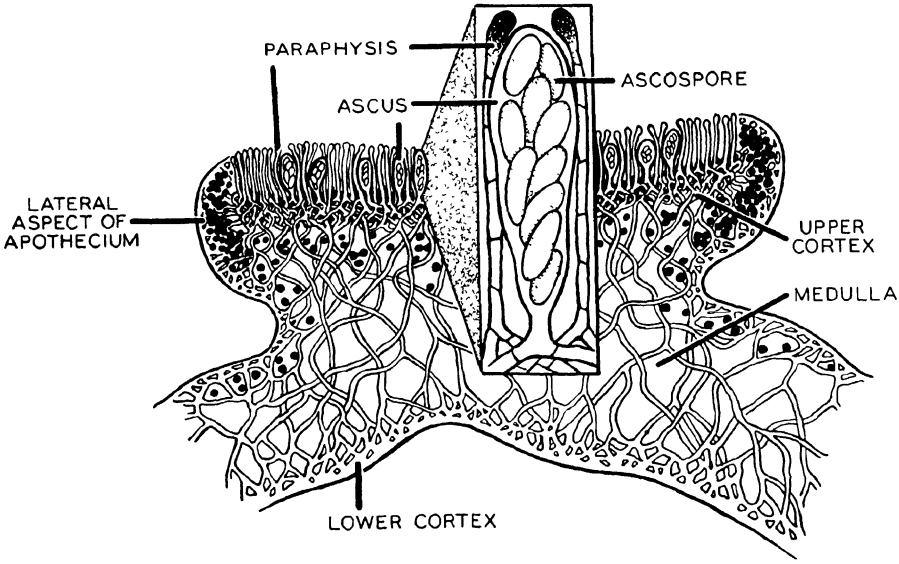


FIG. 25.0 Vertical section of the foliose lichen, *Physcia*. The asci and paraphyses are visualized as contained in an apothecium.

fungal partner obtains food from the photosynthetic algal cells and protects the algal cells from drought by its ability to absorb and retain water. Lichens are able to grow without an organic substrate and under adverse conditions of temperature and moisture. In size they

range from those which are minute to those which are several feet in length. They have a wide distribution on all continents and grow on rocks, on soil, on sand, and on the bark of trees.

The algal components of the lichens belong either to the class Chlorophyceae or the class Cyanophyceae. Examples of such components are *Protococcus, Gloeocapsa, Rivularia,* and *Nostoc.* The fungal component in the great majority of cases is an ascomycete. In a

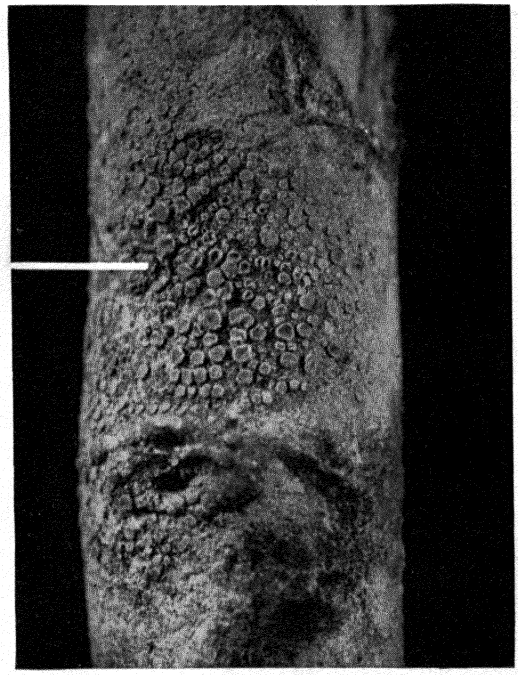


FIG. 25.1 A crustose lichen on the bark of a stem.

limited number of cases it is a basidiomycete. On the basis of the fungal component present, the lichens can be subdivided into the ascolichens and the basidiolichens.

In most lichens the bulk of the plant body is composed of interwoven fungal hyphae, and the algal cells occur in groups enmeshed with the hyphae. Strands of hyphae attach the lichen to the substrate. With respect to the form of the plant body the lichens are divided into three groups: the crustose (Fig. 25.1), the foliose (Fig. 25.2), and the fruticose (Fig. 25.3). The *crustose* lichens appear as crusts on such substrates as rock and bark. The *foliose* lichens are flat and

leaf-like and are usually lobed or branched. The *fruticose* lichens are slenderly branched and are either erect or pendant.

In the foliose lichen *Physcia,* illustrated in vertical section in Fig. 25.0, the uppermost layer, called the *upper cortex,* is constituted of a compacted mass of hyphae from which are seen to arise paraphyses and asci. Directly below the upper cortex is the algal layer. The middle portion, called the *medulla,* is composed of loosely interwoven

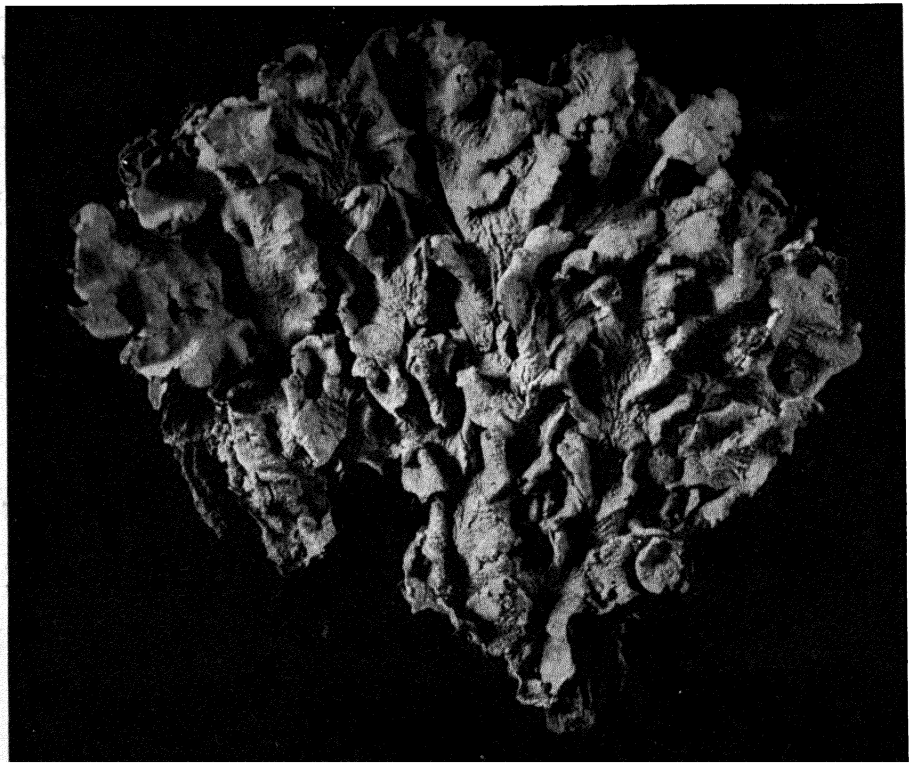


FIG. 25.2 A foliose lichen. Apothecia are discernible.

hyphae. The lowermost layer, called the *lower cortex,* presents a compacted hyphal mass from which arise rhizoidal hyphae.

Reproduction in the lichens is largely by fragmentation or by soredia formation, both of which are vegetative processes of multiplication. In fragmentation a portion of the plant body becomes separated from the remainder of the plant and is disseminated by the wind or water. *Soredia* are minute reproductive bodies consisting of one or

more algal cells embraced by a few fungal hyphae. They appear as outgrowths from the surface of the lichen thallus. When they become separated from the thallus, they are disseminated by wind or water and can develop into a new individual.

In ascolichens ascogenous hyphae arise from fertilized ascogonia. The ascogonia are situated rather deep in the algal layer. Each ascogonium generally terminates in a trichogyne. Flask-shaped bodies,

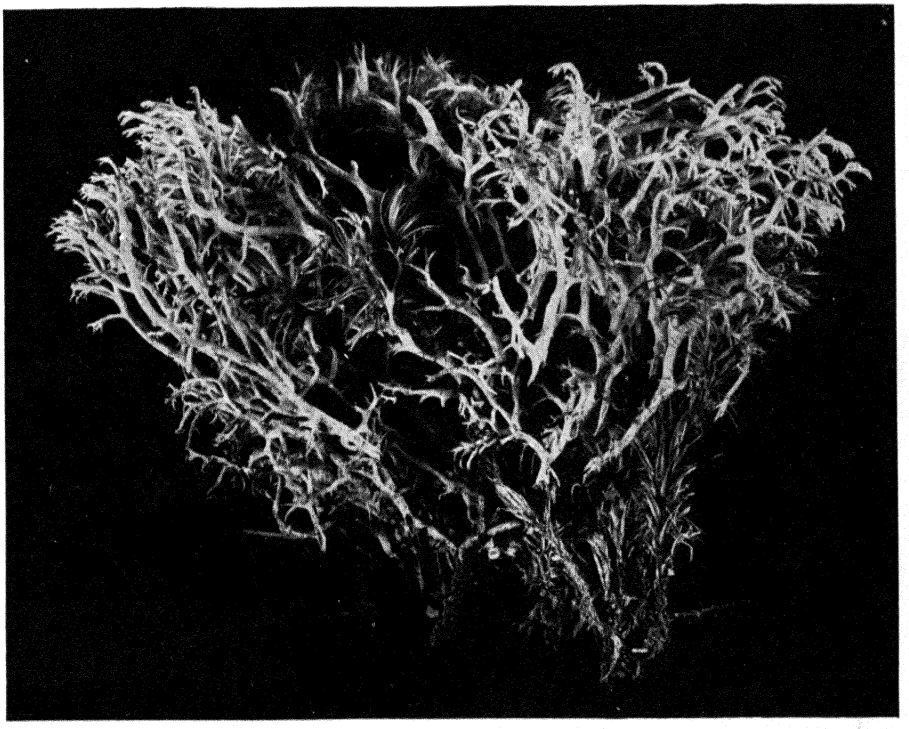


FIG. 25.3 A fruticose lichen.

called *spermogonia,* are generally located near the ascogonia. Within these spermogonia are formed spermatia. On the basis of the observation that many empty spermatia are found closely applied to the trichogyne, it is assumed that the spermatia migrate to the trichogyne and that the protoplasts of the spermatia enter the trichogyne to attain the ascogonial nucleus. In any event, from the fertilized ascogonium arise ascogenous hyphae. These ascogenous hyphae may recurve terminally to form croziers, the penultimate cells becoming asci. The formation of the ascospores is similar to that described for the As-

comycetes, Chapter 22. The ascogenous hyphae with their asci may be ultimately contained in an apothecium (Figs. 25.0 and 25.2) or in a perithecium.

In the basidiolichens, basidia are formed. Each of these basidia bears four sterigmata, each of which is surmounted generally by a basidiospore.

The crustose lichens are the pioneers of the plant world, since they are the only plant organisms which can establish themselves on bare rock and initiate the formation of soil in which other plants can grow. They break down the rock surface probably in two ways. The carbon dioxide produced by the lichen reacts with water to form carbonic acid, and this, together with organic acids excreted by the lichen, dissolves rock. The drying of the lichen thallus during periods of drought results in its shrinkage, and this causes tiny particles of the rock to be torn away. The decay of the older parts of lichens results in the formation of small amounts of humus. The minute rock particles and the humus mixture become a trace of soil, in which some of the mosses can live. Upon the death of the mosses more soil is formed, and the higher plants can then establish themselves.

Lichens are of economic importance other than from the standpoint of soil formation. Various species are used as animal (reindeer and Iceland moss) and human food and as sources of tannins, dyes (e.g., orcein), aromatic substances, and other products.

Chapter 26

THE BRYOPHYTES

THE phylum Bryophyta is a group of relatively small plants embracing approximately 23,000 species which characteristically grow on land in moist and wet situations. They exist in all parts of the world where sufficient moisture is present to permit their growth. They are found on moist soil, on damp rocks, on decaying logs, on the trunks of living trees, and so on. A few species live submerged in fresh water.

Bryophytes lack true roots, true stems, and true leaves. Many of them have structures which superficially resemble these organs of the higher plants, but differ in that they lack the vascular tissues of these organs. The plant body, as in the thallophytes, is a thallus which varies from less than an inch to several inches in length. Root-like filamentous structures, known as *rhizoids*, attach the plant to the substrate and function in anchorage and absorption.

Alternation of generations is firmly established in the bryophytes. The gametophyte, though small, is conspicuous and independent. The sporophyte is the inconspicuous generation and is nutritionally dependent throughout its existence on the gametophyte. The gametangia are more complex than in the thallophytes and are in all cases multicellular. The male gametangium is still termed the antheridium, but the female gametangium is now referred to as the *archegonium*. Though the bryophytes for the most part are terrestrial, water is required for fertilization.

The phylum Bryophyta is divided into two classes: the class Hepaticae or the liverworts and the class Musci or the mosses. The class Hepaticae consists of the thallose liverworts (Marchantiales), the leafy liverworts (Jungermanniales), and the horned liverworts (Anthocerotales). The class Musci includes the bog or peat mosses (Sphagnales), the rock or granite mosses (Andreaeales), and the true mosses (Bryales). The word moss is applied to many plants which are

not mosses in the botanical sense. For example, reindeer moss is a lichen, Spanish moss is a flowering plant, and the club mosses are lycopods.

General Characteristics. The gametophytes of the liverworts are dorsiventral and grow prostrate on the substrate. Some, such as *Riccia* and *Marchantia,* have a leaf-like body, while others, such as *Porella,* are differentiated into a leafy shoot. The mosses resemble in some respects the leafy liverworts. They differ, however, in that the moss spore on germination forms a branching, chlorophyll-containing, multicellular filament, the *protonema,* from which the leafy upright shoots arise; and in that the mature moss gametophyte shows more cellular differentiation. The species of moss is in some instances related to the pH of the substrate. The haircap or pigeon-wheat moss (*Polytrichum*) grows almost wholly in acid substrate. The cord moss (*Funaria*) is largely limited to alkaline or neutral substrates. *Mnium* grows in both acid and alkaline situations.

Economic Importance. Bryophytes are of economic importance in a number of ways. They assist in the prevention of soil erosion. Together with the lichens they build up soil on rocks. Peat, a fuel, is derived largely from *Sphagnum* and other mosses. *Sphagnum,* because of its remarkable water-absorbing capacity, is utilized by florists and horticulturists as a packing material around the roots of shrubs and trees when they are to be transported and replanted. It is also added to soil to increase soil porosity.

The structure and life cycles of *Marchantia polymorpha* (a liverwort) and *Polytrichum commune* (a moss) are now presented to illustrate the general characteristics of the liverworts and the mosses.

MARCHANTIA POLYMORPHA

The conspicuous or gametophytic plant (Fig. 26.0) is a flat, dichotomously branched thallus. Its upper or dorsal surface presents a clearly discernible midrib. A closer examination of the dorsal surface reveals it to be marked by fine lines. These demarcate the surface into a number of polygonal areas, in the center of each of which there is a pore or stoma (Fig. 26.0A). In a microscopic cross section of the thallus, each stoma will be observed to perforate the upper epidermis so as to communicate below with an air chamber. These air chambers are separated from each other by filamentous partitions. From the floor of each air chamber arise short, branched, green filaments of

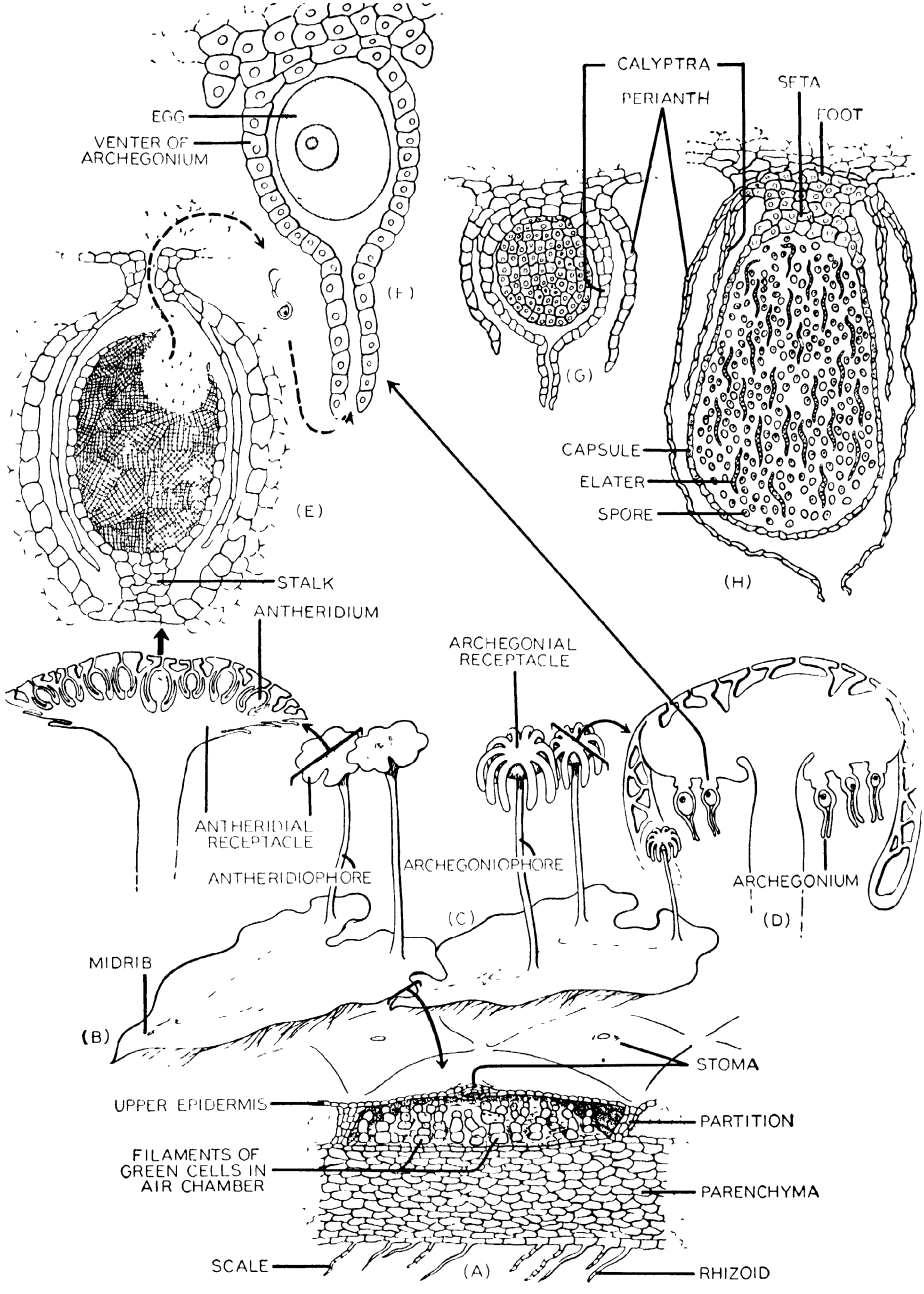


FIG. 26.0 *Marchantia polymorpha:* (A) section through the thallus; (B) thallus with antheridial receptacles, (C) thallus with archegonial receptacles; (D) enlarged view of an archegonial receptacle to show the suspension of archegonia; (E) enlarged view of an antheridium; (F) detailed view of an archegonium; (G) immature sporophyte; (H) mature sporophyte.

cells. These filaments of chlorophyllous cells constitute the main photosynthetic mechanism of the thallus. Below the air chambers are several layers of parenchymatous tissue with a rather sparse distribution of chloroplastids in its cells. The lower or ventral surface is a layer of epidermal cells. Some of these evaginate into rhizoids, the functions of which are anchorage and absorption. From the lower epidermis also issue forth septated outgrowths, called *scales.* The latter are believed to be protective in function.

Antheridia and Archegonia. Marchantia is a dioecious plant; that is, the male and female gametangia occur on separate thalli. The male gametangia or antheridia are contained in separate cavities of a peripherally lobed disc, the *antheridial receptacle* (Fig. 26.0B). This in turn surmounts a slender stalk, the *antheridiophore,* that rises up from the dorsal surface of the thallus. The antheridial cavities of the receptacle open by pores on the upper surface of the receptacle. Within each of these antheridial cavities is contained a single antheridium. Each antheridium (Fig. 26.0E), supported by a cellular stalk, is characteristically pear-shaped and contains a mass of spermatogenous cells enclosed by a single layer of sterile parietal cells. Ultimately each spermatogenous cell undergoes an oblique mitotic division to form two biciliate microgametes. Contact with water causes the disintegration of the sterile parietal cells of the antheridium, with the result that the biciliate sperm are liberated.

On the other hand, the archegonia (Fig. 26.0D) are suspended from the lower surface of a disc-like structure termed the *archegonial receptacle.* From the center of its upper surface originate rays that droop themselves over the peripheral margin of the archegonial disc. These pendant rays characterize the archegonial receptacles. As in the case of the antheridial receptacle, each archegonial receptacle (Fig. 26.0C) surmounts a slender supporting stalk called the *archegoniophore.* Each archegonium is a flask-shaped structure (Fig. 26.0F). The enlarged portion which is suspended from the undersurface of the receptacle is called the *venter* and tapers into a slender neck. The venter contains the egg or macrogamete. When immature the neck of the archegonium is occluded by several neck canal cells, the one nearest the egg being termed the *ventral canal cell.* The free end of the neck is also closed off by cap cells. At maturity the cells in the neck of the archegonium disintegrate, and the cap cells diverge. Thus

there is effected a patent neck for the passage of the biciliate sperm to the egg in the venter.

Note that though *Marchantia* is a terrestrial plant, water is necessary for the biciliate sperm to attain to the archegonia.

Fertilization. Only one biciliate sperm is necessary to fertilize the egg in the venter. The zygote ultimately differentiates into a mature sporophyte which consists of three parts (Fig. 26.0H): the foot, seta, and capsule. The *foot,* an absorbing organ, becomes embedded in the megagametophytic tissue, for the sporophyte throughout its existence is parasitic upon the gametophyte. Extending down from the foot is a small stalk, the *seta,* at the lower end of which there is attached an oval capsule. The wall of this capsule is constituted of a single layer of cells and initially encloses a mass of diploid sporogenous cells. These sporogenous cells divide mitotically to form spore mother cells and elaters. The *elaters* are fusiform cells with spirally thickened walls. Being hygroscopic, the elaters twist and turn in response to moisture changes in the atmosphere and thus play a significant role in the ultimate dispersal of the spores. In the meanwhile the spore mother cells undergo meiosis to produce haploid homospores. As the sporophyte is being formed, the original venter wall becomes commensurately enlarged to enclose the developing sporophyte. The enlarged venter, now termed a *calyptra* (Figs. 20.6G and H), is also ensheathed by a cylindrical sheath, the *perianth,* which has developed from a ring of tissue around the base of the original venter. As the sporophyte approaches maturity, the seta elongates to push the capsule through the enclosing calyptra and perianth. The capsule is ruptured, and the hygroscopic elaters aid in the dispersion of the spores. Each spore possesses a two-layered wall, the outer layer being called the *exine* and the inner one the *intine.* Germination involves the absorption of water by the spore as a result of which the exine is ruptured. The intine then evaginates to form a tube into which passes most of the original protoplasm of the spore. The end of the tube is finally septated by a cross wall to form a terminal cell. This cell subsequently divides to form a cellular mass from which a haploid green thallus ultimately develops.

Vegetative Reproduction (Fig. 26.1). Thus far we have considered only sexual reproduction. However, many thalli of *Marchantia* are able to propagate themselves vegetatively or asexually. On the

dorsal surface of these thalli are found cup-shaped structures, called *gemma cups,* within which are contained stalked discs, termed *gemmae.* These gemmae are easily abstricted from their fragile stalks. Each gemma is simply a fragile cellular mass notched on opposite sides. On coming to rest on suitable substrate, the lower surface of the gemma develops a number of rhizoids. The cells around each notch divide to form a green thallus. Thus each gemma gives rise to two thalli. The central portion of the original gemma, having no part in the formation of the thalli just mentioned, disintegrates.

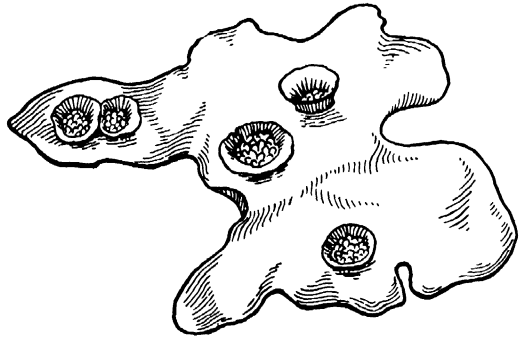


FIG. 26.1 Gemmae cups on the thallus of *Marchantia polymorpha.*

POLYTRICHUM COMMUNE

The gametophyte consists of a "stem" bearing spirally arranged "leaves" (Figs. 26.2A and B). From the base of the "stem" arise septated filaments, called *rhizoids,* that extend into the soil or other substrate. These rhizoids serve to anchor the moss plant and to absorb water and solutes from the soil. It must be emphasized here that *Polytrichum,* or any moss for that matter, does not possess a true stem or true leaves in the strict anatomical sense of these terms. These terms are being utilized simply for convenience of reference. The stem of the moss contains no vascular tissue nor does the leaf possess characteristic mesophyll tissue or stomata. The so-called stem of the moss is composed of an epidermis, a cortex of parenchyma, and a central area of elongated cells, some of which are thick-walled. The cortical cells generally are chlorophyllous and therefore photosynthetic in function, while the central cells are most probably concerned with storage and mechanical support. The leaf of the moss is generally composed of a single layer of chlorophyllous cells except at the so-

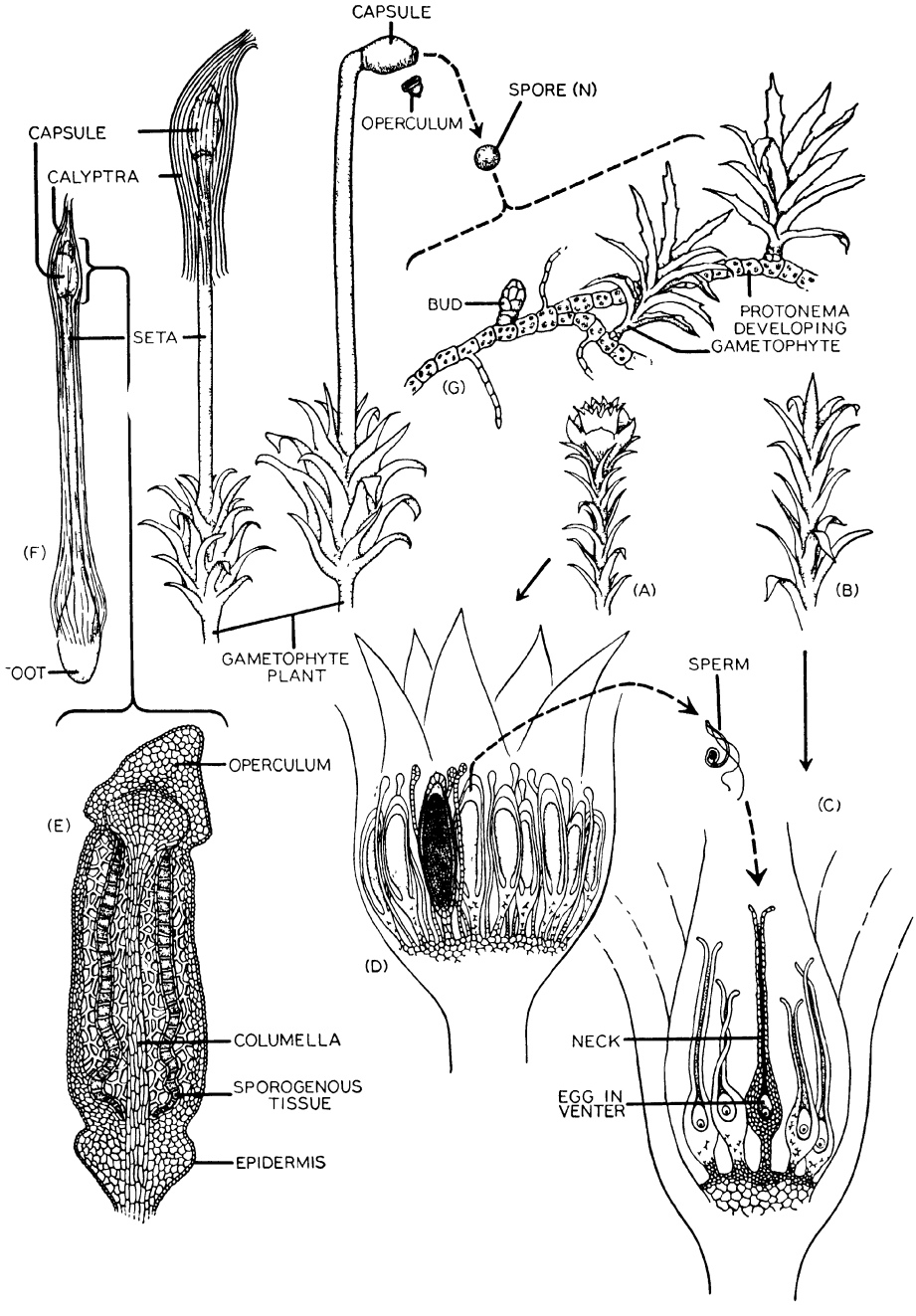


FIG. 26.2 *Polytrichum commune:* (A) male gametophyte; (B) female gametophyte; (C) longitudinal section through the tip of a female gametophyte; (D) longitudinal section through the tip of a male gametophyte; (E) longitudinal section through the capsule; (F) sporophyte; (G) protonema.

called midrib. In *Polytrichum,* however, the leaf is thicker, since vertical rows of chlorophyllous cells rise up from the upper surface of the midrib and adjacent laminate tissue. Thus there is provided a greater surface area for gaseous interchange.

Polytrichum is a dioecious plant, though there are some monoecious mosses. In both the male gametophyte and female gametophyte of *Polytrichum,* the gametangia are borne in terminal clusters at the ends of the stem. The stem of a male gametophyte (Fig. 26.2A) may be readily distinguished from that of a female gametophyte by its terminal antheridial cup, which is due to the fact that the leaves are formed into a rosette around the terminal cluster of the antheridia.

Antheridia and Archegonia The antheridia (Fig. 26.2C), like those of *Marchantia,* are club-shaped and borne on cellular stalks among sterile filaments of cells, called *paraphyses.* The spermatogenous cells in the antheridium divide to form spirally coiled biciliate microgametes or sperm. At maturity the apical portion of the antheridium ruptures, and the biciliate sperm are discharged in a mucilaginous fluid. The archegonia (Fig. 26.2D) are, as in *Marchantia,* typically flask-shaped and each consists of a venter and a rather long neck. At maturity the neck canal cells and ventral canal cell deteriorate, forming a mucilaginous material; the cap cells diverge. It is believed that sugars derived from the mucilaginous mass in the archegonial neck diffuse into the surrounding water and that the sperm respond chemotactically to these sugars. Water obviously is necessary for fertilization.

Sporophyte Generation. The zygote that finally comes about in the venter after fertilization divides to form a mature sporophyte (Fig. 26.2E) consisting of a foot, seta, and capsule. As in *Marchantia,* the wall of the venter and neck becomes enlarged to form a calyptra. The seta rapidly elongates, pushing the capsule ahead of it. The calyptra (Fig. 26.2E) at this time generally becomes detached from the base of the archegonium and appears as a hood draped over the capsule as the seta continues to rise out of the leafy recesses of the female gametophyte. The calyptra finally falls away as the capsule matures.

The capsule (Fig. 26.2F), which is a highly modified structure in contrast to that of *Marchantia,* will now be described in some detail. Macroscopically the capsule is a four-sided sporangium, the free end of which is capped with a lid or *operculum.* Microscopically the capsule possesses an epidermis which may be perforated by stomata

near its basal portion. Beneath the epidermis are generally several layers of parenchyma. Chloroplastids may occur in some of the parenchymatous cells. Beneath the parenchymatous wall cells, there are generally large air spaces traversed by green filaments of cells. Further, within the capsule is a zone of sporogenous tissue which surrounds a central shaft of sterile parenchymatous cells. This central mass of sterile parenchyma is generally referred to as the *columella*. Distally, or at the free end of the capsule, the columellar tissue of the young capsule projects itself as a dome-shaped mass beyond the enclosing sporogenous tissue. The outermost cells of this dome-shaped mass are modified into a lid or operculum. The inner cells contribute to the formation of the epiphragm and peristome. The *epiphragm* is a circular plate of tissue. It is peripherally connected to the apices of small dentations or teeth so disposed as to form a definite fringe, which is attached in turn to the thickened rim (*annulus*) of the capsule in this area. This fringe of teeth is collectively referred to as the *peristome* and is hygroscopic. When the teeth are erect and very closely adherent to each other, the epiphragm is elevated, so to speak, in such a manner as to completely occlude the mouth of the capsule. During periods of dryness, however, the teeth curve inward; the disposition of the epiphragm is altered in such a way as to create a narrow gap between its own peripheral margin and the rim of the capsule. The narrow gap is bridged by the loosely disposed teeth so that there is finally formed a peripheral sieve-like mechanism through which the spores sift out.

Gametophyte Generation. The spores are haploid and result from meiosis of the spore mother cells which collectively make up the sporogenous tissue already mentioned. The spores on the attainment of a suitable environment each germinate to form a branched green filament, the *protonema* (Fig. 26.2G). The protonema is anchored to the soil or other substrate by septate rhizoids. Some of the filamentous branches of the protonema bear buds. From each bud develops an upright stem bearing spirally arranged leaves—the gametophyte. The cycle is thus complete.

Chapter 27

THE HORSETAILS

THE subphylum Sphenopsida of the phylum Tracheophyta consists of the single class, Equisetineae. This class consists of three orders, only one of which, the order Equisetales, is represented by both fossil and living species. The other two orders include fossil forms only. Sporophytes of all Sphenopsida have true roots, stems, and leaves. Distinct nodes are present on the hollow stems. Whorls of generally small leaves occur at the nodes of the aerial stem and its branches. Special stem appendages, called *sporangiophores,* bear sporangia. The sporangiophores are grouped to form cones.

Order Equisetales. The horsetails or scouring rushes constitute the order Equisetales. This order includes fossil forms as well as the sole extant genus *Equisetum,* with its approximately twenty-five species. The members of the genus *Equisetum* are found all over the world except in New Zealand and Australia. A familiar species of *Equisetum* is *Equisetum arvense,* the common horsetail. It is found growing in sandy areas along streams and lakes and also in the dry gravel along railroad tracks and railroad embankments.

LIFE CYCLE OF EQUISETUM ARVENSE

The sporophyte (Fig. 27.0) consists of a horizontal, branching, perennial rhizome, small branching fibrous adventitious roots, and two types of jointed aerial shoots. The distinct nodes of the rhizome bear whorls of scale-like leaves. The nodes of the sterile, green aerial stem bear small, laterally fused scale-like leaves arranged in whorls. Whorls of green branches arise from the axils of these leaves, and they in turn give rise to branches, all of which bear rudimentary leaves at their nodes. The arrangement of the branches gives the sterile shoot a bushy appearance from which the plant derives the name "horsetail." The photosynthetic tissue of this plant is the chlorenchyma of the stem.

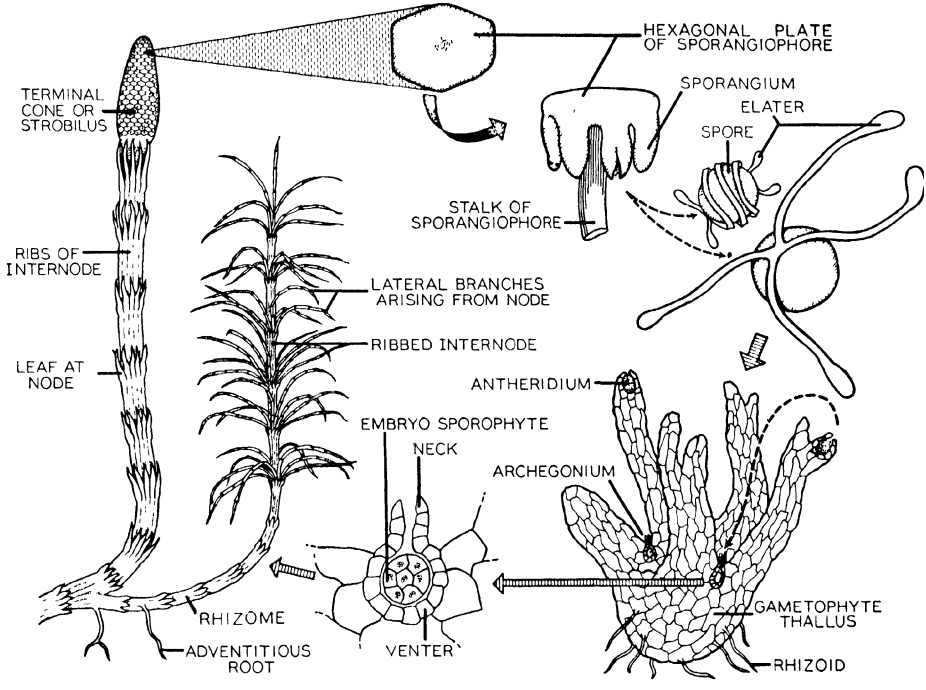


FIG. 27.0 Life cycle of the horsetail (*Equisetum arvense*)

The internodal portion of the stem in cross section is seen to consist of a siphonostele, cortex, and epidermis. The pith of the stele soon disappears, and older stems are hollow. The outer walls of the epidermal cells are covered with a deposit of silica. The presence of this abrasive substance led to the use in former years of the ash of certain species of *Equisetum* for scouring metal household utensils, and hence the name "scouring rushes" for these plants.

The rhizome persists throughout the winter, and new aerial stems develop each year. In the spring the first aerial stems which arise from the rhizome are usually the fertile unbranched aerial stems. When mature they are a few inches to a foot in height. The fertile stem bears a circle of small, partially fused scale-like leaves at each node, and at its apex is a single cone. Each terminal cone consists of a central axis bearing whorls of closely arranged sporangiophores. Each sporangiophore consists of a short stalk at whose outer end is an hexagonal plate disposed at a right angle to the stalk. Each plate bears a number of slender marginal sporangia on its inner surface. The spore mother cells in each of the sporangia undergo meiotic division to form spores. All living species of *Equisetum* are homosporous. When the sporangiophores are mature, they wither, and the

sporangia are split open longitudinally to permit the escape of spores. After spore liberation the fertile branches die. Before spore discharge the outer layer of the spore wall unfolds in the form of four thin, coiled, hygroscopic bands called *elaters*. The four elaters remain attached to the spore at one point. When they are moist, they are coiled around the spore. When they are dry they extend outward. They probably function in spore dispersal.

The spores germinate within a few days after they are shed. Each spore gives rise to a small, green, dorsiventral, prostrate, gametophytic thallus. When mature this consists of a thick, central, discoidal portion several layers of cells in thickness from the undersurface of which rhizoids develop. Irregular-shaped, flattened, erect lobes arise from the marginal regions of the central portion of the thallus. Antheridia and archegonia are borne on the same thallus when the gametophyte grows in its natural habitat. They are sunk in the thalloid tissue.

The antheridia are globular in shape and are borne near the apices of the erect lobes. Each archegonium consists of a venter and a neck and is borne on the upper surface of the central disc near the base of an erect branch.

Numerous multiciliate, spirally coiled sperms are produced in each antheridium. Each archegonium contains a single egg. A single sperm fuses with an egg to produce a zygote. This fusion, or fertilization, marks the beginning of a new sporophyte generation. The zygote undergoes repeated divisions to produce the embryo sporophyte, which later develops into a mature sporophyte in a manner similar to that which occurs in the true ferns, Chapter 29.

Chapter 28

THE CLUB MOSSES

In the Lycopsida the conspicuous plant is the sporophyte, which possesses roots, stem, and leaves. The stem and roots branch dichotomously, while leaves are generally small and spirally disposed about the stem. Sporangia are borne in the axils of sporophylls which are compacted, generally at the ends of upright stem branches, into *strobili.* The vascular tissue of the stem is usually in the form of a *protostele;* that is, there is a central core of xylem circumjacent to which lies a ring of phloem. The xylem may sometimes be peripherally lobed, with the phloem tissue interspersed among the lobes. The phloem is surrounded by a pericycle, adjacent to which lies a well-developed cortex and epidermis. This subphylum possesses one class, the Lycopodineae.

Class Lycopodineae. The class Lycopodineae is composed of five orders. The two main orders are the order Lycopodiales, or the larger club mosses, and the order Selaginellales or the smaller club mosses. The other three orders are the order Lepidodendrales, or the fossil giant club mosses; the order Isoetales, or the quillworts; and the order Pleuromeriales, which includes fossil types incorporating morphological features of both the fossil giant club mosses and the quillworts.

The order Lycopodiales includes the larger club mosses. The sporophytes are herbaceous. The main stem either lies prostrate along the soil surface or occurs as a rhizome just beneath the soil surface. From the main stem arise dichotomously branched upright stems bearing small, spirally disposed, evergreen, sessile leaves. Adventitious roots, sometimes also dichotomously branched, spring from the undersurface of the main stem. In most of the members of this order the sporangia are borne in the axils of the sporophylls, which are compacted in strobilate structures at the ends of the upright stems. The spores, resulting from the meiosis of spore mother cells in the spor-

angia, are all alike (homospores) and present a characteristic tetrad grouping. The plants of this order apparently received their common name because of the moss-like aspect of their leaves and their club-shaped strobili. Because their upright stems look so much like miniature pine trees, these club mosses are often referred to as ground pines and are commonly used as decorative Christmas greens because of their attractive evergreen moss-like appearance. The club mosses are world-wide in distribution, but occur chiefly in tropical and subtropical regions.

The smaller club mosses which constitute the order Selaginellales differ from those of the order Lycopodiales in being smaller and more fragile, and in that two kinds of spores (heterospores) occur in their life cycles. Both microgametophytes and megagametophytes occur. The sporangia are always found in strobili. Though the little club mosses are world-wide in distribution, they are found most abundantly in the tropics. The order Selaginellales consists of a single genus, *Selaginella,* which we will consider as a representative of the subphylum Lycopsida.

LIFE CYCLE OF SELAGINELLA

Some species of *Selaginella* (Fig. 28.0) have dichotomously branching stems which grow along the soil surface, while other species possess a stem whence arise upright branch stems. The stem and its branches bear small pointed leaves disposed into four longitudinal rows along the axis of the stem and its branches. The vascular tissue of the stem is in the form of either a protostele or a siphonostele. Adventitious roots may originate directly from the stem or from leafless branches, termed the rhizophores, of the stem.

Some of the dichotomous branches of the stem terminate in strobili (Fig. 28.0). These strobili are constituted of two types of sporophylls: the smaller sporophylls, the *microsporophylls* (Fig. 28.0), are situated near the apices of the strobili, while larger *megasporophylls* (Fig. 28.0) occur at the bases of the strobili. In the axils of the microsporophylls are located the microsporangia, which are small and ovoid, while in the axils of megasporophylls are situated the megasporangia, which are relatively larger. Initially the megasporangium contains many megaspore mother cells. Generally all of these megaspore mother cells degenerate, with the exception of one. The surviving mother cell subsequently divides meiotically to form a tetrad of haploid mega-

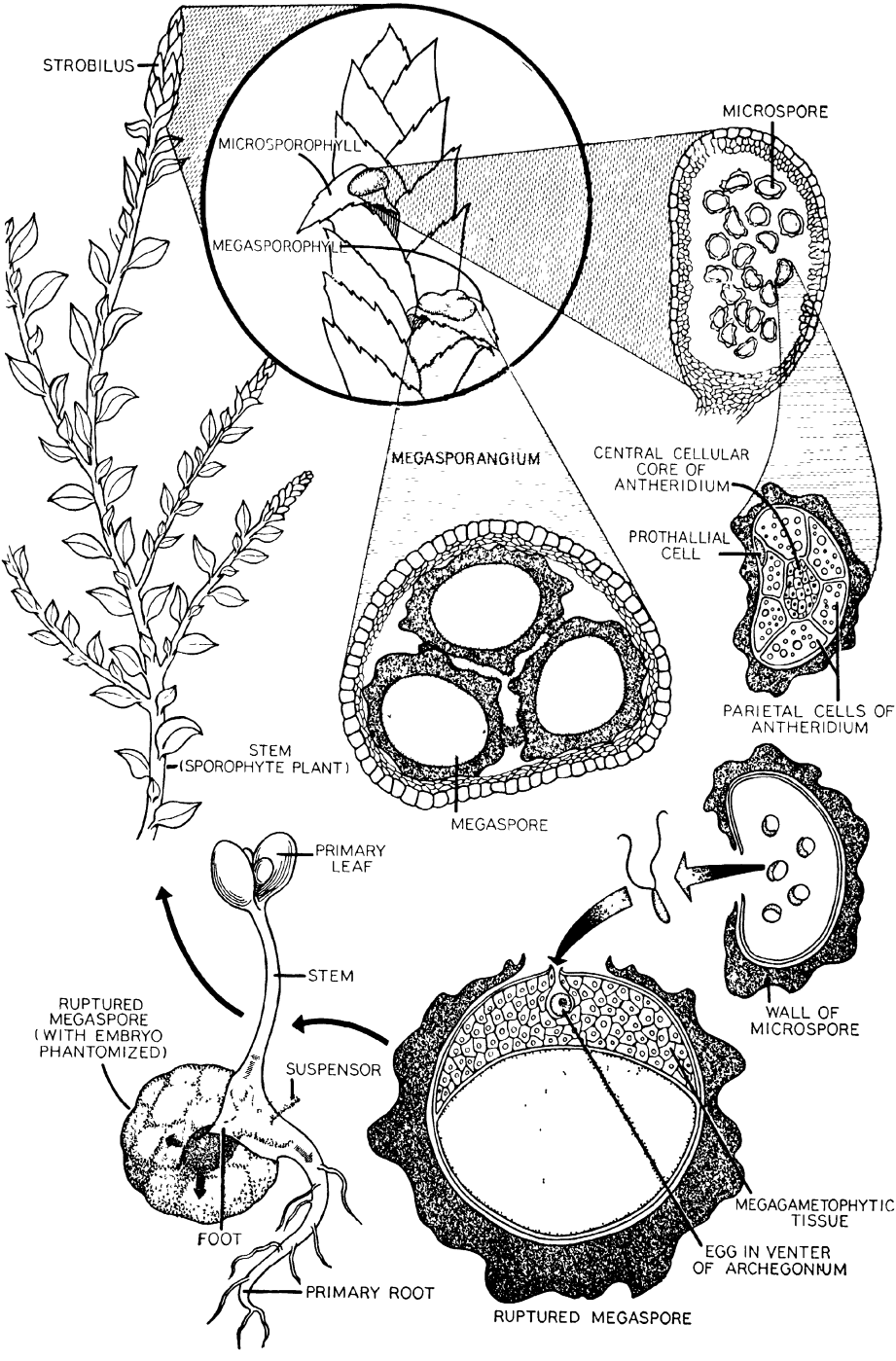


Fig. 28.0 Life cycle of *Selaginella*.

spores. Each of the megaspores becomes so allocated in the megasporangium that the megasporangium finally presents a four-lobed aspect. The microsporangium is filled with numerous haploid microspores, due also to meiosis of microspore mother cells.

Each microspore begins to germinate while still lodged in the microsporangium. The nucleus of the microspore divides; but because of unequal cleavage of the cytoplasm, there are formed within the confines of the microspore wall a large cell and a small cell. The bicellular microspores in many species of *Selaginella* are generally shed from the microsporangium at this time and either sift down among the sporophylls or fall to the ground. The small cell of the microspore is vestigial and is referred to as a *prothallial cell* (Fig. 28.0). The large cell, by mitotic differentiation, culminates in the development of the microgametophyte. Initially the microgametophyte (in this case just a single antheridium and a prothallial cell) is composed of a central core of cells enclosed by a single layer of parietal cells (Fig. 28.0). The central cells each become biciliate microgametes or sperm. With the formation of the biciliate sperm, the microspore wall ruptures, the parietal cells of the antheridium disintegrate, and the biciliate microgametes are liberated. Water is necessary so that these biciliate sperm may swim to the nearby megagametophyte.

On the other hand, the megaspores also germinate before they are shed from the megasporangium. The nucleus of the megaspore divides into a large number of nuclei. The cytoplasm containing these nuclei becomes simultaneously septated to form within the confines of the megaspore a cellular mass, the megagametophyte (Fig. 28.0). At this time the megaspore containing the aforementioned megagametophytic tissue is shed from the megasporangium and falls to the ground. With further increases in the megagametophytic tissue, the megaspore wall is ruptured, and in the exposed megagametophytic tissue there subsequently develop archegonia. Each archegonium, like that of the fern, possesses a venter and a neck. The megagamete or egg is contained in the venter. The lumen of the neck, when it is immature, is occluded by a single ventral canal cell and one neck canal cell. At maturity the lumen of the neck becomes patent with the disintegration of the ventral canal cell and the neck canal cell.

If there exists, as is most generally the case, a film of water between adjacent microgametophytes and megagametophytes on the ground, the biciliate sperm are able to attain the exposed archegonia.

Fertilization ensues, and there is formed in the venter a zygote. The zygote subsequently divides to form two cells: the one vicinal to the neck of the archegonium is called the *suspensor cell,* while the other is the *embryo cell.* The suspensor cell divides to form a suspensor which, as it elongates, serves to press the embryo cell deeper into the megagametophytic tissue. The embryo cell divides mitotically to form an embryo (Fig. 28.0) which is composed of a stem with two primary leaves, a foot, and a primary root. The foot functions as a temporary absorbing organ, for the developing sporophyte is for a very short time parasitic on the megagametophyte, some of the exposed cells of which are photosynthetic. With the emergence of the primary leaves and root from the megagametophytic tissue, the young sporophyte is no longer dependent on the megagametophyte. In the meantime the stem continues its growth, developing its own leaves and adventitious roots.

Chapter 29

THE FERNS

THERE are some eight thousand species of ferns, ranging from the tree-like dimensions of those growing in the tropics to but a few inches in height. The ferns generally seen in the United States are more or less intermediate in size and are exemplified by such common fern plants as the Christmas fern (*Polystichum acrostichoides*), the maidenhair fern (*Adiantum pedatum*), and the bracken fern (*Pteris aquilina*). In our discussion we shall limit our study to a typical representative of the class, the bracken fern or *Pteris aquilina.*

PTERIS AQUILINA

Stem. The stem of *Pteris aquilina* is a perennial rhizome (Fig. 29.0); that is, the stem grows horizontally beneath the soil surface from year to year. It generally bears only a few branch stems. At the end of the rhizome or the terminal part of its branches are found terminal buds. These terminal buds are responsible for growth in length. From the upper surface of the stems at these growing points arise leaves called *fronds* (Fig. 29.0) and from the lower surface emerge adventitious roots.

The microscopic morphology of the rhizome may now be considered (Fig. 29.0C). In a typical cross section of a fern rhizome, we find the following tissues:

(*a*) The outermost layer of tissue is the *epidermis,* which persists, since the fern rhizome does not undergo secondary growth or growth in thickness.

(*b*) Beneath the epidermis are several layers of *sclerenchyma.*

(*c*) The ground tissue of the stem is parenchyma and functions in storage of food and water.

(*d*) Interspersed in the ground tissue are patches of sclerenchyma and closed vascular bundles. Each closed vascular bundle is sur-

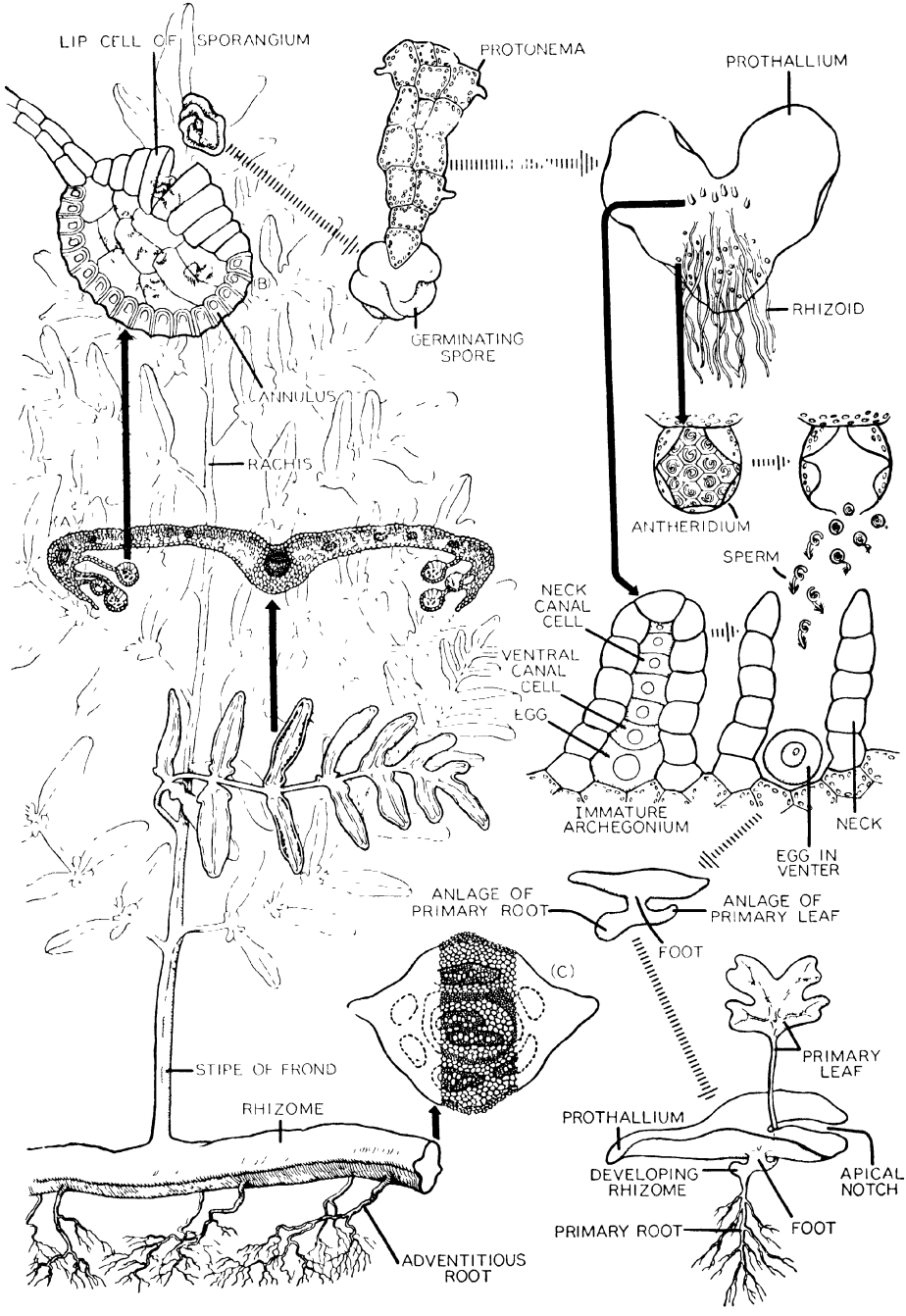


FIG. 29.0 Bracken fern (*Pteris aquilina*): (A) transverse section of a leaflet; (B) stalked sporangium; (C) transverse section of a rhizome showing the disposition of closed vascular bundles.

rounded by a single layer of deep-staining cells, the *endodermis.* Below the endodermis is generally a single layer of parenchymatous tissue, the *pericycle.* The pericycle encloses the vascular tissue. The phloem is situated peripherally and is composed of sieve tubes for the most part, while the xylem is centrally situated.

Roots. The roots are adventitious and present a somewhat wiry aspect. Each root emanates from deep within the stem tissue. The roots possess root hairs and have root caps at their growing tips. Morphologically the roots are comparable microscopically to those already studied under angiosperms.

The Frond (Fig. 29.0). The frond of the fern consists of a petiole, called a *stipe,* which grows up through the soil and supports the aerial portion of the fern. Above the soil the stipe is generally prolonged into a slender axis, termed the *rachis,* to which the leaflets, called *pinnae,* are laterally attached. The pinnae, however, may be divided into smaller leaflets called *pinnules.* The frond of the fern is thus a pinnately compound leaf and has its origin in a small outgrowth on the stem near its growing point.

Morphologically each leaflet is comparable microscopically to the typical leaf which we studied under the angiosperms. It possesses an upper and lower epidermis. Stomata are generally limited to the lower epidermis. Between the two epidermal layers is contained the mesophyll tissue. However, this is not distinguishable into the usual palisade chlorenchyma and spongy chlorenchyma as was the case with the typical leaf which we studied previously.

Sporangia (Fig. 29.0B). In the bracken fern the margins of the leaflet are reflexed or turned under to form an indusium. From the internal surface (generally the vascular area) of the reflexed margin arise stalked sporangia. Groups of such stalked sporangia are referred to collectively as *sori.* Each sporangium possesses a thin capsule, on one side of which two of the capsular cells are radially elongated to function as *lip cells.* These lip cells represent the area where the capsule will be ruptured upon the straightening of the annulus. The *annulus* is a single layer of cells, the inner and radial walls of which are thickened. The annulus extends over the capsule from one side of the stalk to a point closely vicinal to the lip cells. When dry, the annulus straightens and thus causes the capsule to rupture between the lip cells so that the spores may be discharged.

Spores. Initially there are contained in the capsule homospore

mother cells. These diploid homospore mother cells divide meiotically to form tetrads of haploid homospores. These spores represent the beginning of the gametophyte generation. Upon coming to rest on suitable substrate they germinate. Each spore, after the absorption of water, ruptures and sends out a short, septate, green filament of cells, called the *protonema*, from some of the cells of which grow nonseptate root-like protrusions called *rhizoids*.

Prothallium (Fig. 29.0). The terminal cell of the protonema divides obliquely, and by such division there is ultimately formed a heart-shaped, green, flattened cellular structure called the *prothallium*. Suspended from the undersurface of the prothallium are the gametangia. The antheridia, disposed among the rhizoids on the undersurface of the prothallium, are globular in shape. The parietal part of each antheridium is characterized by a unicellular layer of chlorophyllous cells encasing sperm mother cells, whence develop the spirally coiled multiciliate sperm. On the other hand, the archegonia are flask-shaped and are partially embedded in the prothallial undersurface in an area vicinal to the apical notch. Each archegonium has a basally enlarged portion, called the *venter*, which contains the large egg cell or female gamete. The venter is practically submerged into the tissue of the prothallium and thence tapers out into a cellular tube, the neck. The cavity of the neck, when the archegonium is immature, is generally occluded by several cells; the one nearest the egg cell is called a ventral canal cell, and the other two cells in the neck constitute the neck canal cells. On the full maturation of the archegonium, the ventral canal cell and neck canal cells degenerate, and thus there is formed a passage through which the sperm may attain the egg in the venter.

The prothallium, therefore, with its gametangia, represents the mature gametophyte.

Fertilization (Fig. 29.0). Upon the absorption of water, the parietal cells of the antheridia are ruptured. The liberated, spirally coiled sperm then migrate to the archegonia. The sperm enter the necks of the archegonia and fertilize the eggs in the venters. Only one sperm, however, fuses with the egg in an archegonium to form the zygote. The zygote, which represents the beginning of the sporophyte generation since it possesses the $2n$ number of chromosomes, forms a wall round itself and subsequently divides into a four-celled body, called a quadrant embryo. This quadrant of cells, still contained within

the venter, differentiates into a four-lobed body (Fig. 29.0). One lobe, called the *foot*, becomes lodged in the tissue of the prothallium and serves to absorb water and nutriment from the prothallium for the remaining period of sporophyte development. Another lobe grows down into the soil to form the primary root, while still another lobe develops into the primary leaf. The latter is the temporary photosynthetic organ and characteristically grows up from under the prothallium through the apical notch. With the development of the primary root and primary leaf, the foot degenerates and the young sporophyte becomes independent of the prothallium. The fourth lobe develops into the rhizome. With the formation of adventitious roots and a frond from the rhizome, the primary leaf and primary root die. The mature sporophyte, therefore, comprises the rhizome, adventitious roots, and fronds. Thus only one organ, the rhizome, of the young sporophyte persists.

Alternation of Generations. As is obvious from our discussions of the life cycle of the bracken fern, there is distinct alternation of a gametophyte generation with a sporophyte generation. The visible fern plant is the sporophyte generation.

Chapter 30

THE GYMNOSPERMS

THE subphylum Pteropsida of the phylum Tracheophyta is composed of three classes: the class Angiospermae, the class Gymnospermae, and the class Filicineae. In preceding chapters we have made a study of the members of the class Angiospermae (flowering plants) and the class Filicineae in structure and function. This chapter is devoted to a study of the general characteristics and a brief classification of the class Gymnospermae (conifers and their allies) and to the life history of pine (*Pinus*), which is a typical gymnosperm.

General Characteristics of Gymnosperms. The word *gymnosperm* means "naked seed" and refers to the fact that the seeds are borne exposed on the surface of a sporophyll or spore-bearing leaf. They are not enclosed by a pericarp as are the seeds of angiosperms. The sporophyte is a perennial, woody, independent plant, usually an evergreen tree, with true roots, stems, leaves, and seeds. The gametophyte is inconspicuous and is parasitic or dependent on the sporophyte. As in the flowering plants, two types of spores are produced. Megasporangia develop on the surface of megasporophylls (called carpels in the higher vascular plants) and microsporangia develop on the surface of microsporophylls (called stamens in higher vascular plants). The sporophylls are usually organized to form a cone or *strobilus*. In extant species, two types of cones are present: megasporangiate, female or ovulate; and microsporangiate, male or staminate. In many conifers, both types of cones are borne on the same individual plant.

Gymnosperms are the most primitive of seed plants. Certain kinds of them have become extinct and are today known only by their fossil remains. As a group they have a wide geographical distribution. They are found in temperate and tropical zones and also in arctic regions. The class Gymnospermae includes such familiar plants as pine (*Pinus*), spruce (*Picea*), hemlock (*Tsuga*), fir (*Abies*), larch

(*Larix*), redwood (*Sequoia*), juniper (*Juniperus*), cedar (*Cedrus*), cypress (*Cupressus*), and so on. Many of the gymnosperms are of economic importance as sources of lumber, resin, turpentine, wood alcohol, tar, tannins, and other products.

Classification of the Gymnosperms. There are two subclasses of gymnosperms, the subclass Cycadophytae and the subclass Coniferophytae. The subclass Cycadophytae includes the extinct seed ferns (all fossils) and the extinct and extant cycads. Most of the living members of the subclass Coniferophytae are conifers. Hence modern gymnosperms are represented largely by the cycads and the conifers.

The living cycads usually have a short, unbranched, thick stem, from the summit of which arises a crown of large fern-like leaves. A few species have tall columnar trunks and superficially bear a resemblance to tree ferns or palms. Cycads are distributed in tropical and subtropical regions in both hemispheres. Only one genus, *Zamia*, is native to continental United States, and it is found in the state of Florida.

The vast majority of the conifers are tall, richly branched, forest trees. A few species are shrubs. The stems have much wood and little pith. The wood is composed chiefly of tracheids. As the term conifer implies, most of these plants bear cones. The cones are unisexual. Some species of conifers are monoecious and others dioecious. The leaves are usually small and scaly or needle-shaped. Many conifers are mountain-inhabiting plants. They are found growing in almost all parts of the world, but are more prevalent in North America and in Europe and northern Asia.

LIFE CYCLE OF THE PINE

A study of the life history of pine trees (Fig. 30.0) provides a good basis for an understanding of the life cycles of the conifers, even though as a group they show considerable structural diversity. The familiar pine tree with its conspicuous, upright, branched trunk, and needle-like leaves is the sporophyte. These vegetative leaves are borne in clusters of two, three, or five (number varies with the species) on the tips of very short branches called spur branches which arise from the ordinary branches of the trunk.

The reproductive organs are the cones, and they are not produced during the first few years of the life of the plant. The pine produces megasporophylls in female cones and microsporophylls in male cones.

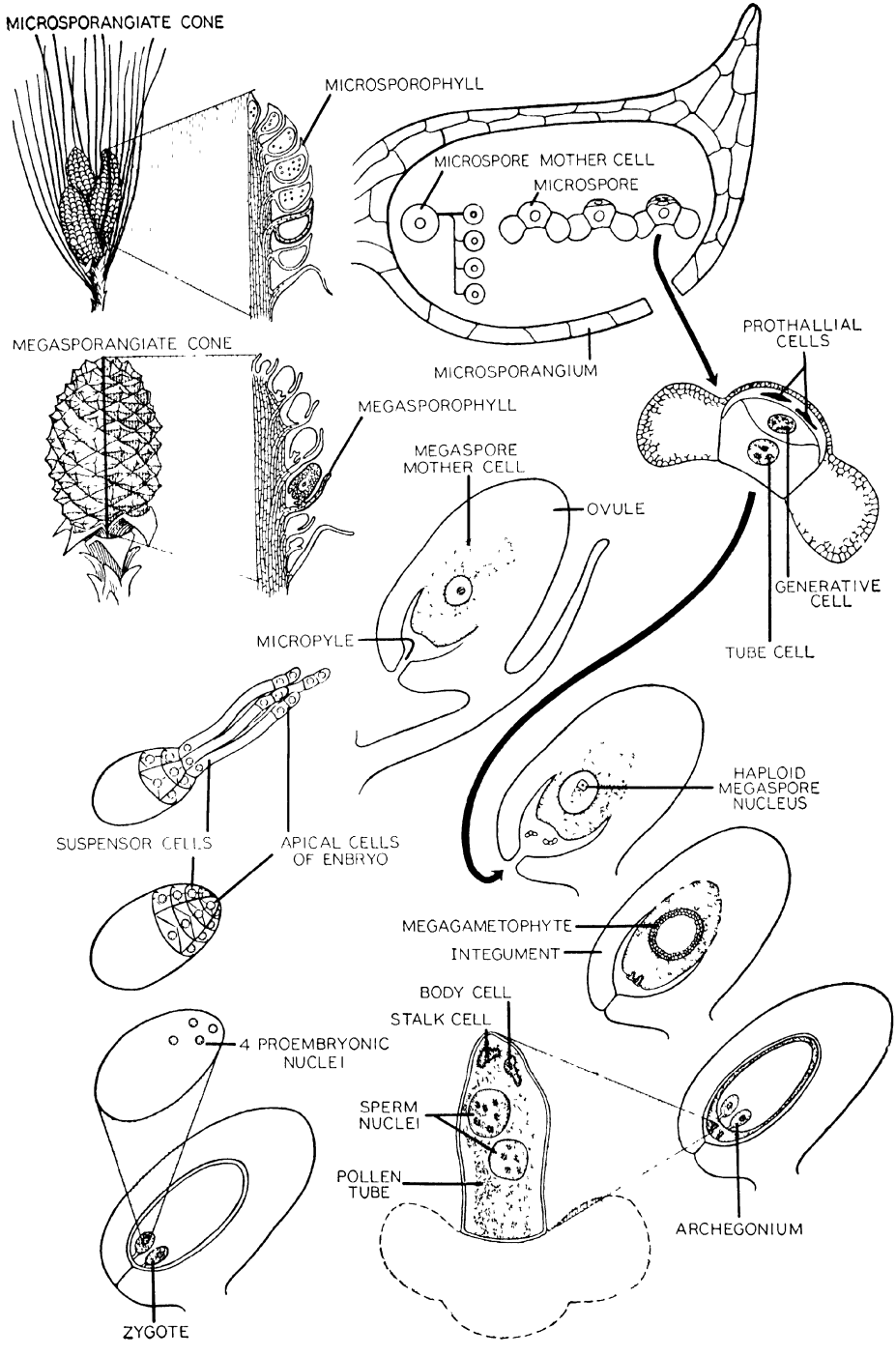


FIG. 30.0 Life cycle of the pine.

Both kinds of cones occur on the same plant. Each cone is composed of a cluster of sporophylls attached to a short central stem.

The smaller microsporangiate, or male cones, are borne in clusters near the ends of long branches. Each male cone consists of a central axis to which many short-stalked, compactly arranged, scale-like microsporophylls are attached in a spiral fashion. Each microsporophyll bears on its ventral surface two ovoid bodies called *microsporangia.* Within the microsporangia, numerous microspore mother cells are produced. Each microspore mother cell undergoes meiosis to give rise to four microspores, each of which develops two lateral wings or air bladders to give it buoyancy. The so-called wings are not cells, but spaces filled with air. The spaces arise by the separation of the exine and intine of the microspore. The microspore has the haploid number (n) of chromosomes and marks the beginning of the microgametophyte. Within the microsporangium, partial development of the microgametophyte begins. Two divisions within the microspore result in the production of two small, lenticular, sterile vegetative or prothallial cells and an antheridial cell. The prothallial cells are considered to be remnants of the male gametophytic thallus of lower plant forms. They occupy one end of the developing pollen grain and begin to disintegrate soon after they are formed. The antheridial cell divides into a small generative cell and a large tube cell. At this four-celled stage the nearly mature microgametophyte, or four-celled pollen grain, is shed from the microsporangium. Pollen grains are transported to the female cones by the wind. This process occurs early in the development of the megagametophytes and in the following spring male and female gametophytic development is completed.

A young female cone consists of a central axis to which many bracts are attached in a spiral fashion. As the cone matures, a scale-like structure larger than the bract, the *megasporophyll,* develops in the axil of each bract. The female cone is usually borne singly and when mature is larger than the male cone.

Each megasporophyll bears two ovules on its upper surface. The young ovule consists of a central mass of cells, the megasporangium, or *nucellus,* together with a single integument which encloses the megasporangium, except at the micropyle. The micropyle is directed toward the axis of the cone. Early in the development of the megasporangium, one megaspore mother cell is formed. This cell undergoes meiosis to give rise to four megaspores arranged in a linear order.

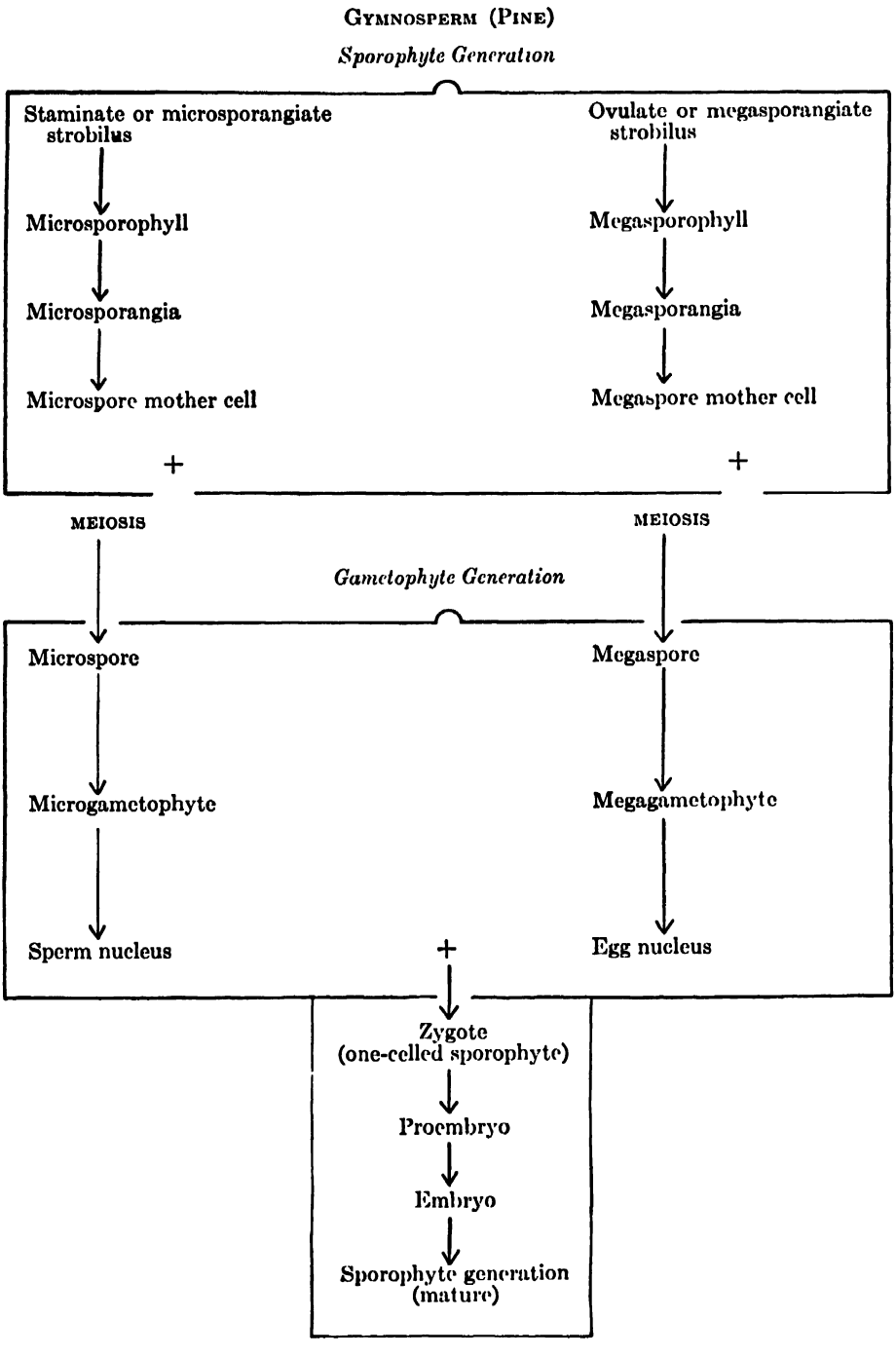
Only one megaspore develops into the mature megagametophyte; the other three undergo early disintegration. The megaspore has the haploid number of chromosomes.

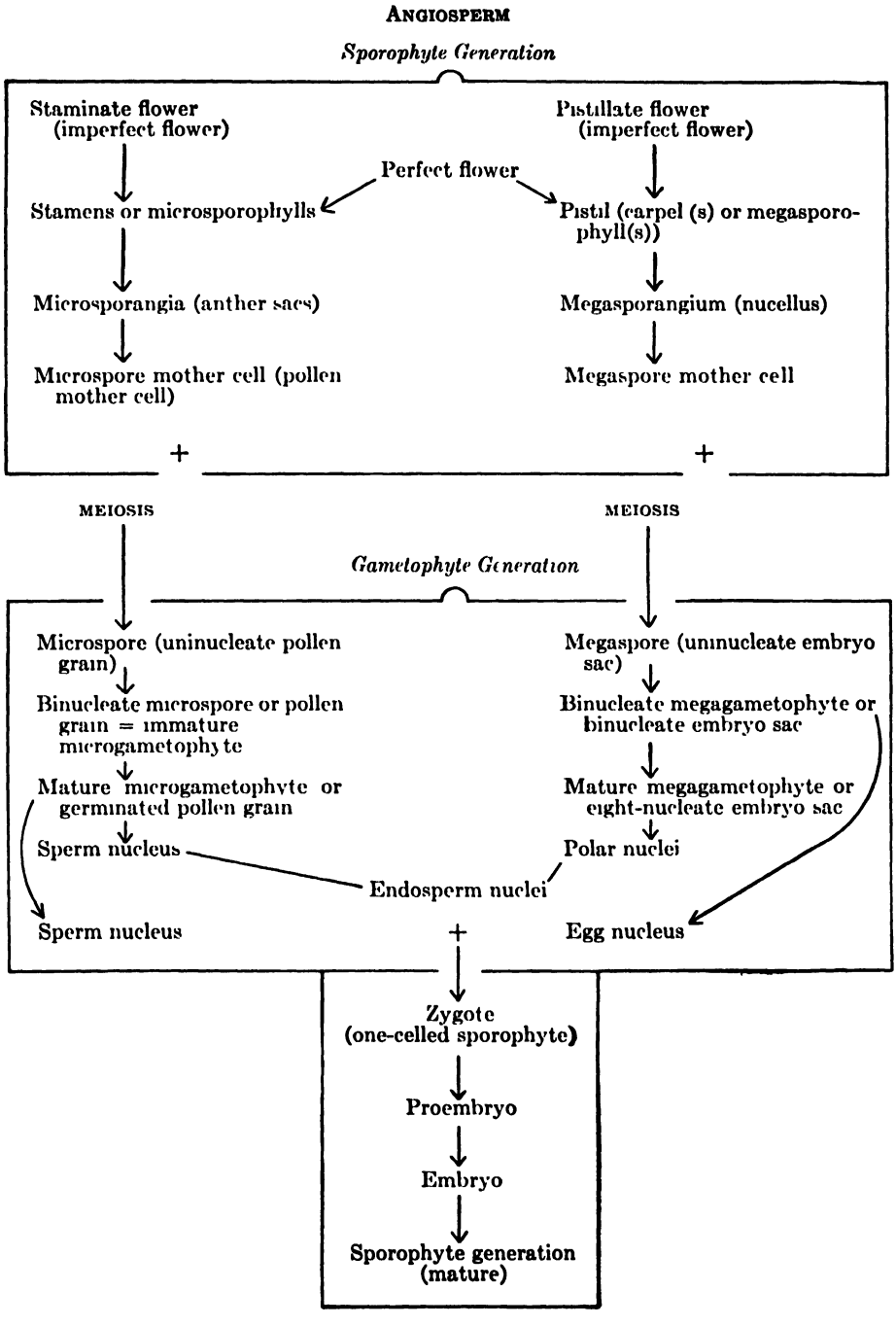
At the time of pollination the ovule consists of one functional megaspore, the megasporangium, and the single integument. Early in the year following pollination, the megaspore enlarges at the expense of the cells of the megasporangium which surround it. Its nucleus undergoes repeated mitotic divisions, but cytokinesis does not occur immediately. Wall formation subsequently occurs, and the result is a solid ovate mass of female gametophytic tissue surrounded by the sporophytic tissue of the megasporangium. Two or three archegonia then develop at the micropylar end of this ovate mass of tissue. Each archegonium takes origin from a single superficial cell of the megagametophyte. The mature archegonium consists of a large egg cell together with the archegonial jacket which is an archegonial wall made up of the vicinal vegetative cells of the megagametophyte. The jacket cells serve to nourish the egg and later the embryo. The mature archegonia are embedded in the mass of megagametophytic vegetative tisue and do not project beyond its surface.

Thus far we have considered the development of the megagametophyte to maturity and the development of the microgametophyte to the time of pollination. We shall now resume our study of the further development of the microgametophyte. At the time of pollen transfer, the ovule exudes a resinous fluid which comes in contact with some of the transferred pollen grains. As this fluid dries, pollen grains are pulled through the micropyle of the ovule and come in contact with the micropylar end of the megasporangium. The tube cell of the pollen grains elongates to form a pollen tube which ceases growth during the cold winter months. During the following spring the pollen tube resumes its growth and ultimately penetrates the megasporangium and an archegonium. Early in the formation of the pollen tube the tube nucleus migrates to the tip of the pollen tube. The generative cell of the microgametophyte meanwhile divides into a stalk cell and a body cell, which also pass into the pollen tube as the pollen tube elongates. The nucleus of the body cell divides to form two nonmotile microgametes, or sperm nuclei.

When the pollen tube penetrates an archegonium, its contents are discharged and a single sperm nucleus fuses with the egg to form the zygote. This process of fertilization in pines occurs in the spring

Table 13. COMPARISON




ANGIOSPERM
Sporophyte Generation
Staminate flower (imperfect flower)
Pistillate flower (imperfect flower)
Perfect flower
Stamens or microsporophylls
Pistil (carpel (s) or megasporophyll(s))
Microsporangia (anther sacs)
Megasporangium (nucellus)
Microspore mother cell (pollen mother cell)
Megaspore mother cell
+
+
MEIOSIS
MEIOSIS
Gametophyte Generation
Microspore (uninucleate pollen grain)
Megaspore (uninucleate embryo sac)
Binucleate microspore or pollen grain = immature microgametophyte
Binucleate megagametophyte or binucleate embryo sac
Mature microgametophyte or germinated pollen grain
Mature megagametophyte or eight-nucleate embryo sac
Sperm nucleus
Polar nuclei
Endosperm nuclei
Sperm nucleus
+
Egg nucleus
Zygote (one-celled sporophyte)
Proembryo
Embryo
Sporophyte generation (mature)

of the year which follows pollination. Formation of the zygote marks the initiation of the new sporophyte generation. The other sperm nucleus, the tube nucleus, and the wall cell disintegrate.

After fertilization the nucleus of the zygote undergoes a series of mitotic divisions. Four nuclei are produced, and they migrate to the lower end of the zygote. Subsequent divisions of these nuclei and development of cell walls result in the production of the proembryo, a structure composed of four tiers of cells with four cells in each tier. The cells of the uppermost tier, that is, those closest to the micropylar end of the proembryo, are not cut off from the cytoplasm of the egg. Each cell in the lowermost tier is an embryo cell and forms an embryo. Since there may be as many as three archegonia in one ovule, twelve embryos may be formed. One embryo arising from a zygote grows more rapidly than the others, and it alone reaches maturity in the seed; the others soon cease growth and disintegrate. The four suspensor cells, which constitute the tier nearest the lowest tier, elongate and push the four cells in the lowermost tier into the food-rich megagametophytic tissue, termed the *endosperm*, at the expense of which they grow.

The seed of pine consists of an embryo embedded in megagametophytic tissue together with a hard protective seed coat which surrounds the latter. The seed coat of the pine seed is derived from the integument of the ovule. In some species of pine a portion of the upper layer of tissue of the megasporophyll splits off to form a wing which remains attached to the base of the seed when it is shed. The megagametophytic tissue continues to grow after fertilization and absorbs the megasporangial cells. The embryo when mature consists of a hypocotyl, an epicotyl, an embryonic root, and from three to twelve cotyledons (the number varies with the species). When the seed germinates, the embryo develops into a seedling in a manner similar to that of a flowering plant.

Chapter 31

PLANT GENETICS

PLANT genetics is the science which seeks to account for the likenesses and differences among plant organisms related by descent. It is because of heredity that these organisms resemble each other. But heredity does not necessarily imply that parents and their progeny are identical in all their traits or *characters* (a term for the observable features of a developing or mature organism, whether they be morphological, physiological, or biochemical). The unlikenesses which exist are termed *variations*. Variations may be due to the environment, to hybridization, or to mutation.

The science of genetics came into being in 1865 when Father Gregor Mendel (1822–1884), a Catholic priest of an Augustinian monastery in Austria, read a manuscript entitled *Experiments in Plant Hybridization* before the members of the Brunn Society of Natural Science. The paper was forgotten until 1900, when three European botanists, de Vries in Holland, Tschermak in Austria, and Correns in Germany, independently rediscovered and verified the experiments of Mendel. Fifty-five years later genetics has developed into a massive body of knowledge which has been integrated with the other biological sciences.

SOME TERMS IN GENETICS DEFINED

The term *genotype* refers to the genetical constitution or to the sum total of the hereditary determinants or genes obtained by offspring from parent (asexual reproduction) or parents (sexual reproduction). The term *phenotype* refers to the sum total of the expressed morphological characteristics and physiological and biochemical processes. Two plants which are genotypically the same for a particular trait, such as height, even when growing side by side in the same field, may be phenotypically different for the trait in question, since

the expression of the genotype is conditioned by external environmental conditions such as the supply of nutrients, light, moisture, and temperature. Phenotypic differences between organisms of the same genotype due to environmental differences are called *modifications.* They persist only in the presence of the particular environment and are not transmitted from parent to offspring.

Hybridization is the process of crossbreeding related organisms which differ with respect to one character or several characters. The offspring of the crossbreeding is termed a *genetical hybrid.* In the hybrid there is a recombination of genes, and the variations due to the recombination are heritable.

The term *mutation,* in the narrow sense, refers to a change in the structure of a gene. It results in a variation that is heritable. In the broad sense it refers to any change in the genotype that is not caused by recombination of genes, and thus it would include gene mutations and chromosomal aberrations. Such aberrations include any change in the number of chromosomes and changes in the arrangements or number of gene loci within a chromosome.

The vast majority of hereditary determinants are transmitted from parent to offspring by way of nuclear constituents. It should be noted, however, that extranuclear determinants of hereditary traits have been demonstrated to exist in some plant cells. These in conjunction with the factors in the nucleus determine some hereditary traits (cytoplasmic inheritance). For example, plastids in the presence of specific nuclear factors will undergo modification and cause leaf variegation.

Chromosomes and Genes. The carriers of hereditary determinants within the nucleus are the *chromosomes.* Arranged in a linear fashion within the chromosomes are the submicroscopic *genes* or hereditary entities which in conjunction with one another and with the environment determine the various traits of an organism. In the somatic cells of the diploid individual which originates as a result of fertilization there are two sets of chromosomes. One set is of paternal origin and the other set is of maternal origin. For each chromosome of paternal origin there is one of maternal origin, which generally corresponds to the one of paternal origin in shape and size and contains genes for the determination of the same characters in the same linear sequence. The members of such a pair of chromosomes are termed *homologous chromosomes.*

The behavior of the chromosomes in mitosis and meiosis is de-

scribed in Chapter 3 and in Chapter 10. When, in mitosis, chromosomal division occurs, each daughter chromosome has the same genes in the same linear sequence. Prior to the longitudinal splitting of each chromosome, there must have occurred a duplication of each gene in the chromosome. Mitosis results in furnishing the daughter cells with the same complement of chromosomes and genes that are present in the mother cell.

In the production of megaspores and microspores in the higher plants, there is involved a specialized type of nuclear division called *meiosis* (Chapter 3) by means of which the diploid chromosomal complement of the megaspore and microspore mother cells is reduced to the haploid number. The result of the meiotic process is not only a numerical reduction of chromosomal number but also the separation of the homologous chromosomes (see Chapter 10). Hence each megaspore or microspore contains only one member of each pair of the diploid chromosomal complement and one member of each pair of genes. The spores on germination give rise to the mature gametophyte generations which reproduce sexually by fusion of heterogametes. Since the nucleus of the zygote contains twice as many chromosomes as the nucleus of a gamete, meiosis is required in the life cycle to keep the chromosome number constant from generation to generation.

Alleles. Two genes at the same locus in homologous chromosomes are termed *alleles*. When the two genes at the same locus in homologous chromosomes are identical, the individual is said to be homozygous for the trait controlled by these genes. An individual is heterozygous for a trait when the two genes at the same locus in homologous chromosomes are different. When one gene of an allelic pair is expressed to the exclusion of the other, it is termed the *dominant gene* and the other member of the pair is called a *recessive gene*.

CROSSING AND ITS PRINCIPLES

Monohybrid Cross (Fig. 31.0). A monohybrid cross is one which involves two parents differing in a single trait or character. In one of his experiments, Mendel crossed garden pea plants which had yellow cotyledons with garden pea plants with green cotyledons. Since self-pollination occurs in the garden pea, he had to remove the stamens of the flowers of one type of parent plant and transfer the pollen from the other type of parent plant to the pistils of the destaminated plants. All of the offspring of the parent plants, or the members

of the first filial generation (F_1), had yellow cotyledons. In this cross, one parent has the dominant genes for yellow cotyledons (YY) and the other the recessive genes for green cotyledons (yy). The members of the F_1 generation received a dominant gene (Y) from one parent and a recessive gene (y) from the other parent. Hence they all had yellow cotyledons, since the gene for yellow cotyledons is dominant.

The members of the F_1 generation were allowed to self-pollinate and 75 per cent of the seeds of these plants had embryos with yellow cotyledons and 25 per cent of them had embryos with green cotyledons. These embryos represent the second filial (F_2) generation. The

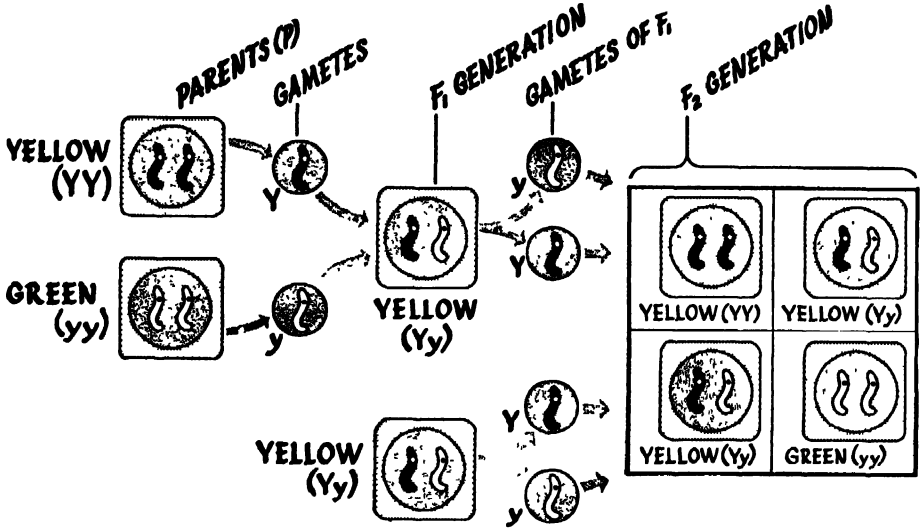


FIG. 31.0 A monohybrid cross.

ratio was 3 : 1. To be exact, 250 plants yielded 8023 seeds, 6022 yellow and 2001 green—a ratio of 3.01 : 1. Both the male and female gametophytic members of the F_1 generation produced two types of gametes. One half of the gametes of each gametophyte contained the gene for yellow cotyledons, and the other half contained the gene for green cotyledons. As a result of random gametic union 25 per cent of the F_2 generation were homozygous (YY) for the dominant gene, 50 per cent were heterozygous (Yy), and 25 per cent were homozygous (yy) for the recessive gene. Hence in the F_2 generation, although there were only two phenotypes, there were three genotypes (YY, Yy, yy) in the ratio of 1 : 2 : 1. In the third filial generation (F_3) the

plants with green cotyledons, on self-pollination, produced only progeny with green cotyledons. But when the YY members of the F_2 generation were selfed, only embryos with yellow cotyledons were produced; when the Yy members of the F_2 generation were selfed, the phenotypic ratio of yellow to green was 3 : 1.

From the various monohybrid crosses made by Mendel, the following principles were formulated:

1. *Principle of unit characters.* The inheritance of various traits by an organism is controlled by factors (genes) and these factors occur in pairs.
2. *Principle of dominance.* One gene in an allelic pair may "hide" the expression of the other member of the pair.
3. *Principle of segregation.* In the formation of haploid reproductive cells such as gametes and spores, only one gene of each allelic pair is received by the gamete or spore.

Types of Mating or Crossing Employed in the Analysis of Plant Inheritance. Three types of mating are employed in genetic analysis: the sib cross, the test cross, and the back cross. In the sib cross, an F_1 plant is selfed or F_1 plants are crossed with each other to obtain the F_2 generation. In the test cross (a type of back cross), the heterozygous F_1 individual is mated with a homozygous recessive; the progeny or test-cross generation, if the cross is a monohybrid one, exhibits a 1 : 1 ratio phenotypically and genotypically. The back cross is made by mating the F_1 hybrids to one or the other of their parents and the progeny obtained constitute the back-cross generation. Both monohybrid back crosses yield a 1 : 1 genotypic ratio; the phenotypic ratio, if full dominance obtains, will be 1 : 1 only in the cross between the F_1 hybrid and the homozygous recessive.

Dihybrid Cross and the Mendelian Principle of Independent Assortment. A dihybrid cross (Fig. 31.1) is one which involves two parents differing in two traits. In pea plants yellow color of seed is dominant over green, and round shape is dominant over wrinkled. Mendel crossed two parent pea plants, one of which was homozygous for yellow round peas (YYRR) and the other homozygous for green wrinkled peas (yyrr). All the peas borne by the F_1 generation were yellow and round (YyRr). He then permitted the members of the F_1 generation to be self-pollinated. Both the male and female gametes of the F_1 generation were of four different types (YR, Yr, yR, yr). Ran-

dom fusion of the gametes of fifteen such plants yielded 556 seeds and of these there were 315 round and yellow, 101 wrinkled and yellow, 108 round and green, and 32 wrinkled and green. This is a 9 : 3 : 3 : 1 phenotypic ratio, or a 3 : 1 ratio multiplied algebraically by 3 : 1. From this and other similar dihybrid crosses was derived the principle of independent assortment. This principle states that *the genes for two or more different traits are distributed to the gametes independently of one another provided they are in different pairs of chromosomes.*

The F_2 phenotypic ratio in a trihybrid cross with each dominant

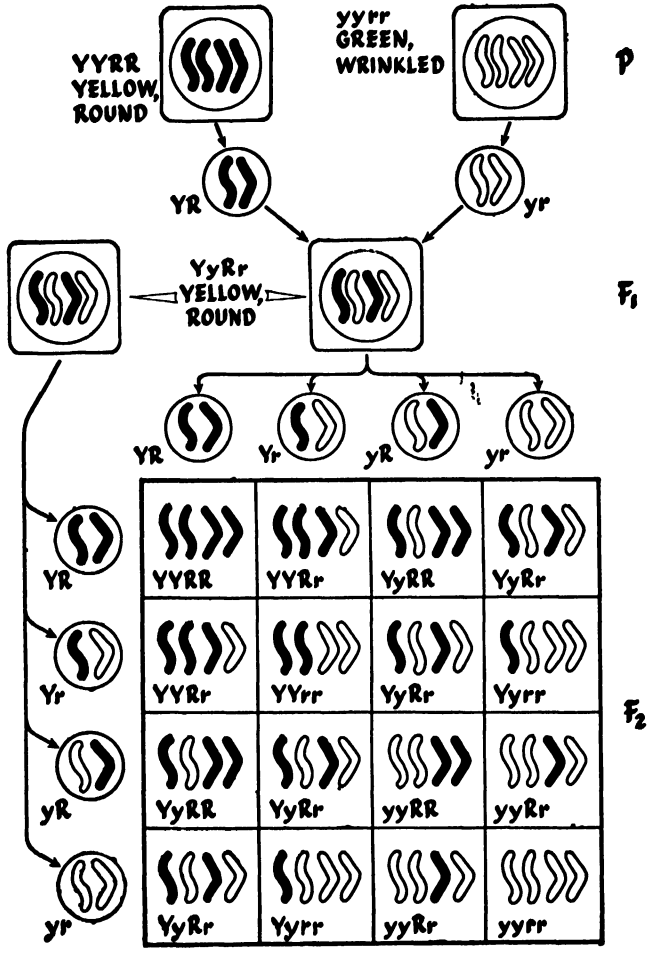


FIG. 31.1 A dihybrid cross.

gene in a different chromosome would be 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1.

Incomplete Dominance (Fig. 31.2). Full dominance does not occur in all genetic crosses. If a homozygous red-flowered four-o'clock is crossed with a homozygous white-flowered four-o'clock, the flowers of the F_1 heterozygous individuals are all pink. When F_1 individuals are mated to obtain the F_2 generation both the F_2 genotypic and phenotypic ratios are 1 : 2 : 1. In the F_2 generation, the members which are homozygous for red are red and those which are homozygous for white are white. The heterozygous individuals are pink. The unique feature of the heterozygous individuals is that they can be visibly distinguished, whereas such is not the case in full dominance.

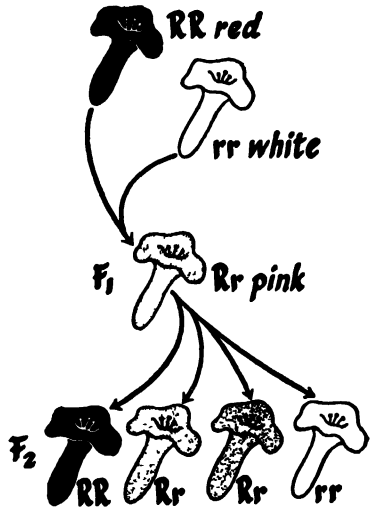


FIG. 31.2 Incomplete dominance from a cross of a red Japanese four-o'clock with a white Japanese four-o'clock.

LINKAGE AND CROSSING OVER

Mendel experimented with seven different pairs of characters in peas and met with no exceptions to the principle of a random assortmnt, since the genes for these characters were caried by different chromosomes. But the Mendelian principle of random assortment is far from universal in its application and is limited to genes in different chromosomes. Each pair of homologous chromosomes carries a large number of gene pairs or alleles. Hence certain hereditary characteristics remain grouped together and are inherited as a unit from generation to generation. The tendency of genes in the same chromosome to remain together is termed linkage. The difference between linkage and random assortment is not due to any difference in the physical behavior of the chromosomes but lies in the relationship of the genes to the chromosomes. Linkage is said to be complete (Fig. 31.3) or perfect between genes when they remain together in the same chromosome through two or more generations. This type of linkage is rare.

In many instances characteristics determined by genes on the same chromosome do not remain linked. The linkage in this case is said to

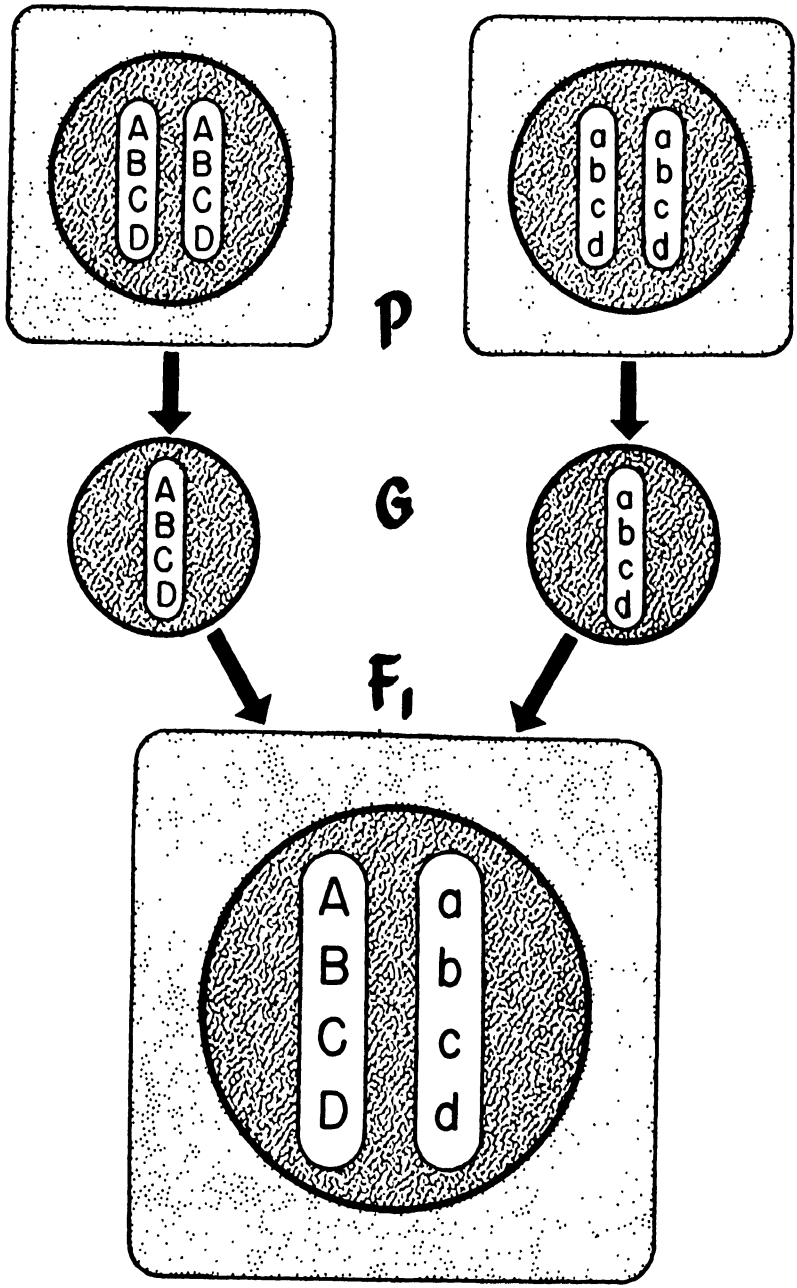


FIG. 31.3 Diagrammatic presentation of complete linkage. The genes on the same chromosome are represented alphabetically.

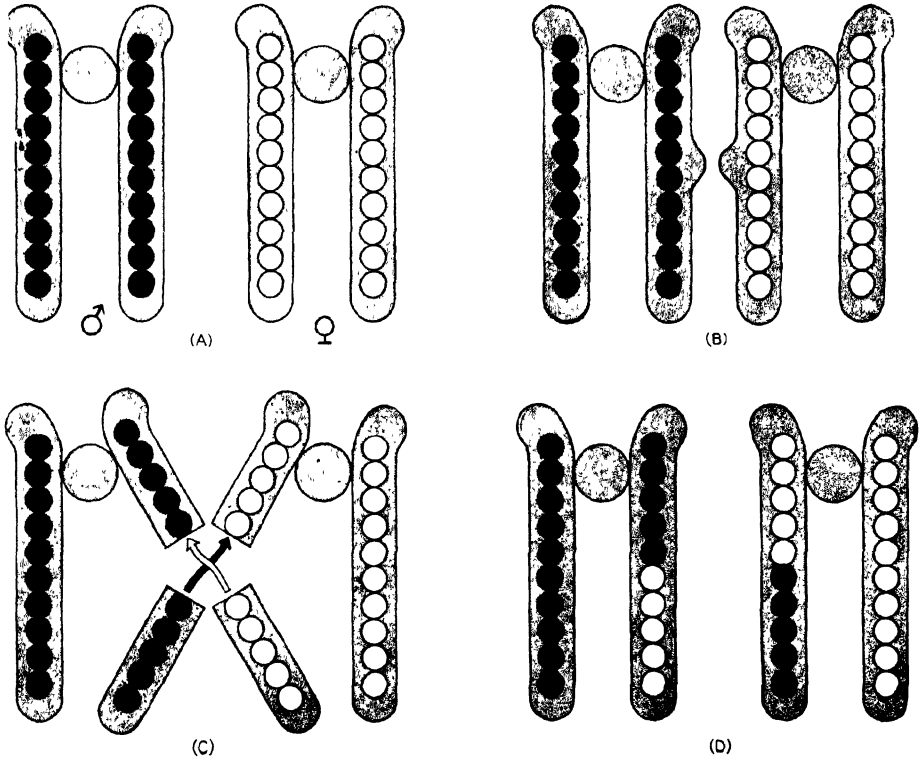


FIG. 31.4 Incomplete linkage due to crossing over: (A) maternal and paternal homologous chromosomes, (B) the same pair of homologous chromosomes in early diplotene, (C) genetical crossover (breakage and reciprocal fusion of non-sister chromatids), (D) result of genetical crossover.

be partial or incomplete, owing to the fact that the linked genes separate. The separation is caused by an exchange of segments between chromatids during the diplotene stage in meiotic cell division. The exchange is termed *crossing over* (Fig. 31.4). The amount of crossing over between linked genes varies directly with their distance apart in the chromosome. The linked genes are quite close together when the percentage of crossing over is low, and they are some distance apart when the percentage of crossing over is high.

SEX CHROMOSOMES

Sex Determination in Plants (Fig. 31.5). Chromosomes concerned with the control of sex are called *sex chromosomes*. All other chromosomes are termed *autosomes*. In plants several types of chromosomal mechanisms exist for the determination of sex. The commonest type of sex determination studied to date in the flowering plants is the XX–XY type. It is exemplified in the dioecious hemp (*Cannabis sativa*). Both

the male and the female plants have a diploid number of 20 chromosomes. The diploid cells of the female plant contain 9 pairs of autosomes and one pair of X chromosomes. The diploid cells of the male plant contain 9 pairs of autosomes and an X and a Y chromosome. These plants, although they are members of the sporophyte generation, are said to be male and female.

All the megaspores produced by the female plant contain 9 autosomes and an X chromosome. The male plant produces two types of microspores: one has 9 autosomes and the X chromosome and the other 9 autosomes and the Y chromosome. If the sperm nucleus with the X chromosome fuses with the egg nucleus in the embryo sac, the

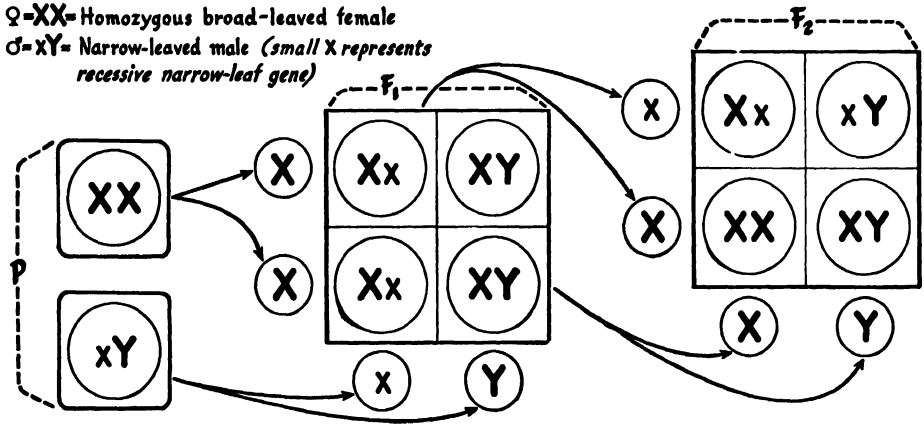


FIG. 31.5 Sex determination and sex linkage as exemplified in *Lychnis diocia*.

diploid plant which develops from the zygote will be female. On the other hand, if the fusion involves a sperm nucleus with the Y chromosome, the diploid plant which develops from the zygote will be male.

Most flowering plants are monoecious or hermaphroditic. Microspores and megaspores are produced in the same or in different flowers on the same plant. As yet research has not elucidated the mechanisms involved in sex determination in these plants.

Sex-linked Characters. The genes which are located in the X and Y chromosomes are termed sex-linked genes. Those in the X chromosome are called X-linked and those in the Y chromosome are termed Y-linked. The characters which the sex-linked genes determine are known as sex-linked characters. Sex-linked characters have been inves-

tigated more extensively in man and other animals than in plants. Hence, for purposes of orientation, an example of this type of inheritance in man is first presented.

Hemophilia or bleeder's disease, characterized by deficiency in the capability of the blood to coagulate, is due to the presence of a recessive gene in the X chromosome of the male. A female with a single gene for hemophilia will not have the disease, since there is present in the other X chromosome a dominant gene for normal clotting time. Such a female, however, is termed a *carrier*. In the male the presence of the gene for hemophilia will cause the disease to develop, since there is no gene for normal clotting time in the Y chromosome. The presence of hemophilia in the female would necessitate the presence of two recessive genes. Many geneticists consider this combination of genes to have a lethal effect in early prenatal development. If a carrier female be mated to a normal male, the female offspring could be normal or a carrier and the male could be normal or a hemophiliac.

One of the earliest examples of sex-linked characters in plants was found in a species of the pink family (*Lychnis diocia,* Fig. 31.5). In this plant, broad leaves are dominant over narrow leaves. When narrow-leaved males were crossed with homozygous broad-leaved females, the F_1 progeny were broad-leaved. All female plants of the F_2 generation were broad-leaved, one half of the male plants were broad-leaved, and the other half were narrow-leaved.

MUTATIONS

The term mutation, as previously indicated in this chapter, applies to both gene mutations and chromosomal aberrations. Most mutant genes are recessive, and since gene mutations normally involve only one member of a pair of genes present in the diploid organism, the mutant genes do not visibly express themselves immediately. Recombination with another similar recessive gene is required to effect a phenotypic variation.

Many chromosomal aberrations involve the loss of a whole set of chromosomes or the multiplication of whole sets of chromosmes. The latter condition is known as *polyploidy*. Plants with three complete sets of chromosomes are triploids; those with four, tetraploids—and so on. One way in which polyploids can originate is through irregularities in meiosis whereby diploid spores or gametes are produced. An effective

method for inducing polyploidy is to treat seeds, pollen, or buds with a weak solution of the alkaloid, colchicine. Other chromosomal aberrations involve changes in the number or arrangement of genes in a chromosome.

Mutations may arise spontaneously in nature or they may be artificially induced. The causative factor or factors involved in spontaneous mutations is still a biological enigma. Cosmic rays are undoubtedly a factor in a limited number of cases. Induced mutations in plants can be effected by the use of such mutagenic agents as X rays, ultraviolet rays, atomic radiation, temperature shock, nitrogen mustard, and colchicine.

A knowledge of mutations is important to the biologist if he is to explain the mechanism of organic evolution. The agronomist, the horticulturist, and other plant scientists are constantly on the alert for new varieties and new species of plants resulting from mutations, since if they are desirable in type, they may be of economic value.

GENETICS AND PLANT BREEDING

The applications of the principles of heredity and variation to the breeding of plants have led to the development of valuable new types of plants, to an increase in the annual crop yield of basic food plants, and to the production of resistant varieties of crop plants. Because it has achieved an important contribution to the world's food supply, one of the most spectacular advances in plant breeding resulting from the application of genetic principles has been the production of hybrid corn.

The principles of constancy of the genes and of genetic recombination are foundations upon which the edifice of modern plant breeding has been constructed, and these principles are illustrated in the production of hybrid corn. The first step involves the isolation of two or more inbred strains selected for their desirable characteristics such as increased yield and resistance to disease. The inbred strains are obtained by self-pollination. Inbreeding for several generations results in the loss of size and vigor, decreased fertility, and increased homozygosity. Two inbred strains can then be crossed (single cross) and the offspring will exhibit increased yielding ability and vigor—a phenomenon called *hybrid vigor* or *heterosis*. In the modern commercial production of hybrid corn, the procedures commonly used are the *double cross* and the *multiple cross*. In the double cross, two desirable

F_1 hybrid lines are secured by crossing such inbred strains as strain $1 \times$ strain 2 and strain $3 \times$ strain 4. The hybrids of the F_1 generation (1×2) and (3×4) are crossed to produce the double cross. The inbred corn seed obtained from the double cross is used in commercial plantings.

The same procedures used in the development of hybrid corn have been applied to such plants as cotton, tomatoes, strawberries, and onions, with desirable results.

Newer plant-breeding methods involve the artificial induction of gene mutations and polyploidy. Some of the mutant plants give a greater yield than their precursors; this is especially true when the material involved is sifted by selection and recombination.

Chapter 32

PLANT EVOLUTION

EVOLUTION in the strict sense has to do with change. Evolution in reference to the plant or animal is basically the transmutation of a previously existent species into a new and distinct species. Perhaps the most concise definition of evolution is found in the words of Darwin himself: "descent with modification." Evolution in reference to either plants or animals is termed *organic evolution,* to distinguish it from *inorganic evolution* relative to the fields of physics and chemistry.

In a textbook of the scope of this one it is impossible, because of the great volume of literature on organic evolution, to present more than the highlights of the subject. It is hoped, however, that this outline may whet the student's curiosity. Accordingly we shall consider briefly the evidences for organic evolution, the older theories as to its mechanisms, and the modern synthesis. Finally we shall present a summary of plant evolution.

EVIDENCES FOR ORGANIC EVOLUTION

The evidences for organic evolution are generally drawn from geographic distribution, paleontology, comparative serology, taxonomy, and genetics.

A. Geographical Distribution. Perhaps the strongest evidence from biogeographical data stems from the studies of plants on oceanic islands—islands formed by volcanic eruption and far removed from the nearest continental shelf. For example, when Darwin visited the islands of the Galápagos Archipelago, some 500 miles off the west coast of South America, he discovered that while the plant life on each of the islands presented a close kinship with each other, they were nevertheless *specifically* distinct. All of the plant life on these islands, he found, evidenced a less close degree of kinship with similar plants on the mainland of South America. It would be difficult, indeed,

to try to explain this distribution on the basis of soil or climatic similarity, for the soil and climate of these islands differ widely from the same ecological factors of the South American mainland. The most plausible, and perhaps the simplest, explanation is that the species of plants on the various islands of the archipelago represent plants which migrated from the mainland and have undergone subsequent modification. Isolation, such as that which obtains on the islands of the archipelago, effects the segregation of a species into small groups and thus sets the stage for expression of mutant genes. Thus these small groups would in time become specifically distinct from one another. Isolation would then sustain the diversification of a species by impeding the crossing of one group with another. To sum up, the kinship between the closely related species on each of the islands of the Galápagos Archipelago and the less close connection with similar species on the South American mainland is an expression of heredity, but the speciation is effectuated by modification through a slow accumulation of mutations preserved from hybridization by isolation.

The effect of isolation in the diversification of species and in the ultimate formation of new genera and families is readily discernible in the general flora of the world itself. In the arctic regions where the continental land masses converge—a conflux dating from not so long ago in terms of geologic time—there obtains a remarkable homogeneity of plant distribution. Different sections of this circumpolar region possess a fairly representative number of the same species, such as junipers, willows, and birches, together with mosses and lichens. However, as the continental land masses extend southward in divergent fashion, plant life, though manifesting *generic* similarity, keeps growing more specifically distinct. Finally, in the latitude of South America and southern Africa, with tremendous oceanic expanses forming the ever-widening isolatory mechanisms, the flora on the continental land masses (South America and southern Africa) present wide diversities at the level of the plant families. Diversity in plant flora, therefore, varies directly as isolation. Certainly one cannot conclude that different species occur in the same latitude of widely separated land masses because of differences in either soil or climate, for plants have been successfully transplanted from one continent to another in the same latitude. The evidence from geographical distribution points significantly to "descent with modification."

B. Paleontology. Fossils, the remnants of life in geological time,

are found in sedentary rocks. The latter type of rock stems from the erosion of previously existent rock at the earth's surface, the product of such detrition being swept away in streams and rivers for deposit on the bottoms of larger bodies of water, such as oceans and lakes. Since sedentary rock is formed in successive strata and is consequently indicative of a definite sequence in the passage of very long periods of time, it follows that fossils buried in the deeper strata are older than those embedded in the relatively more superficial strata. Thus a chronicle of plant life may be obtained in the study of the fossil plants as they occur in sequence from the lowermost to the superficial strata of sedentary rock. An examination of the fossil record, in spite of its incompleteness, indicates a procession of plant forms of progressively increasing complexity. The algae and bacteria occur in the lowermost strata; these organisms are succeeded by the psilophytes, the lycopods and horsetails, the true ferns, and finally the gymnosperms and the angiosperms.

Geologists, in their study of the stratifications of sedimentary rock, have discovered that these strata may be collocated into five large groups, each of which represents an immense duration of time, called an *era*. These eras are, in turn, subdivided into still shorter periods of time, termed *epochs*. From the work of the geologists in their reconstruction of geological time and from the discoveries of paleontologists, the fossil record of plants may be briefly presented in a geological timetable.

C. Taxonomy. Similarity in the morphology and physiology of plants obviously reflects a common ancestral kinship. The degree of this similarity in form and function will also be a measure of the degree of closeness to or remoteness from common ancestors. If the similarity in form and function extends only as far as some rather fundamental character, then the group will be more or less remote from its point of common origin, and this fact will imply at the same time that changes in form and function have occurred. Such a group might be a phylum; for example, the phylum Tracheophyta in which the subphyla share one common morphological and physiological characteristic in the possession of a vascular system. But as we go down the taxonomic scale, let us say, to the various families in a given order, the structural and functional similarities increase rather perceptibly; the differences are not numerous nor as fundamental as those which distinguished the different orders from one another. As we reach the

Table 14 GEOLOGICAL HISTORY OF PLANT LIFE

Era	Period	Epoch	Plant Life	Age
Cenozoic (60 million years)	Quaternary	Recent	Herbaceous plants increase, decline of woody plants	Age of Angiosperms
		Pleistocene	Destruction and redistribution of many plant species because of glaciation	
	Tertiary	Pliocene	Development of flowering plants and monocots	
		Miocene	Reduction of forests	
		Oligocene	World-wide tropical forests, rise of flowering plants and monocots	
		Eocene	Development of forests (angiosperms), with *Sequoias* prominent	
Mesozoic (125 million years)	Cretaceous		Angiosperms come into dominance, decline of gymnosperms, monocots begin to appear for first time	Age of Gymnosperms
	Jurassic	——	Angiosperms appear for first time, conifers and cycads prominent	
	Triassic		Gymnosperms increase, seed ferns become extinct	
Paleozoic (350 million years)	Permian		Decline of horsetails and lycopods	Age of Lycopods and Seed Ferns
	Pennsylvanian	——	Seed ferns and gymnosperms abound in forests	
	Mississippian		Lycopods and horsetails common, gymnosperms spreading over wide areas	
	Devonian	——	Land plants (psilophytes and lycopods) established, appearance of gymnosperms, first forests	Age of Land Plants
	Silurian		First land plants in fossil form, psilophytes, algae are dominant	Age of Algae
	Ordovician	——	Marine algae abound	
	Cambrian		Marine algae, first fossils of plant life	
Proterozoic (900 million years)	——	——	Bacteria and blue-green algae common	
Archeozoic (500+ million years)	——	——	No fossils" "Bacteria"	

level of the various species in a given genus of plants, the similarities become strikingly close and the differences between one species and another are but minor in a comparative sense. Obviously these species, because of their similarity, are as close to the common ancestral species as the phylum is remote. Thus these groupings within groupings postulate not only a common ancestral kinship but also a stepwise series of gradual changes. It would indeed be difficult to say, or even think, that there is no evidence for evolution in plant taxonomy.

D. Comparative Serology. Perhaps the most notable evidence in support of organic evolution comes from the field of comparative serology. Experimental investigations have established the fact that when the proteins of a plant are injected into a rabbit, they behave as antigens and stimulate the production of specific antibodies. In fact the rabbit is said to be immunized against the proteins of the plant; that is, the antibodies in the rabbit's blood will precipitate and destroy the proteins from the same plant on a second inoculation. Further, it has been discovered that the immunized serum of the rabbit will precipitate, in vitro, protein solutions from other related species of plants, but in a progressively diminishing degree as the kinship between the plants becomes more remote. Taxonomic studies of plants on the basis of serological method of determining plant relationship correlate rather closely with similar studies based on morphological data. Thus while varying degrees of serological affinity point to diversification of species, they also underscore a common ancestral kinship.

E. Genetics. Genetics not only has to do with heredity but also with variation. In the latter field, as was indicated in the previous chapter, it has been established that heritable variations may be accomplished through genic mutations and chromosomal aberrations. But heritable variations are basic to speciation—or "descent with modification."

MECHANISMS OF EVOLUTION

Though the fact of organic evolution presents itself clearly from even a short survey of the evidence, the question as to the mechanism or method of evolution still remains. This question brings us to the consideration of the premises of Lamarck, to Darwin's concept of evolution by natural selection, to the mutations of de Vries, and finally to the modern synthesis.

Lamarck's Theory. From the vast fund of taxonomic data which he himself had gathered from his studies in both botany and zoology, Lamarck finally came to the conviction that species were transmuted from previously existent species. In 1801 he put forth a theory as to the mechanisms underlying the evolvement of one species from another. This theory, rather commonly referred to as the *inheritance of acquired characters,* may be condensed into four premises: (1) that a continuing tendency toward increment in size is manifested by living organisms in their evolution; (2) that the production of new organs stems from a need actuated by environmental change; (3) that the development of an organ is attributable to frequent use, and conversely its degeneration and its ultimate disappearance are due to disuse; (4) that the characters acquired during the life cycle of a living organism are transmitted to its progeny.

While some plants may present in their lines of descent a continuing increment in size, it does not follow that they all do. As a matter of fact quite a number of plants in their evolution show a decrease in size. Therefore, his first premise falls because of lack of universality. His second premise is obviously not true. In his third proposition as to the development of an organ being proportional to its use, there is some truth; but there is no evidence that modifications produced in an organ as a result of use or disuse were ever transmitted to the offspring of an organism possessing such a modified organ. Certainly a difference in soil fertility can modify the fruit yield of two plants of the same species: a rich soil will mean a greater fruit yield, while the poor soil reflects itself in slow growth and reduced fruit yield. However, if the seeds from these two plants are put in the same type of soil, the plants which develop from these seeds will be essentially similar both in rate of growth and fruit yield.

In light of modern knowledge, the theory of Lamarck cannot be seriously considered as a *modus operandi* in organic evolution.

Darwin's Concept. Perhaps *Malthus on Reproduction,* a book that Darwin chanced to read, together with his visit to the Galápagos Archipelago, had much to do with his ideas on evolution by natural selection.

It became apparent to Darwin that plants and animals reproduce in numbers far beyond the capacities of the environment to support them. This prodigality of nature is well exemplified in the annual seed production of a mustard plant—730,000 seeds. Because of this over-

production there ensues a struggle on the part of plants for water, light, and food—a struggle for survival which Darwin considered to be of greater magnitude among individual plants of the same species, for the materials necessary for their continued viability would be the same. Now then, no two plants of the same species are exactly alike, for they possess slight variations in structure in much the same way that two brothers in the same family would. In fact, some of the members of the same species, especially if they are somewhat isolated from the others, may show a common pattern of minor variations and constitute a variety or subspecies. Darwin looked upon these subspecies as "incipient species" in the process of modification into distinct species. These variations among members of the same species would be either neutral, favorable, or unfavorable to the plants in their struggle to survive. Darwin, observing that relatively few plants in a given species survived in their struggle for existence, maintained that the variations favorable to the plants in their relations to the biotic and physical aspects of their environment would most probably eventuate in their survival and would be transmitted to their offspring. The preservation of the plants with the favorable variations and the elimination of those with the unfavorable variations were called natural selection by Darwin. The agent of this natural selection was, of course, the environment. Thus *in time* through natural selection, an incipient species could become a distinct species.

Darwin's theory, however, had some shortcomings. It did not account for the presence of nonadaptive characters. Yet these same nonadaptive characters are in many cases the features distinguishing between different species. Darwin himself knew that his theory was weak in reference to the transmission of favorable variations to the progeny of the surviving plants. Darwin did not know of Mendel's work. Left unexplained, also, is the fact of overspecialization that has occurred in the organs of some plants, the flowers of *Yucca* for example. This overspecialization of organs, often quite detrimental to the plants in their struggle for survival, is the result of an extreme degree of variation in structure. However, as will become obvious later, Darwin's concepts still permeate modern scientific thinking in relation to the method of organic evolution.

De Vries' Mutations. In his painstaking work on the evening primrose, *Oenothera lamarckiana,* de Vries discovered that there would appear different and distinct types of *Oenothera.* De Vries, who was

a codiscoverer of Mendel's work, observed that these new types of *Oenothera* would breed true generation after generation. Further, these new types demonstrated such a degree of variation from *Oenothera lamarckiana* that they constituted in a strict taxonomic sense new species. To the hereditary modifications that eventuated in the production of these new forms, de Vries applied the term *mutations*. On the basis of his work, de Vries formulated a theory of evolution by mutation. De Vries held that a new and distinct species could be formed *abruptly* by virtue of mutations. De Vries' idea stands in great contrast to Darwin's concept, for Darwin maintained that a new species resulted from the *slow* aggregation of small variations by natural selection.

It should be emphasized here that de Vries' mutations were actually chromosomal aberrations or chromosomal mutations, to distinguish them from genic mutations (mutations in the strict sense) that play so important a role in evolution according to the modern synthesis.

MODERN SYNTHESIS

The modern synthesis stems, not from a few branches of biology, but from all the biological disciplines. Actually there are two schools of thought in the modern synthesis.

One school, commonly referred to as neo-Darwinism and led by Dobzhansky, holds that evolution is due to:

1. Slow aggregation of small mutations (genic) and sifting of groups of these mutations by natural selection to effect subspeciation.
2. The further modification of the subspecies into a new and distinct species by natural selection, with isolatory mechanisms preserving the subspecies from hybridization in the meantime.

The other school of thought, whose champion is Goldschmidt, submits that the neo-Darwinian concept explains only the formation of a subspecies but is rather inadequate in the explanation of the conversion of a subspecies into a distinct species. The hypothesis of the Goldschmidtian group may be summarized as follows:

1. Formation of the subspecies through the accumulation of small mutations by natural selection.
2. Evolution of the subspecies into a distinct species by chromosomal mutations (chromosomal aberrations).

3. Survival or disappearance of the new species under natural selection. If the species survives, then it subspeciates according to the neo-Darwinian concept.

Both of these hypotheses are sustained by a tremendous amount of evidence, but we still are quite a distance from the real comprehension of the mechanisms involved in organic evolution. However, these two schools of thought represent long strides forward when retrospect takes us to Lamarck and Darwin.

SUMMARY OF PLANT EVOLUTION

From the available evidence it is rather probable that the autotrophic bacteria are the ancestral forms whence evolved all the algae. Though it would appear that the blue-green algae, because of their primitive form, were ancestral to the other algal groups, there obtains practically no evidence to support such a conclusion. The origin of the slime fungi and the higher fungi presents a problem, but there are three possible ways in which they might have evolved: from the algae through the loss of chlorophyll, from the bacteria, or from the Protozoa. The first land plants, the psilophytes, are thought to have evolved from the green algae. The bryophytes are looked upon as a terminal group which originated from the green algae. From the psilophytes arose separately the lycopods, the horsetails, and the ferns. The ferns evolved into the gymnosperms, from which apparently the angiosperms took origin. The origin of the angiosperms from the gymnosperms is at present a rather controversial point among botanists. Most of them are inclined to believe that the gymnosperms and angiosperms originated separately from a common ancestral form along slightly different lines. The dicots of the class Angiospermae are considered to be the progenitors of the monocots.

In the textual material of this book, the following trends in plant evolution have already been noted:

1. The progression from the primitive nuclear body of the bacteria and blue-green algae to the formed nuclei characteristic of the other classes of the algae
2. Colony formation and the ultimate attainment of multicellularity in the algae
3. Sexual reproduction with alternation of generations
4. The decrease in size of the gametophytic generation as the

INDEX

Abscission, 104-105
Abscission layer, 105-106
Absidia cornealis, 260
Absidia corymbifera, 260
Absorption, 25
  active, 33
  passive, 33
Absorption of inorganic salts, 95-96
Absorption of water (root), 95-97
  active, 96
  passive, 96
Achene, 166
Acquired characters, 353
Acquired immunity, 235-236
Actinomorphic flower, 140
Actinomycetes, 233
Active absorption, 33
Active immunity, 235
Adenosine phosphates, 128, 133, 137
Adsorption defined, 84
Adventitious root, 77
Aeciospores, 298
Aeciospore mother cell, 297
Aecium, 298
Aerobic and anaerobic respiration, 132-137
Agar, 217
Agaricus campestris, 289 et seq.
  life cycle of, 290
  morphology of, 289-290
Agglutinin, 235
Aggregate fruits, 164-166
Air vesicle, 210
Albugo candida, 253-255
Albuminous seed, 168
Alcoholic fermentation, 136
Aleurone grain, 168
Aleurone layer, 168
Algae, 175-217
  classification of, 175
    blue-green, 177-181
    brown, 206-212
    diatoms, 200-205
    green, 182-199
    red, 213-217
  definition of, 175
Algae (cont.)
  habitat of, 175
Algal fungi (see Phycomycetes), 250-260
Alkaloids, 22
Alkaloids of ergot, 280
Allele, 151, 237
Alternation of generations, 42, 305
Amanita, 291
Amanita muscaria, 291
Ammonification, 228
Ammonifying bacteria, 229
Amphitrichous bacteria, 221
Amylases, 269
Amyloplast, 20
Anabolism, 22
Anastomoses, 24
Androspore, 196
Angiospermae, 47-172
Animal viruses, 241
  classification of, 241
Annual, 50
Annual rings, 67-68
Annulus, 290, 313, 324
Anther, 140
Antheridial receptacle, 308
Antheridium, 184
Antheridiophore, 308
Anthocerotales, 305
Anthocyanins, 22
Antibiosis, 233
Antibiotics, 233
  against rickettsial diseases, 244
Antibody, 235-236
Antigen, 235
Antihemorrhagic vitamin, 230
Antipodals, 144
Antiseptic, 236
Apetalous flower, 141
Apetaly, 141
Apical cap, 192
Aplanospore, 198
Apothecium, 263-264
Apple mildew (*Podosphaera leucotricha*), 273
Archegonial receptacle, 308

Archegoniophore, 308
Archegonium, 175, 305
Archesporial cells, 160
Arthropod vectors of Rickettsiae, 243
Arthrospores, 285
Ascent of sap, 118-119
  Dixon-Jolly theory for, 118
Ascocarps, 263
Ascogenous hypha, 261, 263
Ascogonium, 261
Ascolichens, 301, 313
Ascomycetes, 261 et seq.
  classification of, 263-264
  general characteristics of, 261
  representatives considered.
    blue and green molds, 273 et seq.
      economic considerations, 275-276
      occurrence, 273
      reproduction, 273-275
      structural aspects, 273
    cup fungi, 280 et seq.
      general characteristics, 280-281
      occurrence, 280-281
      reproduction, 281-282
    ergot fungus, 276 et seq.
      economic aspects, 280
      life cycle, 276-279
      occurrence, 276
    powdery mildews, 270 et seq.
      economic aspects, 273
      morphology, 270
      occurrence, 270-271
      reproduction, 271-272
    yeasts, 264 et seq.
      cytological aspects, 264-265
      economic importance, 268-269
      occurrence, 264
      reproduction, 265-267
  reproduction in, 261-263
Ascorbic acid, 128
Ascus, 261
Asochyta pisi, 285
Asparagus (*Asparagus officinalis*), 75
Aspergilloses, 276
Aspergillus (see Blue and green molds), 273 et seq.
Aspergillus fumigatus, 276
Aspergillus nidulans, 276
Aspergillus niger, 269, 276
Aspergillus oryzae, 276
Aspergillus repens, 273-274
Assimilation, 35
Aster, 20
"Athlete's foot," 285
Atoms, 6-8
Atoms (cont.)
  atomic number, 7
  atomic weight, 7
    isotopes, 7
  electron, 6-7
    definition of, 6
    valence, 7
  ion, 6-8
    anion, 8
    cation, 8
    definition of, 6
  neutron, 6
  proton, 6
  valence, 7-8
    coordinate covalence, 8
    covalence, 8
    deelectronation, 7
    definition of, 8
    electronation, 7
    electrovalence, 8
Atrichous bacteria, 221
Aureomycin, 233
Autoclaving, 231, 236
Autosome, 343
Autotrophic bacteria, 223-224
  chemosynthetic, 223-224
  photosynthetic, 224
Autotrophic plant, 173
Autotrophic soil bacteria, 90
  Nitrobacter, 90
  Nitrosococcus, 90
Auxin, 163
Auxospore, 200, 204
Azotobacter, 229

Bacillariophyceae, 200-205
  auxospore formation in, 204-205
  cell wall of, 202
  economic importance of, 205
  general features of, 200
  locomotion in, 202-203
  occurrence, 200-202
  protoplast of, 203
  reproduction in, 204
Bacillin, 233
Bacillus, 218
Bacillus mycoides, 222
Bacitracin, 233
Back cross, 339
Bacteria (see Schizomycetes), 218-239
Bacterial endospore, 221
Bacterial viruses, 241
Bacteriolysin, 235
Bacteriophage, 238-239
Bacteriostasis, 237
Barberry (*Berberis communis*), 294

Bark, 68
Basidiolichens, 301, 304
Basidiomycetes, 286 et seq.
  general characteristics of, 286-287
    binucleate mycelium, 286
      clamp formation in, 287
    nonseptate basidium, 286
    septate basidium, 286
    uninucleate mycelium, 286
  representatives considered: 288 et seq.
    Agaricus campestris, 288 et seq.
      life cycle of, 290
      morphology of, 288, 290
    Puccinia graminis, 294 et seq.
      economic aspects, 299
      hosts of, 294
      life cycle of, 295-298
    Ustilago maydis, 292 et seq.
      economic significance of, 294
      life cycle of, 292-293
      morphology of, 282
Basidiospores, 286
Basidium(-ia), 286
  nonseptate, 286
  septate, 286
Bast, 56
Bean, castor (*Ricinus communis*), 168
Bean, common (*Phaseolus vulgaris*), 148, 168
Beet (*Beta*), 77
Berry, 166
Biennial, 50
Bilateral symmetry, 140
Binomial nomenclature, 40
Biological oxidations, 123-126
Blastomyces dermatitidis, 283
Blue and green molds, 273 et seq.
  economic considerations, 275-276
  occurrence, 273
  reproduction in, 273-275
  structural aspects of, 273
Blue-green algae (see Cyanophyceae), 177-181
Blue molds (see Blue and green molds), 273 et seq.
Bog mosses, 305
Border parenchyma, 104
Botany, 1
  subsciences of, 1-4
Bottom yeasts, 269
Botulism, 232
Bracken fern (see *Pteris aquilina*), 322-326
Bracket fungi, 291
Bract, 147
Bread making, 269
Bread mold (common), 257-260
Brewers' yeasts (*Saccharomyces cerevisiae*), 267
Bronchomycosis, 260
Brown algae (see Phaeophyceae), 206-212
Bryales, 305
Bryophytes, 350 et seq.
  alternation of generations in, 305
    Anthocerotales, 305
    Jungermanniales, 305
    Marchantiales, 305
  economic importance of, 306
  general characteristics of, 306
  occurrence of, 305
  representatives considered, 306-313
    Marchantia polymorpha, 306-310
    Polytrichum commune, 310-313
Bud, 48-50
  active, 48, 50
  adventitious, 48
  alternate, 48
  axillary, 48, 49
  classification of, 48, 50
  definition of, 48
  dormant, 48, 50
  flower, 48
  leaf, 48
  mixed, 48
  opposite, 48
  terminal, 48, 49
  whorled, 48
Budding, 174
Buffers, 10
  definition of, 10
  types of, 10

Calyptra, 309
Calyx, 140
Cambium of root, 82
  of stem, 64-65
Capillary water (soil), 91
Capillitium, 247
Capsule, 166, 309
Carbohydrate synthesis in higher plants, 128-129
Carbohydrates, 13-14
  classification of, 14
  definition of, 13
Carbon cycle, 227-228
Carotenoids, 20
Carpel, 139
Carpogonium, 215
Carpospore, 216
Carrier, 345

Carrot (*Daucus*), 77
Caruncle, 166
Caryopsis, 166
Catabolism, 22
Catalase, 126
Cation exchange in soil, 85, 89
Cedar (*Cedrus*), 328
Cell, 17-39
  functions of, 25-39
  structure of, 17-25
Cell division, somatic, 35-39
Cell inclusions, 17, 22-23
Cell plate, 38
Cell sap, 22-23
Cell wall, 17-18
Central cells (red algae), 213
Central nodule, 203
Central siphon, 214
Centriole, 20-21
Centromere, 36
Centrosome, 20-21
Centrosphere, 20
Cercospora beticola, 285
Character, 335
Chemical constitution of protoplasm, 10-16
  inorganic constituents, 11
  organic constituents, 11-16
    carbohydrates, 13-14
    lipids, 14-16
    proteins, 11-13
Chemical principles, 6-10
  atoms, 6-8
  colloidal state, 8-9
  ions, 6-9
    anions, 8
    cations, 8
    hydrogen, 9-10
    hydroxyl, 9-10
  molecules, 6
  pH, 10
    buffers, 10
    of protoplasm, 10
Chemical weathering of rock particles, 86-89
Chemotherapeutic agents, 237
Chemotropism, 106
Chiasma, 158
Chlamydospores, 292
Chlorenchyma, 53
Chlorobium limicola, 224
Chloromycetin, 233
Chlorophyceae, 182-199
  economic importance of, 199
  general characteristics of, 182
  representative forms of, 182-199
Chloroplastid, 19-20
Chondriokinesis, 18
Chondriosomes, 18
Christmas fern (*Polystichum acrostichoides*), 322
Chromatid, 36
Chromatin, 24
Chromocenter, 24
Chromomeres, 155
Chromonema (ta), 24
Chromoplasm, 177
Chromoplastid, 20
Chromosome, 36
Chromosomal aberrations, 345-346
Class, 41
Class Angiospermae, 43-46, 47-172
  Ascomycetes, 261-282
  Bacillariophyceae, 200-205
  Basidiomycetes, 286-299
  Chlorophyceae, 182-199
  Cyanophyceae, 177-181
  Deuteromycetes, 283-285
  Filicineae, 322-326
  Gymnospermae, 327-334
  Hepaticae, 305-310
  Musci, 305, 311-313
  Myxomycetes, 245-249
  Phaeophyceae, 206-212
  Phycomycetes, 250-260
  Rhodophyceae, 213-217
  Schizomycetes, 218-239
Classification, 40 et seq.
  modern method of, 41-43
  traditional method of, 44-45
Classification of viruses, 241
Clamp cell, 287
Clamp connections, 287
Claviceps purpurea, 276 et seq.
Clay, 84, 87
Clay particles, 84
Cleistothecium, 263-264
Closterium, 190
Clostridium, 229
Clostridium botulinum, 232
Clostridium tetani, 218
Clover (red) (*Trifolium pratense*), 102
Club fungi (see Basidiomycetes), 286 et seq.
Club mosses, 317-318
  giant, 317
  large, 317
  small, 318
Club mosses (see Lycopsida), 317 et seq.
Club-root disease, 248-249
Cocarboxylase, 127

Coccus, 218
Coenocyte, 196
Coenocytic hypha, 175
Coenogamete, 260
Coenzyme A, 131
Coenzyme I, 127
Coenzyme II, 127
Colchicine, 346
Coleoptile, 168
Coleorhiza, 168-169
Colicin, 233
Collenchyma, 53
Colloidal soil particles, 84
Colony, 47, 177
Columella, 259, 313
Common bean (*Phaseolus vulgaris*), 149, 168
Companion cell, 56
Comparative serology, 353
Comparison (tabular) of gymnosperms and angiosperms, 332-333
Complete flower, 140-141
Compound leaf, 101-102
  palmate, 102
  pinnate, 102
Compound pistil, 139, 142
Conceptacle, 210
Cones, 44, 314
Conidiophores, 261
Conidiospores, 261
Coniferophytae, 328
Conjugation, 174
Coordinate covalence, 8
Coprinus, 291
Cord moss, 306
Cork of root, 83
  of stem, 56, 65
Cork cambium of root, 83
  of stem, 56, 65
Corn (*Zea mays*), 50, 56, 71, 77
Corn smut (*Ustilago maydis*), 292
Corolla, 140
Cortex of stem, 62
Cotyledon, 59, 167-168
Covalence, 8
Cozymase, 127
Crossing over, 343
Crossover, 158
Crozier formation, 263
Crumbs (soil), 86
Crustose lichens, 301, 304
Cryptococcus hominis, 284
Cyanamide process, 229
Cyanophyceae, 177-181
  economic aspects of, 181
  general characteristics of, 177
Cyanophyceae (cont.)
  organization in, 177-178
  representative members of, 178-181
Cycadophytae, 328
Cycads, 328
Cypress (*Cupressus*), 328
Cystocarp, 216
Cytochrome, 125-127, 135
Cytochrome oxidase, 123, 125, 126, 135
Cytokinesis, 36, 38-39
Cytoplasm, 17
Cytoplasmic membrane, 23-24, 30-34
  absorption of nonionic solutes, 32
  definition of, 23-24
  ionic uptake, 33-34
  osmotic relations of, 31-32
  structure of, 30-31
Cucumber (*Cucumis*), 57
Cup fungi, 280 et seq.
  general characteristics of, 280-281
  occurrence of, 280-281
  reproduction in, 281-282
Cuticle, 62
Cuticular transpiration, 115
Cutin, 53

Dandelion (*Taraxacum*), 77
Deamination, 122
Decarboxylation, 122
Decay, 226
Deciduous plant, 50, 105
Dehydrogenases, 124-125
Denitrification, 228-229
Denitrifying bacteria, 229
Dermatophytes, 285
Dermatropic viruses, 241
Desmid, 188-190
Deuteromycetes, 283 et seq.
  definition of, 283
  pathogens considered:
    Asochyta pisi, 285
    Blastomyces dermatitidis, 283
    Cryptococcus hominis, 284
    Diplodia zeae, 285
    Monilia albicans, 284
    Phymatotrichum omnivorum, 285
    Sporotrichum schencki, 284
    Tinea pedis, 285
Development of root, 78, 79, 81
  lateral root from, 82
  vascular tissue in, 81
Development of seed, 149-150
Development of stem, 59-65
Diakinesis, 158
Diastase in wheat, 269
Diatomaceous earth, 205

Diatomin, 200
Diatoms (see Bacillariophyceae), 200-205
Dictyostele, 69, 71
Diffuse root system, 77
Diffusion, 25
Digestion, 35
Dihybrid cross, 339-340
Diphosphopyridine nucleotide (DPN), 125, 127, 128, 134-136
Diplanetism, 252
Diplobacillus, 218
Diploid number, 151
Diplotene, 155
Dioecious flower, 141
Disaccharides, 14
Diseases caused by rickettsiae, 243-244
Diseases caused by viruses, 243
Disinfectant, 236
Disinfection, 236
Dobzhansky, 355
Double cross, 346-347
Downy mildews, 255-257
Drupe, 166
Dutchman's pipe (*Aristolochia sipho*), 62, 63-64

Easter lily (*Lilium longiflorum*), 139
Ectocarpus, 206-210
Edible mushroom (*Agaricus campestris*), 289 et seq.
Elaters, 309, 316
Electron transfer cycle, 133, 135, 137
Electrovalence, 8
Elements, 10-11
  macronutrient, 11
  micronutrient, 11
Elements essential to plant nutrition, 90-91
  table of, 92
Elm (*Ulmus*), 50, 69
Embryo cell, 321
Embryo sac, 143, 162
  eight-nucleate, 162
  four-nucleate, 162
  uninucleate, 162
Endemic fever, 244
Endocarp, 164
Endodermis of root, 79, 81
Endoenzyme, 225
Endogenous spore, 176
Endosmosis, 31
Endosperm, 167-168
  nucleus, 149
  tissue, 149
Endospore (bacterial), 221
Endothecium, 146
Endotoxin, 230
Enzymes, 121-126
  definition of, 121
  factors affecting action of, 122
  reactions catalyzed by, 122-123
  respiratory, 124-126
  various groups of, 121
Epidemic typhus, 244
Epidermal hair, 53
Epidermis, 52
Epigynous flower, 143
Epiphragm, 313
Epitheca, 202
Equisetineae, 314
Equisetum arvense, 314-316
  gametophyte of, 316
  sporophyte of, 314-315
Ergastic substances, 17
Ergonovine, 280
Ergot, 280
Ergotamine, 280
Ergot fungus (*Claviceps*), 276 et seq.
  economic aspects of, 280
  life cycle of, 276-279
  occurrence, 276
Ergot grain, 277
Ergotism, 280
Ergotoxine, 280
Erysiphe aggregata, 272
Erysiphe cichoracearum, 272-273
Erysiphe graminis, 270, 273
Euascomycetes, 264
Eumycin, 233
Evening primrose (*Oenothera lamarckiana*), 354
Evergreen plant, 105
Evolution, 348 et seq.
Exalbuminous seed, 149, 168, 170
Exine, 146, 309
Exocarp, 164
Exoenzyme, 225
Exogenous spore, 176
Exotoxin, 229-230

F_1, F_2 (filial generations), 338
Factors affecting rate of photosynthesis, 114-115
Factors modifying configuration of root system, 78
Facultative anaerobe, 225
Facultative parasite, 173
Facultative saprophyte, 173
Family, 4
Fascicular cambium, 62
Fats, 14-15

Feldspars (soil), 86-87
  decomposition of (tabular), 87
Fermentation, 132, 137
Fermentation (bacterial), 226-227
Ferns (see Filicineae), 322-326
Fertilization, 174
  flower, 149
Feulgen reaction, 24
Fibrous root system, 77
Field capacity (soil), 93
Filament, 177
Filicineae, 322-326
  introduction to, 322
  representative of, 322-326
    Pteris aquilina, 322-326
      alternation of generations in, 326
      fertilization in, 325-326
      frond of, 324
      prothallium of, 325
      root of, 324
      sporangia of, 324
      spores of, 324-325
      stem of, 322, 324
Fir (*Abies*), 41, 50, 327
First filial generation (F_1), 338
Fission, 174
Flagellum, 221
Flavones, 22
Flavoproteins, 125, 127, 128, 135
Flocculation of soil, 86
Floridean starch, 213
Flower, 138 et seq.
  definition of, 138
  fertilization in, 149
    development of seed, 149-150
    formation of fruit, 150
  formation of, 138-139
  fusion of parts of, 141
  germination of pollen grain of, 147-148
  histogenesis of anther, 160
  histogenesis of ovule, 161-162
  inflorescences, 146
  macrosporogenesis, 161-162
  meiosis, 150-151
    phases of, 153-159
  microsporogenesis, 160-161
  structure of mature pistil of, 142-144
    of mature stamen of, 145-146
  typical, 139
    parts of, 139-140
Flowering plants, 47-172
Foliage leaf, 98-106
Foliose lichens, 301-302
Follicle, 166
Food preservation, 230-231
Food spoilage, 230-231
Food synthesis, 34, 128-132
  carbohydrates, 128-129
  lipids, 130-131
  plant hormones, 131
  proteins, 129-130
  vitamins, 131-132
Foot, 309, 321
Foot cells, 295
Formaldehyde as an intermediate photosynthate, 110
Formation of flower, 138-139
Frond (of fern), 322, 324
  (*Fucus*), 210
Fruit, 163-166
  classification of, 164-166
  definition of, 150, 163
  formation of, 150
  induction of development of, 163
  walls of, 164
Fruticose lichens, 302
Fucoxanthin, 206
Fucus, 210-212
Fumagillin, 276
Funaria, 306
Functions of the leaf, 107 et seq.
  photosynthesis,
    current concepts of, 111-113
    definition of, 107
    factors affecting rate of, 114-115
      external factors, 114
      internal factors, 114-115
    formaldehyde as intermediate photosynthate in, 110
    light energy in, 108
    phosphoglyceric acid as intermediate photosynthate in, 113
    previous ideas of, 109-111
      Baeyer, 109
      Wilstatter and Stoll, 110
    products of, 112-113
    raw materials for, 108
      carbon dioxide, 108
      water, 108
    role of chloroplastids in, 107
    utilization of products from, 107
  transpiration, 115 et seq.
    definition of, 115
    rate of, 115
      external factors, 115-116
      internal factors, 117
    types of, 115
  secondary functions, 118
Functions of the root, 95 et seq.
  absorption of inorganic salts, 95-96
  absorption of water, 95-96

Functions of the root (cont.)
active, 96
passive, 96
anchorage, 95
conduction, 97
reproduction, 97
storage, 97
Fungi, 175-176, 218-299
classification of, 176
ascomycetes, 261-282
basidiomycetes, 286-299
deuteromycetes, 283-284
myxomycetes, 245-249
phycomycetes, 250-260
schizomycetes, 218-239
definition of, 175
methods of reproduction of, 176
plant body of, 175-176
Fungi imperfecti (see Deuteromycetes), 283 et seq.
Funiculus, 143
Furrowing, 38-39
Fusion of flower parts, 141

Galvanotropism, 106
Gamete, 174
Gametophyte generation, 42
Gemma cup, 310
Gene, 24, 151, 336-337
definition of, 336
dominant, 151, 337
mutation, 151, 345
recessive, 151, 337
Generation (s), 42
alternation of, 42
gametophyte, 42
sporophyte, 42
Generative nucleus, 146
Genetic crossover, 158
Genetics (see plant genetics), 150-151, 335-347
Genotype, 335
Genus, 41
Geographic distribution, 348
Geological history of plant life (tabulated), 351
Geotropism, 106
Germ tube, 256
Germicide, 237
Germination of pollen grain, 147-148
Gill fungi, 291
Gills, 290
Girdle, 50
diatom, 202
Gloeocapsa, 178
Glycolysis, 134, 136
Goldschmidt, 355
Gooseberry mildew (*Sphaerotheca mors-uvae*), 273
Grain, 166, 168
Gramicidin, 233
Gram-negative bacteria, 221
Gram-positive bacteria, 221
Gram's stain, 221
Grana, 19
Granite mosses, 305
Grape (*Vitis*), 57
Gravitational water (soil), 91
Green algae (see Chlorophyceae), 182-199
Green mold (see Blue and green molds), 273 et seq.
Ground meristem of root, 79, 81
of stem, 62
Growing point of root, 79
Growth, 35
Guard cell, 52, 104-105
Gymnospermae, 327 et seq.
classification of, 328
Coniferophytae, 328
Cycadophytae, 328
general characteristics of, 327-328
life cycle of pine, 328-331, 334
tabulated, 332

Haber-Bosch process, 229
Hair, 53
epidermal, 53
Haploid number, 151
Haustorium, 253
Hemlock (*Tsuga*), 41, 327
Hemophilia, 345
Hemp (*Cannabis sativa*), 343
Hepaticae, 305-310
Herb, 57
Heterobasidiomycetes, 288
Heterocyst, 179
Heterogamete, 174
Heterosis, 346
Heterospores, 43
Heterothallic conjugation (*Rhizopus nigricans*), 260
Heterotrophic bacteria, 224-226
Heterotrophic plant, 173
Heterozygosity, 337
Hill reaction, 112
Hilum, 166
Histogenesis of anther, 160
Histogenesis of ovule, 161-162
Homobasidiomycetes, 288
Homologous chromosomes, 151, 336-337

Homospory, 44
Homothallic conjugation (black molds), 260
Homozygosity, 337
Hop mildew (*Sphaerotheca humuli*), 273
Horizon of soil, 83-84
Hormogonium, 179
Hormones, 131
Horned liverworts, 305
Horse chestnut (*Aesculus hippocastanum*), 50, 102
Horsetails (see Sphenopsida), 314
Host, 173
Hull, 168
Humus, 85, 304
Hybrid vigor, 346
Hybridization, 336
Hydration, 122
Hydrolysis, 122
Hydrostatic pressure, 27
Hydrostatic water (soil), 91
Hydrotropism, 106
Hygroscopic water (soil), 93
Hymenium, 290
Hypanthium, 141
Hypertonic solution, 34
Hypha, 175-176
  definition of, 175
  types of, 175-176
Hypocotyl, 59, 167-168
Hypocotyl arch, 172
Hypogynous flower, 143
Hypotheca, 202
Hypotonic solution, 34

Imbibition, 84-85
Immunity, 233-236
Incomplete dominance, 341
Incomplete flower, 141
Indusium, 324
Infection, 233-235
Inflorescence, 146
  principal types of, 147
Inorganic evolution, 348
Interfascicular cambium, 64
Internode, 48
Intine, 146, 309
Invertase, 268
Irish dulse (*Rhodymenia palmata*), 217
Irish moss (*Chondrus crispus*), 217
Irradiated yeast, 270
Irregular flower, 140
Isoetales, 317
Isogametangium, 174
Isogamete, 174
Isoniazid, 237
Isotonic solution, 34
Isthmus, 189
Ivy, English (*Hedera helix*), 57

Jerusalem artichoke (*Helianthus tuberosus*), 129
Jungermanniales, 305
Juniper (*Juniperus*), 328

Karyokinesis, 35-39
  anaphase, 36
  metaphase, 36
  prometaphase, 36
  prophase, 36
  telophase, 38
Karyolymph, 17, 24
Kelps, 206, 212
Kombu, 212
Krebs cycle, 131, 133, 135, 136-137

Lamina, 99
Laminaria, 212
Larch (*Larix*), 327-328
Lateral conjugation, 188
Lateral root branches, 81-82
Lathyrus odoratus, 140-141
  keel of, 140
  standard of, 140
  wings of, 140
Leaf (foliage), 98-106
  abscission and fall of, 105-106
  arrangement of, 98-99
    alternate, 98-99
    opposite, 98-99
    whorled, 98-99
  coloration of, 102
  definition of, 98
  functions of, 107-120
  internal anatomy of, 102-105
  opening and closure of stomata, 105
  origin of, 98
  parts of, 99
  simple and compound, 101-102
  types of venation, 99-101
Leaf primordia, 98
Leaf scar, 50
Leaf-trace scar, 50
Leafy liverworts, 305
Leaves, secondary functions of, 118
Legume, 166
Lenticel, 50, 65, 67
Lepidodendrales, 317
Leptotene, 155
Leucoplastid, 20
Liana, 57
Lichenes, 300-304

Lichenes (cont.)
definition of, 300
importance of, 304
reproduction in, 302-304
structure of, 301-302
types of, 301-302
Lichens (see Lichenes), 300-304
Life cycles, types of, 153-154
Light, 108
in photosynthesis, 108
quanta of, 108
visible spectrum of, 108
wave lengths of, 108
Lilac mildew (*Microsphaera alni*), 273
Lily (*Lilium*), 76, 139
Linden (*Tilia americana*), 58, 67
Linkage, 340-343
Lip cell, 324
Lipid synthesis in higher plants, 130-131
Lipids, 14-16
classification of, 14-16
definition of, 14
Liverworts, 305
Loam, 84
Lophotrichous bacteria, 221
Lycopodiales, 317-318
Lycopodineae, 317
Lycopsida, 317 et seq.
classification of, 317
Lycopodineae, 317
Isoetales, 317
Lepidodendrales, 317
Lycopodiales, 317-318
Pleuromeriales, 317
Selaginellales, 318
life cycle of *Selaginella*, 318-321
Lysozyme, 234

Macroconidiospores, 285
Macrocystis, 212
Macrocystis pyrifera, 212
Macronutrient anions (soil), 90
Macronutrient cations (soil), 90
Macrosporogenesis, 161-162
Maidenhair fern (*Adiantum pedatum*), 322
Making of malt beverages, 269
Maltase, 268
Manufacture of distilled spirits, 269-270
Manufacture of ethyl alcohol, 268
Manufacture of wine, 269-270
Maple (*Acer*), 50, 100
Marchantia polymorpha, 306-310
Marchantiales, 305
Mash, 268
Mature anther, 161
Mechanisms of evolution, 352 et seq.
Darwin's concept, 353-354
DeVries' mutations, 354-355
Lamarck's theory, 353
modern synthesis, 355-356
Megagamete, 174
Megagametophyte (macrogametophyte), 162
immature, 162
mature, 162
Megasporangia (macrosporangia), 161, 318
Megaspore, 43, 162
Megaspore (macrospore) mother cell, 162
Megasporophylls, 317
Meiosis, 150-151
phases of, 153-159
Membranes, 25-26
permeable, 25
semipermeable, 26
Mendel, 335
Merismopedia, 178
Meristematic tissue, 51-52
Mesocarp, 164
Mesophyll, 104
Metabolism, definition of, 22
Metabolism (see Plant metabolism), 121-137
Metulae, 273
Micrococcus pyogenes aureus, 232
Microgamete, 174
Microgametophyte, 161
immature, 161
mature, 161
Micronutrient anions (soil), 90
Micronutrient cations (soil), 90
Micropyle, 144-166
Microsporangia, 161, 320
Microspore, 43, 161
Microspore mother cells, 161
Microsporogenesis, 160-161
Microsporophylls, 318
Middle lamella, 17, 38
Mineralization (soil), 88
Mitochondria, 18
Mitosis, 35-39
Mnium, 306
Monilia albicans, 284-285
Monoecious flower, 141
Monohybrid cross, 337-339
Monosaccharides, 14
Monotrichous bacteria, 221
Morphology of Rickettsiae, 243

Mosses, 305
Mucor javanicus, 260
Multiple cross, 346
Multiple fruits, 164-166
Munch's hypothesis, 119
Murine typhus, 244
Mutagenic agents, 346
Mutations, 151, 345-346
Mycelium, 175
Mycobacterium tuberculosis hominis, 218
Myxomycetes, 245-249
  economic aspects of, 249
  general characteristics of, 245
  representative forms of, 245-249
    Plasmodiophora brassicae, 248-249
    Stemonitis, 245-248
Myxophyceae (see Cyanophyceae), 177-181

Native immunity, 234
Natural selection, 354
Neck canal cells, 308
Neo-Darwinism, 355
Neoplasms, 242
Nereocystis, 212
Neurotrophic viruses, 241
Nitrate bacteria, 229
Nitrification, 90, 229
Nitrifying bacteria, 229
Nitrobacter, 229
Nitrogen cycle, 227-229
Nitrogen fixation, 229
Nitrogen-fixing bacteria, 229
Nitrosococcus, 229
Nitrosomonas, 229
Nitrosomonas europaea, 223
Node, 47
Nomenclature, 41
Nostoc, 179-180
Nucellar membrane, 168
Nucellus, 143
Nuclear reticulum, 24
Nucleolus(-i), 71, 24-25
Nut, 166

Oak (*Quercus*), 50, 68
Obligate aerobe, 225
Obligate anaerobe, 225
Obligate parasite, 173
Obligate saprophyte, 173
Oedogonium, 190-196
Oils, 14, 15
Onion (*Allium cepa*), 40, 76
Oogonium, 174
Oomycetes, 250
Oospore, 174
Operculum, 312-313
Opsonin, 235
Order, 41
Organic evolution, 348
Organic matter of soil, 85-86
Organoids, 17, 18-21
  centrosome, 20-21
  mitochondria, 18
  plastids, 19-20
    chloroplastids, 19
    chromoplastids, 20
    leucoplastids, 20
Oscillatoria, 180-181
Oscillatoria erythraea, 181
Osmosis, 26-32
Osmotic pressure, 27-32
Ovary, 140
Ovule, 143-144
  anatropous, 144
  orthotropous, 144
  parts of, 143-144
Oxidases, 126
Oxidation, 123

Paleontology, 349
Palisade parenchyma, 104
Pantothenic acid, 131
Pantropic viruses, 241
Paraphyses, 210, 297
Parasite, 173
Parenchyma, 53
Parthenocarpy, 163
Parthenogenesis, 163
Parthenospore, 188
Parts of typical flower, 139-140
  accessory, 140
  essential, 139
Passive immunity, 235
Pasteurization, 231, 236
Pathogen, 234
Pea, garden (*Pisum sativum*), 99
Peat mosses, 305
Pedicel, 147
Peduncle, 140, 147
Penicillin, 233, 275
Penicillium (see Blue and green molds), 273 et seq.
Penicillium
  digitatum, 275
  glaucum, 275
  italicum, 275
  notatum, 233, 275
  olivaceum, 275
  roqueforti, 275
Perennial, 50

Perianth, 140, 309
Pericarp, 164
Pericentral cells (red algae), 214
Pericentral siphon, 214
Pericycle of root, 81
  of stem, 62
Periderm, 56, 65
Peridium, 247
Periplasm, 255
Peristome, 313
Perithecium, 263-264
Peritrichous bacteria, 221
Perizonium, 204-205
Peronospora destructor, 257
Peronospora tobacina, 257
Peroxidases, 126
Petals, 140
Petiole, 99, 104-105
  definition of, 99
  structure of, 104-105
Peziza, 281
Peziza rapanda, 281
Peziza vesiculosa, 281
pH, 10
  of soil, 94-95
Phaeophyceae, 206-212
  economic importance of, 212
  general characteristics of, 206
  representative forms of, 207-212
    Ectocarpus, 207-210
    Fucus, 210-212
Phaeophyll, 200
Phage, 238-239
Phagocyte, 234-235
Phagocytosis, 234
Phellem, 56, 65
Phelloderm of root, 83
  of stem, 56, 65
Phellogen, 56, 65
Phenotype, 335
Phloem, 56
  translocation in, 119
Phloem ray, 65
Phosphoglyceric acid as intermediate photosynthate, 113
Phorphorylation, 123
Photosynthesis, 107 et seq.
  current concepts of, 111-113
  definition of, 107
  factors affecting rate of, 114-115
    external factors, 114
    internal factors, 114-115
  formaldehyde as intermediate photosynthate in, 110
  Hill reaction in, 112
  light energy in, 108
Photosynthesis (cont.)
  phosphoglyceric acid as intermediate photosynthate in, 113
  previous ideas of, 109-111
    Baeyer, 109
    Willstatter and Stoll, 110
  products of, 112-113
  raw materials for, 108
    carbon dioxide, 108
    water, 108
  role of chloroplastids in, 107
  utilization of products from, 107
Phototropism, 106
Phycocyanin, 177
Phycoerythrin, 213
Phycomycetes, 250-260
  economic aspects of, 260
  general characteristics of, 250
  representative forms of, 250-260
    Albugo candida, 253-255
    downy mildews, 255-257
    Rhizopus nigricans, 257-260
    Saprolegnia, 250-253
Phylum, 41
Phylum Bryophyta, 42, 43, 305-313
  classes of, 45
Phylum Thallophyta, 41, 42, 45, 173-304
  subphylum Algae, 45, 175-217
    classes of, 45
  subphylum Fungi, 45, 175-176, 218-304
    classes of, 45
Phylum Tracheophyta, 44-45, 47-172, 314-333
  subphyla of, 44-45
Phymatotrichum omnivorum, 285
Physica, 302-303
Phytohormones, 131
Phytophthora infestans, 257
Phytophthora phaseoli, 257
Phytoplankton, 175
Pig-wheat moss, 306
Pileus, 290
Pine (*Pinus*), 327 et seq.
Pinna, 324
Pinnule, 324
Pistil, 139
  compound, 139
  parts of, 140
  simple, 139
Pistillate flowers, 141
Pith of stem, 63
Pith ray, 63-65
Placenta, 142
Placentation, 142

Placentation (cont.)
axile, 143
free central, 143
parietal, 142
Plant bodies, 47
Plant breeding, 346-347
Plant diseases, 230
Plant evolution, 348 et seq.
definition of, 348
evidences for, 348-352
comparative serology, 352
genetics, 352
geographical distribution, 348-349
paleontology, 349-350
taxonomy, 350, 352
mechanisms of, 352-357
Darwin's concept, 353-354
De Vries' mutations, 354-355
Lamarck's theory, 353
modern synthesis, 355-356
summary of, 357
Plant genetics, 335-347
alleles, 337
chromosomes and genes, 336-337
crossing and its principles, 337-341
dihybrid cross, 339-341
incomplete dominance, 341
monohybrid cross, 337-339
types of mating, 339
crossing over, 341-343
introduction to, 335
linkage, 341-342
Mendelian principles, 339-340
mutations, 345-346
plant breeding, 346-347
sex determination, 343-345
sex linkage, 344-345
Plant metabolism, 121-137
aerobic and anaerobic respiration, 132-137
biological oxidations, 123-126
definition of, 121
enzymes, 121-123
respiratory coenzymes, 126-128
respiratory enzymes, 124-126
synthesis of chemical compounds in higher plants, 128-132
carbohydrates, 128-129
lipids, 130-131
plant hormones, 131
proteins, 129-130
vitamins, 131-132
Plant viruses, 241
Plants affected by viruses, 242
Plasmodesmata, 119
Plasmodiophora brassicae, 248-249
Plasmodium, 245
Plasmolysis, 34
Plasmopara viticola, 257
Plastids, 19-20
Pleuromerlales, 317
Plumule, 59, 167-168
Pneumotropic viruses, 241
Polar nodule, 203
Polar nuclei, 144
Pollen grain, 146
germination of, 147
structure of, 146
Pollen tube, 148
Polypetaly, 141
Polyploidy, 345, 346
Polysaccharides, 14
Polysepaly, 141
Polysiphonia, 213-217
morphology of, 213-214
reproduction in, 215
Polytrichum commune, 310-313
gametophyte generation in, 313
sporophyte generation in, 312
Pome, 166
Pond scum, 185-188
Pore fungus, 291
Porella, 306
Potato, sweet (*Ipomoea batatas*), 77
Potato, white (*Solanum tuberosum*), 75
Powdery mildews, 270 et seq.
economic aspects, 273
morphology, 270
occurrence of, 270-271
reproduction in, 271-272
Precipitin, 235
Primary leaves, 321
Primary root, 77, 321
Principle of dominance, 339
Principle of independent assortment, 339-340
Principle of segregation, 339
Principle of unit characters, 339
Privet (*Ligustrum*), 50
Procambium of root, 79
of stem, 62
Production of citric acid, 276
Products of photosynthesis, 113-114
Proembryo, 149
Progametangium, 260
Promeristem of root, 79
of stem, 59
Prop roots, 77
Proteins, 11 et seq.
classification of, 12
compound, 15
derived, 15

Proteins (cont.)
classification of (cont.)
simple, 14-15
definition of, 11
Protein synthesis in higher plants, 129-130
Prothallial cell, 320
Prothallium (fern), 325
Protoascomycetes, 264
Protococcus viridis, 183-184
Protoderm of root, 79
of stem, 62
Protonema (fern), 325
Protonema (moss), 306, 313
Protoplasm, 10 et seq.
inorganic constituents of, 11
organic constituents of, 11-16
pH of, 10
Protoplast, 17
Protostele, 69, 317
Pseudonucleolus, 24-25
Pseudoperonospora cubensis, 257
Pteropsida, 47-127, 322-333
Ptomaine poisoning, 232
Puccinia graminis, 294 et seq.
economic aspects, 299
hosts of, 294
life cycle of, 295-298
Puffballs, 292
Putrefaction, 226
Pycniospores, 297
Pycnium, 297
Pyrenoid, 182

Q fever, 244
Quillworts, 317

Rachis, 147, 324
Radial stele, 69, 71
Radial symmetry, 140
Radicle, 59, 167, 168
Radish (*Raphanus*), 77
Raphe, 166
Rate of photosynthesis, 114
factors affecting, 114-115
Rate of transpiration, 115-117
external factors affecting, 115-116
internal factors affecting, 117
Receptacle (flower), 140
Receptacle (*Fucus*), 210
Red algae (see Rhodophyceae), 213 et seq.
Redwood (*Sequoia*), 328
Reduction, 142
Reductional cell division, 150-151
Regular flower, 140
Respiration, aerobic and anaerobic, 35, 132-137
Respiratory coenzymes, 126-128
Respiratory enzymes, 124-126
Rhizobium, 229
Rhizomorphs, 290
Rhizophores, 318
Rhizopus nigricans, 257-260
Rhizopus oryzae, 260, 269
Rhodophyceae, 213, et seq.
economic importance of, 217
general characteristics of, 213
representative forms of, 213
Polysiphonia, 213-217
Riccia, 306
Rickettsiae, 243-244
antibiotics as therapeutic agents against, 244
definition of, 243
diseases caused by, 244
shapes and sizes of, 243
vectors of, 244
vertebrate reservoirs of, 244
Ringworm, 285
Rock mosses, 305
Rockweeds, 206
Rocky Mountain spotted fever, 244
Root, 77 et seq.
classification of, 77
development of, 78-79
definition of, 77
functions of, 95-97
absorption of inorganic salts, 95-96
absorption of water, 95-96
active, 96
passive, 96
anchorage, 95
conduction, 97
reproduction, 97
storage, 97
lateral branches of, 81-82
secondary development of, 82-83
systems, 77-78
fibrous root, 77
taproot, 77
vascular tissue of, 81
Root cap, 79
Root hairs, 79
zone of root hairs, 79
Root tip, 79
growing point, 79
root cap, 79
zone of elongation, 79
zone of maturation, 79
Rusts, 294 et seq.

Rye (*Secale cereale*), 276

Sac fungi (see Ascomycetes), 261 et seq.
Saccharification of starch, 269
Saccharomyces, 266
Salmonella group of bacteria, 232
Samara, 166
Saprolegnia, 250-253
Sarcina, 218
Sargassum, 212
Scalariform conjugation, 186-188
Schizocarp, 166
Schizomycetes, 218-239
  agents used to destroy or control pathogenic bacteria, 236-238
    chemical, 237
    chemotherapeutic, 237
    physical, 236
  endospores of, 221-223
  general consideration of, 218-221
  human infection and immunity, 233-236
  importance of to mankind, 226-233
    bacteria and disease, 229-230
    bacteria and other fungi as source of antibiotics, 233
    bacterial digestion of cellulose, 230
    bacterial infections borne by food, 232-233
    fermentation of, 226-227
    food spoilage and food preservation, 230-231
    nitrogen and carbon cycles, 227-229
    putrefaction and decay, 226
    toxemia from foods containing points of bacterial origin, 231, 232
  nutrition and metabolism of, 223-225
  respiration in, 225-226
Schizosaccharomyces, 265, 267
Scientific name, 40
  generic, 40
  specific, 40
Sclerenchyma fiber, 53-54
Sclerotium, 276
"Scouring rushes," 315
Scrub typhus fever, 244
Scutellum, 168, 170
Seaweeds, 206, 212
Second filial generation (F_2), 338
Secondary development in root, 82-83
  in stem, 63-67
Secondary functions of leaves, 118
Secondary phloem (root), 83
Secondary root, 77
Secondary xylem (root), 82
Sedentary rocks, 350
Seed, 149-150, 165-171
  changes occurring during germination of, 170-171
  conditions required for germination of, 170
  definition of, 165
  dissemination of, 168-169
  morphology, 165, 168
    dicot, 165-168
    monocot, 168
Seed coats, 149
  tegmen, 149
  testa, 149
Seedling, 171-172
  definition of, 171
  description of, 171-172
Selaginella, 318-321
  life cycle of, 318
Selaginellales, 318
Semicell, 189
Sepals, 140
Serum, 235-236
Serum globulin, 235
Sessile leaf, 99
Seta, 309
Sex chromosomes, 343-345
Sex determination, 343-344
Sex-linked characters, 344-345
Shaggy-mane mushroom (*Coprinus*), 291
Shoot, 47
Shrub, 57
Sib cross, 339
Sieve tube, 56
Silage, 227
Simple fruits, 164-166
Simple leaf, 101
Simple pistil, 139
Siphonostele, 69, 71
Slime molds (see Myxomycetes), 245-249
Soil(s), 83 et seq.
  atmosphere, 94
  crumbs of, 86
  definition of, 84
  granulation of, 86
  ions, 90
    elements essential to plant life, 90-92
      table of, 92
    essential macronutrient anions and cations, 90

Soil(s) (cont.)
ions (cont.)
essential micronutrient anions and cations, 90
mineralization, 89-90
organic matter of, 85-86
particles of, 84
pH of, 94-95
profile of, 83-84
release of adsorbed cations in, 89
solution, 86-89
water relations in, 91, 93
Solute, 25
definition of, 25
Solutes, diffusion of, 29
Solvent, 25
Soredium, 302
Sorus (fern), 324
Species, 40
Spermatium(-ia), 215, 297
Spermagonium(-ia), 297
Sphacelial mycelium, 277
Sphagnales, 305
Sphagnum, 306
Sphenopsida, 314 et seq.
classification of, 314
Order Equisetales, 314
general characteristics of, 314
life cycle of *Equisetum arvense*, 314-316
occurrence of, 314
Spindle, 36
Spindle attachment, 36
Spindle fibers, 36
Spirillum, 218
Spirogyra, 185-188
Spirochete, 220
Spoilage by yeasts, 270
Spongy parenchyma, 104
Sporangiophore, 176, 259, 314
Sporangiospore, 176
Sporangium(-ia), 45, 174
Spore, 174, 176
endogenous, 176
exogenous, 176
Spore formation, 174
Sporogenous cells (anther), 160
Sporophore, 288
Sporophylls, 44
Sporophyte generation, 42
Sporotrichum schencki, 284
Spring xylem, 67
Spruce (*Picea*), 41, 50, 327
Stamen, 140
Staminate flowers, 141, 145
Staphylococcus, 218
Staphylococcus aureus, 232
Starch (floridean), 213
Starch granule, 23
Stele, 68, 71
definition of, 68
types of, 68, 71
Stem, 47-76
aerial, 57
climbing, 57
creeping or prostrate, 57
erect, 57
annual rings of, 67-68
bark of, 68
comparative aspects of, 67
dicot, 59-71
development of, 59-65
primary growth of, 59-64
secondary growth of, 64-65
structure of, 59-71
functional aspects of, 74-75
herbaceous, 57
in winter condition, 50
monocot, 71-74
development of, 71, 73
secondary growth of, 73-74
structure of, 73-74
periderm formation, 65
steles of, 68, 71
subterranean, 57, 75-76
bulb, 57, 76
corm, 57, 76
rhizome, 57, 75
tuber, 57, 75-76
summary of primary and secondary growth, 70
types of sections, 58-59
radial, 58-59
tangential, 58
transverse, 58
woody, 57-58
Stemonitis, 245-248
Sterigma(-ta), 286
Sterilization, 236
Stigma(-ta), 140
Stipe (basidiomycetes), 288
Stipe (*Fucus*), 210
Stipules, 99
Stolon, 259
Stoma(-ta), 52, 102, 104
definition of, 102, 104
opening and closure of, 105
Stomatal transpiration, 115
Stomium, 145
Stone cell, 54
Strawberry (*Fragaria*), 57
Streptobacillus, 218

Streptococcus, 218
Streptomyces aureofaciens, 233
Streptomyces griseus, 233
Streptomyces rimosus, 233
Streptomyces venezuelae, 233
Streptomycin, 233
Strobili, 317, 327
  megasporangiate, 327, 330
  microsporangiate, 327, 330
Stroma (*Claviceps*), 278
Structure of mature stamen, 145-146
Style, 140
Subclass, 41
  Dicotyledoneae, 43, 46
  Monocotyledoneae, 43, 46
Suberin, 56
Subsoil, 84
Subspecies, 354
Subphylum, 41
  Algae, 42, 45, 175, 177-217
  Fungi, 42, 45, 175, 218-299
  Lycopsida, 44, 46
  Psilopsida, 44-45
  Pteropsida, 44, 46
    classes of, 45-46
  Sphenopsida, 44-45
Subtilin, 233
Suction pressure, 32
Sulfonamides, 237
Summary of plant evolution, 357
Summer xylem, 67
Sunflower (*Helianthus annuus*), 56, 62-64
Suspensor, 149, 260
Suspensor cell, 149
Sweet pea (*Lathyrus odoratus*), 140
Sycamore (*Platanus*), 100
Symbiosis, 182, 300
Symmetry, 140
  bilateral, 140
  radial, 140
Sympetaly, 141
Synandry, 141
Syncarpy, 141
Synechococcus, 178
Synergids, 144
Synsepaly, 141
Synthesis of chemical compounds in higher plants, 128-132
Systematic botany, 40

Tapetum, 160
Taproot system, 77
Taxaceae, 41
Taxonomy, 40, 350
Tegmen, 165
Teliosorus (i), 295
Teliospores, 295
Terramycin, 233
Test cross, 339
Testa, 165
Tetraploidy, 345
Tetrasporangium, 216
Tetraspores, 216
Thallophytes, 173-303
  classification of, 173-176
  definition of, 173
  methods of reproduction of, 173-174
  plant body of, 173
  subdivisions of, 173
Thallose liverworts, 305
Thallus, 42
Thermotropism, 106
Thiamine pyrophosphate, 127
Thigmotropism, 106
Thiobacillus denitrificans, 223-224
Third filial generation (F$_3$), 338
Tinea pedis, 285
Tissue, 51-56
  definition of, 51
  primary permanent, 51
  secondary permanent, 51
  types of, 51-56
    collenchyma, 53
    cork or phellem, 56
    epidermis, 52
    meristematic, 51-52
    parenchyma, 53
    sclerenchyma, 53-54
      fiber, 54
      stone cell, 54
    vascular, 54-56
      phloem or bast, 56
      xylem or wood, 54-56
Top soil, 83
Top yeasts, 269
Torula histolytica, 284
Toxemia, 231
Toxin, 229
Toxoid, 235
Tracheal tube, 55-56
Tracheid, 55-56
Tracheophyta, 47-172, 314-333
Tract, 335
Trama, 290
Transamination, 123
Translocation in phloem, 119-120
  Munch hypothesis for, 119
Transmethylation, 123
Transpiration, 115 et seq.
  definition of, 115

Transpiration (cont.)
rate of, 115
external factors affecting, 115-116
internal factors affecting, 117
types of, 115
Transpiration pull and water cohesion theory, 118
Tree, 57-58
definition of, 57
types of branching, 57
deliquescent, 57
excurrent, 57
Tree mosses, 305
Trichogyne, 215, 263, 297
Trichome, 53
Trihybrid cross, 340-341
Triphosphopyridine (TPN), 127
Triploidy, 345
Tropism, 106
Tube nucleus, 146
Tumors, 242
Turgor pressure, 31-32
Tylose, 68
Tyrocidin, 233

Ulothrix, 184-185
Uredosorus(-i), 295
Uredospores, 295
Ustilago maydis, 292 et seq.
economic significance of, 294
life cycle of, 292-293
morphology of, 292

Vaccine, 235
Vacuole, 22
Vacuolar membrane, definition of, 24
Valve, 200
Vapor pressure, 28
Variation, 335
Vascular bundle, 63, 73
Vascular ray, 65
Vascular rays (root), 83
Vascular tissue, 54-56
Vaucheria, 196-199
Vectors of rickettsial diseases of man, 344
Vein, 104
definition of, 104
structure of, 104
Venation, 99-101
net, 100-101
palmate, 100-101
pinnate, 100
parallel, 100
Venter, 308
Ventral canal cell, 308
Vibrio, 218
Vinegar production, 227
Virulence, 234-235
Viruses, 240 et seq.
classification of, 241
definition of, 240
diseases, 242-243
in man, 243
in plants, 242
Viscerotropic viruses, 241
Vitamin C, 128
Vitamin K, 230
Vitamins, 118, 126-127, 131-132, 230
Volutin, 265

Wall pressure, 31
Walnut, black (*Juglans nigra*), 102
Water relations in the soil, 91, 93-94
Water silk, 185-188
Water table (soil), 91
Waxes, 15
Weathering of rock particles, 86 et seq.
Wheat (*Triticum vulgaris*), 50, 77, 294
Wheat rust (*Puccinia graminis*), 288-289 et seq.
Wilting point coefficient, 93
Wood, 54-56
Wort, 269

Xanthones, 22
Xylem of root, 81
diarch, 81
polyarch, 81
tetrarch, 81
triarch, 81
Xylem of stem, 54-56
Xylem ray, 65

Yeasts, 264 et seq.
economic importance of, 268-269
cytological aspects of, 264-265
occurrence of, 264
reproduction in, 265-267

Zamia, 328
Zone of elongation, 62, 79
Zone of maturation in root, 79
Zooplankton, 175
Zoosporangium, 174
Zoospore, 174
Zygomorphic flower, 140
Zygomycetes, 250
Zygospore, 174
Zygote, 51, 174
Zygotene, 155
Zymase, 136, 268