BIOLOGY

BY

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SECOND EDITION

REVISED AND ENLARGED

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PREFACE

The subject matter of general biology, as presented in current text books, is variously interpreted. In some it means an introduction to the essential structures and vital manifestations of animals and plants. In others it means the discussion of hypotheses and principles of biology. In others it becomes an encyclopoedia of the facts of physiology, hygiene and ecology. With the first method the course is based largely upon laboratory work and the principles are illustrated with specific types. The second and third methods are largely didactic and are illustrated by examples taken at random from the entire animal or plant kingdom.

We believe thoroughly in the type and laboratory method of instruction, and in choosing the types with such care that they serve as points of departure for various lines of development in subsequent course work. The present work is based upon the excellent course outlined in Sedgwick and Wilson's General Biology which occupies so prominent a place in the teaching of American biology, and my only excuse for offering another to the long list of text books is the need, which we have felt at Columbia, of a work along similar lines to cover a course of about thirty class exercises and as many laboratory periods.

The book is planned somewhat differently from that of Sedgwick and Wilson partly because of the enlarged scope, partly because of the excellent general introductory courses offered in up-to-date secondary schools. Emphasis is laid at the outset on cellular activities, especially on the importance of enzymes in metabolism and development, while animal differentiation for the performance of primary functions of protoplasm is the main theme of the entire course. In the development of this theme organisms of one cell, organisms of tissues, and organisms of organs are taken up in succession.

The first is illustrated by yeasts, bacteria, and protozoa; the second by Hydra and the coelenterates; the third by the earthworm. The food of animals and the sources of animal energy are treated in connection with Hydra and illustrated by the unicellular plants and the fern. Further differentiations of organ systems are illustrated by the lobster (or crayfish), and with these are introduced the principles of homology (through study of appendages) and of morphological adaptations. This work is followed by a short study of physiological adaptations as illustrated by parasitism and by some of the phenomena of immunity. As the general theme works out the fundamental principles of evolution are developed in the mind of the student who is prepared for the discussion of the origin and perpetuation of variations, and the modern principles of heredity discussed in the last chapter.

For permission to use many of the figures I am indebted to Professors Sedgwick and Wilson; to the Macmillan Company for cliches of figures 12, 24, 31, 88, 89; to Professor Morgan and the Columbia University Press for cliches of figures 91, 93–101; to Lea and Febiger for cliches of figures 22, 27; and to Miss Mabel Hedge for the original drawings reproduced in figures 55, 57, 69, 86; finally I wish to express my grateful appreciation to Professor J. H. McGregor for reading the manuscript and for many helpful suggestions and criticisms.

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PREFACE TO THE SECOND EDITION

In the present edition, although there is no change in the method by which the subject of Biology is developed, there are many changes in the text, some parts being condensed, others elaborated, in the interest of clearness. Apart from verbal improvements throughout the book, the most important alterations and additions have been made in connection with the subjects of fermentation and enzyme activities; the significance of conjugation; plants, the food of animals; photosynthesis; circulation in the earthworm; and immunity. Three figures in the first edition (numbers 6, 21, and 39) have been replaced by more instructive illustrations, and in all cases where necessary, the legends have been amplified. The glossary, which was introduced with the second printing of the first edition, is considerably enlarged, and a bibliography added. For kindly criticisms and many valuable suggestions in connection with the chapters dealing with plant forms, I gratefully acknowledge here my indebtedness to my friend Professor H. M. Richards of Barnard College, Columbia University.

G. N. C.

April, 1917.

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INTRODUCTION

A biologist is one whose subject of work is, or has been, living matter. The subject Biology, however, like a polyhedron, has numerous faces, each one more or less circumscribed and independent of the others. Each has its group of followers and its particular name and may be looked upon as an independent science, but this independence is quite superficial, for at bottom all are correlated and no one of them is more entitled to the name Biology than any other. It is customary in practice, to divide the biological sciences into two groups of equal value; the one Zoology, dealing with animal life, past and present; the other, Botany, dealing with plant life. They may also be divided into two unequal groups, Morphology and Physiology, the former dealing, descriptively for the most part, with the structures of animals and plants, the latter dealing, experimentally for the most part, with the functions or vital activities of animals and plants. This latter division, however, is quite artificial and has little of real value.

We may enumerate and correlate the biological sciences in some such manner as shown in the accompanying diagram (Fig. 1).

All of the biological sciences enumerated here may have as the subject matter either animals or plants. Thus there is a plant and animal physiology, plant and animal anatomy or morphology, etc. Furthermore, in addition to the main sciences there are numerous subsidiary branches which deal with special groups, such for example as Bacteriology, Algology, Entomology, Protozoology, etc., most of which are specialized subdivisions of one or more of the sciences given above. Of these, Anatomy deals with the general structures of the body and is purely descriptive in character. It has been most extensively developed in connection with the human organism where an accurate knowledge of the muscles, arteries, nerves and various organs of the body is of the greatest importance to medical men.

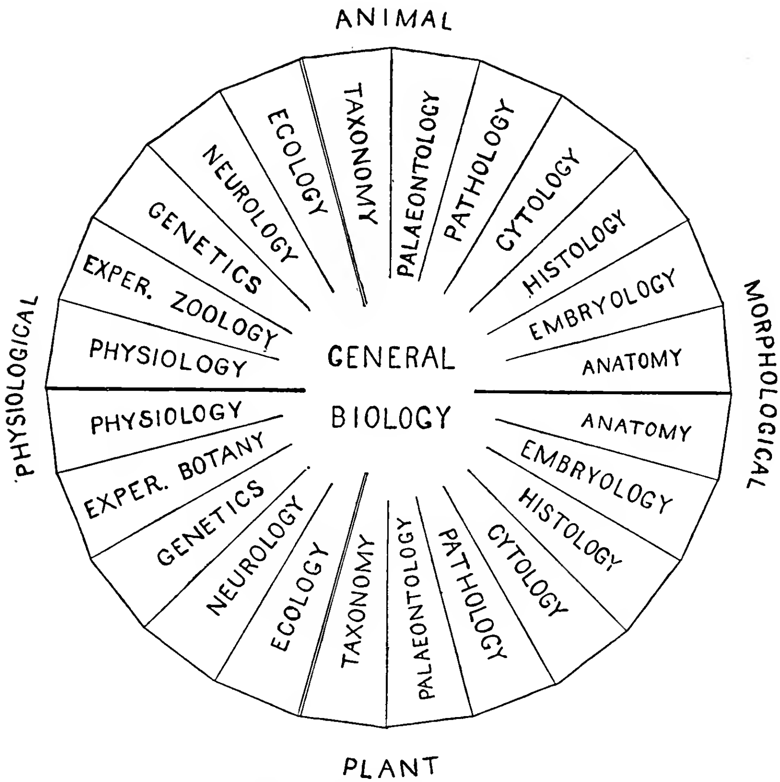


FIG. 1.—Diagram to show the relation of General Biology to the biological sciences.

Comparative anatomy has also been developed as an aid primarily, to the understanding of the various organs in man. Embryology, too, is an important adjunct to anatomy for it deals with the development of organs in the individual. It also has a broader purpose in general biology and has grown into a science quite apart from any particular bearing on human affairs. Cytology is the science dealing with the ultimate units of structure of living things—cells—and has both physiological and morphological sides, while, in connection with the germ cells, it comes in intimate contact with the fundamental problems of general biology. Histology deals with the aggregates of cells in tissues, and this branch, again, is mainly important to students of medicine. Pathology deals with abnormal structures and functions of animals and plants, and is essentially a science of disease. Palaeontology deals exclusively with past life on the earth as revealed by fossil forms of plants and animals. Taxonomy is the science of classification and is dependent upon anatomy, embryology and ecology.

The sciences enumerated above are mainly morphological or based upon the structures of living things, that is upon the mechanisms employed in the performance of vital activities. The remaining five branches are essentially physiological or based upon the actions of the living mechanisms. In this group the science of physiology is the oldest and the best established, dealing, as it does, with the fundamental activities of digestion, assimilation, respiration, excretion, secretion, nerve response and reproduction. Experimental biology, ecology and genetics are more recent and have been developed in connection with the attempts to throw light upon the fundamental biological principles of growth, differentiation, inheritance, variability and organic relationships. Ecology deals with animals and plants as affected by environment, distribution on the earth's surface, and the like. Genetics deals with the different phases of the problems of heredity. Neurology, finally, including psychology, is a science dealing with the nervous system and with the attributes of the brain, while a corresponding science deals with the phenomena of sensation, irritability, etc., in plants.

Other sciences such as Sociology, Anthropology, Political Economy, etc., dealing with man, have a certain claim to relationship with the biological sciences, but, except in a very general way, they are not usually included with this group of sciences.

The diagram (Fig. 1) also illustrates in a general way, the manner in which General Biology is related to the various biological sciences. It must not be understood that the several divisions which we recognize today have grown out of any maternal science of biology. On the contrary the principles of General Biology represent contributions from all the related sciences, and these contributions, for the most part, are fundamental or basic for the special branches involved. Physiology, perhaps more than any other branch, is intimately connected with General Biology; indeed for a long early period General Biology and Physiology were indistinguishable. Anatomy also was, and is yet, intimately correlated with Physiology, and from these two main trunks the secondary branches have developed into special fields of research. One great stimulus for this development was the doctrine of evolution which has been mainly responsible for the distinctly modern sciences of Ecology, Experimental Biology and Genetics.

What then is the subject matter of General Biology? Many naturalists refuse to recognize it or give it a place in their teachings, while the majority of Universities have substituted departments of Zoology and Botany and Physiology for the erstwhile department of Biology.

General Biology deals with the fundamental principles of living matter; specifically, first, with protoplasm and with the manifestations of vitality; second, with metabolism, or the vital processes of waste and repair; third, with the food of animals and plants and with the ultimate sources and transformations of energy; fourth, with the fundamental structures of living things and with the evolution of organic structures; fifth, with the inter-relations of animals, plants, and intermediate organisms; sixth, with the phenomena of vitality, adolescence, age and senescence, fertilization, reproduction, and heredity; and, seventh, with species and the factors of organic evolution. Obviously if we were to study any one of these topics to the limits of our knowledge concerning it, we would compass the entire realm of the biological sciences, so intimately is general biology related to them all. This, however, is just what General Biology should not do; it should, rather, provide a foundation suitable for the further study of any one or all of the many branches of biological science.

CHAPTER I

LIVING AND LIFELESS MATTER

The biological sciences all agree in their fundamental subject matter, *i.e.*, they all deal with things that are, or have been, alive. In this one fundamental fact they differ from the physical sciences. The boundaries between the biological and the physical sciences are very indefinite, however, and investigations into the nature of life, or indeed of any of its manifestations, would be of a very superficial type were not the physical sciences involved. Biological and physiological chemistry, as branches of the science of physiology, are really branches of chemistry, but their subject matter is material that has been living, or has been derived from living things.

What then is living matter as distinguished from non-living matter?

All animals and all plants are made up of a fundamental living substance, together with derivatives from this substance, to which the name Protoplasm was given by Purkinje in 1840. The term protoplasm cannot be accurately defined because it represents a conception rather than a definite thing, there being almost as many protoplasms as there are animals and plants. The term should be used much as we use the terms animal and plant, which refer to no special animal or plant, and it cannot be described any more accurately than can these concepts. Huxley has called it the "Physical Basis of Life," and the physiologist duBois Reymond described it as the "Agent of Vital Manifestations." It is obvious that neither of these definitions would enable us to recognize living substance. The nearest approach to a description of protoplasm is to describe the properties which protoplasms have in common.

The most essential characteristic of this group of similar substances, which we designate Protoplasm, is that they lose their characteristics with life, that is to say they are no longer protoplasm when life is gone. The properties however which living matter possesses alone of all things, are derived from characteristics of protoplasm both in the living state and from its material basis when life is gone. These properties as usually given are (1) the chemical composition; (2) the power of waste and repair; (3) the power of growth by intussusception; (4) the power of fertilization and reproduction, and (5) the power of adaptation.

1. The Chemical Composition

Chemical composition, naturally, is one of the properties of protoplasm which can be obtained only after life is gone, analytical processes invariably killing it. Nevertheless there is no loss of weight after death, so presumably the same chemical elements are present. Analyzed in bulk, material that has been living is known to contain Carbon, Hydrogen, Nitrogen, Oxygen, Sulphur, Phosphorus, Fluorine, Chlorine, Silica and metals Na (sodium), K (potassium), Ca (calcium), Mg (magnesium), Fe (iron), etc. The chemical composition is not easy to determine because protoplasm is not a homogeneous substance but a mixture of different substances; the elements given above are combined in a great variety of ways of which more or less definite compounds called albuminous compounds, or proteins, albuminoids, and nucleo-proteins (all of which are grouped together under the general term proteins) are universally present. Hoppe-Seyler in 1871 analyzing pus cells free from the surrounding fluids, found the following percentages of substances:

Nuclein	34.257 per cent.
Insoluble substances	20.566 per cent.
Lecithin and fat	14.383 per cent.
Cholesterin	7.40 per cent.
Cerebrin	5.199 per cent.
Undetermined albuminoids	13.762 per cent.
Extractives	4.433 per cent.

In the ash he found sodium, potassium, iron, magnesium calcium, phosphoric acid and chlorine. Since then a grea variety of different substances have been obtained from cell and tissues of different living things some of which are giver in the following partial classification of the proteins.

CLASSIFICATION OF THE PROTEINS

- A. Simple Proteins (albuminous bodies)
  - Albumins
  - Globulins
  - Glutelins
  - Prolamines
  - Albuminoids
  - Histones
  - Protamines
- B. Conjugated Proteins
  - Nucleoproteins
    - Nucleic acids
    - Purine bases
      - Uric acid
      - Xanthine
      - 1-methylxanthine
      - Heteroxanthine
      - Theophylline
      - Paraxanthine
      - Theobromine
      - Caffeine
      - Hypoxanthine
      - Guanine
      - Epiguanine
      - Adenine
      - Episarkine
      - Carnine
    - Pyrimidine bases
  - Glycoproteins
  - Phosphoproteins
  - Haemoglobins
  - Lecithoproteins
- C. Derived Proteins
  - Primary derivatives
    - Proteans
    - Metaproteins
    - Coagulated proteins
  - Secondary derivatives
    - Proteoses
    - Peptones
    - Peptides

The above list does not give anything like a complete enu meration of the chemical compounds which make up proto plasm. Most of the above are merely compounds of C, H N, O, and P, and vary in the relative percentages of the differen elements in combination. In the list only the derivatives o the purine bases are given, but each of the others include a similar list of substances. Add to these many compound the various combinations of carbohydrates and fats, and of the minerals Ca, Na, Fe, Mg, etc., and some faint conception may be gained of the enormous number of chemical bodies to be found in protoplasm.

Chemically, living matter may be summarized as consisting of proteins, fats, carbohydrates and salts, the latter playing some important part in the vital processes although, since they all do not appear in all types of protoplasm, each cannot be regarded as a *sine qua non* of living matter. The absolutely essential elements are carbon, hydrogen, nitrogen, oxygen, and phosphorus which enter into the composition of pure nucleinic acid and form the basis of all protoplasm.

While chemical analysis gives an idea of the kinds of elements entering into the composition of protoplasm after death, it allows no conception of the numbers of chemical bodies that are continually being formed during life, and still less conception of the nature of the vital chemical processes. It is generally agreed that pure, ash-free proteins are really inert and lifeless and that salts or electrolytes, either organic or inorganic, are necessary for the vital activities.

Chemical composition, therefore, does not carry us very deeply into the mysteries of protoplasmic composition, nor does it give any clue to the nature of the vital processes. It shows, however, what chemical elements are essential for continued life, *i.e.*, what elements are necessary to provide for in the food, for all living things are constantly using up these substances in vital activities and replacing them from the food materials selected from the environment. This dual process of waste and repair, met with nowhere save in living matter, is a secondary fundamental property of living things and is generally spoken of under the heading **metabolism.**

2. Metabolism or the Power of Waste and Repair

A very good idea of the effects of continued protoplasmic activity in the absence of food may be obtained by keeping some minute animal, for example a protozoon like Paramecium, in a sterile medium for a few days. Paramecium is a microscopic water-dwelling animal to be found in any stagnant ditch or pond. Ordinarily it swims about actively by means of minute motile organs termed cilia and takes in as food still more minute bacteria with the constant current entering the mouth. If it is transferred to a sterile medium it gets little or no food and the protoplasm begins to waste away. The first effect of this uncompensated waste is the appearance of spaces or vacuoles, and after some time in this skeleton-like condition the organism dies (Fig. 2). In other cases the effect may be shown by a

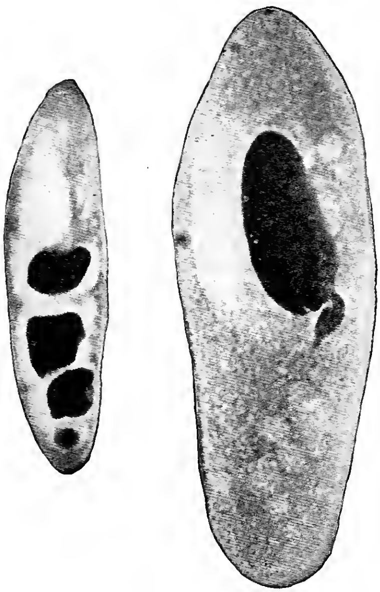


FIG. 2.

FIG. 3.

FIG. 2.—Effect of starvation in *Paramecium caudatum*. Photographs (same magnification) of normal (at right) and starved individuals.

FIG. 3.—Effects of starvation in *Dileptus gigas*. Photographs (same magnification) of preparations of normal individual and individuals starved ten and twenty-one days respectively. All sister cells.

constantly diminishing size; Fig. 3 represents a normal specimen of the protozoon *Dileptus gigas* and sister organisms starved for ten and twenty-one days.

What happens in these small living things finds a rough analogy in a coal fire. The coal, made up of carbon and inorganic matter, is rapidly oxidized, and energy in the form of light and heat is liberated. The potential energy thus changed into light and heat was stored up in the coal, ages ago when it was a part of the earth's vegetation. This process of physical combustion is brought about by the union of oxygen (oxidation) with various elements in the coal. Smoke, carbon dioxide (CO_2), water (H_2O), and an incombustible residue (ash) are formed, while kinetic energy is given off in the form of light and heat. Here then, with oxidation is a change from potential, or stored, to kinetic or free energy, while an organic material with definite properties is changed at the same time into CO_2, H_2O, free carbon and a useless residue.

The famous French chemists, Lavoisier and Laplace, in 1780, were the first to show that animal heat, like that from fire, is produced by combustion involving the consumption of oxygen and the liberation of CO_2, and they found that practically the same amount of heat was produced and the same amount of CO_2 was liberated by a living Guinea pig and by a burning candle. Later, it was discovered that another product occurs in the living animal, viz. urea.

The actively moving, eating, digesting and excreting Paramecium gets the energy for its many vital processes through the oxidation of substances contained in its protoplasmic make-up. As in the combustion of coal, CO_2 and H_2O are formed and liberated while an incombustible residue, termed urea, is analogous to ashes in physical combustion. The energy for movements and for carrying on the many physiological activities of the organism is derived from the chemical energy contained in the complex molecules forming the basis of all protoplasm. The continued activity of Paramecium without a new supply of fuel (food) results in the burning out of the protoplasmic substance as shown by the vacuolization of the body, final exhaustion of the available elements for combustion, and must result in death (Figs. 2 and 3). Similar processes take place in all animals and plants; CO_2, H_2O, and urea or equivalent are formed and excreted in one way or another, while many of the complexities in structure of the higher animals are due to the elaboration of organs for the disposal of such waste products.

To continue the analogy a bit further. New fuel is needed to maintain a fire, so new food is needed to prevent death through continued waste and to provide energy for continued activity. The new coal must first undergo a certain amount of preparation before it undergoes oxidation; it must be broken into small pieces, and must be raised to a certain temperature before active combustion takes place. Similarly, food consisting usually of lifeless proteins, carbohydrates and fats derived from other animals or plants, must be disintegrated and prepared for assimilation, and this finely divided food material is then distributed to all parts of the organism. The process of thus preparing the food is called digestion, and is mainly a process of hydrolysis of food materials. In biology the two processes of waste and repair are usually considered together under the term *Metabolism*, destructive metabolism called *katabolism* being the sum of processes concerned with the breaking down or combustion of protoplasmic substances, and constructive metabolism, called *anabolism*, being the sum of processes having to do with repair and growth. Just how the finely divided food particles are added to the protoplasmic molecules is unknown, but it is certain that the addition takes place uniformly and in all parts of the organism, and that by such uniform additions of new materials growth of the organism takes place. From its mode of addition we have the third property of living matter:

3. Growth by Intussusception

This is distinguished from growth by accretion as seen in the enlargement of a crystal, for example, where new particles are added to the outside of the existing structure. Obviously such growth or increase in amount of protoplasm together with its differentiation, can take place only when the waste or combustion of protoplasmic substances is less than the new materials added. When the constructive processes exceed the destructive, more material is added to the protoplasm than is lost by waste, and growth results. This growth continues until a certain limit of size is reached, every animal and every plant having such a limit to size, and to form as well, and when this limit is reached many of the physiological activities are directed toward reproduction of the race or of kind. Such a stage is spoken of as the period of maturity, and it varies according to the total length of life of the organism. This period of maturity is preceded by a period of active growth when constructive processes are far in excess of the destructive, and is called the period of youth. Succeeding this comes a period, adolescence, of greater equilibrium between constructive and destructive processes, and with this comes a period of maturity with the power to reproduce the species. This power marks a fourth property of protoplasm:

FIG. 4.—Division of *Euplotes patella*. Photograph from a preparation.

4. REPRODUCTION

Reproduction of kind is a phenomenon exclusively confined to living things but the manner of reproduction varies in different cases. In some cases the living organisms divide through the middle to form two similar halves, each of which forms a new organism. This, the most simple method of reproduction, is called simple division or binary fission (Fig. 4). Again, minute bits of the organism may be pinched off the periphery of the parent, and these grow into organisms similar to the parent (Fig. 5). This method is termed budding or gemmation, and the buds thus formed may be single or multiple in number, as in Hydra. Sometimes the entire substance of the parent organism breaks into minute reproductive bodies to which the term spores is applied, the process being known as reproduction by spore-formation or sporulation (Fig. 6). All of the above methods of reproduction are limited to the lower types of organisms, while the higher types reproduce by proc-

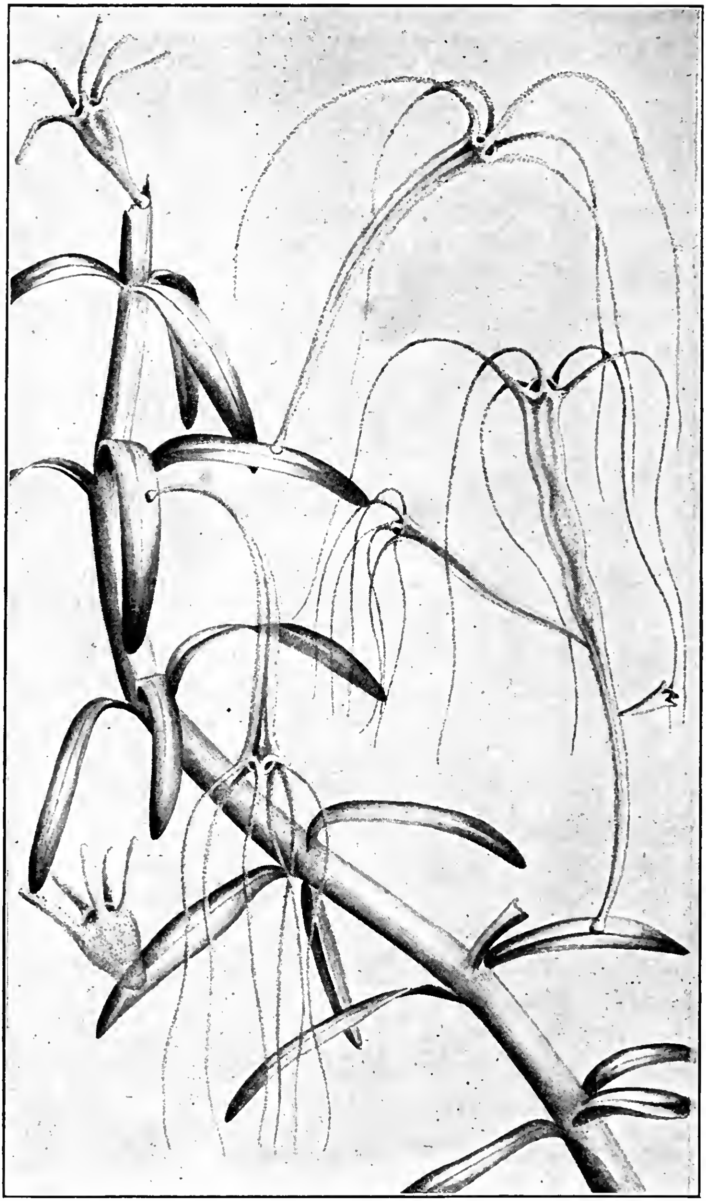


FIG. 5.—Five specimens of *Hydra fusca* on water plant. One individual in process of budding. (From a drawing by S. F. Denton made for E. B. Wilson.)

esses involving sex differentiation, and are called sexual reproduction. These consist, both in animals and plants, in the fertilization of an egg derived from a female organism, by a spermatozoon derived from a male, and after the union of egg and spermatozoon an embryo is produced which grows through many different stages in development (ontogeny) to an adult organism similar to the parent form. In some cases the egg

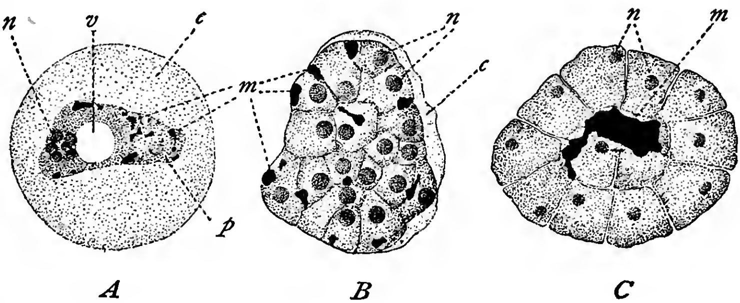


FIG. 6.—Asexual sporulation in malaria organisms. *A*, parasite of tertian malaria (*Plasmodium vivax*) in human blood corpuscle; *B*, multiple division (schizogony) of same; *C*, multiple division of the organism causing quartan malaria (*Plasmodium malariæ*); *c*, blood corpuscles; *m*, melanin granules formed by the parasites and liberated into the blood as a toxin during sporulation; *n*, nuclei of parasite and progeny (merozoites); *p*, cell-body of parasite; *v*, vacuole. From preparations.

proceeds to develop without processes of fertilization, such a method of reproduction being known as parthenogenesis, a result which may be brought about in some cases, artificially, by the use of salts.

5. Power of Adaptation

A fifth property possessed by protoplasm is the capacity to vary under changed conditions of the environment. It is by reason of this power that the myriads of animal and plant forms exist today as distinct species. Such variations, due perhaps to environmental differences, perhaps to mutations or sudden and unexplained appearance, are rarely observed in the making, but the result of the change or changes is spoken of as an *adaptation.* Such adaptations may be in structure or in function, and are accordingly either morphological or physiological. (See Chapter IX.)

These properties, chemical composition, power of waste and repair, growth by intussusception, power of reproduction and adaptability are primary attributes of protoplasm, and serve to distinguish living from all other kinds of matter. It does not follow, however, that non-living things do not manifest one or more of these phenomena. Thus the chemical composition, as we have seen, is that of lifeless protein, while growth by intussusception may be said to take place whenever a solid crystalloid is dissolved in a liquid. Furthermore these properties are of such a nature that if we were dependent upon them it would be difficult in some cases to tell whether an organism is alive or not. To determine its chemical composition it would have to be killed; its growth, waste and repair could not be easily observed, while only a fortunate chance would reveal its reproduction. It is possible, however, to determine by certain characteristics of protoplasm whether a given thing is living matter or not without the necessity of ascertaining its properties, and these we speak of as the evidences or manifestations of vitality.

These are usually included under the heads of appearance, form and movement.

Protoplasmic Appearance.—Under a microscope, protoplasm has a characteristic and recognizable appearance not easy to describe. If seen with a low magnification it appears like a transparent, colorless, somewhat glass-like, semi-fluid substance usually with numerous granules of variable size and with many clear spaces or vacuoles. It is always refringent and never mixes with the surrounding water. It is viscous; has a high power of cohesion and readily absorbs substances by osmosis from the surrounding medium and gives off substances, also by osmosis, to the surrounding medium. It is, therefore, permeable in respect to some substances. If seen under a high magnification the appearance differs with the object. In some cases there is a more or less definite reticulum or network enclosing a more fluid substance; in other cases the protoplasm appears like an aggregate of bubbles in a frothy soap suds, with the walls of the bubbles or, in protoplasm, alveoli, relatively dense and the intra-alveolar substance relatively more fluid; in still other cases the more refringent parts are in the form of minute rods or fibrillæ surrounded by a more fluid matrix. In all forms assumed by protoplasm, there are invariably fine granules, called microsomes, scattered throughout.

These different types of protoplasmic structure have given rise to different theories as to the physical make-up of protoplasm, and the adherents of each theory hold that all other appearances are only modifications of the structures which they believe fundamental. Thus we find biologists who hold to the "reticular" theory, others who hold the "alveolar" theory, others again who adhere to the "fibrillar" theory, and still others who maintain that all apparent structures are secondary and unimportant and that the only vital elements in the physical make-up are the granules or microsomes. Whatever may be the outcome of disputes over the relationship of the different appearances the fact remains that protoplasm consists of an aggregate of fluid-like substances of different densities which may assume a variety of configurations.

Form.—These appearances, even if uniform, could not be relied upon as a sure manifestation of vitality. Lifeless protein, albumen, and even emulsions of oil, water and salt, give similar appearances so that other manifestations must be taken conjointly. Appearance combined with form gives fairly definite evidence of life. Form, however, is closely connected with the configuration of morphological units of protoplasmic structures. With the exception of a small number of amorphous living things, all types of animals and plants have a definite and recognizable form. No living thing consists of a homogeneous sheet or column or ball of semi-fluid protoplasm, but in all higher types the protoplasm is divided among myriads of very tiny units called cells which may become differentiated in the greatest variety of ways. The few amorphous types of living things consist, as a rule, of but one single cell (*e.g.*, Amoeba, Fig. 10). In life the individual cells of an animal or plant cannot be readily made out; some of them are glandular in function, others are muscular, others sensory, supporting, reproductive, etc., the form of the organism being due largely to the supporting cells and products. With the exception of the amorphous types all animals, even the unicellular ones, have fairly definite axes of symmetry. Some, the globular ones, are homaxonic or similar in structure in all planes passing through the center; others are monaxonic, having but one axis of symmetry, with the mouth at, or near, one extremity termed *anterior*, and the tail with vent at the opposite end termed *posterior*. In such forms the mouth side is *ventral*, the opposite or aboral side is *dorsal*. Still other types are polyaxonic and, like Hydra, may be divided by innumerable vertical planes into symmetrical halves.

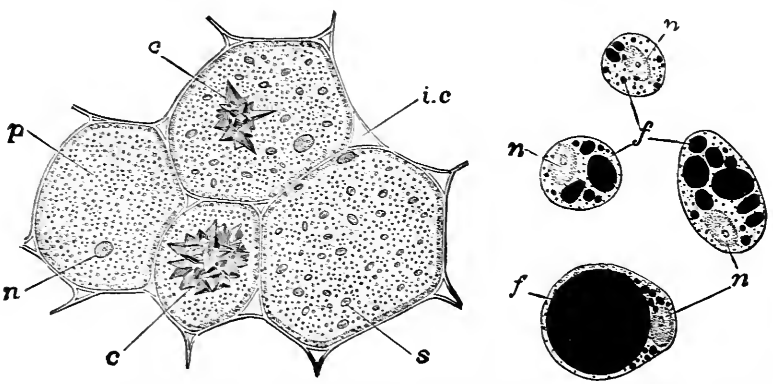


FIG. 7.—Lifeless matter in living cells. *c*, Groups of crystals of calcium oxalate; *i.c.*, intercellular space; *n*, nucleus; *p*, cytoplasm; *s*, starch granules; *f*, fat drops. (From Sedgwick and Wilson.)

The form of an animal or plant, dependent largely upon the presence and activity of the supporting cells, is very often due to the presence of lifeless matter within or around those cells and created by them. In the majority of cases the form is retained for a longer or shorter time after the living protoplasm has died, hence form alone would be insufficient evidence of living matter. Many lifeless things, such as crystals and lifeless products of vital activity, may also have definite forms, hence neither form alone nor form with appearance would give a complete manifestation of vitality. Living and lifeless matter often go together to make up the form of an organism, the lifeless matter being laid down either within the cells or around the cells. Many products of waste metabolism are thus stored up in living cells, perhaps to serve some useful purpose in the functional activities, or to await some means of disposal. Crystals are often found in cells (Fig. 7), and all vegetable and some animal forms make and store up starch grains, sometimes, as in the case of the potato, in great quantities.

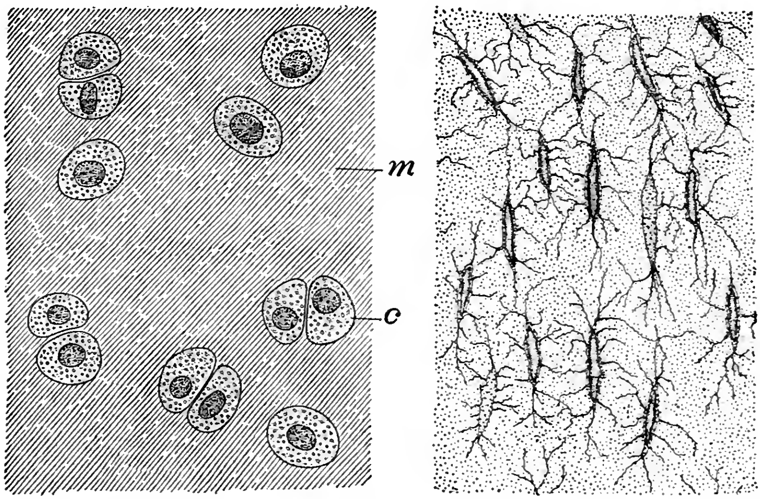


FIG. 8.—Lifeless matter around living cells. *c*, Cartilage cells surrounded by lifeless matrix, *m*; and branching bone cells in the lifeless bony matrix (at right). (From Sedgwick and Wilson.)

Fat also is stored up frequently in cells, and, like starch, becomes a reserve store of nutriment. Again, living cells secrete about themselves different kinds of lifeless matter for purposes of support, protection, defense, etc. Cartilage cells become surrounded by a lifeless matrix of hard resistant cartilage, some kinds of which become replaced by deposition of calcium phosphate and thus become bone with which the living cells of the former cartilage are entirely displaced (Fig. 8). Similarly living blood elements float in a lifeless matrix of fluid plasm. Some products of living activity not infrequently become a poison to the organisms which secrete them, or to other animals which absorb them in one way or another.

Movement.—Appearance and form thus cannot be unmistakable symbols of living matter. No mistake can be made, however, if these two manifestations of vitality are taken together with a third and most important one, viz. movement. A questionable object, if it has the characteristic form and appearance of protoplasm and combines with these the power of independent movement, may be safely interpreted as living matter. Movement alone is not sufficient, for lifeless matter may exhibit spontaneous movements of one kind or another. A drop of water, for example, on a hot surface will move with characteristic activity, or a piece of camphor on the surface of clean water will dance about with considerable vigor, while emulsions of oil, water, and salt will not only simulate the appearance of protoplasm but will also imitate the movements of certain kinds of lower animals. In all of these cases, however, movement is not spontaneous and independent, originating from within the substance, but is due to surface tension or the interaction of the more fluid water and the less fluid substance, and is explained on purely physical grounds. Movement of living things, while it may have at bottom some similar physical principle, is quite different for it originates through the liberation of energy within the living substance.

The types of movement of living things are quite varied but they may all be referred to one or the other of the following kinds: (1) flowing movement; (2) amoeboid movement; (3) ciliary movement and (4) muscular contraction.

Flowing Movement.—The cells of the stonewort (Nitella) are elongate units of structure with heavy walls of cellulose. Within the walls a steady streaming of granules can be made out. This flow is confined to the layer of protoplasm around the periphery of the cell just within the cellulose membrane, the center of the cell being filled by a large vacuole containing water which presses the living substance (primordial utricle) against the walls. The protoplasmic flow is rendered visible by the presence of larger or smaller granules and of "nuclei," which are continually swept up and down in the ever moving mass (Fig. 9).

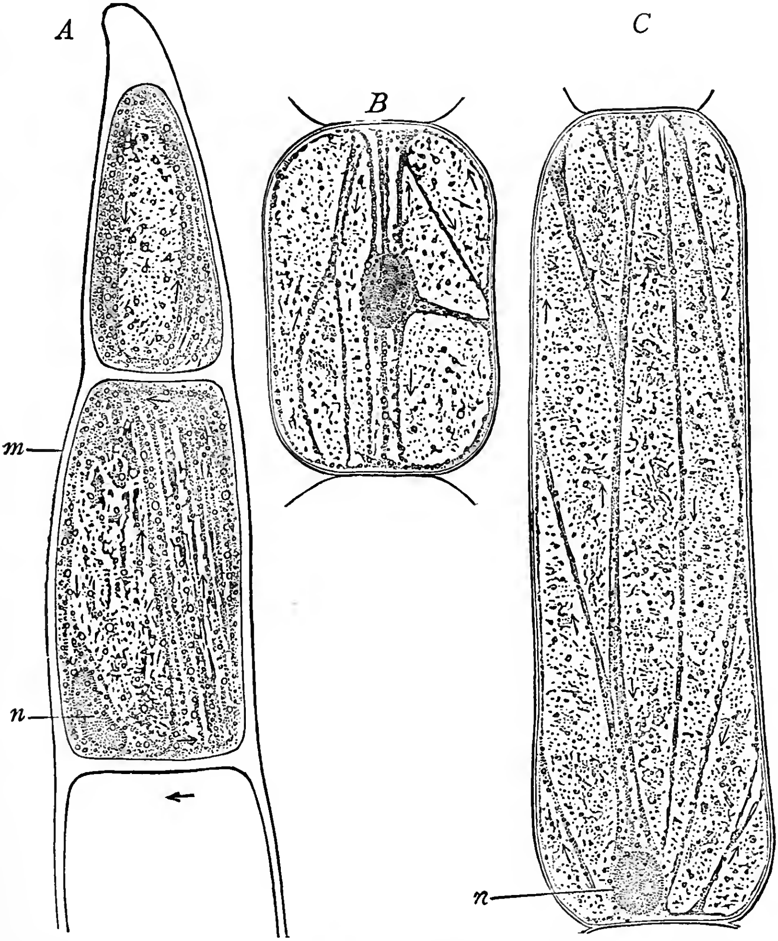


FIG. 9.—*A*, Two cells and a part of a third from a stonewort (Nitella) showing rotation in the direction of the arrows. *m*, Membrane of the cell; *n*, nucleus. *B* and *C*, cells from the stamen hairs of the spiderwort (Tradescantia) showing circulation of protoplasm as indicated by the arrows. (From Sedgwick and Wilson.)

Another type of flowing movement may be seen in the stamen hairs of the spiderwort (Tradescantia) which consist of single rows of cells. Not only is there a flowing of granules and protoplasm around the walls, but streams of flowing protoplasm reach into and pass through the central cavity so that a more or less perfect circulation occurs (Fig. 9 *B*).

Amoeboid Movement.—In flowing movement the fluid protoplasm moves more or less briskly according to the temperature, but it is usually kept within bounds by the firm lifeless cell walls. A free living organism without such walls might be expected to move in any direction and without restraint. Such a form is *Amoeba proteus*, a small animal found in stagnant pools and consisting of one cell only. Here the protoplasmic granules are almost always in motion, and, having no firm covering, the

FIG. 10.—Different forms assumed by *Amoeba proteus*. Photographs from preparations.

periphery gives way and a line of flow is started in the direction of the outbreak. This flow continues until the forces which caused the rupture are expended, or until some point offering less resistance gives way and a new line of flow is started. In this way the bulk of the minute organism moves about in the water, its form constantly changing the while (Fig. 10).

This amoeboid motion is not uncommon in certain cells of higher animals, especially in the white blood cells or leucocytes.

Ciliary Movement.—In both flowing and amoeboid movement the source of energy probably lies in the chemical processes which are transpiring all of the time and in all parts of the protoplasmic substance. In another type of movement, termed ciliary movement, the main liberation of energy is apparently confined to one region of the cell or to specialized parts of the protoplasm of that cell. Manifestations of the liberated energy are expressed solely by such specialized portions or by outgrowths from them. These outgrowths, known as *flagella* and *cilia*, are minute whip-like processes of the cell which undulate in the surrounding medium or lash it like an oar. Flagella are usually single or at most, few in number, but cilia are numerous and their beating moves the cells with considerable rapidity if they are free, or creates currents in the surrounding medium if the cells are fixed. Cilia thus play an important part, sometimes as in protozoa and larval forms of invertebrates, in locomotion, sometimes as in the ciliated cells of various ducts, in creating currents in the surrounding media. Thus the ciliated cells of the trachea sweep particles of dust, mucus, etc., to the outside. For this purpose the stroke of the cilia is upward, and is much stronger than the recovery. Flagella have an entirely different type of motion, acting with a cork-screw or sculling movement. These are rarely found in higher animals save as the motile organs of spermatozoa, but are characteristic of many unicellular animals and of many plant zoospores and motile gametes.

Muscular Contraction.—The most highly specialized type of movement of living protoplasm is undoubtedly muscular contraction. This is limited to special cells of fibrous nature which are usually bound together in bundles, thus forming muscles. Upon irritation a stimulus is transmitted by a nerve to the muscle cells, and contraction results. In this contraction the bulk of the muscle cell remains the same but the form changes, the muscle bundle becoming shorter and thicker (Fig. 11). Muscular action, in higher animals at least, is usually the sole means of locomotion from place to place; in these animals the muscles usually connect movable joints with fixed parts of the skeleton. The majority of muscles are under the control of the organism and can be moved at will. These, the voluntary muscles, are used mainly for locomotion, food getting and other ordinary purposes in the life of the individual. Others, the involuntary muscles, like those of digestive tract and heart, work automatically.

All three of these manifestations of vitality are closely connected. Form and appearance of protoplasm are largely dependent upon movement of the protoplasmic mass, whole or in part. Movement of any type, in turn is dependent upon the conditions of the surrounding medium, or the environment. It is a general truth that heat accelerates and cold diminishes, all within certain limits, the activities of protoplasm. The protoplasm of an Amoeba or of Nitella, the cilia of an epithelium, move faster with a slight increase in temperature. Reduc-

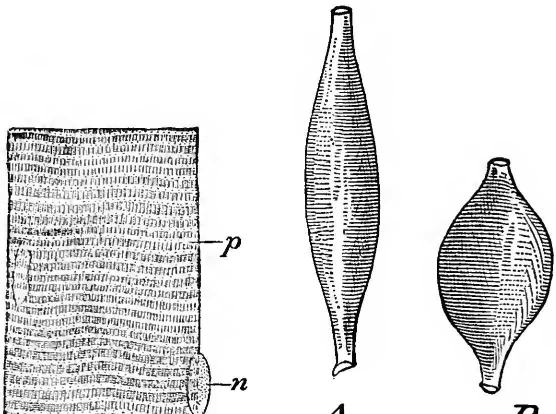


FIG. 11.—Finer structure of a muscle cell (on left) and change of form of a muscle, *A*, at rest; *B*, contracted. *p*, Protoplasm; *n*, nucleus. (From Sedgwick and Wilson.)

tion of temperature, on the other hand, retards these movements, until with increasing cold there comes a temperature in which all activity ceases. Most organisms are destroyed at the temperature of boiling water, although by special adaptations some are able to withstand a much higher temperature (bacteria spores). High temperatures cause the coagulation of certain substances in protoplasm, and lead to what is called heat rigor (rigor caloris), usually between 40° and 50° C. There is no general rule in regard to the most favorable or optimum temperature for all living things; some animals and plants, which are adapted to life in arctic circles or in the depths of the ocean, would die in warmer climates, and vice versa.

CHAPTER II

PROTOPLASM AND THE CELL, AND ORGANISMS OF ONE CELL

If living things consisted solely of protoplasm, the larger forms at least would appear little more than amorphous masses of jelly. We have seen, however, that lifeless matter accompanies living substance, and is laid down by this substance to form supporting structures of one kind or other. Such larger forms are made possible, furthermore, by the fact that the protoplasm is divided up into innumerable units of structure termed cells, each one of which has its own cell wall which is more or less firmly attached to adjacent cells, thus giving mutual support and solidarity to the whole. Lifeless matter deposited in and around these cells adds further support and strength (Fig. 12).

Robert Hooke, an English botanist, in 1665, after studying the structure of wood and higher plants, came to the conclusion that cork and wood generally is made up of minute boxes which he termed Cells. He believed that the walls were the essential parts of the cell since the contents seemed invariably absent. As microscopes improved, this conception of the finer structure of living things became widely recognized, until in 1838–40 the botanist Schleiden and the zoologist Schwann announced their belief that all plants and all animals are composed of minute units of structure to which, following Hooke, they gave the name cells. But even they did not have the idea of cells that we have today but regarded the walls as the vital parts. Protoplasm, as the fundamental living substance, was practically unknown, although in 1835 a French naturalist Felix Dujardin studied the structure of certain foraminifera or naked bits of living matter without cell walls and published his conclusion that this living substance, which he called "sarcode," is a simpler form of living matter than that which composes the bodies of higher animals or plants. It was not until 1863 that protoplasm and sarcode were shown, by Max Schultze, to be the same type of substance. In the meantime research on the finer structure of different animals and plants extended the cell theory of Schleiden and Schwann to form after form, while the older view that the walls are the essential parts was gradu-

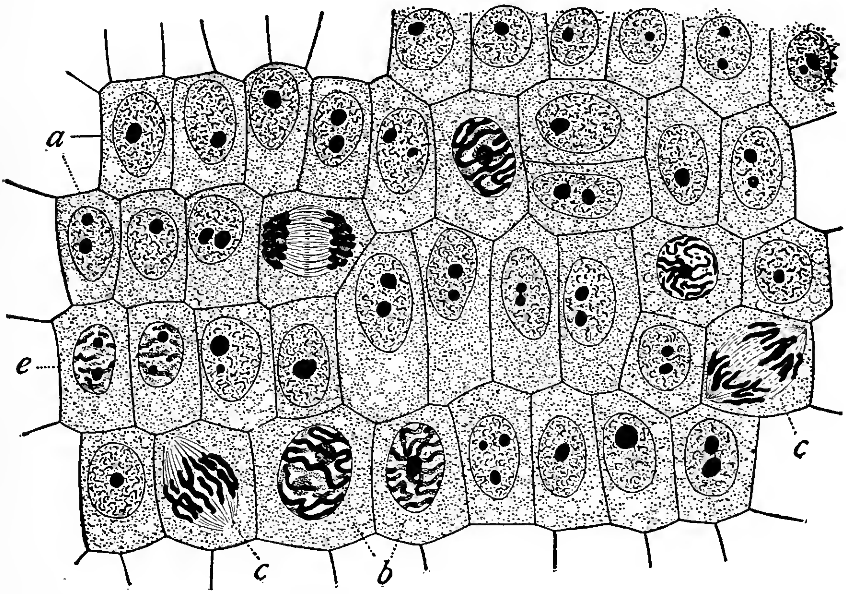


FIG. 12.—General view of cells composing the growing root-tip of an onion; some cells in stages of division (mitosis, see p. 209). *a*, Non-dividing cells; *b*, early stages of nuclear change; *c*, cells in full mitosis. (From E. B. Wilson.)

ally replaced by the modern conception of protoplasm and cell structure.

It thus follows that the term cell, meaning originally an empty box, then a framework with fluid contents, has come to mean finally a small unit mass of living material, while the cellular structure of all living things has no longer the uncertain standing of a theory, but is one of the fundamental and firmly established facts of biology.

All cells have the same general structure; all are composed of protoplasm, of which a part, called the nucleus, is different from the remainder of the cell body, or cytoplasm. In the higher types of living things, where innumerable cells make up the body of the individual, the cells are specialized to perform different functions. Groups or sheets of similar cells, performing a like function or functions, are called *tissues*, and aggregates of different tissues for the performance of some one function are called *organs*, whence the term organism. In both animal and plant kingdoms there are individuals consisting of one single cell; these are known as the unicellular organisms and may be unicellular animals or unicellular plants; if animals they are called *Protozoa*, if plants, *Protophyta*. Higher in the scale we find animals on the one hand and plants on the other, consisting of tissues only—the sponges and coelenterates among animals, and some types of Thallophytes among plants. Still higher in the scale, finally, are organisms consisting of organs, the highest types of living things. In the following pages we will consider first the organisms of one cell, then organisms of tissues, and finally organisms of organs.

The fundamental vital functions are performed by all living things but there is a great difference in the complexity of organs for the performance of such vital activities. We speak of organisms as generalized when all of the physiological activities are performed by a relatively few organs, and as specialized when each of the necessary activities is distributed among a number of organs, each organ contributing a part. With man and the mammals, specialization has gone the farthest; special organs composed of many tissues, each tissue of a congeries of similar cells, perform the vital activities. Each organ contributes its activity or product to the aggregate or individual, and all organs act in harmony for the good of the whole. This phenomenon of dividing the necessary activities among many parts is analogous to division of labor in human communities, and is called the division of physiological labor. With animals at the other extreme of the animal scale from man, all of the vital processes are performed by the protoplasm comprising only one cell. Here organic structures are reduced to their lowest terms, but the functional activities are the same in essence as in higher animals, and the unicellular protozoon is a complete organism, vitally no less complete than a bird, fish or mammal. The several grades in complexity present different aspects of biological principles and justify our division into organisms of one cell, organisms of tissues, and organisms of organs.

The physiological activities of single-celled organisms, while undoubtedly simpler than those of many-celled animals, are nevertheless so marvelously complicated that only a little advance in knowledge has been made. To this advance the minute organisms known as the yeasts have contributed no small part.

A. The Organization and Vitality of Yeast Cells

Yeasts are widely spread in nature, occurring either as "wild" forms or as cultivated commercial types. Wild yeasts live normally upon the surfaces of fruits of various kinds, or on fruit juices; in addition to this habitat, however, there are a great many wild yeasts that live normally in the digestive tract or body cavities of different kinds of animals. A drop of sweet cider gives a good idea of certain species. Baker's yeast, mixed with water, shows myriads of minute yeast cells which cause the milky appearance of the fluid. Brewer's yeast contains several species, two well-marked kinds form the "top" and "bottom" yeast of commerce, the former being used for the manufacture of ales, stout, porter, etc., the latter for "lager beer."

Microscopical examination of baker's or brewer's yeast shows that the individual yeast cells have but little structure. A tiny bit of gray protoplasm is enclosed in a definite double-contoured membrane which, by appropriate treatment, may be shown to consist of cellulose. The cells are spherical or spheroidal in form, and the protoplasm contains, in addition to the ordinary granules of protoplasm, small or larger refractile dots probably of the nature of fat. Several vacuoles are present and a nucleus.

All of these constituents of the cell vary according to conditions. In old cells the cellulose membrane is thicker than in young cells, as can be easily demonstrated by the use of aqueous solution of magenta. The nucleus is larger and more conspicuous in large cells and may be found in the process of division (Fig. 13). Fat droplets and vacuoles, also, vary in number and size according to the conditions.

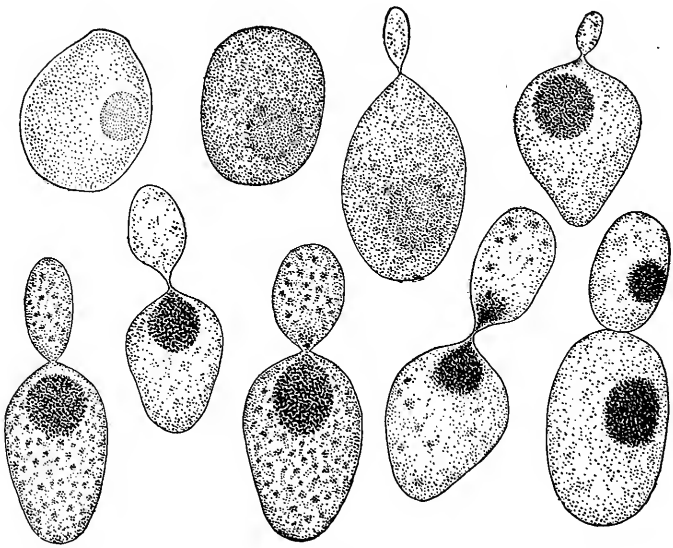


FIG. 13.—Yeast cells showing nuclei and successive stages in the process of budding. (From Sedgwick and Wilson.)

REPRODUCTION

Budding.—In active, growing yeast it is very easy to find cells in the process of reproduction. This is brought about by budding or gemmation, which begins with a local swelling usually at one pole of the spheroidal cell. The membrane appears to give way or to weaken at one point, and the inner protoplasm presses into this region, forcing out the thinned membrane, until a well-marked bud is formed. Later this bud is constricted off and it becomes a separate, young, yeast cell. Frequently the bud continues to grow until mature without breaking away from the parent cell, and may even bud in turn, thus giving rise to chains of yeast cells (Fig. 14).

Spore-formation.—Another mode of reproduction occurs under certain and for the most part unknown conditions. The protoplasm divides, within the cellulose membrane, to form two, three, or four compact, rounded spores (Fig. 15). Under favorable conditions the spore capsules burst or sprout, and the spores emerge as yeast cells which then develop like

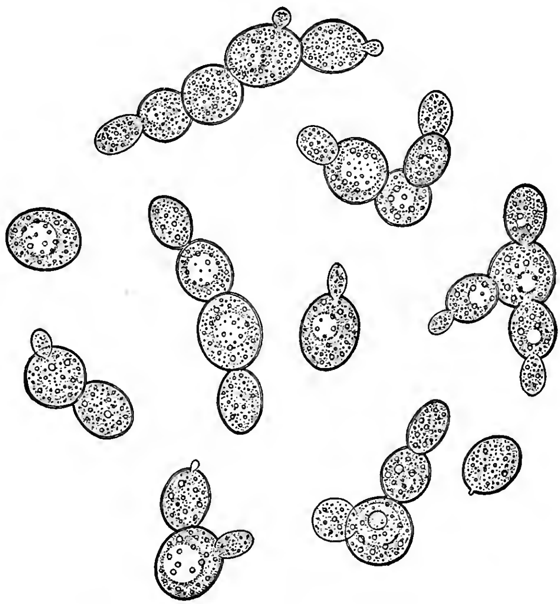


Fig. 14.—Colonies of budding yeast cells. (From Sedgwick and Wilson.)

ordinary forms. Reproduction by this means is called *endogenous* sporulation, which differs somewhat from "spore-formation" in bacteria where there may be no actual reproduction but merely a temporary protection against drying, or other unfavorable condition of the environment.

Culture Media.—The simplicity of structure of yeast cells would naturally suggest a simplification of the vital processes, and lend support to the belief that these might be more readily analyzed than can vital processes in higher types of cells. This belief, indeed, has been realized to a certain extent, although the secrets of constructive and destructive metabolism are still unrecognized. The sweet fluids of fruits offer an excellent medium in which yeast cells grow and multiply. An even more excellent medium is prepared from the proteins, sugar and salts extracted from the young cells of sprouting barley. This medium, known as *sweet wort*, supplies the necessary elements for the living protoplasm of yeast, and the vital processes go on at a rapid rate. Sweet wort, however, and the sugary juices of fruits are too complex to give any more adequate notion of the food value of specific elements, than would the protein food of higher forms of life. Fortunately, however, the yeast processes are so primitive that more direct and exact knowledge is possible.

If a quantity of pure yeast is burned, the mass first chars by the deposit of carbon, then, with continued heat, this is used

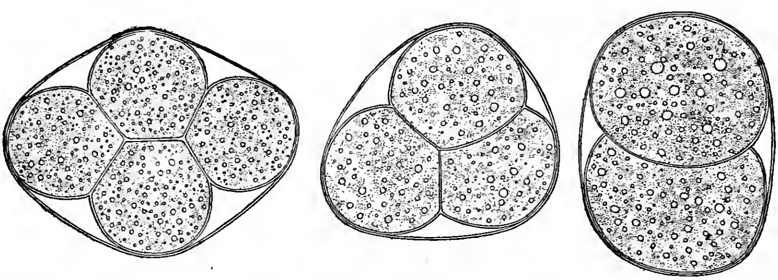


FIG. 15.—Endogenous spore formation in yeast. (From Sedgwick and Wilson.)

up in forming carbon dioxide by union with oxygen, while at the same time the nitrogen of the yeast is given off in the form of nitrogen gas, hydrogen as water vapor, and sulphur as sulphurous acid or sulphur dioxide. Finally nothing remains but a white ash composed of potassium, lime, magnesium, and phosphoric acid.

Pasteur made up a fluid composed of the ingredients thus obtained by analysis, and found that yeast cells would grow and multiply in it as in sweet wort. With such a fluid he was able, by omitting one substance after another, to determine what elements are necessary for the vital activities of yeast. The fluid, known as Pasteur's fluid, has the following percentage composition:

Water H_2O	83.76 per cent.
Cane sugar ($C_{12}H_{22}O_{11}$)	15.00 per cent.
Ammonium tartrate $(NH_4)_2C_4H_4O_6$	1.00 per cent.
Potassium phosphate K_3PO_4	.20 per cent.
Calcium phosphate $Ca_3(PO_4)_2$	.02 per cent.
Magnesium sulphate $MgSO_4$	.02 per cent.

Bearing in mind the essential elements, C, H, N, O, P, S, and some salts, found in all protoplasm it will be seen that the ingredients of Pasteur's solution contain all of the needed elements. On *a priori* grounds it would be possible to leave out some of the ingredients without seriously affecting the vital reactions. If sugar, for example, is omitted, all of the elements which it contains are found in the other ingredients and the yeast cells continue to grow and multiply although fermentation ceases. If some salts are left out, growth is much retarded and vital actions are slow. The one absolutely essential ingredient is the ammonium tartrate. If this is omitted, life processes cease altogether, and a glance at the chemical symbols shows that this alone contains nitrogen.

By means of this simplified medium it is demonstrated that yeast cells are much less complex in their nutritive processes than green plants on the one hand and animals on the other. Green, or chlorophyll-bearing plants, by photosynthesis (see p. 119), manufacture food from far simpler elements than proteins; animals require proteins ready made, and these, as we have seen, are highly complex substances. Yeasts survive and thrive on a nitrogenous compound much less complex than protein and more complex than CO_2 and H_2O which serve as food elements of green plants; they are, therefore, as regards nutrition at least, intermediate between such plants and animals.

Even with this simplified nutrition, however, the finer processes of assimilation and the upbuilding of yeast protoplasm, are as obscure as elsewhere in the living world, but, largely through the study of yeast cells, some good working hypotheses have been formulated and many vital activities have been traced to unstable chemical compounds termed *enzymes* or *ferments*.

B. Bacteria

Bacteria is a term used to designate a great group of minute forms of life intermediate, like yeast, between chlorophyll-bearing plants and animals. Bacteria occur almost everywhere; abundantly in the atmosphere accompanying dust particles; frequently in fresh and salt water; abundantly in the digestive tract of all kinds of animals. They abound in the upper layers of the soil and in exposed fluids containing dead animal or vegetable matter. Some types produce disease in man and other animals, whence they are popularly known as germs or microbes or parasites. Many of them, on the other hand, are positively useful physiologically, in the functional activities of higher animals, and economically and commercially in transforming organic matter into simple salts (nitrites, nitrates, etc.) or in the manufacture of various food stuffs (vinegar, butter, cheese, etc.).

Morphology of Bacteria.—Bacteria are the smallest of the known organisms. Some types placed end to end would require 25,000 to cover a linear inch, and the line would be too fine to be seen; 50,000 such lines side by side would cover a square inch. Other types are larger, varying from 2μ to 60μ in length.[1]

While small, the bacteria nevertheless have fairly definite forms which may be grouped for convenience under three main types: 1. the bacillus or rod; 2. the coccus or ball; and 3. the spiral or corkscrew. They are frequently united in chains or filaments, in plate form (sarcina), or embedded in a gelatinous matrix which they secrete (zoogloea) (Fig. 16).

[1] A μ (micron) equal 1–25,000 of an inch.

The bacteria are usually regarded as single-celled organisms although the complete cell structure is rarely present. The majority have no cell nucleus but contain from one to many granules of chromatin distributed throughout the cell; these granules correspond to the nuclei of tissue cells (Fig. 16, D). The cells are enclosed in firm cell membranes, probably composed of cellulose or an allied substance, which are unbroken except in a small number of forms provided with flagella.

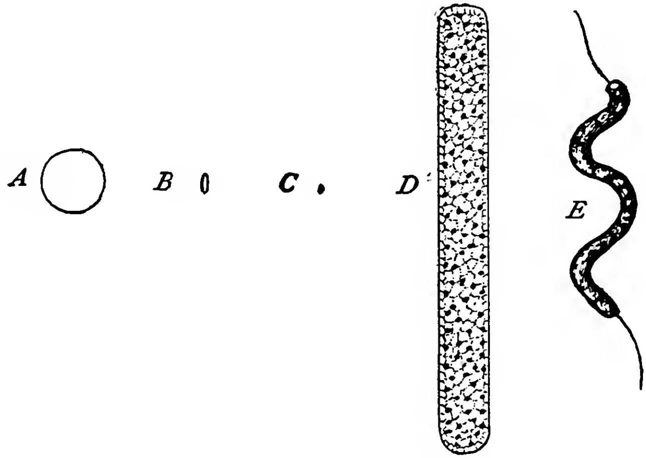


FIG. 16.—Comparative size of *A*, human blood corpuscle, *B*, typhoid bacillus, *C*, influenza bacillus, *D*, giant bacillus from the intestine of a cockroach, and *E*, a common water spirillum.

Reproduction.—All bacteria multiply by transverse division of the cell (Fig. 17). Division is followed by rapid growth, and cycles of growth and division follow one another in quick succession (hay bacillus 30 minutes, cholera vibrio 20 minutes). "It has been estimated that if bacterial multiplication went on unchecked, and the division of each cell took place as often as once an hour, the descendants of each individual would in two days number 281,500,000,000, and that in three days the progeny of a single cell would balance 148,356 hundredweight!" (Jordan, *General Bacteriology*, p. 61.) Such increase does not take place in nature, however, because of various external influences as well as internal influences produced by the bacteria themselves. The environment is soon changed because of their own physiological activities and multiplication is soon checked. Reproduction is quickly stopped by natural factors like dessication, unsuitable temperature, acidity or alkalinity of the medium, but many bacteria have the power to resist such adverse conditions by forming internal spores or *Dauersporen* (enduring spores). These are usually spherical, ellipsoidal or oval in form and possess a dense envelope or spore wall enclosing the majority of the chromatin granules and some cytoplasm (Fig. 17, D). These spores possess a much higher resistance to external influences than do the cells from which they are formed (many for example, can withstand a temperature of from 70 to 100° C.).

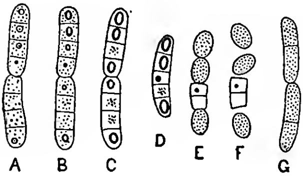


FIG. 17.—Spore formation and germination of spores in bacteria. *A*, A pair of rods forming spores about 2 o'clock P. M.; *B*, the same about an hour later; *C*, one hour later still; *D*, a five-celled rod with three ripe spores which were placed in a nutrient medium after drying for several days; *E*, *F*, the same spores from one to three hours later; *G*, a pair of rods in active growth and movement. (From de Bary after Sedgwick and Wilson.)

One spore per cell is the rule, but in rare instances, two similar spores may be formed. Spore formation in bacteria, therefore, is not always a method of reproduction but may be an adaptation for the preservation of the organism corresponding to what is known as the "encysted state" of many unicellular animals.

Physiology of Bacteria.—The food of bacteria is most diverse. The majority are known as saprophytes, that is, they obtain their nourishment from dead organic matter. Many are parasites, getting their food from other living organisms in the form of complex chemical compounds of protein substance or protein derivatives. Some live in the soil, and get their food supply and their energy from purely inorganic materials. Among these are the so-called nitrifying bacteria, one of which, Nitrosomonas, converts ammonia salts into nitrites while another, Nitrobacter, changes the nitrites into nitrates. Other bacteria utilize free ammonia (NH_3) and still others, free nitrogen (N) in the manufacture of nitrates (see p. 129). These organisms thus perform a most useful economic function in preparing food material in the soil for use by the green plants. But the chief biological interest of these forms is that they are able to build up their own protein molecules directly from relatively simple substances without the aid of chlorophyll, and to get energy from such compounds in which it is locked up for all other kinds of living things. Thus urea, thrown off by animals and plants as a useless and to them harmful waste matter, is a source of food and energy for some bacteria which convert it into free ammonia, carbon dioxide and water.

C. Enzymes, Hormones and Vitamines

Alcoholic Fermentation.—The control of alcohol production in practical ways was well understood long before the explanation of its production was worked out. The term fermentation was early given to all processes involving the generation of gas, probably because of the froth or foam which appears during alcohol formation or when acids are allowed to act on carbonates. In the 17th century, however, a distinction was drawn between alcoholic fermentation and acid fermentation, and it was recognized that alcohol is a new product of the fermentation process and quite distinct from the *gas vinorum* (CO_2) arising at the same time. In the 17th century also, Leeuwenhoek, the first microscopist, discovered that the scum or deposit which is always present during fermentation is made up of small spherical bodies which he did not attempt to identify as animal or plant. With Lavoisier in the 18th century, chemistry became a more exact science and, in connection with alcoholic fermentation, it was found that the sugar in fermenting fluids breaks down into alcohol and CO_2 gas, with traces of glycerine and acetic acid. As with most other chemical processes, fermentation was regarded by Lavoisier as a process of oxidation, and the spherical bodies discovered by Leeuwenhoek were considered unimportant. Early in the 19th century, however, a reaction set in against many of Lavoisier's views, and its effects are seen in the interpretation of alcoholic fermentation. On the negative side, Schwann showed that oxygen had nothing to do with the process. By simply heating the air about fermentable fluids which had been properly prepared (sterilized), he found that no fermentation took place, whereas fermentation does occur in such fluids if they are exposed to the ordinary atmospheric air. Schwann concluded that something in ordinary air is destroyed by heating, and fermentation is prevented. On the positive side Erxleben in 1818 suggested that the globules discovered by Leeuwenhoek might be the cause of fermentation. This view was elaborated and confirmed by Cagniard de Latour in 1835, and was finally conclusively proved by the epoch-making experiments of Pasteur (1857–1863).

Yeast was thus proved to be the agent of alcoholic fermentation by acting in some way on the sugar contents of nutrient media. By this action about 95 per cent. of the sugar is broken down into alcohol and CO_2; about 4 per cent. is decomposed with the formation of glycerine, succinic acid, and CO_2; and about 1 per cent. is used by the yeast cells as food. The small amount of acetic acid that is usually present is not due to the activity of the yeast cells but to oxidation, through the agency of bacteria, of the alcohol already formed.

The approximate chemical reactions involved in the formation of alcohol and acetic acid are as follows:

$$C_6H_{12}O_6 \text{ (sugar)} + \text{yeast} = 2C_2H_6O \text{ (alcohol)} + 2CO_2$$
$$C_2H_6O \text{ (alcohol)} + O_2 + \text{bacteria} = C_2H_4O_2 \text{ (acetic acid)} + H_2O.$$

The acetic acid is finally oxidized to water and CO_2 through the action of bacteria again. Thus

$$C_2H_4O_2 + 2O_2 + \text{bacteria} = 2CO_2 + 2H_2O$$

The next step in the investigation of alcoholic fermentation was to determine just what yeast does in effecting the transformation of sugar into alcohol. Büchner in 1897 was the first to demonstrate that yeast cells contain a substance which causes the same destruction of sugar that living yeast cells do. This was accomplished by grinding yeast cells in diatomaceous earth, then compressing the mass and obtaining a clear fluid free from yeast. The clear fluid, which he called *zymase*, extracted in this manner from the living yeast, was thus shown to be the active agent in alcoholic fermentation. Such agents in chemical activities are called *ferments* or *enzymes* (from Greek *en*, in, and *zyme*, yeast). Still later investigations have shown that a second enzyme, called co-enzyme and also produced by the yeast cell, is necessary to activate the zymase.

Enzymes in Vital Activities.—The zymase and its co-enzyme, which can thus be extracted from the protoplasm of yeast, are normal products of the vital or metabolic activities of the organism and are examples of the many analogous ferments which yeast is capable of producing. Macfadyen, Morris, and Rowland as well as other investigators, have devised methods of cutting up minute organisms in mass, thus breaking down the cells more perfectly than had been done before. In this way it has been possible to isolate from yeast not only a powerful zymase but other enzymes as well, including maltase, invertase, endotryptase, rennin, and traces of two others, all of which must be present in the protoplasm of normal yeast cells.

One of the characteristics of the chemical activities in protoplasm which distinguishes them from similar activities in physical nature is the speed with which they take place. Thus sugar dissolved in water and exposed to the air oxidizes very slowly. There is no difference in kind between this process and the oxidation of sugar in the living cell, but there is a great difference in speed. Such differences in the rapidity of chemical actions in living and lifeless matter are due, as we now know, to the presence of innumerable enzymes in all kinds of living cells. The first hint of these elusive agents in vital activities was given as early as 1836 by Berzelius when he discovered the action due to what he called "catalytic force." Subsequent researches have shown that his catalyzers, which we now know as enzymes, are chemical substances which participate in chemical reactions by forming compounds of unstable and intermediate character. The compounds break down easily, thus freeing the enzymes and enabling them to repeat the process, so that they appear to be unaltered by the reactions which they undergo. These enzymes are probably organic bodies or compounds of which the exact composition is unknown, although for certain starch-dissolving enzymes (amylases), Mathews concludes that "the indications are that the active part of the molecule is a protein, probably colloidal, and that this active principle is usually combined with a colloidal, carbohydrate gum" (*Physiological Chemistry*, p. 330).

While the chemical composition of enzymes is at present unknown, we have a rapidly accumulating fund of information concerning their classification and activities in animal organisms. Thus in the general function of nutrition where the digestive enzymes are hydrolytic agents throughout, we find some that are proteolytic (*i.e.*, that break down proteins), some lipolytic (*i.e.*, that destroy fats), and some that are amylolytic (*i.e.*, that break down carbohydrates).

Some of the more important proteolytic enzymes are: (1) pepsin, which acts in an acid medium to break down proteins into peptones; (2) trypsin which acts in an alkaline medium to break down proteins and to transform products of peptic digestion into amino-acids and polypeptids; and (3) erepsin which splits peptones and polypeptids to amino-acids. Among the fat-transforming enzymes, *i.e.*, enzymes which split fats to form glycerine and fatty acids, are different forms of lipase from stomach, intestines and the pancreas (steapsin). Among the more important amylolytic ferments are the amylases or diastases which convert insoluble starch into soluble sugars, such as ptyalin of the saliva, diastase of the pancreatic juice, and other amylases of the digestive fluids. Here also belong the enzymes which transform disaccharid sugars into monosaccharids, such as maltase of the saliva, which splits maltose; invertase of the stomach and pancreatic juices, which splits cane sugar; and lactase of the stomach and pancreatic juices, which splits milk sugar.

Enzymes having to do with the digestion of food substances may act either within the cells of the body (phagocytes, protozoa and coelenterates), or in cavities lined by the cells which secrete them. In addition to these digestive enzymes there are many others in protoplasm which have to do with the various processes of constructive and destructive metabolism, and these always act within the cell, hence they are often called the *endoenzymes*. They are best known in connection with destructive metabolism, the modern conception being that endoenzymes are the causes of a series of progressive chemical decompositions. Each chemical process is presided over by a specific endoenzyme which acts only on certain chemical substances and gives rise to other chemical substances to be acted on in turn by other enzymes. "The processes which years ago were considered as due to the peculiar vital properties of the tissue cells, and which were supposed to be entirely dependent upon their morphological and functional integrity, are now seen to be due primarily to a great variety of enzymes, manufactured indeed by the living cells, but capable of manifesting their activity even when free from the influence of the living protoplasm. The varied processes of tissue katabolism are the result of orderly and progressive chemical changes, in which cleavage, hydrolysis, reduction, oxidation, deamidization, etc., alternate with each other under the influence of specific enzymes, where chemical constitution and the structural make-up of the various molecules are determining factors in the changes produced." (Chittenden, *The Nutrition of Man*, pp. 75, 76.)

Hormones.—A second group of enigmatical chemical substances produced by living organisms includes the hormones. These are extremely difficult to study, and facts regarding them have come to light only recently. A good example is the hormone *secretin* in man, which causes the pancreas cells to secrete the digestive ferments of the pancreatic juice. This *secretin* is formed after contact of the acidified contents of the stomach with the mucous membrane of the small intestine. The acid food stuffs do not stimulate nerves which start secretion in the pancreas, but they act apparently upon a substance formed in the cells of the mucous membrane, transforming this substance into a heat-resisting hormone *secretin* which reaches and stimulates the appropriate nerves through the blood and these, in turn, stimulate the pancreas cells to secrete. Other hormones are responsible for many of the phenomena of growth and differentiation, and possibly they play an important part in early development of the individual. Again, there is strong reason to suppose that secondary sexual characteristics are developed at maturity through the action of hormones secreted by the reproductive glands into the blood. A close relation exists also between the glandular patches known as the *corpora lutea* on the mammalian ovary, fixation of the fertilized eggs to the wall of the uterus, and stimulation of the mammary glands. If these small glands on the ovary are removed, the developing egg will not attach at all, and it is supposed that a hormone is secreted which reaches the uterus through the blood and causes the cells of the uterus to react to the embryo. Again the pituitary body in the brain plays an important part in regulating growth of the organism, diseases of this gland giving rise to acromegaly, one of the symptoms of which is the excessive development of parts of the organism far removed from the brain.

Vitamines.—Still another group of elusive chemical bodies are the so-called *vitamines*, named by Casimir Funk. Like enzymes and hormones, these are substances of unknown chemical composition which appear to be necessary for the proper nourishment of the body. They are undoubtedly organic in nature but are neither proteins, carbohydrates, nor fats. They may be extracted from these normal foods by alcohol, and are destroyed by heat and by alkalies. They contain nitrogen, but no phosphorus, and are probably reducing substances. Vitamines are best known in connection with the disease known as Beri-beri which is caused by eating white polished rice as a sole or staple article of diet. While such rice contains abundant nourishment, the body cannot utilize this nourishment without the aid of vitamines which should go with the rice. The outer coatings of the rice kernels, which are removed in the preparation of white or polished rice, contain such vitamines, and if these husks are eaten with the rice, a proper nourishment results. Scurvy is another disease which apparently results from the absence of vitamines. All normal foods, whether proteins, carbohydrates, or fats, contain these essential substances but in different degrees, and all such food substances can be rendered innutritious by previously extracting the vitamines while, on the other hand, excellent results in growth and increase in weight may be obtained by adding vitamines thus extracted from nutritious proteins to the ordinary milk or cereal of infants suffering from malnutrition and cessation of growth (Eddy).

From this brief survey of a vast field of biology into which we are led by the activities of the simple organism Yeast, we learn that vital activities of animals and plants consist of a series of intricate reactions through the agency of enzymes and other subtle chemical bodies. Partly by experiment in the hands of eminent physiologists like Hoppe-Seyler, Ostwald, Hofmeister, Mathews and others, and partly by theory, we are brought to the present-day conclusion that not only cleavage processes which occur during the preparation for assimilation of foods, not only all of the processes of destructive metabolism with the consequent liberation of energy in the form of light, heat, electricity, or movement, but also all of the synthetic processes in protein formation, from the union of the simplest beginning materials like carbonic acid, water, and nitrogen-holding salts to the most complicated albumen compounds, are, one and all, effects of specific chemical bodies, each of which plays its part.

CHAPTER III

ORGANISMS OF ONE CELL. *Continued*

THE UNICELLULAR ANIMALS

In cells of tissues in higher animals some one vital function predominates over all others and gives to the cell its particular character. With muscle cells, the function of contractility or movement overshadows all others; with nerve cells, irritability or nervous response to external stimuli is predominant; with epithelial cells, the function of secretion predominates, and so on, each type of cell performing its own work but all working for the good of the organism as a whole. Some of the vital functions indeed are lost with such differentiation; the function of digestion, for example, is confined to cells of the alimentary tract while the latter have lost all power of independent movement. Such cells in which one function overrides all others may be spoken of as *physiologically unbalanced* cells, while other cells in which the functions or vital activities are equally developed may be spoken of as *physiologically balanced.* Such balanced cells are illustrated by the entire group of protozoa or animals consisting of one cell only, a group comprising some of the most perfect of single cells and at the same time the simplest in structure of all animals.

A. Amoeba proteus

Few organisms have been studied more frequently than this minute protozoon, and nothing gives a better idea of living matter than this fascinating bit of protoplasm with its enigmatical movement and its vital activities. It is found in the greatest variety of places but is not as plentiful as many text books would lead one to suppose. It may be found, however, among the superficial dead leaves and slime in many ponds or on the stems of ordinary water plants where amoebae and allied forms are often abundant. *Amoeba proteus* varies in size from 1/200th to 1/75th of an inch and undergoes different form changes which at times make it difficult to recognize. There is some question whether some of the forms described as different species of amoeba are not in reality one and the same; the matter can be decided only by knowledge of the complete

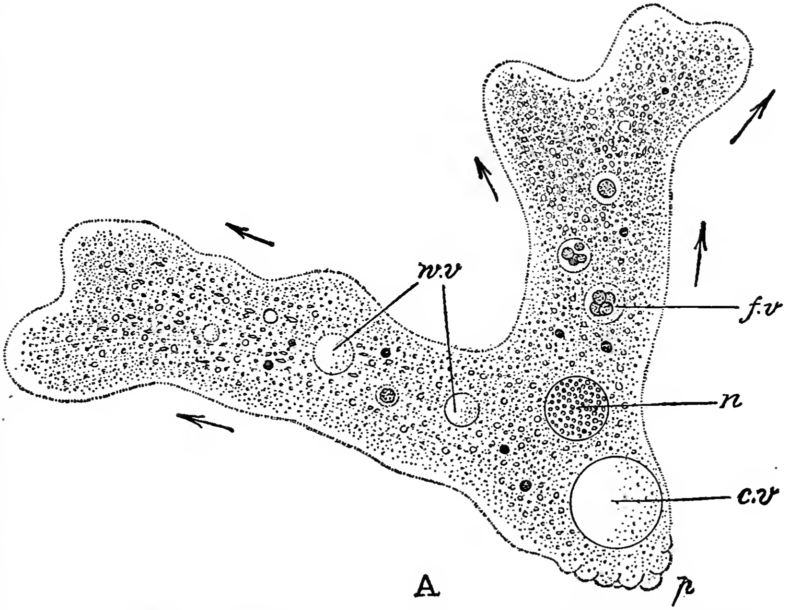


FIG. 18.—*Amoeba proteus* in active moving condition. *c.v.*, Contractile vacuole; *f.v.*, food vacuole; *n*, nucleus; *p*, remains of former pseudopodia; *w.v.*, water vacuoles. The arrows indicate the direction of protoplasmic flow. (From Sedgwick and Wilson.)

life history. Sometimes the organism is flattened or spatulate in form, changing slowly, if at all, in shape. Again it becomes a quickly moving drop of protoplasm quite transparent and long drawn out as a single thread of substance. All intermediate grades between these forms are known, and in a general way the form and movements indicate states of nutrition, for the flat spatulate types are usually dense with undigested food while the rapidly moving forms are relatively clear and transparent (Fig. 18).

Nucleus.—While the form of *Amoeba proteus* is continually changing, the structure remains practically the same. It is always one protoplasmic unit, a cell, and like other cells it is differentiated into cell body, called cytoplasm, and nucleus. This nucleus is composed of slightly different protoplasm from that of the cell body, and is chiefly characterized by the greater affinity for basic stains, while the protoplasm of the cell body has an equivalent affinity for acid stains. The substance of the nucleus which takes the stain is called chromatin, and is composed chiefly of nucleins or nucleo-proteins particularly rich in phosphorus. The nucleus can be seen in life as a pale circular disc moving with the flow of granules from one part of the cell to another, and turning as it moves, showing now the circular outline, again the flattened edge view.

Endoplasm and Ectoplasm.—The cytoplasm is not entirely homogeneous but is differentiated into an inner and an outer portion. The former, in which the nucleus is found is called the *endoplasm*, or sometimes, the endosarc. The latter, called the *ectoplasm* or ectosarc, although soft and gelatinous, is firmer and denser than the endoplasm and is more transparent, for it has none of the refractive bodies found in the endoplasm. It is to be regarded as a protective layer, since it is the part that comes in contact with the surrounding medium, and through it all intercourse between the amoeba and the environment must take place. In other forms of protozoa it is this ectoplasm which becomes differentiated in the greatest variety of ways for purposes of protection, locomotion, and sensation.

The endoplasm, on the other hand, contains the vital organs of the cell, a number of which can be seen with little effort. Large particles more or less disintegrated, and surrounded by clear fluid, are food bodies recently ingested and are undergoing digestion in the fluid-filled spaces, which, for this reason, are called *gastric vacuoles*. The bodies in these vacuoles may frequently be recognized as portions of other minute animals or plants. Another fluid-filled sphere, usually best seen near the periphery of the cell, is perfectly clear and without solid particles of any kind. It suddenly disappears, the contained fluid being excreted to the outside through the ectoplasmic layer. It shortly reappears as a small clear space which rapidly grows in size until it again disappears by contraction. From its rhythmic dilatation and contraction this organ of the cell is called the *contractile vacuole;* its pulsations are fairly constant and regular in the same temperature but the rate varies with changes in temperature. This organ was formerly believed to be a beating heart, but is now generally regarded as an excretory or possibly respiratory center.

Movement.—In the course of its "amoeboid movement" Amoeba throws out blunt protoplasmic processes termed *pseudopodia.* The ectoplasm gives way at one point as a result of unknown inner forces; the endoplasmic granules may be seen streaming toward this point until a blunt finger-formed pseudopodium results. Sometimes the entire mass of the Amoeba flows through this extended portion, and the organism then will have moved a distance equal to its diameter. In the meantime, however, other pseudopodia may be forming and the direction of movement changed. As the cell changes in moving direction the older pseudopodia are withdrawn, and these may be seen as small blunt processes of the cell on the side opposite that in advance (cf. Fig. 10).

Metabolism.—The constant streaming of protoplasm and the constant formation of pseudopodia require energy. The history of energy transformation resulting in the advance of an Amoeba involves the entire history of metabolism and, if understood, would make the matter of "vital activities" an open secret. Some few points, however, are known. The immediate source of energy for such movements is the combustion or oxidation, through the action of enzymes, of parts of the cellular protoplasm, and if no food were taken in, the organism would soon die from loss of its vital parts. This loss, however, is constantly made good by capture and digestion of food, functions involving the primary and fundamental activities of all animals and plants, these functions being the central factors in the development of the multifold structures in the living world.

Amoeba proteus captures food and draws it into the body protoplasm through the agency of the pseudopodia, or rather, the protoplasm of the organism streams into pseudopodia around the prey, thus engulfing it (Fig. 19). Some water is engulfed with the food particle and this forms the chief portion of the liquid of the gastric vacuole. This water usually is alkaline in reaction when taken into the body; soon, however,

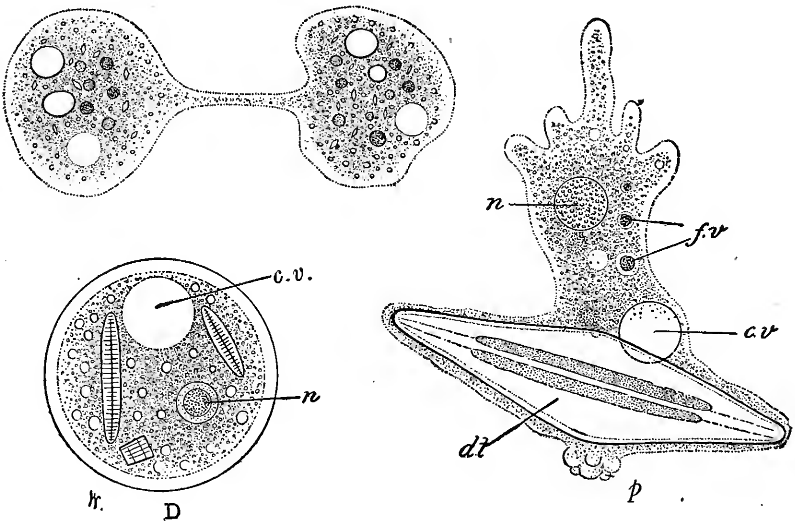


FIG. 19.—Amoeba dividing (*A*), ingesting food, and encysted (*D*). *p*, Retracted pseudopodium; *dt*, diatom taken in as food; other letters as in Fig. 18. (From Sedgwick and Wilson after Leidy and Howes.)

it changes in reaction from alkaline to acid, the change being brought about by the secretion of an acid digestive fluid from the surrounding endoplasm. Through the action of this acid (supposed to be HCl), the food particle, if living, is first killed and then disintegrated.[1] Later the reaction of the contents of the vacuole again changes from acid back to alkaline, and in this medium the further processes of digestion are accomplished. The end result of this series of chemical actions on the food is the formation of proteoses from the protein sub-

[1] No enzyme analogous to pepsin and acting in this acid medium is known to occur in *Amoeba proteus*.

stances which, as soluble materials, are then taken into the body protoplasm of the organism; the food particles are said to be digested.

When the protein food is thus digested it is only prepared for the first stages of protoplasm re-building, and many more steps must be taken before the essential elements are added to the protoplasmic molecules. These further steps are generally included under the comprehensive term, *assimilation*, and their exact nature is hidden in the deepest obscurity. Little by little chemical research is throwing light on the processes, so that we have now a basis for working hypotheses as to the manner in which protoplasmic molecules are built up. We now know that cells in all kinds of tissue possess chemical properties hitherto unsuspected. These have to do, in the main, with enzymes which act upon the partially broken down food matters and cause their disintegration into finer particles, until they are prepared for anchorage in the protoplasmic molecules, and begin the series of integrations and disintegrations characteristic of vital processes. It has been found by experiment that portions of the cell without a nucleus cannot form such enzymes, and the conclusion is drawn that these vital activities are dependent upon substances derived from the chromatin. It was largely through experiments in cutting minute forms like Amoeba that this discovery was made. Nusbaum, Hofer, Verworn and others found that if an amoeba is cut in two pieces with a scalpel, both parts would continue to live for some days but one would die ultimately, while the other part, containing a nucleus, would continue to live and multiply indefinitely. The portion without a nucleus is unable to digest and assimilate food, or even to capture it.

Thus while the exact processes of assimilation are unknown in amoeba, it is quite probable that the finer changes are carried on in the same way as with cells in higher animals, that is, through the agency of enzymes. These act in a linked series, the product of one chemical action furnishing the material for the next until finally the elements derived from the protein food are added to the protoplasmic molecules.

Knowledge of the anabolic or building processes is much more hypothetical than that in regard to the katabolic or breaking down processes, the latter taking place whenever energy is expended. These processes take place in the cell body or cytoplasm and are due to enzymes which probably come from the inter-action of cell nucleus and cytoplasm. They are oxidizing enzymes which bring about the union of oxygen with receptors of the protoplasmic molecules. The ultimate result of such combustion is the formation of simple compounds, the hydrogen leaving the protoplasm molecule to unite with the oxygen, forming water; carbon with oxygen, forming carbon dioxide, and the ammonium combination (NH_3), forming with carbon and oxygen the compound urea $(NH_2)_2CO$, which still contains some energy. This urea, however, cannot be used by the animal protoplasm as a further source of energy but is voided to the outside as waste matter. The energy, however, is not wasted in nature for, as we have seen, bacteria have the power of breaking urea into free ammonia, carbon dioxide and water, and of converting the contained energy into the energy of their own vital processes.

As urea is of no use to the animal but rather a menace in case of its undue accumulation, it is necessary for the animal to get rid of it. In all animals this is accomplished by means of special organs which form the excretory systems. In mammals and vertebrates generally, the kidney and associated organs are set apart for this purpose; in lower animals like worms, crustacea, etc., special funnel-like organs termed "nephridia" perform this function. In all types of animals in short, there is some structure or structures of more or less complicated type which are devoted almost exclusively to this end.

In *Amoeba proteus* there is a special organ which has the function of disposing of waste matters and is analogous, therefore, to the kidney of higher types. This is the "contractile vacuole" which pulsates with a regular or rhythmic contraction, the rate of pulsation varying with the temperature. It is not improbable that the contractile vacuole has other functions than that of urea excretion, but this has never been demonstrated, while the presence of uric acid crystals has been shown in the fluids of the vacuole. After a vacuole has contracted, the new one is formed in the vicinity of the nucleus by union of small and at first unnoticeable vesicles, one or more of which may be left over by the incomplete emptying of the preceding one. This coalescence continues until the new vacuole becomes large enough to be seen with low magnification. As it grows by the continual addition of fluids it increases in bulk and is less easily carried in the moving protoplasm, so that it becomes left behind, so to speak, until it bursts to the outside, usually in that region which for the time being is posterior.

Irritability.—As a spark may cause an explosion so may certain agents in the environment produce sudden and violent reactions on the part of a living organism. Such reactions are due to the local expenditure of energy. In higher animals special "sensory" organs are activated by heat, light, sound, electrical or other agents called stimuli. The energy released as a response to such stimuli is far in excess of the energy represented by the activating agents, and may involve reactions by every part of the organism.

In *Amoeba proteus* there are no sense organs but the organism has the property of reacting to every marked change in external conditions in its environment. This property is called *irritability*, and is analogous to more complicated reactions to stimuli in higher animals. Innumerable kinds of stimuli may produce these reactions but may be classified according to their qualities into a few large groups, such as mechanical, chemical, photic and electrical, all of which indicate changes in the immediate environment of the organism. The responses of organisms to the great variety of stimuli are so diverse that only the most general definition will cover them all. The physiologist Verworn gives such a definition as follows: "Irritability of living substance is its capacity of reacting to changes in its environment by changes in the equilibrium of its matter and its energy" (Lee, Translation, p. 353).

With *Amoeba proteus* irritability is indicated by more rapid movement, as under the stimulation of increased temperature; or by withdrawing of pseudopodia and rounding out of the body, as under the effects of mechanical, electrical or chemical stimuli. These various responses frequently subserve a useful purpose in capturing food or avoiding difficulties, and represent a prototype of higher conscious actions. There is absolutely no ground for believing that Amoeba does anything intentionally or wilfully but all of its activities can be explained on the ground of responses to environmental stimuli. An interesting analogy to vital processes in Amoeba is shown by a drop of chloroform which, through surface tension, will draw in, and roll up, a filament of shellac. Another species of Amoeba, *A. verrucosa*, captures and rolls up a filament of Oscillaria in exactly the same way, and the inference is that both processes are due to the same fundamental physical laws.

Reproduction.—In all forms of life the process of reproduction when reduced to its simplest terms is the same, viz. cell division, and the young forms invariably begin life as single cells which, after the stimulus of fertilization or its equivalent, begin to divide. The products of this continued division soon begin to differentiate into tissues and organs, the various phenomena constituting the subject matter of the science Embryology. In *Amoeba proteus*, however, the cell is never more than a single unit and might at all times be considered the equivalent of an egg. There is evidence, although proof is not certain, that only at definite periods is Amoeba really similar to an egg cell, and requiring fertilization for its continued activities. At other times the cell divides as does the fertilized egg of other animals, but, unlike the products of cleavage of the egg, the daughter cells of Amoeba do not remain attached to one another but separate and live as independent organisms similar to the parent. Here then, as with the yeast cell, reproduction is reduced to its lowest terms, simple division. In this process the nucleus of the cell first divides and then the cell body (Figs. 19 and 20).

Encystment.—When the environmental conditions become unsuitable for life, an Amoeba will secrete about itself a wall or *cyst* of chitin, within which it is protected against adverse conditions such as drought. When conditions are again suitable the cyst wall is ruptured, and the organism comes out for a new cycle of growth and reproduction.

B. Flagellated Protozoa. Chilomonas and Allied Forms

When protein matter, a piece of beef or vegetable, is left in water for a day or so it disintegrates and putrefies under the action of bacteria. In addition to the swarms of these minute

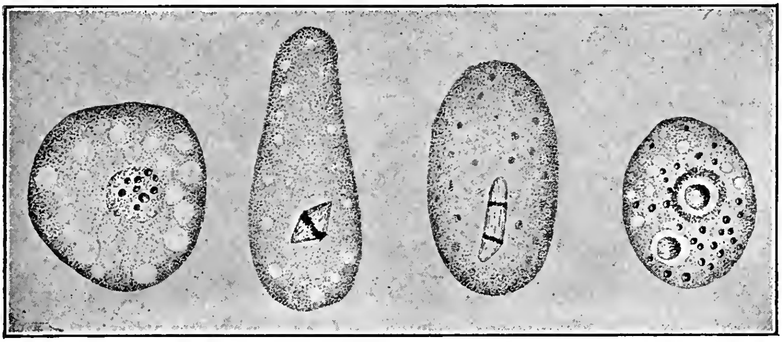


Fig. 20.—Entamoebae from the intestine during division stages of the nucleus. From preparations.

bacteria there may also appear in the water enormous numbers of small flagellated protozoa, *Chilomonas paramecium*. Compared with the smaller bacteria these minute animals are of considerable size, but compared with *Amoeba proteus* they are quite small, having a length of about 25 to 30μ (1/1000 to 1/800 of an inch.) In form they are somewhat like an elongated foot-ball with an obliquely truncated end, which we may term the anterior end since this is the end in advance when swimming (Fig. 21). The posterior end is rounded and blunt, and has no structural features of importance. The animal moves through the water by means of two parallel *flagella* which extend out to a distance equal to the total length of the body, the latter being dragged along by the vigorous lashing of the water by these flagella, and turning round and round on its long axis as it moves forward.

It is because of the flagella that Chilomonas is classified as one of the Mastigophora or whip-bearing protozoa.

The flagella are extremely delicate, and impossible to see when the organism is moving, but when the cells are killed with iodine they can be made out easily. They are of uniform diameter

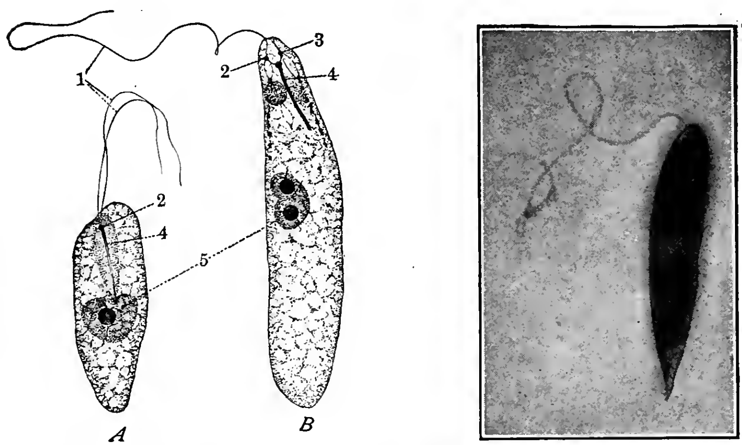


FIG. 21.—Flagellated protozoa, Chilomonas, Peranema, and Euglena. *A*, *Chilomonas paramecium*; *B*, *Peranema trichophora* at beginning of division. 1, Flagella; 2, basal bodies of flagella; 3, basal body with young flagellum growing from it; 4, parabasal body; 5, nuclei. Drawings and photograph from preparations.

throughout, entering the body at about the center of the truncated plane and continuing into the protoplasm as far as the nucleus. The latter has a different structure from the nucleus of *Amoeba proteus*, and consists of a relatively large granule (division center) surrounded by minute granules of chromatin, and with a delicate nuclear membrane. Between the nucleus and the truncated end of the cell is a somewhat cone-shaped mass of denser protoplasm which is probably the main seat of food assimilation. The remaining protoplasm has a distinct alveolar structure, the alveoli about the periphery being much more regular and compact than those within, the whole giving a very excellent demonstration of the finer structure of protozoan protoplasm. A contractile vacuole, finally, can be seen at one side of the truncated end.

Chilomonas differs from Amoeba structurally in having a definite and constant body form due to the presence of a firm cell membrane, easily seen in stained specimens. It also differs from *Amoeba proteus* and from the majority of animals physiologically in that no solid food is taken in to be digested, as in a gastric vacuole of Amoeba. Nevertheless it could not live without protein food in some form, and the fact that it does live and multiply to enormous numbers shows that it obtains suitable food. This it gets from the relatively small amount of protein matter coming from the meat or vegetable that is dissolving in the water and absorbed by osmosis into the protoplasm, the chief area of absorption being the truncated end. This method of feeding, widely distributed among similar lower forms of life, is called *saprophytic* or *saprozoic* nutrition, while that of Amoeba and higher animal forms is called *holozoic* nutrition. Many plants like bacteria and fungi take food in a similar way, the process being called *saprophytic* nutrition, while in typical green plants, where the methods of feeding are entirely different, the term *holophytic* nutrition is employed. While the latter method of feeding (to be explained in detail in connection with the fern) is almost exclusively confined to the plant kingdom, there are some few animals, as, for example, Euglena and its allies, which may make their food by the plant method.

We are ignorant of the finer processes of assimilation in Chilomonas but are justified in assuming that it differs in no essential respect from the processes in Amoeba, after the protein food materials are dissolved. As there are no solids the cell contains no undigested food matters, and there is no defecation. Urea, however, is undoubtedly formed since the organism is constantly doing work, and this is probably excreted by means of the contractile vacuole, although it may also pass out by exosmosis, as must be the case in many protozoa in which no contractile vacuole can be found.

Chilomonas may frequently be seen in pairs swimming along side by side; these are sister cells not yet fully divided and they have originated by the longitudinal division of the cell. Reproduction thus is of the simplest type, the nucleus always dividing first, then the cell body, while new flagella

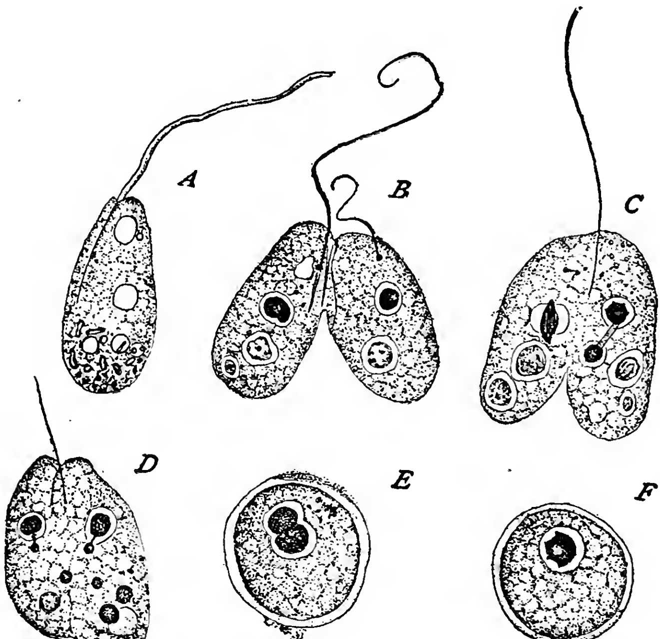


FIG. 22.—A flagellated protozoon, *Copromonas subtilis*. *A*, A normal adult cell before division; *B*, two individuals in conjugation; *C*, *D*, *E*, and *F*, later stages in the fusion of cells and nuclei, and formation of protective cyst. (From Dobell.)

are formed as outgrowths. It is not known how these originate in Chilomonas but from analogy with other forms of flagellates where the process is known, two of the four at least must be new growths; in some cases the old flagella are withdrawn and new ones are formed; in other cases one of the two flagella goes to each daughter cell.

The processes of feeding, growing and dividing continue for days before other activities occur. Indeed for Chilomonas so far as known they may continue indefinitely, but from analogy with other forms of Mastigophora where the full life history is known, these ordinary vegetative processes are sooner or later replaced by processes involving a simple kind of fertilization or sexual union. In Copromonas, for example, two similar cells after a long period of divisions, meet and fuse; the flagellum of one of them is discarded while that of the other is used as a motile apparatus for the pair. Fusion of nucleus and cell body continue until a single cell results. This then secretes a membrane and becomes quiescent, or it divides and behaves like an ordinary individual. Here there is typical fertilization but no difference between the conjugating cells so far as can be detected (Fig. 22).

FIG. 23.—*Synura uvella*, a colony of flagellated protozoa in which the individuals are attached at a common center. From a photograph.

Allied Forms.—Many hundreds of species of flagellated protozoa are known and may exhibit the most manifold variations in structures and functions. Many of them have only one flagellum, as Peranema or Euglena, for example, which are common organisms in infusions of different kinds. It is a remarkable and fascinating sight to see a relatively large cell like Peranema drawn steadily forward by the undulations of the tip of its long and easily seen flagellum. In this case the entire flagellum does not vibrate, but only the tip, whereas in Euglena the whole flagellum is in constant motion and almost invisible.

Nutrition in Peranema, as in Chilomonas, is saprozoic, but it is entirely different in the case of Euglena which has the power to manufacture its food in the same way that the higher green plants do. This holophytic nutrition is accomplished through the agency of *chloroplastids* or color-bearing structures distributed throughout the protoplasm of the Euglena cell (Fig. 21).

The color is due to a substance termed *chlorophyll* which, with the aid of sunlight, is able to manufacture starch; this, in turn, is built up into protein matter which serves as food (see Chapter V). Another colored structure is also found in Euglena, although it is not so conspicuous as the green chloroplastids. This is the red-colored spot or stigma which is more sensitive to light than other parts of the protoplasm, and is often spoken of as a rudimentary "eye-spot." In many cases it is accompanied by a lens-like body which may concentrate light rays

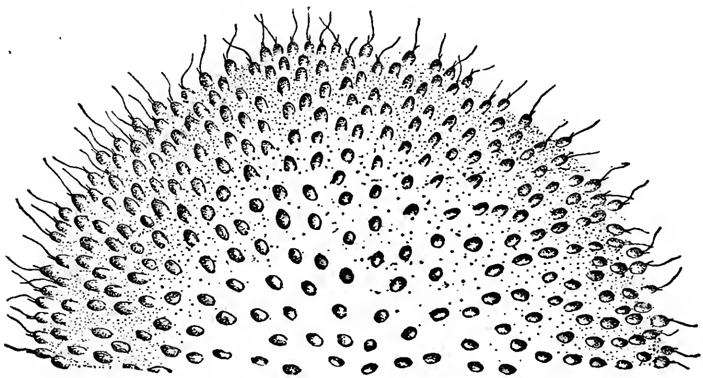


FIG. 24.—*Uroglena americana*, a colony of flagellated protozoa in which the individuals are embedded in a common gelatinous matrix.

on a particular spot and so act as a directive agent; at any rate this spot is usually turned toward the source of light and it serves therefore as a rudimentary sense organ.

Colonies.—Both Peranema and Euglena reproduce by longitudinal division which is not different in any way from the division of Chilomonas. The daughter cells separate after division, and lead an independent existence. In some forms of flagellated protozoa, however, the cells after division do not separate completely but remain attached to each other in one way or another (*e.g.*, by the basal ends as in *Synura uvella* (Fig. 23), thus forming aggregates of cells or individuals of a second order to which the term *colony* is given. Sometimes the cells thus formed are embedded in a common jelly, the aggregate forming relatively large spherical masses (Fig. 24). Again they are limited to a certain number of cells, and this number always reappears upon reproduction so that the multicellular individual is much more specific in nature, as in *Gonium pectorale* where the individual always consists of 16 cells (Fig. 25).

These colony forms are of peculiar interest in that they have many features in common with the higher animals and plants,

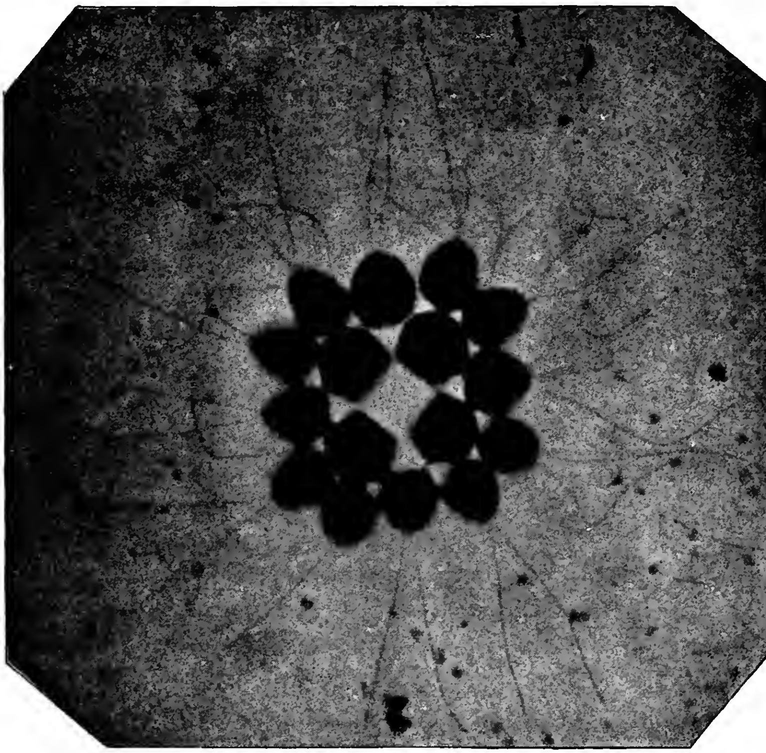


FIG. 25.—*Gonium pectorale*, a colony of flagellated protozoa consisting of sixteen cells arranged in a flat plate, three on a side and four in the center. Each cell carries two flagella. Photograph from a preparation.

but the cells are not differentiated for the performance of different functions, each one acting for itself rather than for the aggregate as a whole. They represent, therefore, a phase in complexity of form and function intermediate between the unicellular organisms (protozoa, protophyta) and the multicellular (metazoa and metaphyta).

C. A Ciliated Protozoön, Paramecium caudatum

An infusion of vegetable or animal matter becomes the feeding ground not only of bacteria and flagellated protozoa, but also, after some considerable time, of ciliated protozoa as well. From the fact that all of these organisms appear in such infusions, the term Infusoria was formerly employed to designate all of them indiscriminately. The bacteria were first recognized as having no systematic relation to the other forms, and were separated in classification from the protozoa found in infusions. Later the flagellated forms were recognized as entirely different from the ciliated ones and were classified under the name Mastigophora, so that finally, the term Infusoria is used today to include only the ciliated forms of protozoa. Of these there is a great number of different types, one of which, Paramecium, formerly known as the "slipper animalcule" common in every ditch, pool, or stagnant water, may serve as a type for all.

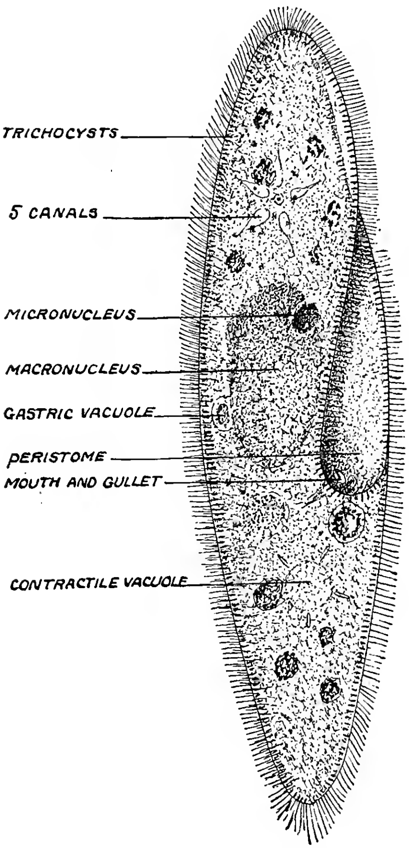


Fig. 26.—Diagram of structures of *Paramecium caudatum* from an individual about 1/125 of an inch in length.

Paramecium is an elongated, somewhat cigar-shaped organism, consisting of a single cell which moves rapidly through the water, turning the while on its long axis. The movement is brought about by the synchronous beating of the water by myriads of minute cilia uniformly distributed over the surface in diagonal lines, while the rotation on the long axis is due partly to this arrangement and partly to the action of cilia covering an asymmetrical groove called the *peristome,* extending from the anterior end backward to about the middle of the body. This peristomial area does not run in a straight line from the anterior end to the center but curves from the left dorsal extremity to the right, ending to the left of the middle of the ventral surface at the mouth. The area deepens from in front backward, until at the mouth a conspicuous pocket is formed (Fig. 26). The mouth is a circular opening leading into a short gullet which bears an undulating membrane on one side.

Structure.—The finer structure of Paramecium differs considerably from that of Amoeba and Chilomonas owing to the fact that Paramecium cells are much more highly differentiated into cellular organs. We can recognize, however, a distinct endoplasm and ectoplasm and note that the chief differentiations are in the latter. The endoplasm is made up of alveoli similar to those of Amoeba, and we find the same granular microsomes and larger food particles in various stages of digestion. The protoplasm also undergoes streaming movements or cyclosis, the movement being entirely within the cell, however, and irregular so that it appears to be different from the movement involving pseudopodia formation in Amoeba. Nuclei and contractile vacuoles are quite different and more complex than in Amoeba or Chilomonas.

Nuclei.—Paramecium and the Infusoria, in general, are different from all other cells in having two kinds of nuclei, macronuclei and micronuclei. One of these, the macronucleus, is large and conspicuous; the other, the micronucleus, is very small and usually partly embedded in the substance of the larger nucleus. While not fully proved it is probable that these two kinds of nuclei have different functions to play in the vital activities in the cell, the macronucleus being the chief seat of metabolic activities, while the micronucleus is mainly concerned with reproduction and maintenance of the race.

Contractile Vacuoles.—The contractile vacuole of *Amoeba proteus* is a single spherical vesicle which moves in the endoplasm with the other endoplasmic organs. Paramecium is more highly differentiated in this respect by having two vacuoles which are fixed in the cell, and open to the outside by permanent pores in the membrane. One of the vacuoles is in the anterior third of the body; the other in the posterior third. A conspicuous feature in regard to them is that special canals feed them by bringing waste matters from all parts. When these canals are full a characteristic radiate structure about the vacuole can be made out with ease. Systole or rupture of the vacuole and diastole or filling are independent in the two organs, but both radiate structures may be seen at the same moment (Fig. 26).

The waste matters that are collected and excreted through the vacuoles consist, probably, of urea and carbon dioxide resulting from the processes of destructive metabolism. As in Amoeba, murexid crystals have also been demonstrated in these vacuoles showing the presence of uric acid.

Ectoplasm.—The ectoplasm of Paramecium is much more complicated than the endoplasm, and more so than the ectoplasm of amoeba. It is covered by a lifeless "pellicle," equivalent to the cuticle of higher animals. The membrane or cortical plasm is relatively thick and forms a firm but plastic covering for the cell, by means of which the organism retains a definite form or "morph." The cilia are inserted in it, each cilium taking its origin from a minute basal granule, from the substance of which it is apparently formed. The ectoplasm is further complicated by the presence of peculiar rod-like elements termed *trichocysts.* When the organism is irritated in any way the material forming these trichocysts is shot out with considerable force and a network of threads is formed about the cell. The trichocysts thus serve as a means of protection against small enemies which are prevented by the weft of threads from reaching the cell. In some forms of Infusoria similar trichocysts have an offensive as well as a protective function, the minute organisms being able to sting and paralyze other organisms preparatory to devouring them. This paralysis is due to a minute quantity of poison contained in the thread; in Paramecium, however, there is no evidence to show that the trichocysts are poisoned. The extrusion of trichocysts may be seen by adding a small quantity of dilute acetic acid to the medium.

Nutrition.—Paramecium lives primarily on bacteria which are always present in infusions. A constant stream of water passes into the mouth and down the gullet, and bacteria carried by the stream are constantly taken into the endoplasm. A gastric vacuole forms at the bottom of the gullet which gradually fills with water and bacteria. The vacuole is then carried away from the mouth by the streaming protoplasm (cyclosis) and the process of digestion begins, as in Amoeba, by the secretion into it of a mineral acid. The bacteria are killed by this acid and begin to swell preparatory to dissolution. After from 10 to 15 minutes the vacuoles show an alkaline reaction, and the further processes of digestion, requiring several hours, are completed in this alkaline medium. In well-fed Paramecia the cell becomes loaded with these vacuoles containing bacteria in various stages of digestion. As in Amoeba again, this later digestion is brought about by a proteolytic enzyme which acts like trypsin. Finally the liquid of the vacuole disappears, as the digested food becomes intimately mixed with the protoplasm, and assimilation, presumably as in *Amoeba proteus*, takes place.

An instructive picture of the protoplasm of Paramecium can be obtained by systematically over-feeding it for a long period, *e.g.*, for some months on a rich hay infusion diet. The protoplasm becomes filled with dark granules, the vacuoles of the protoplasm become indistinct or lost, the contractile vacuoles lose their rhythmic action, and movements are slow and irregular. At such a time the organism is said to be in a state of depression. It is loaded down with reserves of food partly digested, and seems to be unable to assimilate (Fig. 27). If a small quantity of salt be added (potassium phosphate or potassium chloride), the dense structure slowly disappears, first in the region around the nucleus; in a few days the protoplasm becomes as clear and vigorous as ever. Such experiments show either that some of the oxidative ferments are exhausted so that the organisms become gradually overpowered by the products of their own metabolism, or that the formative processes are not properly functioning. They also show that salts or electrolytes were probably no longer present in the cells and that oxidative processes had ceased, because the simple addition of salts to the medium resulted in the restoration of vital activities. Finally they indicate that the nucleus of the cell is probably the seat of manufacture of the oxidative ferments or catalyzers.

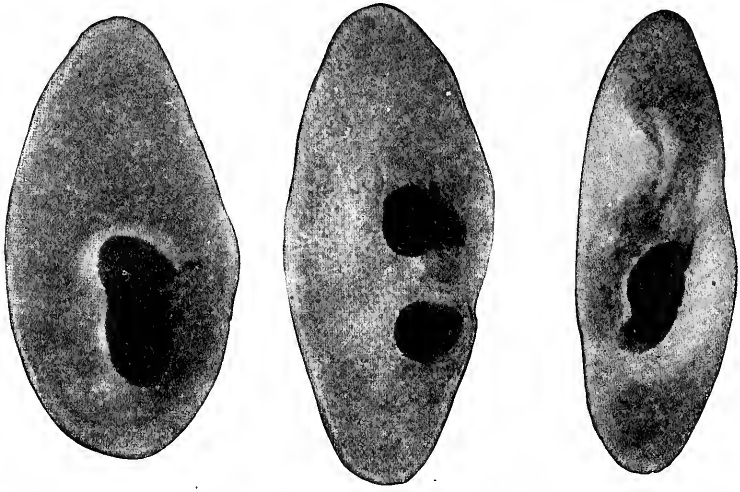


FIG. 27.—*Paramecium caudatum* in the condition of depression and recovery through the use of salts. The individual on the left has densely packed protoplasm, the others were similar individuals which were treated with potassium phosphate. From photographs of prepared specimens.

Reproduction.—Like *Amoeba proteus* and the flagellates, Paramecium reproduces by simple division, the micronucleus dividing first. The cell divides transversely through the middle of the macronucleus which is passively divided with the rest of the cell (Fig. 28). One new mouth and new contractile vacuoles are formed by the daughter cells which separate and begin an independent existence. The entire process requires from half an hour to two hours according to the temperature.

Irritability.—Like *Amoeba proteus* again, Paramecium responds to external stimuli, but having definite motile organs its responses are more definite and more easily studied. It answers to all sudden stimuli by a definite reaction termed a "motor response." It backs away by reversal of its ciliary action, then turns on its axis and moves forward again. If the offending object is still encountered it repeats the action until finally its forward movement is unimpeded. It reacts definitely to the action of a galvanic current, and always moves toward the negative pole, thus showing a well-marked galvanotaxis. With strong acids and alkalis it gives the characteristic motor response.

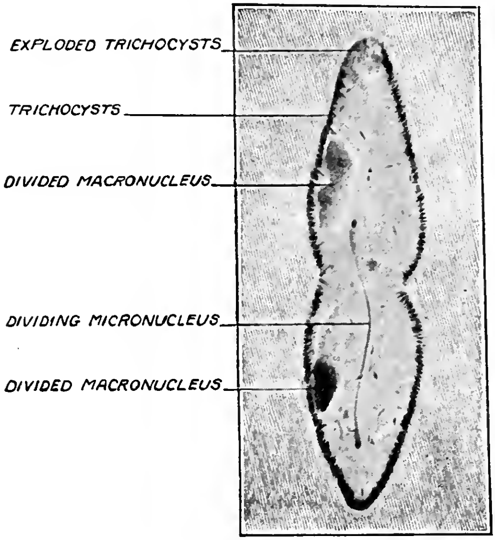


FIG. 28.—Paramecium in division. Photograph of a section.

D. Some General Biological Problems Associated with Protozoa

The single-celled animals have been intimately connected with some of the deepest problems in general biology, for since vital manifestations are everywhere the same, physiologists have turned for their solution to these simple organisms where processes, like structures, are relatively uncomplicated. Some of these problems, such as the distinction between animals and plants, have only an academic importance; another, spontaneous generation, has only an historical importance, but others, like old age, the origin of death, the significance of fertilization are all deep problems which rest upon the very foundations of biological science.

Animals and Plants.—At first glance it would appear to be a simple matter to distinguish between animals and plants, and superficial observers do not hesitate to do so with full assurance. But when we come to examine them more closely we find that no definite boundary line can be drawn between them, and no single characteristic belongs absolutely to one or the other group. Formerly it was argued that plants are quiescent while animals move, and the power of spontaneous movement was regarded as sufficiently characteristic to distinguish them. But numerous sensitive plants, the Venus fly trap for example, and many algae have the power of movement quite as well developed as do many animals, while many animals, as for example the sponges, are quiescent. Again it was thought that chlorophyll, giving well-defined colors to plants, is a definite and distinctive feature. But many animals such as Euglena and many other flagellates are similarly colored by chlorophyll. The presence of chlorophyll indicates a power of manufacturing starch and sugars, while plant cells generally have a definite membrane of cellulose which is closely allied to starch in chemical composition. Cellulose therefore was also regarded as a specific plant characteristic. But again a number of animals have the power of manufacturing cellulose; the Dinoflagellates, for example, have a thick cellulose wall, while some of the higher animals, notably the group known as the ascidians, have well-defined tests of the same material. Still later it was maintained that plants do not eat solid food in the form of proteins while animals do; but the Venus fly trap Dionaea not only moves but also catches and digests insects of various kinds. On the other hand, a number of animals, especially the unicellular ones, do not take in solid food but manufacture it, as do the plants, through the aid of chlorophyll. Similarly with every other distinctive feature we find some exceptions on one side or the other, showing that physiological processes in nature are nowhere monopolized by any one type of organisms.

While it is impossible to draw a definite line between animals and plants it is possible, nevertheless, through the sum of characters to determine whether an organism is either plant or animal, or some form of life intermediate between them. For the determination of a given questionable type it is necessary to take into consideration not only form, movement, and mode of nutrition but also the immediate relations. Thus Euglena has many of the physiological characteristics of plants of which the mode of nutrition is the most important; but it itself and a nearly-related type, *Chromulina flavicans*, have the power of both holophytic and holozoic nutrition and can live in the dark on solid protein matter, or in the light without solid food where it manufactures its food. An allied form, Astasia, lives solely on solids. The structures and life history of Euglena place it unmistakably with the animal flagellates.

It is now known that plants, like animals, renew their protoplasm with oxygen, salts and proteins, and give off CO_2 and other waste matters the same as animals do, the only essential difference being their power to manufacture the proteins to be used as food. Their functions, therefore, are fundamentally constructive while animals are destructive; all plant tissues and organs are differentiated to subserve this great function while those of animals are mainly differentiated for the procuring of food, digesting and assimilating it. The two great lines of living things have thus developed in different directions, and the higher we go in either scale the more easily we are able to distinguish between animals and plants by these structural differences.

Spontaneous Generation.—"But expectation is permissible where belief is not; and if it were given me to look beyond the abyss of geologically recorded time to the still more remote period when the earth was passing through physical and chemical conditions which it can no more see again than a man can recall his infancy, I should expect to be a witness of the evolution of living protoplasm from non-living matter." (Huxley, Biogenesis and Abiogenesis.)

All biologists are practically agreed that living matter originated on the earth's surface from salts and other inorganic matter at a time when conditions of temperature, atmosphere and other physical characteristics of the globe were very different from the conditions today. At the present time, while ignorant of the first causes all are agreed that living matter cannot arise spontaneously from non-living matter, and that all plants and all animals come from the germs of their ancestors. All theories to the contrary have been based upon ignorance, and the gradual clearing away of these dark clouds forms an interesting chapter in modern biology. A characteristic of the human mind is to explain what cannot be seen or comprehended, by the most plausible hypotheses based upon what is known. This is why in the 17th century it was generally believed that insects are spontaneously generated in decaying meat, the myth being disproved by the simple experiment of Redi, an Italian naturalist, who kept fresh meat under a fine netting upon which he saw flies deposit their eggs; these he watched develop into maggots and later into flies. Thus a set of phenomena was removed from the unknown into the known, and Redi concluded from his observation that all living things come from pre-existing living things, a conclusion formulated in the well-known dictum credited to Harvey (?), *omne vivum ex vivo*. Redi's conclusions, however, were not to be fully accepted for more than two hundred years, for shortly after his experiments were carried out, the world of microscopic organisms was discovered by the Dutch naturalist Leeuwenhoek, and ignorance of their origin resulted in a new life for the theory of spontaneous generation. This theory, therefore, finally died out only in our own times with the famous experiments of Pasteur and Tyndall upon the smallest visible forms of living organisms, bacteria and yeasts.

The Problem of Age and Natural Death.—With full and unhindered processes of metabolism there is no *a priori* reason why living matter contained in the single-celled organism, apart from tragic or accidental death, should not live indefinitely. So far as we know, however, all living things experience a weakening of these fundamental biological activities, and pass through a longer or shorter period of physiological weakness, which we term old age, ending in natural death. The length of life varies within wide limits, animals on the whole having shorter lives than plants; some of the giant trees of California, for example, live for tens of centuries while some of the insects (May-flies) are born and live out their adult life within a single day. On the other hand, some animals like the tortoise may live for hundreds of years.

Senescence.—In the higher animals or metazoa the cells are differentiated for the performance of different functions, and the various activities of metabolism are relegated to different types of specialized cells. These are the links in the chain of vital phenomena which weaken, give out and lead to old age. The secreting cells, for example, ultimately cease functioning one by one, and their places in the tissue are taken by non-functioning connective-tissue cells; when enough of these are thus worn out and replaced, activity of the organ is impaired and the general vitality of the entire organism is correspondingly weakened. In the human organism this process results in hardening of the tissues, leading, for example, to cirrhosis of the liver or kidney, sclerosis of arteries, etc., ending inevitably in death after a longer or shorter time.

FIG. 29.—*Paramecium caudatum* in conjugation. The micronuclei can be seen in the process of dividing. The organisms are united in the peristome region. From a photograph of a preparation.

The problem of old age therefore resolves itself into the question, why do the individual cells give out? It would seem that these differentiated cells of the body are endowed with a limited possibility of action, or with a "potential of vitality," which is gradually exhausted by continued use. Yet some of these epithelial cells, under circumstances abnormal to the organism, have the capacity to live far beyond the limits of the natural life of the organism to which they belong. Thus epithelial cells of the mouse, under abnormal conditions which we call cancer, may be transplanted from mouse to mouse for years after the normal length of life of the original animal, a fact demonstrating that epithelial cells, at least under these abnormal conditions, have a far greater potential of vitality than is represented by the ordinary length of life of the individual. Weakness and death of the individual cells, therefore, must be due to some defect in the inter-relations of the many differentiated cells and organs of the body of the metazoön; this defect is cumulative until the organisms are unable to carry on the necessary functions, and die. The same result may be brought about by the local destruction of cells through disease; thus bacteria may destroy the cells of the lungs in pulmonary tuberculosis, a loss resulting in the weakening of other cells in the body, and finally in death through inability to obtain oxygen and gives off CO_2.

This gradual weakening of the cells and vital activities in general led Weismann, a famous German biologist, to the conclusion that old age and natural death are penalties which the higher organisms must pay for their privilege of differentiation, while the unicellular organisms, dependent only upon themselves, have an unlimited capacity of life, *i.e.*, are potentially immortal. These conclusions have been repeatedly challenged on the ground that all protoplasm is subject to the same laws of physiological usury, and numerous experiments beginning with those of Maupas, 1888, have been undertaken to show that protozoa, like metazoa, undergo senescence, and die from old age. It follows from the negation of spontaneous generation, however, that all living things are composed of protoplasm that has been living continuously since life appeared on the earth, and it is obvious that all organisms contain some cells endowed with the potential of physical immortality. These, called the *germ cells*, hand down the race from generation to generation. The experiments of Maupas and of subsequent investigators have shown that it is only in this sense that protozoa are physically immortal. Maupas isolated Oxytricha, Stylonychia, and other unicellular animals, and kept the descendants isolated, in order to prevent fertilization, through 316, 319, etc., generations of simple division. Toward the end of the time the cells became reduced in size and abnormal in structure through loss of cilia and other organs, and all finally died under conditions similar to senile degeneration in higher animals. Many other types of Infusoria, also, have been watched through many hundreds of generations by different observers, but the physiological activities in every such experiment save one, weakened, and sooner or later, abnormal or deformed specimens brought the race to an end. The one apparent exception is the case of *Paramecium aurelia* which Woodruff has carried on for many years (over 6000 generations) without conjugations. At regular intervals, however, the race of Paramecium under observation showed a reduced vitality as measured by the division rate, and it was found that, during these periods of depression, the macronucleus breaks up into fragments, and the micronuclei divide. New macronuclei develop from some of the products of division of the micronuclei, functional micronuclei from others, while some degenerate. The fragments of the old macronucleus and the degenerating micronuclei are absorbed in the cytoplasm, and this addition of relatively large quantities of nucleo-proteins makes a decided change in the chemical organization of the entire protoplasm. As a result of this process of nuclear and cytoplasmic reorganization which Woodruff calls *endomixis*, all of the vital activities are accelerated so that the organisms grow and divide at a more rapid rate than during the process of endomixis or just prior to it. This high vitality then gradually decreases until the next period of depression when the process of endomixis is repeated.

In essence, therefore, it appears that the unicellular organisms agree with the multicellular in possessing physiological powers which gradually wear out. To be sure, the single cells of the majority of generations do not die. They cease to live as the same cells, but the protoplasm continues to live in the daughter cells arising from divisions; but the same is true of any individual cell of a metazoon, since the adult organism is formed by the continued division of a single original egg cell. The entire race of Paramecium derived from a single ancestral cell, and not any single cell of that race should therefore be compared with a metazoon, the race of Paramecium in most cases may die from old age no less surely than the race of cells composing the metazoon. Old age and natural death, therefore, appear to be characteristic of animals whether single cells or many celled.

In spite of the fact that protozoa, should they escape the thousands of their natural enemies, may die of old age, they nevertheless exist in more or less abundance in natural waters, and will undoubtedly continue to exist in the future. The question then arises, how is this physiological weakness overcome and what means are employed in nature to perpetuate the species? One means of accomplishing this end is the chemical reorganization following endomixis as described above; another and an essentially similar means is the chemical reorganization of the protoplasm which follows fertilization through the act of conjugation. Bütschli in 1876 observed that a culture of Paramecium, after some weeks in a watch glass, showed hundreds of pairs in conjugation, the cells being united in the region of the peristomial area. This union or conjugation, lasting from eighteen to twenty-four hours, is followed by separation of the two individuals (Fig. 29). From this observation Bütschli concluded that conjugation is for the purpose of renewing the vitality of the race, or is a means of protoplasmic rejuvenescence, and this interpretation, while it has been questioned, has never been disproved or improved.

Conjugation or Fertilization.—Conjugation of protozoa is essentially the same as fertilization in metazoa, and in one form or another represents a phenomenon practically universal in animals and plants. It is, therefore, one of the fundamental activities of living things (see page 15). It is usually associated with reproduction, but reproduction may go on without it, as in the case of division, spore formation, etc., of the protozoa, or budding in Hydra and plants, or parthenogenesis in insects. Strictly speaking, therefore, it is not a process of reproduction but a process of protoplasmic reorganization, followed by renewal or re-birth of all vital activities including that of reproduction.

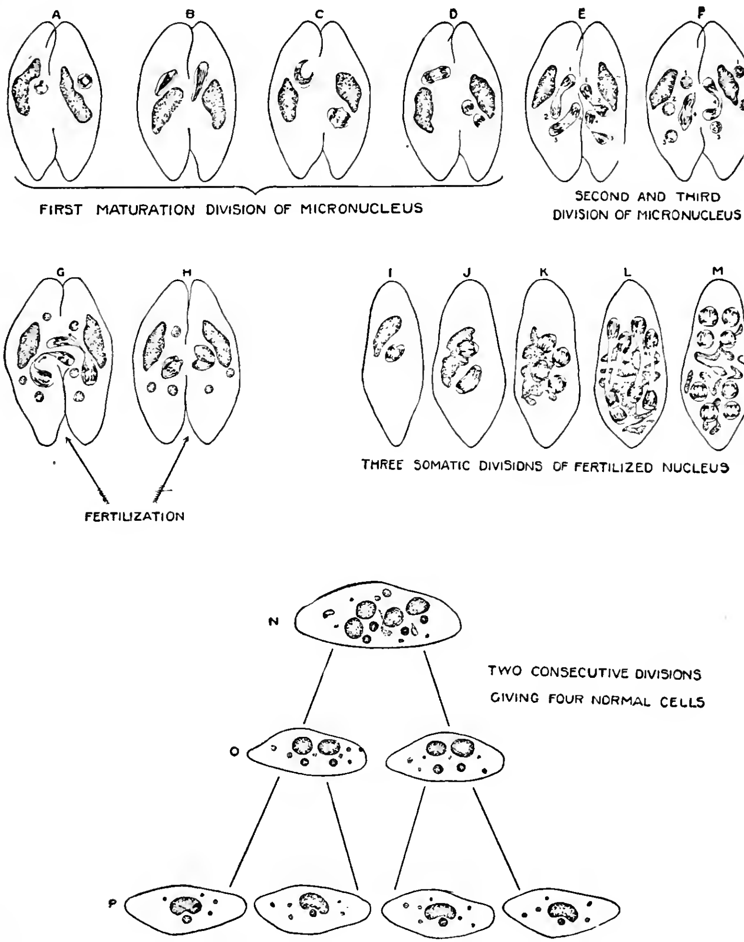


FIG. 30.—Diagram of the consecutive stages in conjugation of *Paramecium caudatum*.

Investigations subsequent to those of Bütschli have revealed all the happenings during the process of conjugation in Paramecium. The micronuclei in each cell first begin to swell by the absorption of fluids from the endoplasm; the chromatin increases enormously in quantity and becomes drawn out in the form of rods termed *chromosomes*, too numerous to count. Each of these chromosomes is then divided into two equal parts, after which the micronuclei divide through the center, each daughter micronucleus receiving one-half the original chromatin. There are now two micronuclei in each cell, and all four divide once again, forming eight in all or four in each cell. Of these four, three degenerate and are absorbed in the endoplasm, leaving one micronucleus in each cell. These then divide once again, forming what are called *pronuclei*, one of which migrates from its cell into the other cell so that a mutual exchange of pronuclei takes place. Each wandering pronucleus unites with the stationary pronucleus of the opposite cell and fuses completely with it, forming a fertilization nucleus (Fig. 30, A–H).

In the meantime the macronucleus of each cell begins to break into pieces and to degenerate, and sooner or later it entirely disappears, although this final disappearance does not occur until some time after the two cells separate and divisions have begun. After separation of the conjugating cells the fertilization nucleus gives rise, by divisions, to eight micronuclei. Four of these begin to swell, change in character, and develop into four new macronuclei. After twenty-four to forty-eight hours the exconjugant divides. Two macronuclei and two micronuclei pass into each daughter cell, and after another twenty-four hours these cells divide again, one micronucleus and one macronucleus going to each daughter cell. With this final division the normal relations of the cell are restored, and the processes of conjugation are ended, the resulting cells having each one macronucleus and one micronucleus (Fig. 30, I–P).

With the breaking up of the old macronucleus the protoplasm becomes loaded with nuclear stuffs, as in endomixis, and these probably renew the supply of material for the production of the various endoenzymes needed in the vital reactions.

With the conjugation of Paramecium, therefore, the ordinary cells are metamorphosed into germ cells with extraordinary activities, the protoplasm of the race is completely reorganized by the interchange of nuclear material, by the formation of new macronuclei and new micronuclei of a different chemical make-up, and by the formation of a new cytoplasm through the absorption of the old macronucleus and three-quarters of the old micronucleus. It now contains the potential of a new race of cells, exactly as in the case of a fertilized metazoan egg, and in the race of cells derived from it, some will be germ cells, just as in the case of the metazoan. So far as immortality is concerned, therefore, the unicellular organisms resemble the multicellular; there is a reorganization of the cytoplasm, a new combination of physico-chemical elements, and a new individuality in protozoa, exactly as in metazoa. There is no essential difference in the vital phenomena, only a difference in their manifestations. Old age, followed by natural death, is a biological and inevitable termination of vital activities, which, so far as we know, can only be prevented by fertilization, or by endomixis the equivalent of parthenogenesis, and then only in the germ cells, since epithelial cells, muscle or nerve cells have no possibility of similar reorganization.

CHAPTER IV

ORGANISMS OF TISSUES

VERY little observation is needed to show that a Paramecium is a complicated mechanism, despite the fact that it is only a single cell. The various parts of the cell are differentiated for the performance of different functions, whereas in Metazoa the same functions are performed by aggregates of cells and tissues. Such cells and tissues, like the parts of the protozoan cell, are specialized for different functions. Fundamentally alike in their physiological activities, there is, nevertheless, a vast difference between organisms of one cell and organisms of many cells. With the aggregate of cells there is a great possibility of differentiation which is absent in unicellular forms, and with this differentiation the possibility of structural complications is vastly increased.

Could we collect and hold together all the progeny of a fertilized Paramecium cell into a harmoniously working whole, the result would be an organism composed of tissues, or in this case, of a single tissue, for all the cells would be fundamentally alike and performing the same functions. While this condition does not exist for Paramecium, there are protozoa in which the progeny after division remain connected, forming aggregates of many cells. These protozoan aggregates, colonies, are designated according to their method of formation, as gregaloid, sphaeroid, arboroid and catenoid. In all of these, except the first, the colony results from the incomplete division of the cells and their products. Gregaloid colonies differ in that they are formed by the coalescence of adult cells into a loose group, as in the case of *Microgromia socialis*. A catenoid colony is formed by the attachment, end to end or side by side, of sister cells resulting from division. An arboroid colony is formed by the daughter cells of one organism remaining attached to the parent; both parent and offspring then reproduce in the same way until a branching tree-like colony results (Fig. 31). Sphaeroidal colonies, finally, differ from the others in that the cells resulting from division remain embedded in a gelatinous matrix secreted by the parent organism (Fig. 24). Such colonies are usually spherical, the constituent cells being arranged about the periphery. When this condition in develop-

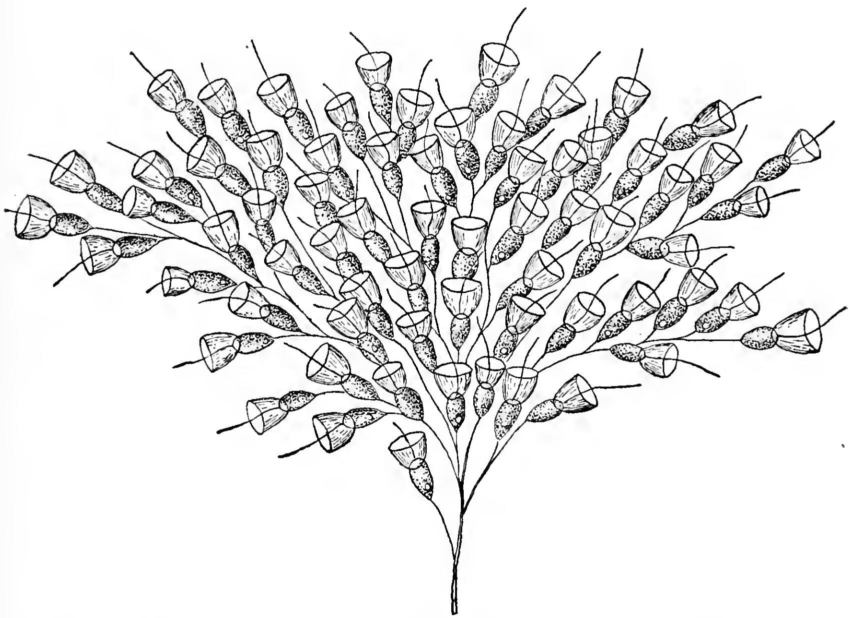


FIG. 31.—An arboroid colony of flagellated protozoa, *Codosiga cymosa*, Sav. Kent. (From Calkins after Kent.)

ment is reached it is not a long step to the simplest type of metazoan, and we find cases where there is even a regional differentiation in the colony. A Proterospongia, for example, is a gelatinous mass with cells arranged about the periphery; when abundantly fed these cells migrate one by one to the interior of the jelly mass, losing their flagella in the process. Within the jelly they divide, and the cells then wander back to the periphery to take their place with the feeding cells of the colony. Here then is a temporary differentiation into vegetative or somatic cells, and reproducing or reproductive cells. The differentiation is carried a step farther in the case of Pleodorina where twenty-eight of the cells are capable of reproducing, while the remaining four cells, making up the thirty-two cell colony, are purely vegetative and do not reproduce. Here there is a permanent differentiation in the colony and a long step toward the metazoan condition. In some colonies finally, as in *Gonium pectorale*, the method of development approaches

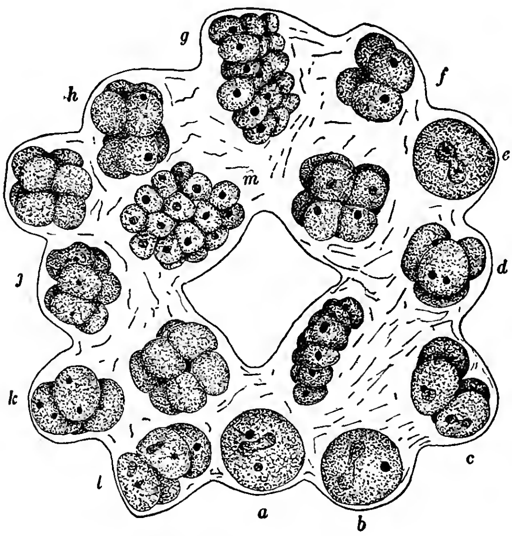


FIG. 32.—Reproduction of *Gonium pectorale*. Each of the sixteen cells of the ordinary colony (see Fig. 25) divides until a sixteen-cell stage results; the old colony then breaks up and the sixteen young colonies grow independently.

closely to that of metazoa. The organism consists of sixteen cells arranged as in Fig. 25. When ready to reproduce, each cell of the colony divides first into two cells; these cells do not separate but while still connected they divide again into four, these four divide into eight, and the eight ultimately into sixteen. Each cell of the parent organism, therefore, gives rise to a new colony of sixteen cells, each of which is liberated as a colony by dissolution of the original jelly mantle (Fig. 32). Here then is a process of development, an embryology in the case of a protozoön, in which all of the constituent cells are potentially germ cells. Furthermore, the first two division planes are vertical and the third horizontal, exactly as in the case of holoblastic cleavage in metazoa.

The primordial cell (fertilized egg cell) of a higher animal develops by continual cell division until myriads of cells constituting the adult organism are formed. In the typical case and in the majority of forms the early stages of this development follow the course illustrated in Fig. 33. The process of holoblastic cleavage, so-called, is a regular and symmetrical division of the egg cell. The first cleavage in a vertical plane results in the formation of two similar cells—the two-cell stage; the second cleavage, also vertical, gives four similar cells; the third cleavage differs in being horizontal, crossing the first two planes at right angles and resulting in eight cells; in the majority of cases this third cleavage brings about the first trace of differentiation in the cells, those of one pole (vegetative) being larger and containing more yolk than those of the smaller pole (animal). The fourth cleavage is again vertical, and the difference between the two poles is further emphasized, the sixteen cell stage presenting eight larger vegetative and eight smaller animal cells. At this stage also the cells begin to separate, leaving a cavity in the center. This cavity, termed the *segmentation cavity*, in the majority of types is later closed up, and plays no part in the adult organism. After the sixteen cell stage cleavage becomes more or less irregular, the cells of the animal pole dividing more rapidly than those of the vegetative, until a many celled hollow sphere results. At this stage the organism is termed a *blastula* (Fig. 33). Up to this time the developing metazoon differs but little from some colony forms of protozoa. After the blastula stage a step in development is taken which is found nowhere but in metazoa, and represents therefore a great advance over protozoa. The cells of the lower pole invaginate or turn in until their inner sides come in contact with the inner sides of the cells of the animal pole. This process is termed *gastrulation*. The *gastrula* thus formed is a double walled sack enclosing a cavity, which becomes the enteric or digestive cavity of the embryo, and in most cases the digestive tract of the adult is formed directly from this enteric cavity. Because of this ultimate fate the cavity is called the *archenteron* or primitive gut, while the opening to the outside is termed the *blastopore* or larval mouth. At this stage in development the water dwelling types usually leave the egg membrane and swim about in the water, taking in food through the blastopore and digesting it in the archenteric cavity. We see, therefore, that the larger cells of

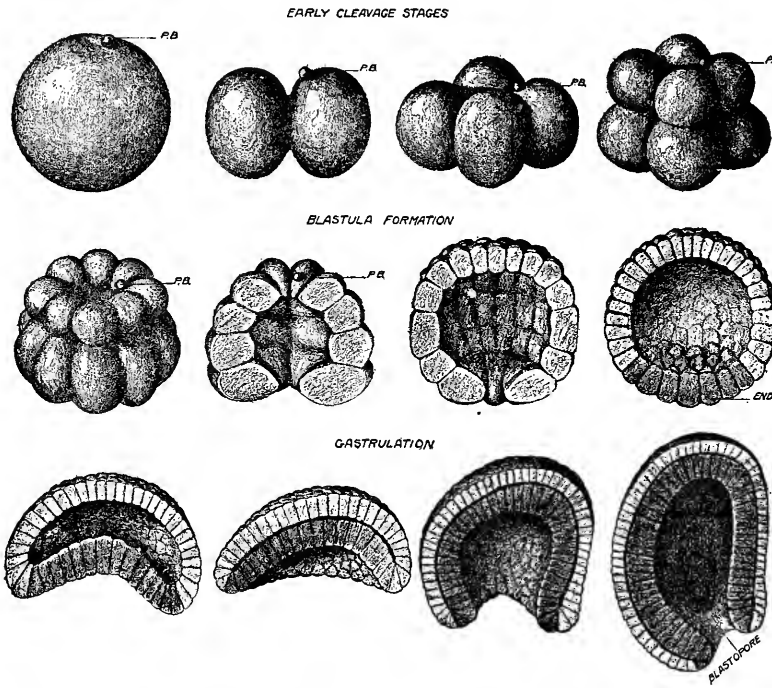


FIG. 33.—Holoblastic cleavage and gastrulation of Amphioxus. P.B., polar body (see p. 213). (From Ziegler models.)

the vegetative pole of the blastula become the functioning cells of the digestive tract of the adult and are internal in position, forming a lining of cells called the hypoblast or *endoderm*. The cells of the animal pole remain outside, covering the endoderm cells and forming a continuous sheet of cells termed the epiblast or *ectoderm*. The two layers together constitute the *primary germ layers* of the organism. At first each sheet consists of entirely similar cells having a similar function, but as development progresses the cells become differentiated in groups for the performance of different functions, some cells of the ectoderm forming the outer covering or skin, the nervous system, etc., while cells of the endoderm become differentiated for different processes of digestion. Tissues are aggregates of similar cells having the same function. In the gastrula there are two tissues, endoderm and ectoderm, but in later development many different tissues are formed from these two, *e.g.*, epithelial, nerve, muscle, connective tissue and the like. In the majority of higher animals a third germ layer, termed the *mesoderm*, is formed between the ectoderm and the endoderm. This third layer gives rise to muscle tissues, endothelial, supporting or connective, and germinal tissues (see Chapter VI). Organs are aggregates of tissues for the performance of one function; digestive organs, the stomach, liver, etc., consist of secreting, muscular, nerve, vascular, and connective tissues. Organs finally are grouped in *systems* for the performance of the fundamental vital processes of metabolism. The digestive system includes all of the organs necessary for the digestion of food; the muscular and supporting systems, the organs of locomotion; the excretory system, the organs for disposing of waste matters; the respiratory system, the organs for obtaining oxygen and removing CO_2; the nervous system, the organs for receiving and transmitting stimuli, and the reproductive system, the organs for maintaining the race. At the bottom of all of the complicated structures is the single cell, the minute, active, and mysterious unit of living matter. Cells form the tissues; tissues form organs; organs form systems; and the systems working harmoniously together form the normal living organisms.

All types of metazoa start with an analogous egg-to-gastrula stage in development, and differentiation begins from this point, although in many cases differentiation may begin even before this. Naturalists divide the animal kingdom into great groups, termed phyla, according to the degree and nature of the differentiation which follows from this gastrula stage. The simplest of the metazoa are those which depart least from the gastrula type of structure, while from these to the most complex organisms there is every grade of complexity. Just as the egg cell of metazoa is represented by organisms—the protozoa—which never go beyond this single cell condition, or the blastula by colony forms which do not develop beyond this stage, so the gastrula is represented by one group of organisms, termed Coelenterata, which do not develop beyond the gastrula or two layered stage in the development of metazoa.

Forming as they do the lowest branch of the metazoan tree, the coelenterates demand particular attention, because through them we are introduced to many of the essential problems in the general biology of higher animal forms. A good type to begin with is the common fresh water Hydra.

A. Hydra fusca and Hydra viridis

Like the majority of protozoa, Hydra always lives in water, and usually in fresh water although some types live in salt water. They are sedentary forms attached by one end, termed the pedal disc, to water plants or other objects. The body is cylindrical, a double wall of ectoderm and endoderm enclosing one single cavity, the *enteron*, and terminates in a mouth-bearing or oral end. The mouth is surrounded by a crown of tentacles which vary in number, usually from five to eight (some allied forms of Hydra, *e.g.*, Microhydra and Protohydra have no tentacles). The pedal extremity is somewhat dilated, forming a sucking disc for attachment to foreign objects. Thus attached, it sways about with the currents in the water, with its tentacles widely spread for the capture of prey (Fig. 5, p. 14).

Radial Symmetry.—Because of its cylindrical body it is possible to cut Hydra vertically through the mouth in an infinite number of planes, each of which would result in two symmetrical halves. In the majority of other metazoa only one plane, that passing through the mouth vertically, will divide the body symmetrically; such higher animals are *bilaterally symmetrical*, whereas Hydra is said to be *radially symmetrical*. Radial symmetry in animals is supposed to be due to the fact that they have lived as attached organisms, not moving from place to place in search of food. As a result of the attached mode of life radial symmetry is supposed to have developed because of equal pressure on all sides. Another group of organisms, the Echinodermata (star fish, sea-urchins, sand dollars, etc.), have partially acquired through attachment at some time and in some past age, similar radial symmetry, but their phylogenetic history is far more complex than that of the Coelenterata. Both cases, however, are excellent illustrations of the effect of the mode of life upon body forms of animals.

HISTOLOGY

Several different types of cells make up the two layers, ectoderm and endoderm, of Hydra. Excepting the reproductive cells these several types are not bound together into definite aggregates or organs, but are distributed over the entire organism, forming diffuse tissues. Between the two layers is a structureless and non-cellular, gelatinous intermediate layer termed the *mesogloea* or supporting lamella (Fig. 34). The mouth is at the top of a small rounded or conical prominence, called the *hypostome*, and lies in the center of the crown of tentacles. It opens directly into the digestive cavity, thus corresponding to the blastopore which opens into the archenteron of the gastrula. Hydra and the coelenterates in general are often called the diblastic or two-layered animals, as distinguished from the triploblastic or three-layered higher animals made up of ectoderm, endoderm and intermediate layer, the mesoderm.

The different types of cells of Hydra perform their functions for the good of the entire organism, and represent, morphologically, the incipient stages of organ systems in more highly differentiated animals.

A. Ectoderm Cells.—Six types of cells are present in the ectoderm: (1) epithelio-muscle (neuro-muscle) cells; (2) nettle or stinging cells; (3) nerve cells; (4) sensory cells; (5) germ cells; (6) formative or interstitial cells. The bulk of the body covering is made up of the epithelio-muscle cells, while sensory cells are rare and limited to the regions about the mouth and the pedal disc. The nettle or stinging cells are superficially placed on the epithelial cells and partly embedded in them. The nerve and interstitial cells lie between the bases of the epithelial cells and upon the supporting lamella.

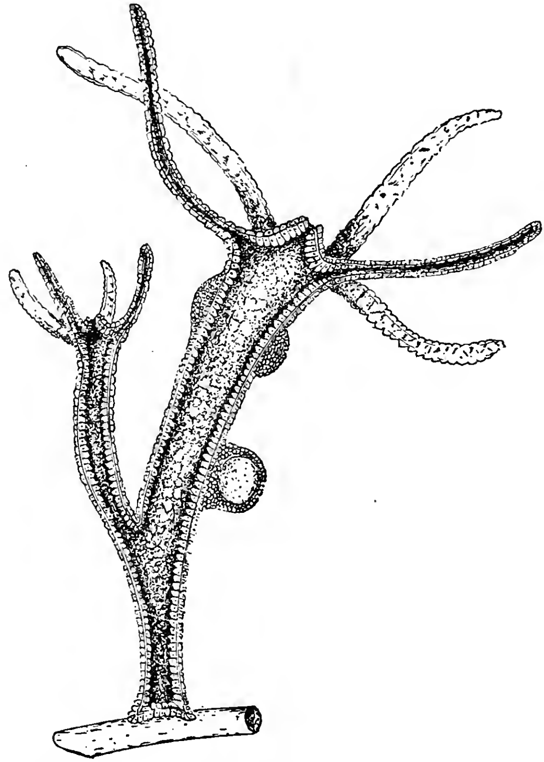


FIG. 34.—*Hydra fusca* as seen in optical section through the enteric cavity; two testes are shown just below the tentacles and an ovary farther down; on the opposite side a well-developed bud. (Modified after Marshall and Hurst.)

1. *The Epithelio-muscle Cells.*—There is no muscular system in Hydra, the covering, or epithelial cells, possessing contractile processes which take the part of muscles in higher animals. These cells are much elongated in the gonad region and on the pedal disc where the cells are loaded with granules of secretion

(Fig. 35). On the tentacles they are much flattened, while in other regions of the body their size is intermediate. The trunk epithelial cells are more or less vacuolated. All forms of these epithelial cells are characterized by the presence of muscular fibers (myofibrils) in the basal parts of the cells. These fibers run up and down the body, thus forming a complete longitudinal muscular investment for the entire animal, giving it, with the transverse muscle processes of the endoderm cells, the power of movement in all directions.

In addition to the contractile power, the epithelio-muscle cells of the pedal disc and of the tentacles have the power of forming

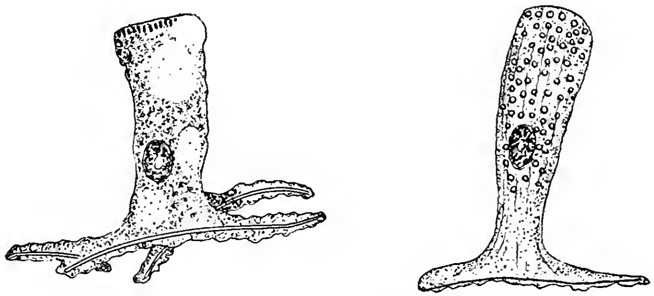


FIG. 35.—Epithelio-muscle cells from *Hydra fusca* showing myofibrils and secretory granules. (From Schneider.)

pseudopodia by means of which Hydra attaches itself to the sub-stratum, alternately by tentacles and pedal disc, and thus moves from place to place.

2. *Nettle or Stinging Cells.*—These peculiar cells are typical of coelenterates and are not found elsewhere, although we have seen analogous structures in the trichocysts of Infusoria. They are absent on the pedal disc but are particularly abundant on the tentacles and on the hypostome, where they are arranged in groups, usually one large one surrounded by a crown of smaller ones. They are called nettle or stinging cells because of the presence of a coiled thread which is thrown out when the cell is irritated. The tip of the thread contains a trace of poison, so that minute animals struck by them are paralyzed and become an easy prey for the tentacles and mouth. These cells, which

are sometimes called *nematoblasts* or cnidoblasts, thus perform functions of offence and defence.

Each stinging cell possesses a sensory hair or "trigger," called a *cnidocil*, at the free end, and a thread-holding capsule, the *nematocyst*, within. The thread is formed from a cell growth which is spirally wound in the capsule, while capsule and its contents are all formed by differentiation of a single nucleated cell of the ectoderm. During growth of the capsule and thread the young nettle cells first lie near the supporting

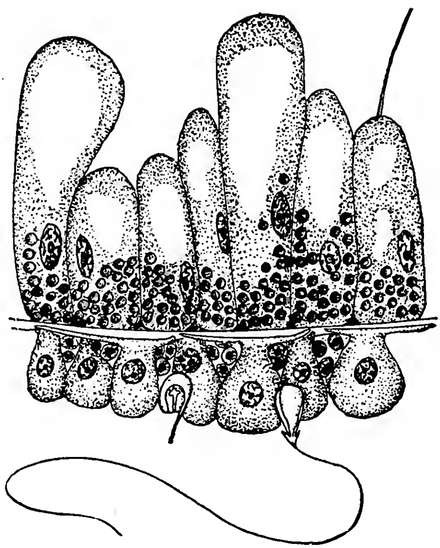


FIG. 36.—Diagrammatic figure of the cells from a small portion of the body wall of *Hydra viridis;* the ectodermal cells with nematocysts below (one with protruded thread), and the large vacuolated endoderm cells above. The symbiotic algæ are grouped near the supporting lamella at the bases of the endoderm cells. (From Marshall and Hurst.)

lamella in the region of the mouth, but they migrate during the period of their formation, and finally come to lie on the surface of the ectoderm around the mouth or on the tentacles and body, the cnidocils ultimately projecting slightly beyond the surface of the body in the surrounding medium (Fig. 36).

3. *Nerve Cells.*—The nerve cells of Hydra and the coelenterates represent the special differentiation of cells for the per-

formance of the single function of irritability. All cells of Hydra, like all protoplasm, are irritable and respond to external stimuli, but the nerve cells are especially adapted in this respect, receiving stimuli from the epithelio-muscle cells, from special sensory cells or from other nerve cells, and transmitting them to other nerve cells and to the plexus of muscle fibers around the organism. While more numerous in the region about the mouth they are not combined into special nerve centers or ganglia, but, like the muscle processes, they form an interlacing network throughout the animal.

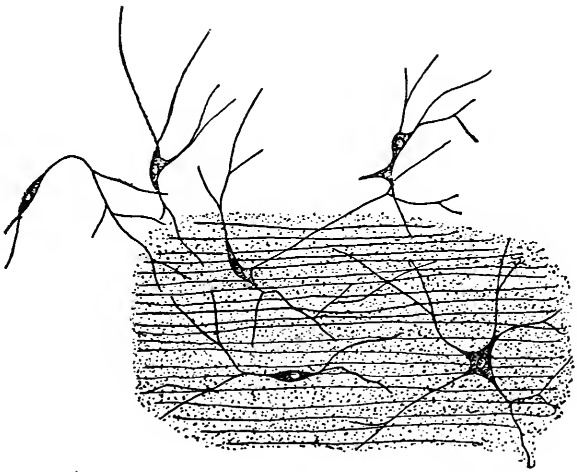


FIG. 37.—Plexus of nerve cells in the ectoderm of *Hydra fusca;* the parallel lines represent the longitudinal muscle fibers on the supporting lamella. (From K. C. Schneider.)

The small cell bodies are either bipolar or multipolar in form, and fine fibers or processes extend from the poles, often for considerable distances, into the surrounding tissues (Fig. 37). These fibers are the means of communication between nerve cells, nerve cells and muscle processes, and nerve cells and nettle cells, and through their coordinating activities the entire organism acts as a unit.

4. *Sensory Cells.*—Special cells for receiving external stimuli are much more common in the endoderm than in the ectoderm, but are found sparingly about the mouth and on the pedal

disc. They are fine thread-like cells crowded in between the epithelial cells, and run out at the basal ends into branching fibers which connect the sensory cells with nerve and muscle cells.

5. *Reproductive Cells.*—Hydra is hermaphrodite, that is, provided with both male (spermatozoa) and female (ova) germ cells. The former are aggregated into gonads called testes, the latter into gonads called ovaries. When immature, the germ cells cannot be distinguished from other formative cells, but when the organism is mature, the germ cells accumulate between the epithelial cells, forming characteristic swellings of the male and female gonads. The male gonads, which are usually multiple, develop as a rule before the latter, and usually in the vicinity of the tentacle bases, while the ovaries usually form near the foot (Fig. 34). A mature testis contains multitudes of spermatozoa which may be seen in active movement within the gonad; but only one egg develops in the ovary.

6. *Formative Cells.*—The formative or interstitial cells, finally, are present as minute rounded cells heaped up between the epithelial cells on the supporting lamella, and are especially numerous on the hypostome. They form the cell reserves of Hydra, replacing nettle cells and nerve cells when exhausted, and give rise by growth and division to the reproductive cells. During regeneration after injury the new epithelio-muscle cells are likewise derived from these reserves. They are, therefore, typical embryonic or generalized cells from which all other elements of Hydra may be replaced.

B. THE ENDODERM.—The endoderm of Hydra, like the ectoderm, is made up of six types of cells: (1) nutritive muscle cells; (2) slime cells; (3) albumen cells; (4) sensory cells; (5) nerve cells; and (6) formative cells. The nerve and formative cells, as in the ectoderm, lie between the bases of the epithelial nutritive cells, and are comparatively rare. The slime and sensory cells are almost exclusively limited to the mouth region.

1. *The Nutritive Muscle Cells.*—These are elongated cylindrical cells somewhat enlarged at the distal rounded ends which may bear flagella (Fig. 36). The cytoplasm is highly vacuo-

lated, and is frequently loaded with food substances taken into the cell through the activity of pseudopodia which may also be formed at the free ends. In *Hydra viridis* the nutritive cells contain living algae (zoochlorellae) which give the green color to the animal. At the basal ends the cells are developed into muscle processes similar to those of the ectodermal cells, but they are usually finer and shorter and run at right angles to the long axis of the body. The contraction of these muscle processes lengthens the animal while contraction of the longitudinal muscle processes shortens it.

2. *Slime Cells.*—These are very numerous in the region of the mouth and gullet where, as short cylindrical cells, they lie between the nutritive muscle cells and usually at some distance from the supporting lamella. They are usually filled with granules which on discharge from the broader distal end form a slimy secretion surrounding the prey taken in as food.

3. *Albumen Cells.*—These are similar to the slime-forming cells but are more widely distributed, and each cell is drawn out at the base in a thin process which rests on the supporting lamella. At the opposite free end they have, like the nutritive cells, two or sometimes three long flagella. The large granules of secretion usually lie in vacuoles.

4. *Sensory Cells.*—These fine thread-like cells are much more numerous here than in the ectoderm. They may bear two flagella, like nutritive cells, or only one flagellum, while occasionally there is none at all. The basal ends of these cells are prolonged into fine branching nerve processes which form, with the nerve fibers, a plexus on the inner layer of transverse muscle processes.

5. *Nerve Cells.*—These agree throughout with the ectodermal nerve cells, and while less numerous are distributed in much the same way, but are apparently absent from the endodermal cell of the tentacles.

6. *The Formative Cells.*—These also are less numerous than in the ectoderm, their chief reparative activity apparently being the new formation of albumen cells, since nettle cells and reproductive cells are absent. In regeneration after injury, how-

ever, they give rise, as in the ectoderm, to the various cells of the inner layer.

C. The Supporting Lamella.—The mesogloea, separating ectoderm and endoderm and broken only at the mouth, is the only supporting structure of the organism. It is derived from both layers by secretion from the cells which abut against it. It is homogeneous throughout, and the muscle processes are slightly embedded in it.

PHYSIOLOGY

In its functional activities Hydra stands midway between the unicellular protozoa and metazoa with well defined organs. In protozoa the protoplasm is differentiated for different functions, the ectoplasm for locomotion and food getting, the endoplasm for digestion and assimilation and for the elaboration of various parts of the cell. Hydra is made up of multitudes of cells, most of which are physiologically unbalanced, that is, some one function predominates over all others. Of these there are eight distinct types, while one additional type—the formative cells—is physiologically balanced. These nine types of cells do not get beyond the tissue stage in differentiation and internal organs or aggregates of like cells, and tissues for performing special vital functions are not developed. Some advance in this direction, however, is seen in the tentacles, the mouth and hypostome, and the gonads.

While the apparatus for performing them is relatively simple the vital activities of Hydra are exactly the same as in other living animals, and may be grouped under the headings: (*a*) nutrition; (*b*) excretion; (*c*) respiration; (*d*) irritability and (*e*) reproduction.

A. Nutrition.—The food of Hydra consists of any minute living thing in the surrounding water but it seems to be particularly fond of small crustacea and embryos of various water-dwelling animals. A passing Cypris touches a tentacle and is stung by the poisoned threads of the nettle cells; this poison, called "hypnotoxin," paralyzes the prey while the threads anchor it to the captor. Other tentacles turn to it, and it is passively drawn to the mouth and swallowed. It enters the large sac-like enteron where digestion takes place. This is accomplished by a combination of methods of higher animals and of protozoa. As in the stomach of a higher animal digestive ferments are poured into the digestive cavity from the gland cells. The slime cells, as shown above, are limited to the oral region, and no gland cells are on the pedal disc. The prey, apparently in accord with this distribution, is kept in the upper region of the enteron and in the vicinity of the mouth. There is some uncertainty as to the nature of the ferment in Hydra but in distant related coelenterates (Actinians) its reactions are similar to those of trypsin. Starch-dissolving ferments are absent, and starch grains fed to Hydra are thrown out unaltered.

The result of ferment activity is the dissolution of the prey into soluble substances and fine particles of solid matter, and it is in connection with the latter that the protozoon method of digestion is involved. The small solid particles are seized by pseudopodia formed by the nutritive muscle cells and drawn into the protoplasm of these cells. Here intra-cellular digestion takes place exactly as in an Amoeba or allied form. Such seizure and intra-cellular digestion is called *phagocytosis* and the cells, because of this function, are known as *phagocytes*. Similar functions are performed by white blood cells (phagocytes) of higher animals, but not in connection with metabolism (see p. 200). Nothing is known about the process of absorption of the digested food; presumably it takes place by absorption from cell to cell since there is no blood system to carry the products of digestion to different parts of the organism.

The undigested food substances like starch, cellulose, chitin, etc., are defecated through the mouth, so this organ acts both as mouth and anus. In this respect many of the protozoa (ciliates) are more specialized than Hydra in having a definite anal opening quite as distinct as the mouth and, in some cases, with special cilia to aid in defecation.

In animals higher in the scale than Hydra the digestive system gradually becomes more and more perfected. In the round worms and annelids it becomes a long tube with mouth at one end and anus at the other. After this the chief advance is in the concentration of different cell types and specialization of the tube into receptacles and digestive glands. The mouth becomes an organ with jaws and teeth for masticating food, and with salivary glands to moisten it; through a gullet the food passes to a single or multiple digestive viscus, the stomach, and thence through a long intestine where the products of digestion are usually absorbed into the blood vascular system. Intra-cellular digestion ceases entirely; the cells instead are differentiated into various kinds of ferment producers whose secretions are poured into the digestive tract and combine to make all kinds of food,—proteins, fats, and carbohydrates, ready for absorption through the walls of the intestine. Gradually the digestive organs acquire a close relation with the excretory organs, so that useless or damaging products of digestion may be removed in the liver from the loaded blood before distribution to the general system. In this way an organ system is slowly evolved from a primitive digestion apparatus like that of Hydra with its protozoa-like peculiarities. Similarly with other organ systems, specialization and continued division of labor result in the complex aggregates of cells, tissues and organs which we know in the higher animal types.

B. Excretion and Respiration.—Practically all cells of Hydra are in contact with the surrounding water, the ectodermal cells directly with the surrounding medium, the endodermal system with water taken in with food. As with protozoa, no special organs are necessary for excretion and respiration but the waste matters of metabolism are given off directly by transfusion from the cells, and oxygen is absorbed by the protoplasm from the water. In respiration this is exactly the manner in which higher animals get their oxygen; the only difference is that the cells of hydra absorb it from the medium water while the cells of higher animals absorb it from the medium blood or the medium air (insects and other tracheates).

C. Irritability—Hydra reacts to external stimuli of all kinds by contraction of the muscle processes of the epithelial cells. Contraction of the ectodermal cells results in shortening of the body or in local movements of the tentacles. The stimuli are received by either the sensory cells or by the ectodermal epithelio-muscle cells, a function which has led to the name neuro-muscle cells sometimes applied to them. The impulse thus received is transmitted to the nerve cells especially endowed with the power of transmission, and a general co-ordinated reaction follows.

The Nervous System.—It is important to note that with the nervous system a delicate function of protoplasm, irritability, is singled out and made the special function of a complicated series of cells and fibers. It is the centralizing and unifying system of the organism, whereby the most widely separated parts of the individual are made to act in harmony for the capture of food or escape from enemies. No such specialization is found in protozoa—apparently there is no need for it since the single cell must act as a whole. In Hydra there is such need, but we find that the nervous system or apparatus for co-ordinating muscular actions is extremely simple, consisting of a nerve-cell plexus enveloping the whole animal. There is no evidence of a centralized nervous system to which impulses due to external stimuli are sent and from which motor impulses to muscle groups are transmitted. This comes first in higher forms, and is accomplished by aggregation of nerve cells into *ganglia* of the central nervous system. One part of this system, the brain, with further advance and specialization, becomes the special center for reception, analysis of external and internal stimuli and for utilization and co-ordination of multifarious impressions and responses, functions which we associate together under the head of consciousness. The term loses its meaning when used to describe reactions of animals in which the co-ordinating center has not reached a certain degree of complexity, but there are undoubtedly different grades or degrees of consciousness, just as there are different grades of complexity in the nervous system.

With Hydra there is no such centralization, but a step in this direction is seen in Hydra and in the higher types of coelenterates, in the accumulation of nerve cells around the mouth which thus becomes the most sensitive or irritable part of the body.

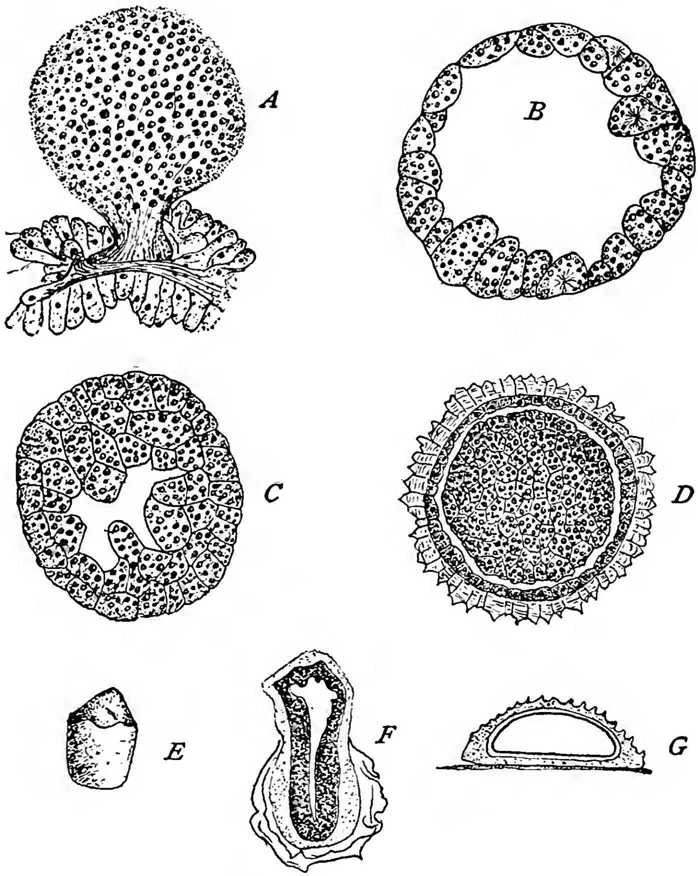


FIG. 38.—The egg of Hydra and its development. *A*, The mature ovum full of yolk granules; *B*, section of blastula formed by segmentation of the ovum; *C*, formation of the inner mass of cells by transverse division and immigration of the outer cells; *D*, solid mass of endoderm and ectoderm cells, and cyst-like outer membrane; *F*, embryo emerging from membrane; *E*, discarded membrane; and *G*, separation of endodermal cells to form the enteric cavity. (From Dendy, after Bourne and Brauer.)

D. REPRODUCTION.—The naturalist Trembley, living in the 18th century, discovered that a Hydra might be cut into many pieces, and that each piece would continue to live and would develop into a complete Hydra. This power of regeneration, or re-growth of the whole animal from a part, is a characteristic of all of the lower animals and is an evidence of their generalized character. Some forms of the lower animals (certain worms for example) actually reproduce by spontaneously breaking into pieces. Hydra does not reproduce in this way but, in addition to sexual reproduction, has a more simple method of propagating its kind, namely, by budding. At certain times, on healthy well-nourished Hydras, swellings appear near the foot. Such a swelling, which involves both layers ectoderm and endoderm, soon takes the form of a young Hydra, mouth and tentacles appearing on the distal end and the trunk growing until it has nearly the length of the parent organism. The bud or young Hydra then separates from the parent by constriction of the foot and starts on an independent career (Fig. 5).

Among the cells of Hydra, distributed here and there in the tissues, are male and female germ cells which collect from time to time in definite regions to form the gonads. Of these the testes or male organs are formed near the base of the tentacles, while the female organ or ovary is formed nearer the pedal disc.

The spermatozoa are developed from the formative or interstitial cells of the ectoderm, and collect in large numbers between the epithelio-muscle cells. They do not change directly into spermatozoa, but each one is a primordial sperm cell which divides two or more times before transforming into spermatozoa. When mature the spermatozoa are liberated by rupture of the outer walls of the testis, and live for a longer or shorter period in the water until they come in contact with egg cells; otherwise, they die.

There is usually only a single ovary, and in the ovary only a single egg. But the female gonad, like the testes, starts with an accumulation of formative cells which divide and produce a number of potential egg cells. Only one develops, however, the others being devoured by the successful egg, which, as an amoeboid cell, puts out pseudopodia and feeds upon the sister cells (Fig. 38, A). The ovum grows to a relatively large size and becomes loaded with yolk bodies; the external cells of the ovary finally break away, leaving the ovum exposed. A spermatozoon bores its way into the egg and fertilizes it.

Development begins while the egg is still attached to the parent Hydra. A hollow ball of cells, or blastula, is formed, consisting of a single layer of cells enclosing the segmentation cavity (Fig. 38, B). Cells then begin to migrate from the periphery into the segmentation cavity which ultimately is filled by the mass of hypoblast cells, thus forming a solid endoderm (Fig. 38, C, D). The outer layer of cells, ectoblast, secretes a horny protective envelope about the embryo, which now leaves the parent and rests without further development for some time on the bottom of the pond. Finally development begins again; the cyst or shell is ruptured, and the embryo escapes. The endoderm cells begin to separate from one another, leaving a hollow in the middle; this is the enteric cavity from which a mouth breaks through, and tentacles develop around it (Fig. 38, F). The gastrula stage, or two-layered pouch with blastopore, is attained with the formation of the mouth, but the method of gastrulation differs from that described on p. 80. The same result is reached, in typical development by invagination, here by inwandering or immigration of ectoblastic cells.

SYMBIOSIS

In addition to Microhydra (a form without tentacles) and *Hydra fusca* (brown Hydra), there is another and an equally common species of fresh water forms—*Hydra viridis*. As the specific name indicates, this Hydra is colored green, the color being due to the presence of minute unicellular plants, *Chlorella vulgaris*. The plant cells are situated in the basal parts of the nutritive muscle cells where they form an almost complete sheath of investing plant organisms, the cells of the ends of the tentacles alone being free from them. Buds, when formed, include the accompanying plants and are quite as green as the parent.

The chief interest, biologically, of these green cells lies in their physiological relations to Hydra. They are not parasites, for parasites are organisms living at the expense of other organisms to which they are detrimental, either structurally or functionally. Hydra is not inconvenienced in any way by the presence of these green cells, but lives, grows, and reproduces normally. On the contrary there is every reason to believe that the foreign cells are beneficial to Hydra, for green plants are essentially constructive in their vital activities and make use of CO_2 for the construction of starch. This CO_2 is a waste product of metabolism of the Hydra cells, and the green cells are of service in freeing them of it; thus *Hydra viridis* will live much longer in an atmosphere of CO_2 than *Hydra fusca* (Hadzi). Furthermore the active green cells give off oxygen which the Hydra cells need. *Hydra viridis* may be freed from its accompanying plant guests by being kept in dilute glycerine, and will continue to live as a white Hydra although it does not have the same vitality, and its growth and reproduction are much slower (Whitney). It is probable, therefore, that the green cells are beneficial in supplementing the normal metabolic processes of Hydra.

Just what advantages the green cells obtain from this peculiar habitat are less obvious. They are protected by the animal and probably receive a constant supply of CO_2. Out of the sunlight, as at night, they require oxygen and give off CO_2 just as animal cells do; the oxygen at such times may be obtained from the surrounding water by diffusion in the same way that the Hydra cells obtain it, while the CO_2 and other waste matters are probably disposed of in the same way as in the case of *Hydra fusca*, by osmosis. On the whole, therefore, there is some gain to both types of organisms by this joint housekeeping, the advantages, which we can only guess at, being proved by their thriving vitality.

This phenomenon of living together is termed *symbiosis* or messmateism, and differs from parasitism in the fact that no structural or functional harm is done to either organism, host and guests living together for mutual benefit.

POLYMORPHISM. COLONY FORMATION AND INDIVIDUAL DIFFERENTIATION

The individual *Hydra fusca* in its relation to other individuals may be compared with an Amoeba or Paramecium where, after division, the daughter individuals separate and live independently. There are many species of Coelenterates, however, more or less closely related to Hydra, in which the individuals, after their formation by budding, remain attached to the parent organism, thus forming colonies similar in origin and mode of growth to many colonies of protozoa. Obelia is such a colony form, the adult being a graceful, much branched aggregate of individuals, resembling a small bush in its appearance and mode of growth, a fact which led Aristotle to name such organisms Zoophyta or animal plants. Obelia begins as a small hydroid (Hydra-like), one-sixty-fourth to one-thirty-second of an inch in height with mouth and tentacles; it reproduces by budding, while stalks or stems are formed by the secretion of a nitrogenous material, chitin. New buds are continually added to the colony, until the latter attains the height of several inches and consists of thousands of individuals with main stems and side branches enclosed within chitin, the entire colony being connected by living substance.

Such hydroid colonies differ from colonies of protozoa in that some individuals may become differentiated for the performance of different functions. This phenomenon, termed *polymorphism,* is represented by Obelia in a relatively simple form. The only differentiation here is the formation of reproductive individuals distinct from the nutritive individuals. When the colony is mature, certain individuals produce buds which differ from the ordinary hydroid buds in structure. These buds, instead of remaining attached as do the hydroids, are detached and swim away as "medusae" or jelly fish. The jelly fish bear the gonads (testes or ovaries), and are the sexually differentiated individuals of the colony. When eggs and spermatozoa are ripe, they are discharged into the water where fertilization takes place, the fertilized egg developing into a young hydroid which begins the formation of a new colony by budding. A hydroid, thus, may be polymorphic; Hydra is not.

Other types of hydroids present different grades in complexity of this phenomenon of polymorphism, some individuals being

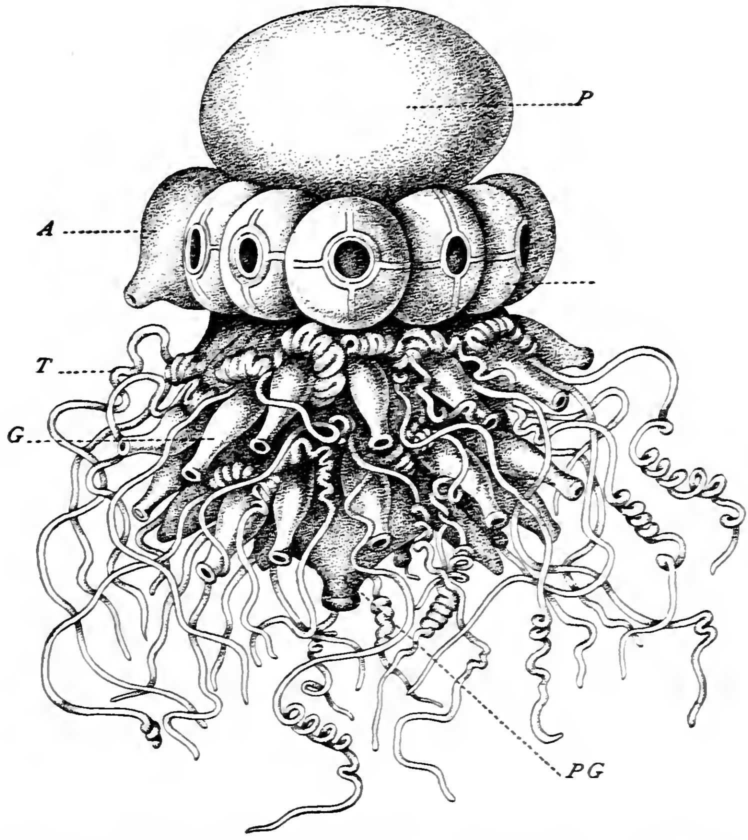


FIG. 39.—*Stephalia corona.* A siphonophore colony illustrating polymorphism. *A*, aurophore, a modified medusa; *G*, secondary gastrozooid or feeding polyp; *T*, tentacle of gastrozooid; *PG*, primary gastrozooid, *N*, nectophore, one of the locomotor individuals of the colony and with the general form of a medusa; *P*, pneumatophore or air sac. (From Lankester after Haeckel.)

differentiated for purposes of locomotion, others for protection and defence, and others for reproduction. The highest development of this coelenterate polymorphism is found in the group of Siphonophora, where no less than seven different kinds of individuals may be present in the same colony, all working for the common good and each dependent on the others for some vital function (Fig. 39). We have in forms like Stephalia and the Portuguese Man-of-War, therefore, a distinct type of individual composed of many individuals, originally of a common type. Such forms have been termed individuals of a second order, and their evolution may have been a parallel of the evolution of metazoa where cells with different functions, working for the good of the whole, were gradually evolved from colonies of protozoa in which the cells are of one type.

One other phenomenon of general biological importance was briefly mentioned above in describing the sexual reproduction of Obelia. The jelly fish or medusa produces eggs which, when fertilized, develop not into medusae but into hydroids which produce other hydroids by asexual reproduction. This phenomenon, termed *alternation of generations* or "metagenesis," is not often met with in animals but it is widely spread in the plant kingdom, an asexual generation giving rise to a sexual generation and this, in turn, to an asexual in regular alternation.

B. Summary of Points of General Biological Interest Shown by Hydra

Hydra and its allies are important to the student of biology because of their intermediate position between organisms composed of one cell and organisms composed of organs. One essential characteristic of the metazoa is represented by them in the differentiation of cells for the performance of the different vital functions. Nerve and sensory cells, muscular and supporting cells, nematoblasts and digestive cells are physiologically unbalanced, in that they exhibit some one function which predominates over all of the others. In Hydra, at least, these differentiated cells are not bound together into specialized and centralized organs which perform certain functions for the entire individual, but are more or less uniformly distributed over the body. Thus the nervous system is diffuse, that is, it consists of external nerve and sensory cells with their long fibers or cell processes which inter-cross with one another and with muscle cells. In higher animals, similar nerve cells come together in groups to form ganglia, and these ganglia are aggregated into more or less complicated central nervous and peripheral sensory systems.

Similarly with the muscle cells of Hydra; they are not bound together in complicated muscle bundles, but, like nerve cells, are distributed over the entire organism, and are connected only in a primitive way with the nerve fibers by which they are stimulated to contract. Histologically, therefore, Hydra differs from higher animals and perhaps indicates the generalized type of structures from which higher animals have been derived.

While Hydra itself does not show the concentration of cells into definite specialized organs, we do find types of coelenterates, especially the siphonophores, where specialized organs are developed, but in quite a different way from organ formation in higher animals. Polymorphism, a second feature of general interest, is a form of organ development in which individuals themselves are modified as organs for the performance of some one chief function. Medusae are reproductive in function, and are special organs for sex-cell formation and distribution, produced on blastostyles or reproducing individuals. Dactylozooids are individuals specialized for purposes of offence and defence. Gastrozoids are feeding individuals, and Nectophores or swimming bells are individuals specialized for locomotion. Each specialized individual performs its particular function for the good of the whole colony, and their colony organization has led to the descriptive phrase, "individuals of a second order."

A third feature of general biological interest is an outcome of these individualized organs. The medusa becomes free-living as an individual of the sexual generation; it forms eggs or spermatozoa (the sexes are separate), and the fertilized eggs develop into Hydra-like asexual individuals, called *hydroids*, which reproduce by budding. This phenomenon is called metagenesis or alternation of generations, since one (sexual) generation (medusa) alternates with another (asexual) generation (hydroid).

Other features of general interest mentioned under different headings above may be summarized as (4) the bilamellate or diblastic structure of Hydra representing a permanent gastrula; (5) symbiosis or living together of two different types of organisms for mutual benefit; and (6) the combination of extra-cellular and intracellular digestion, thus combining the digestive processes of higher metazoa with those of the protozoa.

CHAPTER V

PLANTS, THE FOOD OF ANIMALS AND THE SOURCES OF ANIMAL ENERGY

Helmholz, when he outlined the great theory of the conservation of energy, is said to have been widely criticized for his "play of fancy" in believing that all living things get their energy from the sun, transforming it into vital activity. Today this "fancy," refined through thousands of experiments on the physiology of animals and plants, is an accepted fact. It is known that not all living things can use the solar energy directly, plants alone having this power, while animals obtain it indirectly through the vegetable world. The importance, therefore, of the plant organism in general biology cannot be overestimated. In the present chapter we will trace back this energy through the food of animals to its ultimate source.

A. The Food of Animals

Hydra, as we have seen, like Paramecium or Amoeba, takes in solid food in the living state, digests and assimilates it. The protoplasmic molecules throughout select from the dissolved proteins the elements needed for their reconstruction. This food, rich in potential energy, consists mainly of minute crustacea, rotifers, protozoa, unicellular plants and bacteria. The potential energy carried over by these organisms must in turn be traced back to *their* food. The crustacea, rotifers, protozoa, etc., are animals, and live upon solid living materials as Hydra does, but being minute, their food must be correspondingly small. Could Hydra be cut up in small enough pieces, minute Crustacea, rotifers and protozoa might equally well get their nourishment from its protein, a type of retaliation with which Huxley has made us familiar in the possible mutual gastric relations of man and lobsters.

We have seen that Paramecium and perhaps the majority of protozoa live on bacteria, extracting from these minute cells the elements necessary for their protoplasmic reconstruction and growth. Rotifers and crustacea feed upon the larvae of animals, on smaller crustacea and rotifers, and upon unicellular animals and plants such as protozoa, diatoms, desmids and other algae. These crustacea, rotifers and larvae live on unicellular animals and plants. The food of Hydra, therefore, traced back upon any line, finally brings us to the minute chlorophyll-bearing plants and bacteria. These ultimate food materials of Hydra, therefore, are living things some of which have the power to manufacture their nutriment from simple elements with the aid of the sun, while the others live upon dissolved protein matters from decomposing animal and plant tissues, or else utilize waste matters like urea and relatively simple chemical compounds for their sources of energy.

The higher animals, like Hydra, must likewise turn to the plant world for food, but to trace back the connection in some cases would involve a far more complicated chain of organisms than in the case of the simple coelenterate. Man is almost omnivorous, taking his food directly from the vegetable kingdom in his green vegetables, cereals, etc., and from the animal in his beef, mutton, fish, or fowl. Cattle, sheep and birds, in turn, are herbivorous or graminivorous and get their main nourishment from plants. Birds, indeed, eat worms and insects to a great extent but worms and insects feed upon leaves and other vegetable matter, so this food is only one step removed from green matter. Man eats fish, oysters and other marine food; the larger fish eat smaller ones, these still smaller and so on until the smallest eat crustacea, larvae, protozoa and other micro-organisms which, like rotifers, subsist finally on microscopic algae and bacteria. Carnivorous animals live almost entirely without green plants or their products, and with them the ultimate plant-eating forms serving as food are still more remote; in the end, however, we find the same dependence upon the vegetable world for proteins and potential energy.

The work of Hydra and higher animals is done at the expense of energy which is transformed from the stored-up energy in proteins and other foods, which in turn is derived from the energy of foods obtained from other animals or plants, where in turn it is obtained from other foods, until finally this energy is traced back to the green plants. Green plants, in turn, get their energy from the sun. A necessary step, therefore, in the biology of animals is to trace out as far as possible the transformation of solar energy into that of protoplasm. The initial steps in the process are connected with the structures and functions of plants, and enough of these will be described to pave the way for a clear understanding of the work which the plants do in nature.

The lines of development of the two great kingdoms are widely different. While at bottom the vital activities of plants and animals are the same, the structural differentiations have followed lines of entirely different requirements. The activities of animals have been directed toward food getting and food digestion and protection against enemies who would make food of them, functions involving highly developed muscular systems, closely correlated nervous responses and centralized nervous systems, and complicated organs for the digestion of many different kinds of food. Their metabolism, therefore, involves active destructive processes and the formation of excessive waste matters, for the disposal of which complicated excretory organs have been evolved. Higher plants, on the other hand, are stationary; their food material being everywhere about them, locomotor organs are not developed and their nervous response is limited to protoplasmic irritability; waste matters are relatively unimportant and easily disposed of, requiring no complicated excretory organs. Their plan of development, like that of animals, has been essentially in the service of nutrition. Great trunks and branches have been evolved, apparently in response to the need of presenting maximum chlorophyll-bearing leafy surfaces to the air and light, while great subterranean roots absorb water and salts from the earth. Strong frameworks of lifeless wood, giving resistance to winds and weather, have been evolved for the support of the heavy aerial structures, while complicated canal systems for the transportation of salts and foods in solution penetrate the entire plant organism from the tiniest rootlet to the tips of the highest leaves. The reproductive organs, finally, are equally well developed in plants and animals, the maintenance of species being a universal biological need.

Plants, like animals, are divided into two great groups, protophyta and metaphyta, although these designations are not often used in classification. The metaphyta bear the same relation to the protophyta that the metazoa bear to the protozoa, viz., many-celled as contrasted with single-celled organisms. For our purposes a glance at each type will suffice to give a clear understanding of the essential relationships of animals and plants, and show that, except for the functions of nutrition, the fundamental biological principles in animals and plants are the same.

B. Pleurococcus pluviatilis and Sphaerella lacustris

These two organisms are good types of the unicellular plants, the former existing as quiescent non-motile cells, the latter having two phases, one motile, the other not. As unicellular forms they are allied to a large number of low types of plants included in the group known as *Algae*, in which some forms are included which cannot be accurately determined as plants or as animals. Some of these, like the Peridiniales or Dinoflagellata and the Volvocidae, are included by botanists as plants, by zoologists as animals.

Pleurococcus is widely distributed in damp places, where it exists as a green covering to stones, tree trunks, ground, etc. Each cell is composed of protoplasm differentiated into cytoplasm and nucleus, and contains minute grains of starch. Green coloring matter, chlorophyll, is uniformly distributed throughout the cell, which, finally, is covered by a transparent coating of cellulose, a characteristic plant product similar in chemical composition to starch but with a different arrangement of molecules. Reproduction occurs by simple division, the daughter cells separating when formed, or remaining to-

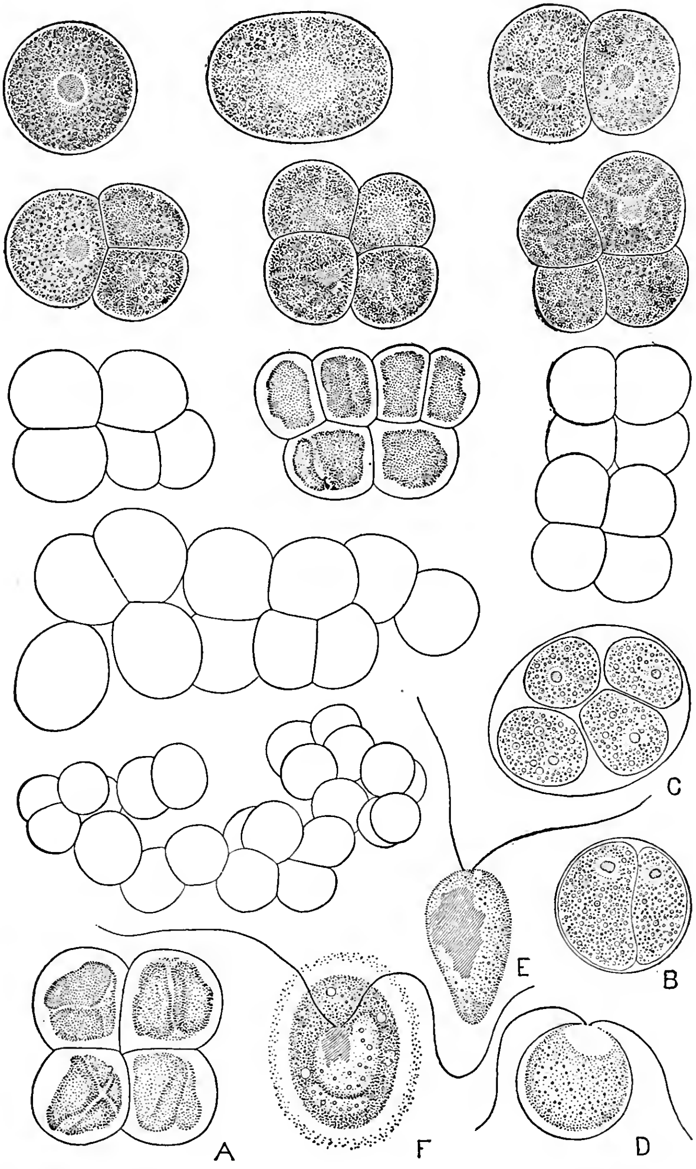


FIG. 40.—Pleurococcus, from the bark of an elm tree in active vegetation. *A*, Dried cells; *B*, division within a cyst; *C*, cyst contents divided into four cells; *D*, motile form of Protococcus (?). (From Sedgwick and Wilson.)

gether in groups of two, three or more cells, sometimes eight or nine forming a loosely arranged colony. The union is only

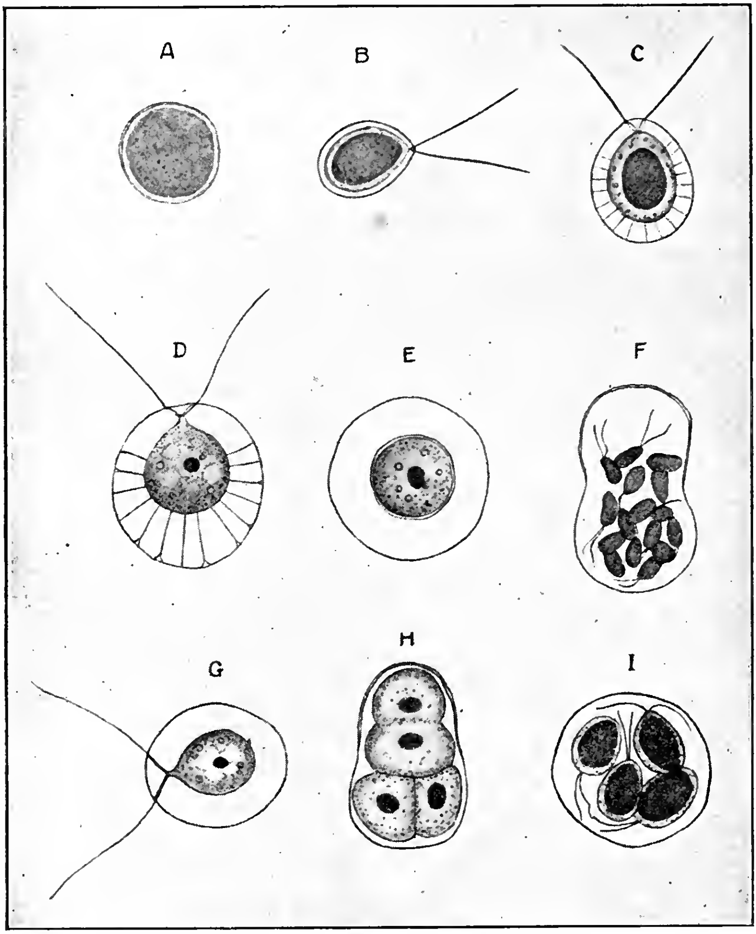


FIG. 41.—*Sphaerella lacustris.* Various stages in vegetative life and spore formation. *A*, a typical red-colored, resting cell; *B*, a red individual with two flagella and a yellow-green border of chlorophyll; *C*, an older individual with more chlorophyll and a widely-distended cell-wall; *D*, a mature green individual with red eye-spot; *E*, individual that has lost its flagella and developed a thick cell-wall; *F*, 16 microzooids formed in the mother-cell; *G*, mature megazooid; *H*, *I*, megazooid formation. (From Hazen.)

temporary, however, for ultimately the cells separate and live as independent units (Fig. 40).

Sphaerella lacustris in its quiescent phase is similar to Pleurococcus, save for the presence of what are termed *chloroplastids*, products of the cell, which are specialized for the purpose of manufacturing chlorophyll, now confined to these bodies. At times the green color is replaced by a distinct red haematochrome, which is only a masked form of chlorophyll and is known to be a condition brought about by lack of nitrogen. The flagellated phase of Sphaerella is quite different in appearance from the resting form. The chief structural difference is the presence of two definite flagella, originating from basal granules in the cell protoplasm and extending through the coating of cellulose to the outside, where their undulations in the water lead to energetic and jerky movements of the entire organism. A red so-called "eye-spot" is also present, and represents a more sensitive bit of protoplasm, especially in respect to light (Fig. 41).

Like Pleurococcus, Sphaerella reproduces by simple division, but the cells do not form colonies or remain connected after division. At times, furthermore, the protoplasm of the cell, protected by the firm cell membrane, divides repeatedly until from thirty-two to sixty-four minute cells are formed. These ultimately break out of the cyst and swim about by means of two flagella. Two of these small products, upon meeting, fuse, lose their flagella, and settle down as a resting cell. This process of conjugation is a primitive type of sexual reproduction, and the minute cells may be called gametes.

The chief interest of Pleurococcus and Sphaerella lies in their physiological activites. Surrounded by a membrane of cellulose and an even more resistant cell membrane, solid matters cannot enter the cell. Salts, however, dissolved in water can be absorbed by osmosis through the body wall, and gases can diffuse through the cellulose. In this way the plant cells take in CO_2, water, salts of various kinds, and give out CO_2, free oxygen, and waste matters, none of which has much chemical energy. The carbon dioxide and water are broken down into their constituent parts through the energy of sunlight acting through the chlorophyll, and the elements thus freed are ultimately recombined into sugars and starch, from which, by a series of changes which can best be described, in connection with a higher type of plant, they are finally made into protoplasm; this, when life is extinct, becomes protein, the main food of animals.

The plant forms serving as food for the higher animals are far more complicated than Pleurococcus and Sphaerella, and just as the higher animals become progressively differentiated with complicated organs for the performance of the functions of food getting, digestion, assimilation, excretion, nervous response and reproduction, so do the higher plants become progressively differentiated with complicated organs for the performance of their metabolic and reproductive functions.

To trace the food of animals, therefore, it is necessary to examine the structure and functions of the higher plants, a good example of which is the common fern or brake, *Pteridium aquilinum*, formerly called *Pteris aquilina.*

C. Pteridium aquilinum

The common brake or fern, *Pteridium aquilinum*, is widely distributed upon the earth's surface, growing in damp or shady places and resisting various kinds of unfavorable conditions of the environment. At one time in the earth's history—the age of Pteridophytes—ferns formed the chief type of vegetation, and some of them grew to an enormous size (up to sixty feet), while even today some ferns are tree-like in size and mode of growth (tree-ferns). Others, like the maiden hair, are extremely delicate, growing only in the most favorable localities.

For purposes of description, Pteridium may be regarded as composed of two distinct parts; the one, aerial or above ground, is termed the *frond* or leaf and consists of the chlorophyll-bearing parts and their supporting and nutritive organs; the other, underground, is termed the *rhizome* and consists of a stem

FIG. 42.—*Pteridium aquilinum.* The underground stem or rhizome (*rh.*), one frond (l^1) of the present year in full leaf, the other (l^2) of the past year; *ab*, apical bud bearing apical cell at the extremity of a branch bearing stumps of leaves of previous seasons; l^1, mature active leaf; l^2, dead leaf of the preceding year; *l.m.*, lamina of leaf; *p*, pinna; *x*, younger pinna shown enlarged at *B*. (After Sedgwick and Wilson.)

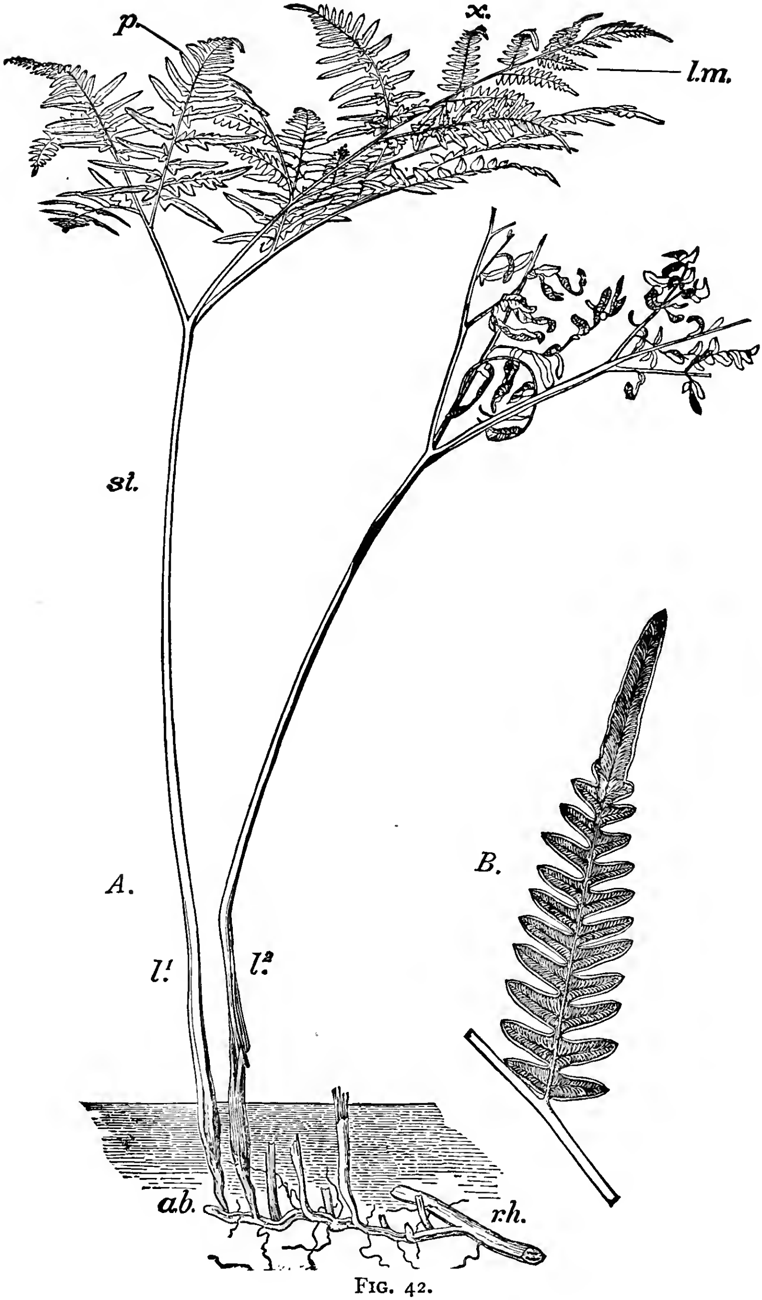


FIG. 42.

with roots and rhizoids stretching out in all directions for the absorption of water and salts. The fronds grow up at intervals from the underground stem, a single, vigorous rhizome often bearing several fronds (Fig. 42).

The Rhizome.—The main stem of the underground part may be a simple root-like structure of practically uniform size and several feet in length, or it may be branched, with numerous lateral rhizomes penetrating the earth in different directions. The main rhizome and its branches lie a few inches below the surface and always parallel with that surface, while roots grow out from it into the earth below. In addition to the roots there

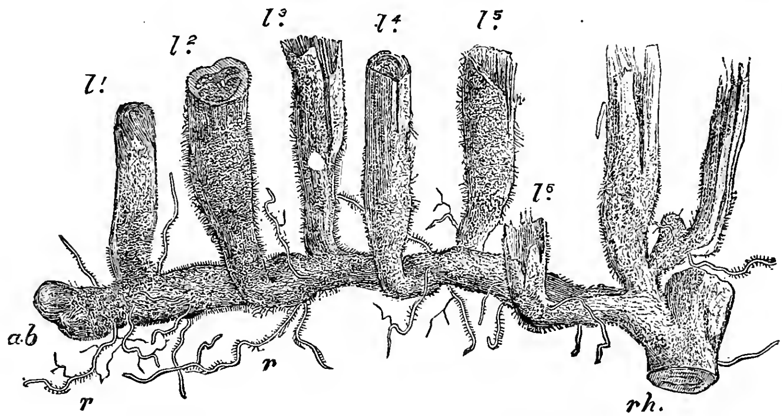


FIG. 43.—Branch of a rhizome of Pteris showing the apical bud (*a.b.*) stumps of numerous leaves (l^1, l^2, etc.), and a part of the main rhizome (*rh.*); *r*, roots. (From Sedgwick and Wilson.)

are numerous filamentous outgrowths, termed hairs or rhizoids, which differ in finer structure from the roots. One end of the rhizome consists of soft white tissue quite different in appearance from the black surface. These are the growing points of the rhizome and branches, all growth of the underground trunk or stem being in a linear direction, and new cells are added by growth of the terminal cell, termed the *apical cell* (Fig. 43).

HISTOLOGY

A cross section of a rhizome (Fig. 44) shows that it is not quite circular in outline, the transverse axis being somewhat longer than the vertical; the two sides, furthermore, show somewhat flattened ledge-like surfaces which are turned upward, a differentiation offering more resistance to up-rooting than would be the case if the sides were smoothly rounded. The cross section also shows various cellular differentiations. On the outside is a layer of cells termed the cortex, consisting of an outer black and lifeless layer to which the name *epidermis* is given, while below this is a layer of hardened, almost wood-like,

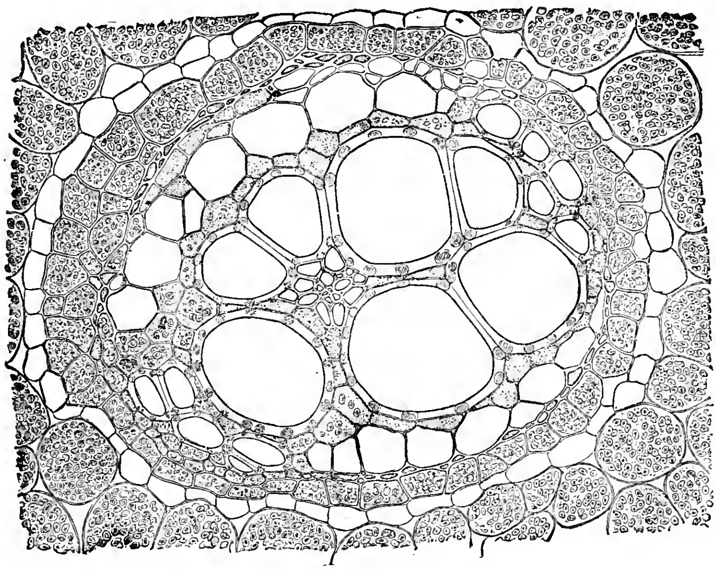


FIG. 44.—Transverse section of a vascular bundle surrounded by fundamental tissue. The conducting system of the plant. (From Sedgwick and Wilson.)

cells forming the bulk of the cortex. These cortex cells are hardened by the lignification of the protoplasmic structures, this *lignin* forming the chief element in the composition of the still more hardened wood tissues within the rhizome. Within the cortex is a mass of living *parenchyma* cells with soft and undifferentiated protoplasm, well supplied with starch, and forming the bulk of the mass of the rhizome. Scattered among these parenchyma cells are two large masses and other smaller patches of dark brown material formed by the lignification of the fundamental cells, all firmly attached, and forming a tough and resisting framework or skeleton, giving strength and rigidity to the whole. These woody masses are together called the *stereome*. Finally there are smaller and more or less circular patches of cells with thick cellulose walls, which form the most important organs of the rhizome, the aggregates being termed *vascular bundles*.

If we examine a vertical or horizontal section of the rhizome (Fig. 45) we find that these internal masses of stereome and the vascular bundles are composed of elongate woody and cellular structures, firmly attached end to end so that continuous sup-

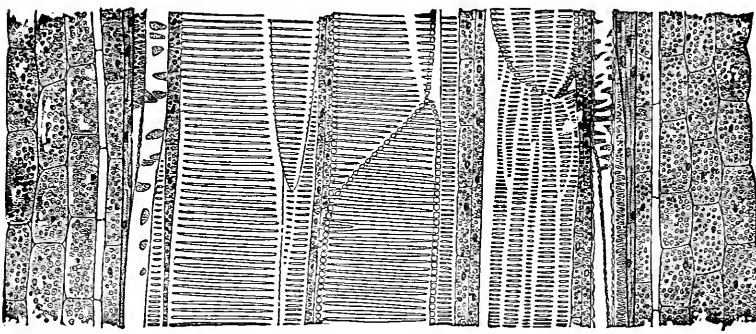


FIG. 45.—Longitudinal section of a vascular bundle showing the conducting system of the plant in lengthwise section. (From Sedgwick and Wilson.)

porting structures and tubes traverse the rhizome from end to end, the former serving as an internal skeleton, the latter as conducting and feeding organs.

In the immediate vicinity of the growing tip of the rhizome the cells, with the exception of the apical cell, are practically all alike and of the fundamental parenchyma type forming the primary *meristems*, but they become differentiated at a short distance from the apical cell to form cells of varying structure and function, some becoming vascular cells, while others are transformed into lifeless stereome.

These various groups of cells, tubes, supporting structures, etc., are not only continuous throughout the main trunk of the rhizome but are also continuous, through branches, in every root and every leaf stalk, the root hairs alone being free from them. The canal system leading into the stalks of the fronds are the most important, forming, as they do, the only means

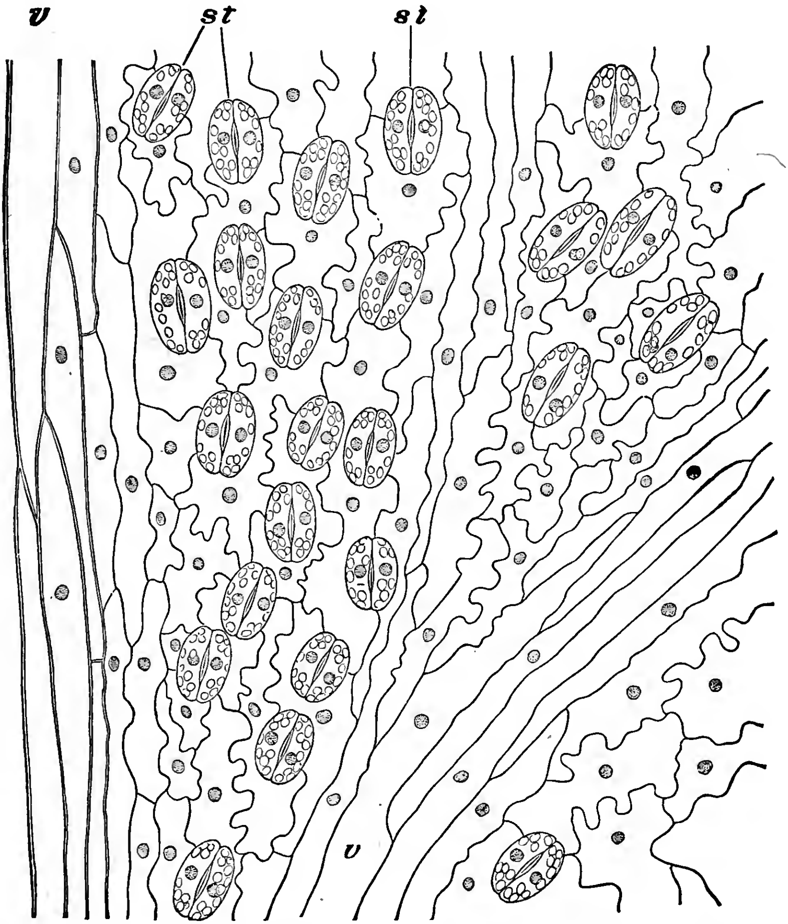


FIG. 46.—Epidermis from the under side of a leaf, showing the wavy outlines of the epidermal cells, the veins (*v*) covered by thickened epidermal cells, and guard cells (*s.t.*) enclosing the stomata. (From Sedgwick and Wilson.)

of communication between the aerial frond and the underground parts of the fern.

The Leaf or Frond.—The aerial part of Pteridium consists of a main branch or stem arising as an outgrowth from the rhizome.

Its branches, termed *pinnae,* in turn give rise to the flattened chlorophyll-bearing structures analogous to leaves of higher plants, but here termed *pinnules.* (In the comparative morphology of plants analogous parts do not always bear the same names, thus the leaf of the fern is the entire aerial part of the plant while the rhizome corresponds to the trunk of a tree. The trunk is underground, the leaves alone being exposed.)

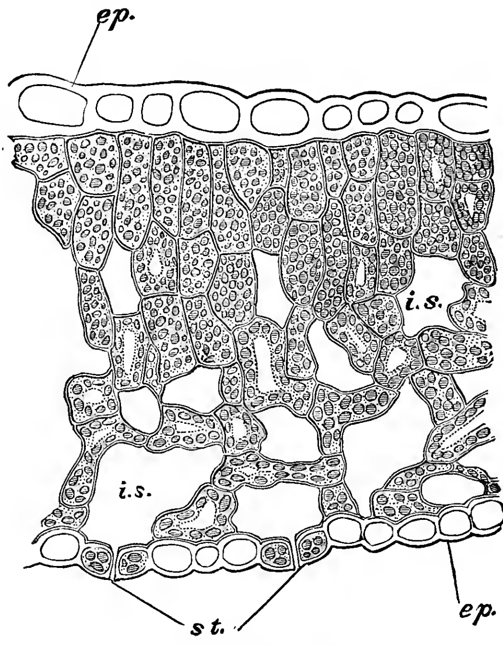


FIG. 47.—Cross section of a portion of a leaf showing the epidermis (*ep.*), the palisade mesophyll (above) and the spongy mesophyll (below). Sections through the guard cells and stomata (*st.*) show the openings into the inter-cellular spaces (*i.s.*). (From Sedgwick and Wilson.)

The stalk of the frond is somewhat thickened at the point where it enters the ground, thus giving greater resistance to wind, etc. It is generally supposed that the frond is only a much thinned or flattened outgrowth of the stipe or stem. It is composed of the same series of cells as those found in the rhizome, but some of them have undergone modifications. The epidermis cells of the rhizome are lifeless, but here they are living and elaborated into flattened epidermal cells with curious wavy outlines, which form the outer covering for both the upper and the under sides of the leaf. The epidermis cells are colorless for the most part, but here and there among them bright green chlorophyll-bearing cells may be seen in pairs (Fig. 46, s.t.). These cells are bean-shaped and surround a minute pore termed the *stoma*, which connects the inner air spaces of the leaf and the surrounding atmosphere. They further have the function of swelling or of decreasing in size with the humidity of the air, and thus regulate the openings of the stomata; for this reason, the term *guard cells* is usually given them. On the upper surface of the leaf the epidermal cells are continuous, and guard cells are absent but they are widely distributed on the lower surface.

The fundamental parenchyma of the rhizome is continued into the leaf, but a new function is there undertaken by the generalized cells. They become large cuboidal cells, closely packed together on the upper side forming a *palisade mesophyll* layer, while on the under side they are loosely arranged with relatively great gaps or chambers, forming the *spongy mesophyll*. The chambers are in communication with the outer air by means of the stomata. The term mesophyll, or sometimes chlorenchyma, is applied to these cells because of the universal presence of chloroplastids colored green by chlorophyll (Fig. 47).

The vascular bundles break up in the leaves into a series of fine tubes which are differentiated for collecting food substances, and for conducting fluids, while the stereome is reduced to a minimum.

Throughout the protoplasm of the mesophyll cells are products of cellular activity in the form of minute spherical or tabloid granules, termed *chloroplastids*. They are only a modified form of protoplasm and have the power to reproduce themselves by division; hence they are living elements of plant protoplasm and are often colorless, especially in the dark. In the light these chloroplastids have the power of forming an oily fluid substance of green color, the *chlorophyll*, which disappears after some time in the dark, but can be reformed in the light. Its chemical composition is very complex and is of the nature of protein, its formula, as given by Willstätter, being something like $(MgN_4C_{32}H_{30}O)(COOCH_3)(COOC_{20}H_{39})$. If white light be passed through a prism it is broken up into the colors of the spectrum; if passed through a chlorophyll solution it shows absorption bands in the red, yellow, green, blue and violet, thus indicating the absorption by the chlorophyll of the sun's rays richest in actinic energy. This energy is utilized by the plant in reducing CO_2 and H_2O, a first step in the manufacture of the plant's food. Chlorophyll, finally, is easily split up into *cyanophyll* with a blue-green color, and *xanthophyll* with a yellow color, while, in the presence of acid, the Mg is replaced by hydrogen, giving a magnesium-free yellow derivative, termed *phaeophytin*.

GENERAL PHYSIOLOGY

Food materials for the fern include a large variety of simple elementary compounds found everywhere in the soil and air. From the soil, salts of different kinds are absorbed by the roots, and pass by means of the vascular bundles to all parts of the plant; water, holding salts in solution, is also taken in by these organs, and passes by osmosis and root pressure, aided by evaporation in the leaves, to the highest parts of the aerial plant. From the air, carbon dioxide and oxygen are taken in, and by aid of the energy taken from sunlight, the carbon is dragged away from the oxygen, and the hydrogen likewise from oxygen, leaving these elements ready to recombine preparatory to the formation of sugars and starch. For this process it was formerly supposed that a number of molecules of carbon were united with twice as many molecules of water, but now it is considered more probable that the base of the operation is the hydroxyl OH. The reaction is usually expressed in the following manner, although the equation does not represent all of the actions taking place: $n5H_2O + n6CO_2 = nC_6H_{10}O_5$ or starch $+ n6O_2$. It is more probable that the reaction is brought about through the formation of intermediate products, thus: $CO_2 + H_2O = CH_2O + O_2$. Or possibly, $CO_2 + 3H_2O = CH_2O + 2H_2O_2$, the latter, hydrogen peroxide, breaking down into H_2O and O_2. CH_2O is a poison, formaldehyde, and must be condensed immediately upon its formation, presumably changing into a simple hexose sugar by addition and rearrangement of its molecules, thus $n6CH_2O = nC_6H_{12}O_6$ or glucose from which starch is formed by the loss of water, thus $nC_6H_{12}O_6 - nH_2O = nC_6H_{10}O_5$ or starch. This starch is stored temporarily in the leaves, or it is gathered up as glucose, which is soluble, by the collecting tubes and carried through the vascular bundles to the rhizome where, in the parenchyma cells, it is permanently stored as starch to be used as needed by the plant. At night, in this way the starch is removed from the leaves, but with the advent of daylight the manufacturing process begins again. This process of starch manufacture by *photosynthesis* is the essential difference between animals and plants, and the plant has this power by virtue of chlorophyll.

Recent investigations in the chemistry of chlorophyll indicate that the reactions taking place in the formation of hexose sugars are far more complex than those outlined in the preceding paragraph. Thus pure, extracted chlorophyll, used as a sol with water as the dispersion medium, in a closed vessel containing only *carbon dioxide*, and exposed to light, will not produce formaldehyde. The carbon dioxide and water form carbonic acid, and this causes the displacement of the chlorophyll magnesium, thus producing yellow phaeophytin (Willstätter). On the other hand, similarly prepared chlorophyll in a closed vessel containing *oxygen* and exposed to the light, will lose its color entirely, while formaldehyde is formed in variable quantities depending on the length of time of exposure, while the acidity of the system continually increases. This production of formaldehyde may be interpreted as due to oxidation and destruction of the chlorophyll molecule through splitting off and reduction of the alcohol ester (phytol) contained in that molecule, while the increasing acidity may be due to the further oxidation of the formaldehyde to formic acid (Jörgensen and Kidd).

If formaldehyde production in the living plant is a necessary step in the formation of plant sugars, and if it is formed in the manner outlined by Jörgensen and Kidd, then the process of sugar formation is not a direct result of constructive metabolism, but rather a direct effect of destructive metabolism through oxidation. In the test tube the chlorophyll is destroyed by this chemical change, but chlorophyll in the test tube is quite another matter from chlorophyll in the living leaf where, if such reactions are necessary in the formation of sugar, they are balanced by the synthesizing activity of the chromogen complex ($MgN_4C_{32}H_{30}O$) in the presence of CO_2 and H_2O and with the energy of sunlight. The chromogen complex would thus play the part of a synthesizing enzyme activated in both constructive and destructive phases by the energy of light. Present knowledge, however, is very incomplete in regard to photochemistry of the chloroplast, and such deductions, while alluring, must be regarded as purely hypothetical, although no more hypothetical than the long-accepted view of the direct union of CO_2 and H_2O in the formation of hexose sugars by photosynthesis.

From this point on in nutrition, animals and plants alike have the power to manufacture proteins. In the plant, the process can be followed more easily than in animals; some of the simpler compounds like asparagin consist of nitrogen added to the carbohydrate ($C_4H_8N_2O_4$), and from this relatively simple amide, protein may be formed by the addition of the essential elements. The formation of these substances is obscure, the action, presumably, being brought about through the agency of synthesizing enzymes. In animals, the protein materials taken as food provide the necessary elements for this synthesis, but in plants the proteins must be built up step by step. Plants thus are essentially constructive while animals are destructive.

In the manufacture of starch more oxygen is liberated from combination than can be used, and this diffuses through the leaves and into the air, while carbon dioxide is taken in. Plants and animals, therefore, would seem to be well adapted for mutual existence side by side. But the plant does more or less work and utilizes its substance in providing the energy necessary for this work, while waste matters, in the form of CO_2 and water and nitrogenous substances, are formed. As in animals, the CO_2 is given off into the air while oxygen is taken into the plant from the air, but this fundamental process of respiration is masked by the more active processes going on under the action of chlorophyll, so that, in sunlight, the oxygen needed is provided by the residue of oxygen after starch is formed, the remainder being given off, while the waste matter CO_2 is reduced and ultimately manufactured into starch. The essentials of respiration, therefore, go on all the time, but CO_2 is actu-

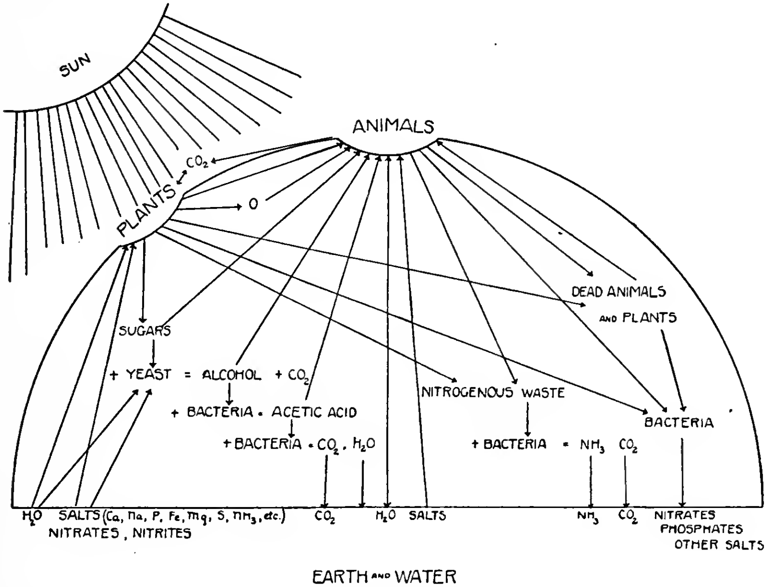


FIG. 48.—Diagram illustrating the cycle of living matter and energy in animals, plants, yeast and bacteria.

ally given off by the plant only in the absence of sunlight. The oxygen given off cannot be considered a waste matter or product, since it has not been a part of the plant organism but is only a by-product of chlorophyll activity. Nitrogenous waste may be disposed of, when present in small quantities, by being stored in the leaves, and finally cast off by the annual shedding of leaves and their contents.

Cycle of Matter and Energy.—The autotrophic nutrition of the fern, and of plants generally, is the starting point for the wonderful cycle of matter and energy in nature whereby living things are all interrelated and balanced. Plants manufacture proteins which are built up into animal protoplasm. Plants also produce glucose which, acted upon by yeast, is transformed into alcohol and CO_2. The alcohol is acted upon by bacteria and changed to acetic acid and water, other bacteria act upon this acetic acid and change it to CO_2 and water. Plants and animals die, their protoplasm, as protein, is acted upon by bacteria and broken down into free ammonia, nitrites, nitrates, sulphates, phosphates and other salts, all of which are returned to the earth to be taken up by the roots of plants and built again into plant protoplasm. Animals, and to a less extent, plants, produce nitrogenous waste as a product of metabolism. This is acted upon by bacteria and turned into NH_3 and CO_2 and water. In this way there is a continual cycle of simple salts and gases converted into starches, sugars, plant and animal protein with high potential energy which is ultimately transformed into energy of heat, light, electricity and movement, giving the infinite variety of vital manifestations. This protein, through oxidizing agents and nitrifying agents, is finally brought again to the state of elementary compounds. All may be shown in a simple diagram (Fig. 48).

REPRODUCTION OF THE FERN

The rhizome of the fern may give rise now and then to branch rhizomes which start up independent plant growths, and thus bring about a form of reproduction somewhat analogous to budding in Hydra. This, however, is only an exceptional method of reproduction and does not amount to much in the distribution of the fern. The chief methods of reproduction do not involve the rhizome at all, but take place as a result of activity of the frond cells. As in hydroids, reproduction here involves an alternation of generations, sexual and asexual generations following each other in regular succession.

The Asexual Generation (*Sporophyte*).—The ordinary fern plant is the asexual generation, *i.e.*, it does not form the sex cells but, like the hydroid, it gives rise without fertilization to an organism different from itself. These dissimilar organisms are formed from spores which develop on the under surfaces of the

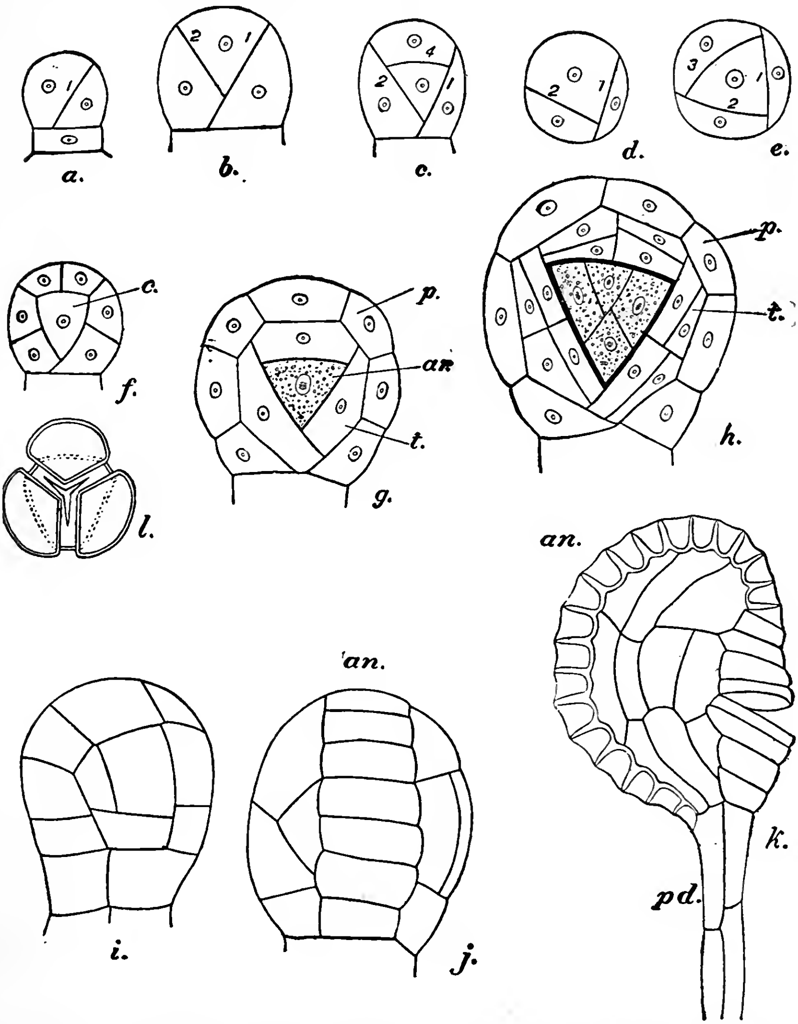


FIG. 49.—Development of a fern (Aspidium) sporangium. *a*, The young sporangium-forming cell just divided from its parent epidermis cell; *b*, *c*, *d*, *e*, *f*, different aspects of the dividing cells of the spore capsule; *g*, origin of the tapetal cells and formation of the spore-producing cell or archesporium (*ar*); *h*, increase of the tapetal cells (*t*) and formation of the spore mother cells; *i*, *j*, *k*, further stages in the development of the sporangium; *an*, annulus; *pd*, pedicel. (From Sedgwick and Wilson.)

leaves. In nature, sporulation of Pteridium usually occurs in August, and in allied forms sometime during the summer months. The margins of the mature leaves, when ready for spore formation, turn under and form elongated pockets which extend throughout the length of the pinnules. This inturned shelf of tissue is termed the *false indusium*, while another shelf of tissue, derived from the epidermis of the under surface and extending out to the false indusium, is called the *indusium*, the spore-bearing organs being formed in the chamber enclosed by the true and false indusia and the under surface of the pinnule.

In other types of fern the spore chambers are somewhat differently constructed. In the maiden-hair, for example, the entire edge of the pinna is not turned in, but three or more spots on the edge become localized spore-forming centers, each covered by an indusium. In the Boston fern a row of similar spots on each side of the median line on the under surface are spore-forming centers; each spot, termed a *sorus*, is covered by an indusium.

The spores develop in peculiarly shaped spore-cases called *sporangia*, many of which are formed in a sorus, and multitudes in the spore chambers of Pteridium. Each sporangium begins by the division of an epidermal cell (Fig. 49, a-h) until a capsule is formed, with a ridge (annulus) of specially hardened cells. Within the capsule a single germ cell, the *archesporium*, divides six consecutive times, forming 64 spores, each spore being enclosed in a firm covering (shell or epispore, Fig. 49, l). When ripe, the sporangium bursts open by contraction of the cells of the annulus, and the spores are scattered from the leaves to the ground.

The Sexual Generation (*Gametophyte*).—After some months on the ground the spores absorb moisture, the epispore bursts open, and the spore cell or endospore begins to swell and to

Fig. 50.—Germination of the spore and formation of the prothallium. *A*, Young plant leaving the spore case; *B*, similar stage after one cell division has occurred (*p*, protenema; *s*, spore case; *r*, root). Later stages in formation of the young prothallium are shown on the left, and below a fully developed prothallium with archegonia and antheridia. In the notch above is a figure (life size) of the same prothallium. (From Sedgwick and Wilson after Suminski.)

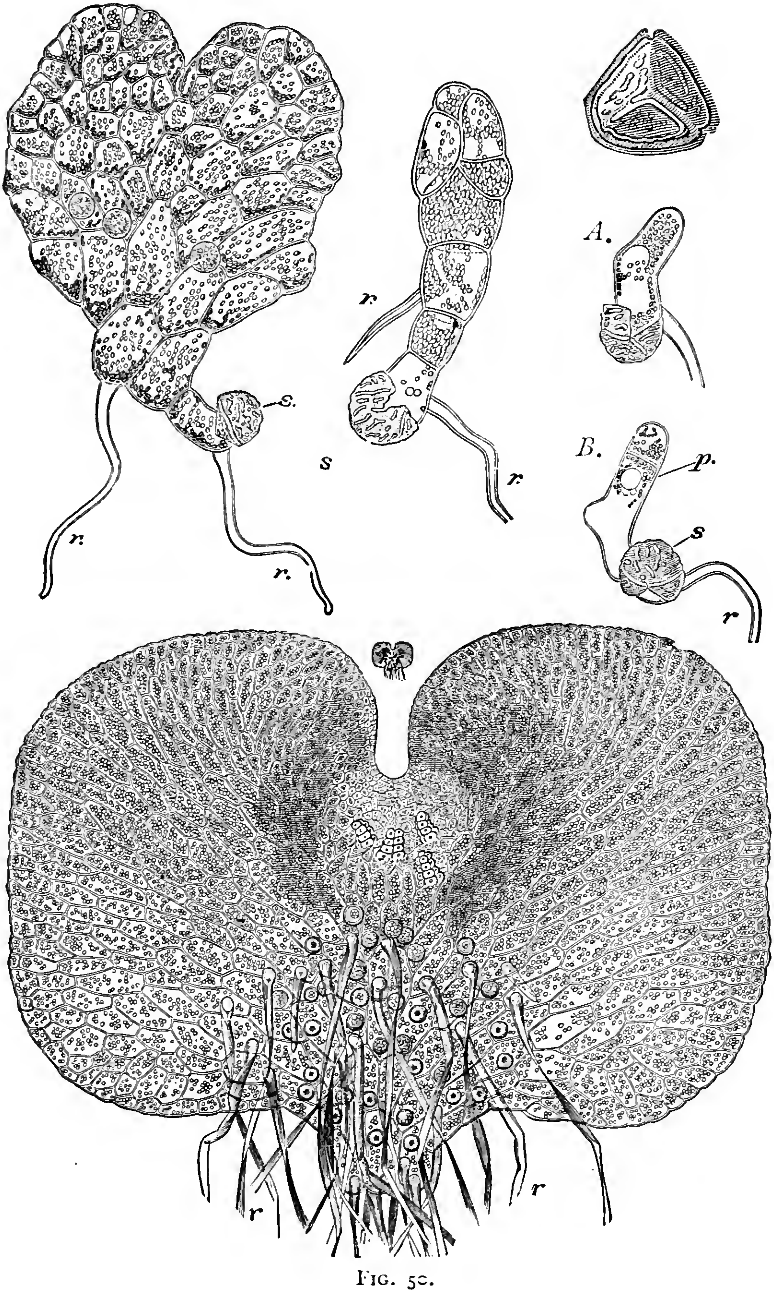


FIG. 50.

divide, forming root-like hairs (rhizoids) and the embryonic plant termed the *protonema* (Fig. 50). The end cells of the protonema develop *chlorophyll*, divide, and ultimately form a flattened plate of cells closely applied to the ground, to which it is anchored by the rhizoids. This flat plate of cells, or thallus, is the sexual generation of the fern and is called the *prothallium* (Fig. 50). It is entirely unlike the fern plant, but when mature it bears the sex cells which, after fertilization, develop into the fern. It thus resembles the medusa of a hydroid, an organism quite different from the hydranth from which it came, but the sole agent in the formation of the male and female germ cells which, on fertilization, give rise to the hydroid.

The sex cells of the fern are formed in characteristic organs on the under side of the prothallium. The oöspheres or egg cells are developed and contained in peculiar chimney-shaped structures termed *archegonia* (Fig. 50); while the male cells are formed in smaller rounded or hemispherical structures termed *antheridia* (Fig. 50). The two types of structure are each formed by continued division of an epidermal cell. In the archegonium these divisions result in a solid column of cells, with the oösphere embedded at the base of the column. The central cells of the column undergo liquefaction, thus forming a passage filled with a mucilaginous liquid from the apex of the archegonium to the egg cell. The antheridia are formed by divisions of similar epidermal cells which develop into a solid hemispherical mound, the internal cells of which divide repeatedly; the final divisions form the male cells or *antherozoids*, each, when mature, bearing a spiral filament covered with cilia.

The antherozoids usually develop first, and are distributed on the ground where they make their way in the moisture on the under side of the prothallium to the archegonia of the same or of different origin. They are attracted toward the chimney-like opening of the archegonia; one or more penetrate the gelatinous passage to the egg cell, and one antherozoid unites with it. The entire process of fertilization takes place within the tissues of the prothallium.

Development.—The fertilized egg cell or oöspore begins at once to divide, first into two, then into four cells. Of these first four cells, two form the foot or attachment organ by which the young embryo retains its position in the tissues of the prothallium;

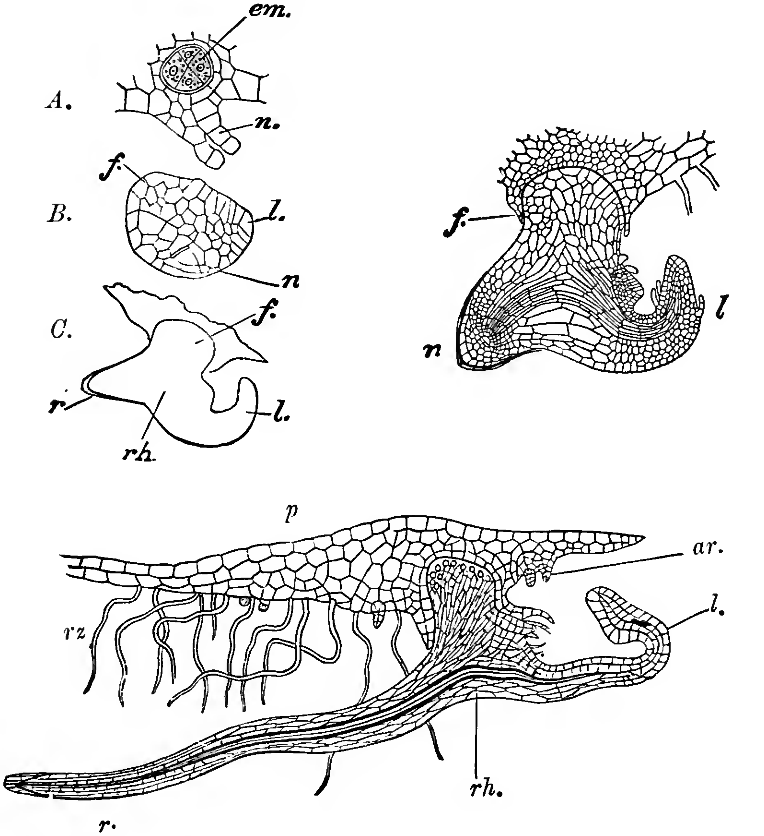


FIG. 51.—Development of the fern embryo. *A*, Section showing the closed neck (*n*) and the planes of division of the embryo into four cells (*em*); *B* and *C*, later stages of the embryo showing the beginning of apical growth and formation of the first leaf and rhizome. The other figures represent later stages in development. *ar*, old archegonia; *f*, foot; *l*, leaf; *p*, prothallium; *r*, root; *rh*, rhizoids. (From Sedgwick and Wilson, after Hofmeister and Sachs.)

one forms the rhizome, and one the first frond or leaf (Fig. 51). The young fern thus develops while anchored to the sexual generation. A second leaf is soon started from the basal portion; the first leaf unfolds in the light and the cells become filled with chlorophyll; the rhizome elongates by apical growth through the ground, until the young fern plant is fully established and is ready to make and store up starch. The prothallium gradually shrivels up and disappears.

The work done by the fern is duplicated by every type of plant life provided with chlorophyll. Sugars, starches, proteins and lifeless woods are manufactured and stored in roots, fruits, seeds, and trunks, and with them is locked up the potential energy to be transformed into kinetic energy through physiological and physical combustion by man and the lower animals. Nothing is wasted in the life cycle of matter and energy. Sugars, in addition to their food value for animals and plants, in the presence of yeast are transformed into alcohol and carbon dioxide, and their contained energy is changed into heat, energy of yeast protein and that of alcohol. Alcohol, in the presence of bacteria, is turned into acetic acid, the potential energy being converted into that of bacteria protein and that of acetic acid. The latter is acted upon again by bacteria, and changed into carbon dioxide and water in which the contained energy is nil, the bacteria protoplasm again storing up that which was contained in the acetic acid.

The proteins, carbohydrates and fats, derived mainly from plants, in the last analysis are the main foods of all animals and their chief sources of energy. Both plants and animals release the stored energy in the form of heat, light, electricity or movement, and in metabolism give off nitrogenous waste, carbon dioxide, and water. Of these, only the nitrogenous substances retain some energy of combination. Under the action of bacteria this small store is transformed into energy of bacterial protein, while free ammonia, carbon dioxide and water are returned to the earth and the air $(NH_2)_2CO + 2H_2O = 2NH_3 + CO_2 + H_2O$. The proteins of the dead bodies of plants and animals, after furnishing food and energy for scavengers of many kinds, are finally attacked by the army of nitrifying and other bacteria, and slowly transformed into nitrites, nitrates, sulphates, phosphates and other salts, and into free ammonia, carbon dioxide and water. Other bacteria are able to reduce nitrates and nitrites, and thus to liberate free nitrogen. These are relatively few in number, including, however, the well-known species *Bacillus coli*, *B. typhosus*, *B. fluorescens* and *B. pyocyaneus*. This action probably follows a condition of oxygen hunger on the part of the bacteria when oxygen is wrested from the nitrogen, leaving the latter as a free gas. Nitrogen, thus liberated, cannot be utilized by the higher plants, and were it not for the activity of other specially adapted organisms there might be a leak in the current of matter and energy. It is still a disputed question whether some of the lower algæ and some of the common molds have the power to "fix" this free nitrogen and so bring it back into the cycle of living things. This function is performed, however, by certain groups of bacteria, some of which are able to bring about the oxidation of free ammonia (NH_3) to nitrates, while still other bacteria can fix free nitrogen of the air (*Clostridium pastorianium*, two species of Azotobacter, and various species of Bacillus). All products of vital activity are thus, sooner or later, returned to the earth or atmosphere to be again taken up by the green plants and animals, and drawn once again through the living vortex of matter and energy.

The food of Hydra thus is only a link in the endless chain of matter- and energy-transformations shown in the diagram (p. 121). Above and throughout the entire marvelous chain of activities is the silent penetrating agency of the sun, the source of all energy.

CHAPTER VI

ORGANS AND ORGAN SYSTEMS

1. General

In *Hydra fusca*, we have studied an animal composed only of tissues, and a form representing the gastrula stage in development of all higher animals. We have seen, moreover, that some cells of Hydra, especially those of the ectoderm, are differentiated for special functions, particularly those for protection and nervous response. Such cells, however, are isolated and not combined in compact tissues or special organs. In higher animals, we find similar cells derived from the ectoderm of the gastrula developing into complex organs of the skin and into still more complicated organs of special sense, and finally into marvelously intricate organs like the human brain, spinal cord, and sympathetic nervous system. In these higher animals also, cells from the endoderm of the gastrula form all of the organs of the usual animal metabolism. All of the usual mesodermal structures, like bone, cartilage, muscles, connective-tissues, mesenteries, blood, etc., are derived from cells originally set apart from the vegetative cells of the gastrula.

An organ differentiated for the special performance of some vital function or part thereof never consists solely of the one tissue mainly responsible for that function. The stomach, for example, in which the first stages of protein digestion occur, does not consist merely of secreting epithelial cells from the endoderm. but is a complicated aggregate of connective tissue, muscle tissue and blood vessels from the mesoderm, and nerve tissue from the ectoderm, giving support, contractility and food to the functioning epithelial cells. The stomach, furthermore, performs only a part of the function of food digestion; other organs are associated with it for complete digestion. All of these, like the pharynx, oesophagus, liver, pancreas, and intestine and rectal organs, are similarly composed of different tissues, all aiding in the one function of preparing food for the body or of eliminating indigestible and harmful matters.

Such an aggregate of organs for the performance of a primary function constitutes an *organ system*. The aggregate of stomach and accompanying organs is termed the digestive or alimentary system. All of the nerve organs together form the nervous system. Similarly we find in all higher animals an excretory system; a supporting and muscular system; a respiratory system; a blood vascular system and a reproductive system, each composed of organs for the performance of one function or part of one function. All of the vital functions, like digestion, secretion, respiration, nervous response, reproduction, etc., performed by the single cell of Amoeba or Paramecium, are here performed by complex organ systems.

All human beings are familiar in a general way with the structures and functions of their own bodies, and they realize, in some degree at least, how complicated and difficult it is to understand human anatomy and human physiology. It is not only desirable but essential, therefore, for the beginner in biology to become familiar with simple types of organ systems and with some of the factors which have led to the differentiation of such relatively simple into more complex systems, before undertaking a study of the highest animal or deepest biological problem in detail. It is to this end that the present and the following chapters are devoted.

II. Structures and Functions of the Earthworm, Lumbricus Sp.

The earthworm occupies a position in the animal scale similar to that occupied by the fern in the plant scale. All the essential organ systems are present, but the general organization, while markedly higher than that of Hydra, is relatively simple when compared with crustacea, insects or vertebrates.

A. Occurrence, Habits and Mode of Life of Earthworms.—Earthworms are widely distributed over the earth, and six or seven different species are known, some growing to giant size (three to four feet long). Closely allied forms are partly earth-dwelling, partly water-dwelling forms, and some live entirely in water, while one type (Dendrobaena) burrows in the green ice of glaciers as an earthworm burrows in the earth.

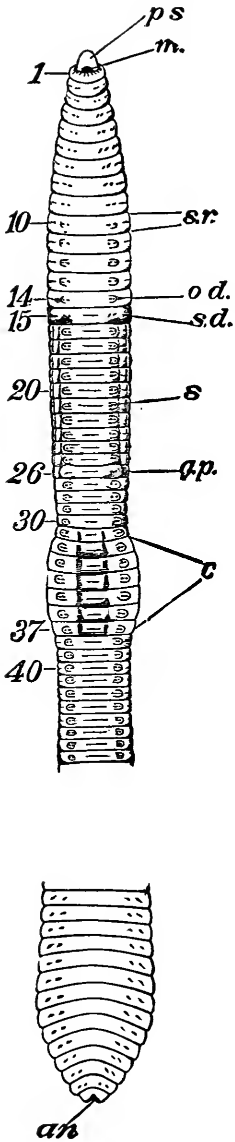
Earthworms live in winding burrows formed by eating their way through the earth, the burrows running through the soil at a depth of from five to six inches to several feet. The worms are nocturnal for the most part, coming out of their burrows at night to forage. During the day they lie in their burrows, mouth end up and close to the surface; at night they emerge, but usually remain anchored by their tails, exploring the region of their burrows throughout the area covered by their body radius. Pebbles, dirt, leaves and other small objects lying within this radius are swallowed or dragged into the burrows, where the small stones are used to line the walls and to cover the opening in the daytime. The dirt that is swallowed with nutritious matter, such as leaves, animal remains, etc., is slowly passed through the digestive tract; the nutritious parts are digested out, while the residue, consisting mainly of dirt, is voided to the outside through an opening at the opposite end, the anus. This defecated material is deposited on the outside of the burrow, where as small mounds, or "castings" or "fæces," they are familiar to every observer. Darwin, who made a special study of earthworms, has shown that enormous masses of earth pass in this way through the bodies of worms, as much as eighteen tons per acre per year in regions where earthworms abound. He has also shown that the entire surface of a field with great rocks upon it, in the course of several years, will be buried by the castings of worms, while walls and even buildings are similarly sunk into the earth in the course of time.

As a creeping, crawling, and burrowing thing, the earthworm is well adapted to its mode of life. Its long flexible body makes it particularly adapted to its burrowing habits, and a thoughtful student will puzzle over the problem whether its elongated body and various organs are the result of its mode of life, or whether it adopted this mode of life because of its peculiar structures. The same problem recurs in connection with all types of living things and may be expressed by the question: does the environment and mode of life of an animal type cause the race to become adapted to its surrounding conditions, or does the animal type choose the environment most suitable to its peculiar structures? We may leave the discussion of this question for the present with the non-committal statement that all animals are more or less perfectly adapted to the conditions of their environment, and will take up the problem of the significance of such adaptations in a later chapter.

B. Regional Differentiation.—A superficial examination of the worm is sufficient to show that it has quite definite structures.

Metamerism.—The entire body is divided by faint ring-like constrictions or annuli into short segments called *somites* or *metameres*, which on first view seem to be all alike. These rings are characteristic of a great group of worms called Annulata or annelids from this peculiarity, and all are metameric animals in which only slight modifications of the metameres occur. With metamerism, however, the possibilities of differentiation are almost unlimited, and we find that all of the higher types of animals, with the exception of the phyla of the soft-bodied molluscs and spiny-skinned Echinoderms, are built on this plan of structure. It is plainly evident in crustacea, insects, fish, and snakes, but is limited to the vertebral column in the majority of vertebrates.

Antero-posterior Differentiation.—Even in the earthworm, where the metameres seem to be all alike, there is some regional differentiation. If the mouth end of the worm be tickled, it will be found to be more sensitive than the middle region or the opposite end. If a bright light is suddenly thrown on the mouth end, the worm will react vigorously. This end of the worm, therefore, is more irritable than the other. Furthermore, at or near this end there are several external openings of internal organs not found elsewhere; thus on the eighth, ninth,



fourteenth, and fifteenth somites there are different openings of the reproductive system, while several enlarged somites from the twenty-eighth to the thirty-seventh, forming what is called the *clitellum*, are also associated with reproduction. The mouth end of the earthworm is thus differentiated from the remainder of the worm. We can hardly speak of it as the "head" end for there is no head nor tail, but we speak of this type of differentiation as *antero-posterior differentiation*, or anterior and posterior ends. In higher types of animals this type of differentiation leads to very definite head formation and centralization of the nervous system, while the posterior end always bears the vent or anus (Fig. 52).

Dorso-ventral Differentiation.—The worm always crawls on one surface. If turned over on its "back," it objects vigorously and quickly resumes its normal position. The surface on which it crawls also appears different from the other; it is more flattened; many papilla-like whitish glands are present, especially in the anterior part, and the various external openings (mouth, anus, reproductive, excretory) are found here. Furthermore peculiar bristle-like *setae*, which can be felt by gently drawing the worm between the fingers, are found on this surface. There is, therefore, a fairly well-marked differentiation between the

FIG. 52.—Enlarged diagram of the anterior and posterior parts of the earthworm as seen from the ventral side. *an*, Anus; *c*, clitellum; *g.p.*. glandular swellings on the twenty-sixth somite; *m*, mouth; *o.d.*, external openings of the oviducts; *ps*, prostomium; *s*, setae; *s.r.*, openings of the seminal receptacles; *s.d.*, external openings of the sperm ducts; 1–40, numbers of the somites beginning behind the prostomium. (From Sedgwick and Wilson.)

crawling surface or belly and the opposite more rounded surface or back, and the phenomenon is called *dorso-ventral differentiation*, which becomes more plainly marked in higher types of animals.

Bilateral Symmetry.—All of the organs of the body which do not lie on the median line are found in pairs, one on each side of a plane passing through the longitudinal center of the body. The mouth, anus, and entire digestive tract are unpaired and lie in the median plane; so do the main blood-vessels, but all of the reproductive organs, excretory organs, nervous system, musculature, setae, etc., are paired structures, so that one entire side of the earthworm is an exact replica of the other. This phenomenon, also characteristic of the higher animals, is called *bilateral symmetry*.

External Apertures.—Some of these are too minute to be seen, but others can be easily made out. Two pairs of minute pores (openings of the seminal receptacles) are on the ventral surface between the 9th and 10th and 10th and 11th somites; a pair of male genital openings are on the 15th and a pair of female genital openings are on the 14th. On the ventral surface also there are two extremely minute openings of the excretory organs (nephridia) in each somite, except the first three or four and the last. With the exception of the anus, all of the openings posterior to the male genital pore are too minute to be seen.

While most of the external openings are on the ventral surface, some are on the dorsal surface. Here, for example, are the dorsal excretory pores, one to each somite, after the 10th, in the annular creases, and very difficult to see.

Setae.—There are no true appendages on the worm's body, but if the animal is drawn gently through the fingers, fine bristle-like structures may be felt. These are setae or bristles, easily seen with a hand lens. There are eight setae to each somite, arranged in four double rows on the ventral surface and the sides. They aid the worm in locomotion by catching into the earth which acts as a fulcrum. The flattened tail of some forms (*Lumbricus terrestris*) also serves a useful purpose in anchoring the animal in its burrow, while the anterior end moves freely about in a small radius around the hole.

C. INTERNAL STRUCTURE.—A first impression is that the internal structures of an earthworm consist of a tube within a tube, the inner tube being the alimentary tract continuous from the mouth at the anterior end to the anus at the posterior (Fig. 53). The outer tube, formed by the body wall, is strictly speaking, not one continuous tube but a multitude of minute

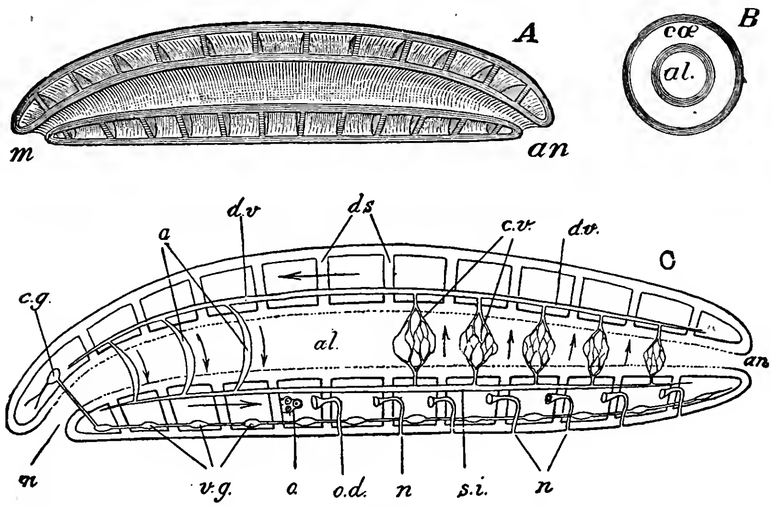


FIG. 53.—General diagrams of the earthworm as seen in longitudinal section. *A* and *C*, and transverse section *B*, showing the two tubes, the coelom, and the dissepiments. *a*, Aortic loops; *al*, digestive tract; *an*, anus; *c.g.*, cerebral ganglia; *coe*, coelom; *c.v.*, parietal vessels; *ds*, dissepiments; *d.v.*, dorsal vessel; *m*, mouth; *n*, nephridia; *o*, ovary; *o.d.*, oviduct; *s.i.*, ventral vessel. (From Sedgwick and Wilson.)

tubes (150 more or less), formed by the transverse partitions, *septa* or *dissepiments*, attached to the body wall where the annuli mark their positions. The cavities between these dissepiments are termed *coelomic cavities*, or simply the *coelom*. The body wall is relatively thick and muscular, being made up of epithel-

FIG. 54.—Anterior part of the body of the earthworm as it appears when the dorsal wall is removed. *ao*, Aortic loops; *ph*, pharynx; *c.g.*, cerebral ganglia; *oe*, oesophagus; *s.v.*, seminal vesicles; *s.r.*, seminal receptacles; *c.gl.*, calciferous glands; *c*, crop; *g*, gizzard; *d*, dissepiment; *s.i.*, stomach intestine; *d.v.*, dorsal vessel. (From Sedgwick and Wilson.)

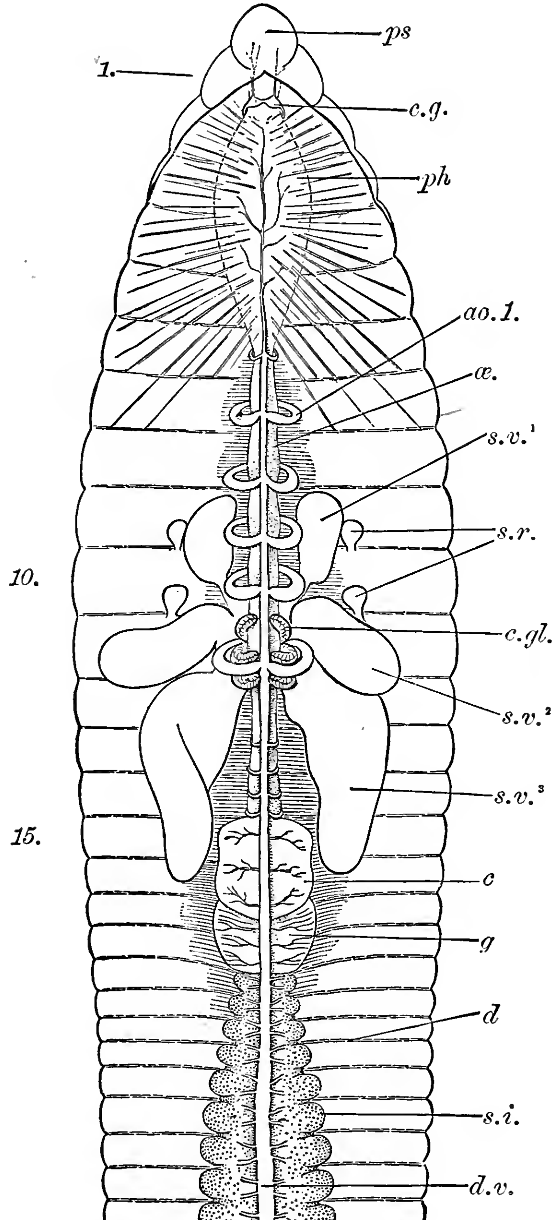


FIG. 54.

ium, muscles, nerves, glands, connective tissue, blood vessels, and endothelium, and the whole is covered on the outside by a delicate lifeless coat termed the *cuticle.*

The Digestive System.—The food of an earthworm consists of leaves, grass, animal tissues of any kind, and the minute forms of life found in the ordinary dirt. Quantities of this dirt are continually taken in by the animal and are passed, unaltered, through the alimentary tract to be defecated through the anus.

The apparatus for food digestion and absorption is much more complicated than in Hydra, where digestion is largely intracellular. In the worm, it is inter-cellular and occurs in cavities, into which the lining cells secrete digestive ferments. The anterior end of the digestive tract is covered by a thick muscular wall. This part, the pharynx (Fig. 54, ph), is used as a sucking mechanism for drawing in food matters. Posterior to the pharynx is the oesophagus, a thin-walled tube extending from about the sixth or seventh somite to the fourteenth or fifteenth, covered over from the seventh or eighth to the fifteenth by the large yellowish vesicles of the reproductive system, and encircled by the fine "aortic arches" of the blood vascular system. Posterior to the reproductive organs and on the ventral side of the oesophagus are three pairs of bright yellow organs called the *calciferous glands,* the secretions of which serve to neutralize the acids taken in with the food. Immediately behind the calciferous glands the alimentary tract expands into a larger thin-walled pouch, termed the *crop,* which serves as a food reservoir. The crop opens into a thick-walled reservoir or muscular pouch, called the *gizzard,* where the food materials are ground up into fine particles, the dirt, sand grains, etc., serving a useful purpose in the process. Posterior to the gizzard, from about the twenty-sixth somite to the posterior end of the worm, the digestive tract consists of a uniform tube lined by secreting cells. This tube is called the *stomach-intestine* from its combined functions, and it is covered with a thick layer of brownish-yellow glandular cells termed the *chlorogogue cells.* These are richly supplied with blood vessels, and are supposed to have some function connected with excretion. Finally, at the posterior end, the stomach-intestine opens to the outside through the anus by a short section of non-functional tissue, called the *proctodaeum.*

In the cavities between the digestive tract and the body wall lie all of the other important organs of the worm. They are, therefore, morphologically speaking, inside the worm while undigested food, dirt, etc., although inside the digestive tract, are, morphologically, outside of the animal. Some of these internal organs, like those of the excretory system, are repeated in each somite; others, like the blood, vascular and nervous systems, are continuous from one end of the body to the other, while still others, like the reproductive system, are concentrated in one part, occupying only a few somites.

D. PHYSIOLOGY OF THE DIGESTIVE SYSTEM. *Buccal Cavity and Pharynx.*—The mouth is covered by a dorsal prolongation of the first somite, functioning as an upper lip or prostomium. A much smaller under lip completes the border. The buccal cavity is a relatively spacious hollow reaching as far as the third somite, and its walls are provided with special muscles reaching to the body wall. This cavity opens into a larger and more muscular pharynx. The lips do not act as grasping organs for ingestion of leaves, but the prostomium is rather an organ of smell, while the pharynx with its heavy muscles acts as a suction pump for drawing leaves into the burrows and for ingesting them afterward. The leaves line the walls of the burrows or partly extend out of them, masking the openings. If such a partially visible leaf is pulled out, the part inside the burrow will be found to be a mere skeleton, the mesophyll structures having been sucked into the pharynx of the worm by the action of the muscular pump. This action is facilitated by the secretion from the mouth and pharynx of a digestive fluid of alkaline reaction which, however, only softens and does not digest, although Darwin suspected the presence of tryptic protease and amylolytic ferments.

The Oesophagus.—The oesophagus stretches from about the sixth to the fourteenth somites; it is somewhat laterally compressed with longitudinal and annular muscles. In the posterior part of the oesophagus the walls are considerably thickened to form three pairs of peculiar calciferous glands. These glands consist of numerous flat and broad pockets of tissue radially arranged on the oesophagus as axis. The flattened pockets are enclosed in a muscular sheath and lie in a blood-filled sinus, while between the pockets are collections of lime. These "glands" are not true glandular diverticula of the oesophagus, but are mesodermal in origin and are merely the walls of the blood vessels. The cells of the pockets take crystals of calcium carbonate from the blood and secrete them in a milky fluid into the oesophagus. (See Combault, Harrington, etc.)

The function of the glands is not entirely clear, although several assumptions have been made which are more or less well grounded. Claparede and Darwin believed that the milky fluid may be an excretion of the great quantity of lime which is contained in fallen leaves and accumulates in the blood after digestion of the leaves. Harrington, on the other hand, found that secretion of lime from the glands diminishes if the worms are fed with calcium carbonate, but increases if fed with acidified food, and he accepts a second hypothesis of Darwin's, *viz.*, that the lime plays a rôle in digestion. This rôle is to neutralize the humus acids contained in decomposing vegetation, and to prepare a suitable alkaline medium for the action of tryptic ferments.

A third view advanced by Combault is that the calciferous glands form a sort of internal breathing organ for removing CO_2 from the blood, combining it with calcium and excreting it as lime into the oesophagus. This view, which is also supported by experimental evidence, does not exclude the possibility of a digestive function, but if true, it indicates the further function of preventing a surplus of CO_2 in the blood.

The Crop and Gizzard.—In the 14th segment the digestive tract enlarges to form a thin-walled expansion called the crop, extending from the 14th to the 16th somites. No special function, apart from storage, is attributed to this organ, but it opens directly into a thick-walled gizzard provided with powerful circular muscles. The contraction of these muscles, acting on the contained food material mixed with gravel, results in the trituration of the solid food materials and prepares them for digestion in the stomach intestine.

The Stomach Intestine.—This, the most important organ of the alimentary system, begins at about the 18th somite and runs in a straight course to the posterior end of the worm. It consists of epithelial, vascular, circular and longitudinal muscular tissues and is covered on the outside by peculiar yellowish-brown *chlorogogue cells*, derived from the coelomic endothelium. Along

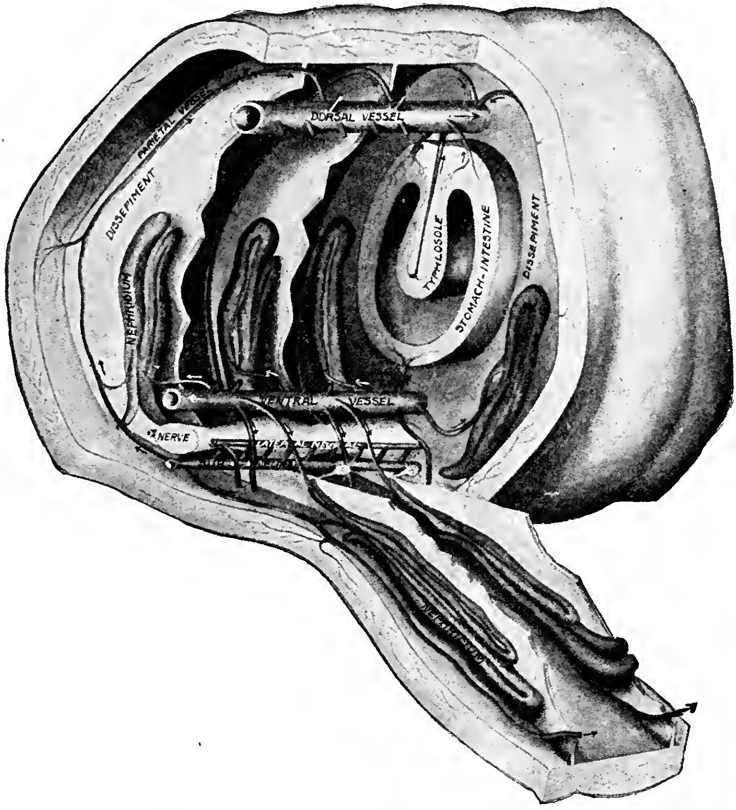


FIG. 55.—Stereogram showing the relations of organs in the posterior part of the earthworm. (Worked out by Professors McGregor and Calkins, and drawn by Miss Hedge.)

the dorsal median line a longitudinal fold of tissue coming from the dorsal wall of the intestine runs the entire length of this organ as far as the rectum. This fold, called the *typhlosole* (Fig. 55), has a different form in different regions of the body and contains additional blood vessels and chlorogogue cells, thus increasing the area of the digestive surface. The intestine, finally, is constricted at each dissepiment so that its structure follows the general metamerism of the body.

The digestive fluid secreted by the wall cells of the intestine corresponds in its essential features with the pancreatic juice of mammals. Free acids cannot be detected in the gut, where the fluids in general show a slightly alkaline reaction. According to Lesser and Taschenberg, albumin is broken down under action of this digestive fluid in 3 1/2 hours at 37° C. if the medium is slightly alkaline, and in 28 1/2 hours if it is slightly acid. According to Abderhalden and Heise, a peptogenic ferment is also present, which accounts for the slow digestion in an acid medium. The same observers also extracted an amylolytic ferment which changes starch into sugar (maltose), and found traces of a fat emulsifying ferment.

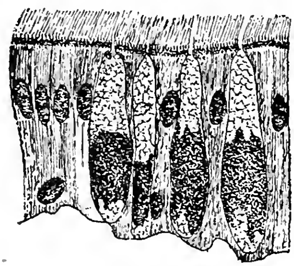


Fig. 56.—Cells from the endoderm of a worm showing enlarged gland cells with secretions, and between them, the absorptive cells. (From K. C. Schneider.)

The digestive ferments are secreted by gland cells distributed among absorbing cells of the gut epithelium (Fig. 56). In prepared sections, they may be distinctly made out, if filled with granules which have an albuminous nature, but if emptied of granules, they become so small and compressed that they are difficult to find.

The absorption cells are columnar, ciliated, epithelial cells, somewhat broader at the ciliated end. In each there is a typical and characteristic closing apparatus. The free surface possesses a cuticle-like covering which bears a hedge of fine, stiff rods, through which the cilia pass from their basal bodies in the cell to the lumen of the gut. These cilia are absent on the cells of the typhlosole, where fat absorption is the chief rôle (Greenwood). The function of the minute rods is unknown but they occur very generally on absorption cells. Granules of absorbed food-stuffs are often visible in these cells, some of which may be recognized. Thus, if powdered carmine or indigo is mixed with the worm's food, the colored granules

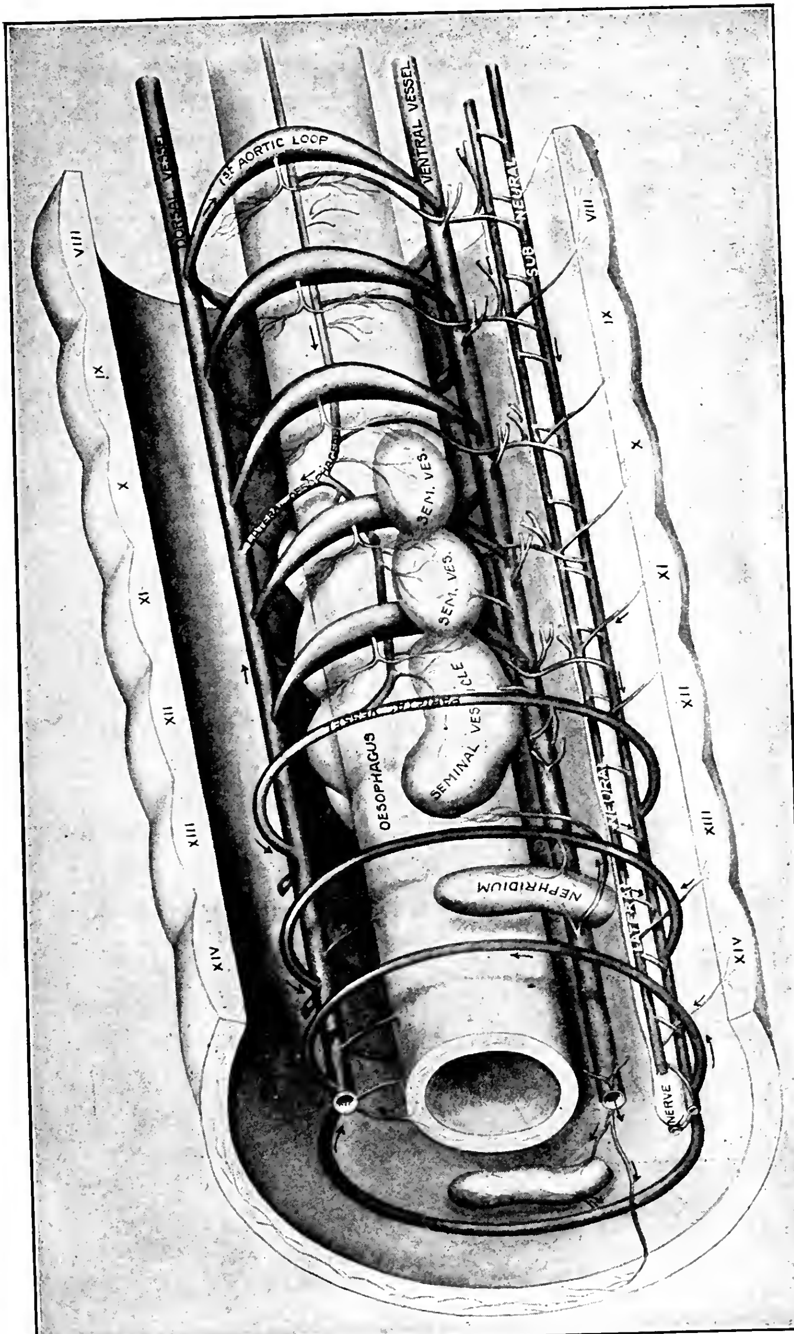


FIG. 57.—Stereogram showing the relation of the circulatory and other organs in the anterior part of the earthworm. (Worked out by Professors McGregor and Calkins, and drawn by Miss Hedge.)

reappear in the absorptive cells; chlorophyll and fat have also been detected.

The Rectum.—The rectum of the earthworm is the posterior part of the intestine, which bears no typhlosole. It opens to the outside through the anus which is provided with a sphincter muscle. According to Hensen, each worm deposits 1/2 gram of faeces in 24 hours, and these faeces make up the castings shown by Darwin to have great economic importance.

Further Fate of the Absorbed Nutriment.—The gut walls of the earthworm are richly supplied with blood vessels and finer capillaries which form a vascular network throughout the entire intestine. It is highly probable, although never demonstrated, that the absorbed food material is passed directly into the blood through the walls of these vessels.

E. Blood Vascular System.—In the earthworm it is the plasm or fluid that is colored red by haemoglobin, while the living cells of the circulation are colorless. As in vertebrates, the blood flow is continuous, the circulation being closed throughout, *i.e.*, the blood is always in tubular vessels. The main trunks are (1) a dorsal vessel lying on the digestive tract and giving off in the anterior segments five pairs of enlarged vessels, the so-called "aortic arches" or loops. These loops are connected below the oesophagus with (2) a ventral vessel also running the entire length of the animal below the digestive tract. Both dorsal and ventral vessels give off branches to the adjacent tissues. One pair (parietals) run from the dorsal vessel in each somite and along the dissepiment to the body wall, where they split into numerous fine branches (capillaries), penetrating the dermal musculature and the epithelium. Other branches of the dorsal vessel are given off to the digestive tract, ending in capillaries in the walls of the stomach-intestine and other organs. In the anterior region two lateral vessels are given off, which supply the reproductive organs. Three other longitudinal ventral vessels run the length of the worm; one, the sub-neural vessel, lies below the nerve cord, while two others, lateral-neurals, are embedded in the connective tissue about the nerve cord, one on each side (Figs. 55 and 57).

Vascular Circulation.—The circulation of the blood is brought about by peristalsis or the consecutive contraction of the circular muscles in the walls of the blood vessels. This wave of contraction proceeds in the dorsal vessel from the posterior end toward the anterior, the blood being forced ahead of the wave of contraction, as one might force water from a rubber tube. The details of the path followed in the circulation of the blood are not fully known, but there is abundant evidence that the essential features in the following account are correct (cf. Figs. 55 and 57).

The blood passes into the pharyngeal vessels anterior to the aortic loops; also through the aortic loops into the ventral vessel, where the flow is from the anterior toward the posterior end. From the ventral vessel branches are given off to the digestive tract, the nephridia, and the body wall. In the digestive tract these vessels branch repeatedly until they result in fine capillaries running throughout the vascular area of the digestive system. Similar capillaries connect with these and conduct the blood, now loaded with products of digestion, into larger vessels which, in turn, open into the dorsal vessel. It is possible that the waste matters (urea), contained in the blood thus directed into the digestive system, are disposed of through the agency of the chlorogogue cells. The blood vessels which enter the nephridia likewise break up into capillaries where the blood probably gives up its urea. The purified blood then passes into the parietal vessels, or into the body wall, and is ultimately conducted back to the dorsal vessel. In the same way, the vessels which enter the body wall ultimately end in capillaries distributed throughout the general surface of the body. Here the blood loses its CO_2, and takes in oxygen, and is then carried through progressively larger vessels back to the lateral-neural vessels, from which it passes directly to the sub-neural vessel, and then, by way of the parietals, back to the dorsal vessel. Within each of the parietal vessels, near its point of union with the dorsal vessel, is a conspicuous valve which may be seen in the living worm. This valve is so placed that blood can flow from the parietal into the dorsal vessel after a peristaltic wave has passed, while blood is prevented from flowing back into the parietal vessel by closure of the valve, due to pressure of the oncoming peristaltic wave.

The dorsal vessel thus functions like a heart, the force necessary to propel the blood through the large vessels and capillaries coming from the consecutive contractions, or peristalsis, of its circular muscles, and the force, in turn, comes from the transformed energy, due to oxidation, in the muscle cells.

Coelomic Circulation.—Another circulating fluid is contained in the body cavity, or coelom, which is continuous throughout all of the somites of the worm through dorsal apertures, in the form of slits, between the dissepiments and the digestive tract. This fluid is made up of a colorless plasm with white blood cells or leucocytes. It is washed back and forth by movements of the worm, thus bathing the endothelium lining the coelom, but there is no definite circulation.

F. The Excretory System.—*Nephridia.*—The waste matters of metabolism are disposed of through the action of small but complicated organs, called *nephridia*, a pair of which may be found in all of the somites after the first four. Each nephridium consists of similar parts, the most important of which are: (1) the funnel or nephrostome, (2) the ciliated neck, (3) the coiled narrow tube, (4) the wide glandular tube, and (5) the ejaculatory duct opening to the outside (Fig. 58).

The ciliated neck of the nephrostome passes through the anterior wall of the somite, close to the mid-ventral line. The nephrostome, therefore, lies in the somite anterior to the one containing its own nephridium, so that waste matters of any one somite are expelled to the outside by the nephridium of the next posterior somite. The nephrostomes or mouths of the nephridia are flattened fan-like structures, consisting of two flattened lamellae or plates with a narrow slit-like opening between them; the great cells lining the opening are covered with powerful cilia which maintain a constant current toward the tubular part of the nephridium. These tubes are developed in coils which lie in the posterior parts of the somites, three coils or turns in each, the third ending in an enlarged portion opening to the outside on the ventral wall of the somite (Figs. 55 and 58). All of the turns are richly supplied with blood vessels.

If carmine powder is injected into the coelom, it is taken up by the chlorogogue cells, which then break down, freeing the carmine together with fragments of the chlorogogue cells, and all are caught up by the current made by the nephrostome, and carried through the nephridium to the outside. From this experiment the conclusion has been drawn that some, at least, of

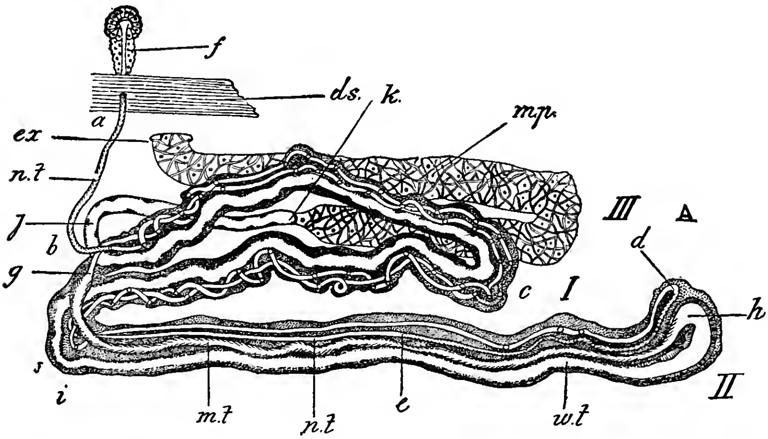


FIG. 58.—Nephridium of Lumbricus. *f*, Funnel or nephrostome; *ds*, dissepiment; *n.t.*, narrow tube, ciliated between *a* and *b*, *d* and *e* and at *c*; *m.t.*, middle tube ciliated between *h* and *i*; *w.t.*, wide tube; *m.p.*, muscular part; *ex*, external opening. (From Sedgwick and Wilson, after Benham.)

the waste matters of the tissues are brought in the circulation to the chlorogogue cells, and are acted upon by the fluids of these cells. The products of this activity are liberated into the coelom by the fragmentation of the cells, and then are excreted from the worm by the nephridia.

Dorsal Pores.—Excretion is also carried on to a limited extent through dorsal pores situated in the annuli in the mid-dorsal line.

G. THE MUSCULAR SYSTEM.—The main muscular and supporting system of the earthworm is relatively simple, consisting of two walls of muscle fibers which form a continuous sheath from anterior to posterior ends of the worm. Being united with the skin to form the body wall, it is known as *dermal musculature.* The inner wall consists of longitudinal fibers running from somite to somite, and their contraction results in drawing head and tail end together, or in shortening the worm (Fig. 59). The muscle fibers are closely packed together, giving the appearance of many muscles. The outer wall consists of fibers running around the somite at right angles to the longitudinal

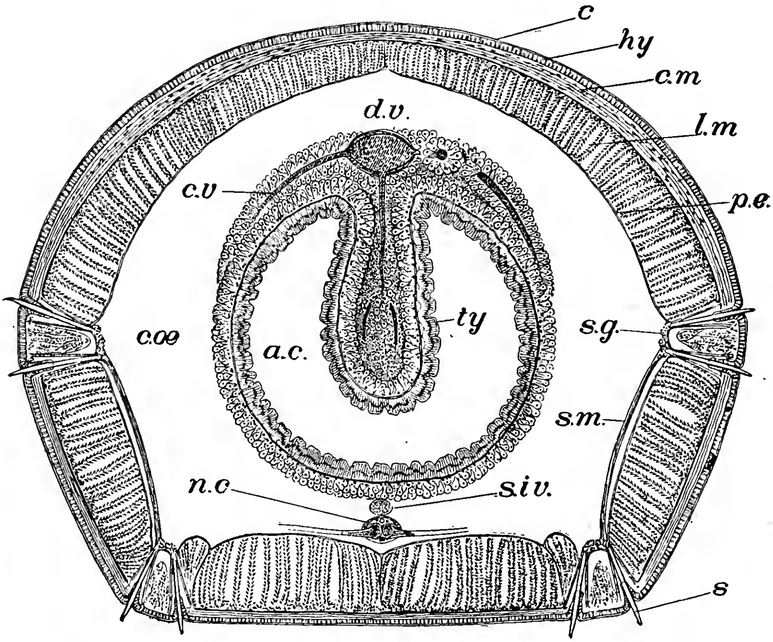


FIG. 59.—Transverse section of the earthworm behind the clitellum. *a.c.*, Cavity of the digestive tract; *c*, cuticle; *coe*, coelom; *c.m.*, circular muscles; *c.v.*, parietal vessel; *d.v.*, dorsal vessel; *hy*, hypodermis; *l.m.*, longitudinal muscles; *n.c.*, ventral nerve chain; *p.e.*, peritoneal endothelium; *s*, seta; *s.g.*, setigerous gland; *s.i.v.*, ventral vessel; *s.m.*, muscle connecting two groups of setae on the same side; *ty*, typhlosole. (From Sedgwick and Wilson.)

fibers, and their contraction results in shortening the diameter of the somite and thus in elongating the worm. Both sheaths of muscle are broken in four places at points where setae are formed, and here special muscles for moving the inner ends of the setae are developed; by their contraction the setae are moved one way or another. These setae are lifeless rods of chitin, somewhat sharpened at the outer ends and formed from special glands termed the seta-sacs. These are often of large size, and are conspicuous when the worm is opened. Between the two setae of each pair, a few longitudinal bundles of muscle fibers help to strengthen the body wall and to complete the muscular sheath, while smaller muscles connect the adjacent setae on each side (Fig. 59 *s.m.*).

Other special muscles form the walls of the pharynx, and by their contraction and relaxation they shut and open this organ, thus making it a sucking pouch which draws in dirt, leaves, and other extraneous matters.

Still other special muscles form the walls of the gizzard, making it a grinding organ for cutting up food received from the crop. Circular and longitudinal muscles also form part of the wall of the stomach intestine, and by their successive contraction force the enclosed undigested food materials toward the anus, thus acting by peristalsis as do the blood-vessel muscles which form a part of the walls.

H. THE NERVOUS SYSTEM.—The nervous system is closely connected with the muscular system, and it is well to get in mind the muscle-nerve combination, for one always involves the other, sensory cell, central nervous system, and muscle all working together in what is termed a "reflex action."

The Sensory System.—The cells of the skin are of different kinds, the majority being epithelial or columnar cells, with secreting or goblet cells interspersed here and there, which form the slimy secretion poured out when the worm is irritated. In addition to these, there are many small sensory cells which receive stimuli when the worm is irritated. These are much more numerous in the anterior part of the worm than elsewhere, making this the most sensitive or irritable portion of the whole body. The irritation received by these sensory cells is passed as a nervous impulse through prolongations of the sensory cells in the form of nerve fibers to the central nervous system which runs from end to end of the worm. There are no aggregates of sensory cells to form sense organs, but the entire skin is sensitive.

The earthworm marks a great advance in the organization of the nervous system. In Hydra and the coelenterates there is nothing like the highly co-ordinated nervous system of the annelids and higher types generally. Nerve cells are present, it is true, in Hydra, and, as we have seen, they form a more or less complete nervous network throughout the organism, but they consist of sensory cells and isolated nerve cells whose processes connect with the equally isolated epithelio-muscle cells.

In the earthworm, in common with all higher animals, the sensory cells do not connect in this direct manner with the muscles, but act through a central nervous system. The condition in Hydra may be compared with a primitive telephone system, where everyone rushes to the phone whenever a bell rings in the system, while the earthworm condition may be compared with a well-equipped and efficient modern telephone plant, where all peripheral calls are sent directly to the central exchange and there properly classified and transmitted. We distinguish, therefore, two distinct parts of the nervous system of the earthworm (1) the sensory or peripheral system, described above, and (2) the central nervous system.

The Central Nervous System.—The central nervous system consists of a double nerve cord lying below the digestive tract, with a large double swelling in each somite. These swellings are termed *ganglia*, and they are made up of masses of nerve cells. The ganglia are connected from somite to somite by the heavy double nerves termed *commissures*, so that the entire worm is bound together by a continuous system of commissures and ganglia which form a fairly homogeneous central nervous system (Fig. 60).

The central nervous system is connected with the sensory cells of the body wall, and with all of the organs of the somites, by three pairs of nerves which leave the ganglia as shown in Fig. 60. These nerves are supported by the dissepiments and body wall and branch and sub-branch, until they are lost in a network of fine fibers penetrating muscles and epithelium. Each of the main nerves is a bundle of fine fibers which transmit sensory impulses to the ganglia, and motor impulses from the ganglia.

At the anterior end of the ventral nerve chain there is a pair

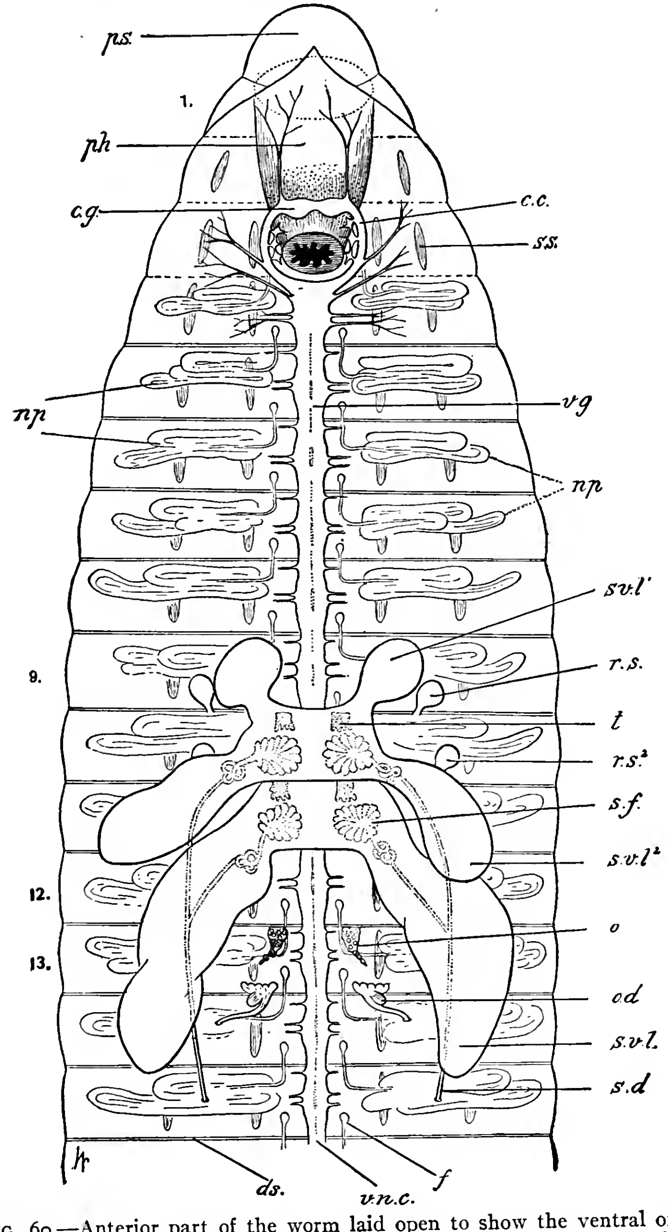


FIG. 60.—Anterior part of the worm laid open to show the ventral organs. *c.c.*, Circum-oesophageal commissures; *c.g.*, cerebral ganglia; *ds.*, dissepiment; *f*, funnel of nephridium; *np*, nephridium; *o*, ovary; *od*, oviduct; *ph*, pharynx; *ps*, prostomium; *r.s.*, seminal receptacle; *s.d.*, sperm duct; *s.f.*, sperm funnel; *s.v.l.*, lateral seminal vesicle; *t*, testis; *v.g.* and *v.n.c.*, ventral nerve cord. (From Sedgwick and Wilson.)

of larger ganglia, known as the sub-oesophageal ganglia. The commissures from them pass around the oesophagus, one on each side, and connect with a pair of ganglia in the peristomium, dorsal to the mouth. Because of their course around the oesophagus, these commissures are called the *circum-oesophageal commissures*, and the two dorsal ganglia are called the *cerebral ganglia* (c.c. and c.g.). This pair represents the only morphological element comparable with a brain of higher animals, but it is probable that they have no functions different from those of the ordinary ganglia of the ventral chain. As there are more sensory cells in the anterior region of the worm, it is probable, however, that their functions are more frequently called into play, so that it is a more active organ than any of the other ganglia.

A Reflex Action.—Consciousness, as we understand it in human beings, probably does not exist in the earthworm, but the relation between nervous impulse and muscular response is so delicately adjusted that movements are produced, which in human beings we would interpret as conscious acts. The complicated movements of a worm, in its efforts to free itself from some irritating environment, may all be traced back to a relatively simple series of processes termed a reflex action (Fig. 61). Each reflex action involves five distinct elements of the nervous system: (1) A sensory cell which receives the stimulus from the outside; (2) a nerve fiber bearing the sensory or afferent impulse transmitted from the sensory cell; (3) a central nerve cell in the ganglion which receives the sensory impulse, and transforms it into a motor or efferent impulse, which now travels over (4) an efferent or motor nerve to (5) a muscle cell. The stimulus, thus conveyed, starts contraction in the muscle. It is probable that other centers of activity are stimulated, and that, by nerve cells and their processes, the nerve fibers transmit impulses from one ganglion to another along the entire course of the central nervous system. This is probable because of the presence in the ventral nerve chain of different kinds of nerve fibers, some of which originate in the ventral ganglia and send processes in both directions along the ventral cord, without leaving the cord at any point. Such cells and fibers, known as *co-ordinating* cells, extend from somite to somite, and give rise to co-ordinating impulses which cause the entire worm to act as a single unit.

The ventral cord and ganglia have other cells than those mentioned, which may be grouped together as (1) afferent nerve cells which receive impulses, (2) efferent nerve cells which trans-

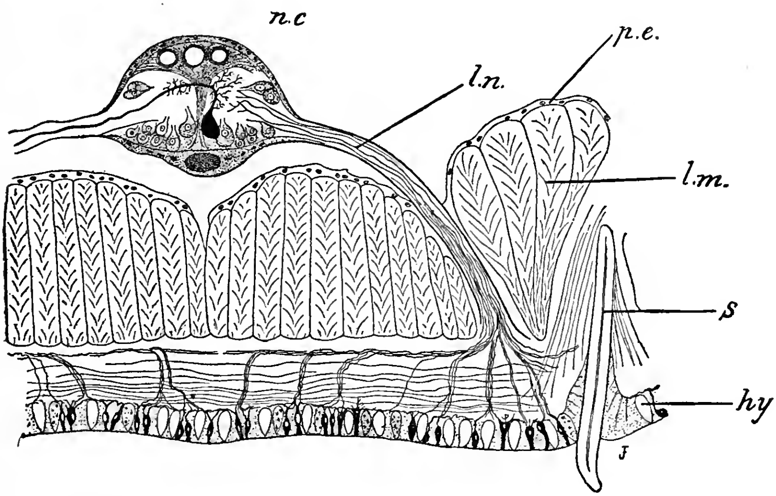


Fig. 61.—Portion of a transverse section of the ventral part of the body of Lumbricus, to show the nerve connections. *n.c.*, Ventral ganglion giving off a lateral nerve *l.n.*; *p.e.*, peritoneal endothelium; *l.m.*, longitudinal muscles; *hy*, hypodermis; in the nerve *l.n.* are sensory fibers proceeding inward from the sensory cells (in black) of the hypodermis, and terminating in branching extremities; *s*, seta. (From Sedgwick and Wilson, after Lenhossek.)

mit impulses to motor fibers, (3) co-ordinating cells which bring about concerted action of the entire chain of somites, (4) giant fibers, the functions of which are somewhat problematical, but which may have both supporting and co-ordinating functions, and (5) glia cells which form the matrix or main body of the chain (Fig. 62).

Each young nerve cell in development first forms an axial process called the *axon*, which carries impulses away from the cell. Other processes of the cell are termed *dendrites*, which are shorter and more branched than the axon, and they receive

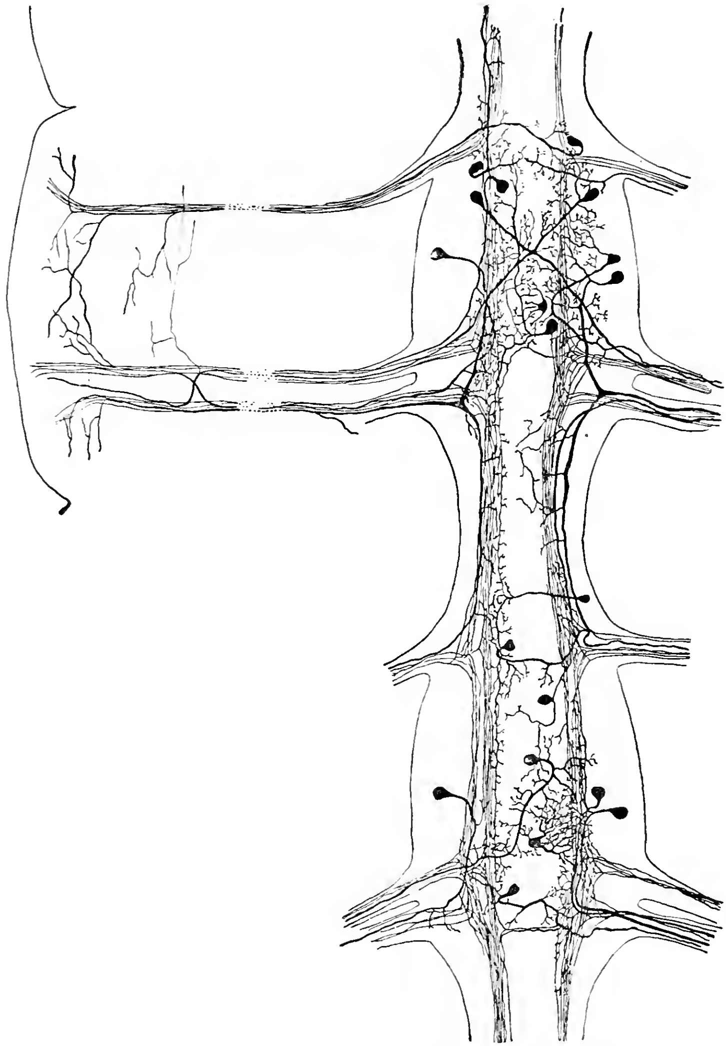


FIG. 62.—Portion of the ventral nerve cord with two ganglia and six pairs of lateral nerves. The sensory nerves end in terminal branches which connect with the dendrites of the motor and co-ordinating nerve cells of the cord. (From Retzius.)

and carry impulses to the cell. The entire system of cell body, axon, and dendrites constitutes a nerve unit called the *neuron*. Every neuron is separate and distinct, and adjacent neurons, while in contact, do not fuse; impulses, however, are transmitted from one to another by contact.

The muscular and nervous systems are sometimes grouped together as organs of relation, since it is through them that the organism is in touch with its environment. These systems, together with those of nutrition, circulation and excretion are organs of the individual, and have to do only with one animal. One other system of organs—the reproductive organs—has little to do with the individual, since it consists of organs having nothing to do with metabolism, secretion, excretion or nervous response, but is, primarily, a system of organs of the race, with the one common function of perpetuating the species by reproduction of the same kind of worm. Hence we consider it separately.

I. THE REPRODUCTIVE SYSTEM.—Like Hydra and the fern, the earthworm is hermaphrodite, having both male and female organs of reproduction. These are somewhat complicated, and involve two sets of structures, one set for the receiving and storing of spermatozoa received from another worm during copulation, the other set for the manufacture, development and emission of the mature spermatozoa and eggs.

The receptive organs, termed *seminal receptacles* (Fig. 63), consist of two pairs of globular sacs in the 9th and 10th somites, with openings to the outside on the ventral surface. They are small spherical sacs close to the dissepiments, and one pair, at least, may be hidden by the overlying *seminal vesicles* or organs for the manufacture of spermatozoa. At the period of maturity, these receptacles are usually filled with mature spermatozoa which have been formed in another worm. When the eggs are mature these spermatozoa are squeezed out, and fertilization takes place on the outside of the body.

The spermatozoa-forming organs are more complicated, consisting essentially of three pairs of closed sacs, called the seminal vesicles, united in the median line and enclosing the sperm mother cells derived from the *testes*. Strictly speaking, there is but one sac, for the cavities of the seminal vesicles are all in open communication, the walls of the sac being drawn out in three pairs of lobes. The testes are small and difficult to find in the mature worm, for the dorsal wall of the vesicle sac must first be removed. One pair are situated on the posterior side of the anterior wall of the 10th somite, and another pair are in the corresponding position on the anterior wall of the 11th

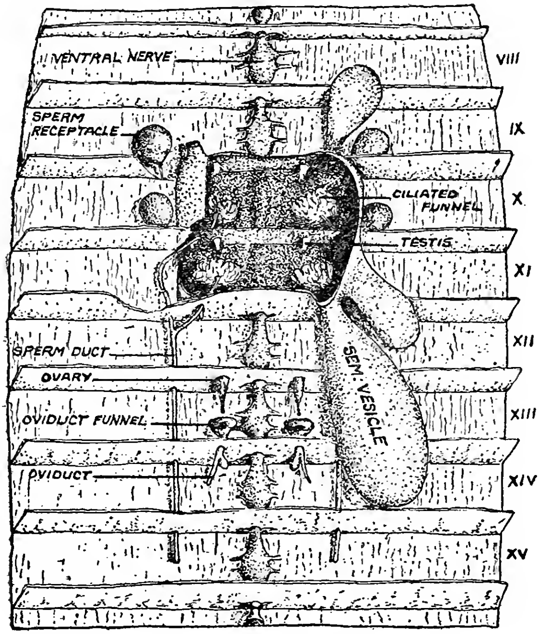


Fig. 63.—Diagram of the reproductive system of the earthworm showing the central chamber of the seminal vesicles and the internal position of the testes.

somite. When the sperm mother cells have reached a certain stage of development, they drop off the testis and continue their development as free cells in the cavities of the vesicles (Figs. 63 and 64).

The primordial germ cells which give rise to the spermatozoa are formed in the testes. Here the nuclei divide without cell divisions, until multinucleated protoplasmic masses are formed, which break loose from the testes and continue their development in the seminal vesicles (Fig. 64).

The nuclei increase by division and take a position at the periphery of the protoplasmic mass, where further multiplication follows until there are from 32 to 64 nuclei. Protoplasmic furrows then cut in around each of

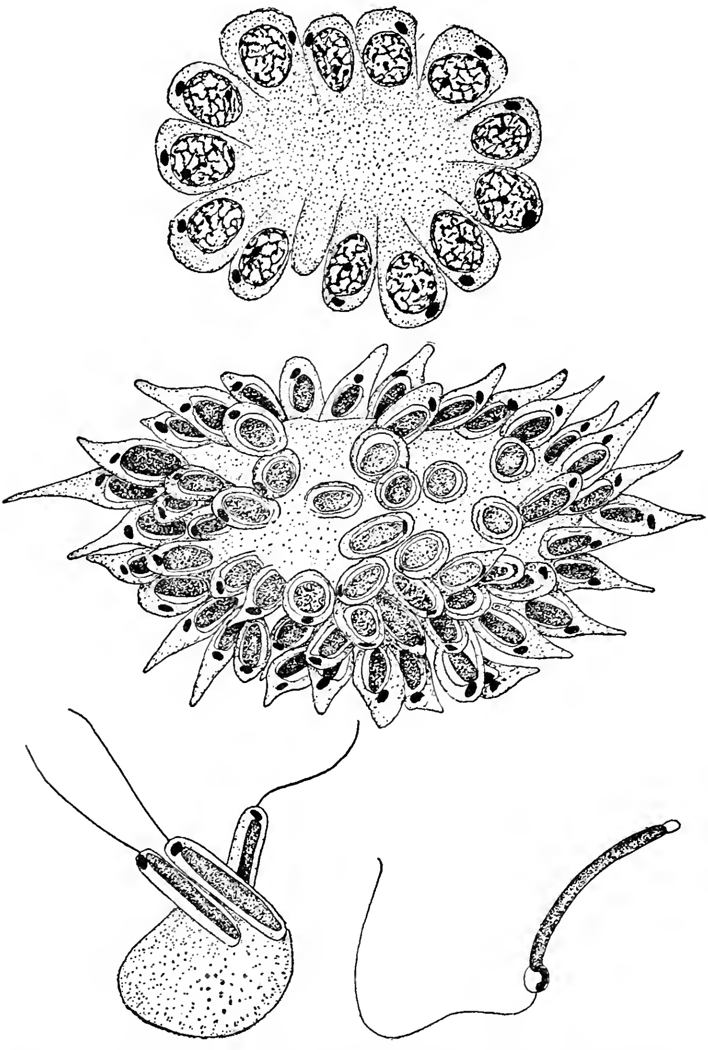


FIG. 64.—Stages in the development of spermatozoa of the earthworm. (From Calkins.)

the peripheral nuclei. Each of these nuclei then begins to elongate, and to transform into a spermatozoon. The nucleus forms the head of the spermatozoon, which remains attached to the parent protoplasmic mass (blastophore); the centrosome forms the middle piece, while the cytoplasmic tail grows out at the distal end. The bulk of the spermatozoon thus is derived from the nucleus.

Under the dorsal wall of the median vesicle and directly opposite each testis there is a large convoluted, ciliated opening of the *sperm duct.* These ciliated funnels draw the mature spermatozoa into them, and thence they are conducted to the outer opening of the ducts on the 15th somite. The ducts from the ciliated funnels on each side of the worm unite to form a common duct leading to the 15th, so that two common sperm ducts, known as the *vasa deferentia,* open on the ventral surface (Fig. 63, sperm duct).

Female Organs of Reproduction.—These are much simpler in structure than the male organs, consisting of one pair of relatively large ovaries on the posterior face of the anterior wall of the 13th somite. The eggs, when mature, drop into a large-mouthed thin-walled funnel-like oviduct which opens on the ventral surface of the 14th somite (Fig. 63).

J. REPRODUCTION. FERTILIZATION AND DEVELOPMENT.—Fertilization of the earthworm eggs takes place after copulation, which leaves the sperm receptacles of the worm filled with mature spermatozoa. A tough resistant girdle is formed around the clitellum of each worm, and after the worms separate this girdle is worked forward, collecting albumen from the glands on the ventral surface, mature eggs as it passes the 14th, and mature spermatozoa as it passes the 9th and 10th somites, or openings of the sperm receptacles. When the girdle passes off the anterior end, it closes at the front end and afterward at the posterior end. The girdle thus forms a cocoon, which hardens later into a chitinous spindle-shaped vessel containing reproductive cells and albuminoid food material (Fig. 65). The eggs are fertilized in the coccoon by the spermatozoa, and development begins at once, continuing under the protection of the cocoon.

Cleavage of the egg is regular up to the 16-cell stage, with four vegetative cells at the lower, and smaller animal cells at the upper pole. The lower cells invaginate and form a typical two-layered gastrula. Up to this stage, development closely follows the type described on page 79, but from here on, it becomes complicated by the formation of a third germ layer, called the mesoderm. This arises from two *pole cells*, coming from the vegetative pole and taking an initial position in the segmentation cavity (Fig. 66). They then divide, forming a sheath of cells on each side of the median line and filling the segmentation

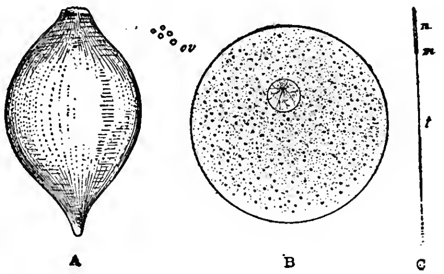


FIG. 65.—*A*, Egg capsule, enlarged five diameters (a few eggs, *ov.*, are shown near by on the right enlarged to the same scale); *B*, an ovum highly magnified; *C*, a spermatozoon still more highly magnified; *n*, nucleus or head; *m*, middle piece; and *t*, tail. (From Sedgwick and Wilson.)

cavity. In the meantime, the embryo has elongated in the main or antero-posterior axis passing through the blastopore; new ectoderm cells are pushed in from the ectoderm, and secondary mesodermal pole cells are separated from the mesoderm. The former are the first stages of the nervous sytem, and are known as *neuroblasts*. The latter are of different kinds, with different functions to play later. Some are muscle-forming cells called *somatoblasts*, and some are nephridia-forming, known as *nephroblasts*. All give rise to sheets of cells which become differentiated into the ultimate adult structures—nervous system, muscles and nephridia.

Meanwhile, the masses of mesoderm cells on each side of the median line begin to show traces of a loose structure, and later, well-marked spaces or cavities are developed from these spaces and assume regular shapes. They are first clearly formed in the region of the blastopore, as regularly arranged cavities lined by mesoderm cells. These cavities are the coelomic cavities of the adult, and their anterior and posterior walls form the dis-

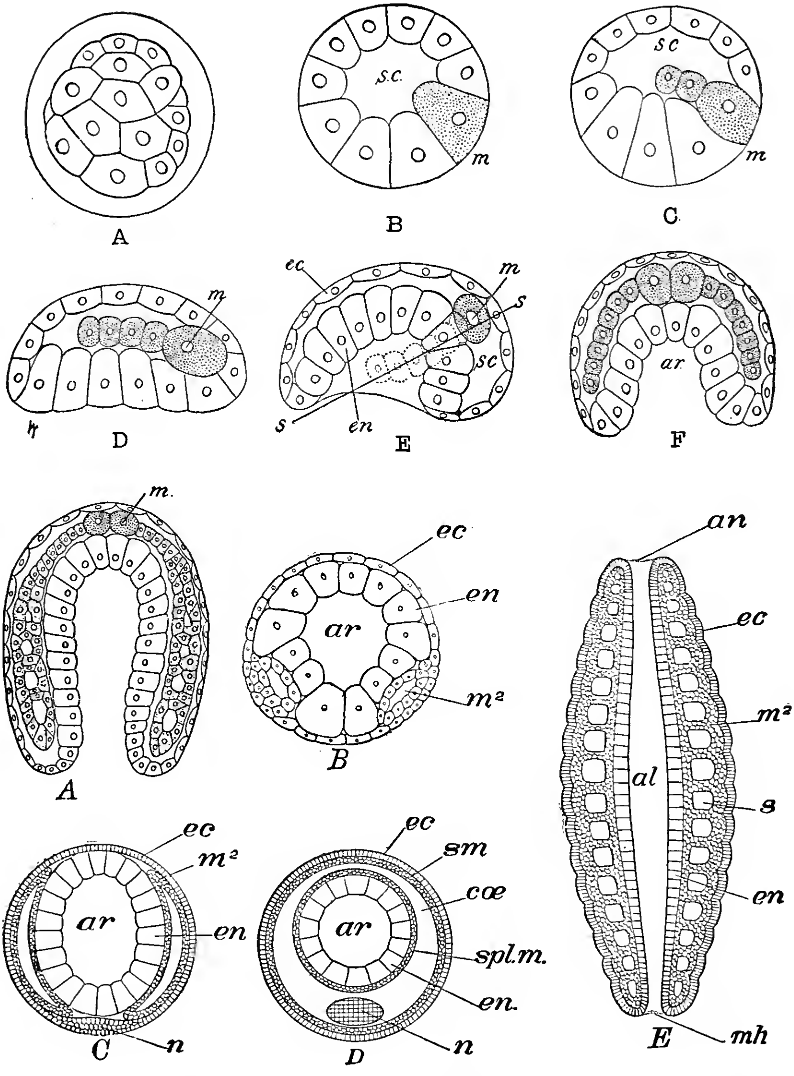


FIG. 66.—Diagrammatic figures of the early and embryonic stages in development of the earthworm. *A–F*, gastrulation showing the formation of the two layers ectoderm and endoderm, and the beginning of the mesoderm arising at the outset from the cells shown at *m*; the lower five figures show the origin of the coelomic chambers and the dissepiments. *al*, alimentary tract; *an*, anus; *ar*, archenteron; *cœ*, coelom; *ec*, ectoderm; *en*, endoderm; *m*, mesoblast pole-cell; m^2, mesoblast tissue; *mh*, mouth; *n*, nerve cord; *sc*, segmentation cavity; *sm*, somatic mesoderm; *spl.m*, splanchnic mesoderm; 8, eighth coelomic cavity. (From Sedgwick and Wilson.)

sepiments marking out the metameres of the mature animal. Thus the coelomic cavities are mesodermal in origin and are lined by mesoblast, this lining, known as endothelium, thus having a different origin from the epithelium of the gut which comes from the primary endoderm, or from the epithelium of the skin which comes from the primary ectoderm. The primitive enteric cavity of the gastrula gradually develops through a series of changes into oesophagus, crop, gizzard, and stomach intestine. The ectoderm turns in at the mouth end and at the posterior end, where the anus breaks through. Two regions of the digestive tract are thus lined by ectoderm, that of the mouth, termed the *stomodaeum*, and that of the anal end, called the *proctodaeum*. The chlorogogue cells are formed from mesoderm, as are also the blood vessels, muscles, reproductive organs and seta sacs. The young worm is now ready for an independent life, and it leaves the cocoon after from two to three weeks.

Summary of The Derivatives of The Germ Layers

Endoderm.	Ectoderm.	Mesoderm.
Oesophagus	Outer epithelium	All muscles
Crop	Nervous system	Endothelium of coelom
Gizzard	Stomodaeum	Chlorogogue cells
Stomach-intestine	Proctodaeum	Calciferous glands
	Ends of nephridia	Blood vessels
		Dissepiments
		Nephridia, functional parts
		Seta sacs
		Reproductive organs

CHAPTER VII

HOMOLOGY AND THE BASIS OF CLASSIFICATION

SYSTEMS of organs similar to those of the earthworm are found in all animals higher in the zoological scale than Hydra and the coelenterates. In some cases the organs are even simpler than those of the earthworm, but in the great majority of animals they are more complex. The complexity is brought about by the specialization of parts, leading to more extensive and more detailed division of labor. The power of modification possessed by animals makes possible an infinite number of minor differences, as well as a great number of major differences, by which we mean easily recognizable structural differences. A *species* is a group of animals or plants in which the individuals differ by no major structural differences. It is estimated that more than 500,000 species of animals exist at the present time.

Species of like nature are grouped into *genera*, or aggregates of animal types, which agree in the main elements of structure and function. Genera in turn are grouped into *families*, families into *orders*, orders into *classes*, and classes into races or *phyla*. Different phyla have few characters in common; classes have numerous common features, orders still more, and so on down to species in which all characters are similar, except for minor variations, such minor features giving the basis for varieties.

One great interest to biologists in the study of comparative anatomy is to trace out the relationships of parts which have become differentiated from generalized organs. Another series of problems has to do with the causes which have led to such differentiation; and still another series has to do with the possibility of inheritance of such differentiations.

Zoologists recognize some seventeen primary phyla or races of animals as follows:

Group comprising Amoeba, Euglena Paramecium, etc., upward of 10,000 species — Phylum Protozoa

Group comprising sponges upward of 800 species — Phylum Porifera.

Group comprising Hydra, sea-anemones, etc., upward of 3000 species — Phylum Coelenterata

Group comprising comb-bearing jelly forms, upward of 500 species — Phylum Ctenophora

Group comprising tape worm and flat worms, upward of 1600 species — Phylum Platyhelminthes

Group comprising round worms, filaria, etc., upward of 1000 species — Phylum Nemathelminthes

Group comprising ringed worms, earthworm types, upward of 2500 species — Phylum Annelida

Group comprising lobster, crab, shrimp and allies, upward of 8000 species — Phylum Crustacea

Group comprising insects breathing by tracheae, upward of 300,000 species — Phylum Insecta

Group comprising centipedes, spiders, ticks, etc., upward of 5000 species — Phylum Arachnida

Group comprising clams, snails and allies, upward of 22,000 species — Phylum Mollusca

Group comprising star fish, sea cucumbers, etc., upward of 2500 species — Phylum Echinodermata

Group comprising fish, frogs, reptiles, birds, mammals, upward of 25,000 species. — Phylum Vertebrata

In addition to these there are several minor races which are recognized by biologists, but in which the number of species is comparatively small; here, for example, are the phyla Rotifera (350 species), Polyzoa (700 species), Brachiopoda (100 species) and Tunicata (300 species).

No one has made an accurate enumeration of the existing species of animals, but it is safe to say that more than 350,000 species are known and grouped into distinct phyla.

In each phylum, although the type is the same throughout, the structures may be so modified as to give very distinct forms of animals. Different types of vertebrates give the most familiar examples of this, mammals, birds, reptiles, amphibia and fish being widely different from one another, yet all belong to the same phylum. Birds, being fundamentally of one type, are grouped together as a class; mammals, reptiles, etc., form other and fairly homogeneous classes, five classes in all, in the race of vertebrates.

Further subdivision is necessary for the complete classification of animals. The classes which form the most comprehensive groups within the phyla are frequently broken up into sub-classes, and these into orders, the basis of classification being structures or mode of life, or some other pronounced characteristic or aggregate of characteristics. The sub-class Oligochaeta, for example, includes a group of worms inhabiting fresh water, and another group which burrow into the earth. The former are classified as an Order Limicola, while the latter are placed in the Order Terricola. Orders, in turn, are sub-divided into sub-orders and families, and the families into genera, the basis of classification, as before, being structures where possible, or some prominent characteristic. Thus Megascolex, Allolobophora, etc., are similar to Lumbricus, the earthworm, forming different genera in the common family, Lumbricidae. According to such a scheme, therefore, the animals studied here are classified as follows:

Genus	Species	Family	Order	Class	Phylum
Amoeba	proteus	Gymnamoebidae	Rhizopoda	Sarcodina	Protozoa
Euglena	viridis	Euglenidae	Euglenida	Mastigophora	Protozoa
Paramecium	caudatum	Paramecidae	Holotrichida	Infusoria	Protozoa
Hydra	fusca, viridis	Hydridae	Leptolina	Hydrozoa	Coelenterata
Taenia	solium	Taeniidae	Polyzoa	Cestoda	Platyhelminthes
Lumbricus	terrestris	Lumbricidae	Oligochaetida	Chaetopoda	Annelida
Homarus	Americana	Astacidae	Decapoda	Malacostraca	Crustacea
Callinectes	hastatus	Cancridae	Decapoda	Malacostraca	Crustacea

At first glance it is often difficult to classify animals even to the phylum, and in some cases only a prolonged study furnishes the key to relationships. Animals that fly, for example, including bats, birds, and insects, all have wings, and might be classified in one group as "beasts of the air." But study of bats and birds shows that they belong to two entirely different classes, the bats having wings like the arms and fingers of a mammal and the mammary glands of the mammals, while birds have especially modified fore limbs, entirely different bone structure and other organs, which place them in the class Aves. Birds and insects are also different, both in the character of the wings and in the absence of an internal bony skeleton in the latter. While the functions of wings of birds and insects are the same, their anatomy shows an entirely different mode of origin and different secondary structures. In such cases the organs are said to be *analogous*. When organs have the same ancestry, that is, when they come from some common part of an ancestral type, they are said to be *homologous*. The wings of a bird have had the same ancestry as the fore-legs of beasts or the arms of man; so too have the wings of a bat—hence arms, fore-legs of beasts, and wings of bat or bird are homologous structures. It is quite otherwise with the wings of a bee or fly. These have had an entirely different ancestry from the wings of a bird and are not homologous with the latter. Wings of different insects, however, are homologous.

Homology, or *genetic relationship* of organs and structures in general, is the ground principle of classification of species. Two organs on different animals may be homologous whether they perform the same functions or not, and conversely, the same functions may be performed by organs not homologous. The study of homologies therefore is one of the most important in comparative anatomy and in taxonomy. The walking legs of vertebrates and those of a lobster are the same in function and are analogous organs, but no one would compare them morphologically, and they are not homologous in any sense. It is quite otherwise, however, with the legs of lobsters, of crabs and of shrimps, which are homologous, having had a like origin. All of the appendages of a lobster or crab, furthermore, although they have widely different functions and are quite different in form and appearance, are serially homologous with one another. The crustacea therefore give excellent subject matter for the study of homology.

I. The American Lobster, Homarus Americanus

Habits, Mode of Life.—Lobsters live in comparatively shallow waters along the Atlantic coast from Labrador to Delaware, in depths of from one to 100 fathoms. They are predatory, but usually capture their prey by stealth, while hidden in weeds on the sea bottom. They are also well-known scavengers, and will quickly discover and devour dead fish to which they are attracted through an acute sense of smell. Ungainly on land, their movements in water are graceful, where they may run about with agility or shoot backward with surprising speed. When enemies are about they are pugnacious, but at the same time wary and resourceful, and are well able to defend themselves. A closely related species is the European lobster (*Homarus gammarus*), while somewhat similar forms are the *langouste* of the French coast, and the so-called Norwegian lobster (*Nephrops norvegicus*).

General Structure and Systems of Organs.—Like the earthworm, the lobster and all of its allies are metameric animals. The somites or metameres may easily be seen in the abdomen, where they are separate, but in the anterior region they are fused together, those of the head (cephalon) fusing with those of the thorax to form the main part of the animal, termed the *cephalothorax* (Fig. 67). All parts of the body are covered by a firm lifeless cuticle of chitin which, on the back (dorsum) and on the side (tergum), is impregnated with calcium salts, until quite solid. In some species this covering becomes almost rock-like in its solidity, containing much pure limestone. The chitin and lime are secreted by cells of the skin, which is drawn down over the sides of the cephalothorax in two great folds like the front flaps of a coat; the two flaps thus cover and protect two branchial chambers on the two sides of the cephalothorax, where the gills lie, and are called the *branchiostegites* or gill protectors. On the under side of the body, especially in the abdomen, the chitin is thin and transparent, with heavier ribs of chitin for muscular support, while, in the region of the cephalothorax, these heavier bars are united to form an internal skeleton-like structure, termed the *endophragmal* skeleton. This forms the floor of the body cavity, and protects the ventral chain of ganglia (Fig. 69, p. 171).

APPENDAGES AND SERIAL HOMOLOGY.—The metameric structure of the body is well indicated by the appendages, of which there is one pair to each somite. The relation of the appendages to the somite is clearly shown in the abdominal region where the

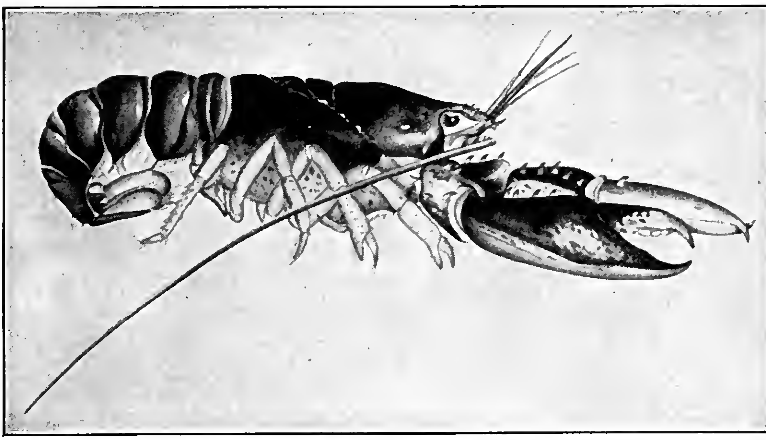


FIG. 67.—The American lobster, *Homarus americanus*, showing regions of the body.

somites are free, but in the cephalothorax where the somites are fused, their external signs are given only by the several pairs of appendages lying closely packed over one another. Some of these belong to the head, and some to the thorax. The number of somites in lobsters and in all of the higher types of crustacea is limited to 20, of which 5 form the head, 8 the thorax, and 6 the abdomen (some zoologists allow 6 for the head). Corresponding to these somites, there are 19 (or 20) pairs of appendages which are named according to their functions, and are distributed as follows:

Head	Antennae Antennules Mandibles or jaws 1st maxillae 2nd maxillae	Thorax	1st Maxillipedes 2nd Maxillipedes 3rd Maxillipedes 1st Ambulatory (chelae) 2nd Ambulatory 3rd Ambulatory 4th Ambulatory 5th Ambulatory
Abdomen	Copulatory 1st swimmerets 2nd swimmerets 3rd swimmerets 4th swimmerets 5th swimmerets, or caudal appendages Telson (unpaired)		

The terminal joint of the abdomen, termed the telson, bears the anus, and is not usually regarded as a somite.

Different as they are in function and different as they appear to be in structure, the appendages are all built upon the same plan, and throughout the series we can trace the same homologous parts. The simplest of all are the appendages of the abdomen, where three fundamental parts can be easily distinguished, a basal portion, termed the *protopodite*, attached to the body, and two distal portions, one of which is inside, that is near the median line of the animal, the other outside. The internal part is called the *endopodite*, the external part the *exopodite* (Fig. 68). In the male, the first abdominal appendages show considerable modification from the others. Here the external parts have disappeared, leaving only the endopodites which are tightly fused with the protopodites to form the copulatory organ. In the female, the appendages of this somite are degenerated, as shown by the entire absence of distal parts, leaving only the protopodites which are drawn out into plume-like organs. The terminal appendages are similar to the other abdominal appendages, but are much enlarged in all parts and strengthened by chitin and lime salts.

The thoracic appendages are highly modified. All ten of the ambulatory consist of one distal branch only, the endopodite,

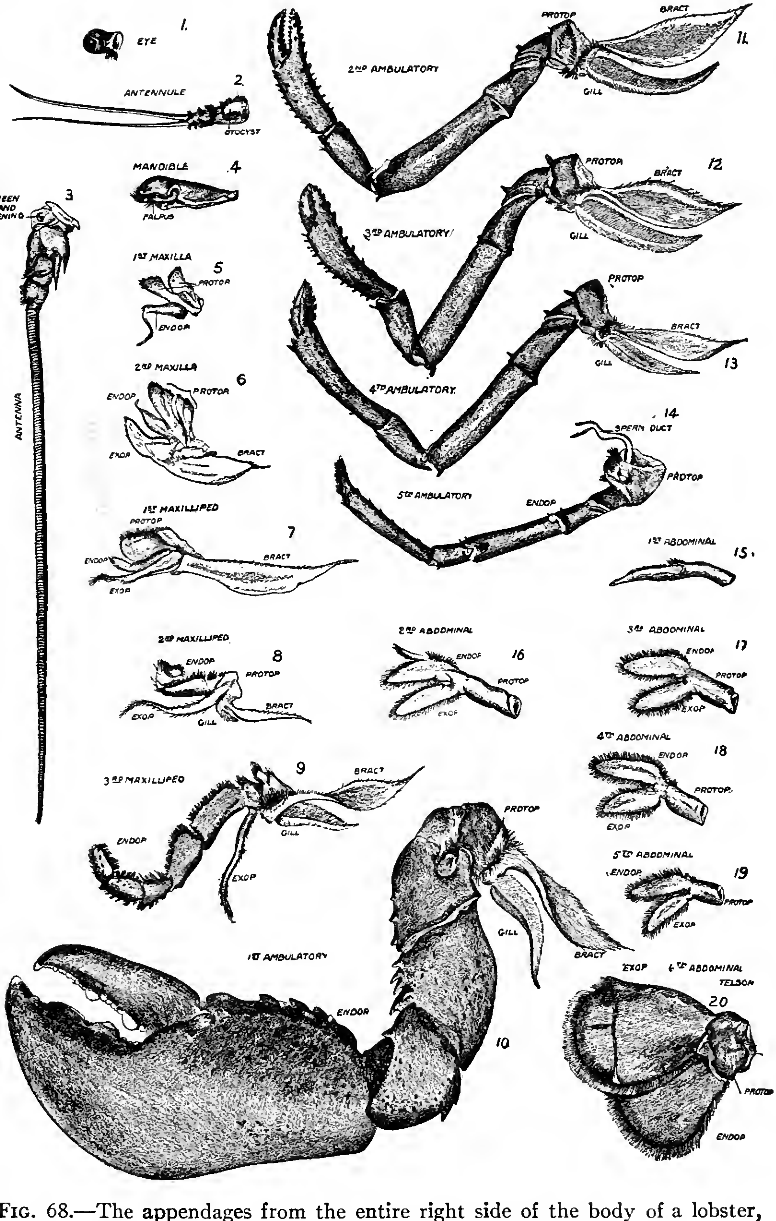


FIG. 68.—The appendages from the entire right side of the body of a lobster, arranged serially to illustrate serial homology.

attached to the protopodites which, in turn, are freely attached to the body. On the fifth ambulatory protopodites and on the internal surfaces, are the openings of the male organs of reproduction (Fig. 68, 14). Here also the skin or membrane of the protopodite is drawn out into a leaf-like organ, termed the bract or flabellum, a structure which reappears in each of the thoracic appendages and serves as a partition wall between the gills in the branchial chamber. All of the other ambulatory appendages are like the fifth in consisting of one shaft, the endopodite, but on the protopodites of the first four, in addition to the bracts, there are outgrowths of membrane which form the gills in the branchial chamber (Fig. 68, gill). The endopodites are jointed, consisting of five parts or joints termed podomeres. There is nothing in their structure to show that they are endopodites and not exopodites, this fact being established by embryology, all of the thoracic limbs appearing first as biramous appendages with both exopodites and endopodites (see Fig. 78). The exopodites wither and disappear as growth progresses, leaving only the endopodites. Similarly with the antennae, jaws and antennules, the exopodites have disappeared or are so highly modified as to be indistinguishable, leaving only the inner branches. The remaining appendages of head and thorax are not so highly modified that homologous parts cannot be made out, although they must be studied part by part with the principles of homology in mind. These parts are well shown in the accompanying figures.

All of these diverse appendages have been developed from the primitive simple type of the biramous appendage of the abdomen, and well illustrate the principle of adaptation for particular functions. The walking legs, for example, are adapted for this means of locomotion, and the anterior pair for offence and defence; the jaws for crushing food; the maxillae and maxillipedes for seizing, sifting and propelling food into the jaws. It would seem as if unnecessary parts of the appendages had disappeared, leaving only those portions which are useful for the purpose of the particular appendage. Many biologists hold that such adaptations come through use or disuse of parts, the useless por-

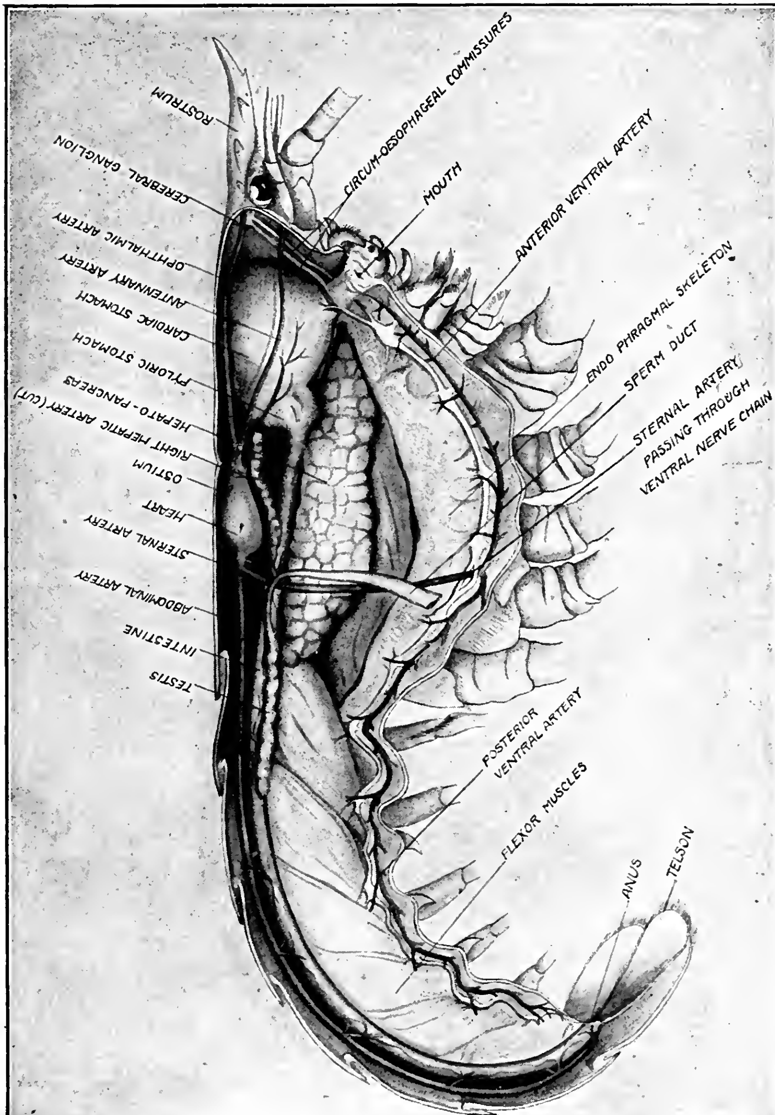


FIG. 69.—Longitudinal section of the lobster showing the arrangement of the internal organs.

tions degenerating, the useful parts increasing in usefulness by continued activity. Another group of biologists, however, take the very opposite view, viz., that the function or use of an organ depends upon its position, the maxillae and maxillipedes, for example, crowded together in the thorax, have the functions of seizing, sifting and propelling food matters forced upon them, and could not do otherwise. In either case, there is general agreement that all appendages are derived from one ancestral biramous type of appendage, which is regarded as a generalized organ capable of differentiation and development along different lines, until structures result of widely different appearance, although homologous throughout. The study of comparative anatomy is, in large part, only the ferreting out of such homologies in animals of the same or allied groups (see Chapter IX).

Digestive System.—The lobster is primarily a scavenger, and eats all forms of dead and decaying protein matter. For this purpose, it has a highly developed digestive apparatus, capable of extracting the nutrient material out of all sorts of food.

The most conspicuous part of the digestive system is the chitinous fore-stomach or cardiac stomach into which the oesophagus opens (Fig. 69). In the walls of this organ special chitinous processes are developed, forming tooth-like accumulations which are worked by special muscles attached to the body wall. These teeth form a grinding machine, known as the *gastric mill*, which triturates the food passed on by the jaws. They also form a sieve, guarding the opening into the functional or pyloric stomach and preventing all bones or large materials from entering the physiological stomach, in which digestive juices are poured from the large digestive glands known as the *hepato-pancreas*. After action by these fluids, the undigested residue is passed on to the intestine which lies over the dorsal sides of the ventral muscles.

Not only are digestive fluids poured into the pyloric stomach, but some of it also goes into the cardiac stomach, where the food particles are softened and prepared for passing the gastric filter between the cardiac and pyloric portions. Food thus passed through is distributed in the various diverticula of the hepato-pancreas, where the bulk of digestion takes place. Here also are the absorbing cells which take up the digested foods and turn them over to the blood (Jordan). The end gut or intestine plays no rôle either in digestion or in absorption. The absorption cells have the same general structure as those of the earthworm. The connective tissue in which the hepato-pancreas is embedded is richly supplied with blood vessels and lymph spaces, which probably receive digested food directly from the absorption cells.

The digestive fluid which comes from the hepato-pancreas is very complex. It is of yellowish-brown color, not viscous, is rich in albumen, contains a free alkali, and gives a flocculent precipitate with acids. This precipitate, filtered and washed, gives all of the reactions of a globulin. The digestive ferments contained in this juice are (1) a protease or proteolytic ferment similar to the protein digestive ferments of the earthworm and other invertebrates; (2) a lipase or fat emulsifying ferment; (3) an amylase or starch converting ferment. In other allied forms of crustacea, still more ferments have been obtained from the digestive juices, and these may be present in the lobster. Thus a cellulose dissolving ferment (cytase) was discovered by Biedermann and Moritz from the crayfish.

The digestive tract of the lobster thus shows a considerable advance over that of the earthworm or other lower types. The functional digestive part is removed from the main tract, but is derived from it as an outgrowth or diverticulum. It represents a step toward still higher types of development, where secretions from different glands are poured into a digestive sac or stomach and intestine. Here in the lobster, the digestive gland still acts as a part of the glandular tube of a worm; the food is contained in it, and digestion and absorption take place in it instead of in the main digestive tube. In higher animals, all of the glands pour their digestive fluids into the main tube.

The Blood Vascular System.—In the lobster and other forms of arthropods, all of the blood of the organism passes sooner or later from the main arteries into the general cavity of the body, where the food material is taken up. Such a circulation of blood is spoken of as an *open circulation*, as opposed to the *closed circulation* of organisms like the earthworm, which have both arterial and venous capillaries so that the blood is always within specialized blood vessels. The body cavity of the lobster, therefore, is quite different from the coelom of an earthworm and other animals. It is not lined by endothelium, and

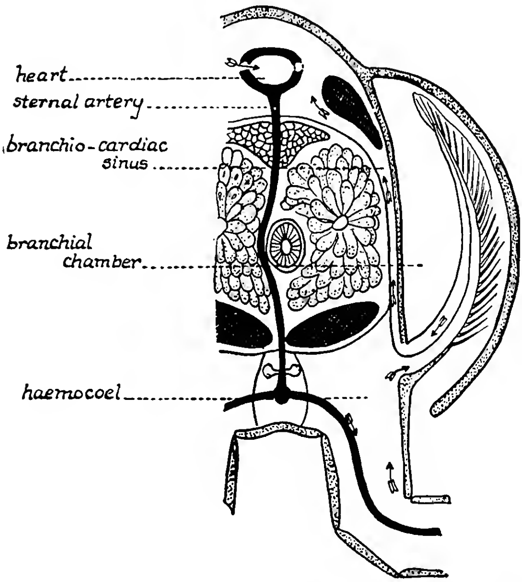


FIG. 70.—Transverse section through the thorax of a lobster to show the relation of the gills to the bronchial chamber, the haemocoel, and the chamber of the heart. (Modified after Lang.)

does not contain the opening of the excretory organs (nephridia), nor do its walls give rise to the germ glands. It corresponds rather to a large blood sinus, and for this reason is termed a *haemocoel* and not a coelom. The real coelom of these forms is limited to the small cavities of the nephridia and the germ glands.

Gills.—The blood mixed with digested food, in the haemocoel, passes slowly into the gills, where it is aerated. The gills are pockets of tissue derived from the epithelium, drawn out in the form of long triangular pyramids with broad bases and pointed tips (Fig. 70). Each gill, in turn, is drawn out into innumerable flaps or lamellae, closely packed together like leaves of a book. In each gill there are two blood vessels, one ventral, one dorsal. The blood from the body cavity enters the ventral vessel, passing into the gills; here capillary vessels branch into the lamellae, and are continuous with similar capillaries emptying into the dorsal vessel. In the gills, therefore, there is a small closed circulation from one venous ventral tube into another dorsal tube, in which it passes toward the heart. The thin-walled lamellae of the gills are in contact with water, which passes through the branchial chamber by activity of the scoop or *scaphognathite*, which consists of the fused bract and exopodite of the second maxilla (Fig. 68). The blood is thus brought in contact with fresh water and is aerated, giving off CO_2, and taking oxygen before passing to the dorsal branchial tube.

Various parts of the body wall are drawn out to form these triangular gill pockets. Some are on the appendages and are termed *podobranchs;* others are on the basal joint of the appendage and do not come out when the appendages are removed. These are termed *arthrobranchs*, from their position on the joints; still others originate on the body wall itself, and are termed *pleurobranchs* or side-wall gills. The number of each kind gives the basis for a gill formula, which differs with each species of crustacea; the formulae for the lobster and the crayfish are given below:

	Podobranchiae	Arthrobranchiae	Pleurobranchiae
Crayfish (Astacus)	6	11	3 (2 rudimentary)
Lobster (Homarus)	6	10	4

After aeration in the gills, the blood is slowly passed on into large branchial sinuses (*branchio-cardiac sinuses*), which lead into the pericardial chamber containing the heart. The latter has the form of a pentagonal shield with six openings or *ostia*, of which one pair is dorsal, one lateral, and one ventral. Blood from the pericardium enters the heart through these ostia and is prevented from going back again by valves on the inside, which are closed upon pressure due to contraction of the heart. This pressure forces the blood out into arteries as follows:

one unpaired median artery, *ophthalmic*, which conveys blood to the eyes and surrounding organs; one pair of *antennary* arteries from the anterior sides of the heart, leading to the antennae and adjacent organs; one pair of *hepatic* arteries from the lateral ventral part of the heart, which are quickly lost in

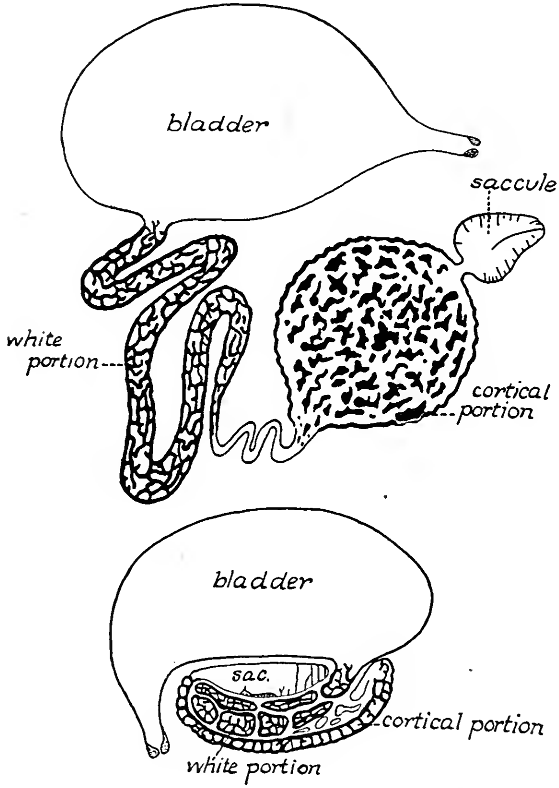


FIG. 71.—Diagram of the kidney of a crayfish (*Astacus fluviatilis*). (From Parker and Haswell after Marchal.)

branches in the hepato-pancreas; one unpaired dorsal *abdominal* artery from the posterior angle of the heart, and one unpaired *sternal* artery, which passes directly downward from the posterior ventral portion of the heart to the ventral surface, where it enters the *ventral* artery which traverses the entire ventral surface. The dorsal abdominal continues posteriorly to the telson, giving off one pair of large arteries in each somite (Fig. 69).

The vascular system thus consists of an arterial system and a great body cavity, which forms a blood sinus, taking the place of a venous system in other animals. The pressure forcing the blood through the gills comes from the constant addition of blood to the body cavity through muscular heart beats, aided by the vacuum produced when the heart is emptied. Movements of the appendages also tend to keep up a constant circulation in the sinuses.

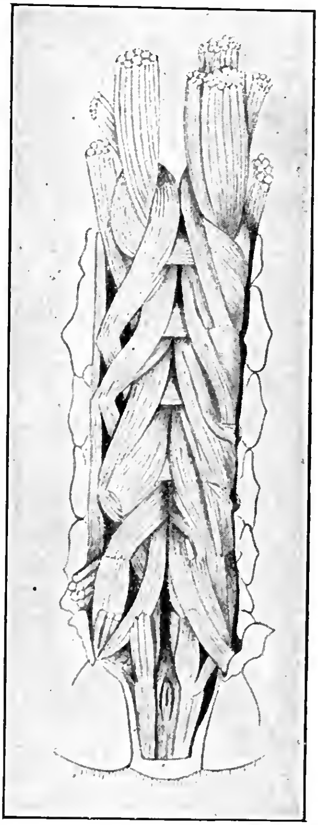


Fig. 72.—The abdominal musculature of the lobster to show the complicated arrangement of extensors and flexors. (From Gerstaecker, after Milne-Edwards.)

The Excretory System.—Excretion in the lobster must be comparatively sluggish, for the organs for the purpose are small and poorly placed for active function. This may be due to the fact that the lobster and similar forms are naturally sluggish animals, lying in wait for prey, feeding on carrion, etc., rather than moving about actively in search of food. The nephridia are small flattened coiled organs at the bases of the antennules, and consist of a rather large "bladder" and a small glandular part (Fig. 71). From their characteristic color they are also known as the green glands. The external openings of the nephridial ducts are on the inner faces of the basal segments (Fig. 68, 3). Some excretion of waste matters may also take place through the skin.

The Muscular System.—The muscles of the lobster are

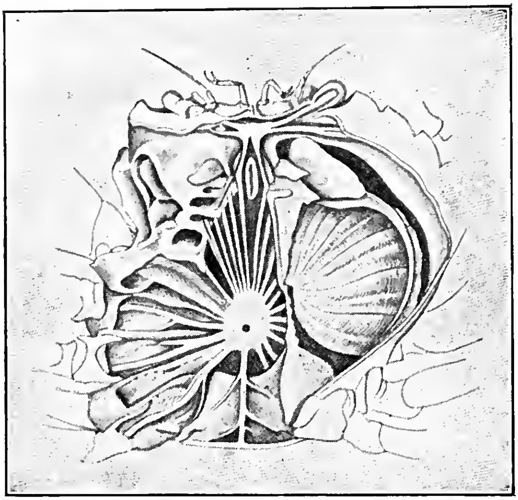
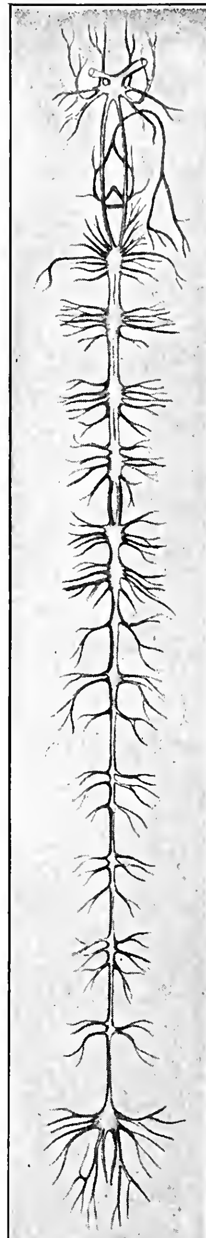


FIG. 73.—The central nervous systems of the lobster and the crab. The ventral chain of ganglia in the crab are concentrated in one ventral mass, the sternal artery passing through it. (From Gerstaecker after Cuvier.)



highly developed, the large ventral muscles of the abdomen being remarkably powerful. These are inserted anteriorly on the inner walls of the cephalothorax (Fig. 72), one on each side. In the abdomen they twist around one another like a huge muscular rope, and are intimately connected with the ventral exo-skeletal parts of each somite. Contraction of the muscles results in the simultaneous ventral turning of all the abdominal somites, and the vigorous flop of the lobster results. Similar, but smaller and straight muscles lie on the dorsal surface of the huge ventral muscles, and are similarly connected with the dorsal exo-skeleton. When these muscles contract, the abdominal segments are straightened out. These *flexor* and *extensor* muscles thus act quite differently from the dermal musculature of the earthworm. Other important muscles work the various appendages, of which those of the giant chelae are the most highly developed. Still others manipulate the gastric mill, theeyes, etc.

The Nervous System.—In general arrangement, the nervous system of the lobster is strikingly similar to that of the worm; here again we find a ventral chain of nerve ganglia which, however, are dorsal to the ventral blood vessel. A pair of cerebral ganglia, close to the eyes, innervates these and adjacent organs. A long pair of circumoesophageal commissures connects the cerebral with the first ventral or sub-œsophageal ganglia. These, however, represent a fusion of thoracic ganglia, for just as the somites here have merged to form the cephalothorax, so these ganglia have fused into one. Between the fourth and fifth ganglia, the double nerve cord splits and allows the sternal artery to pass through. In the abdomen, the nerve chain is quite regular and similar to that of the earthworm, in having one pair of ganglia to each somite (Fig. 73).

Fig. 74.—The otocyst of the lobster opened, showing sensory hairs and otoliths. (From Gerstaecker after Farre.)

Sense Organs.—In the earthworm, we have seen that there is a well-marked advance in nerve-organization over forms like Hydra, with grounds for dividing it into peripheral sensory and internal central nervous systems. The peripheral system consists of more or less isolated sensory cells with their nerve processes, more plentiful about the anterior end, but distributed nevertheless about the entire body.

In arthropods we find a great advance, over annelids, in complexity of the peripheral, or sensory, nervous system. Here similar sensory cells are grouped together to form different kinds of sensory organs of more or less complexity. In the lobsters we recognize: (1) tactile organs; (2) olfactory or smelling organs; (3) auditory or primitive hearing organs, and (4) organs of vision or eyes.

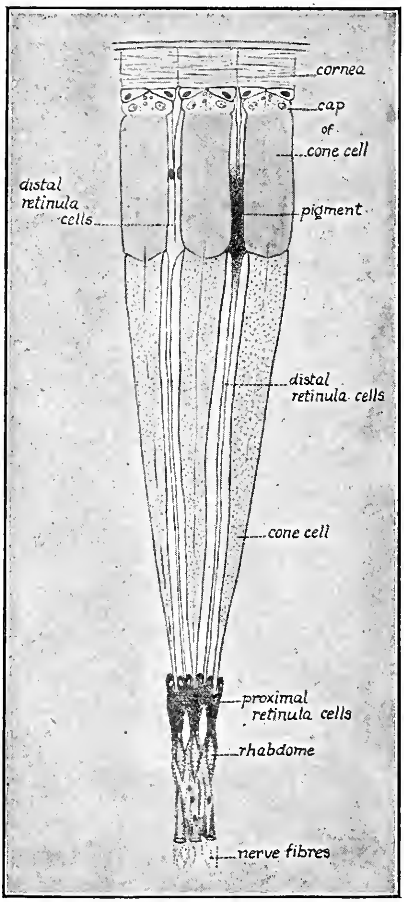


FIG. 75.—Three ommatidia from the compound eye of the lobster. (Modified after Parker.)

1. *Tactile Organs.*—The organs of touch are distributed over the body, usually on the appendages and in large numbers in the cephalic region, in the form of hairs. Each hair contains a nerve, with delicate nerve endings in cells forming the walls of the hair, and each hair contains a small ganglion.

2. *The olfactory organs* are similar to the tactile, but differ in the position of ganglia and arrangement of the nerve endings. They are distributed mainly on the antennules.

3. *The auditory organs* are technically termed "otocysts," and their functions are incited through the action of small crystalline foreign bodies, termed "otoliths." The cysts or capsules are located on the inner side of the basal joints of the antennules,

and open to the outside by a hair-protected aperture at the distal angle of the membranous wall of the capsule (Fig. 74). Inside the capsule is a gelatinous mass of semi-fluid material, through which fine sensory hairs, innervated from a main sensory branch, are abundantly distributed. The otoliths or crystals are also distributed throughout the gelatinous matrix. When the equilibrium of the organism is disturbed these otoliths impinge on the sensory hairs, and thus originate stimuli and motor responses by which the animal regains its balance. Sound vibrations may also have the same effect on the hairs directly. The so-called "auditory" organ perhaps has less to do with sound vibrations than with the balance or equilibrium

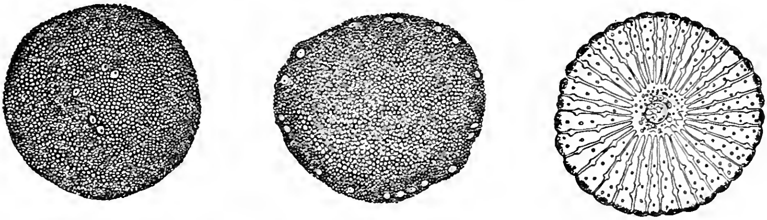


FIG. 76.—Centrolecithal type of egg and cleavage in the crayfish. The nuclei, after several divisions, pass to the periphery of the egg after which radial cleavage planes divide it into cells. (From Parker and Haswell.)

of the body, and compares with the lateral organs of fishes or the semi-circular canals of vertebrates.

4. *The Eyes.*—The eyes of arthropods are entirely different from those of higher groups of animals. Vision is compound, the eyes being made up of thousands of minute units, termed *ommatidia*, each ommatidium having a complex structure (Fig. 75). The facets (cornea), like mosaics, form the outer cuticle of the eye.

REPRODUCTIVE SYSTEM.—The sexes are separate in the majority of crustacea, and the gonads are relatively much larger than in the earthworm. The testes are long, beaded organs, white in color, lying dorsally to the hepato-pancreas, one on each side of the dorsal blood system. The male gonoduct or vas deferens originates about two-thirds of the length from the anterior end, and runs downward through the body cavity to open to the outside on the basal segment of the fourteenth appendage (Fig. 68, 14). From this opening the spermatozoa, packed together in bundles called spermatophores, are caught by the tubular exopodites of the fifteenth pair of appendages, and placed on the genital groove of the female during copulation.

The ovaries are similar in general shape and in position, but are bright orange in color, and the female gonoduct or oviduct, while it originates in the same relative position, opens to the outside on the basal segment of the twelfth appendage. The eggs are fertilized as they pass out, and are covered with a gelatinous mucus by which they stick to the hairs bordering the swimmerets or abdominal appendages. Thousands of them become thus attached, to be swayed back and forth by the movements of the swimmerets during the early stages of development.

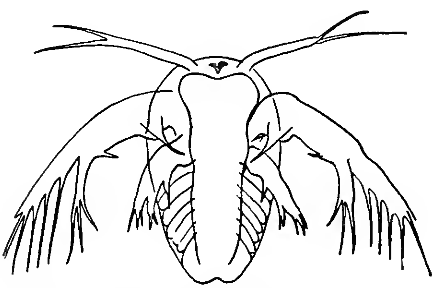


Fig. 77.—A typical nauplius larva of the copepods with three pairs of appendages.

Development and Metamorphosis.—The development of the earthworm, as of Hydra, begins with the division of the egg cell into two cells or blastomeres, each with one-half of the fertilization nucleus. Development of the lobster begins with the division of the nucleus, without division of the egg substance. The second, third, etc., up to the eighth division are the same, a multinucleated cell resulting, in which the nuclei arrange themselves around the periphery of the egg. Then the outer zone of protoplasm divides around each nucleus, the cleavage planes passing radially toward the egg center (Fig. 76). This type of cleavage is characteristic of the arthropods, and is called meroblastic, as opposed to holoblastic. The yolk is collected in the center of the egg, which for this reason is called *centrolecithal.*

Metamorphosis.—In the more generalized types of crustacea this method of cleavage leads to the formation of a free living embryo or *larva*, termed the *nauplius*. This larva has little resemblance to the parent, consisting of a small ovoidal body, with mouth, three pairs of biramous appendages and a median unpaired simple eye (Fig. 77). The appendages are the first three pairs of the adult, and in this stage have little similarity to the later antennules antennae and mandibles. Each consists of exopodite, endopodite and protopodite, which, with development of the larva, become transformed into the specialized organs of the head.

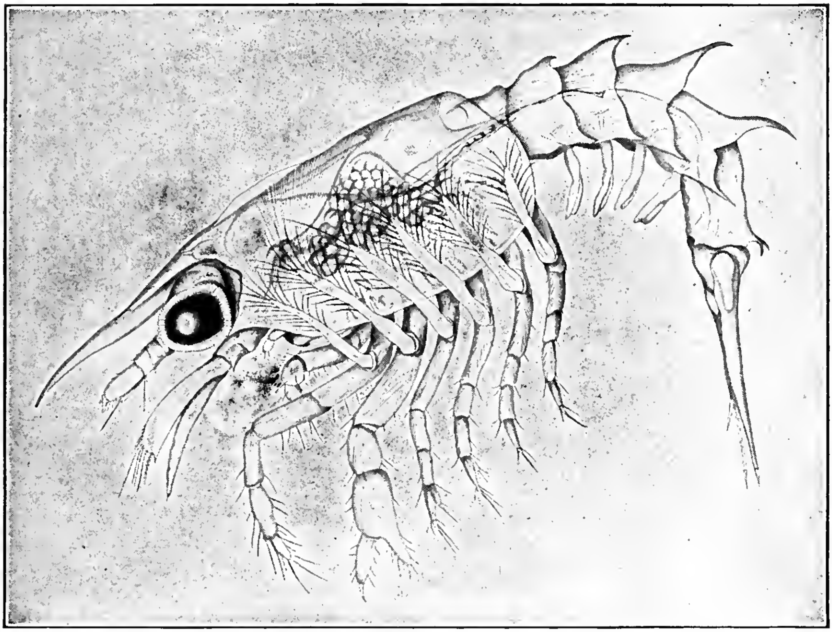


FIG. 78.—"Mysis" stage in the development of the lobster; a stage in which the thoracic appendages are all biramous (*cf.* Fig. 87). (From Herrick.)

Growth of the larva results in elongation of the body and the formation of somites at the posterior end. The terminal somite is formed first, and new somites are added by a process of growth, analogous to budding, which occurs between this terminal somite and the body. After each somite is thus formed, paired biramous appendages develop on it as outgrowths. A larval form thus develops from the nauplius, in which all of the appendages are provided with exopodites and endopodites ("Mysis" stage, Fig. 78).

Even in the early stages the body is covered by a carapace of chitin. This is by no means as heavy and tough as in the adult; nevertheless, it is highly resistant and unyielding. Growth of the body thus results in an organism with a covering too small for it—it outgrows its clothes. The chitin carapace then splits along the mid-dorsal line, and the organism detaches its tissues from the exo-skeleton and pulls itself out of its cramped quarters. A new chitin covering is then secreted, which lasts

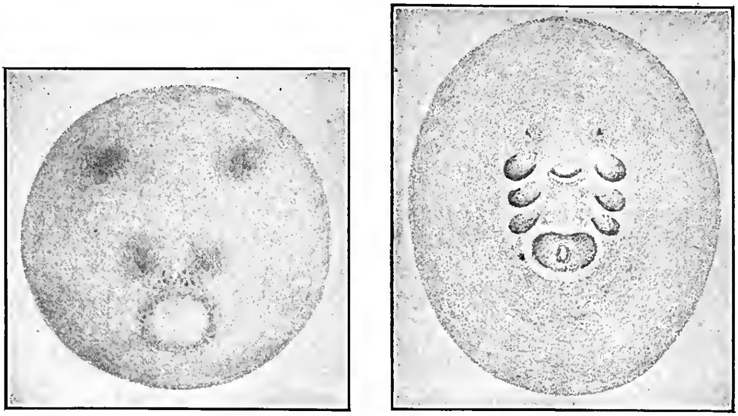


Fig. 79.—Stages in the early development of lobster homologous with the nauplius larva of the copepods. (From Parker and Haswell after Lang.)

until continued growth demands a new change. This process of moulting—termed *ecdysis*—is characteristic of the crustacea, and continues at lengthening intervals throughout the life of the individual. The "soft-shell" crab has just shed its old coat and has not yet produced a new one.

The lobster's development differs from that of more generalized crustacea, in that the embryo does not leave the egg membrane as a nauplius larva, but continues its embryonic development within the egg membrane, until it has grown into the general form of the parent. It then leaves the egg case (Figs. 79, 80), and grows by successive moults into the adult.

II. General Biological Interest of the Lobster

The structures and life history of the lobster teach, by analogy, the story of evolution. Structural adaptations of animals to different modes of life, interpreted on the principle of homology, furnish evidence of the origin of species from generalized types. The appendages of the lobster are originally all alike, and of a primitive biramous type. From this primitive type by

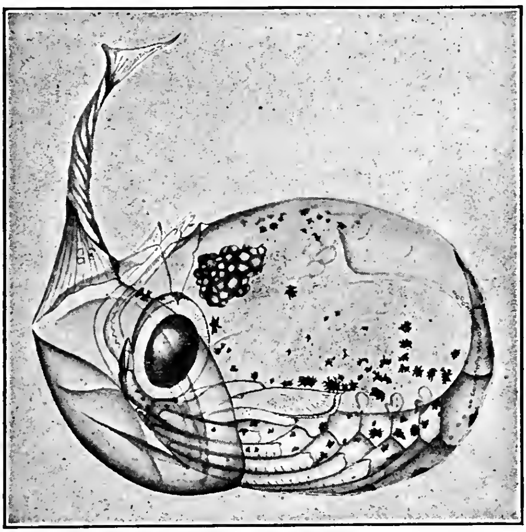


Fig. 80.—A young lobster leaving the egg case (on left). (From Herrick.)

various modifications, several different forms of the adult appendages are derived. These appendages, furthermore, are utilized for different purposes, thus illustrating the principle of *adaptation*—a generalized type of organ may become adapted to several different kinds of uses.

What happens among homologous parts in the individual lobster can, theoretically, take place in allied organisms of a given group, although the process cannot be watched as it can be in the lobster. We find, in existing animals, structural adaptations which we can interpret best on the theory of common origin. Thus, in this one group of crustacea to which the lobster belongs, we find that eight pairs of thoracic appendages is the rule. In the lobster, we see that five of these pairs are adapted for walking or locomotion, and three of them for assisting in procuring and manipulating food. So too, the crab, or shrimp, and many allied forms have the same distribution of the thoracic appendages, and zoologists group them together as an order of crustacea, called Decapoda. In other groups, however, we find different distributions of the eight pairs of thoracic appendages. One such group has only three pairs of walking legs; the remaining five are adapted for food manipulation (Order Stomatopoda). In another group, all eight are rudimentary, none being developed for walking (Order Cumacea), while in another, seven of the eight pairs are developed for walking, and only one pair serves for food manipulation (Order Arthrostraca). The assumption is made that all of these different types of Crustacea, because of their striking similarities, must be closely related, and must have had a descent from common ancestors. Such ancestors could not have been more specialized than are these types today; they must have been more generalized forms, from which different lines of adaptation could come.

Such generalized ancestral forms of the crustacea are represented among existing types, which form a sub-class (Entomostraca) of the crustacea. Their appendages and somites are more numerous than twenty pairs, and the appendages are of the primitive biramous type. How the more specialized forms of crustacea were derived from these more generalized types is a matter of speculation, involving the factors of inheritance and evolution which will be considered in a subsequent chapter.

III. Insects

Another series of illustrations of homology may be found in the group of insects, of which more than 200,000 are known. In these myriads of forms, the adaptations of wings and mouth parts are particularly striking.

Superficially, the insects are so similar to crustacea that formerly they were all classed together in the common phylum

Arthropoda. Some of the insects, however, have quite as close an affinity to the annelid worms, one genus, Peripatus, having many annelid characteristics. Biologists, therefore, agree in making crustacea and insects independent phyla, with common ancestors in annelid-like forms.

Like crustacea, the insect body is composed of somites which are regionally fused to form more or less independent head,

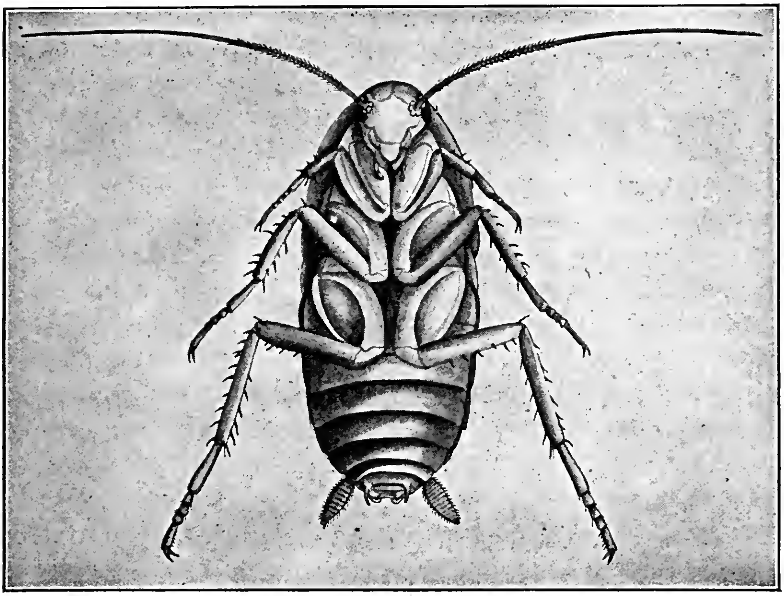


FIG. 81.—A cockroach, from the ventral surface.

thorax and abdomen. The head consists of five somites, the thorax of three, and the abdomen of eleven or less, the number of somites being highly variable in the abdomen, but fixed in head and thorax. The head always bears compound eyes and, very often, simple eyes in addition. It also carries one pair of antennae, and two pairs of pre-maxillae (Fig. 81). In the cockroach, the latter are united to form a labrum overhanging the mouth (Fig. 82). The head also bears one pair of mandibles or jaws, and two pairs of maxillae. In different orders of insects these mouth parts are adapted for different modes of nutrition. For biting and chewing in orthoptera (grasshoppers, cockroach, etc.), coleoptera (beetles), hemiptera (bugs), and hymenoptera (ants, bees and wasps); for sucking or licking, diptera (flies, mosquitoes, etc.), lepidoptera (butterflies, moths), and neuroptera (dragon flies, etc.). Just as we may trace homologies of the crustacean appendages, so we may trace the homologous parts of different insects in which the appendages are adapted for different functions (Fig. 82).

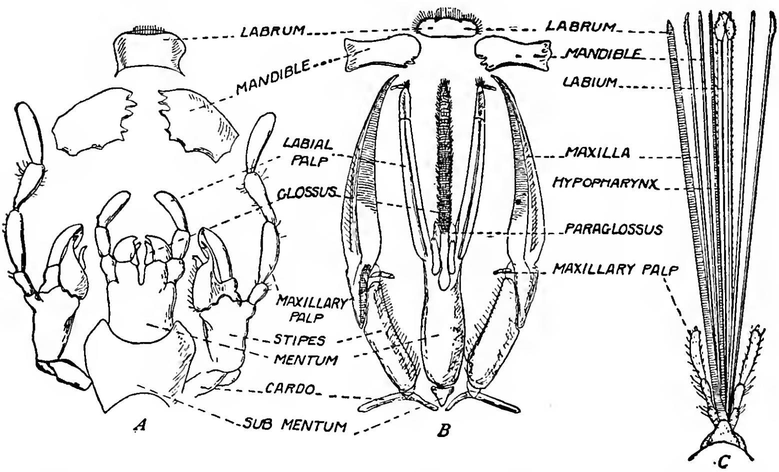


FIG. 82.—Homologous mouth parts of cockroach (left), bee (center) and mosquito (right). (Combination of figures from Hertwig.)

The thorax of the cockroach consists of three fused somites, termed the pre-, meso-, and meta-thorax, and, as in the lobster, it bears the most important organs. Each somite carries one pair of legs, and these three pairs of legs are so constant in the insects that the phylum is sometimes called the Hexapoda. These legs are adapted for many different activities.

The thorax also carries the wings. These are thin bags of cuticle drawn out from the dorsal angles of the meso- and metathorax, which become expanded and stiffened in the air, and are the most characteristic of the external appendages of insects, distinguishing them from all other animal forms. The wings, like other appendages, are also subject to wide variations in form and function.

The internal organs of insects are especially adapted for an aerial mode of life. The most characteristic are adaptations for breathing air. There are, obviously, two possible different ways in which organs, tissues, and cells of the body may obtain fresh oxygen; each tissue may get it directly from the outside by osmosis, as in the coelenterates and earthworms, or each cell may get it from some specially modified oxygen-carrying agent. The blood vascular system forms the agent in the majority of higher types, but in the insects the blood system has no such functions, and in many cases is absent altogether. Air is carried from the atmosphere directly to the tissues and cells by special tubes called *tracheae*, which form a complicated system or branching system of vessels distributed throughout the body. The main trunks end in external openings termed *spiracles*, which may be variously placed in different types of insects. In some cases, there is only one pair of such openings; again there may be a pair to each somite of the abdomen and thorax (cockroach, grasshopper), or many openings may be distributed about the body.

CHAPTER VIII

PARASITISM: PHYSIOLOGICAL ADAPTATION

A. The Tapeworm, Taenia sp.

Many types of adaptation can be traced back directly to the effects of the environment. These may be either structural or functional or both. A tapeworm has no mouth or digestive tract, but obtains its food by absorption of dissolved proteins from the host. It has little need for movement—if it were necessary for it to move, it could not do so easily, for the body musculature is inadequately developed. It might be inferred from its position in the digestive tract that such a parasite would need some apparatus of attachment. Suckers and hooks are developed for this purpose. Absence of muscular development indicates lack of need for nervous system. The nervous system is most primitive. So, too, are organs of excretion. All of these structural features indicate an adaptation for the particular mode of life of an intestinal parasite. Physiological adaptations must also have been developed with the change from independent individualism to dependent association. The loss of digestive tract could not have occurred in the ancestry of our cestode, so long as there was need of it for life of the worm (Fig. 83).

The greatest physiological adaptation, however, is apparent in the reproductive system. The entire construction of the tapeworm seems bound up with this particular activity. The young worm, attached to the intestinal wall, grows by absorption of food digested and prepared for assimilation by the functioning digestive cells of the host. The first trace of reproduction is the formation of a somite-like bud at the posterior end of the parasite. Continued growth involves continued new bud-formation with enlargement of the older buds, until a long chain of similar buds growing from the attached "head" end (called scolex) results. The completed worm then has a superficial resemblance to a segmented form such as an annelid, but the resemblance is only superficial, for the segments (called proglottids) are not typical metameres or somites and have little

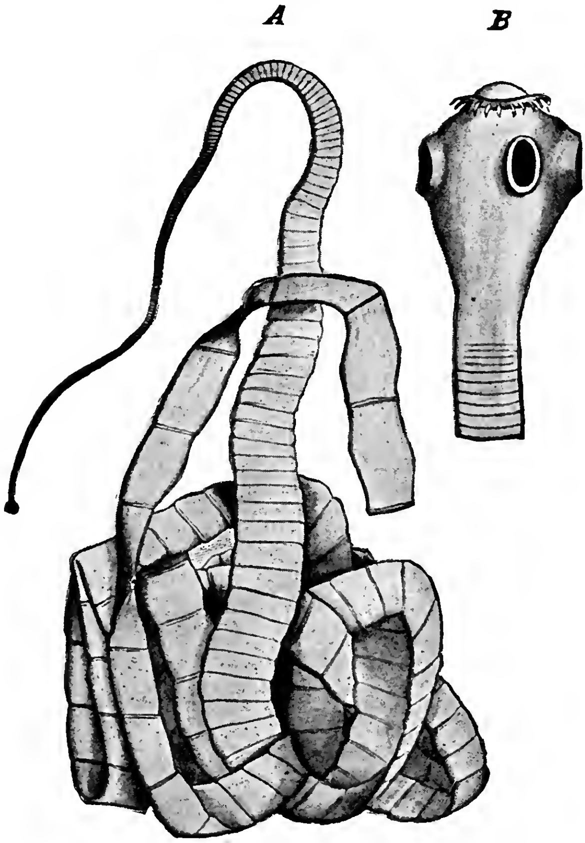


FIG. 83.—*Taenia solium.* *A*, Entire tapeworm with proglottids; *B*, scolex with sucking discs and crown of hooks. (From Leuckart.)

organic relation to the whole worm. Each segment has a complete set of reproductive organs which are quite as complex as the reproductive organs of annelids or other animals of similar grade (see Fig. 84). When mature, the proglottids are detached from the end of the tapeworm and are defecated with the faeces of the host to the outside. Each proglottid has the power to produce thousands of eggs which are fertilized when mature,

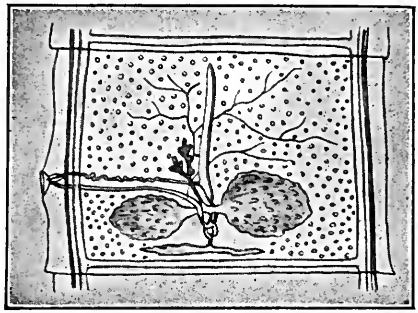


FIG. 84.—A single proglottid of *Taenia solium* enlarged to show the reproductive organs. (From Leuckart.)

and stored up in the uterus of the proglottid, ready for development. When detached, a ripe proglottid then has thousands of embryos, each capable of giving rise to a new tapeworm. But these are deposited with the faeces, and before they can develop into a new Taenia must undergo partial development in the pig. In one way or other, they find their way into the food of a pig; the embryos are liberated by action of the pig's digestive fluids, and when liberated make their way through the walls of the digestive tract into the muscles of the pig. Here their development is arrested, and, as *cysticercids* or bladder-worms, they give rise to what is called measly pork. Such pork eaten in an uncooked state is a source of human infection. The bladder-worms are freed in the digestive tract, become attached as scolecids to the lining epithelium, and begin to bud out proglottids.

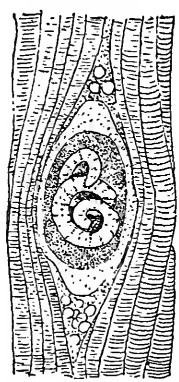


FIG. 85.—*Trichina spiralis*, encysted in muscle tissue. (From Hertwig after Boas.)

Here, there is a very characteristic physiological adaptation, in which the difficulties of maintaining the species are balanced by the enormous number of embryos formed.

In a similar way, thousands of species of animals become adapted to a parasitic life in different types of host. Furthermore, there are different grades of parasitism; some are *obligatory* parasites, requiring a particular host and a particular organ, very often, of that host. Others are *facultative* parasites, not absolutely dependent on a given host, but capable of living in such a host if chance brings them there. Thus the round worm, Trichina, is an obligatory parasite of man, and a facultative parasite of domesticated animals, including the pig. The embryos are eaten with infected meat; liberated in the human intestine, they penetrate the walls of the digestive tract and multiply in the body cavity, ultimately penetrating muscle bundles where, in the muscle cells, they finally encyst. If the unfortunate victim does not die from trichinosis before such encystment occurs, recovery is possible, for once encysted, the parasites do no further damage. Trichinosis, however, is usually fatal, the infected muscles of the victim often containing millions of the parasites (Fig. 85).

B. Animal Associations

Animals of different kinds may live together in harmony and without ill effects on either; or different types of living organisms may live together for mutual benefit. Such a form of partnership is called *symbiosis*, an example of which we have seen in the case of *Hydra viridis*—or this association may become obligatory, so that neither organism can live without the other. Where the association does not confer mutual benefit, or any obvious advantage to both, we speak of the association as *commensalism*. A good example of this is the union of the glass sponge, Euplectella, and a crustacean; a pair, male and female, enter the pores of the sponge in the larval stage, and grow to adult size within the chosen prison, which they cannot leave after they grow up (Fig. 86). Numerous examples may be found, in the human intestine, of both commensalism and symbiosis; many innocuous protozoa and bacteria live there, while many bacteria also are symbionts which play an important

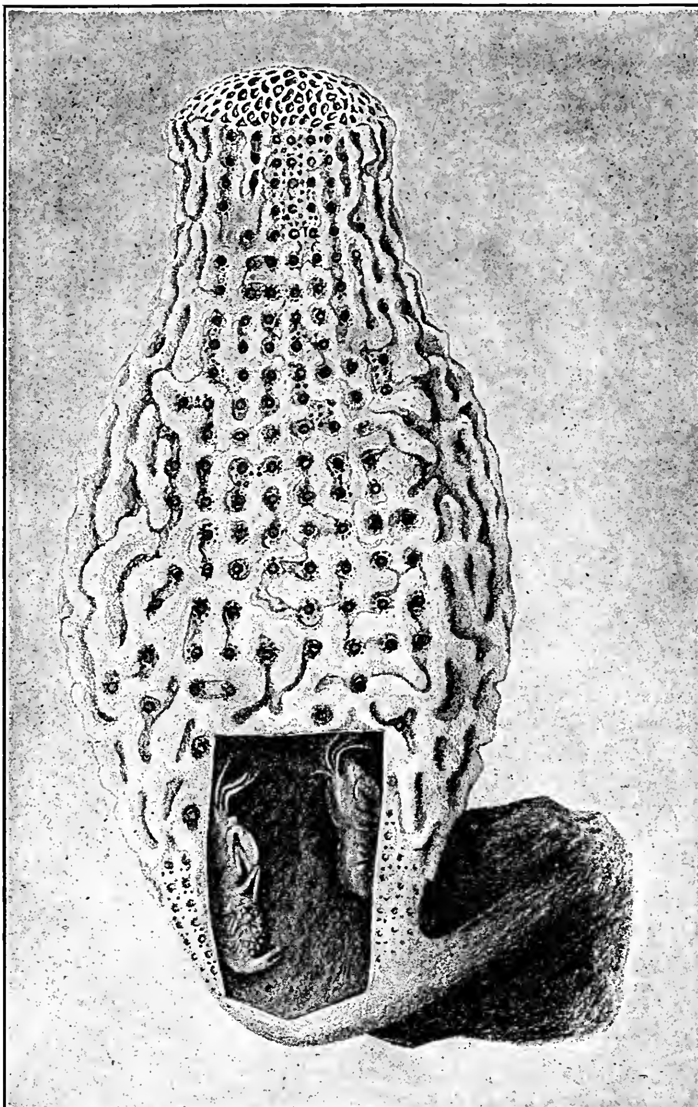


FIG. 86.—A glass sponge (Euplectella) with commensal crustacea, male and female, in the sponge cavity; the female is carrying eggs.

part in intestinal digestion, thereby contributing to the functioning activities of the host while thriving on the products of digestion in the intestine. Parasites, finally, live at the expense of their hosts. These are all illustrations of physiological adaptations on the part of symbionts, commensals, or parasites, but adaptations do not stop here.

C. Adaptations against Parasites

Parasites, especially some forms of bacteria, give off products in the form of nucleo-proteins or other chemical compounds, which act as poisons on the host's cells and tissues. Sometimes, as in typhoid fever or cholera, these poisons from the intestine are absorbed into the vascular system and are carried to all parts of the organism. The action of such poisons differs in different cases. Very frequently the protoplasm and walls of the cells of the digestive tract are dissolved, a phenomenon known as *lysis* (hence cytolysis, hemolysis, karyolysis, etc.) and local or distributed areas of functioning organs are ulcerated and destroyed, leading to various forms of enteritis or intestinal inflammation. Or the parasites may become localized in other parts of the body, pneumococcus in the lungs giving acute congestion characteristic of pneumonia; or the bacillus of tuberculosis in the lungs, which forms a poison causing destruction of the lung cells as in consumption. The organisms of tonsilitis and diphtheria accumulate in the throat and give off poisons which act on the entire system; the organisms of smallpox and scarlet fever collect in the skin, those of hydrophobia in the nerve cells of the peripheral and central nervous system, while some find their way into the blood and multiply there; for example, Streptococcus and Staphylococcus cause blood poisoning or malarial organisms cause malaria.

These various parasites have become adapted to this parasitic mode of life in the human organism. They live at the expense of the latter, and in the course of their various metabolic activities they give off substances which interfere with the normal activities of metabolism of the host, usually by the direct or indirect destruction of organ cells by which normal functions are carried on. The result is disorder in the physiological balance of the human organism, leading to morbid symptoms, and, if uncontrolled, to death.

Moreover, just as these parasites have become adapted to a new mode of life in the host organism, so the host organism has become physiologically adapted to resist them. These adaptations are (1) physical, through the activity of white blood cells or leucocytes (phagocytes), and (2) chemical, through the formation of chemical bodies which counteract the poisons created by the parasites.

(1) *Phagocytosis*.—If we inject a bit of capsicum into the skin of a salamander or other amphibian, the result is a collection of blood, or inflammation, in the vicinity. If the experiment is made on the web of the foot, and the foot fixed under the microscope, the course of the blood in the veins and in the capillaries can be easily watched. From time to time white or colorless cells come along, hesitate in the blood flow, stop and then begin to work through the walls of the capillary. They pass through this wall and into the surrounding fluids, the process of migration being known as *diapedesis*. Thus by amoeboid motion they move toward the seat of irritation, and if yeast cells or powdered carmine be injected in the skin, the white cells can be observed to engulf them exactly as an amoeba takes in food. These white cells are the phagocytes of the blood—microphages and macrophages—and their function is to surround and engulf any foreign bodies or irritating substances in the organism. This function is phagocytosis.

In a similar manner, the phagocytes may attack and engulf bacteria or other harmful foreign objects. Once engulfed, they are digested by intracellular digestion in the same way that amoeba engulfs and digests living food. The phagocytes, therefore, contain some digestive substance fatal to bacteria; provided the bacteria are engulfed by them, and just as alcoholic fermentation is possible through the action of zymase without the living yeast cell, so extracts of phagocytes would be capable of destroying bacteria. This apparently happens under conditions of disease. The invading bacteria, in some cases, produce poisons which destroy cells of the body and phagocytes; with their destruction the contained digestive fluids or chemicals are liberated; these in turn react on the bacteria and kill them. Thus, if rabbits are inoculated with the bacilli of anthrax, the parasites multiply in the blood, over-run every organ of the body and ultimately kill the rabbit. If, however, the bacilli are placed in rabbits' blood that has been drawn out into a test-tube, the bacteria are killed (Nuttall and Buchner). This result, as it is usually interpreted, is due to the death and disintegration of phagocytes, whereby some chemical substance (called *alexine* by Buchner), which is fatal to the bacteria, is liberated from the disintegrating protoplasm. Alexine is supposed to be the same substance which brings about digestion of bacteria ingested by living phagocytes.

Some types of bacteria in the blood are attacked and killed by the phagocytes. This was demonstrated by Metschnikoff who, using a strain of bacteria which are thus killed in the blood, enclosed some in collodion sacs which he placed in the body cavities of different animals. These sacs allowed the free interchange of fluids, including bacterial products and various substances contained in the blood, but the bacteria themselves could not get through, nor could the phagocytes reach the bacteria which lived and thrived in the collodion sacs.

Again, some types of bacteria in the blood are not touched by phagocytes under ordinary conditions, but if animals containing such bacteria are inoculated with phagocyte-free blood, which is immune to these bacteria, the phagocytes immediately devour them. Something in the serum has produced a change in the bacteria which, while it leaves the bacteria uninjured so far as their vital processes are concerned, renders them susceptible to attack by phagocytes. Wright, who discovered this phenomenon, gives the name *opsonin* to the substance which makes bacteria susceptible to phagocytes (opsono—I prepare the food).

(2) *Anti-bodies and Immunity.*—While phagocytes are thus a potent physiological adaptation for protecting the organism

against disease, they do not form the sole means of protection. The phenomena of immunity furnish another and more subtle illustration of physiological adaptation.

Everyone is familiar with the ordinary facts of immunity from disease. In a community in which some contagious or infectious disease is epidemic, some individuals do not acquire the disease, if exposed to it. These individuals are said to be immune, and of these there are usually two classes; in one class, the individuals have never had the disease, but enjoy what is called *natural immunity*. Again, other individuals take the disease but have it in mild form; they are said to be slightly susceptible to the disease, but have sufficient natural immunity to make it a light case. Still others are *highly susceptible*, and succumb.

In a similar way, entire races may be naturally immune to diseases that are ordinarily fatal to other races. Thus the horse and ass are highly susceptible to the organism of glanders, but cattle, sheep and fowls can be injected with large doses of the glanders organism without ill-effects—they are naturally immune. Many diseases of lower animals, such, for example, as hog cholera, swine plague, chicken cholera, mouse septicaemia, etc., fatal to these animals, are harmless to human beings. On the other hand, some diseases of man, like scarlatina, whooping cough, yellow fever, etc., are harmless to lower animals, while some others like anthrax, tuberculosis, etc., are equally dangerous both to man and lower animals.

Most of us have passed through the ordinary diseases of childhood ourselves—whooping cough, chicken-pox, mumps, and some through smallpox and scarlet fever, none of which we expect to have a second time because of the *acquired immunity* which these diseases have left in us.

Again, most of us have been vaccinated against smallpox, and some of us against typhoid fever, and neither of these diseases may be expected after such vaccination, which has given us an acquired immunity. This vaccination has produced changes in the physiological mechanism similar to the changes produced by the diseases themselves. Thus acquired immunity may be of two types (a) *active immunity*, through experience of the disease or by vaccination with organisms which produce the disease, or by their products, and (b) *passive immunity*, by injection of a serum from an actively immunized animal, carrying with it certain substances by which protection is conferred. If organisms are introduced with vaccination, they are rendered comparatively harmless by preliminary treatment. Thus, experience has shown that the organism of smallpox is rendered harmless to man by passing it through the calf, which is only mildly suceptible to the disease. When recovered from the calf, the organisms (virus), are weakened in such a way that upon inoculation into man they produce only a local disturbance, but enough to change the chemical make-up of the blood, which will then protect the body against smallpox for years.

A very striking case of passive immunity is furnished by the modern treatment of diphtheria. The ill effects of the disease are due to poisons produced by the parasite of diphtheria—these spread through the victim, and by their cumulative effect either cause death or stimulate the cells of the body to produce an antidote in sufficient quantity to neutralize the poison. The actual existence of such an antidote was discovered in 1890 by Kitasato and von Behring, and named by them an anti-body. It was found, furthermore, that lower animals could be employed as the source of the anti-body. The horse, for example, may be inoculated with the organisms of diphtheria—after some days the blood of the horse contains quantities of the anti-body, so that the serum, if injected into a human victim of diphtheria, counteracts the poison produced by the diphtheria organisms of the victim. It is a case of acquired active immunity in the horse, and acquired passive immunity in the human.

D. The Mechanism of Immunity

What is the nature of this change in the blood, whereby organisms or their poisonous products are counteracted? The fundamental principle underlying immunity is that the blood contains something which it did not contain before. Substances which produce this change are called *antigens*, and the new responsive bodies are called *anti-bodies.* Now the facts of immunity are established and there is an increasing multitude of such facts, but the explanations are purely theoretical. There are two main hypotheses at the present time; one is Metschnikoff's development of phagocytosis, the other is Ehrlich's famous side-chain hypothesis. According to the former, all responses of anti-body formation to antigens take place in the phagocytes, of which there are two kinds—microphages and macrophages. The former are the leucocytes of the blood, which engulf bacteria and other minute bodies, and digest them by the aid of an enzyme clled *microcytase.* The latter are modified organ cells of the body, which have become dissociated from their tissues, and roam about as scavengers in the blood supply, producing an enzyme called *macrocytase*, and digesting larger bodies than bacteria. When broken down under the action of antigens, they liberate chemical substances which form the counteracting chemical anti-body. The reaction thus is purely chemical or physiologico-chemical in nature.

In Ehrlich's theory there is an attempt to visualize the actual process of the physiologico-chemical action. The unknown myriads of molecules which make up protoplasm are imagined to have unsatisfied groups of atoms, ready to unite with food substances or other substances from the blood. These free groups are called side-chains. Instead of uniting with food substances, one or many may unite with molecules of poison, which are thus introduced into the protoplasmic substance, resulting in the destruction of the side-chains. If the number of such molecules of poison is limited, the protoplasm is able to regenerate the atom groups thus used, but if the poison accumulates, the new groups are combined as soon as formed, and fatal poisoning results. In the case of diphtheria, the horse undergoes such direct poisoning, but not extensive enough to produce fatal results. Its blood, however, becomes loaded with anti-bodies. According to Ehrlich's theory, this is explained by the assumption that atom groups of the molecules in protoplasm, when thus destroyed by the poison molecules, are regenerated, and these regenerated groups are cast off from the protoplasm into the blood as *free* atom groups, which are then capable of uniting in the blood with the poison molecules. In this way, chemical union of antigen and anti-body takes place outside or apart from protoplasm, and when thus united, the poison is made harmless, because of its inability now to unite with any protoplasmic group—its valencies have been satisfied. Furthermore, Weigert has shown that the quantity of protective substances in the blood (anti-bodies) is out of all proportion to the quantity of toxin which stimulated the reaction. In other words, hyper-regeneration follows such toxic injuries to the protoplasm. Thus, in the case of diphtheria it has been shown that one unit of diphtheria toxin is sufficient to produce 100,000 units of anti-body. Immunity, therefore, is explained by Ehrlich as the condition whereby the blood is loaded up with free chemical substances, which unite with and render harmless the specific poison of a disease-causing parasite. It is a most pregnant theory, and has been developed with surprising ingenuity to satisfactorily account for all of the complications connected with zymotic diseases. One only of these complications will be given here, as the subject of immunity is vast and perplexing. The case of opsonin formation and action is a relatively simple adaptation of the theory. Some bacteria in the blood, *e.g.*, tubercle bacilli, are relatively unharmed by the phagocytes under normal conditions, but if immune serum be added, the bacteria are immediately devoured, or in some cases dissolved without being engulfed. According to Ehrlich's theory, there is no chemical attraction or proper grouping of atoms in the bacterial cell to enable the protecting substances to unite with them. With the addition of immune serum, however, the union is effected—the substances contained in it being able to unite with both the bacteria and the phagocyte. In such a case, the phagocytes or dissolving anti-bodies form the *complement*, the molecules of immune serum form the connecting links, and are known as *amboceptors*. Hence, without the amboceptors, the anti-bodies in the blood are unable to unite with the toxins, any more than pepsin can digest proteins in an acid-free medium.

It is not our purpose here to examine deeply into the secrets of immunity—the magnitude of the subject forbids anything more than the briefest exposition of the phenomenon of physiological adaptation, which immunity suggests. What this phenomenon means to the organism can be imagined, when the same individual becomes successively immunized to chicken-pox, whooping cough, measles, mumps, smallpox, and half a dozen other diseases. The fact of minute reactions bringing about great adaptations against disease is only one more instance of the marvelous powers of adaptation which protoplasm manifests.

CHAPTER IX

THE PERPETUATION OF ADAPTATIONS

WE have seen that the appendages of the crustacea are built primarily on the same type of structure, and that, in different orders, the several appendages have become modified in one way or another for the performance of different functions. In the Malacostraca, the appendages are reduced to twenty pairs in all, but in the more primitive forms included in the group Entomostraca, there are large numbers of pairs made up of primitive biramous appendages, all performing practically the same functions. The twenty pairs (in one order, Phyllocarida, there are twenty-one pairs) are distributed in the same way in all of the Malacostraca (Fig. 68); five belong to the head, eight to the thorax, and six to the abdomen. The abdominal appendages retain the original biramous condition, but the other thirteen pairs are variously modified for the performance of different functions. Examining only the thoracic appendages, we find one order (Schizopoda), in which all eight pairs are biramous and of the generalized type, all serving for swimming (Fig. 87). In the other orders they are adapted for feeding and walking in a variety of ways. In the order Stomatopoda, five pairs are modified for food getting, and only three pairs for walking; in the order Decapoda, three pairs are modified for food getting, and five are devoted to walking; in the order Cumacea, only two pairs are for food getting, while six are devoted to walking; and in the order Arthrostraca, only one pair is for food getting, the other seven for walking. In all of these cases, the morphology of these organs indicates that the most highly differentiated appendages and the most generalized ones are built on the same plan of structure. The study of the development of the individual crustacean indicates that the most highly differentiated appendages appear first as generalized biramous structures which, with growth, lose their generalized structure and become specialized. In different regions of the same organism and in different organisms, therefore, the same generalized type may become adapted for quite diverse activities. Thus the fourth pair of thoracic appendages in Mysis (Schizopod), Squilla (Stomatopod), and the lobster (Decapod) are, at some period in development, the same in structure, and resemble one another, but in Mysis they remain biramous and lamella-like; in Squilla they become modified into characteristic maxilli-

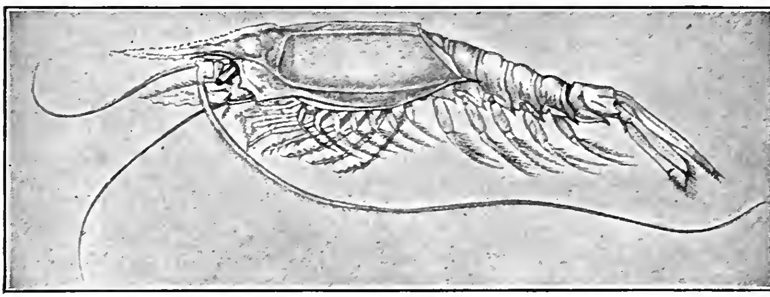


Fig. 87.—A schizopod (*Gnathophausia gigas*) with permanent biramous thoracic appendages (*cf.* schizopod stage in development of the lobster, Fig. 78). (From Sars.)

peds or food getting organs, and in the lobster they change into the powerful offensive and defensive chelate walking legs characteristic of the Decapods. Such differences form the basis of animal species.

A. Animal Descent

The lesson taught by the structures and functions of the lobster's appendages may be extended to all animals. As the specialized appendages of different crustacea may be traced back to generalized structures, so may animals, no matter how modified, be traced back, more or less accurately, to more generalized types from which they have descended. This descent is often difficult to make out, for some of the primitive structures may have become so modified, through functional activity or otherwise, as to be unrecognizable; others, like the exopodites of the walking legs of the lobster, may have disappeared entirely, and even the embryological evidence may have been eliminated in the rapidity of development of the individual; finally, new structures may have appeared without recognizable homologies in the primitive forms. All of these possibilities offer problems for the student of animal descent, and their solution is at first hypothetical, such hypotheses being based upon different biological evidence, sometimes upon the facts of comparative anatomy, sometimes upon transient embryological structures, sometimes upon geographical distribution, but usually upon two or more of these lines of evidence taken together. The value of such hypotheses of the origin of different types of animals depends upon the amount and the nature of such evidence, which may be so convincing as to make the hypothesis an established truth. This is, indeed, the case with the theory of evolution itself, the evidence upon all sides being so conclusive that no other general hypothesis of the origin of the present day living beings is tenable.

It is within the memory of many men still living, that the different species of crustacea comprising the orders mentioned above would have been interpreted by intelligent people as especially created types of animals having no genetic relationship. Today, such organisms are universally believed, by people who have the right of opinion, to be blood relations and to have had a common ancestry from generalized crustacea.

B. Evolution

The change in point of view was due to the acceptance of the doctrine of evolution which, in its modern form, had its start with the publication of Charles Darwin's book on The Origin of Species in 1859. This volume embodied the observations of a keen naturalist, running over a period of thirty years, with an argument for evolution, through natural selection in the struggle for existence, of all kinds of living things.

The effect of this one book, and of the acrimonious controversy which it brought about, was a revolution in human thought.

Biologists of all countries and thinking men of all walks in life were drawn into the controversy. Living nature was searched everywhere for evidence bearing on evolution. Habits and instincts, coloration and mimicry of animals, living and fossil forms were studied minutely in the search for proof, and little by little, with the accumulation of facts the opponents of evolution were won over, until finally the conception of evolution was universally accepted as the explanation of the origin of modern types of living things.

In the meantime, however, another controversy arose, this time among biologists themselves who, having accepted what has taken place through evolution, did not agree as to how it has taken place nor in regard to the factors involved. Darwin believed that natural selection, by which those organisms best adapted to survive in the struggle for existence would continue to live and breed, was the chief means of the maintenance of diverse types, although not the only means. Some later biologists believed that this process of natural selection is itself the source of variations, as well as the means of perpetuating them after adaptations had arisen, useful adaptations being selected and conserved, useless adaptations, being a hindrance, would lead to extinction. Still other biologists could see little basis for the origin of variations on Darwin's theory of natural selection, and turned back to the view advocated by Lamarck in 1815, to the effect that animals may become changed or adapted to conditions of their environment during their individual lifetime, and then transmit such acquired changes or adaptations to their offspring. These Neo-Lamarckians thus believed in the inheritance of acquired characteristics, which Darwin himself believed might play some slight rôle in the origin of species.

One effect, in large part, of this controversy among biologists was to introduce a new method of research in biological science, and experimental biology grew up. At first, animals were mutilated in various ways to see if such mutilations would have any effect upon the offspring. The failure of such experiments was no check upon the use of the experimental method, which in the different fields of experimental zoology, botany, embryology, and genetics introduced many new problems for solution, while the attempts to solve them threw a brilliant flood of light, not only on the old question of evolution, but over the entire field of biological phenomena. Indeed, it may be safely stated that all of the great strides in modern biology have been along the lines marked out through use of experimental methods.

The greatest of these strides has been taken along the line of heredity or genetics, and a new point of view of the origin of variations has resulted. It is not the work of any one man, nor has the advance always been definite, but certain names stand out prominently, and certain achievements mark successive outposts of advance.

C. Conformity to Type

A female lobster produces thousands of eggs, each of which, after fertilization, has the potential of a new adult lobster, and all of the brood are essentially similar to one another and similar to those produced by other lobsters. If one or more claws of two parent lobsters are cut off early in life and kept cut off after successive regenerations, the fertilized eggs resulting from these two individuals will develop again into normal adult lobsters with perfect appendages. I am not aware that such an experiment has actually been made with lobsters, but it has been worked out in so many other cases that we are justified in assuming the result with these crustacea. The main point is that the visible changes or defects of the parents have no apparent effect on the eggs and embryos produced by them. In other words, the germ cells conserve the particular type of organism producing them, not necessarily that of the immediate parents, but of the race to which the parents belong.

If the various types of crustacea which are known today have had common ancestral forms in some more generalized type, why did not the eggs of that generalized type produce organisms similar to the parents, and when and how did changes occur? It is the old problem of the hen and the egg; the egg came first, but the hen gradually evolved from generalized ancestral forms quite dissimilar from the modern fowl. How were the successive changes or variations impressed on the egg, until such changes became normal to the modern types?

D. Somatic and Germ Plasm

The old enigma has been partly solved through the experimental method in modern biology. The full solution is indeed far from reached, but the key apparently has been found. As usual in science, imagination led the way in the search for this key, which is now generally believed to be bound up in the conception of the germ plasm as outlined in a series of hypotheses by Darwin, Dalton, Spencer, Nägeli, and especially by Weismann in his famous essays on Heredity. According to Weismann's conception, our lobster, like all animals, is made up of two kinds of protoplasm, *somatic plasm* and *germ plasm.* The somatic plasm forms the structures of the individual, including all of the systems of nutrition and relation; the germ plasm, in the female, is confined to the eggs and to the endothelium from which eggs are formed, and in the male, to the sperm cells and to the endothelium from which sperm cells are derived. The somatic plasm wears out and ultimately dies from old age, but the germ plasm is handed down and continues to live in generation after generation of descendants. The individual thus is a nurse or carrier of the potentially immortal germ plasm; his inheritance comes not from the somatic protoplasm of either parent, but from the germ plasm of both, and here is the secret of the conformity to type—the race is preserved in the germ plasm, and the race changes with changes in the germ plasm.

The development of this idea forms one of the most interesting chapters in the history of biological science. While highly speculative, especially at the outset, it was nevertheless developed on a basis of facts. These facts are connected with the phenomena of mitosis or cell division, which were worked out by many different observers during the two decades from 1870 to 1890. It was found that every characteristic type of animal or plant cell reproduces its like by cell division, and that the characteristic and most important changes of the cell during division were connected with the nucleus. It was shown that the chromatin of the nucleus during vegetative stages is distributed, in the form of granules, on a network of achromatic material called *linin* (Fig. 88, A); that these granules collect and coalesce in one or more spirally wound threads of chromatin called the *spireme* (Fig. 88, B, C); that these spireme threads divide longitudinally throughout the entire length, and that the double spireme then segments into a number of short double rods called *chromosomes* (Fig. 88, D, E). It was discovered that the number of these chromosomes is always the same in individuals of the same species and in all types of the tissue cells of the same individual. At the same time, it was shown that the chromosomes collect in the center of a peculiar spindle-formed body, derived from achromatic material of the cell, and having characteristics peculiar to itself in the form of *centrosomes* at the poles of the spindle, with spindle fibers running from one centrosome to the other (Fig. 88, D, E, F). It was found that these centrosomes arise by the division of a single centrosome lying on the periphery of the nucleus, and by separation of the daughter-centrosomes through an arc of 180°; also that the nuclear membrane disappears at this time, while new fibers (mantle fibers) grow out from the centrosomes, and connect with the chromosomes. It was seen that the two equal parts of each chromosome then separate from one another, each half going toward one of the two centrosomes, so that the entire mass of chromatin material is equally divided between the two daughter-nuclei which are bounded by new nuclear membranes (Fig. 89, G, H, I, J). It was noted, finally, that nuclear division is completed by disintegration of the daughter-chromosomes into the distributed chromatin granules characteristic of the vegetative nucleus, and that, after this nuclear division, the cell body divides by a plane, passing through the center of what was the nuclear division figure.

This complicated chain of processes with its involved activity of chromatin, centrosomes and spindle fibers was named *karyokinesis* by Schleicher 1878, and *mitosis* by Flemming 1882, and both names are found in current literature.

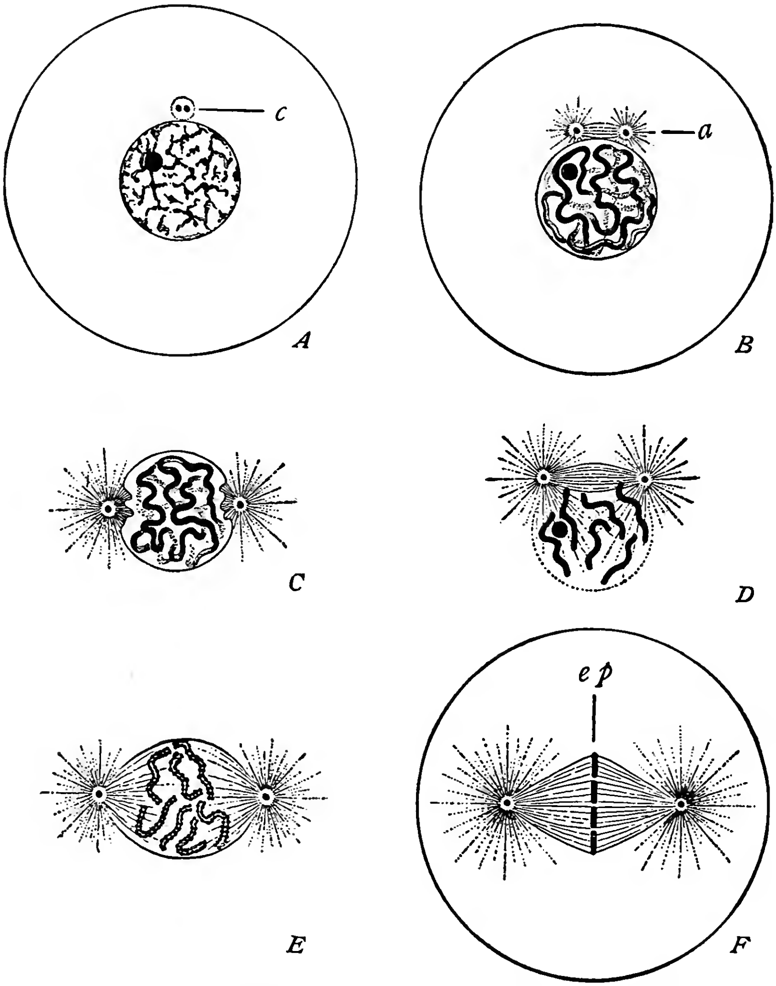


FIG. 88.—Diagram showing the early stages of mitosis. *A*, Resting cell with reticular nucleus and nucleolus; at *c*, the attraction sphere with two centrosomes; *B*, early prophase, the chromatin in the form of a continuous thread or spireme; the centrosomes have separated forming a spindle figure between them; this is the amphiaster (at *a*); *C*, *D*, two later stages in the prophase of division in which the spireme is divided into segments, the chromosomes; *E*, formation of the mitotic figure with centrosomes at the poles and with the chromosomes split longitudinally; *F*, the mitotic figure fully established. *a*, Amphiaster; *ep*, equatorial plate. (From Wilson.)

Wilhelm Roux, speculating on the significance of these nuclear phenomena, suggested that the minute and exact halving of these fundamental structures of the cell, and the complicated processes by which this halving is brought about, must have some important bearing on deeper biological problems, and he concluded that karyokinesis is the means by which hereditary characteristics, contained potentially in the chromosomes, are distributed to all cells of the organism. This conception in connection with the germ cells was taken up by Weismann and worked into an elaborate theory of inheritance, which was published in complete form in his book on The Germ Plasm in 1892. The chromosomes were regarded as aggregates of different elements, each element (called a biophor) representing some specific characteristic or group of characteristics of the adult organism. With longitudinal division of the chromosomes, each element is equally divided.

Maturation Phenomena.—In the meantime, the discovery had been made that the mature germ cells, when ready for fertilization, contain only half the number of chromosomes characteristic of the species, so that upon union of egg and spermatozoon the normal number is restored, the resulting offspring inheriting equally from the two parents. It had also been found that this halving in number of chromosomes takes place in the germinal endothelium during the process of ripening of eggs and spermatozoa, and at the time of the preliminary mitoses which accompany the formation of the germ cells. These peculiar divisions became known as the *maturation divisions*.

After the discovery of the reduced number of chromosomes, and in accordance with his conception of the chromosomes as the bearers of hereditary characteristics, Weismann in 1888 prophesied that, in one of the maturation divisions, it would be found that the chromosomes do not divide longitudinally but transversely, so that the hereditary characteristics, instead of being equally partitioned between the daughter cells, would be divided crosswise, so that the daughter cells would receive dissimilar groups of biophors. The ordinary longitudinal division of the chromosomes he called an *equation division*, and the extraordinary hypothetical division during maturation, the *reduction division.*

The fulfilment of this prophecy by a host of different observers was a remarkable justification of the imagination in science.

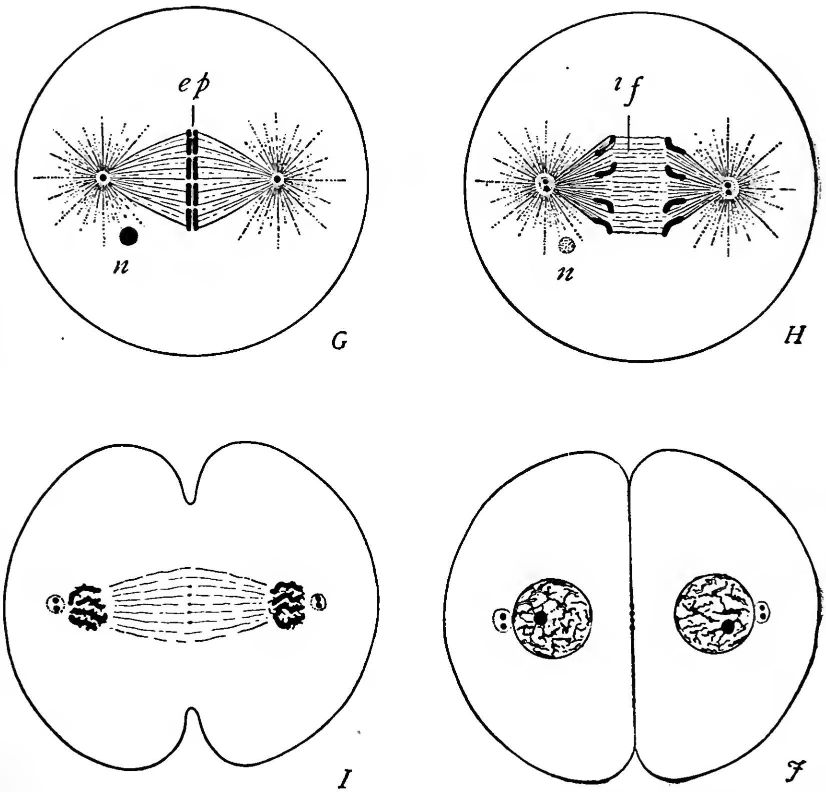


FIG. 89.—Middle and end phases of mitosis. *G*, Metaphase showing the longitudinal split of the chromosomes; *H*, the end phase or anaphase with the daughter chromosomes separating, between them the inter-zonal fibers (*if*); the centrosomes are divided in preparation for the next following mitosis; *I* and *J*, final stages in daughter nuclei formation and division of the cell; *n*, the discarded nucleolus; *ep*, equatorial plate. (From Wilson.)

The reduction division, in some form or other, often complicated and atypical, was revealed in type after type of animals and plants, until today it is generally, if not quite universally, accepted as a typical phenomenon of maturation.

The Maturation Divisions.—The maturation divisions in male and female organisms, while similar so far as the chromatin is concerned, do not result in the formation of the same number

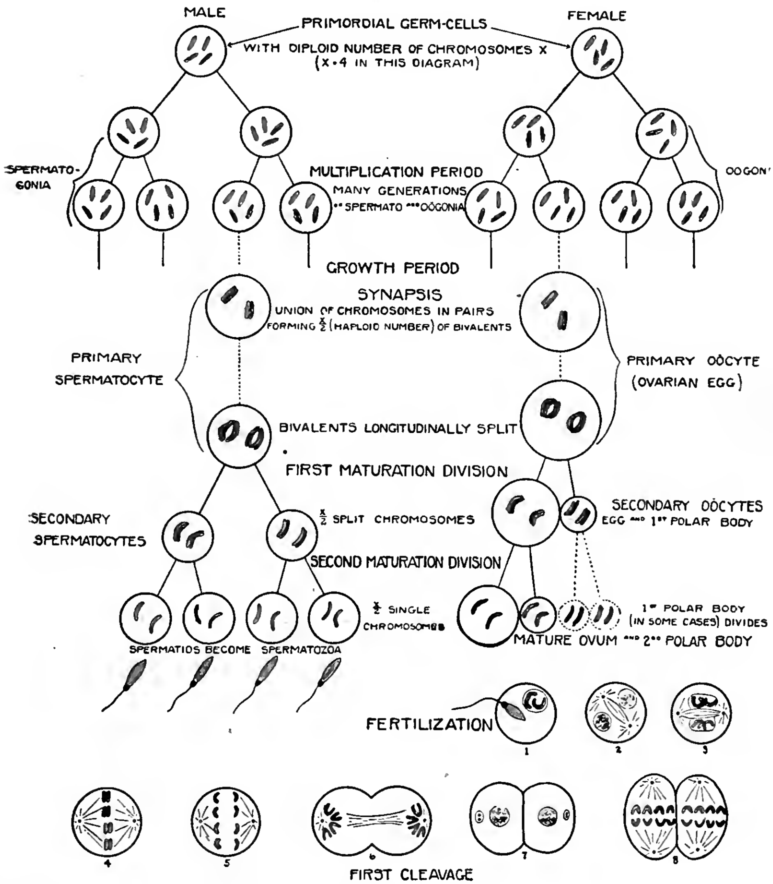


FIG. 90.—Diagram of the maturation divisions of the male and female germ cells. Four chromosomes are present in all cells of the body of the case illustrated. (The polar bodies are represented as much larger than they actually are in relation to the egg cell.)

of mature germ cells. From each primordial egg cell only one mature egg is formed, while three rudimentary eggs called *polar bodies* are formed, which have no part in development, but degenerate and die. From each primordial cell of the spermatozoon, on the other hand, four functional spermatozoa are formed, each of which may fertilize an egg. In each case, the primordial germ cells of the germinal endothelium are similar; each has the number of chromosomes characteristic of the species (in modern terminology, the *diploid* number), but the egg-forming cells, at an early period, begin to enlarge and to deposit stores of yolk in the cell body. The chromatin of the nucleus collects in a thick fibrous mass on one side of the nucleus (*synapsis* stage), and from it emerge one-half as many chromosomes as are formed at ordinary vegetative divisions (in modern terminology, this is called the *haploid* number). Each chromosome, however, is double, consisting of two chromosomes lying side by side or end to end (Fig. 90). Reduction, therefore, at this stage has not actually taken place, hence the phrase *pseudo-reduction* is applied to it. The two parallel parts of each chromosome then divide longitudinally, and the entire chromosome, in many cases, contracts into a smaller four-parted chromosome termed a *tetrad* (Fig. 90). A mitotic figure is then formed, which migrates toward the periphery of the egg, and the nucleus divides equally, one-half of each tetrad passing into a daughter nucleus. While the nucleus divides thus equally, the egg cell divides unequally; only enough egg protoplasm is divided off to surround the one daughter nucleus. This becomes pinched off at the surface of the egg to form a minute bud-like cell termed the *polar body*. Both nuclei then pass directly into a second division phase, the chromosomes undergoing no further change. By this second division, each remaining half tetrad (now called a *dyad*) is separated into its two component parts, one going to each daughter nucleus, and a second polar body is formed from the egg. The first polar body meanwhile may have divided to form two small cells, which with the second polar body and the functional egg make up the four cells derived from the primordial germ cell. In many cases the first polar body does not divide, and in some cases these maturation divisions do not take place until after the spermatozoon has entered the egg; sometimes the first polar body is formed before, the second polar body after, entrance of the sperm.

Reduction in number of chromosomes also occurs in the plant world. Here, in many cases, the germ cells with a reduced number continue to proliferate, and even to give rise to an entire plant (gametophyte). Thus in the fern, reduction in the number of chromosomes occurs at the time of formation of the spores (*cf.* p. 122). Each spore, and all of the cells of the sexual generation formed from it (prothallium), thus have only one-half the number of chromosomes contained in the cells of the asexual generation (sporophyte), the full number being restored by union of the spermatozoid and the oosphere. While details differ slightly in animals and plants, the essential facts are the same.

The male cells resemble the female in the germinal tissue, but in many types of animals characteristic changes soon appear, which make these early germ cells distinctly different from early egg cells. These differences have to do with the determination of sex, which will be considered in a later section. In other types of animals no such visible sex-indicating differences appear, and in these the nuclear changes, formation of tetrads in haploid number, and double division take place as in the egg. No polar bodies are formed, but four functional spermatozoa result (Fig. 90).

The Germ Cells after Maturation.—If, on Weismann's hypothesis, the chromosomes are made up of a series of factors determining adult structures, they must be variously distributed in the germ cells. In Ascaris, a nematode worm, for example, there are four chromosomes in the early germ cells. We may follow a hypothetical group of characters in one of these in spermatogenesis, as shown in Fig. 91 (upper series). The light end on one of these four chromosomes (A and B) represents such a group. In the first maturation division (C), this group passes undivided into one of the daughter cells (D), while the other daughter cell (D′) contains no part of it. At the second maturation division (D), the group is equally divided by a longitudinal division of the chromosome, while D′ divides into two cells with no part of the group. Of the four spermatozoa which result, two (E, E) contain the group of characters which is not

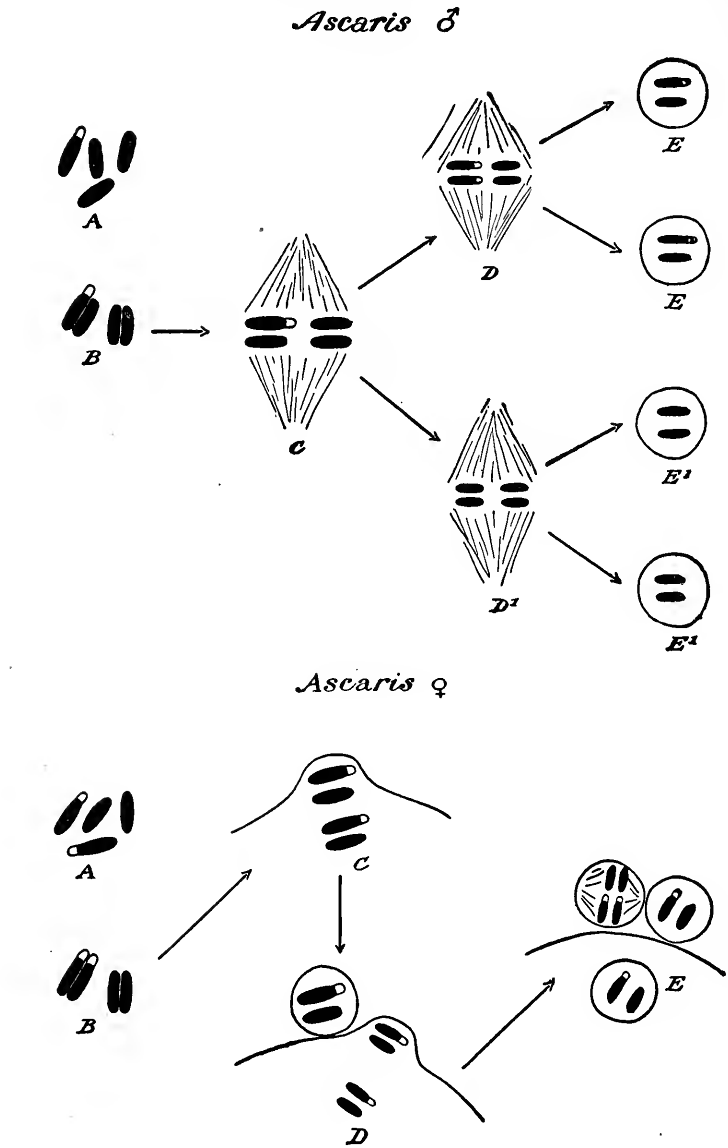


Fig. 91.—Diagram showing the distribution of the chromosomes in the two maturation divisions of the male (♂) and female (♀) germ cells of the nematode worm Ascaris. The light spot at the end of some of the chromosomes may represent a group of characteristics (*e.g.*, sexual characters), and its distribution to spermatozoa and mature eggs is shown in the history of the two divisions. (From Morgan.)

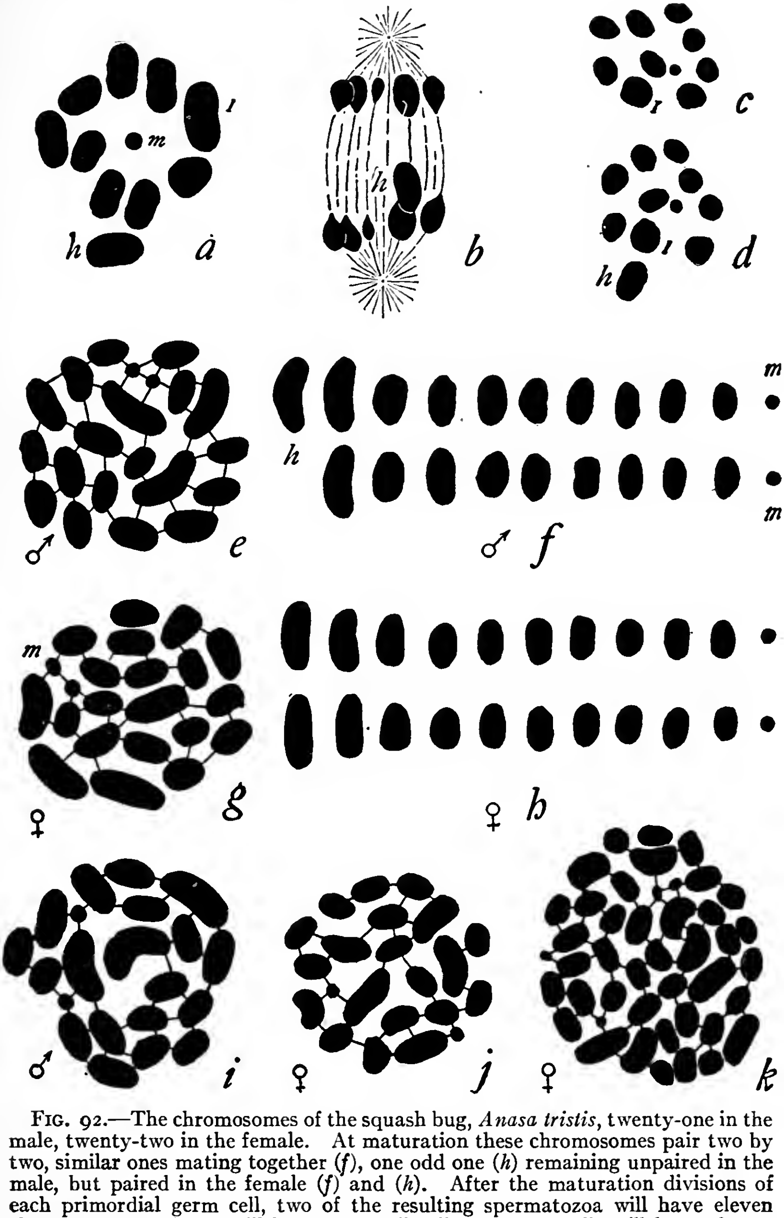


FIG. 92.—The chromosomes of the squash bug, *Anasa tristis*, twenty-one in the male, twenty-two in the female. At maturation these chromosomes pair two by two, similar ones mating together (*f*), one odd one (*h*) remaining unpaired in the male, but paired in the female (*f*) and (*h*). After the maturation divisions of each primordial germ cell, two of the resulting spermatozoa will have eleven chromosomes and two will have ten, while all of the egg cells will have eleven. If one of the first two fertilizes the egg the result will be a female with twenty-two chromosomes; if one of the latter two unites with the egg the resulting individual will be a male with twenty-one chromosomes. (From Wilson.)

represented in the other two (E′, E′) (Fig. 91, A-E). Fertilization may be accomplished by either E or E′, and different types of adult will result. There is a similar result with the maturation processes of the egg, where three polar bodies and one egg cell are formed. The eggs resulting will be different, according to the disposal of the group of characters during maturation.

Weismann finds in these phenomena a possibility of the origin of variations which, once originated, may be maintained or exterminated by natural selection.

The Significance of Pseudo-reduction.—The significance of pseudo-reduction has only recently been made out. The diploid number of chromosomes is reduced to the haploid number by union of the chromosomes, two by two. This union is not haphazard, but takes place with remarkable order and precision. It is best shown in those animals in which the chromosomes are dissimilar in size and shape, as in *Anasa tristis* (squash bug), where the twenty-one chromosomes of the male differ in size. It has been demonstrated that these chromosomes occur in two sets of chromosomes, as shown in Fig. 92 (*e, f*). When union of chromosomes takes place at the period of pseudo-reduction, a unites with a, b with b, c with c, etc., so that the resultant tetrads are symmetrical.

These two sets of chromosomes represent the sum total of character factors, received from the two parents at the time of fertilization of the egg, which developed into the adult whose germ plasm we may be studying. Each set of chromosomes contains all of the factors necessary for the complete individual (as shown by parthenogenesis, artificial or normal). Each chromosome represents certain structures of the adult (as determined by experiment), and the union at pseudo-reduction of two similar chromosomes is thought to be the union of the factors having to do with the same characteristics of the adult, one chromosome representing these characteristics in the female parent, the other representing the like character group in the male parent. Hence it follows from the happenings at maturation (Fig. 91), if the light area represents certain characteristics of the female parent, these characteristics will be transmitted by the spermatozoa E, E, and not by spermatozoa E′E′, which transmit the male parent equivalent of these characteristics. After fertilization with these spermatozoa, the offspring of E will inherit this set of characteristics from the paternal grandmother, while those from E′ will inherit from the paternal grandfather, subject of course, in both cases, to modifications brought into the union by the egg cells, in which similar maturation processes have taken place.

E. The Mendelian Principles of Heredity

The preceding account of the cytological changes during maturation, and their interpretation on the basis of Weismann's theory of the germ plasm indicate, if the theory is correct, that the germ cells, when ready for fertilization, are pure in respect to any given characteristic, *i.e.*, they carry inheritance of that characteristic from either the male or the female parent and not from both.

The same conclusion was reached, entirely independently of cytology or of Weismann's hypotheses, through experimental breeding of plants and animals, and is embodied in the so-called Mendelian principles of heredity. The great field of modern genetics is the outcome of experiments in selected breeding first carried out scientifically in 1865 by Gregor Mendel, a Silesian monk, in the gardens of the monastery at Brünn. The results of his experiments and the conclusions he drew from them were published in an obscure journal, where they remained buried for thirty-five years. In the year 1900, the botanists de Vries, Correns and Tschermak, working independently, each brought out evidence confirming Mendel's conclusions, and the full value of his work was finally recognized. Soon after, Bateson demonstrated that Mendel's principles apply to animals as well as plants.

A. Heredity of One Pair of Characters.—Mendel's principles of heredity can be best illustrated by a simple case of his own, involving only one pair of characters, in which one of the pair comes from the female parent, the other from the male. Mendel crossed two types of garden pea, one parent plant producing yellow peas, the other green peas. A hybrid (F_1 generation) resulted from this cross, which produced only yellow peas. These yellow peas produced plants which were

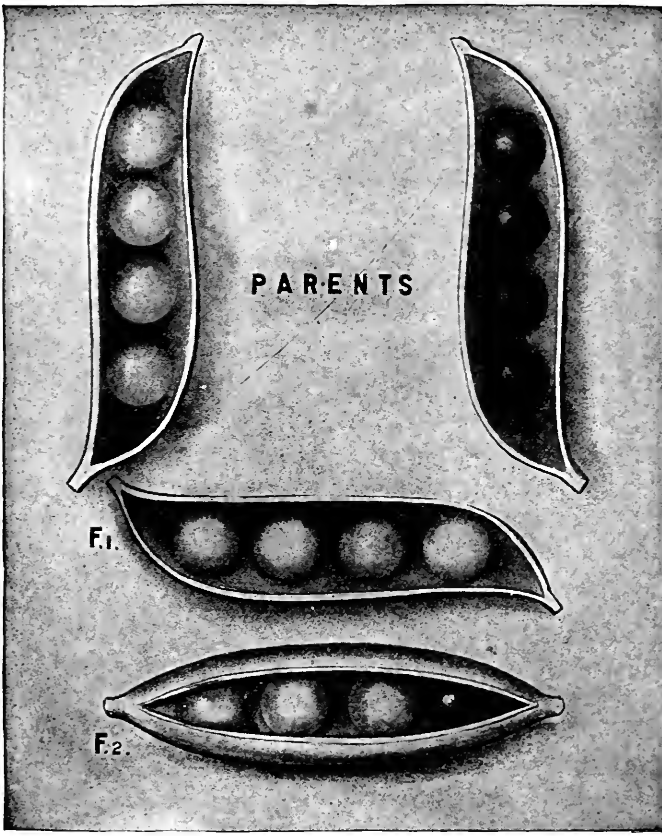


FIG. 93.—Mendelian inheritance resulting from the crossing of yellow and green peas. (From Morgan.)

then intercrossed or self-fertilized, and the resulting peas (F_2 generation) were found to be mixed, the pods containing both yellow and green peas in the proportion of three yellow to one green (Fig. 93). These, in turn, were grown and again self-fertilized, when it was found that the green peas produced only green peas, while the yellow peas were found to be different; some produced only yellow peas, while others produced yellow and green peas, again in the ratio of three to one. The pure yellow peas were found to be just one-third of the total number of yellow peas produced, or one-quarter of the total number of peas—thus, 1 green: 2 mixed, 1 yellow.

In reasoning out the significance of his results, Mendel concluded that something is carried into the germ cells which produces color in the seeds. One original parent contained a factor for yellow, the other a factor for green; fertilization of the germ cells from the two parents brought both factors into the ovule

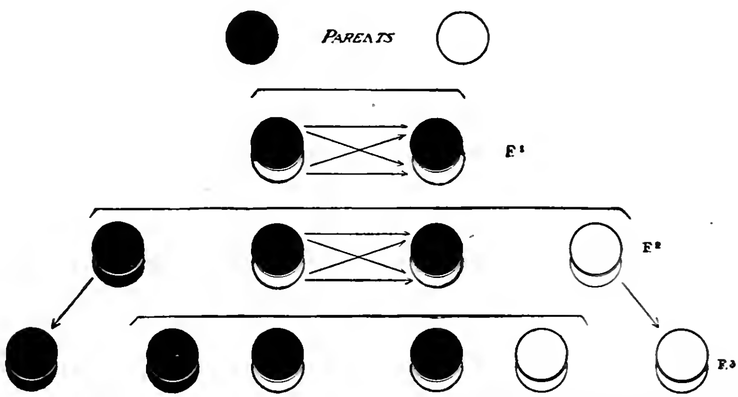


FIG. 94.—Diagram to show the segregation and re-combination of the factors (black and white) in the gametes, and the presence of both in the hybrid *F'*. (From Morgan.)

which developed into the hybrid. Both factors do not come out when the peas are formed; one—*recessive*—remains latent, the other—*dominant*—predominates over the other, with the result that all peas are of one color, in this case, yellow. The principle of *dominance*, where two factors for the same character lie together in the fertilized egg, was thus recognized. The same reasoning is applied in respect to all other characteristics of the adult organisms.

Mendel's experiments were carried out long before the essential features of maturation were known; nevertheless he suggested that some process must take place during the formation of the hybrid germ cells, whereby the yellow and green factors are separated from one another, so as to produce germ cells having only one factor for green or for yellow. This is known as Mendel's principle of *segregation.* The hybrid ovule containing both factors is said to be *heterozygous*, and the two factors for the same character (here color) are called *allelomorphs*, one of which is dominant, the other recessive. If only one type of factors is present in an ovule, it is said to be *homozygous.*

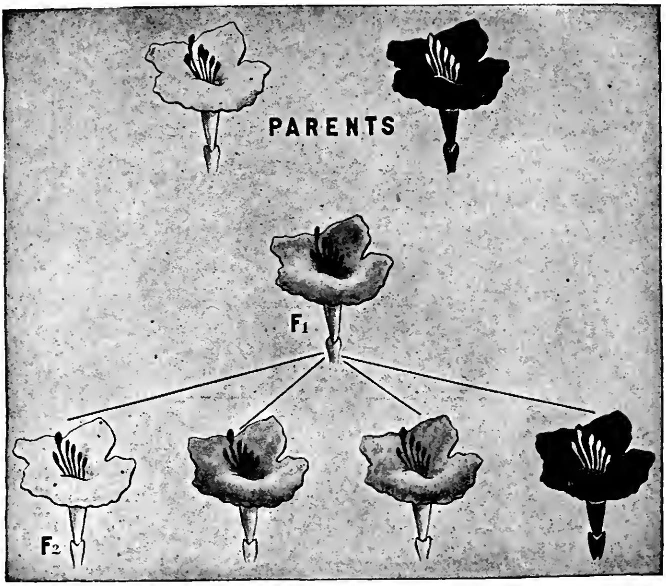


FIG. 95.—Example of Mendelian inheritance in which the hybrid (F_1) is intermediate between the two parents, but showing segregation of the two factors in the germ cells giving in the F_2 generation the proportion of 1 : 2 : 1. The cross is made between white and red races of *Mirabilis jalapa* (the "four o'clock"). The hybrid (F_1) is pink, and these when inbred give white, pink, and red flowers in the proportion of 1 : 2 : 1 (F_2). (From Morgan.)

Now if the hybrid plants are self-fertilized, *i.e.*, through union of their own germ cells, and if segregation of factors occurs during the formation of these germ cells in both anthers and ovules, then the following combinations may occur (Fig. 94). The green-bearing anther may unite with a green-bearing ovule, and the result is green (homozygous); or a green-bearing anther may unite with a yellow-bearing ovule, and the result is a heterozygous yellow, since yellow is dominant. Or a yellow-bearing anther may unite with a yellow-bearing ovule, giving a homozygous yellow; or finally a yellow-bearing anther may unite with a green-bearing ovule, giving a heterozygous yellow. Thus there will be three yellows to one green or one pure yellow, two heterozygous yellows and one pure green (Fig. 94, F2 generation).

Mendel found further, that these pure greens, if continually self-fertilized, never gave rise to yellow peas, and that the pure

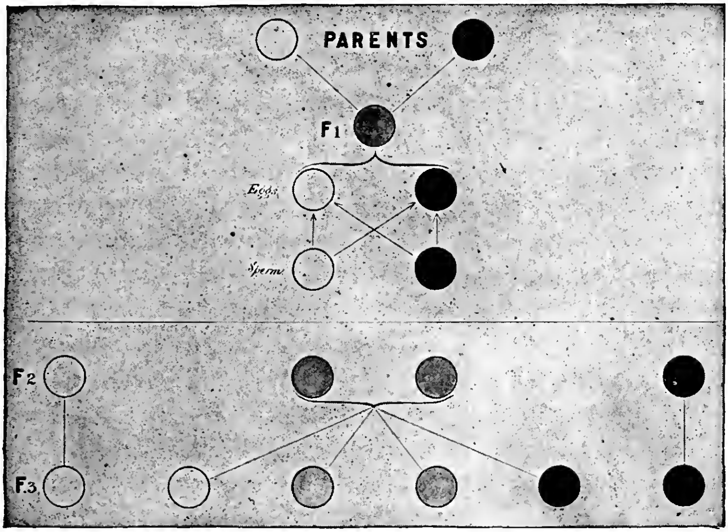


FIG. 96.—Diagram to illustrate the history of the gametes of crossed white and red Mirabilis. A gamete with factor for white and one with factor for red unite to form the pink zygote of F_1. The gametes in F_1 are homozygous for red or white, and these, by random mating, give the Mendelian ratio. (From Morgan.)

yellows never gave rise to green peas, while the mixed yellows and greens, on self-fertilization, always produced offspring in the proportion of three yellow to one green.

A similar result is obtained with white and red races of *Mirabilis jalapa*, the "four o'clock," in which the hybrid (F), is pink (Figs. 95 and 96). Here both allelomorphs for color take part in the hybrid flower, forming a composite pink (F_1) which, on self-fertilization, produces pure whites, pure reds, and the composite pinks.

The same result may be worked out theoretically along the lines of Weismann's hypothesis of the significance of maturation. The chromosomes which unite at pseudo-reduction contain allelomorphs which are separated from one another during the maturation divisions (Fig. 90). Two kinds of spermatozoa and two kinds of eggs result. On self-fertilization, one kind of sperm may unite with an egg containing its like kind, or it may unite with an egg containing its allelomorph. Or the other sperm may unite with its allelomorph or its like, the result being the Mendelian proportion of three to one.

B. Heredity of Two Pairs of Characters.—Mendel worked out the principles of heredity in cases where two or more pairs of characters are involved, and found the same underlying principles of dominance and segregation as in the case of a single pair. He crossed a pea producing yellow and round seeds, with one producing green and wrinkled seeds. The F1 generation or hybrid seeds were yellow and round, showing that the round characteristic is dominant over the wrinkled. The F1 plants, when self-fertilized, produced some yellow and round peas, some yellow and wrinkled, some green and round peas, and some green and wrinkled in the proportion of 9 : 3 : 3 : 1. The explanation is the same as for the simpler cases of one pair of characters. One parent produced germ cells containing the factors for yellow (Y) and round (R); the other parent produced germ cells containing the factors green (G) and wrinkled (W). The fertilized eggs, or F1 generation, must therefore have contained YRGW, the allelomorphs being YG and RW. These allelomorphs are separated during maturation, the germ cells containing either YR, YW, GR or GW, since these are the only possible combinations. If the hybrids are self-fertilized, there would be four kinds of male and four similar kinds of female gametes, which would give sixteen possible combinations as shown in Fig. 97.

These experiments have been so often repeated, and on so many different plants and animals with many different characteristics, that the main conclusions of Mendel are now universally accepted. Many characters, however, do not seem to segregate or Mendelize, at least not in any simple way that can be predicted, and these are the problems that modern experimentalists are working on.

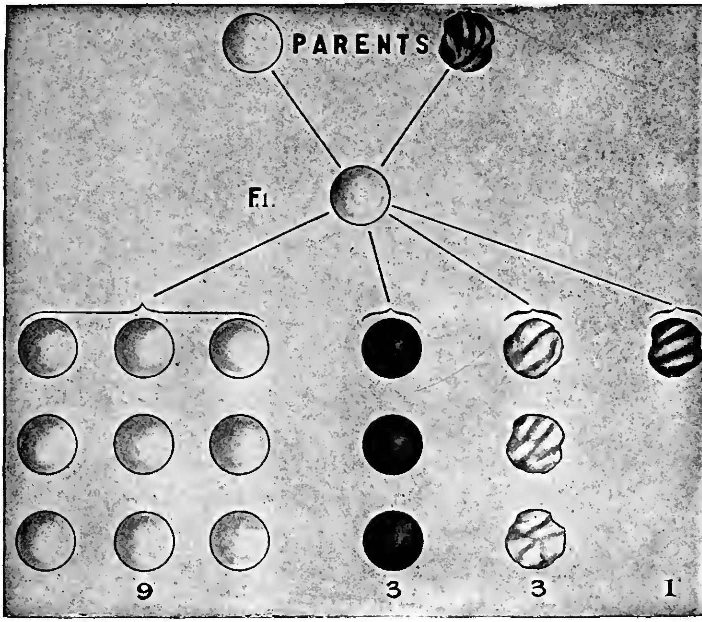


Fig. 97.—Diagram iilustrating Mendelian inheritance when two characteristics are involved. A yellow-round and a green-wrinkled pea are crossed. The F_1 generation gives only yellow and round peas, these being dominant over green and wrinkled. These when inter-bred segregate out in the proportion of 9 : 3 : 3 : 1. (From Morgan.)

C. Heredity of Sex. *Cytological evidence*.—Sex, with many of the secondary characters which go with it, is recognized today as an aggregate of Mendelian characteristics. The evidence on which this generalization is based is partly cytological, partly experimental, and while many perplexing problems connected with sex are still unsolved, the evidence in favor of the heredity of sex is so strong that it may be accepted as the most plausible working hypothesis at the present time.

On p. 215 reference was made to divergent results in regard to the number of chromosomes in development of the sperm cells of certain animals. In a great many insects (belonging to the orders hemiptera, diptera, homoptera, phylloxerans, etc.), in nematode worms (Ascaris, Ancyrocanthus), and in Guinea pigs, the process of spermatogenesis does not exactly accord with the description given. For example, the bug Protenor has thirteen chromosomes in the cells of the male, and fourteen in those of the female, instead of the same number in both sexes. Of the thirteen male chromosomes, one is considerably larger than the others. At synapsis the smaller chromosomes unite in pairs according to the usual rule, but the large one remains unpaired (Fig. 98, ♂ A). At the first maturation division, all of the chromosomes divide, six small and one large passing into each daughter cell. At the second maturation division, the six small ones divide again, while the large one passes undivided into one of the daughter cells (Fig. 98, ♂ D). Thus two types of spermatozoa result, one type possessing six chromosomes, the other, seven.

In the female germ cells (Fig. 98, ♀ A, B), there are fourteen chromosomes, of which twelve are smaller than the other two. The latter unite in synapsis and behave like the smaller chromosomes during maturation divisions, the resultant eggs all receiving seven chromosomes (Fig. 98, ♀, D, E,). Now if a spermatozoon with six chromosomes fertilizes one of these eggs, the result is a male with thirteen chromosomes; if one with seven chromosomes fertilizes the egg, the result is a female with fourteen chromosomes. The large, odd chromosome, therefore, is a sex determining chromosome.

Another excellent illustration is given by the nematode worm Ancyrocanthus, where the number of chromosomes may be counted in the living germ cells. The male, as in Protenor, produces two kinds of spermatozoa, one with five chromosomes, the other with six. The eggs all contain six chromosomes. Fertilization with one type of spermatozoa produces a male with eleven chromosomes; fertilization with the other type produces a female organism with twelve.

In man, there is some evidence that a similar difference in

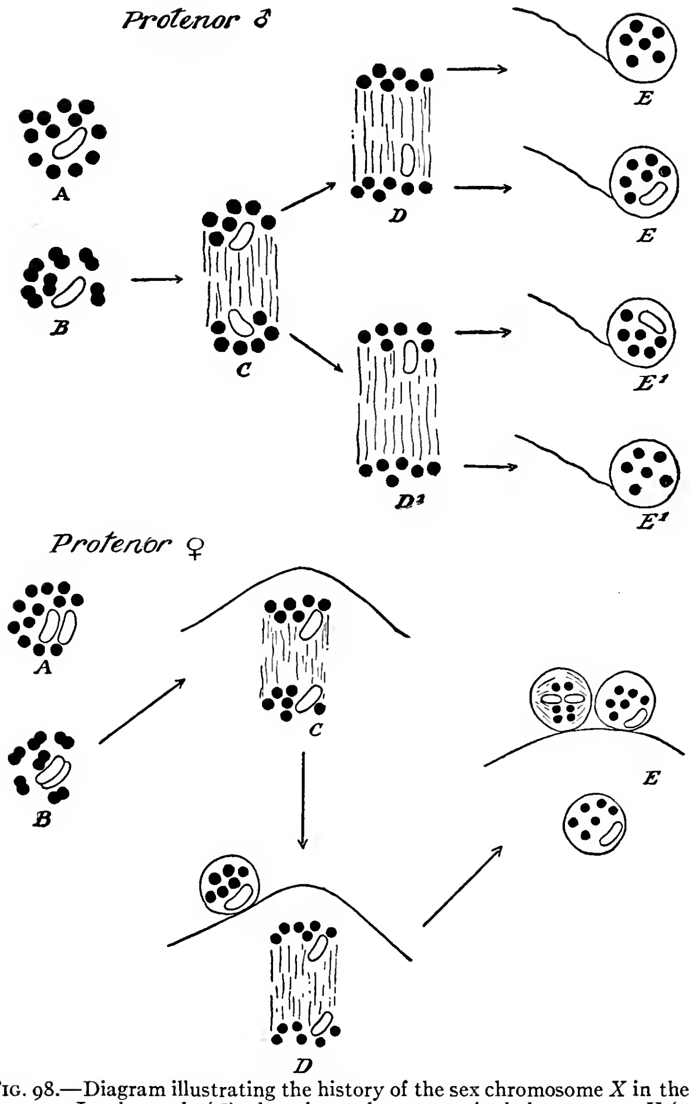


FIG. 98.—Diagram illustrating the history of the sex chromosome *X* in the bug Protenor. In the male (♂) there is one large, unpaired chromosome *X* (represented as blank) in *A–E′*. *B*, Union of the chromosomes in pairs except the *X*-chromosome. The two successive maturation divisions (*C*, *D*), show the distribution of *X* in the resulting spermatozoa (*E*, *E′*), two of the four having *X*, two having no *X*. The latter have only five chromosomes, and on uniting with eggs, produce only male individuals. The female organisms have two *X*'s which pair in maturation like the other chromosomes, so that the resulting eggs and polar bodies all have one *X*. A spermatozoon with *X*, uniting with an egg, produces a female organism. (From Morgan.)

spermatozoa is present, although the small size of the chromosomes and their large number makes counting difficult, so that observers disagree as to the facts. According to one careful observer (von Winiwarter), the male cells contain forty-seven chromosomes which unite to form twenty-three pairs and one odd chromosome (Fig. 99). Two types of spermatozoa result, one with twenty-four, the other with twenty-three chromosomes.

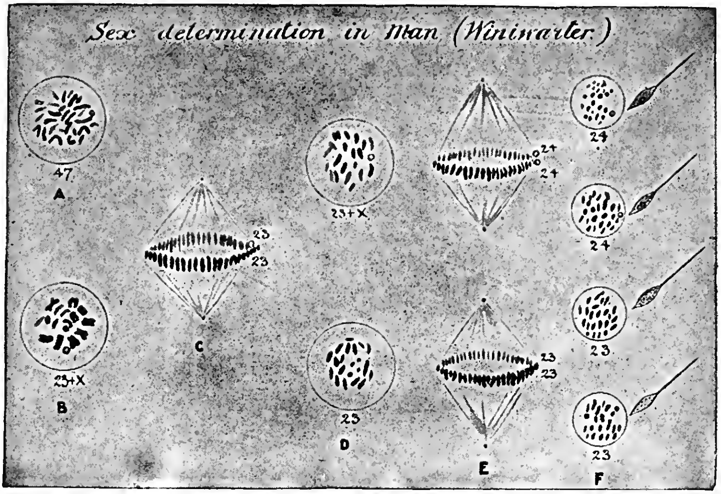


Fig. 99.—Diagram of the history of the male cells in human spermatogenesis. *A*, Spermatogonium with forty-seven chromosomes; *B*, first spermatocyte with the haploid number of chromosomes in pairs and the sex chromosome (open circle); *C*, first maturation division; *D*, two resulting cells (spermatocytes) from the first maturation division; *E*, division of the second spermatocytes giving *F*, four resulting spermatozoa, two female producing (above), two male producing (below). (From Morgan.)

Female cells have forty-eight chromosomes, according to this observer's best counts, twenty-four being present in the mature egg. Fertilization results in an embryonic cell with forty-eight or forty-seven chromosomes, according to the type of spermatozoon uniting with the egg cell, and the resultant individual is female or male, according to the type of spermatozoon.

The cytological evidence, therefore, affords some very clear proofs that, in some cases at least, sex varies with the presence or absence of one chromosome, and we cannot get away from the conclusion that, in such cases, this chromosome itself is the

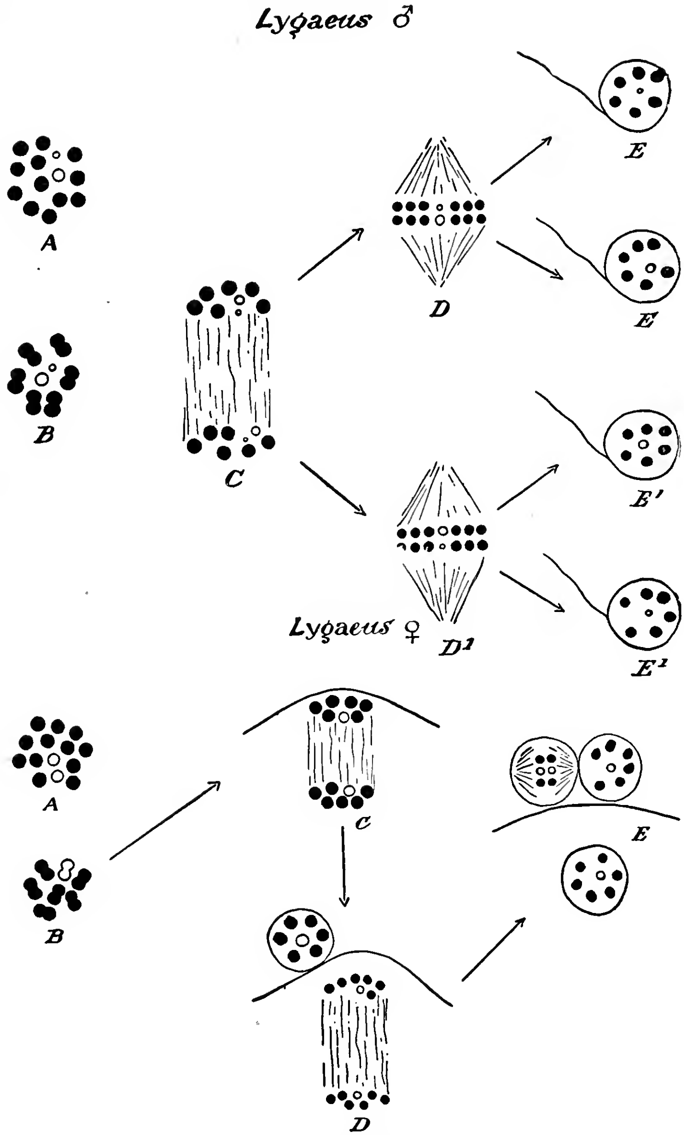


FIG. 100.—Diagram illustrating the history of the sex chromosome when accompanied by a smaller *x* or *Y* chromosome, as in *Lygaeus bicrucis*. The male cells have twelve ordinary chromosomes and two sex chromosomes, one larger (*X*) than the other (*Y*). The resulting spermatozoa from each primordial cell differ; two have *X* and produce females on uniting with eggs, two have *Y* but no *X* and produce males. (From Morgan.)

essential factor in sex determination. In other cases, the evidence is equally clear, but it is found that the sex chromosome is not always alone, *i.e.* unpaired at maturation. In some cases, its history may be easily followed because of some size difference or other peculiarity. Thus in the bug Lygaeus, the sex chromosome of the male (X), unites at synapsis with a smaller element (Y), the end stages of maturation giving again two types of spermatozoa, one type containing the sex chromosome (X), the other its smaller mate (Y) (Fig. 100). The female, on the other hand, contains the full number of chromosomes including two X's. After maturation there is one X in each egg. Fertilization results in embryos with either one X or two X's. In the former case, the individual is a male, in the latter case a female.

In still other types of bugs, the corresponding X and Y chromosomes are of equal size and cannot be distinguished morphologically, but males and females are produced in equal numbers, and the conclusion is justified that one of the chromosomes is the sex determining or X chromosome (see Ascaris, Fig. 91).

Experimental Evidence.—The modern conception of sex determination, as outlined above, is beautifully supported by direct experiments in breeding. It is quite conceivable, *a priori*, that the sex chromosome X should contain factors standing for other characteristics of the adult than sex alone. If this is true, then certain peculiarities should appear only when the sex chromosome is present as a pure Mendelian segregation character. An actual experiment will make this clear. Prof. Morgan has carried out breeding experiments on the small fruit fly, *Drosophila ampelophila*, for several years. The wild fly has typical red eyes, but during the experiments a white-eyed male appeared. This was mated to a typical red-eyed female (Fig. 101). The offspring were all red-eyed. These were then in-bred, and the resulting brood contained (1st) red-eyed females, (2nd) red-eyed males, and (3rd) white-eyed males, and in the proportions of 50% of the 1st, 25% of the 2nd and 25% of the 3rd, a true Mendelian proportion.

On the chromosome basis, this result is as easily explained along the lines of Mendelian segregation as is the case of sweet peas. The sex chromosome (Fig. 101) may be represented by X, the black X representing red eyes, the open X white eyes, and O in males, no X. After maturation of the original white-eyed male, one type of spermatozoa has the open X, the other type has no X as in the case of Protenor (Fig. 98). Fertilization affords an equal chance for both types of spermatozoa. The egg

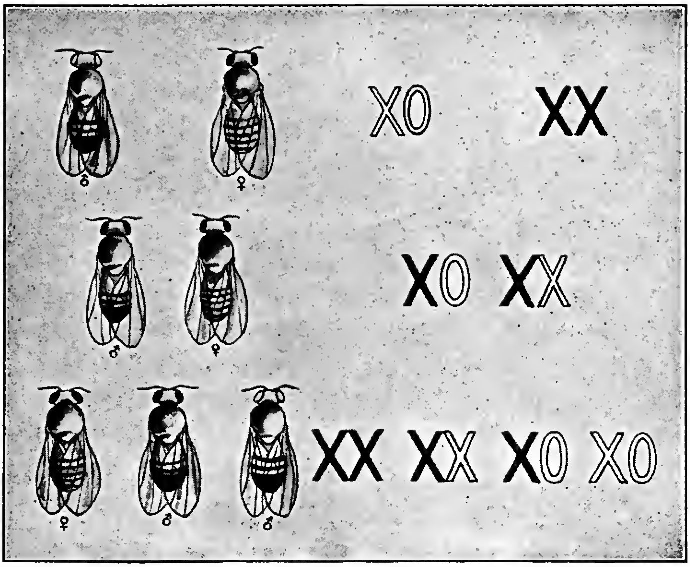


Fig. 101.—Sex-linked inheritance of white and red eyes in Drosophila. Parents, white-eyed ♂ and red-eyed ♀; F_1 red-eyed ♂ and ♀; F_2, red-eyed ♀, red-eyed ♂ and white-eyed ♂. To right of flies the history of the sex chromosomes XX is shown. The black X carries the factor for red eyes, the open X the factor for white eyes, O stands for no X. (From Morgan.)

cells contain one black X. The F1 generation will all contain a black X which is dominant over the open X, and of course over no X. When these are interbred, two black X's, a black X with an open X, a black X with no X, and an open X with no X may result, and the proportions are three red to one white.

In this experiment, only males appeared with white eyes, a fact which might be interpreted as sex-limited inheritance, males only having white eyes. This, however, is not true, for white-eyed females may be produced by mating the above red-eyed grand-daughters (containing a black X and an open X) with the white-eyed male (containing an open X and no X). Two white X's are brought together, and females with white eyes are produced, as well as females with red eyes, and males of both types.

This feature, eye color, therefore is not *sex-limited*, but is said to be *sex-linked, ie.* connected with the sex chromosome, and is distributed with the distribution of the sex chromosome.

Prof. Morgan has found no less than seventy-five of these sex-linked factors, all of which have been worked out experimentally on the fruit fly, and all conform to the case illustrated above. Other characteristics have been found which have nothing to do with the sex chromosomes, but are bound up with others. These results thus appear to be a brilliant confirmation of Weismann's hypothesis of the constitution of the germ plasm.

F. The Origin of Variations

The results described above from cytological and experimental work would seem to indicate that variations would be extremely difficult to originate. If the characteristics of the adult are contained in the germ plasm, then the individual is preordained, and the germ plasm would pass on to descendants with the same characteristics. The individual which develops may change, by reason of environmental influences, in many somatic characteristics, but how is it with the germ plasm and the characteristics of the parents? Examples from mutilations would seem to bear out the Weismann view, that somatic changes of the individual have no effect on the germ plasm which that individual carries and transmits. Nevertheless, variations do arise, are transmitted by inheritance, and fostered or obliterated by natural selection. How they arise is still a matter of speculation, more or less founded on fact. Amphimixis, mutation, inheritance of acquired characteristics, are upheld by various biologists as accounting for the origin of variations.

Amphimixis.—The union of germ cells brings together (amphimixis) the traits of two lines of ancestry, and with the union a possibility of different combinations in the segregation of characteristics. Or by such union, recessive characteristics may be brought out, leading to divergent types in the race. This principle, advocated by Weismann, leaves unexplained the origin of the factors in the germ plasm, but interprets the changes that may arise, as due to shuffling about of the characters already present. Other biologists interpret amphimixis as bringing about the exactly opposite result, viz., keeping the race true to type, and preventing variations.

Mutations.—A number of biologists believe that new types arise suddenly, by jumps or mutations, which first appear as freaks of nature or "sports." The botanist de Vries discovered a variety of primrose which underwent a spontaneous change of type, sufficiently well marked to make of it a new variety, if not a new species. It bred true to its type, and showed no tendency to revert to the ancestral form. De Vries concluded, and many biologists agree with him, that freaks or sports appear infrequently in the history of every species, and serve as centers of departure from old types. Such mutations were known to Darwin and the earlier evolutionists, the race of Ancon sheep being an historic example.

Mutations may be due to the chance union of recessive characteristics, which, as in Prof. Morgan's flies, would be lost again by promiscuous or indiscriminate breeding. Prof. Tower has been able to breed in the laboratory distinct types of the potato beetle, which differ markedly from the ancestral type from which they sprang, and he has found the same distinct types existing wild in nature and regarded as different species. Here an experiment was performed in the laboratory, which had been done on a larger scale in nature, with the advantage in the laboratory, because the starting point, a mutant, was known. But again the result may be interpreted as due to shifting of germinal characteristics, followed by discriminating breeding.

If, in any of these cases, the variation is useful to the organism in its struggle for existence, the chances of living and of mating are increased, which would result in the numerical increase of the mutant type, until possibly the ancestral or original type is crowded out. Thus by natural selection, a new species and one better adapted to the environment would result. Or it is conceivable that dominance may shift about with environmental changes, thus leading to change of type. Speculations as to the origin of variations based on the theory of mutations are endless, and there is apparently good ground for many of them.

The Inheritance of Acquired Characteristics.—Beginning with Lamarck (1744–1829), many biologists have held that changes brought about in structures of the individual, during that individual's lifetime, are transmitted by inheritance to the offspring. This conception, extremely difficult to prove experimentally, involves the fundamental principle of use and disuse of organs as affecting the descendants and the race.

Everyone knows that continued use of an organ strengthens it—a time-worn illustration is the blacksmith's arm—but there is no evidence that this over-developed organ is transmitted to the offspring, no evidence that the blacksmith's children differ from other children in muscular development. This point could not be satisfactorily proved, however, until a hundred or more generations of successive blacksmiths have been studied. The imagination fails in trying to account for the origin of the lobster's chelate appendages through use and inheritance, but readily conceives how such an organ might have arisen by mutation and been transmitted by inheritance, and which, being useful, is preserved in the race by natural selection. On the other hand, the effects of use seem to be shown in the single-toed horse of today, which has descended from ancestral forms having four toes and a rudimentary fifth (Eohippus) on the front legs, and from forms having three toes, one of which is large and functional, the other two reduced (Hipparion, Merychippus). This appears to be a case where continued use has resulted in the modern structure.

The effect of disuse may be readily imagined. Vestigial organs are evidence of structures which in the past have been useful in one way or other. The lateral toes of the fossil horse, of little use apparently even to Hipparion, have entirely disappeared in the modern horse. The digestive tract of intestinal parasites shows various degrees of degeneration through disuse. In some of the thread worms (nematodes), it consists in part of a single row of perforated cells; in the tape-worm, it has entirely disappeared.

In order that they may be perpetuated, any changes that may occur in the individual must be represented in the germ plasm. The individual is mainly somatic, and as such is mortal, but he is also the nurse or protector of the germ plasm which is potentially immortal. Whether or not he can impress his individual stamp on the germ plasm, and send it on with the new impress, is the very crux of the problem of species. Modern biology gives no positive solution of this problem. Weismann and his school maintain that all changes are due to re-combinations of factors in the germ plasm; Neo-Lamarckians, that the germ plasm responds directly to the changes in the body, and these in turn go back to the conditions of the external environment.

The limits of this text-book do not permit an examination of the evidence for and against these two points of view; indeed many important questions which bear upon it have not been even mentioned. Morgan has recently summed up the general problem as follows: "It is true that the germ plasm must sometimes change—otherwise there could be no evolution. But the evidence that the germ plasm responds directly to the experiences of the body has no substantial evidence in its support. I know, of course, that the whole Lamarckian school rests its argument on the assumption that the germ plasm responds to all profound changes in the soma; but despite the very large literature that has grown up dealing with this matter, proof is still lacking. And there is abundant evidence to the contrary.

"On the other hand there is evidence to show that the germ plasm does sometimes change or is changed. Weismann's attempt to refer all such changes to re-combinations of internal factors in the germ plasm itself has not met with much success. Admitting that new combinations may be brought about in this way, yet it seems unlikely that the entire process of evolution could have resulted by re-combining what already existed; for it would mean, if taken at its face value, that by re-combination of the differences already present in the first living material, all of the higher animals and plants were foreordained. In some way, therefore, the germ plasm must have changed. We have then the alternatives. Is there some internal, initial or driving impulse that has led to the process of evolution? Or has the environment brought about changes in the germ plasm? We can only reply that the assumption of an internal force puts the problem beyond the field of scientific explanation. On the other hand, there is a small amount of evidence, very incomplete and insufficient at present, to show that changes in the environment reach through the soma and modify the germinal material" (T. H. Morgan, *Heredity and Sex*, pp. 17–18).

The origin of adaptations thus, specifically in our group of crustacea, is still difficult to explain. Some advance of a sure kind has nevertheless been made. We know that a fundamental property of protoplasm is its power to vary, to adapt itself to changed conditions of environment. In higher animals the somatic protoplasm certainly exhibits this property, and there is no *a priori* reason why the germ plasm also should not possess it. We know also that changes in one organ bring about compensatory or regulating changes in others, and again there is no *a priori* reason why the germ plasm should not partake in this reaction. An adaptation in our crustacea may have originated as a useful mutation; in the germ plasm, it may have been present as a simple Mendelian characteristic, subject to segregation during the maturation stages. Later it may have become too deeply impressed in the germ plasm to undergo segregation, and became a fundamental part of the racial plasm no longer subject to extinction by natural selection, while the environment remained the same. Such an origin, especially for all of the variations in a present-day phylum, and in different phyla, demands time. The history of the earth, as written in modern geology, allows some hundred millions of years for modern types to have evolved, and if seventy-five mutants of a single species may be experimentally produced in seven years, it is conceivable that 500,000 species of animals might have been produced in one hundred millions of years, since each species possesses the power to vary.

The power to vary is not possessed by all organisms in equal degree; this is shown by the very fact of the enormous differences in organization of modern animals, some of which do not vary in any marked degree from forms deposited some fifty million years ago, and found today as fossils. If the dictum *omne vivum ex vivo* is true, then all protoplasm must be of approximately the same age, whether found in an amoeba or in man. If protoplasm of all animals is equally old, it follows that some forms of it were endowed with a greater possibility of variations and adaptations than others, or with a greater "potential of evolution," so that certain types developed into marvelously complicated organisms in the same period required by other types to develop into lower forms. Thus if man and the coelenterates are equally old, the protoplasm which was to develop into man must have been endowed with a much greater potential of evolution than that which developed into the coelenterates, provided they had a similar environment.

It is conceivable also that, in the period when protoplasm was formed from non-living matter, the conditions were not always the same, and that the "best" protoplasm, in the sense of possessing the highest potential of evolution, was formed during a limited part of the protoplasm-forming period, while protoplasm less highly endowed was formed at other times, when conditions were less propitious. Bacteria and the lowest forms of both plants and animals might be conceived as having come from protoplasm formed during an unpropitious period, and so poorly endowed with the potential of evolution that some of them never reach the stage of a perfect cell; others, like the present day infusoria and higher protozoa generally, never progressed beyond the single-celled stage.

If from the coelenterates up, a monophyletic hypothesis is adequate to explain present-day phyla, then we must admit that, with different types and under the conditions of their development, unlimited variations and evolution were impossible, and that certain types of structure would permit of many more variations than do other types. Some modifications were capable of great development; these were "lucky strikes" so to speak, in evolution, which enabled the organisms to respond more quickly or more adequately to changes in environment. One of the greatest of these probably was the development of metameric structure; another was the development of the internal osseous skeleton; still another was the development of air tubes or tracheae for respiration, and others will occur to every student.

GLOSSARY

Acquired Character. A character which originates during the life of an individual and due to environmental causes.

Adolescence. Youth, or the period of life between sexual maturity and full development. Usually employed in connection with young of the human race.

Allelomorph. One of two factors standing for the same character in inheritance.

Alternation of Generations. A phenomenon in the reproduction of animals or plants, whereby an organism resulting from fertilization or parthenogenesis gives rise to other organisms by some asexual method of reproduction (division, budding, or sporulation).

Amboceptor. An intermediate chemical body acting as the linking factor between two other chemical bodies.

Amino-acid. An acid containing the amino-group NH_2.

Amoeboid. Pertaining to or resembling Amoeba.

Amphimixis. The union in the fertilized egg of germ plasm and hereditary factors from different individuals.

Amylase. A ferment capable of dissolving starch.

Amylolytic. Starch dissolving.

Anabolism. Processes of constructive or ascending metabolism, whereby energy is absorbed and stored up.

Antherozoid. A minute male germ cell of the fern and other cryptogams.

Antibody. A chemical substance capable of counteracting or neutralizing a toxic substance.

Antigen. Any substance capable of entering into combination with protoplasmic molecules and of stimulating the formation of antibodies.

Apical Cell. The single cell which in higher cryptogams constitutes the growing point.

Archegonium. Female sexual organ of the fern and higher cryptogams.

Archenteron. Primitive or first gut of developing animal embryos.

Archesporium. A spore-producing cell.

Autotrophic. Capable of independent or self-nourishment.

Axon. The main nerve process from a nerve cell; also called the axis-cylinder.

Basal Body. Part of the kinetic complex of a flagellated protozoan which gives rise to the flagellum.

Blastomere. Any cell in the early cleavage stages of the developing egg.

Blastophore. Sperm mother-cell in earthworm spermatogenesis.

Blastopore. The opening or mouth of a gastrula.

Blastula. An early stage in development of the egg prior to the gastrula or two-layer stage.

Branchiostegite. Lateral gill-protecting portion of the crustacean exoskeleton.

Buccal Cavity. Mouth cavity.

Carbohydrate. Any organic body containing carbon, with hydrogen and oxygen in the proportions represented by water (H_2O).

Cell. A unit mass of protoplasm consisting of nucleus (or nuclei) and cell body or cytoplasm.

Centrolecithal. A type of ovum in which the yolk material is mainly collected in the center.

Centrosome. The center of radiations in a dividing cell.

Cephalothorax. Fused head and thorax of the majority of the higher crustacea.

Chitin. A lifeless organic substance which forms the basis of protective membranes, integuments, shells, and exoskeletons of invertebrates.

Chlorophyll. The coloring matter of plants which, under the action of sunlight, decomposes carbon dioxide and water and recombines the elements in the form of carbohydrates.

Chloroplastid. A green, chlorophyll-bearing structure in plant or animal cell.

Chromatin. The deeply staining substance of the nuclear network and chromosomes.

Chromogen. The nitrogen-holding portion of the chlorophyll molecule.

Chromoplastid. A color-bearing structure other than chloroplastids in plant cell.

Chromosomes. Deeply staining bodies formed by aggregations of chromatin during the process of indirect cell division.

Clitellum. A glandular swelling in the region of the 30th to 37th somite of the earthworm. It produces the girdle by which two worms are held together at copulation.

Coelom. The periaxial body cavity of a metazoon with mesodermal wall and containing the internal opening of the excretory organ.

Colony. An aggregate or association of individuals.

Commensalism. Living together in harmony without necessarily conferring mutual benefit or harm.

Commissure. A connecting nerve between ganglia.

Complement. A chemical substance in the blood which acts only through association with an intermediate body or amboceptor.

Conjugation. The temporary sexual union in protozoa and lower plants.

Corpora Lutea. Firm yellow bodies formed in the Graafian vesicle after the discharge of an ovum.

Crustacea. A group of arthropods with firm exoskeletons.

Cuticle. The lifeless outermost covering of the body of an animal.

Cyanophyll. A greenish-blue substance derived from chlorophyll.

Cyclosis. The streaming movements of protoplasm within the cell.

Cysticercus. The encysted state of the larva of a tape-worm.

Cytology. The science which deals with cells.

CYTOPLASM. The protoplasm of the cell apart from that of the nucleus; the cell body.

DENDRITES. The protoplasmic branching processes of a nerve cell.

DIASTASE. A ferment which transforms starch into sugar.

DIFFERENTIATION. The evolutionary process or result by which originally indifferent parts or organs become changed or specialized in either form or function; specialization.

DIPLOID. Refers, in connection with chromosomes, to the double or normal number, half from the male, half from the female parent.

DISSEPIMENT. A septum or partition between the somites of annelids.

DOMINANT CHARACTER. A character inherited from one parent which develops, while the factor for the same character from the other parent remains latent or undeveloped (recessive).

ECDYSIS. Moulting, or the act of shedding an outer coat or integument.

ECTOBLAST. The outer primary cell layer in the embryo of any metazoan animal; the ectoderm.

ECTODERM. The completed outer layer of cells in all metazoan animals, formed by the cells of the ectoblast.

ECTOPLASM. The outermost recognizable living substance of a cell.

ENCYSTMENT. The process of forming a tough resistant covering or cyst within which the organism remains alive.

ENDODERM. The inner layer of cells surrounding the enteron in all metazoa.

ENDOENZYME. A ferment formed, and normally acting, within the protoplasm of a cell.

ENDOMIXIS. Asexual re-organization of the cell (Protozoa).

ENDOPLASM. The inner protoplasm of a protozoan cell.

ENDOPODITE. The inner one of the two main divisions of the typical limb of a crustacean.

ENDOTHELIUM. Superficial layer of cells derived from the mesoderm.

ENTERON. The intestine, alimentary canal, or digestive space which is primitively derived from the endoderm.

EPIDERMIS. The non-vascular outer layer of the body.

EPISPORE. The outer covering of a spore.

EPITHELIUM. Any superficial layer of cells of mucous membranes including the proper secreting tissues of glands, etc.

EXOPODITE. The outer one of the two main divisions of the typical limb of a crustacean.

FACTOR. A specific cause in a germ cell of a developed character.

FÆCES. Excrement voided from the anus; "castings."

FERMENT. A chemical substance which stimulates chemical activity in other substances.

FERMENTATION. A chemical change produced in an organic substance by the activity of ferments usually derived from living things.

GAMETE. A reproductive germ cell, male or female.

GAMETOPHYTE. The sexual generation of a plant.

GANGLION. An aggregate of nerve cells, nerve fibers, and supporting cells.

GASTRULA. A stage in development in which the embryo consists of two germ layers enclosing the archenteron.

Gastrulation. The process of gastrula formation.

Gemmation. Asexual reproduction by budding.

Genetics. The science of heredity.

Germ Plasm. The reproductive protoplasm distinguished from the somatic or organ-forming protoplasm of the individual.

Gonad. A reproductive organ in which the germ cells are formed.

Haematochrome. A red coloring matter formed from chlorophyll.

Haemocoel. A body cavity containing blood, and different from a coelom.

Haploid. Refers, in connection with chromosomes, to the half number subsequent to reduction.

Hepato-pancreas. The digestive gland of the crustacea.

Heredity. The appearance in offspring of characters, the factors for which are in the germ cells.

Hermaphrodite. An organism with both male and female organs of reproduction, or capable of producing both eggs and spermatozoa.

Heterozygous. Containing two factors or allelomorphs for the same character in heredity.

Holoblastic. Cleavage in which the division planes cut through the entire cell mass.

Holophytic. Like green plants in the manufacture of food.

Holozoic. Animal-like in mode of nutrition.

Homology. Genetic relation of parts; implies morphological likeness or structural affinity.

Homozygous. In heredity, containing one kind only, of two alternative factors for the same character.

Hormone. An internal secretion necessary for the full activity of some organ at a distance.

Hydranth. A single asexual individual of a hydroid colony.

Hydroid. Hydra-like, or pertaining to Hydroidea, a group of coelenterates.

Hydrolysis. A form of chemical decomposition by which a compound is resolved into other compounds by taking up the elements of water.

Hydrolytic. Capable of producing dissolution through the addition of water.

Immunity. Protection against disease.

Indusium. Membrane covering a sorus or fruit-dot in ferns.

Intussusception. Reception of foreign matter by all parts at once of living matter, leading to interstitial growth as opposed to growth by accretion or addition on the outside.

Irritability. The property possessed by all protoplasm of responding to stimuli.

Karyokinesis. The phenomena of nuclear division involving the formation and the division of chromosomes; same as mitosis.

Katabolism. Destructive metabolic processes in the living organism, whereby protoplasm and its derivatives are broken down, forming compounds of lower energy potential and transforming stored energy into energy of heat and movement.

Linin. The substance of the nuclear reticulum other than the chromatin.

LIPASE. An enzyme which converts fats into glycerine and fatty acids.

LIPOLYTIC. Capable of disintegrating fats.

MACROCYTASE. Digestive ferment of the macrophage.

MACRONUCLEUS. The larger nucleus of a protozoan cell in which dimorphic nuclei are present.

MATURATION. The series of processes in the formation of germ cells by which the number of chromosomes is reduced to one-half.

MEDUSA. A free-swimming, gonad-bearing sexual generation of coelenterates.

MELANIN. A toxic pigment formed by malaria organisms.

MERISTEM. Unformed and growing cell tissue found at the ends of young stems, leaves and roots.

MEROBLASTIC. Applied to eggs in which the division or cleavage planes do not cut through the yolk mass; superficial cleavage.

MEROZOITE. An asexually reproduced germ-cell.

MESODERM. The middle germ layer of an animal embryo in the three-layer stage.

METABOLISM. The aggregate of chemical changes in living organisms involving the building up of protoplasm (anabolism), and the breaking down of protoplasm (katabolism).

METAGENESIS. See alternation of generations.

METAMERISM. Segmentation of the body along the main axis, resulting in a series of more or less similar parts which are serially homologous.

MICROCYTASE. A digestive ferment produced by microphages.

MICRONUCLEUS. The smaller nucleus of an infusorian in which dimorphic nuclei are present.

MICROSOMES. The minute granules embedded in the ground substance of protoplasm.

MIMICRY. The simulation of something else in form or color, usually having protective value to an organism.

MITOSIS. The processes involved in nuclear division, including formation and division of the chromosomes. Same as karyokinesis.

MORPHOLOGY. The science which deals with form.

MUTATION. The process of originating a new species or a new specific character at a single step; discontinuous variation.

NEMATOBLAST. A nettle thread-forming cell of Hydra and allied forms.

NEMATODE. A round- or thread-worm.

NEPHRIDIUM. The excretory organ of invertebrate animals.

NEPHROBLAST. Initial cell of a chain of cells in development destined to form an excretory organ or part thereof.

NEPHROSTOME. Mouth or internal opening of a nephridium.

NEUROBLAST. Initial cell in a chain of cells in development destined to form the nervous system or part thereof.

NEURON. Morphological and physiological unit of the nervous system consisting of a nerve cell, its nucleus, axon, and dendrites.

NUCLEUS. A differentiated portion of the cell protoplasm consisting of membrane, chromatin, linin, nucleoli and ground substance.

Ommatidium. A radial element or segment of the compound eye of an arthropod.

Ontogeny. The developmental history of a given organism as distinguished from phylogeny or history of the race.

Oogenesis. The development of the ovum from a primordial sex cell.

Otocyst. A vesicle associated with the sense of equilibration in lower animals; a primitive auditory organ.

Otolith. A mineral element or concretion in an auditory vesicle.

Oxidation. The action or process of taking up or combining with oxygen.

Parabasal Body. A part of the kinetic complex of a flagellated protozoan.

Parenchyma. The fundamental cellular tissue of plants.

Parthenogenesis. Development without fertilization of an egg into a normal individual.

Pericardium. The membrane around the heart.

Peristalsis. Wave-like involuntary contraction of circular muscles of a tubular organ.

Peristome. The region around the mouth.

Phagocyte. Amoeboid cell of the blood able to engulf other cells or foreign objects.

Phagocytosis. The process of engulfing by a phagocyte or white blood cell.

Photosynthesis. The process by which green plants utilize the energy of sunlight in the manufacture of starch.

Phylogeny That branch of biology which treats of the ancestral history of animals or plants.

Phylum. Any primary group in the animal or vegetable kingdom.

Phytol. A primary alcohol composing part of the chlorophyll molecule.

Pinnæ. The smaller branches of a branching structure.

Pinnules. The smallest branches of a branching structure.

Plasmodium The cause of malaria, a protozoan.

Polar Body. A minute abortive cell given off by an ovum during maturation.

Polymorphism. Capacity of an animal or plant to exist under different forms or types.

Proctodaeum. The posterior part of the digestive tract of an animal formed by the ingrowth of ectoderm.

Proglottid. One of the posterior segments of a tape-worm.

Prostomium. The lobe in front of or overhanging the mouth of an annelid.

Protease. An enzyme capable of transforming proteins into diffusible bodies.

Protein. That group of chemical substances which consist essentially of amino acids and their derivatives.

Proteolytic. Capable of breaking down, or dissolving, protein.

Proteose A secondary protein derivative.

Prothallium. Sexual generation derived by germination of the spore in the higher cryptogams and bearing the sexual organs.

Protonema. Outgrowth from the germinating spore in higher cryptogams, which develops into the prothallium.

Protoplasm. The living substance of animals and plants.

PROTOPODITE. The first or basal division of an appendage of a crustacean.

PSEUDOPODIUM. A temporary prolongation or protrusion of the protoplasm of amoeboid cells.

QUARTAN MALARIA. Recurrent chill and fever on every fourth day. Caused by *Plasmodium malariae.*

RECEPTOR. The molecule in protoplasm with which a toxin or various metabolic elements may unite.

RECESSIVE. In heredity, a factor which, although present in a heterozygous individual, remains undeveloped.

REDUCTION. The halving of the number of chromosomes in the nucleus of a germ cell during maturation.

REGIONAL DIFFERENTIATION. Specialization of a part of the body not duplicated in other parts.

RHIZOID. Resembling a root.

RHIZOME. An underground trunk or stem.

ROTIFER. Minute multicellular animal with rings of powerful cilia; "wheel-animalcule."

SAPROPHYTIC. Food-taking by absorption or osmosis; applies to some plant forms.

SAPROZOIC. Same, applying to animal forms.

SARCODE. A term proposed by Dujardin, replaced by term protoplasm.

SCHIZOGONY. The process of asexual multiplication in certain types of parasitic protozoa.

SCOLEX. The "head" or attaching segment of a tape-worm.

SEX-LINKED. Any character the factor of which is associated with the sex determiner.

SINUS. A cavity or hollow in tissues.

SOMATIC PLASM. Protoplasm of the body organs and tissues as opposed to the reproductive or germinal plasm.

SOMATOBLAST. A particular cell in early development destined to give rise to the ventral plate of the embryo.

SORUS. One of the aggregates of spore cases on the fronds of ferns.

SPERMATOGENESIS. The development of spermatozoa from the primitive or primordial sex cells.

SPERMATOPHORE. A special capsule, case or sheath containing spermatozoa.

SPIRACLE. An aperture for admitting air.

SPIREME. A coiled mass of chromatin in thread form at the beginning of nuclear division.

SPORANGIUM. The case or sac within which spores are produced.

STEAPSIN. A fat-transforming enzyme.

STEREOME. The woody elements which impart strength to vascular bundles and other tissues of plants.

STIMULUS. Anything acting on living matter which calls forth a response.

STOMA. Mouth; a breathing pore in plant leaves.

STOMODAEUM. The anterior part of the digestive tract formed by ingrowth of ectoderm.

SYMBIOSIS. Obligatory living together of two organisms for mutual benefit.

SYNAPSIS. The union of maternal and paternal chromosomes prior to the maturation divisions.

TAXONOMY. The science of classification.

TERTIAN MALARIA. Chill and fever on every third day. Caused by *Plasmodium vivax*, a protozoan parasite.

TETRAD. Bivalent chromosomes which appear to be 4-parted in the maturation divisions.

TISSUE. An aggregate of similar cells or cell products having the same function.

TOXIN. A poison; usually employed to indicate products of protein breakdown during the metabolic processes.

TRACHEAE. As used here, the air-holding tubes of insects and allied forms.

TRICHOCYST. One of the minute hair-like bodies developed in the cortical protoplasm of an infusorian.

TRYPSIN. A proteolytic ferment capable of rapidly digesting albumins.

TYPHLOSOLE. A fold of the intestine of certain annelids and other invertebrates, formed by the inturning of the wall of the intestine along the dorso-median line and projecting into the intestinal cavity.

UREA. The final product of protein decomposition in the body, forming the chief solid constituent of the excretory fluid of many animals.

VASCULAR BUNDLE. An aggregate of woody fibers, cellular ducts, and columnar cells, found in vascular cryptogams and higher plants.

VITAMINES. Substances of unknown chemical composition necessary for nutrition of the body.

XANTHOPHYLL. A yellow-green substance derived from cholorophyll.

ZOOGLOEA. A mass of bacteria embedded in jelly of their own secretion.

ZYMASE. The enzyme of yeast which causes the breaking up of sugar into alcohol and carbon dioxide, or alcoholic fermentation.

ZYMOGEN. Substance from which enzymes are formed by internal changes.

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