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GENERAL ZOOLOGY

BY

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THIRD EDITION

McGRAW-HILL BOOK COMPANY, INC.

NEW YORK AND LONDON

1938

PRINTED IN THE UNITED STATES OF AMERICA

THE MAPLE PRESS COMPANY, YORK, PA.

PREFACE TO THE THIRD EDITION

With the exception of perhaps a dozen pages in which only minor changes have been made, the preparation of the present edition has entailed the complete rewriting of the text of the preceding edition. This has been necessary for the accomplishment of desired changes in emphasis and in the order and arrangement of subject matter. Some new material on the frog has been added with the idea of correlating the subject matter of the text more closely with that of the laboratory program and, as a result, the frog assumes a position of importance in the early chapters of the book. This emphasis on the frog is in keeping with the common practice of using the frog as the subject of laboratory study at the very beginning of the introductory course in zoology. The primary reasons for selecting the frog for this purpose are that it is a common animal, large enough for the inexperienced student to study with profit, and also that it displays easily recognizable resemblances to the human body in both structure and function. In addition, the frog and allied forms have played an important part in the hands of investigators in the development of the science of biology.

Another departure from the preceding editions consists in the attempt to avoid a cleavage between structure and function in the descriptions of individual organs and organ systems, by combining the discussion of structure with that of function, as far as possible. The aim, of course, is to emphasize the essential unity of structure and function. Thus metabolism is discussed in connection with the structure of the individual organs concerned rather than pigeonholed in a separate chapter. Similarly, examples of different tissues are described as they are encountered in the study of gross anatomy rather than under a separate heading at the beginning of the book, where they have but little meaning for the student.

The chapter on endocrines has been completely reorganized and brought up to date. A more logical order has been followed in the treatment of the topics of heredity, evolution, and adaptation. A short chapter on environment and distribution has been added. The final chapter on systematic zoology has been considerably enlarged. A glossary has been included and also a list of references for further reading. Some fifty additional illustrations have been inserted.

The author is grateful to his colleagues, Dr. C. K. Weichert and Dr. W. A. Dreyer, for helpful suggestions and criticisms, and to his wife for invaluable aid in preparing the index.

H. L. Wieman.

University of Cincinnati,
May, 1938.

PREFACE TO THE FIRST EDITION

The present volume is the product of some years' experience in developing an introductory course in zoology designed to meet the needs of general college students and at the same time to satisfy the technical requirements of various groups of pre-professional students, especially those preparing for medicine. The foundation for such a course must be laid in the actual study of animal forms in the laboratory but the limitation in time precludes the presentation and demonstration of many important and interesting aspects of the subject by the usual laboratory methods. For this reason the author, sharing the experience of others, has found it advisable to devote two or three lecture or recitation periods weekly to the enlargement and rounding out of the student's knowledge of the subject by class-room discussions of those phases of zoology not adequately dealt with in the laboratory. The problem of a suitable text for this work has been met by the compilation of the contents of this book, which is a rather condensed account of some of the outstanding facts and principles of zoology, selected and arranged to serve the student as a guide; the form of the text having been kept as flexible as possible to permit of expansion or extension in whatever direction the instructor may see fit. The references listed at the end of each chapter are easily available works which the author has been in the custom of assigning for collateral reading.

The book begins with a consideration of such general topics as morphology and physiology, the protoplasmic doctrine, the cell doctrine, taxonomy and adaptation; followed by an outline of organology illustrated by examples from common laboratory animals, considered largely from the morphological side. Then follows a section dealing primarily with the functional side of the animal organism, centering in metabolism. Next come the main facts of ontogenesis, followed in turn by a discussion of phylogenesis, evolution and heredity. To cover this ground takes the greater part of a year, the remainder of which is devoted to a general survey of the animal kingdom, as outlined in the final chapter, paying particular attention to life histories and the systematic side of zoology, which the author believes should form an integral part of the course. Such a systematic survey can best be undertaken toward the end of the year when the student through his laboratory work has obtained sufficient familiarity with animal forms and taxonomy to make it worth while. Incidentally there is perhaps no better way to review or summarize the course and to bring out vividly the applications of biological principles. The author realizes that principles are based upon facts and that logically facts should come first; the plan of presentation followed here is a compromise which is successful with beginning students and which at the same times does not violate standards of scientific method.

In the laboratory the endeavor is made to have the student obtain a substantial knowledge of a relatively few animal forms as whole organisms rather than a smattering acquaintance with parts of many. Selection of animal forms for laboratory study is a matter of judgment guided by experience. The author has found it best to begin with a relatively large animal, like the frog, then turning to Protozoa and working up the scale. This general program is broken into from time to time with special demonstrations, collecting trips and visits to the zoological garden. For the laboratory work mimeographed directions are used similar to those used in the work in other places.

Naturally it is not always possible to correlate lecture and laboratory work but the class-room instructor constantly bears in mind what the student is doing in the laboratory and, so far as possible, makes full use of the student's laboratory experience in dealing with the subject under discussion. Free use of special demonstrations helps to obviate this difficulty.

In the compilation of the material for this book the author has made use of many sources which are acknowledged in the text and in the lists of references at the ends of chapters. The majority of the illustrations are new drawings based upon the author's material or figures of others; the remainder have been taken directly from other works with the permission of the publishers whose courteous cooperation is duly appreciated. The author is also indebted to his wife for valuable assistance of a miscellaneous sort at each stage of the book's progress; and to Dr. C. V. Piper for helpful editorial suggestions.

CINCINNATI, O. H. L. WIEMAN.
June, 1925.

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CHAPTER I

THE STUDY OF ZOOLOGY

Biology, a word compounded of two Greek nouns, *βιος* (bios), life, and *λογος* (logos), discourse, is believed to have been used for the first time as a scientific term by Gottfried Reinhold Treviranus (1776–1837) in his work entitled "Biologie; oder die Philosophie der lebenden Natur" (Biology; or the philosophy of living nature), published between 1802 and 1805. It was adopted by the French naturalist, Jean Baptiste Lamarck (1744–1829), and has since spread into general use. Biology is the science of organisms, the study of living things. Since living things for the most part fall into two general categories—animals and plants—the two major fields of biology are concerned with these two natural groups. Zoology, from *ζωον* (zoön), animal, and *λογος* (logos), discourse, deals with the animal side of biology, while botany, from *βοτανη* (botane), plant, has to do with the study of plants.

In zoology a knowledge of the nature of life is sought by studying animal organisms at rest and in various stages of activity, under natural and controlled conditions. A knowledge of the structure and function of the animal body is highly important in reaching a scientific view of the nature of life because the collective phenomena constituting what we call life are only manifested in association with the material substance of the organic body. Matter without life is common enough, but life without matter is unknown to science. As a first step in seeking a solution of the problem of life and explaining it in scientific terms a careful study of the organic body in all of its structural and functional details is necessary.

Approach.—The common aim of all biological studies is an understanding of the origin and nature of life. The biologist attempts to reach such an understanding by assuming, as a working hypothesis, that life had its origin in natural rather than supernatural causes and that it is therefore a phenomenon subject to the laws and principles of the basic sciences of physics and chemistry. The ultimate goal of the scientific searcher—the explanation of living phenomena in terms of scientific phenomena—is still far from achievement; in fact it may be impossible of achievement for the reason that life may involve some factor or principle outside the realm of chemistry and physics. However that may be, the broad, general, and practical lines of approach to the study of the problem of life are relatively few in number and may be summarized as follows:

1. The study of the physical and chemical properties of *protoplasm*, the living matter of which organisms are composed and with which life is always associated. Such work falls largely in the province of the biochemist who deals with protoplasm as a substance to be analyzed by appropriate chemical laboratory methods.

2. The study of the *morphology* or the form and structure of animals and plants. This is commonly subdivided into:

a. Gross anatomy, which is morphological study in its broad aspects, carried on by the dissection of the bodies of animals. In gross anatomical studies the analysis of structure is made with the unaided eye, *i.e.*, without the use of a magnifying lens.

b. Microscopic anatomy or *histology*, the study of the more minute structure of tissues and organs, in which special preparations are made for examination and study under the microscope.

c. Cytology, the study of the finest structural details of cells, the morphological units of which tissues and organs are composed; the microscopic study of protoplasm as distinguished from histology, which is primarily concerned with the study of the structure and arrangement of cells.

d. Embryology, the study of the development of an organism; the study of embryogeny. In embryology the methods of dissection and microscopic study are both used.

3. *Physiology*, the study of the functions of organs considered separately and in relation to the organism as a whole. It deals with the process of waste and repair in living things, food, and the sources and transformation of energy. It also has to do with the

underlying causes of animal behavior. In its method physiology is largely experimental.

4. *Ecology*, the study of the relations of an animal or plant to its environment both animate and inanimate. It is fundamentally physiological in character but involves also a consideration of morphological features of animals and plants as well as attention to such factors as temperature, moisture, light, pressure etc., which make up the nonliving environment.

5. The study of *evolution*, the process through which, there is much reason to believe, the great wealth and diversity of life and its distribution in time and space have been brought about. Evolution is a central principle in biology which holds that the present condition of life on the earth has been arrived at through changes extending over long periods of time, and that in general higher forms of life have evolved from lower forms, through natural processes. The fields of study devoted principally to the topic of evolution are:

a. Paleontology, the study of prehistoric forms of life, a record of whose existence has been preserved in the form of fossils embedded in the earth. It deals with the distribution of organisms in time.

b. Zoogeography, the study of the distribution of animals in space.

c. Genetics, the study of the origin of the individual organism as distinguished from evolution in which the problem is the origin of kinds of organisms. Genetics is the science of heredity.

6. *Taxonomy* or *systematic zoology*, the science of classification of organisms, which is concerned with naming organisms and indicating as far as possible the relationship between different kinds.

Structure and Function.—In the various methods of approaching the subject of biology, structure of the organism and function form the background of the study. Structure and function represent two aspects of the organization of the living body. A general distinction is sometimes made between structure and function in which structural details are regarded as representing the static side of organization, in the sense that the actual form and structure of the components of the animal body stand for the visible machinery by means of which functions are carried out;

while function, since it is concerned fundamentally with the production of motion, is considered dynamic in nature. Such distinction is of value in a general way only, since matter, and particularly living matter, is constantly changing and therefore never absolutely static. In other words, living objects like nonliving objects exist not only in a space relationship but also in a pattern of time. The organism therefore should not be regarded as matter (structure) *plus* motion (function) but rather as matter *in* motion, or as structure *in* function. It is not necessary to decide whether structure causes function or function causes structure, for neither exists without the other. Structure and function are complementary.

Though structure and function considered separately have no real meaning, for purely practical reasons the study of organisms is pursued along two general lines, morphological and physiological. Ideally, these should be carried out simultaneously or as nearly so as possible, but for the beginning student it seems best to begin by acquiring a sound knowledge of morphology as a background for physiology. In such preliminary morphological studies, questions as to the possible or probable functional significance of structural relationships constantly arise. Such questions should be raised even though a satisfactory answer may not be forthcoming until a later time. Morphological detail is meaningless without functional interpretation, nevertheless in most cases a preliminary mastery of morphology facilitates the attack on physiology and is the method followed in this book.

Morphology and physiology are merely convenient terms for classifying two fairly distinct groups of findings and the assignment of a field of study under one head or the other is always subject to some limitation. Thus embryology is ordinarily considered a morphological subject because its study consists to a great extent in the examination and study in considerable detail of the form and structure of embryos at different stages of development; but since this is done for the purpose of piecing together a history of the process of development, an embryological study that does not give due weight to the physiological aspects of development becomes a series of lifeless descriptions of embryo anatomy.

By means of gross microscopic dissections of an animal, combined with carefully planned laboratory experiments to demonstrate functional features, a detailed knowledge of its anatomy and physiology may be obtained; yet a far from satisfactory conception of the animal as an organism is gained unless laboratory observations are supplemented by studying the animal in its natural state in the field and thus noting its relationships to other organisms and to its environment generally. Ecological field studies often supply the key to morphological and functional adaptations because adaptations are adjustments to environmental conditions. Since different animals occupy different stations or levels in the living world, a complex interlocking environmental relationship has been built up, a knowledge of which is necessary in order to gain a full understanding of any given organism. But even after exhausting these avenues of approach, the problem of the organism still presents difficulties which can be removed—and not completely at that—only by applying all the refinements of technique of the sciences of physics and chemistry. The problem of the living thing is beset with difficulties many and diverse because of the presence in it of so many variable factors.

The Protoplasm Doctrine.—From the point of view of the biologist protoplasm is the living substance of which the bodies of animals and plants are composed. The protoplasm doctrine of life assumes that life is a development of protoplasm or that life results from a certain physical and chemical combination of matter such as occurs in protoplasm; that protoplasm is life. This doctrine has not been proved—it is merely a working hypothesis that has been more serviceable than any other hypothesis in extending our knowledge of the nature of the processes that go on in the living body. As a working hypothesis it will be adhered to so long as its application yields results.

Physical Properties of Protoplasm.—All of the material of the animal body is not living matter. Certain parts of the body such as the hard covering of an insect or parts of the bone of the vertebrate skeleton are products of the activity of the protoplasm; *i.e.*, they are formed through the agency of living tissue and serve definite functions but are not, strictly speaking, alive. Such substances can scarcely be regarded as typical protoplasm. Rather than call such substances dead material they may be regarded as inert substances subject to the control of active protoplasm and which form part of the picture of the anatomy of some animals.

A small mass of living protoplasm viewed through the microscope appears as a faintly grayish, jellylike substance in which granules are suspended. Sometimes a streaming or flowing movement of materials can be seen. Protoplasm is heavier than water and somewhat more refractive to light.

Protoplasm has a semifluid consistency which is known as a *colloidal* state of matter. This means that some of its constituents at least, instead of being in the form of a true solution, consist of suspensions of molecular aggregates dispersed in a medium. The medium in this case is largely water. In a true solution these aggregates of molecules would separate as individual molecules which in turn might dissociate into ions. The molecular aggregates are therefore much larger than the particles making up the solute in an ordinary solution. Their size varies roughly between 0.0001 and 0.000001 mm. in diameter. In protoplasm there seem to be three physical systems, *viz.*, *true solutions*, *emulsions*, and *gels*, of which the latter two are colloidal systems.

The colloidal state is common enough in nonliving nature where the components may be solid, liquid, or gaseous, in various combinations. Thus smoke is a colloidal mixture of solid in a gas; foam, of gas in a liquid; fog, of liquid in a gas, etc. Protoplasm seems to be largely an emulsion, *i.e.*, the components consist of liquid phases, such for example as is produced when oil is shaken up in water. In an oil-and-water mixture the components usually separate in the course of time, if undisturbed, unless some other substance is added that serves to keep one liquid phase dispersed in the other. This is accomplished in the preparation of mayonnaise dressing by adding yolk of egg to an emulsion of oil and water (vinegar). The yolk of the egg serves to preserve the colloidal state of the oil in the aqueous medium by acting as a binder. The physical state of protoplasm is roughly approximated by the physical state of mayonnaise dressing.

Substances in the colloidal state diffuse slowly or not at all through animal membranes, which partially explains why living protoplasm does not dissolve in water. Colloids within limits have the power of changing from a fluid or *sol* state to a more solid or *gel* state and back again.

From the purely physical side, protoplasm resembles substances like glue or gelatin rather than crystalline substances like cane sugar or sodium chloride. When living cells are subjected to dissection under the microscope with extremely fine needles, the more solid portions (gels) can be drawn out into thin threads having considerable tenacity. The viscous properties of protoplasm can also be demonstrated by centrifuging living cells. Under the pull of the centrifugal force the heavier components are dragged through the cell and become arranged in layers according to density. If the centrifugal force is great enough, the cells can be pulled into dumbbell shapes, the protoplasm between the heavier and lighter half being drawn out into a thin strand, which may finally snap.

The mere touch of a needle to a living cell may cause liquefaction or the reverse change, gelation, to occur with extreme rapidity. The reversibility from solid to liquid, or liquid to solid, is one of the striking features of protoplasm and one which may be regarded as a characteristic of the living colloid.

Composition of Protoplasm.—Protoplasm is not a definite chemical compound in the technical sense. It is rather a chemical complex of substances, the percentage composition of which is not the same for all kinds of protoplasm. The same kinds of substances occur in all forms of protoplasm, but the proportions and the actual composition of the different constituents vary. The most abundant constituent is water, which accounts for from about 75 per cent to more than 90 per cent of the total weight of the protoplasm. Water is utilized as a solvent and as such plays an important part in bringing about chemical reactions. It is also required to maintain the colloidal state. In some marine forms as in jellyfishes, water forms 99.8 per cent of the body weight. The human body contains about 65 per cent of water, the weight of the bones lowering the average. *Inorganic salts* such as sulphates, chlorides, phosphates, and carbonates of sodium, potassium, magnesium, and calcium, and small amounts of iron make up about 5 per cent of the whole. Small amounts of iodine, manganese, copper, zinc, barium, and silicon are present in varying amounts. Of the remaining constituents, *viz.*, *proteins*, *carbohydrates*, *fats* and extractives, which are organic in nature, protein seems to be the most important and forms about 15 per cent of the human body. Protein is a very complex substance which has never been synthesized. Chemical analysis shows that it contains carbon, hydrogen, nitrogen, oxygen, sulphur, phosphorus, and sometimes iron. Fats and carbohydrates contain carbon, hydrogen, and oxygen, but in different proportions and combined in different ways. Starches and sugars are examples of carbohydrates. Extractives include substances like *urea*, $CO(NH_2)_2$, *creatinine*, $C_4H_7N_3O$, *inosite*, $C_6H_6(OH)_6$, all of which are soluble in water by means of which they can be extracted from coagulated protoplasm.

The substances making up protoplasm are determined by chemical analysis, which gives but little more than the percentage composition of these constituents. Such an analysis shows that protoplasm is made of chemical elements of common occurrence in inorganic nature and also that there is no chemical element peculiar to protoplasm. Such a simple analysis throws little light on how the chemical elements are combined. For example, the amount of water in a sample of protoplasm is determined by driving off the water by means of heat; the difference in weight before and after representing the percentage of water. Thus by this method mammalian meat is found to contain 76 parts by weight of water. If the same piece of tissue is reduced to ash by incineration, the weight of the residue represents the total of inorganic salts which in this case is about 1 per cent of the whole. Other methods show that this same kind of tissue is composed of 21.5 per cent of nitrogenous material and 1.5 per cent of fat. The real problem is to explain how these various components are combined in protoplasm. Certainly the inorganic salts and organic substances are not present as such in living matter but are combined in a chemical complex along with the water in a very intricate manner. If we are to look upon protoplasm as a form of physicochemical system, it differs from other systems in its internal atomic or molecular organization. In other words, the difference between protoplasm and other chemical combinations is not in the chemical elements concerned but in the manner in which they are combined chemically and physically. A random mixture of constituents in the proportions and concentrations as determined by a chemical analysis of protoplasm would not produce a system having the properties of living matter. In order to produce a living system, what is required in addition is a knowledge of the structure or arrangement and the physical state of the constituents, both of which are necessary to provide a basis for the orderly interactions that characterize living matter.

Metabolism.—An organism maintains itself by taking in substances from the environment and at the same time excreting other substances, most of which are of no value to it. The energy generated in an organism and utilized in various ways is, in the case of animals, obtained from food. In the body the food is transformed; some of it is built up into protoplasm and the remainder undergoes oxidation with the release of energy. What are called waste products are the end products of chemical reactions and are of no further use to the body as sources of energy. The organism functions as a transformer of energy and remains alive only as long as it is capable of carrying out this function. Metabolism is a collective term which includes all the chemical and physical changes involved in the transformation of food, the elimination of water, and the functional activity of all the organs of the body. In general it consists of a twofold process of disintegration, or *catabolism*, and reintegration, or *anabolism*. In disintegration, complex chemical compounds are broken down, in the course of which energy is released and waste substances, poor in energy content, are produced. This process may take place in certain food substances before they are incorporated as a part of living protoplasm and it also occurs in protoplasm itself. The reintegrative phase of metabolism is the constructive process which makes good the losses accompanying disintegration of protoplasmic constituents. The two general processes are taking place continuously in the living organism. When metabolism ceases, death ensues.

The principal difference in the metabolism of animals and pigmented plants lies in the fact that animals require food of an initial complexity for the support of life while the colored plant is capable of manufacturing food from raw materials of relatively simple composition. Chlorophyll-bearing plants in the presence of sunlight are capable of utilizing water and carbon dioxide to synthesize starch and other energy-containing substances from them. The carbon dioxide comes from the air, the water from the soil. Protein is synthesized from substances in the soil. Nitrogen for the use of protein building comes largely from nitrates in the soil, which also supplies other necessary elements including sulphur and phosphorus. The process of synthesizing starches under the influence of light is called *photosynthesis*. Only plants possessing chlorophyll or other similar substances are capable of carrying out this function. In photosynthesis, carbon dioxide and water are absorbed by the plant and oxygen is given off. In animal respiration, oxygen is absorbed and carbon dioxide and water given off. There is thus a reciprocal relation between animals and plants in the use of these substances. Similarly, other waste products of animal metabolism can be utilized by the plants in synthesizing proteins, after such nitrogenous waste products have been acted on by bacteria present in the soil.

Photosynthesis does not occur at night or in the dark. Under these conditions oxygen is taken in and carbon dioxide is given off, just as in animals, regardless of light conditions. Respiration of oxygen, then, is a characteristic of metabolism in all organisms. Photosynthesis is a process which accompanies respiration in plants, taking place when light is available. During photosynthesis, respiration is overshadowed by the constructive activities of the plant tissues. Properly speaking, oxygen is not a food, if one defines food as a fuel or a means of repair. Oxygen is a necessary element in processes of oxidation which accompany all energy-releasing reactions of the body.

Movement.—Nonliving things as a rule move under the influence of gravity. Occasionally, as in a volcanic eruption or an explosion of dynamite or similar substances, nonliving objects may be moved by the action of forces generated by processes of combustion. The power of controlled or independent movement exhibited by animals results from internal processes of combustion or oxidation. The energy liberated is utilized in producing movement. Movement is one of the outstanding characteristics distinguishing animals from plants. In plants movement is largely limited to changing positions of the foliage in response to sunlight. It is true of course that in some plants, as in *Mimosa*, the sensitive plant, whose leaves fold up in response to touch, movements of parts resemble similar movements in animals; but on the whole movement has been much more highly perfected in animals than in plants.

Irritability.—Animals respond when subjected to disturbing influences. The disturbing influence or stimulus may be produced by impact, heat, light, sound, electricity, chemical action, etc. Irritability refers to this ability to respond to stimuli of various sorts. Knowledge of the external world is gained from influences which stimulate part or all of the sensory mechanism of an animal. Movements are the result of stimulation of the motor apparatus by nervous impulses acting on muscle tissue. The flow of digestive juice may be invoked by the chemical stimulation of the walls of the digestive canal by food substances. The entire mechanism for the coordination of functional activities in different parts of the body depends ultimately on the irritability of protoplasm to certain stimuli.

Growth.—Organisms subsist on materials taken from the environment. During metabolism a certain portion of the absorbed food products is built up into protoplasm by what is known as intussusception, which means the deposition of new particles of material among those embodying the living substance. Protoplasm is constantly growing from material supplied from the outside but incorporated from the inside. This occurs after undergoing preliminary changes, in chemical and physical form, called digestion. Food in the process of digestion is changed into a form in which it can pass through surfaces of cells and be assimilated. Only a fraction of the digested food is required for anabolic processes. Most of it is oxidized without ever becoming an actual part of living tissue. The immediate cause of increase in size of an organism is the multiplication of individual cells by a process of cell division. When the adult stage is reached, cell division ceases in the body generally. The growth process characterizing the preadult period results from an excess of anabolic over catabolic processes, accompanied by cell multiplication.

Size and Form.—Another peculiarity of living things is that each kind has a determinate size and form, which is reproduced as a rule generation after generation within rather narrow limits of variation. Lifeless objects may be of almost any size and form as, for example, water may be in the form of a rain drop or a lake; a stone may be a pebble or a mountain. The distinctive size and form of any given species are due to factors that are rooted in the organization of the protoplasm of that particular species.

Reproduction.—Living things reproduce their own kind. In Protozoa, unicellular animals, reproduction consists in the division of the entire animal into halves, each of which then grows to the original size. In multicellular animals, this same simple method may take place, but only in lower forms. The method of reproduction common in all forms above the Protozoa is far more complicated and its discussion must be postponed until a later period. Suffice it to say, that the elements of the reproductive process are an egg cell, produced by the female and a sperm cell produced by the male. These unite in fertilization and out of this relatively simple beginning the organism gradually develops into the adult form. Each stage of development is alive. The different stages represent the organism in stages of transformation. Under some conditions the egg alone may reproduce the adult animal, showing that at least in some forms the potency for reproduction is possessed by the egg alone.

Vitalism and Mechanism.—The list of attributes of protoplasm as outlined above constitute a definition of an organism. Can these attributes be explained in terms of the protoplasm doctrine or is it necessary to assume the presence of some supernatural, vital factor in addition to known chemical and physical factors? Formerly, the idea that the living body is presided over or directed by some kind of vital force or energy such as the "soul" of Descartes or the "entelechy" of Driesch met with more general acceptance than at the present time. The proponents of such a view are usually spoken of as "vitalists," and their doctrine is known as *vitalism*. According to the vitalists, a living thing is protoplasm plus some unknown something that is absent in nonliving objects. The unknown thing is called the vital factor, without which life cannot exist. The objection to such a view from the scientist's standpoint is that it bars the way to investigation. If investigators of living matter must always admit the presence of a factor which cannot be seen, felt, weighed or measured, that is to say, a factor that cannot be controlled, his attempt to solve the riddle of life in scientific terms is doomed to failure from the start. Such a view discourages investigation and creates an atmosphere of hopelessness which is not conducive to success. It does not help but actually hinders further investigation into the problem. For this and other reasons many biologists are inclined to support the protoplasm doctrine which is a mechanistic theory of life to the extent that it attempts to explain the phenomena of life in terms of chemistry and physics. The rejection of the vitalistic hypothesis by biologists generally must not be attributed to narrowness on their part, but simply to the lack of satisfactory evidence to support the vitalistic doctrine. Since the vital factor does not exist, scientifically speaking, the scientist is compelled to do without it, since he can deal only with those facts and factors in the problems of protoplasm that are amenable to scientific analysis and measurement. The main support of the mechanistic interpretation, from a practical point of view, is the fact that its application has actually overthrown hypothetical vitalistic explanations of many phases of metabolism and replaced them with understandable explanations in terms of chemistry and physics. Such a view recognizes a common background for all natural phenomena and assumes that living and lifeless objects are forms of matter and energy. On this basis the organism is a physicochemical system which owes its peculiar properties to its physicochemical make-up, and which differs only in its internal arrangement from known nonliving physicochemical systems.

Cells.—Protoplasm exists in the form of small structural units more or less distinctly marked off from one another, and known as cells. In the Protozoa, the entire body of the animal is a single cell; but in all higher forms, the Metazoa, the body is composed of many cells, structurally and functionally differentiated. In 1838, Mathias J. Schleiden, a botanist, and Theodor Schwann, a zoologist, each published observations on the structure of plant and animal tissues which led to the formulation of what is known as the *cell theory*. The central idea of this theory—that the bodies of animals and plants are composed of cells and the products of cells—was undoubtedly held by R. J. H. Dutrochet as early as 1824, but a clear description of the cell nucleus by Robert Brown in 1831 enabled both Schleiden and Schwann to distinguish between cells and other structures, and led them to a more accurate conception of the cellular structure of organisms. Schwann in 1839 published a very precise account of cell structure in a variety of animals which surpassed in accuracy and completeness that of any of his predecessors. The protoplasm doctrine is a much later development and not until 1861 was it clearly understood that cells are really masses of protoplasm and that protoplasm is essentially similar in all organisms. This was a logical conclusion that united the cell theory and the protoplasm doctrine, and provided a material basis for a scientific theory of life. Protoplasm is a living substance and this substance has a cellular structure.

A cell may be defined as a small mass of protoplasm containing one or more nuclei. The cytoplasm or cytosome forms the body of the cell in which the nucleus is embedded. This means that the protoplasm of the cell is made up of two regions, nuclear and cytoplasmic. These two regions are not merely topographical distinctions, but they actually mark the boundaries of two different kinds of protoplasm which have distinct chemical attributes. It also happens that under certain conditions the boundaries between cells are not sharply marked off, forming what is known as syncytial tissue structure; therefore, the significance of cells does not depend so much upon their morphological distinctness as upon the fact that each cellular region is made up of a nuclear and a cytoplasmic component. The cell is something more than a building block with sharply defined boundaries. It is a functional unit which functions with or without cell boundaries.

Cells do not conform to a standard shape. Free cells, such as egg cells, particularly those deposited in water, are often spherical in form. Tissue cells generally, owing to the pressure of the surrounding cells, take on some other form. Under conditions of relatively uniform pressure, as in the liver, cells are polyhedrons with approximately equal faces. At the outer surface of the body, cells tend to become flattened and thin, as in the surface layer of the frog's epidermis. Nerve cells have a round or irregular region in which the nucleus is located and from which slender processes extend, in some cases for several feet. Muscle cells are usually spindle-shaped. Pigment cells have irregular branching processes extending in all directions. In general some correlation exists between the shape of the cells and its function (Figs. 1, 2, and 3).

The nucleus is usually a centrally located body whose shape conforms with the general shape of the cell. Thus, in a spherical cell the nucleus is rounded, whereas in a columnar cell the nucleus is elongated in the main axis of the cell. In the tissue cells of the metazoan animals, as a rule, there is but one nucleus in a single cell. In syncytial tissue, where cell boundaries are lacking, a cytoplasmic mass may contain numerous nuclei, all of which are alike. Protozoa often show two kinds of nuclei in a single cell. Thus in Paramecium (Fig. 2) there is a small spherical micronucleus embedded in the side of the large kidney-shaped macronucleus. In some species there are two or more micronuclei. By microdissection it can be demonstrated that the nucleus is bounded by a definite membrane. Some cells, such as mammalian red blood corpuscles in the blood stream, lack a

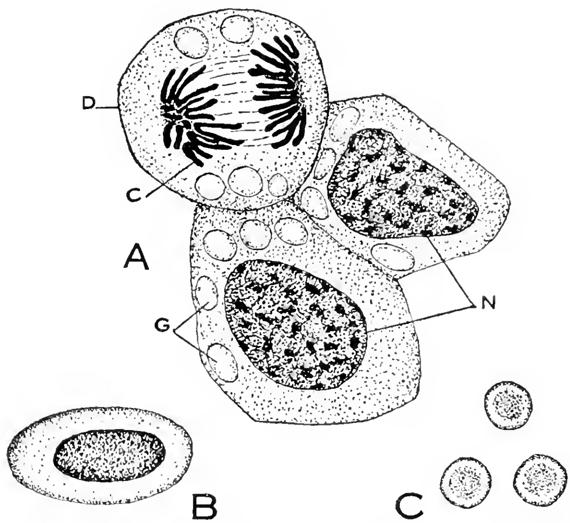


Fig. 1.—Cells. A, three cells from the outer layer of the skin of the salamander one of which (D) is dividing. C, chromosomes; G, yolk globules; N, nucleus; B, blood cell of the salamander, nucleated. C, human red blood cells, non-nucleated. × 900.

nucleus though each corpuscle is a nucleated cell at an earlier stage of its development. Properly speaking, such a corpuscle is only part of a cell and its life in the blood stream is of short duration (about ten days in the case of man).

The nucleus contains an important substance called *chromatin* which, unless the cell is dividing, appears in fixed and stained sections as *flocculent masses* of irregular outline. In the course of cell division the chromatin is transformed into very distinct bodies called *chromosomes*, each of which then divides in half, so that both daughter cells receive the same number and kinds of chromosomes. Chromosomes are important in connection with

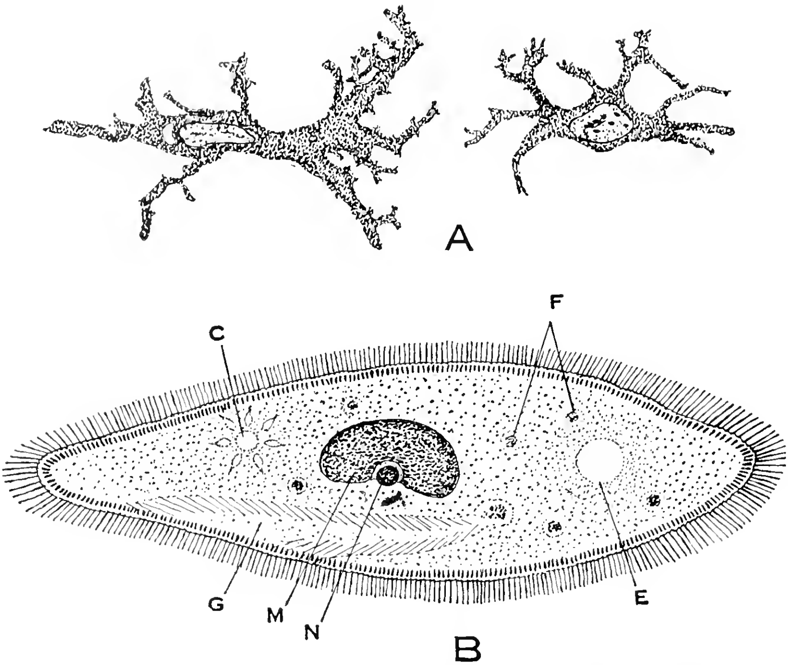


FIG. 2.—Cells. A, two pigment cells from the skin of the salamander. B. Paramecium, a ciliated protozoan, a single-celled animal. C, contractile vacuole, expanding; E, contractile vacuole, expanded; F, food vacuoles; G, gullet, a primitive alimentary tract; M, macronucleus; N, micronucleus. × 300. The contractile vacuoles are filled with cell fluid which is emptied on the outside when the vacuole contracts, thus maintaining an intracellular circulation. Food vacuoles are simple organs of digestion.

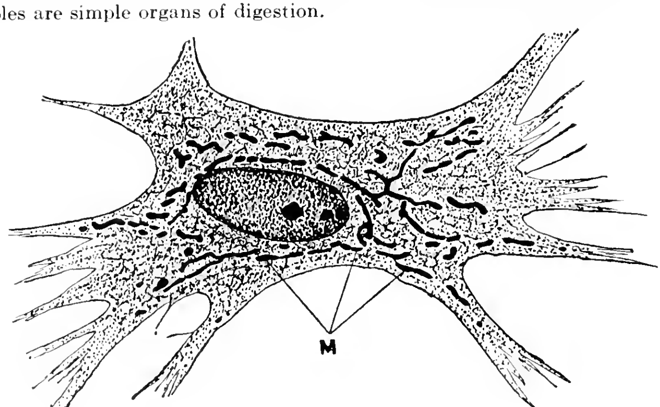


FIG. 3.—Endothelial cell from a tissue culture of the chick embryo, grown in a culture medium on a glass cover-slip inverted over a hollow-ground slide; stained to show mitochondria, M. × 1080. (*From a photo by W. H. Lewis.*)

heredity. A detailed account of cell division and the behavior of the chromosomes is reserved for a later chapter. A *nucleolus* is also usually present in a nucleus. It is as a rule rounded in shape and stains differently from the chromatin. Its function is unknown. The remainder of the nucleus is composed of *karyolymph* which serves as a matrix in which the chromatin and nucleolus are suspended. This ground substance is semifluid in character.

In the cytoplasm the principal formed elements common to all cells are the *mitochondria* and the *Golgi material* (Figs. 3 and 4). The mitochondria are minute objects, usually rod-shaped, that occur in large numbers in the cytoplasm. The Golgi material is usually in the form of a closed network of fine threads or canals which may extend throughout the cytoplasm or be confined to a more restricted area. Both mitochondria and the Golgi material can be seen in living cells. Materials such as fat, oil globules, yolk, glycogen, etc., occur in varying amounts as inclusions in the cytoplasm of cells. The ground substance of the cytoplasm in which these structures and materials are suspended or dispersed is optically homogeneous. Cilia (short hairlike processes), flagella (long whip-shaped structures), and membranellae (delicate fin-shaped membranes) may develop as cytoplasmic structures at the surface of some cells. In general there is a greater degree of variability in differentiation and form in the cytoplasm than in the nucleus.

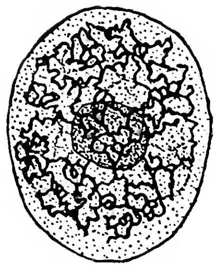


FIG. 4.—A spinal ganglion cell of the rabbit showing Golgi material in the form of a network in the cytoplasm. The rounded central object is the nucleus. (*After Golgi.*)

The complex nature and orderliness of the chemical reactions that take place in the living cell seem to call for some sort of structural protein framework within the cell by means of which the cytoplasm is subdivided and supported. Such a structural framework has been demonstrated in the following manner: Fresh cells such as those of the liver of the rabbit, are frozen in liquid air at −30°C. and dried under partial vacuum for 12 hours, and then ground to a flour in a mortar. If the ground up powder is then treated with salt solutions all of the soluble protein in the form of globulins can be extracted. The solid residue from which the extraction is made when examined under the microscope is found to consist of fragments of liver tissue in which the typical outlines of liver cells can be seen (Fig. 5). These fragments are also protein in nature. Thus in cells from which all of the soluble protein has been extracted there still remains what may be considered a structural protein upon which the morphology of the cell depends. The structural protein is colloidal, *i.e.*, its demonstration depends upon the fact that it is less soluble than the other protein constituents.

Cells as a rule are microscopic in size. Cells of macroscopic proportions are the result of special conditions. Thus the

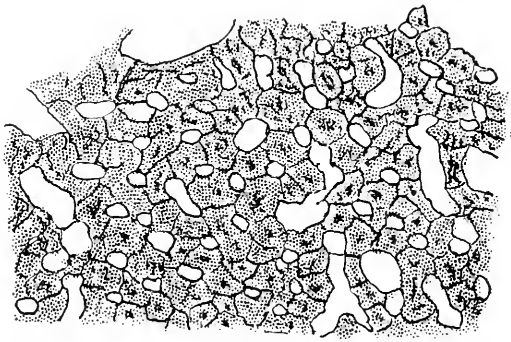


Fig. 5.—Section of the liver of rabbit frozen in liquid air, dried at −30°C., extracted for 48 hours with salt solution, 48 hours with distilled water, fixed in formalin and stained. Cell form and protoplasmic structure is still intact and some remains of nuclear content may be seen. × 300. (*After R. R. Bensley and N. L. Hoerr.*)

unfertilized egg of the domestic fowl is a cell which is approximately the size of the yolk of the laid egg. (The white of the egg and the hard shell are protective coverings.) In this case the large size of the cell is accounted for by the yolk material stored in the cytoplasm of the egg cell. The yolk-free cytoplasm and the nucleus are of microscopic volume. The large size of eggs generally is due to the presence of yolk material in the cytoplasm. The common unit of linear measurement employed in microscopy is the *micrometer* or *micron,* abbreviated as μ (Greek letter μ), which is a length of 0.000001 meter. Human red blood cells measure 7.5 to 8.5 μ in diameter; some leucocytes about 10 μ; a skeletal muscle fiber, which is really a multinucleated cell, may be 1 in. long and 50 μ in width.

In the years following the publication of the cell theory there was an almost total lack of understanding as to how cells arise.

The first step toward the final solution of this question was taken by Carl von Nägeli, who in 1844 stated, as a result of his studies, that cells always come from preexisting cells and that they do not arise from a generative matrix of some sort, as do crystals from a liquid. Cells come from preexisting cells by a process of cell division, but the discovery of the details of the process came to light slowly because of their complicated nature. In cell reproduction the division process is initiated in the nucleus, where the transformation of the chromatin into chromosomes takes place and where all of the intricacies of the division mechanism seem to center. The importance of the nucleus in cell division was recognized by Eduard Strasburger, a botanist, and in 1879 led him to state that a nucleus always comes from a preexisting nucleus, a conclusion confirmed in 1882 by W. Flemming in studies of animal cells. It is largely due to the work of these two men that the complicated details of cell division were worked out. The term *karyokinesis* means division of the nucleus and refers to the changes undergone by the nucleus in the process of cell division. *Mitosis* is a synonym for karyokinesis. A fuller discussion of mitosis is reserved for Chap. XI, and it need only be mentioned at this point that, as a rule, division of the nucleus is accompanied or followed by division of the cytoplasm, resulting finally in the production of two cells of equal size, each of which in the course of time grows to the size of the parent cell. The division of the cytoplasm is called *cytokinesis*.

The development of an animal from an egg is usually preceded by the fertilization of the egg by a spermatozoon. One of the earliest observations of the entrance of the spermatozoon into the egg was made in the case of the frog's egg by Newport in 1854, but it was not until 1861 that it was clearly shown by the comparative anatomist Karl Gegenbaur that the egg is really a cell. The same conclusion regarding the spermatozoon was reached in 1865 by Schweigger-Seidel and La Vallette St. George. In fertilization the essential feature is the union of the egg nucleus with a nucleus derived from the spermatozoon, so that the fertilized egg is really a cell with a nucleus of *biparental* origin. These demonstrations of the cellular character of the egg and spermatozoon have been verified many times since and have tended to emphasize the importance of the cell in developmental processes. Since the egg and spermatozoon must contain all the hereditary qualities derived from the parents the problem of heredity centers in explaining how an adult organism develops from a cell.

Unity in Organisms.—In Protozoa, the individual animal is bounded by a single plasma membrane which is comparable to the cell membrane of a metazoan cell. Within the bounds of this membrane there may be one or more nuclei. If a cell be defined as a small mass of protoplasm containing one or more nuclei, then a protozoan is a cell, and the individual organism and the cell are one and the same. The cell in this case is organized as an individual animal. In Metazoa, the animal body is made up of many cells or, the metazoan body may be said to be more or less subdivided by many plasma membranes, represented by the cell walls. Schwann believed that each cell is, within certain limits, an individual, an independent whole; that the vital phenomena of one cell are repeated, entirely or in part, in all other cells of the body, and that the individual cells are not arranged side by side as a mere aggregate, but that they operate to produce a harmonious whole. "The whole organism subsists only by means of the reciprocal action of the single elementary units." This idea is in keeping with the fact that the organization of a single cell is capable of maintaining itself in the case of Protozoa; that the metazoan animal starts from a cell and develops as new cells are produced; and that the individuality or unity of the cell as represented in the fertilized egg *may* be repeated in each cell formed from the egg. From this point of view the cell is the unit of organization. In Protozoa, the unity of the cell and the unity of the individual organism coincide; in Metazoa the unity of the organism is made up of a number of cell units, cooperating in some way to produce the whole. In either case the cell would be the unit of organization.

Others have maintained that the fact that the protozoan is a cell should not be permitted to overshadow the equally pertinent fact that the protozoan is also an organism, but an organism whose size is so small that it is possible for it to be contained within a single plasma membrane. The organization of a protozoan is the organization of an individual animal that happens to conform in a general way to a definition of a metazoan cell. If in the case of the metazoan we also regard the organism as the unit in organization, the individual cells composing it lose their significance as primary units of organization. Sachs recognized this long ago when he said (in 1865) that "cell formation is a phenomenon, very general it is true, in organic life but still only of secondary significance; at all events it is merely one of the numerous expressions of the formative forces which reside in all matter, in the highest degree, however, in organic substance."

The view that the organism and not the cell is the unit of organization in living nature is now generally accepted and is known as the *organismal theory*. On this basis the important difference between protozoan and metazoan animals is not primarily in the number of cells but in the difference in the organization of the protoplasm in the two cases, which in the final analysis means difference in the chemical and physical constitution of the two kinds of protoplasm.

The problem of cell *versus* organism in determining the location of organic unity is, of course, a problem only in metazoan animals, for the simple reason that in protozoans the cell and the organism are identical. The criteria for determining unity are primarily physiological. It is a common observation that reactions to stimuli are adaptive, *i.e.*, reactions tend to preserve the condition of wholeness in the organism. Isolated groups of cells of metazoan animals as a rule do not survive, or if they do survive, under natural conditions, they tend to organize themselves along the lines of the organism from which they came, rather than as cell units.

Evolution.—There exists abundant evidence for the belief that the present population of the earth, and the condition of the earth itself, are the results of a process of change or evolution that has extended over enormous periods of time. The only alternative to such an explanation is some form of *Special Creation*, which raises more problems than it solves. The theory of evolution implies that animals and plants were not always as they are now, but that they have *descended* from more primitive forms of life through the action of slow processes of *divergence* which for the most part have been adaptive in character.

Evolution has been the guiding thought of biology for more than half a century, thanks largely to the painstaking work of the great English naturalist, Charles Darwin, whose publications, beginning with the "Origin of Species" in 1859, rank as the most notable contributions to biological literature of the nineteenth century, and perhaps of all time. The nature and extent of the evidence upon which the theory of evolution rests will be considered more in detail in later chapters.

Taxonomy.—The science of classification is known as taxonomy. The theory of evolution teaches that all living things had

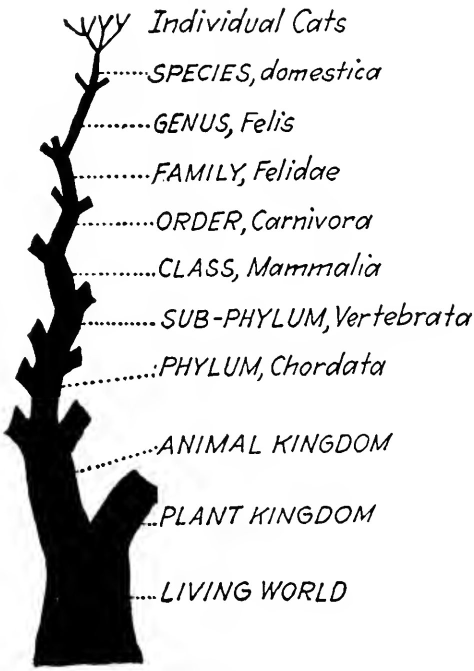


Fig. 6.—Diagram to show the tree-like form assumed by a natural system of classification, as illustrated by the classification of the house cat, *Felis domestica.*

an origin in some simple form or forms of protoplasm. From these hypothetical ancestral organisms there first arose, presumably, the simpler forms of plant and animal life, and from these in turn the higher forms. Thus it follows that a *relationship* of varying degree exists between all forms of life—even animals and plants being connected by simple unicellular forms, some of which combine both animal and plant characteristics. Lamarck was the first to express this relationship diagrammatically by means of a tree whose trunk divides almost at once into two main stems, one for the plant kingdom and one for the animal kingdom, each stem in turn sending out branches that represent the subdivisions of plants and animals (Fig. 6). Such a tree would show the relationships between organisms in a very exact manner if knowledge of the evolutionary processes were complete, but since this knowledge is at its best rather fragmentary, the construction of the tree of life is a difficult matter and subject to continual alteration.

Descent.—When it is held that the higher animals are derived or descended from animals simpler in form and organization, it is not meant that the lower animals living today are the ancestors of the higher ones. Thus, it would be incorrect to speak of monkeys or apes as the ancestors of Man, although it is true that Man is more closely related to them than to any other animals. The fact is that Man and monkey probably had some *common ancestor* from which monkeys were evolved on one hand and Man on the other—the common ancestor having in the meantime disappeared from the living fauna. Since the same principle applies to other groups of animals and plants, it follows that the part of the genealogical tree that represents the living population of the earth includes only the *twigs*—the trunk and its branches, representing the *connecting links* between living forms, having dropped out and become extinct.

Natural Affinities.—Evidence of relationship between organisms may be obtained from a study of living animals and plants. The great Swedish naturalist, Linnaeus (1707–1778), who founded the modern system of classification, was not an evolutionist, but he was able nevertheless to classify animals and plants with a remarkable degree of accuracy by carefully noting their resemblances and differences. The point is, however, that these resemblances, or *natural affinities*, as Darwin called them, find their rational explanation in the theory of evolution, with the result that the application of the evolution principle has had a clarifying effect on the problems of classification.

Species.—In the modern scheme of classification the species constitutes the basic group of individuals. A *species* may be simply defined as the offspring of similar parents. The members of similar species resemble one another because they are descended from common ancestors. Species have become more or less sharply differentiated from all other species by the disappearance of intermediate forms. Owing to *variation*, the individuals composing a species are never identical, and the individual differences which constitute these variations make it difficult to define the limits of a species. Such gradations among or between species are exactly what would be expected on an evolution basis; while, on the other hand, variations have been a stumbling block to upholders of the doctrine of special creation, who with Linnaeus believed that species did not develop gradually but were made outright, and that all species were therefore *fixed*. At present, the idea that species are fixed is no longer tenable because of the vagueness of the boundaries between them, but the employment of the term "species" is useful in describing the basic unit in the system of classification.

Scheme of Classification.—Species are arranged in groups of higher order called *genera*. A number of similar species constitutes a *genus* in much the same way that a number of similar individuals makes up a species. The characteristics which distinguish one genus from another are more deep-seated and fundamental than those that distinguish species. Related genera, in turn, are combined into *families*, families into *orders*, orders into *classes*, and classes into *phyla*. The phylum, then, is the largest group in either the *plant* or *animal kingdom*. Each group is sometimes made up of subgroups, such as *subphylum*, *subclass*, etc.; and occasionally entirely new terms are introduced to meet the needs of classification. The custom of employing Latin or Greek derivatives in the technical naming of these groups is now universally followed and makes for clearness in identification.

Binomial System.—Every known kind of animal and plant has a scientific name, consisting of the name of its genus, capitalized, followed by the specific name in small letters. Thus, the name of the house cat is *Felis domestica;* a common species of frog (Leopard frog) *Rana pipiens;* Man, *Homo sapiens*. This method of naming was formulated by Linnaeus and is known as the binomial system of nomenclature. It is also customary to follow the scientific name with name of the author who originally proposed it.

Trinomial System.—It sometimes happens that the difference between two kinds of animals is so slight as to scarcely warrant placing them in separate species, and yet requires some practical method of classification. In such cases the intraspecies distinction is made by adding a subspecies name to the name of the genus and species; thus the mountain salamander is known as *Desmognathus fuscus carolinensis* and the closely related brook salamander as the *Desmognathus fuscus fuscus*. These two forms are varieties of the same species, and so far as one knows, are not connected by intermediate forms at the present time.

Animal Phyla.—The animal kingdom is composed of 17 animal phyla, of which the names of those commonly used in laboratory study, with examples of each, are as follows:

Protozoa, unicellular animals, microscopic in size such as Amoeba and Paramecium.
Porifera, sponges.
Coelenterata, hydra, jellyfishes.
Ctenophora, sea walnut, comb jelly.
Platyhelminthes, flatworms, tapeworms.
Nemathelminthes, roundworms or threadworms.
Trochelminthes, rotifers.
Annelida, segmented worms, such as the earthworm.
Arthropoda, crayfish, crabs, insects, spiders.
Mollusca, snails, clams, oysters.
Echinodermata, starfishes, sea urchins.
Chordata, animals with a notochord, of which the most important subdivision is the Vertebrata, animals with a backbone.

The classification of animals is considered in some detail in the final chapter (XVIII), which should be consulted whenever a new or unfamiliar animal is mentioned in the text. Since a very definite part of the program of an introductory course in zoology is a mastery of the fundamental facts of animal taxonomy, the student is expected to learn the names of all the animal phyla and their principal subdivisions and to acquire more detailed knowledge of those phyla, of which examples are studied in the laboratory. This knowledge can best be acquired by a process of gradual absorption, learning the important facts about a single phylum, one at a time, until the entire system has been mastered.

CHAPTER II

THE ANIMAL ORGANISM

The fundamental biological functions of animal organisms are the same in all forms of animal life. The principal differences between different kinds of animals lie in the manner in which these functions are carried out and in the degree of morphological differentiation that accompanies functional differentiation. Thus the Protozoa, the lowest phylum in the animal kingdom, consist of animals in which the body is a single cell, free-living, or united with other similar cells to form a colony. Protozoa are capable of maintaining and reproducing themselves, in a favorable environment, with as much success as any higher form of life. In the ascending scale of animal life one finds that the organism takes on an ever-increasing structural and functional differentiation of its parts that is absent or at best only very feebly expressed in Protozoa. The elaboration of structural and functional features found in higher forms is an inevitable accompaniment of their greater size. It is inconceivable that a frog could exist as a frog in the form of a single cell.

The varying degree of structural differentiation found in different kinds of animals lends itself to an analysis in terms of cells, the common though variable structural units of which their bodies are composed. In forms above the Protozoa—Metazoa or multicellular animals—larger morphological units composed of groups of cells constitute what are called *tissues* and *organs*. A tissue is a group of histologically similar cells, such as the cells forming the outer layer of the frog's skin. An organ is composed of different kinds of tissues, characterized by a distinctive histological structure, and capable under proper conditions of performing one or more distinct functions in the animal body. Tissues and organs are the visible evidence of differentiation in the bodies of metazoan animals.

The Frog.—A study of the biology of an individual animal might begin with any animal as the subject matter. Logically, perhaps, one should start with the Protozoa and work up the scale, but practically more rapid and satisfactory progress is made if the beginner starts with a larger animal and one with which he is to a certain extent familiar, such as the leopard frog or grass frog, *Rana pipiens*, or any other species of frog. The leopard frog is classified as a member of the phylum *Chordata*, the subphylum *Vertebrata*, the class *Amphibia*, the order *Salientia*, the family *Ranidae*, the genus *Rana*, and the species *pipiens*. It is therefore a member of the highest phylum, Chordata, and also of the subphylum Vertebrata to which Man also belongs. It is an example of a vertebrate animal, which refers specifically to the fact that it has a vertebral column or backbone.

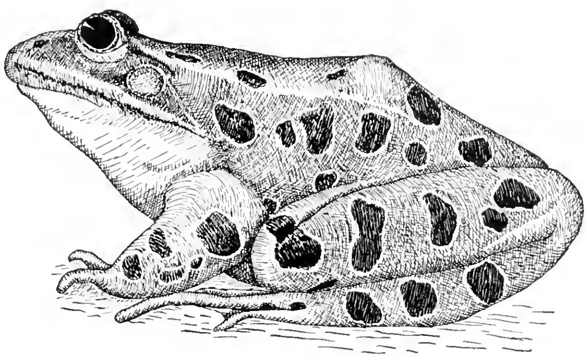


FIG. 7.—*Rana pipiens*, sketched from life.

The leopard frog is found in nature living near ponds, lakes, and streams of fresh water of the North American continent east of the Pacific slope. The winter months are spent in hibernation, during which active feeding ceases and all bodily activities are reduced to a minimum. Several varieties of the species differing from one another in color pattern are known. In the variety illustrated in Fig. 7 the dorsal side of the head and body, and the upper sides of the legs, are marked by large brownish spots, bordered by narrow light iridescent green edges, on a background of lighter brown. The sizes of the spots and the pattern vary in different races. The throat, the ventral side of the body and the inner sides of the legs are whitish and unmottled.

The skin of the frog is smooth and is rendered slippery by *mucus*, a viscid secretion poured out on its surface by skin glands. The skin is held loosely to underlying parts by *sub-*

cutaneous connective tissue, divided into inner and outer layers by large *lymph spaces.* These spaces are readily seen when the skin is removed from the frog. A thickened ridge in the skin extends back from the eye on either side of the body to form a *lateral dermal fold* or *plica.* In addition to mucus-secreting glands, which are very numerous, the skin also contains smaller numbers of *poison* glands, located principally in the skin of the dorsal body surface, lateral dermal plicae and in the skin of the hindlegs. The poison is in the form of a whitish fluid. It is not so toxic as the secretions of the poison glands of toads.

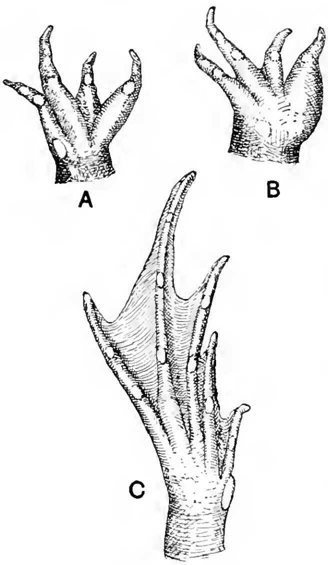


FIG. 8.—Palmar surfaces of feet of *Rana pipiens.* A, right forefoot of female; B, right forefoot of male; C, hindfoot.

In a sitting posture the body rests on the folded hindlegs and the extended forelegs. From this position the sudden extension of the hindlegs sends the animal through the air in a long leap. This is its usual form of locomotion on land. In water the swimming strokes are also provided by the hindlegs. The hindfoot has five elongated toes connected by *interdigital membranes* which increase the surface of the foot and add power to the swimming stroke. Each forefoot has four toes and a very rudimentary thumb. A padlike enlargement on the proximal segment of the first digit is present in the male and is practically the only external anatomical distinction between the sexes (Fig. 8).

The eyes are prominent structures at the sides of the head. Each eye has an immovable upper eyelid in the form of a thick fold of the integument. The lower lid is well developed and can be moved upward, covering the eye. When this happens the eyeball is withdrawn into the socket by a special muscle, the *retractor bulbi.* The upper part of the lower lid is thin and transparent and is called the *nictitating membrane.* When the lower lid is withdrawn, the nictitating membrane folds inside on the lower thicker part of the lid. On the forehead between the eyes an unpigmented spot, the *brow spot,* can usually be seen.

This spot shows the location, beneath it, of the *pineal organ*, which is a dorsal outgrowth of the diencephalon of the brain. In the embryos of some amphibians and reptiles the tip of the pineal organ enlarges to form an eyelike structure beneath the integument. The pineal organ with its distal enlargement is regarded as a vestigial organ which in modern amphibians has lost its original function and much of its structure. On either side of the head behind the eye is the *tympanic membrane* or eardrum, a flattened circular area flush with the surface of the head.

A live frog at rest exhibits pulsating movements in the region of the throat which are concerned with respiration. On the

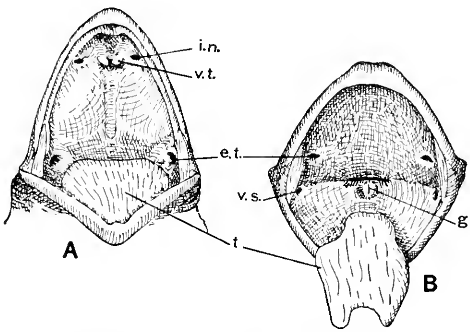


Fig. 9.—Two views of the oral cavity of *Rana pipiens*. A, tongue in place in floor of mouth; B, tongue pulled forward. e.t., Eustachian tube; g, glottis; i.n., internal naris; t, tongue; v.s., vocal sac openings; v.t., vomerine teeth.

dorsal side of the snout not far from the tip are located the two *external nares*, leading to respiratory and olfactory passages which open into the anterior end of the *oral* or *buccal cavity*. If the frog's mouth is held open (Fig. 9) several structures can be seen. In the roof of the mouth on either side near the anterior end is a small opening, the *internal naris*, and between the two nares is a pair of white *vomerine teeth*. Small bluntly pointed teeth are also found in the upper jaw which forms a frame for the roof of the mouth (Fig. 9, A). On either side, near the angle formed by the articulation of the upper and lower jaws, is the opening of the *Eustachian tube*, which connects with the *tympanic cavity* or *middle ear*. The tympanic cavity is closed to the outside by the tympanic membrane. In the mid-line between the two openings of the Eustachian tubes is the constricted opening into the *esophagus*. The most conspicuous structure in the floor of the mouth is the *tongue* with its free, forked end pointed back toward the esophagus. Between the spread tips of the tongue is a slightly raised circular area with a longitudinal slit, the *glottis,* which opens into the larynx. On either side of the floor of the mouth in the male is a pit leading to a *vocal sac,* which is a small pocket of the oral epithelium that can be expanded with air. The lower jaw is without teeth. When the mouth closes the lower jaw meets the upper jaw in a groove, the *sulcus marginalis,* which lies inside of the tooth-bearing margin of the upper jaw. The *tuberculum prelinguale* is a rounded conical prominence at the tip of the lower jaw.

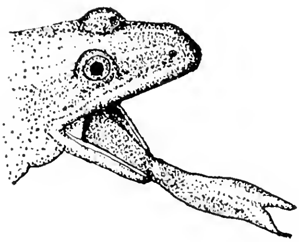


FIG. 10.—Showing tongue of frog fully extended.

Live insects and worms form the principal diet of frogs. In capturing insects, the tongue, coated with an adhesive secretion is extended (Fig. 10), forked end foremost, and then retracted with the prey sticking to it. The nature of the teeth restricts their function largely to grasping and holding. The food moistened by the saliva is swallowed, passing down the wide esophagus to the stomach and intestine where it is digested and absorbed. If a longitudinal slit is made in the abdominal region of a frog, the cut passes through the skin and a thin layer of muscle. The skin can be easily separated from the underlying muscle, which is the real supporting element of the abdominal wall. To expose the underlying parts between the forelegs it is necessary to cut through the *sternum* which is part of the skeleton. Likewise the pubic portion of the *pelvic girdle* between the hind limbs must be severed to follow the termination of the alimentary canal. The cavity thus exposed is the *pleuroperitoneal cavity* or *coelom,* in which lie the lungs, liver, pancreas, spleen, alimentary tract, kidneys, and reproductive organs (Fig. 11). The heart, it will be noted, is in a sac, the *pericardium,* which is really a subdivision of the coelomic cavity. The wall of the coelom is lined by a thin epithelium, the *peritoneum* or *parietal peritoneum,* which is continued over the organs, in whole or in part, as an investing membrane, the *visceral peritoneum.* The sac surrounding the heart, the pericardium, represents the parietal peritoneum in that region. The small intestine is attached to the dorsal part of the body cavity by a thin membrane, the *mesentery*, which provides a pathway for blood vessels and nerves to the intestine. The mesentery really consists of two thin sheets, right and left, continuous at the point of insertion in the body wall with the parietal peritoneum, and surrounding the intestine at the free edge, where it forms the visceral peritoneum, or *serous membrane*.

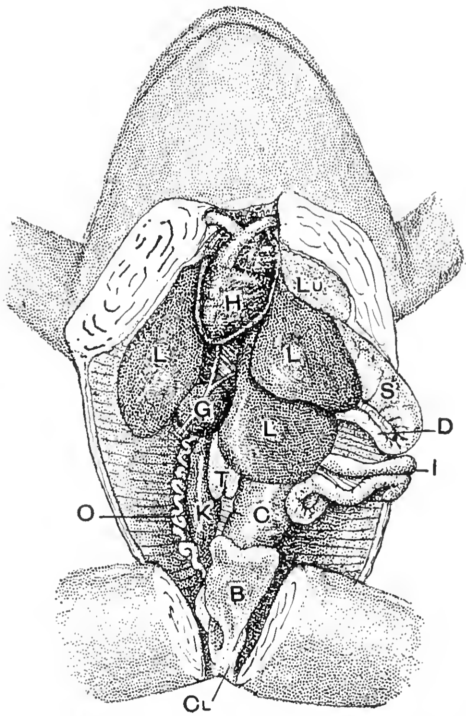


Fig. 11.—*Rana pipiens*, male; ventral half of abdominal wall and parts of pectoral and pelvic girdles removed to show internal anatomy. B, bladder; C, colon (large intestine); Cl, cloaca; D, duodenum; G, gall bladder; H, heart; I, ileum; K, kidney; L, liver; Lu, lung; O, oviduct; S, stomach; T, testis.

The visceral peritoneum, the mesentery, and the parietal peritoneum are therefore different parts of a continuous epithelium. The lungs, liver, and pancreas have a similar relation to the peritoneum. The kidneys, on the other hand, are *retroperitoneal* —behind the peritoneum—which refers to the fact that the parietal peritoneum is fastened against the ventral faces and edges only of the kidneys. The dorsal surfaces of the kidneys are attached directly to the body wall. The term mesentery, in strict usage, applies to the portion of the peritoneum between the intestine and the body wall, but it is often used for the suspensory or supporting membrane of other viscera.

The form of the entire alimentary tract can be seen if the liver and other overlying parts are removed, as in Fig. 12. The posterior continuation of the broad, ciliated, buccal cavity is the *pharynx*, which is also ciliated, and leads in turn to the *esophagus*, a wide muscular tube, lined by a ciliated epithelium and creased by longitudinal folds. Like the mouth, the esophagus is provided with mucous glands. The *esophageal glands*, located near the lower end of the esophagus, secrete *pepsin*. The demarcation between the esophagus and stomach is indicated externally by a constriction, but on the whole it is not very distinctly marked. If unpalatable food reaches the stomach, it may be regurgitated by a reversed peristaltic action which turns the stomach inside out, sometimes causing it to bulge outside of the mouth. The soft glandular lining of the stomach secretes pepsin and hydrochloric acid, in addition to mucin. Pepsin is a digestive enzyme which in the presence of hydrochloric acid acts upon protein food. The curved stomach lies with its convex surface to the left and is attached to the body wall by the *mesogaster* and to the liver and small intestine by the *gastrohepatoduodenal ligament*. These attaching structures are examples of mesenteries.

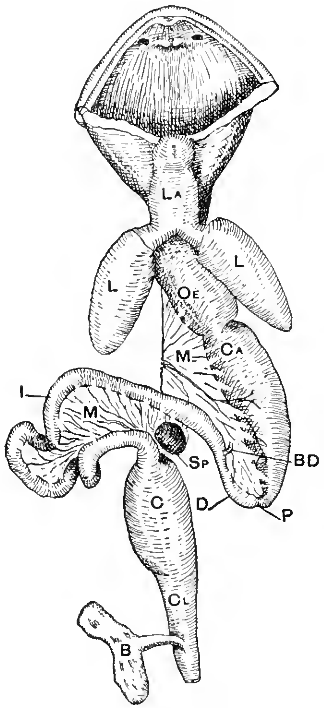


FIG. 12.—Alimentary tract of *Rana pipiens*. B, bladder; BD, bile duct; C, colon (large intestine); CA, cardiac end of stomach; CL, cloaca; D, duodenum; I, ileum; L, lung; LA, larynx; M, mesentery; OE, esophagus; P, pylorus; SP, spleen.

The lower end of the stomach leads to the *small intestine*, a sharp constriction at the *pylorus* marking the junction. The first part of the small intestine makes a sharp bend at the pylorus, turns forward and parallels the course of the stomach. This is the *duodenum*. In the loop between the duodenum and the stomach lies the *pancreas*. At the top of the loop the duodenum passes over into the *ileum*, which turns back and follows a coiled path to the *large intestine*, from which it is marked off by a constriction. The *spleen*, a small globular structure, reddish in color, is attached to the mesentery near the upper end of the large intestine. It is really a part of the circulatory system. The *liver* consists of three main lobes from which *bile* is collected by a system of *hepatic ducts*, which unite to form a *common bile duct*. The latter passes through the tissue of the pancreas and opens into the middle region of the duodenum. Since the bile duct also collects the secretions of the pancreas, the lower part of the duct serves as a *hepato-pancreatic duct*. The *gall bladder* is an enlargement on one or more of the hepatic ducts where bile is stored, until liberated from time to time into the bile duct (Fig. 13).

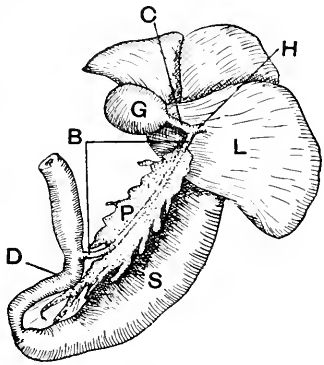


FIG. 13.—*Rana Pipiens*. B, bile duct; C, cystic duct; D, duodenum; G, gall bladder; H, hepatic duct; L, liver; P, pancreas; S, stomach.

The lining of the small intestine is folded into longitudinal and transverse ridges, which increase the absorptive surface and delay the passage of food. Digestion of protein started in the stomach by pepsin is continued in the intestine by *trypsin*, one of the constituents of the pancreatic secretion. *Amylopsin* or *amylase*, and *lipase*, also produced in the pancreas, act on starches and fats, respectively. Amylase converts starches into sugars and lipase changes fats into fatty acids and glycerin. The bile has no digestive function but facilitates fat digestion. The liver is not primarily an organ of digestion. It serves to store sugar absorbed from the intestine, in the form of *glycogen* or animal starch, and also is concerned in the storage and utilization of fat and in the conversion of certain nitrogenous metabolic products of the blood into *urea*, which is excreted through the kidneys. *Fibrinogen*, from which the *fibrin* of clotted blood is formed, is produced in the liver.

The large intestine opens into a chamber, the *cloaca*, which in turn opens to the outside. The cloaca also receives the openings of *reproductive* and *urogenital systems* and the mouth of the *bladder*. The large intestine serves to store fecal matter until it can be voided.

The frog obtains oxygen by absorption through the skin, the surface of the buccal cavity, and the lining of the lungs. If the alimentary canal is dissected out as shown in Fig. 12, the *lungs* are seen as two conical sacs connected to an oblong structure, the *larynx*, attached to the ventral surface of the wall of the pharynx. The glottis, a slitlike opening, seen in the floor of the pharynx behind the tongue when the mouth is opened, leads to the larynx. From the internal surface of the lung, septa project inward and divide the lung cavity into *alveoli*, all of which open into the central, undivided cavity of the lung (Fig. 14). Bands of muscle

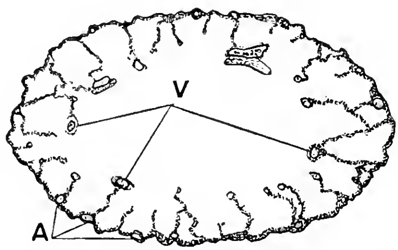


FIG. 14.—Cross section of lung of *Rana pipiens*. A, arteries; V, veins.

are found on the inner, free edges of the septa, from which thinner strands of muscle extend through the septa to the wall of the lung, which likewise contains scattered muscle tissue fibers. The contraction of this muscle tissue under certain conditions collapses the lung and almost completely empties it of air. The cells at the free edges of the septa are ciliated and among the ciliated cells are found mucus-secreting goblet cells. Elsewhere the alveoli are covered by a flattened layer of cells. The septa are richly supplied with blood vessels, through which oxygen is absorbed from the air in the lungs and from which carbon dioxide is given off.

A living frog displays two kinds of *respiratory movements* in the throat region: (1) a regular series of shallow pulsations, and (2) a deeper lowering and raising of the throat repeated several times. During the period of shallow respiratory movements, the external nares are open, the glottis closed, and air is drawn in and out of the buccal cavity through the nasal passages. The ventilation of the buccopharyngeal region is accompanied by the absorption of oxygen through the lining of the mouth. When these shallow movements are interrupted by a deep lowering of the throat, an increased volume of air is drawn in; but since before the completion of this movement the external nares are closed and the glottis opened, air passes from the lungs into the buccal cavity. The vigorous contraction of the throat, which now follows, forces the mixed air back into the lungs. One or more repetitions of these deeper respiratory movements of the throat muscles cause the air to surge back and forth from the lungs to the mouth, after which the glottis closes, the nares open, and the shallow respiration is resumed. The closure of the external nares is effected by a slight forward movement of the lower jaw which wedges the *tuberculum prelinguale* of the lower jaw between the two elements forming the tip of the upper jaw, the *premaxillary bones*, spreading them and closing off the nares.

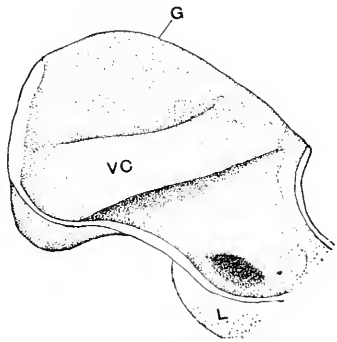


Fig. 15.—View of interior of right half of larynx of *Rana pipiens*. G, margin of glottis; L, lung; VC, vocal cord, attached at its ends and along its length to the wall of the larynx.

It is known that oxygen is absorbed through the skin of the frog throughout the entire year. This rate of oxygen absorption through both lungs and skin reaches its maximum during the spawning season. It is interesting that a greater amount of carbon dioxide is released from the skin than from the lungs. During the winter, with a general reduction of respiratory activity, the amount of carbon dioxide given off is at its lowest level. The respiratory function of the skin is highly important in the frog. A damp or moist environment is necessary for a frog, since the skin cannot prevent the loss of body fluids, in a dry warm atmosphere.

The *vocal cords* are folds in the lateral walls of the larynx forming thickened lips, lying parallel to the edges of the glottis. They can be seen best by laying open the larynx with a cut through the ventral wall (Fig. 15). In producing sounds, air is forced back and forth from the lungs to the buccal cavity, thus causing the vocal cords to vibrate. Since sounds can be produced without taking in air from the outside, frogs can call under water. In the male the volume of sound is increased by the vocal sacs, which are merely extensions of the floor of the mouth at each angle of the jaw, capable of dilation when filled with air and which act as resonators. They are lacking in the female.

The frog has a well-developed blood-vascular system, consisting of a heart, arteries, veins, and capillaries, through which the blood is circulated. The *heart* is a pump which furnishes the motive power, by means of which the fluid blood is propelled through the system. The blood is forced from the heart through *arteries* which eventually break up into thin-walled *capillaries* from which the blood is returned to the heart by *veins*. There are two vascular circuits in the frog: (1) a *pulmonary circuit* connecting the heart and the lungs, and (2) a *general systemic circuit* connecting the heart with all other parts of the body. The *blood* itself is made up of a fluid *plasma* and several different kinds of cellular *corpuscles* suspended in the plasma. It functions as a vehicle for the conveyance to the cells of the body of nutritive material, absorbed from the alimentary canal, and of oxygen, absorbed from the lungs, skin, and buccal cavity. It also absorbs from the tissues generally, products of metabolism, including carbon dioxide, which are excreted through the kidneys, lungs, and skin.

The *lymphatic system* is related to the blood circulatory system both structurally and functionally. It consists of large and small spaces, between and within body tissues, all connected, and drained into the blood system by means of four *lymph hearts*. Lymph also enters the blood stream through ciliated openings in the ventral surface of the kidneys which lead from the coelomic cavity to the renal veins. The subcutaneous lymph spaces are large and abundant, as a result of which the skin seems to be loosely attached to the underlying muscles. A large lymph space within the body is known as the *cisterna magna* which occupies most of the space above the dorsal side of the body cavity. The anterior pair of lymph hearts pumps lymph into the vertebral veins and the posterior pair pumps it into the transverse iliac veins. The general direction of flow of the lymph is from the tissues toward the veins, which in turn lead toward the heart. The lymph supplements the action of the blood in absorbing excretory products from the tissues.

The *skeleton* of the frog consists of bones which serve as a supporting framework for the body. Bodily movement is brought about by the contractions of *muscles* which are located external to the skeleton. The body musculature is composed of numerous distinct bundles of muscle tissue each of which is known as a muscle, whose action is under the control of the central nervous system. *Joints* between skeletal elements make possible the movement of different portions of the body. The extension or flexion of a segment of a limb, for example, is brought about through the action of two antagonistic sets of muscles extending over the joint, the contraction of one set producing an effect opposite to that of the other. The muscles are attached to the bones by means of *tendons* and it is usually the tendon from the distal end of the muscle that extends over the joint to be inserted on the bone. A muscle produces movement by contraction, which draws its ends, and any parts attached to them, toward each other. Relaxation of the muscle is passive and does not produce a pushing effect.

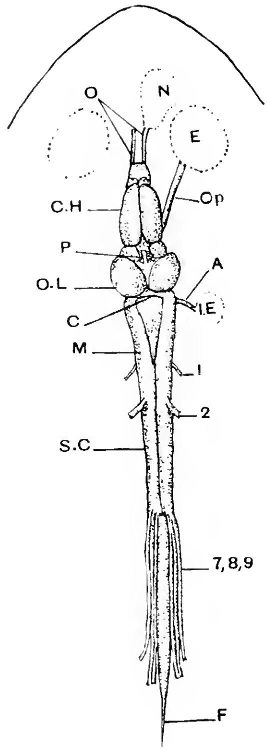


FIG. 16.—Dorsal view of central nervous system of *Rana catesbeiana*. A, auditory nerve; C, cerebellum; C.H., cerebral hemisphere; E, eye; F, filum terminale; I.E., internal ear; M, medulla; N, nasal cavity; O, olfactory nerve; Op, optic nerve; O.L., optic lobe; P, pineal organ; S.C., spinal cord; 1,2,7,8,9, spinal nerves.

The frog has a *central nervous system* consisting of the *brain*, enclosed in the *cranium* of the skull, and a *spinal cord* lying in the channel formed by the *neural arches* of the vertebrae of the backbone. Connected with the brain are ten pairs of *cranial nerves* distributed mainly to various parts of the head. The tenth cranial nerve, the *vagus*, has important connections with the viscera. There are also ten pairs of *spinal nerves* connected with the spinal cord which are distributed to the trunk and limbs. The chain ganglia of the *sympathetic nervous system* consist of a pair of nerve trunks which extend from within the cranium posteriorly along the dorsal surface of the body cavity. These trunks are connected by means of *rami communicantes* with the spinal nerves and certain of the cranial nerves. Enlargements on the trunks are known as *ganglia*. Nerves extending from the chain ganglia are distributed among the viscera and the walls of blood vessels. The regulation of the heart beat, the secretion of digestive fluids, the contraction of the *nonstriated*

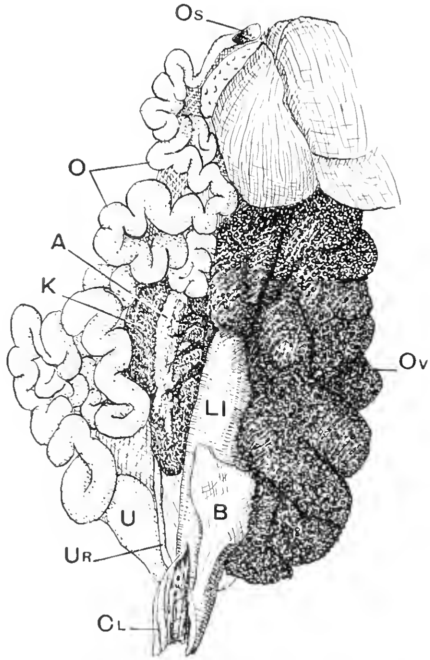


Fig. 17.—Female reproductive system of *Rana pipiens*, ventral view, right ovary removed. A, adrenal gland; B, bladder; CL, cloaca; K, kidney; LI, large intestine; O, oviduct; Os, ostium of oviduct; Ov, ovary; U, uterus; UR, ureter.

muscles in the walls of the alimentary tract, and other functional activities of the viscera are controlled through the agency of the sympathetic nervous system and the closely related *parasympathetic* nervous system (Chap. IX). All of these activities are involuntary and *autonomic*. The central nervous system, with its peripheral connections, furnishes a mechanism for controlling and coordinating bodily activities of all sorts (Fig. 16).

Reproduction in the frog results from the fertilization of an egg. The reproductive organs of the female consist of a pair of *ovaries*, which are attached by mesenteries to the body wall at the level of the anterior end of the kidneys. Each ovary has the appearance of a mass of black and white beads, which are developing eggs. During the breeding season the ovaries become so large as to exceed the rest of the viscera in volume. The younger eggs or ova are small and white in color. As they grow older, they become black at the *animal* pole and white at the opposite, *vegetative* or *vegetal* pole, where most of the *yolk* is concentrated. When mature, the eggs are released by ruptures in the wall of the ovaries and, propelled by the action of cilia located on the surface of the liver, pericardium, and peritoneum, eventually find their way into the oviducts. Each oviduct is provided with a wide mouth or *ostium* at its anterior end, located near the base of the lung, through which the eggs enter. As they pass through the coils of the oviducts, the eggs are covered with three layers of an albuminous secretion of the walls of the oviducts. At the lower end of each oviduct, just before it opens into the cloaca, an enlargement, the *uterus*, serves as a storage place for mature eggs before they are discharged through the cloaca (Fig. 17).

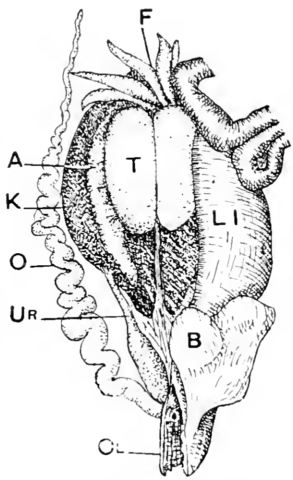


FIG. 18.—Male reproductive system of *Rana pipiens*, ventral view. A, adrenal gland; B, bladder; CL, cloaca; F, fat body; K, kidney; LI, large intestine; O, oviduct; T, testis; UR, ureter.

The reproductive organs of the male consist of two yellow, bean-shaped *testes*, attached by mesenteries to the body wall between the anterior ends of the kidneys. Spermatozoa pass from each testis by way of a small number of *vasa efferentia* into the corresponding kidney, from which they leave by the *ureter*, a duct passing from the outer border of the kidney to the cloaca. The ureter in the male thus serves a double function in that it provides a passageway to the cloaca for both the urine from the kidney and the spermatozoa from the testis. In the male oviducts are present but reduced in size. They are not functional (Fig. 18).

The reproductive organs reach the height of their development in the early spring when spawning occurs. The eggs are fertilized in the water by a single spermatozoon entering each egg. The jelly surrounding each egg swells to several times its original diameter and serves as a protective covering for the developing *embryo*. When the embryo reaches the length of six or seven millimeters it hatches by wiggling out of the gelatinous capsule. This takes place about two weeks after fertilization, depending upon the temperature of the water, a low temperature prolonging the time. The embryo, now a *larva*, has a blunt head and a short median fin, but no limbs or even a mouth. At either side of the head are rudiments of external *gills*. A mouth soon forms from an indentation (invagination) in the outside layer of cells covering the ventral surface of the head, communicating with the anterior end of the pharynx. The larva then begins to feed on water plants and grows rapidly. The external gills become enclosed in a fold of the skin, called the *operculum*, which forms a respiratory chamber, opening on the left side by a *spiracle*. With the formation of the operculum, the external gills are resorbed and are replaced by internal gills, which develop on the edges of *gill slits* located in the wall of the pharynx on either side. The forelegs develop inside of the operculum and at first are not visible externally. The hind limbs appear later at the base of the tail.

At about the end of the third month of larval development *metamorphosis* takes place. Metamorphosis involves profound changes, both external and internal. Briefly, these consist in the completion of the development of the lungs with accompanying changes in the circulatory system; an enlargement of the stomach and liver and a shortening of the intestine; the resorption of the operculum and the liberation of the forelimbs; disappearance of the gills and closure of the gill slits; and finally the resorption of the tail. During the larval period the mouth is provided with horny jaws which are cast off with the molting of the skin accompanying metamorphosis. During the larval period the diet is largely plant material. After metamorphosis, the frog becomes more carnivorous in its feeding habits. Correlated with this there occurs a shortening of the alimentary tract, in keeping with well-known fact that flesh eaters have relatively shorter digestive tracts than plant eaters.

Hibernation.—Following the breeding season and throughout the summer the frog is an active feeder, storing up a reserve supply of energy to carry it through the winter. Late in the autumn the frog buries itself in mud below the frost line and passes the cold months in a state of suspended animation. Respiration is reduced to a minimum and is confined to the skin. The body temperature drops until it is only slightly above the temperature of the ground. Metabolic activity is displayed in the activity involved in producing a circulation of the blood and in the development of the eggs and spermatozoa. When the frog emerges from hibernation in the spring it still possesses sufficient reserves of energy to complete spawning before resuming feeding.

The foregoing is a summarized statement of the general plan of the structural and of the functional activities of the frog. In the following chapters the discussion of organization is continued by comparing organ systems of selected animals, both structurally and functionally, using the frog as the basic form, for the purpose of obtaining a bird's-eye view of the conditions found in as many different types of animals as can be conveniently studied. It must be remembered, however, that the organism as a whole is the real unit in living nature and that the comparison of organ systems is a comparison of parts of the organism unit. The alternative to such a plan is to consider only entire organisms, a procedure that is entirely sound but one which limits the scope, if the time available for study is to be considered. However, a basis for the appreciation of the comparison of organ systems is provided by the laboratory work in which a number of selected forms are studied as whole organisms. With the laboratory experience as a background, the comparative study of organ systems serves to bridge the gaps left by the laboratory programs and offers a practical method of securing a general survey of the field in the shortest time.

CHAPTER III

INTEGUMENT

Integument or skin is the covering of the body. Its form, thickness and physical consistency, in all cases, provide some degree of protection from mechanical injury. Combined with this purely passive function of the skin is a nervous function maintained by sensory-nerve endings located just below the surface of the body. Since the entire nervous system evolved from the primitive integument or ectoderm, the nervous function of the skin is one of its primary functions. Respiration, the absorption of gaseous oxygen and the evolution of carbon dioxide, is another primary function of the integument and one that persists in the integument of many animals. The protective function of the integument, provided by its toughness or texture, is further extended in some cases by the presence of glands capable of secreting poisonous, slimy, or malodorous substances. Sebaceous glands, producing oil, and sudoriparous glands, producing sweat, are found in the skin of some animals.

Integument of the Frog.—The outer layer of the integument of the frog is known as the epidermis. Beneath this is the corium or dermis. These two layers occur in the skin of all vertebrates.

Epidermis.—The epidermis consists of two regions: the *stratum corneum* at the surface, and the *stratum germinativum* below, both of which are epithelial in structure (Fig. 19). An *epithelium* may be defined as one or more layers of cells, compactly arranged, covering an external or internal surface of the body of an animal or derived from such a surface. The stratum corneum, an example of a *simple squamous* epithelium, is composed of broad flattened cells of a horny texture, and serves as the outermost protecting layer of the skin. From time to time this layer is shed as a whole, a process known as *molting* or *ecdysis.* The stratum germinativum is composed of several layers of cells, forming a *stratified epithelium.* The innermost or basal layer of this epithelium is composed of columnar cells, while the cells of the upper layers are polygonal in outline,

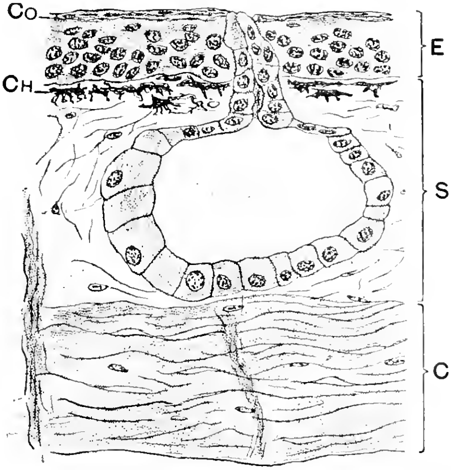


Fig. 19.—Section of skin of *Rana pipiens*, showing a mucous gland. C, stratum compactum; Co, stratum corneum; Ch, chromatophores; E, epidermis; S, stratum spongiosum.

becoming definitely flattened next to the stratum corneum. When the stratum corneum is lost at molting, its place is taken by the outermost layer of the stratum germinativum, and new cells, formed by cell divisions in the basal layer, are pushed up from below. All of the cells of the epidermis originate in the basal layer. A peculiar histological characteristic of the cells of the stratum germinativum is the presence of delicate processes, called *intercellular bridges*, connecting adjacent cells (Fig. 20).

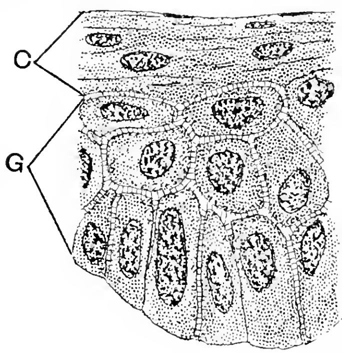


Fig. 20.—Section of epidermis of *Rana pipiens*, highly magnified, showing intercellular bridges. C, stratum corneum; G, stratum germinativum.

Pigment cells or *chromatophores* occur in small numbers in the epidermis. Cutaneous innervation is supplied by nerves terminating in the lower layers of the epidermis. The epidermis is pierced by ducts leading from glands located in the corium.

Corium.—The histological structure of the corium is entirely different from that of the epidermis. It is composed of two layers: an outer *stratum spongiosum* and an inner *stratum compactum,* both containing a large amount of connective tissue fibers. These fibers are of two kinds: *white fibers,* which are inelastic and unbranched; and *yellow fibers,* which are elastic and branched. The fibers of the spongiosum layer form a more or less open network, in which are found blood vessels, lymph spaces, nerves, and glands. At various points this layer is elevated to form dermal papillae, each of which contains a touch corpuscle composed of a conical group of flattened cells supplied with sensory nerve endings. Most of the chromatophores lie in the upper layer of the corium.

The fibers of the stratum compactum appear in sections as a wavy layer of compact tissue, traversed at intervals by vertical bands extending upward into the stratum spongiosum and the epidermis. The fibers are both branched and unbranched. Here and there are nonstriated muscle fibers whose contractions move the skin. Nerves and blood vessels also occur.

Beneath the stratum compactum is a layer of loose connective tissue, the subcutaneous connective tissue, which is divided into an inner and outer layer by large lymph spaces. The lymph spaces are separated by septa joining the two layers of subcutaneous tissue. This tissue attaches the skin to the underlying parts.

In general, connective tissue is characterized by the presence of a large amount of *intercellular* material, which in the case of the corium is fibrous. Connective tissue cells are found in and among the fibers, but the fibers themselves lie outside of cells. We shall see later that bone and cartilage are also forms of connective tissue, but in these cases the intercellular material is represented by the matrix of bone or cartilage, in which the cells are embedded.

Glands.—The cutaneous glands of the frog are of the simple alveolar type. This means that each gland consists of a globular *alveolus,* whose wall is composed of a single layer of cells, connected with a short straight *duct* whose wall is also a single layer of cells (Fig. 19). The duct opens on the surface of the skin, but the alveolus is located in the stratum spongiosum. However, both alveolus and duct originate as a downgrowth from the basal layer of the epidermis and are therefore epithelial structures.

Microscopic sections stained with haematoxylin (blue stain) and eosin (pink stain) show two types of glands differing both in structure and in the staining reactions of the cytoplasm of the alveolar cells (Fig. 21). In one, the mucous type, the cytoplasm is in the form of a network and takes the blue stain; in the other, the poison type, the cytoplasm is granular and stains a deep pink. The size and shape of the cells of both types vary with the activity of the gland. Cells filled with secretion enlarge until they practically fill the cavity of the alveolus. As the secretion is discharged, the cells shrink to a low cubical form. Each type of gland is surrounded by a muscular and connective tissue tunic, the contractions of the muscles aiding the discharge of the secretion.

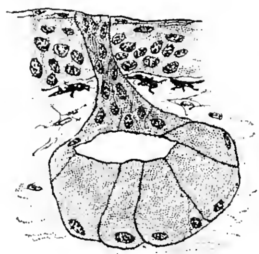


Fig. 21.—Section of a small immature poison gland.

Respiration.—The skin of the frog plays an important part in aerating the blood, supplementing the respiratory functions of the oral epithelium and the lungs. The cutaneous blood vessels are separated from the surface of the body by at least the thickness of the epidermis, so that oxygen absorbed from air or water must diffuse through the epidermis and the walls of blood capillaries in order to reach the blood. Carbon dioxide given off from the blood passes from the blood in the reverse direction. In this respiratory exchange, therefore, the gases pass through several layers of cells, though the total distance is not very great.

Water.—Water passes in either direction, to or from the blood stream, through the frog's skin. Experiments indicate that the rate of diffusion of water under pressure through the skin is much greater from without than from within. Water thus passes in more readily than out. The limited control of water loss through the skin makes it necessary for the frog to live in a moist environment. In a dry, warm room a frog will die overnight as a result of the loss of water.

Human Skin.—Though built on the same general lines as frog's skin, human skin differs in a number of structural and functional features. Human skin is much thicker and tougher, gives rise to different types of glands, and is richly supplied with a variety of specialized nerve endings. It is impervious to water and does not function in respiratory processes. It may develop hair (Fig. 22).

The human epidermis is composed of many layers of cells, morphologically differentiated into distinct regions which, beginning with the lowest or innermost layer, are as follows: (1) *stratum germinativum*, (2) *stratum granulosum*, (3) *stratum lucidum*, and (4) *stratum corneum*. The basal layer of the

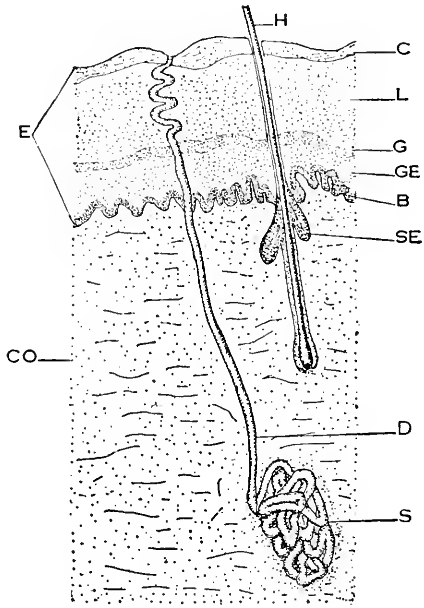


Fig. 22.—Vertical section of human skin, semidiagrammatic. B, basal layer of epidermis; C, stratum corneum, the outer layer of epidermis; CO, corium; D, duct of sweat gland; E, epidermis; G, stratum granulosum; GE, stratum germinativum; H, hair; L, stratum lucidum; S, sweat gland; SE, sebaceous gland, opening into hair follicle.

stratum germinativum produces all of the epidermis and from it also develop hair follicles and hair, sweat and oil glands, mammary glands, and nails. It is composed of five or six layers of cells, graded in shape from a columnar outline in the basal layer to a flattened polygonal form in the outer layers. The stratum granulosum is about two cell layers in thickness and gets its name from the fact that the cytoplasm of the cells in this layer has undergone a granular degeneration, the product being known as *keratohyaline granules*. The condition of the cells of the stratum lucidum represents an advance in degenerative changes in which the keratohyaline granules of the granulosum cells are converted into a substance called *eleidin*, which gives the stratum lucidum a glassy appearance in sections. The stratum corneum is composed of numerous layers of dead, dry, squamous cells that are constantly rubbed off piecemeal. The loss of cells at the surface of the skin is made good by the production of new cells in the basal layer of the epidermis, whence they spread to the outside. The various layers of the epidermis, above the basal layer, represent progressive stages in cell degeneration.

The corium of human skin is made up of white and elastic connective tissue fibers, blood vessels, nerves, and glands projecting into it from the epidermal layer. The *stratum subcutaneum* lies beneath the corium to which it is firmly attached. It is composed of loose, fibrous connective tissue, with numerous fat cells and is connected below by connective tissue with muscle or with the periosteum of bone. Human skin is more firmly anchored to underlying structures than is the skin of the frog.

There are no chromatophores in human skin. The color of the skin is due to pigment granules in and among the lowest layers of the epidermis. A few granules are also found in the corium.

There are two general types of glands in human skin, *sweat glands* and *oil glands*. Sweat glands, epidermal in origin, are long unbranched tubes, extending from the surface of the epidermis into the deep part of the corium or into the subcutaneous tissue, each tube terminating in a coil. Ordinarily, the secretory cells, located in the coiled portion of the gland, secrete an oily fluid for the lubrication of the skin, but under nervous stimulation the secretion becomes more watery and by evaporation serves to cool the surface of the body. Sebaceous glands, also derived from the epidermis, are branched or unbranched glands located in the upper layer of the corium and usually attached to the sheath of a hair. On the margin of the lip they occur independently of hair. The secretion consists of fat and cell debris. In its production the gland cells fill with fat and then break down, the fat and cell debris forming a semifluid material. The *mammary glands*, which may be regarded as modified sweat glands, are made up of a branching system of ducts terminating in alveoli, *i.e.*, rounded vesicles, which extend from their point of origin in the epidermis, at the nipple, into the corium and subcutaneous tissue of the breast. In the secretion of milk, the free end of the gland cell ruptures and discharges fatty droplets along with cell substance. The empty cells then fill up. Few gland cells are cast off. The *ceruminous* (wax) *glands* of the external auditory meatus are also modified sweat glands.

Nails and Claws.—A cross section of a finger through the nail shows that the nail is composed of a layer of cornified cells overlying a stratum germinativum (Fig. 23). The corium of the nail bed consists of fibrous and elastic connective tissue running vertically from the periosteum of the bone (phalanx of the finger) to the stratum germinativum, and also of connective tissue fibers running the length of the finger. The cornified layer of the nail represents modified epidermal cells. In the embryo this

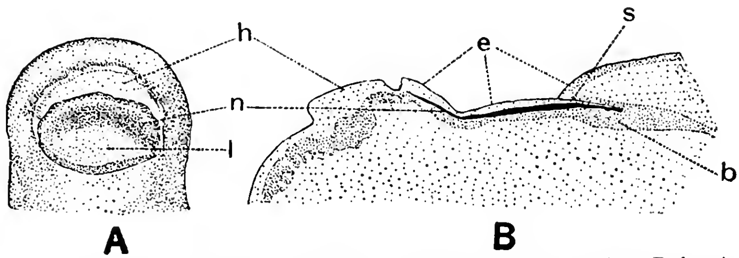


FIG. 23.—The nail of a human fetus of 10 weeks. A, dorsal view; B, longitudinal section; b, nail bed; e, eponychium; h, hyponychium; l, lunula; n, nail; s, nail sulcus. (*After Kollman.*)

layer is covered by the *eponychium,* which in the adult is reduced to the thin layer at the base of the nail, continuous with stratum corneum of the contiguous skin. The nail is produced from the stratum germinativum at the root of the nail and as far forward as the boundary of the *lunula,* the crescentic white area at the base of the nail. Claws are similar modifications of the epidermal layer.

Hair and Feathers.—In the embryo, the development of a hair begins as a solid downgrowth of the basal layer of the epidermis, terminating in a bulb, which becomes indented from below. The indented region is occupied by cells from the corium, forming the papilla which in later stages is provided with blood vessels. The central part of the column above the papilla separates from the peripheral cells to form a core, from which the shaft of the hair develops (Fig. 24). The peripheral cells of the hair column form the sheath of the hair. The sebaceous glands develop from the cells of the hair sheath. Later, a connective tissue sheath is formed from the corium around the lower half of the hair follicle. The *arrectores pilorum* are bundles of nonstriated muscle extending from the fibrous tissue of the corium to the connective tissue sheath of the follicle. Their contractions raise the hair on end. The hair grows by additions of cells from the bulb. The shaft of the hair is formed of cornified cells derived from stratum germinativum of the bulb which, as they are pushed out, adhere

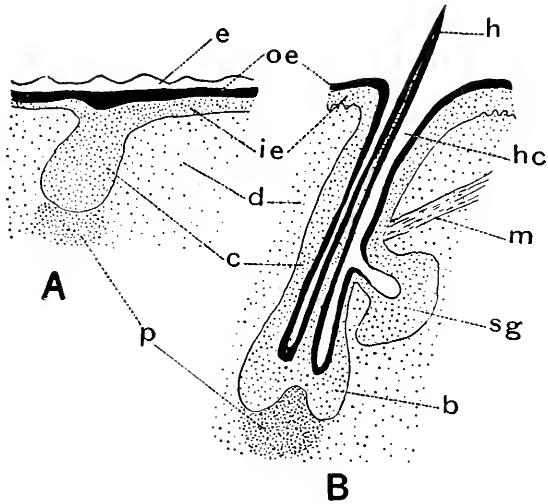


FIG. 24.—Diagrams showing the development of hair. A, the formation of the hair column from the stratum germinativum of the epidermis; B, the hair at birth. b, hair bulb; c, hair column; d, corium; e, epitrichium; h, hair shaft; h.c., hair canal; i.e., inner layers of epidermis; m, muscle (arrector pili); oe., outer layer of epidermis; p, hair papilla; s.g., rudiment of sebaceous gland.

in the form of the hair. The feathers of birds, though somewhat more complicated in structure than hairs, are also composed of modified epidermal cells and develop in a somewhat similar manner.

Scales.—The scaly covering of reptiles, such as snakes, is composed of the stratum corneum of the epidermis, which is shed as a whole when the animal molts. On the other hand, the scales of fishes are primarily subepidermal structures. Of these the most primitive type is represented by the *placoid scale* of the elasmobranchs (sharks). Such a scale consists of a flattened base of *dentine* from the center of the external surface of which a spine projects. As the bony basal plate and its spine are laid down in the corium, the overlying epidermis secretes a hard enamel covering upon the dentinal base and spine. The rough "sandpaper" surface of the shark's skin is thus due to numerous sharp spines, each projecting outward from a basal plate. The exposed, enamel-covered spines are like so many short sharp-pointed teeth on the surface of the body, the basal plates remaining embedded in the corium below and the epidermal layer above. This type of scale is thought to be the forerunner of vertebrate teeth and dermal bone (Fig. 25).

The scales of teleost fishes, such as the perch or bass, consist of bony plates developed in the dermis and overlaid by the epidermis. Scales of this type may be hard and bony or soft and flexible. The epidermis takes no part in their development.

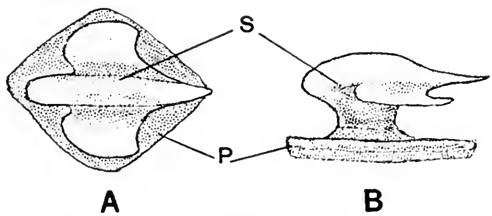


Fig. 25.—Placoid scale. A, view from above; B, side view. s, spine; p, basal plate.

Horns, Hoofs, Antlers.—The horns and hoofs of sheep, goats, and cattle represent cornifications of the epidermis and resemble nails and claws in their general composition. Usually horns are not shed, a notable exception being the horns of the prong-horn antelope, *Antilocapra americana,* of Western U. S. Antlers are outgrowths of the frontal bones of the skull and are at first covered with skin which may persist throughout life, as in the giraffe, but which in forms like deer, elk, etc. becomes worn off, exposing the bone. The antlers are shed each year, the succeeding ones displaying a greater number of tines, which thus serve as an index of age.

Invertebrate Integument.—The outermost layer of the integument of some invertebrate animals is cellular, as in the flatworm, *Planocera,* in which it consists of short columnar epithelial cells, one cell layer in thickness, and provided with cilia on the outer surface (Fig. 26). In many other invertebrates a typical condition consists in the presence of a noncellular structure, the *cuticle* or *cuticula,* at the surface of the body. The cuticle is a substance secreted by the underlying epidermal cells, varying in different animals in its thickness, texture, and composition. It is pierced by openings of small size through which secretions of glands are discharged. Other openings are occupied by sense organs of touch, taste or smell connected with nerve endings coming in from below.

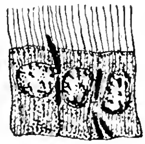


FIG. 26.—Ciliated cells of the epidermis of the turbellarian, *Planocera inquilina.* The darkly stained rods are *rhabdites*, secreted by the epidermis.

The cuticle of the earthworm is a very thin but tough layer which, if stripped off and examined under the microscope, shows a crisscross arrangement of fibrils which give it the appearance of a piece of thin-woven cloth (Fig. 27). Numerous small openings provide a passage for secretions of unicellular mucus glands. The fibrillar structure of the cuticle may be the result of stresses and strains set up in the cuticle during its formation. In both the flatworm and the earthworm the integument has a respiratory function.

In the group *Arthropoda,* which includes animals like the lobster, crayfish, spiders, insects, etc., the cuticular layer develops into a stiff armor. Joints between segments of the body and between segments of appendages such as legs or antennae, are provided by a softer cuticle connecting adjacent segments. The soft cuticle is protected by a telescoping of the hard cuticle of one segment over the end of the adjoining one. In insects the cuticle is composed of an organic substance called *chitin* which is not only hard and tough but also resistant to the action of acids and alkalis. In the crayfish the cuticle consists of an organic material impregnated with lime salts. Beneath the cuticle are the epidermal cells which secrete it. The cuticle of the arthropods not only serves as a protective outer covering but also acts as an *exoskeleton* to which the body muscles are attached. Figure 28 shows a section of the integument of the lobster. The cuticle, above, is laid down in stratified layers. The epidermal cells immediately below this layer are large columnar cells containing vertical fibrils. On the left side of the figure, the fibrils of the epithelial cells seem to be continuous with fibrils connected with muscle cells below. The muscles are attached to the

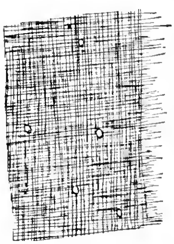


FIG. 27.—Piece of cuticle stripped from an earthworm.

cuticle through the agency of epidermal cells. The epidermal layer lacks a basement membrane, and the lateral walls of the cells are poorly defined.

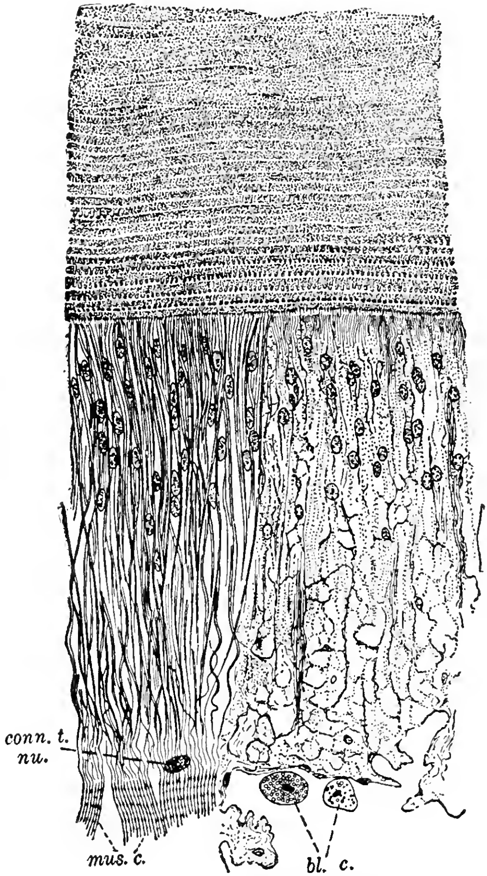


FIG. 28.—Portion of the new integument of a lobster, *Homarus*, as seen in section. The cuticle is shown above in stratified layers. *conn.t.nu.*, connective-tissue nucleus; *bl.c.*, blood cells; *mus.c.*, muscle cells. (*From Dahlgren and Kepner, Principles of Animal Histology, The Macmillan Company. By permission.*)

Animals with a hardened cuticle undergo periodic molting or *ecdysis*, during which the cuticle splits in definite places and the animal crawls out. The new cuticle is then secreted, and while it is still soft and elastic, the animal grows in size. A soft-shell crab is one that has recently shed its cuticle.

The shell of molluscs such as the snail, clam, and oyster is also the product of the activity of cells at the surface of the body. The secretion consists of organic matter, *conchiolin*, richly impregnated with calcium carbonate. The shell increases in size by additions at its edge and, unlike the cuticle of arthropods, is not shed.

The hard integument of the starfish and sea urchin consists of calcareous plates developed in the subepidermal region of the skin. The epidermis is a thin simple epithelium overlying the plates except where points of the plates project. These plates act as an armor protecting the internal organs and constitute an exoskeleton though differing in origin and development from the exoskeleton of the arthropods.

General.—A comparison of the integument of invertebrates with the integument of vertebrates brings out the following points: (1) In both groups an epidermal layer of cells, representing the primitive covering of the body, is present. Among invertebrates, the epidermis may secrete a cuticle of variable hardness and chemical composition which serves as a protective covering and also provides points of attachment for body muscles and other internal organs. Among vertebrates, on the other hand, the surface layer of the body remains cellular, though the cells may be highly transformed, as in the outer layer of the shell of turtle which is epidermal in origin. In snakes the hardened outer layer of the skin is the stratum corneum of the epidermis. (2) The subepidermal layer of the invertebrate skin is as a rule poorly developed. An exception is found in *Echinodermata*, such as the starfish, in which the hard calcareous plates of the exoskeleton develop below the epidermis. The corium of vertebrates is a well-developed layer that provides the skin with its tough and at the same time flexible character. Leather is the chemically treated corium of hides. In those vertebrates in which the skin takes on the form and consistency of an exoskeleton, such as in many fishes, turtles, alligators, crocodiles, and some mammals (armadillo), the condition is the result of the development of scales or bony plates in the corium.

CHAPTER IV

ENDOSKELETON AND VOLUNTARY MUSCLE

Many invertebrate animals are soft-bodied and lack a hard, rigid supporting or protecting skeletal structure. If a skeleton is present, it is in the form of an exoskeleton enveloping the body. An internal supporting hard framework is absent. The invertebrate skeleton is integumentary in both origin and location. In sharp contrast, all vertebrates possess an internal skeleton regardless of the fact that in some cases an exoskeleton may also be present. The vertebrate type of skeleton is called an endoskeleton because it is situated internal to the body muscles. In the invertebrate type of skeleton the muscles are internal to the skeleton (Fig. 29).

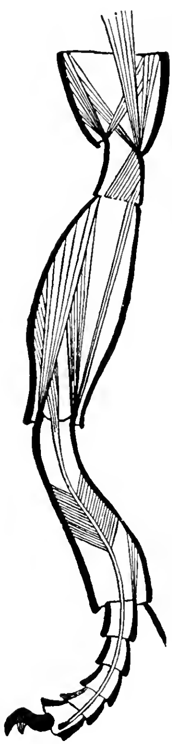


FIG. 29.—Relation of muscle to hard parts in the leg of an insect. (*After Berlese, from Shull, LaRue and Ruthven; Animal Biology.*)

The endoskeleton is composed of *cartilage* or *bone*, or a combination of both, and in its development it is closely associated with the development of the voluntary musculature of the body. Such a skeleton provides an internal framework to which the body muscles are attached. Joints between the parts of the skeleton permit movement of the parts upon or about one another, while the movement itself is produced by the contractions of the attached muscles. Skeleton and muscle are intimately related functional as well as structural components of a system responsible for body movements, controlled through nervous connections by the central nervous system.

Two general regions are recognized in the endoskeleton of vertebrates: (1) the *axial skeleton*, which includes the skull and vertebral column or backbone, and (2) the *appen-*

dicular skeleton, made up of the skeleton of the limb girdles and the skeleton of the paired appendages, such as the paired fins of fishes or the arms and legs of terrestrial forms. Ribs and the

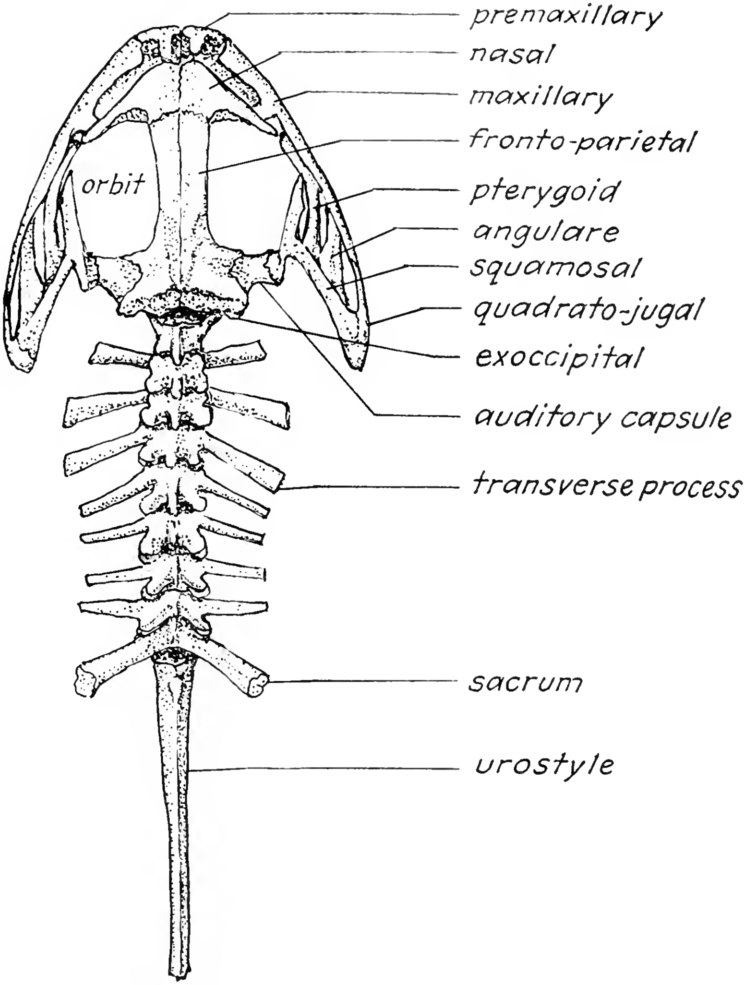


FIG. 30.—Axial skeleton of *Rana catesbeiana*, dorsal view.

skeleton of unpaired fins if present belong to the axial skeleton. The sternum or breast bone seems to be a development of the anterior limb girdle and therefore a part of the appendicular skeleton.

Cranium of the Frog.—The skull is composed of two parts: (1) the *cranium,* which encloses the brain, the inner ears, and olfactory organs, and (2) the *visceral skeleton,* made up of the upper and lower jaws and the hyoid apparatus. The cranium of the frog occupies the central region of the skull. Beginning at the posterior end are two bones, a right and left *exoccipital* bone, between which is a large opening, the *foramen magnum,* through which the spinal cord passes from the cranium to the neural canal of the vertebral column (Fig. 31). Each exoccipital bone, on its posterior face has a rounded projection, the *occipital condyle,* one on each side of the foramen magnum. The two condyles articulate with the atlas or first vertebra. At the side and just in front of each occipital condyle is a foramen for the passage of the ninth and tenth cranial nerves.

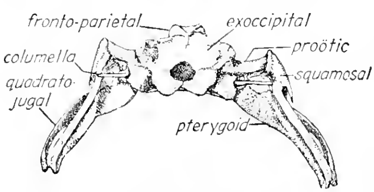


Fig. 31.—Posterior view of skull of *Rana eatesbeiana.*

The *prootic* bones, which form the auditory capsules, are short cylindrical bones at the sides and in front of the exoccipital bones. On the lower lateral surface of each prootic bone near the outer edge is an opening, the *foramen ovale,* which faces the middle ear (Fig. 31). The foramen ovale is closed by a cartilage which in turn articulates with the broad, inner end of the *columella,* the principal ossicle of the middle ear. From the broad base, the columella extends outward as a slender, slightly curved rod to the tympanic membrane to which it is attached. Vibrations of the tympanic membrane are transmitted through the columella and the cartilage at its inner expanded end to the inner ear. At the front and toward the ventral side of each prootic bone is an opening serving as a passageway for the fifth, sixth, and seventh cranial nerves.

The *frontoparietal* bones, one on either side, extend forward from the exoccipital bones to form the greater part of the roof of the portion of the cranium enclosing the brain (Fig. 30). These two bones are firmly united in the mid-line by a median suture. From the side of each a wing extends downward to form a portion of the side wall of the cranium. The greater part of the floor of the cranium is formed by the unpaired *parasphenoid* bone. This bone consists of a transverse process spanning the region beneath and between the prootic bones, from the center of which a narrow longitudinal tongue extends forward (Fig. 32).

The anterior end of the cranial cavity is closed by the cylindrical *sphenethmoid* bone which is overlapped above by the frontoparietals and below by the anterior end of the parasphenoid. In front of the sphenethmoid is the *nasal cavity*, which is divided by a median partition. The side walls of the cranium between the sphenethmoid in front and the prootic bones behind, and the frontoparietals above and the parasphenoid below, are formed of cartilage. The large spaces on either side of the frontoparietal bones are the *orbits* of the eyes.

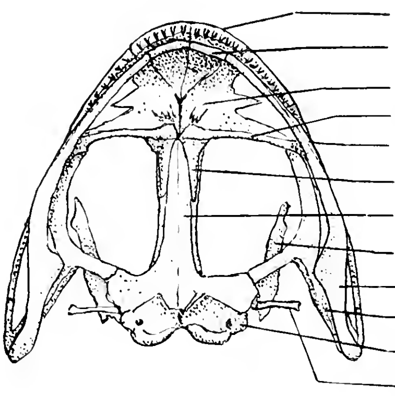


FIG. 32.—Ventral view of skull of *Rana catesbeiana*.

The paired *nasal* bones, lying just in front of the frontoparietals, meet in the mid-line, overlying the cartilaginous *nasal capsules*. From each nasal bone a narrow process extends laterally to the upper jaw. Below the nasal capsules and forming the floor of the cranium in front of the sphenethmoid bone are the paired *vomer* bones. Each vomer bone bears a tooth on its ventral face.

Suspensorium of the Frog's Skull.—Three pairs of bones, the *squamosals*, *pterygoids*, and *palatines*, attach the jaws to the cranium and constitute the suspensory apparatus of the skull. The squamosal bone can be seen best in a side view of the skull (Fig. 33). It consists of a narrow stem extending from the angle of the jaw diagonally upward to a shorter cross piece, which is articulated at its upper end to the prootic bone and whose lower end curves downward toward the upper jaw. The pterygoid can be seen in a ventral view of the skull (Fig. 32). Beginning at the angle of the jaw, it curves forward beneath the stem of the squamosal to the upper jaw at its middle where it is also connected to the lower end of the cross piece of the squamosal by cartilage. From the center of this arched portion of the pterygoid bone an arm projects medially to the outer end of the prootic bone. Each palatine bone extends from the anterior end of the

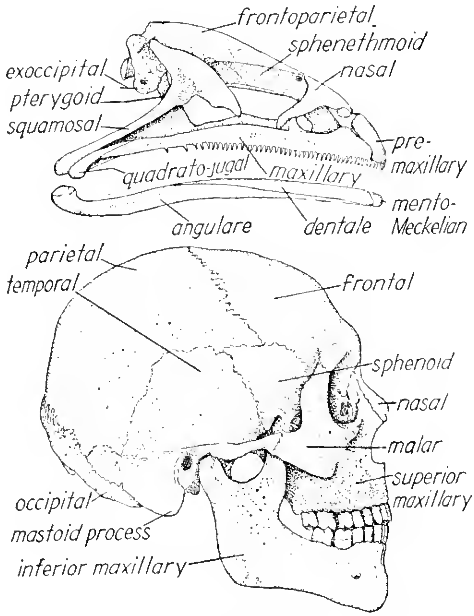


FIG. 33.—Side view of skull *Rana catesbeiana* and of human skull, reduced in size for purpose of comparison.

sphenethmoid outward to the upper jaw, directly beneath the lateral processes of the nasal bones.

Jaws of the Frog.—The upper jaw is composed of three pairs of bones. In front are the two *premaxillary* bones, short segments, from each of which a short *facial process* curves upward and back toward the external nares. A *maxillary* bone forms the long segment, on either side, extending from the premaxillary in front to the *quadratojugal* bone behind. The quadratojugal bone articulates with the *squamosal* and *pterygoid* bones at its posterior end. Teeth are borne by the premaxillary and maxillary bones (Fig. 33).

At the tip of each half of the lower jaw is a short segment, the *mentomeckelian* bone, directly beneath the corresponding premaxillary bone in the upper jaw. The mentomeckelian bone continues backward to the angle of the jaw as *Meckel's cartilage*, passing between two overlapping bones, the *dentale* in front and outside of the cartilage, and the *angulare*, inside of and below the cartilage. The posterior half of the cartilage runs in a groove on the upper surface of the angulare, widening out to form an articulating surface at the end of the jaw. In prepared skeletons, the cartilage is often absent, but the groove in the angulare can be clearly seen. There are no teeth in the lower jaw. The *coronoid process* of the angulare offers a point of attachment for muscles that close the jaw.

The tips of both upper and lower jaws are movable. When the tip of the lower jaw is thrust upward, the premaxillaries are raised, pushing the prefacial processes of the latter against the sides of the external nares, closing them.

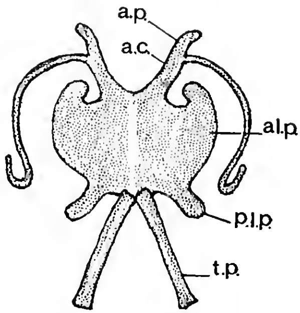


Fig. 34.—Hyoid apparatus of *Rana catesbeiana*, ventral view. a.c., anterior cornu; a.p., anterior process; al.p., alary process; p.l.p. posterior lateral process; t.p., thyroid process.

Hyoid Skeleton.—The frog in the tadpole stage is provided with gills and gill clefts, perforating the pharynx on either side. When metamorphosis occurs, the gills disappear and the branchial skeleton supporting the gills becomes converted into the hyoid skeleton of the adult, most of which is cartilaginous (Fig. 34). The *body* of the hyoid is a flat plate of cartilage, roughly quadrilateral in shape, located in the floor of the mouth cavity. The *anterior cornua* of the hyoid are a pair of slender rods curving backward and upward, one to each prootic bone. The *alary processes* extend laterally, one on each side just behind the corresponding anterior cornu. The *posterior lateral processes* extend from the body behind and at the sides. Between them are the ossified *thyroid processes* which enclose and support the larynx.

Chondrocranium.—The primitive vertebrate skull was cartilaginous. In higher vertebrates parts of this chondrocranium are ossified or replaced by membrane bone. In the frog much of the cartilaginous cranium remains. The exoccipitals, prootics, and sphenethmoid of the cranium are *cartilage bones*, by which is meant that they are first laid down in cartilage, and later converted into bone. The remaining cranial bones, the frontoparietal, parasphenoid, nasal, and palatine bones are *membrane bones*, *i.e.*, they develop directly out of connective tissue and are not preformed in cartilage. If they are carefully removed, the cartilaginous cranium is found beneath them enclosing the brain completely except for several openings in the roof.

It has already been pointed out that the core or axis of the lower jaw is formed by Meckel's cartilage. The upper jaw likewise is built on a cartilaginous basis continuous with the chondrocranium. Excepting the quadratojugal and mentomeckelian bones, the components of the suspensory apparatus and the jaws are membrane bones.

Some of the general and more obvious differences between the human skull and that of the frog are shown in Fig. 33. In the human skull there has been an enormous increase in size of the cranium as compared with the frog. The frontoparietal region of the frog is flat; in the human skull it is highly elevated and convex. The human cranium is also relatively wider and more elongated posteriorly above the occipital region. The human jaws are relatively shorter than those of the frog. The human skull is completely ossified. The human face results from the increased size of the cranium accompanied by a relative and actual reduction in visceral skeleton.

Vertebral Column.—The vertebral column or backbone of the frog consists of a series of nine *vertebrae*, all of which are based on a common structural plan, followed by a tenth, the rodlike *urostyle*. The urostyle represents the caudal vertebrae of the frog tadpole which become fused into a single bone during the process of metamorphosis. Each of the first nine vertebrae, except the first and ninth, consists of (1) a *centrum*, a solid ventral portion, concave in front and convex behind, and (2) a *neural arch*, forming the dorsal half of the vertebra (Fig. 35). The space between the arch and the centrum is occupied by the spinal cord. On the dorsal side of the arch in the mid-line is a projection, the *neural spine*. From either side of the neural arch a *transverse process* extends laterally. In a fresh specimen each transverse process bears at its outer end a short cartilaginous segment, which represents a rudimentary *rib*. Ribs are therefore practically absent in the frog. Extending forward from the anterior edge of each neural arch is a pair of spoon-shaped articulating surfaces, the *anterior zygapophyses*, which face upward and inward. A pair of *posterior zygapophyses*, projecting backward from the neural arch, faces downward and out, fitting over the anterior zygapophyses of the following vertebra. These articulations between the vertebra at the level of the neural arch together with the ball and socket union between the centra permit a limited amount of movement in the body axis.

The vertebrae are held together by means of *hyaline cartilage* between the ends of the centra and by ligaments extending along the sides of the centra and between the neural arches and between

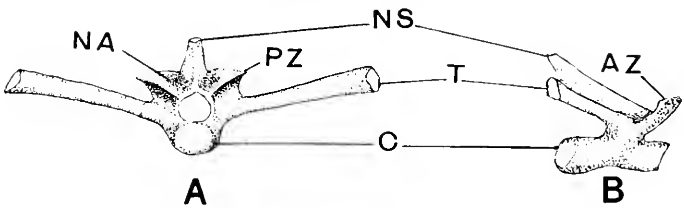


FIG. 35.—Fourth vertebra of *Rana catesbeiana*. A, posterior view; B, right side view. AZ, anterior zygapophysis; C, centrum; NA, neural arch; NS, neural spine; PZ, posterior zygapophysis; T, transverse process.

the neural spines. The *intervertebral foramina* are spaces between adjacent neural arches through which the spinal nerves emerge.

The first vertebra, or *atlas*, lacks transverse processes and anterior zygapophyses. In place of the latter there is on either side of the centrum a deep concave surface which articulates with an occipital condyle of the exoccipital bone of the cranium. The ninth vertebra lacks posterior zygapophyses. A pair of rounded knobs, which project from the posterior face of the centrum, articulates with a pair of cavities on the anterior face of the urostyle. The transverse processes of the ninth vertebra are well developed and are attached to the ilia of the pelvic girdle. The urostyle has a small vertebral canal into which the spinal cord extends. The last pair of spinal nerves passes out through small openings near the anterior end.

In the higher vertebrates the vertebral column is differentiated more completely into regions than is the case in the frog. Thus the *cervical* region, which in the frog is represented by the single atlas vertebra, in higher forms consists of a number of vertebrae characterized by a reduction in the size of ribs or by the complete absence of ribs. In the higher forms the cervical region is followed by the *thoracic* region, provided with well-developed ribs; the *lumbar* region, usually without ribs; the *sacral* region, made up of several vertebrae, fused together and firmly united to the pelvic girdle; and the *caudal* or tail region (Fig. 36). The caudal region is sometimes reduced or modified as in the case of the *pygostyle* of birds (Fig. 44), or the *coccyx* of man (Fig. 63).

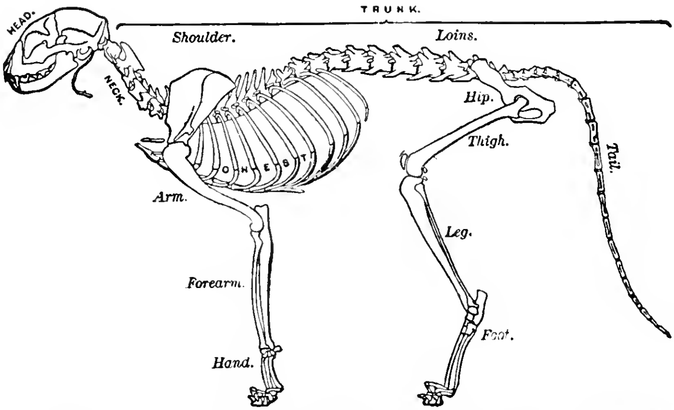


Fig. 36.—Regions of the vertebrate skeleton (cat). (*From Jayne, Mammalian Anatomy, J. B. Lippincott & Co. By permission.*)

Unpaired Appendages.—The *dorsal*, *caudal*, and *anal* fins of fishes and the continuous *median* fin of larval amphibians, such as the tadpole of the frog, are examples of unpaired appendages. They are located in the midplane of the body, and in fishes are supported by cartilaginous or bony spines. In amphibians skeletal elements are lacking. Median fins, by extending the lateral surface of the trunk and tail, enlarge the pushing surface of the trunk and tail and thus increase the efficiency of the swimming strokes.

Notochord.—In the lowest vertebrates, the *Cyclostomata*, there is a rudimentary vertebral column with poorly developed neural arches. The centra of the vertebrae are absent and in their place is a long unsegmented cylindrical rod, the *notochord*, which serves as a body axis. The notochord develops in all vertebrate embryos (Fig. 37). In fishes, vertebrae are developed, but the notochord is not completely replaced even in the adult stage and can be recognized as a thin thread extending through the centra of the vertebrae and as rounded masses between the concave ends of the centra, so that the actual form of the notochord resembles a string of beads (Fig. 37, B). In vertebrates above fishes the notochord is more and more completely replaced by the centra of the vertebrae until in mammals it vanishes completely in the adult. The notochord may be

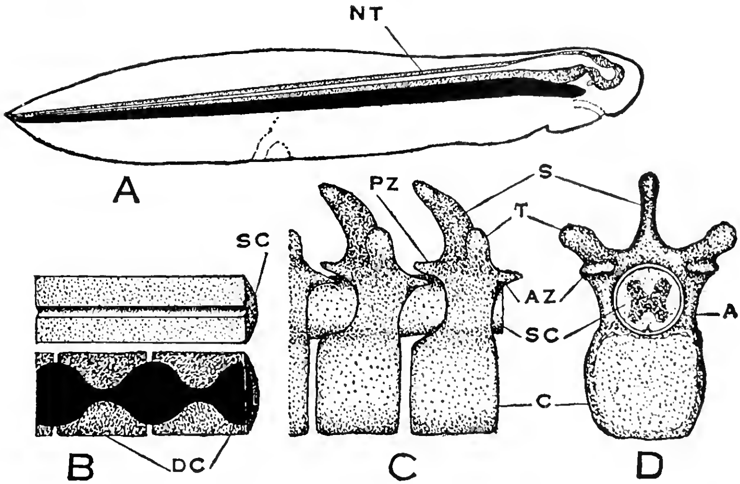


FIG. 37.—A, the notochord (in solid black) as seen in a longitudinal section of the larval salamander in which it represents the axial skeleton. The neural tube (NT) lying above consists of the brain and spinal cord. B, diagram of a median view of the spinal cord (SC) and developing centra (DC) split lengthwise. The notochord (in black) is partially replaced by the enveloping centra which give it a beaded appearance that remains a permanent condition in fishes. C, a diagrammatic side view of two completely developed vertebrae of a mammal, showing the intervertebral foramina through which nerves and blood vessels pass. The nerves and blood vessels are omitted in the drawing. D, vertebra from the anterior side with the spinal cord shown in section in the vertebral canal. A, neural arch; C, centrum; S, neural spine; SC, spinal cord; T, transverse process; AZ, anterior zygapophysis; PZ, posterior zygapophysis.

regarded as the primitive skeletal axis of vertebrates which in the higher vertebrates is replaced by the vertebral column.

Ribs.—There are two kinds of vertebrate ribs: (1) *hemal* ribs, occurring in fishes and some amphibians and reptiles, and (2) *pleural* ribs, which may occur in all vertebrate groups. In the frog there are no hemal ribs. Pleural ribs are represented by the small projections on the ends of the transverse processes of the vertebrae. In birds and mammals only pleural ribs are present.

In fishes the hemal rib extends from the side of a centrum of a vertebra into the muscle of the body wall. In the caudal region the ventral ends of the ribs meet in the mid-line to form a *hemal arch,* enclosing blood vessels (Fig. 38). A caudal vertebra in such a case is provided with a neural arch above the centrum and a hemal arch below.

The pleural ribs of man are restricted to the thoracic region of the body. The first seven vertebrae are the vertebrae of the neck or cervical region. The next twelve vertebrae belong to

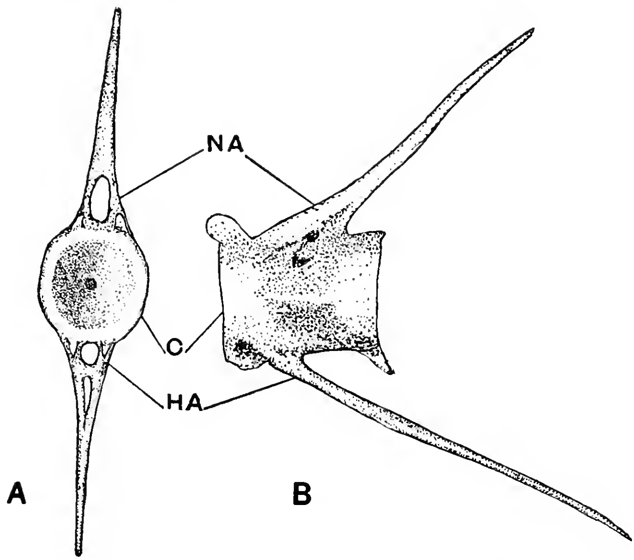


Fig. 38.—Posterior (A) and side view (B) of a caudal vertebra of a teleost fish. c, centrum; ha, hemal arch; na, neural arch.

the thorax and it is to the thoracic vertebrae that the dorsal ends of the ribs are articulated at two points, *viz.,* the *head* and *tubercle* (Fig. 39). The head or capitulum, at the dorsal end of the rib articulates with a facet on the centrum of the vertebra called the *parapophysis.* The facet on the centrum may be entirely on a single vertebra, as in Fig. 39, or it may be shared by two adjoining vertebrae. The tubercle or tuberculum of the rib articulates with the *diapophysis,* a facet in the transverse process of the vertebra. The neck of the rib is the region between the head and the tubercle. The first ten pairs of ribs are connected at their ventral ends by means of costal cartilages to the *sternum* or breast bone. The eleventh and twelfth pairs of ribs are known as floating ribs. In many birds and some reptiles a thoracic rib may bear an *uncinate process* directed backward and overlapping the rib behind, thus reinforcing the thoracic framework (Fig. 44).

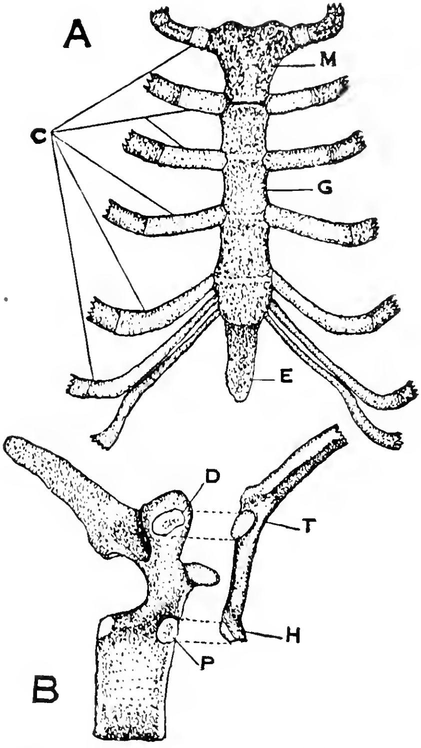


FIG. 39.—A, sternum of Man showing the manner in which the ribs are attached by costal cartilages, C. E, ensiform process; G, gladiolus or body; M, manubrium. B, view of a thoracic vertebra from the right side with the dorsal end of the corresponding rib rotated so as to show its posterior aspect and the manner in which it articulates with the vertebra. D, diapophysis; H, capitular head of rib; P, parapophysis; T, tubercular head of rib.

Pectoral Girdle and Sternum.—There is a difference of opinion as to whether the sternum evolved in connection with the anterior limb girdle or from ribs. In the frog the sternum is an integral part of the pectoral girdle, the combined elements forming a bony structure almost completely encircling the body at the level of the forelimbs. On each side of the body, the girdle is composed of three bones, the *scapula*, *clavicle*, and *coracoid*, which meet at the shoulder. The scapula extends dorsally from

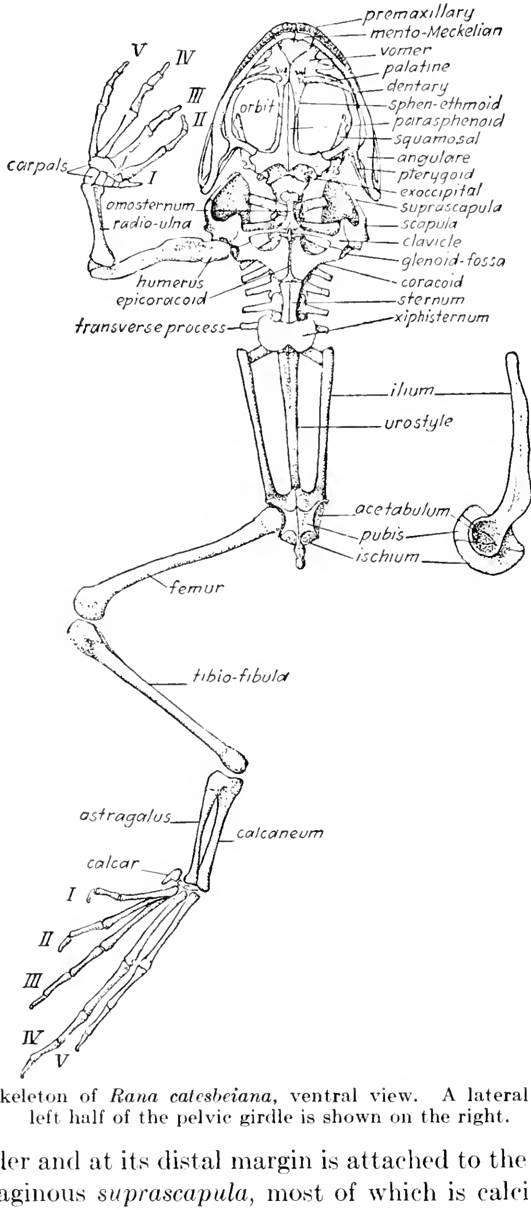


FIG. 40.—Skeleton of *Rana catesbeiana*, ventral view. A lateral view of the left half of the pelvic girdle is shown on the right.

the shoulder and at its distal margin is attached to the broad and flat cartilaginous *suprascapula*, most of which is calcified. The clavicle in front and the coracoid behind extend from the shoulder medially and slightly ventrally to the *epicoracoid cartilages* in the mid-line (Fig. 40). The *glenoid fossa* is a shallow cavity at the junction of the scapula and coracoid, most of it being located on the posterior side of the scapula. This cavity receives the head of the humerus of the arm. The clavicle joins the scapula at the *acromium* of the latter, directly in front of the glenoid fossa.

The calcified edges of the epicoracoid cartilages, closely united in the mid-line between the median ends of the clavicles and

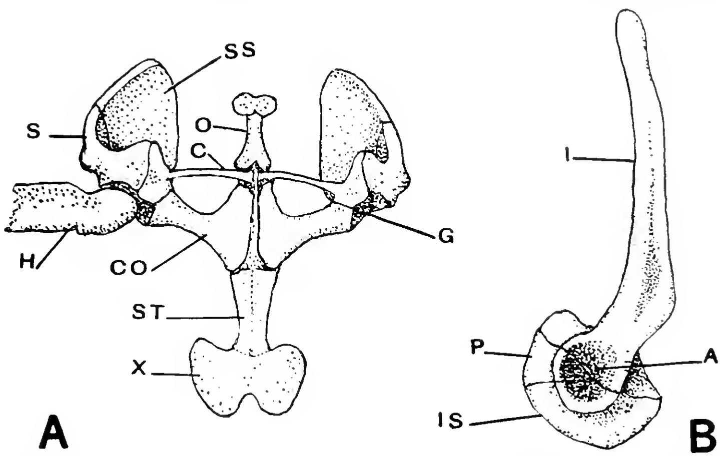


Fig. 41.—Ventral view of pectoral girdle (A) and lateral view of left half of pelvic girdle (B) of *Rana catesbeiana*. A, acetabulum; C, clavicle; CO, coracoid; G, glenoid fossa; H, humerus; I, ilium; IS, ischium; O, omosternum; P, pubis; S, scapula; SS, suprascapula; ST, sternum; X, xiphisternum. The epicoracoid cartilages make up the narrow region compressed between the median edges of the coracoid bones.

coracoids, represent the middle section of the sternum. The remainder of the sternum is composed of the *omosternum* in front and the *sternum* behind (Fig. 41). At the anterior end of the omosternum is an expanded cartilaginous segment, the *episternum*. A somewhat larger cartilaginous disk strongly notched, the *xiphisternum*, is attached to the posterior end of the sternum.

In man the sternum is of more importance in connection with the ribs than with the pectoral girdle. The suprascapula is absent and the coracoid is reduced to the *coracoid process* of the scapula. The clavicle extends from the acromium of the scapula to the anterior end of the sternum. The glenoid cavity is located entirely on the scapula (Fig. 42). The human sternum is an unpaired structure consisting of the *manubrium* in front (above), the *gladiolus* in the middle, and the *ensiform process* behind (below). To the gladiolus are attached the intercostal cartilages which link it with the ventral ends of the first ten pairs of ribs. Its only contacts with the pectoral girdle are through the clavicles and these are of minor importance as far as supporting the sternum is concerned (Fig. 39).

Pelvic Girdle.—The pelvic girdle is much like the pectoral girdle, with which it may be compared part for part. Thus, the *pubis* is on the ventral side in the same relative position as the clavicle; the *ischium*, lying posteriorly to the pubis, corresponds to the coracoid; and the *ilium*, extending dorsally, to the scapula (Fig. 41). The pelvic girdle, however, differs from the pectoral girdle in its relation to the axial skeleton in all forms above the fishes. In fishes, both girdles are free of the vertebral column, but in the higher groups the pelvic girdle is firmly united to the sacrum on each side by a *sacroiliac* ankylosis, a fusion of the sacrum and ilium. This, together with the fact that the pubic portions may meet in the midventral line, makes the pelvis a firm, rigid structure. This is especially important in *bipeds* like birds and man, where the entire weight of the trunk rests upon the pelvis. In man, the three elements of each side of the pelvis, though separate in the embryo, are fused in the adult into a single bone, the *os innominatum*.

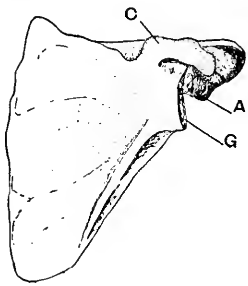


FIG. 42.—Left human scapula from the front. A, acromium process; C, coracoid process; G, glenoid cavity.

Paired Appendages.—The anterior and posterior pairs of *fins* of fishes are relatively simple structures, used in maintaining balance and to a certain extent in swimming. They may be classified as organs of locomotion, though the important strokes in swimming are produced in the fish by the contractions of the body muscles, which push the trunk and tail against the water. The skeleton of the fin consists of cartilaginous or bony rods, which support the tough membrane making up the rest of the fin. Save for differences in details and some cases of special adaptation, the paired fins are uniform in shape and structure, in keeping with the uniform nature of the fluid medium, water, in which they live. The paired appendages of the terrestrial vertebrates, though based on a common plan of structure, show a wide variety of structural forms, in conformity with the fact that they may be adapted for crawling, walking, running, swimming, or flying.

Forelimb of the Frog.—The fore- and hindlimbs of the frog are made up of similar parts based on the same structural pattern. The proximal element of the skeleton of the upper arm is an elongated bone, the *humerus,* whose head articulates with the glenoid cavity of the pectoral girdle to form the shoulder joint (Fig. 40). The *deltoid ridge* is a narrow elevation running from the head of the humerus to its middle. The lower end of the humerus terminates in a large rounded articulating surface, which fits into a depression in the *olecranon* of the forearm to form the elbow joint. The skeleton of the forearm is a single unit, the *radioulna,* formed by the incomplete fusion of two bones, the radius and ulna. The olecranon is a prolongation of the ulnar portion of the radioulna and lies on the postaxial (away from the head) side of the limb. The lower end of the radioulna is definitely bifurcated into a preaxial radial component, in front, and a postaxial ulnar component, behind. The bones of the wrist or *carpus* consist of six small irregularly shaped bones, known as *carpals,* arranged in two transverse rows. Beginning on the preaxial side, the proximal row is made up of the *centrale,* the *radiale* and, the *ulnare;* in the distal row are the *first carpal,* the *second carpal,* and the *outer carpal,* the latter representing a fusion of three bones. The skeleton of the palm or *metacarpus,* which adjoins the wrist, is composed of five cylindrical bones of which the preaxial one is greatly reduced in size, especially in the female. Only four *digits* or fingers are present and these correspond to digits II, III, IV, and V of the human hand, the thumb (I) being absent. The bones of the fingers are called *phalanges,* of which there are two in digits II and III and three in digits IV and V.

Hindlimb of the Frog.—The skeleton of the upper leg is the *femur,* which corresponds with the humerus of the forelimb. It is a cylindrical bone in the form of a slightly reversed curve. Its rounded head fits into the *acetabulum* of the pelvic girdle to form the hip joint. Its distal end is enlarged to form an articulating surface with the *tibiofibula* of the lower leg or crus. The tibiofibula like the radioulna is a fusion of two bones. The double origin of the tibiofibula is indicated by deep grooves in either end of the shaft, the tibial component being preaxial and the fibular postaxial. The ankle or *tarsus* of the frog is highly modified. Adjoining the distal end of the tibiofibula are two long bones, united at either end but separate in the middle, called the *tibiale* or *astragalus* and the *fibiale* or *calcaneum*, preaxial and postaxial, respectively. Beyond these are two or three smaller *tarsal* bones, the largest of which represents the fusion of two bones. There are five *metatarsal* bones, corresponding to the five metacarpal bones. There are five toes of which digits I and II contain two *phalanges* each, digits III and V three each, and digit IV, four. On the preaxial side of the first digit is the *prehallux* or *calcar*, composed of one or two parts, and regarded by some as a rudimentary digit.

Limbs in General.—The similarity in the structural plan of the fore- and hindlimbs of the frog is also true of the limbs of other vertebrates. The limbless condition of snakes is secondary and is the result of loss of limbs. All vertebrates above fishes are believed to have had limbs at some time. If one wishes to get some idea of what the primitive vertebrate limb was like, one should study an amphibian in which the limbs are not highly developed. The frog does not serve for this purpose because of the obvious structural and functional specialization of its limbs. Instead, one should turn to a tailed amphibian, such as *Ambystoma microstomum*, which has relatively simple limbs. Its locomotion consists of slow crawling movements in which the body is raised just high enough to clear the ground, the tail dragging. The limbs move principally in a horizontal plane, the entire *volar* or *plantar* surface of the foot touching the ground at each step. This type of foot posture is known as *plantigrade*. In more rapid movements the body is thrown into snakelike, side-to-side undulations by contractions of the trunk and tail muscles, which accompany the movements of the legs. The undulatory movements resemble the swimming movements of these animals, except that in swimming the legs are not used.

The proximal element of the limb skeleton of the salamander is a single bone, the humerus in the forelimbs and the femur in the hindlimb. The radius and ulna of the forelimb are separate bones as are also the tibia and fibula of the crus. The carpal and tarsal bones are relatively unspecialized and vary from seven to nine in number. The foot is provided with four or five digits and seems to be derived from a *pentadactyl* type. Such a limb is regarded as a fairly close approximation to the primitive type of vertebrate limb from which the limbs of all vertebrates have been derived.

Departures from this primitive amphibian type of limb are numerous in the higher vertebrates. Thus in the frog the radius and ulna are fused and, likewise, the tibia and fibula. In other animals, one component in the forearm or leg may be distinct and the other greatly reduced. An extreme example of this

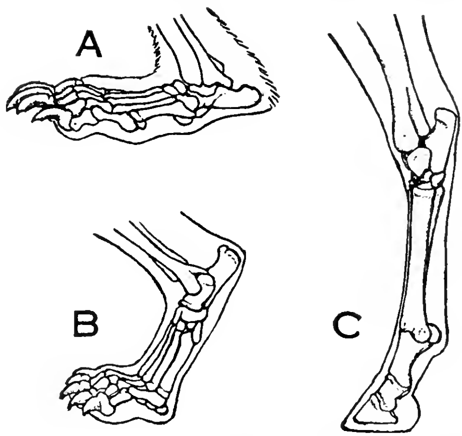


FIG. 43.—Foot postures. A, plantigrade, bear; B, digitigrade, hyena; C, unguligrade, horse. (*A and B after Lull, Organic Evolution, C after Pander and D'Alton.*)

among mammals is found in the horse, in which the fibula is distinct but reduced in size to a thin rod. There is a reduction of parts through loss as well as diminution in the more distal elements of the limb of the horse. Thus metacarpal III is the principal element of the metacarpus, metacarpals II and IV being reduced to splints, while metacarpal V is missing. A similar condition is found in the metatarsus. Of the digits only digit III is present. The horse walks on the nail (hoof) of its middle finger or toe. This type of foot posture is *unguligrade* (Fig. 43).

Dogs and cats are *digitigrade*, *i.e.*, they walk on their toes. Strangely enough, the human limb has retained a number of primitive features, such as distinct radius and ulna in the forearm, and distinct tibia and fibula in the leg, though the fibula is much reduced; a pentadactyl hand and foot, and a plantigrade foot posture. Of the larger mammals, bears alone have plantigrade feet.

The skeleton of the limbs of birds in the course of evolution has undergone considerable modification (Fig. 44). In the wing

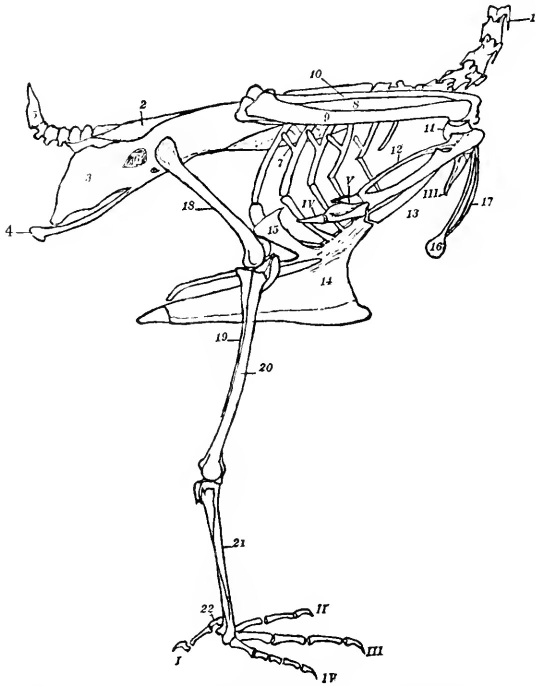


Fig. 44.—Skeleton of trunk and appendages of domestic fowl. 1, cervical rib; 2, ilium; 3, ischium; 4, pubis; 5, pygostyle; 6, ilio-sciatic foramen; 7, uncinate process of thoracic rib; 8, humerus; 9, ulna; 10, radius; 11, ulnar carpal; 12, metacarpal of ulnar digit; 13, coracoid; 14, sternum; 15, metasternum; 16, hypocleidium; 17, clavicle; 18, femur; 19, fibula; 20, tibiotarsus; 21, tarsometatarsus; 22, metatarsus of first digit. I, II, III, IV, V, digits. The digits of the fore limb should be labeled II, III and IV instead of III, IV and V respectively.

of the domestic fowl, ulna and radius are both present, the ulna being the larger. Carpals and metacarpals are reduced by fusion. Of the metacarpals, II, III, and IV can be identified, and adjoining these are the corresponding rudimentary digits. The proximal element of the skeleton of the hindlimb is the femur. The next segment consists of a very much reduced fibula and a long cylindrical *tibiotarsal* bone, formed by fusion of the tibia with proximal tarsals. Distal to the tibiotarsal is another cylindrical bone, the *tarsometatarsal*, formed by fusion of distal tarsals with metatarsals. As a result the ankle joint in birds is intertarsal instead of between the tarsals and the tibia and fibula. This condition also occurs in reptiles. Four toes are present in the fowl, digit V being absent.

Histology of Cartilage and Bone.—Bone and cartilage are forms of connective tissue. Cartilage is composed of cells embedded in a matrix of solid material that is a mixture of *collagen* (a substance also found in white connective tissue fibers), *chondroitin-sulphuric acid* in a combined form, and *albuminoid* substances. *Hyaline cartilage*, which is translucent

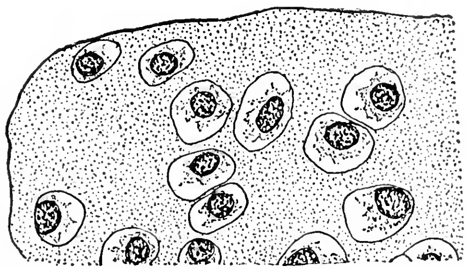


Fig. 45.—Cartilage, larval salamander. × 300.

and pale gray in color, forms the articulating surfaces of bones, the nasal cartilages, the costal (rib) cartilages, and the rings of the trachea (windpipe) and bronchial tubes. *Elastic cartilage* is yellowish in color, owing to the presence of yellow elastic fibers. It occurs in the external ear of mammals. *Fibrocartilage* contains in its matrix dense connective tissue composed mainly of white fibers. In man it is found in the disks between the centra of the vertebrae. The matrix of cartilage is produced by the cells embedded in it (Fig. 45).

Bone resembles cartilage in the topographical and functional relations of cells and matrix. The matrix of bone in the early stages of its histogenesis is soft and at that time is composed of *collagen*, *osseomucoid*, and usually some connective tissue fibers. The bone hardens as a result of deposition of inorganic salts, of which the most abundant is calcium phosphate. *Cartilage bone* is bone that passes through a cartilage stage in its development. *Membrane bone*, on the other hand, is formed directly from connective tissue without passing through a cartilaginous stage. The greater part of the skeleton is laid down in cartilage, which, except in those forms in which the skeleton is permanently cartilaginous, is replaced by bone tissue formed about the cartilage as the latter is resorbed. In the frog some of the primitive cartilaginous skeleton survives in the adult, though the greater part of it is converted into bone. Membrane bones, such as those of the face, the flat bones of the skull, parts of the jaw, etc., may be formed regardless of whether the original cartilaginous skeleton becomes ossified or not. The calcified cartilage of sharks is almost as hard as bone.

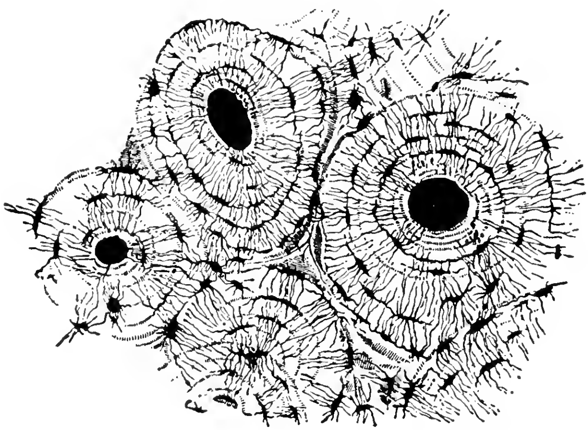


FIG. 46.—Cross section of compact bone from the shaft of the humerus showing the ground substance in white. The large black areas are occupied by blood vessels, the bone cells lying in the smaller spaces arranged in concentric circles. × 150. (*From Schäfer, Textbook of Microscopic Anatomy, Longmans, Green & Co., after Sharpy. By permission.*)

The nature of the process of histogenesis is the same for both cartilage and membrane bone. The preliminary formation of cartilage in the formation of cartilage bone probably signifies the existence of a primitive ancestral cartilaginous skeleton in which the homologues of the membrane bones were not represented. Therefore, membrane bone would seem to be a later addition to the skeleton.

A cross section of a decalcified human long bone (Fig. 46) shows large black spaces, *Haversian canals*, surrounded by concentric circles of smaller spaces, *lacunae*, with fine radiating lines connecting the circles. The Haversian canals contain blood vessels and some nervous tissue, which enter from the periosteum covering the bone. The lacunae enclose bone cells from which processes extend into the fine radiating canals.

Skeletal Muscle.—If the skin is removed from the body of a frog, the superficial skeletal muscles are exposed. Muscles are usually attached by one or both ends to bones by *tendons*, which are composed of white connective tissue fibers. *Fasciae* are slightly elastic connective tissue membranes covering muscles, and uniting with the tendons at the ends of the muscles. The *origin* of a muscle is the end that remains stationary, or relatively so, when the muscle contracts. The *insertion* is the end that moves during contraction. Since movements are brought about by the contractions of muscles, the flexion or extension of a body part at a joint is the result of the actions of two sets of antagonistic muscles known as *flexors* and *extensors*, respectively. *Adduction* or *abduction* refers to movements of the arms or legs toward or away from the mid-line of the body, or in the case of fingers or toes, toward or away from the principal axis of the arm or leg. A *rotator* muscle causes a part to rotate about its main axis. In connection with the jaws a *levator* muscle raises the lower jaw and a *depressor* lowers it. The description of the muscles of the bullfrog, *Rana catesbeiana*, in the following paragraphs, is confined to those muscles that can be exposed by the removal of the skin and fasciae and by a small amount of dissection as illustrated in Figs. 47 and 48.

Muscles of the Head and Trunk.—Beginning at the ventral side of the head, the *submaxillaris* muscle, forming the floor of the mouth, can be seen. Its fibers run transversely between the rami of the lower jaw. It is important in swallowing and respiratory movements. If one-half of the submaxillaris is removed, three other muscles are exposed: (1) the *submentalis*, a very small muscle joining the tips of the dentary bones that aids in closing the external nostrils by drawing together the two halves of the lower jaw and thus raising the premaxillary bones; (2) the *hyoglossus* and (3) the *geniohyoideus*, two ribbon-shaped muscles extending from the submentalis posteriorly. The outer one, the geniohyoideus, arises from the lower jaw and is inserted on the hyoid bone. The inner one, the hyoglossus, has its origin in the hyoid bone, runs forward uniting with the muscle of the opposite side and passes into the tongue at the anterior end of the mouth, where it turns back and continues to the tip of the tongue.

The following muscles are found on the ventral and lateral walls of the trunk. The *deltoideus*, arising from the clavicle, precoracoid, omosternum, and scapula, is inserted on the deltoid ridge of the humerus. Its contraction draws the limb forward. The *sternoradialis* arises in the mid-line from the omosternum and epicoracoid, passes outward, piercing the distal portion of the deltoid, and is inserted on the radioulna. It corresponds to the human biceps muscle and its contraction flexes the forearm. The *recti abdominis* muscles of each side meet in mid-line in a tendinous union, called the *linea alba.* Each rectus muscle is also traversed by four or five transverse *inscriptiones tendineae*, which are tendinous insertions in the muscle. As each rectus muscle passes forward from its origin in the pubis, it widens and at the second inscriptio tendinea from the rear divides into two parts: a median portion continuing straight forward to the xiphisternum and beyond; a lateral portion branching off to the shoulder to form the abdominal component of the *pectoralis* muscle. The continuation of the median portion beyond the xiphisternum forms the *sternohyoideus,* which is inserted on the hyoid bone. The pectoralis muscle consists of three parts; of which the *sternalis anterior*, in front, and the *sternalis posterior*, just behind, both have a broad origin from the epicoracoids, sternum, and xiphisternum, while the *abdominalis* portion arises principally in the rectus abdominis. All three portions of the pectoralis muscle are inserted in the humerus. If the pectoral muscle is removed (right side of Fig. 47), the *coracohumeralis* is exposed. This is a narrow muscle having its origin in the coracoid near the sternum and its insertion on the middle of the humerus. Posterior to the coracohumeralis a small portion may be seen of the *obliquus internus* (or *transversus*) muscle, which forms the inner layer of the abdominal wall. Its origin is principally in the ilium and transverse processes of the last six vertebrae. Its points of insertion are various, such as the xiphisternum, coracoid, esophagus, pericardium, and the linea alba. The *obliquus externus*, whose fibers run almost at right angles to those of the obliquus internus, forms the outer wall of the abdominal cavity except ventrally where it is overlaid by the recti abdominalis and pectoral muscles.

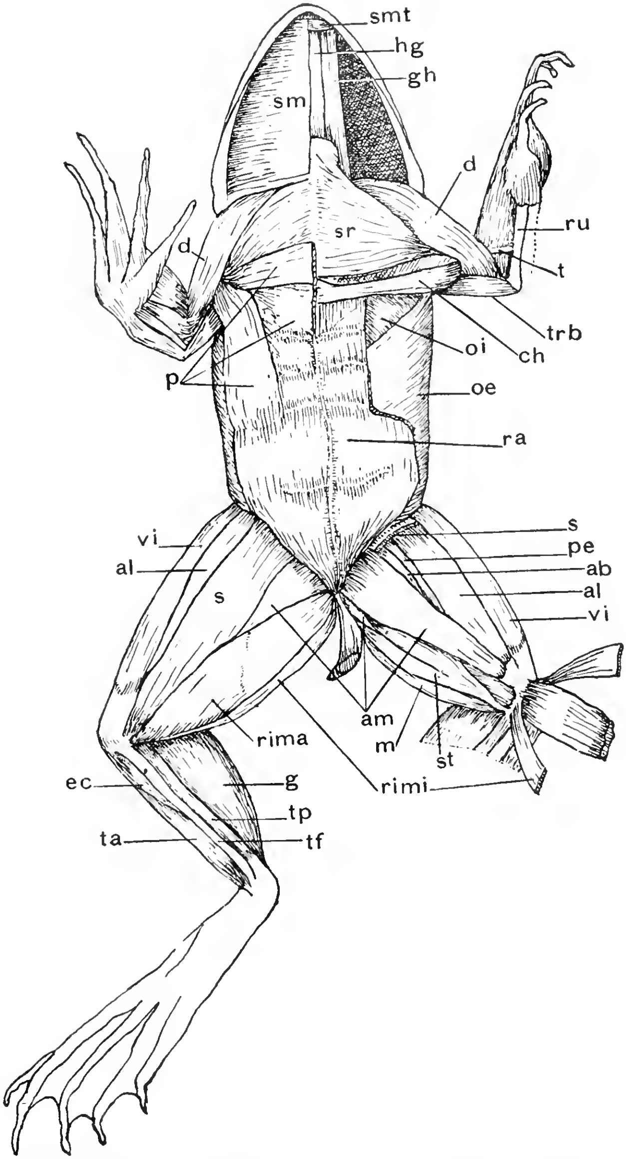


Fig. 47.—Muscles of *Rana catesbeiana*, ventral side. ab, adductor brevis; al, adductor longus; am, adductor magnus; ch, coracohumeralis; d, deltoideus; ec, extensor cruris; g, gastrocnemius; gh, geniohyoideus; hg, hyoglossus; m, semimembranosus; oe, obliquus externus; oi, obliquus internus; p, pectoralis; pe, pectineus; ra, rectus abdominis; rima, rectus internus major; rimi, rectus internus minor; ru, radioulna; s, sartorius; sm, submaxillaris; smt, submentalis; sr, sternoradialis; st, semitendinosus; t, tendon of sternoradialis; ta, tibialis anticus; tf, tibiofibula; tp, tibialis posticus; trb, triceps brachii; vi, vastus internus.

The *triceps brachii* is an important muscle of the upper arm whose contractions extend the forearm. A portion of it may be seen in Fig. 47 at the posterior side of the upper arm. It arises by three heads: (1) from the scapula and from the capsule of the glenoid cavity; (2) from the proximal half of the inner surface of the humerus; and (3) from the outer surface of the humerus. It is inserted by a single tendon on the radioulna. The muscles of the forearm consist of extensors and flexors of the wrist and fingers, a description of which will be omitted.

Muscles of the Head and Trunk, Dorsal Side.—A portion of the *temporalis* muscle can be seen between the orbit and the tympanum (Fig. 48). This muscle has its principal origin in the prootic bone, from which it passes out beneath the squamosal and over the pterygoid, between the latter and the maxillary and quadratojugal to its insertion in the coronoid process of the angulare. A portion of its fibers also come from the anterior border of the tympanic ring and from the squamosal bone. It is an important levator muscle of the lower jaw. The *depressor maxillae inferioris*, overlapping the temporalis posteriorly, arises (1) from the dorsal fascia and (2) from the squamosal and the posterior and inferior border of the tympanic ring; it is inserted in the posterior angle of the lower jaw. Its action depresses the jaw and opens the mouth. The *infraspinatus* muscle, arising from the suprascapula, and the *latissimus dorsi*, from the dorsal fascia, are both inserted by a common tendon in the outer surface of the deltoid ridge of the humerus. The *longissimus dorsi* arises from the urostyle and is inserted in the spinous processes of the first five vertebrae and in the lateral processes of the first six vertebrae. The *coccygeosacralis* arises from the anterior lateral surface of the urostyle and is inserted in the neural arch and transverse process of the last vertebra. The *coccygeoiliacus* arises from nearly the entire length of the urostyle, and is inserted in the anterior two-thirds of the ilium. The *obliquus externus*, a portion of which may be seen in the dorsal view, has its origin in the scapula and the dorsal fascia, and its insertion on the xiphisternum and in the rectus abdominis on the ventral surface of the body.

Muscles of the Thigh, Ventral Side.—The *sartorius*, a long thin muscle traversing the midventral region of the thigh, arises from the posterior end of the ilium and is inserted in the head of the tibia, just beyond the knee joint. Its contraction pulls

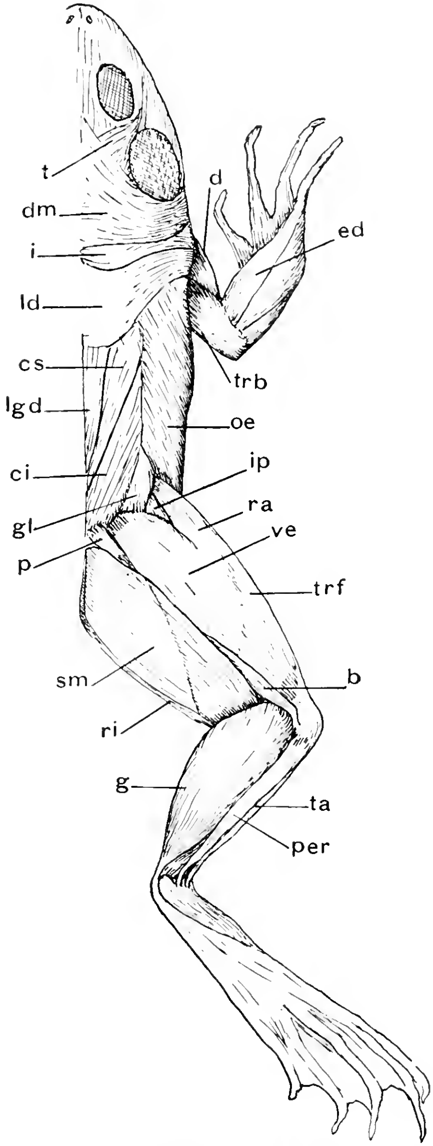


FIG. 48.—Muscles of *Rana catesbeiana*, dorsal side. *b*, biceps; ci, coccygeo-iliacus; cs, coccygeosacralis; d, deltoideus; dm, depressor maxillae; ed, extensor digitorum; g, gastrocnemius; gl, gluteus; i, infraspinatus; ip, iliopsoas; ld, latissimus dorsi; lgd, longissimus dorsi; oe, obliquus externus; p, pyriformis; per, peroneus; ra, rectus femoris anticus; ri, rectus internus minor; sm, semimembranosus; t, temporalis; ta, tibialis anticus; trb, triceps brachii; trf, triceps femoris; ve, vastus externus.

the hindlimb forward in a ventral direction. The *rectus internus major* (*gracilis major*) is a large muscle occupying most of the inner half of the ventral surface of the thigh, marked by an oblique tendinous insertion across its middle. It arises from the posterior border of the ischium and is inserted at two points in the head of the tibiofibula. Its contraction draws the thigh backward and may flex or extend the crus, depending upon the degree of bend in the knee joint at the time of contraction. Thus, if the crus is partially extended, contraction of the rectus major internus will extend it still more. If the crus is at an angle of less than a right angle, contraction of the muscle will flex the crus. The *rectus internus minor* (*gracilis minor*) is a long narrow muscle at the inner edge of rectus internus major, having its origin in the ischium and its insertion in one of the tendons of the rectus internus major. The actions of the two internal recti muscles are similar (Fig. 47).

Between the sartorius and the rectus internus major a portion of the *adductor magnus* can be seen (left side of Fig. 47). If the sartorius and rectus muscles are removed, the adductor magnus is fully exposed (right side of Fig. 47). Just distal to its origin in a tendon attached to the pubis and ischium, this muscle divides into two parts, between which passes the tendon of one of the heads of the *semitendinosus* muscle. Distally the two parts of the adductor magnus reunite and join with a small slip from the semitendinosus. The adductor magnus is inserted in the distal end of the femur and it acts either as an abductor or adductor, depending upon the position of the thigh at the beginning of contraction. If the centers of its origin and insertion lie in a line behind the head of the femur, contraction of the muscle adducts the thigh, *i.e.*, draws it back to the mid-line. If this line lies in front of the head of the femur, contraction draws the thigh forward, *i.e.*, away from the mid-line, and ventrally. The *semitendinosus*, located to the inner side of the adductor magnus, arises by two distinct heads from the pubis, the anterior head dividing the adductor magnus near the head of the latter. Its insertion is a tendon which, with that of the sartorius, forms a connective tissue arch joined with the fascia of the crus, beneath which the tendons of the internal recti muscles pass.

The *adductor longus* arises from the ventral part of the ilium and is inserted with the adductor magnus in the middle of the femur. Between the upper ends of the adductor longus and the adductor magnus can be seen two small muscles, the *adductor brevis* and the *pectineus*, both of which originate in the pubis and are inserted in the proximal half of the femur.

Muscles of the Thigh, Dorsal Side.—The *vastus externus* which can be seen at the outer surface of the thigh in the ventral view, is a part of the triceps femoris which can be better understood from the dorsal view (Fig. 48). The *triceps femoris* forms the front of the thigh and arises by three heads: (1) the *vastus internus*, from the outer covering of the acetabulum at the junction of the ischium and pubis; (2) the *rectus femoris anticus*, from the ventral side of the middle of the ilium; and (3) the *vastus externus*, from the crest of the ilium. The fibers of the rectus femoris anticus join those of the other two components at the middle of the thigh, forming a single muscle that is inserted by a single tendon passing over the knee joint to the proximal end of the tibiofibula. Its action extends the crus and pulls the whole leg forward. The *semimembranosus* is a large muscle occupying the inner half of the dorsal surface of the thigh, arising from the posterior margin of the ilium and, passing under an arch formed by the tendon of origin of the gastrocnemius muscle, ends in a tendon inserted on the dorsal surface of the tibiofibula. It is divided obliquely into anterior and posterior halves by a tendinous insertion. This muscle adducts the thigh and may extend or flex the crus, depending upon whether the crus is in an extended or flexed position when the muscle contracts.

The *pyriformis* is a narrow muscle originating at the tip of the urostyle and is inserted on the inner surface of the femur. The *iliopsoas* extends from the ilium to the outer surface of the femur. The *gluteus* arises from the posterior two-thirds of the ilium and is inserted on the femur near the head. The *biceps* or *iliofibularis* can be seen near the lower ends of the semimembranosus and the vastus externus. Its tendon of origin passes from the ilium between the pyriformis and the iliopsoas, under and behind the origin of the vastus externus. It has two points of insertion: one on the inner surface of the femur and the other on the dorsal surface of the femur and on the tibiofibula.

Muscles of the Crus.—The *gastrocnemius* muscle forms the calf of the leg or crus. One of its two heads arises from a tendinous arch extending from the femur to the tibiofibula and the other from the tendon of the triceps. It terminates in a strong tendon, the *tendo Achillis*, which after passing over the ankle joint spreads out in a connective tissue sheet over the plantar surface of the foot. Its contraction flexes the crus and extends the foot. The *tibialis anticus* (Fig. 47) lying at the front of the leg, originates on the distal end of the femur, its ligament passing

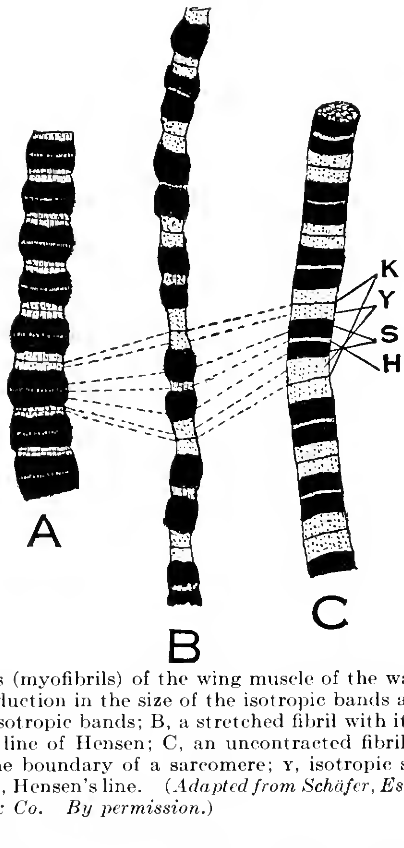


Fig. 49.—Fibrils (myofibrils) of the wing muscle of the wasp. A, contracted fibril showing a reduction in the size of the isotropic bands and a corresponding increase in the anisotropic bands; B, a stretched fibril with its anisotropic bands constricted at the line of Hensen; C, an uncontracted fibril. K, membrane of Krause forming the boundary of a sarcomere; Y, isotropic substance; S, anisotropic substance; H, Hensen's line. (*Adapted from Schäfer, Essentials of Histology, Longmans, Green & Co. By permission.*)

beneath the tendon of the triceps. This muscle divides at about the middle of the leg, the inner half being inserted on the astragalus and the outer half on the calcaneum. It extends the foot and flexes the tarsus. The *peroneus* muscle, seen in a dorsal view of the leg (Fig. 48) between the tibalis anticus and the gastrocnemius, originates in a tendon attached to the distal end of the femur and ligaments of the knee joint; it is inserted in the end of the tibiofibula and in the calcaneum. It extends the leg and may either flex or extend the foot. The *extensor cruris*, seen in the ventral view of the leg, arises from the inner condyle of the femur and is inserted on the outer (anterior) surface of the tibiofibula. It extends the leg. The *tibialis posticus* lies between the gastrocnemius and the tibiofibula. It arises from the entire length of the tibiofibula and is inserted on the astragalus. It flexes or extends the foot (Fig. 47).

Histology of Skeletal Muscle.—A skeletal muscle is made up of numerous muscle *fibers*, separated from one another by thin sheets of connective tissue, continuous with connective tissue enveloping the muscle. The muscle fiber may be regarded as an elongated cell, tapered at the ends, and containing many nuclei. A vertebrate muscle fiber may be $\frac{1}{2}$ in. or more in length. Sometimes, as in the frog's tongue, the fibers are branched. In mammals the nuclei occupy a peripheral position in the fiber, directly inside of the *sarcolemma*, except toward the ends where they may be centrally located. The sarcolemma is the wall of the fiber. In the frog the nuclei are scattered through the fiber. The cytoplasm of the muscle fiber contains numerous striated *myofibrils*, or *sarcostyles*, occurring in groups known as *muscle columns*, so arranged that the dark parts of one fibril are opposite those of adjacent fibrils, with the result that the muscle fiber as a whole has a striated appearance. For this reason skeletal muscle is sometimes called *striated* or striped muscle. The muscle columns are separated from each other by clear *sarcoplasm*. A clear hyaline material also separates individual myofibrils. The structure of a myofibril is shown in Fig. 49. Under polarized light, the dark bands are *anisotropic* (doubly refractive) and the light bands are *isotropic* (singly refractive). Each anisotropic band is crossed by a median membrane, *Hensen's line*. In the same way each isotropic band is divided by *Krause's membrane*. Krause's membrane is thought to be a continuous membrane extending from one myofibril to another, dividing the muscle fiber into disklike segments called

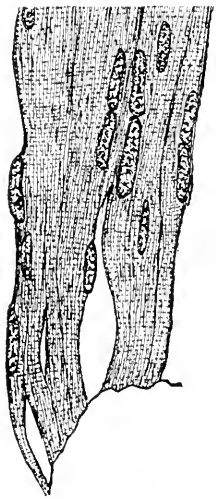


Fig. 50.—Section of skeletal muscle of larval salamander.

sarcomeres. Thus a single sarcomere would include the parts of each myofibril, within two adjacent membranes of Krause, lying at the same level. Usually, however, the longitudinal cohesion is greater than the lateral with the result that some striated muscle fibers cannot be made to cleave transversely into disks. Figure 50 illustrates the appearance of a longitudinal section of skeletal muscle of a larval salamander.

Action of Skeletal Muscle.—Skeletal muscle is voluntary in its action, *i.e.*, its action is under the control of the central nervous system, the brain and spinal cord. This is in sharp contrast to the involuntary activity of the *plain* or *unstriated* muscle cells of the walls of the alimentary tract and blood vessels. *Cardiac* muscle, though striated, is also involuntary in its action.

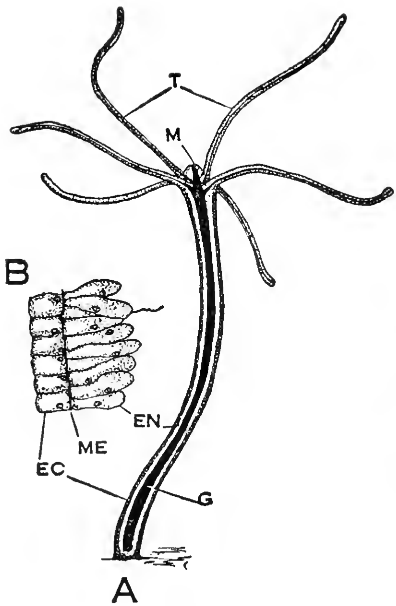
CHAPTER V

ALIMENTATION

The energy-producing substances of an animal's diet consist of chemically complex compounds, *viz.*, proteins, carbohydrates, and fats, each of which undergoes digestion before being absorbed. Water, simple sugars, and some inorganic salts, such as sodium chloride, taken with food do not require digestion. In the higher forms, the organs of digestion include, in addition to the alimentary canal in which digestion and absorption take place, a number of glands, such as the oral (salivary) glands, the pancreas, and the liver, though the last in vertebrates does not produce a digestive enzyme.

Gastrovascular Cavity.—A simple kind of alimentary tract is that of the common *Hydra*, a tube-shaped animal found in fresh water, its length in different species varying from 2 to 60 mm. The closed end of the tubular body is attached by a basal disk to the substratum, which is usually a plant; the opposite free end is open and serves as a mouth. The mouth is surrounded by from six to ten long, narrow, tubular tentacles. The body wall consists of two well-defined cellular layers, an outer *ectoderm* and an inner *endoderm*, with some indication of a third layer between them. The third layer, known as the mesoglea, is noncellular and of jellylike consistency. Since only two embryonic germ layers, the ectoderm and endoderm, are developed, the animal is said to be *diploblastic*. Each tentacle likewise consists of an inner layer of endoderm and an outer layer of ectoderm. The cavity of the tube, the *gastrovascular cavity*, is the digestive cavity (Fig. 51).

Food captured by the tentacles passes through the mouth into the gastrovascular cavity, where it is acted upon by a secretion of the cells lining the cavity. Some of the food is digested in this way; and some of it apparently is engulfed by the endodermal cells to undergo *intracellular* digestion. The products of *extracellular* digestion are absorbed by the endoderm and any undigested remains are cast out through the mouth. From the endoderm, absorbed food is distributed to the ectoderm by cell-to-cell transfer. The simple digestive tube of Hydra may be regarded as an early step in the evolution of the digestive tract of



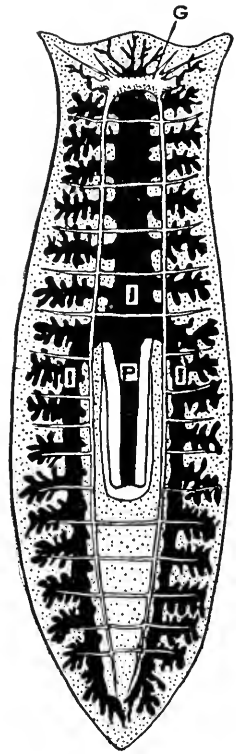


Fig. 51. Fig. 52.

Fig. 51.—A, *Hydra*, expanded, diagrammatic; B, longitudinal section of body wall. ec, ectoderm; en, endoderm; g, gastrovascular cavity, shown in black; me, mesoglea; m, mouth; t, tentacles.

Fig. 52.—Digestive and nervous system of a flatworm, *Euplanaria;* the digestive system shown in solid black. g, ganglionic mass; i, intestine; p, pharynx.

higher forms. A more complete description of the histology of the hydra is given on page 389.

The flatworm, *Euplanaria*, may be utilized to illustrate a modification of the same type of canal (Fig. 52). This animal is also a fresh-water form, of common occurrence in ponds. Its body measures about 12 mm. in length, and in shape it is flattened and elongated, being blunt at its anterior end and pointed posteriorly. A ciliated layer of ectoderm covers the outside, and an inner layer of endoderm lines an alimentary tract. Between the two are muscle tissue and other organs derived from a third germ layer, the *mesoderm*. Euplanaria is, therefore, *triploblastic*. The opening into the alimentary tract is on the ventral surface of the body near the middle through which a muscular tube, the *pharynx*, can be thrust like a proboscis. Inside the body the pharynx connects with an *intestine* consisting of three main trunks, one forward and two backward, from each of which numerous smaller branches, ending blindly, penetrate among the tissues. Digestion, both intracellular and extracellular, takes place in the intestine, which also serves to distribute the products to the tissues by means of its collateral branches.

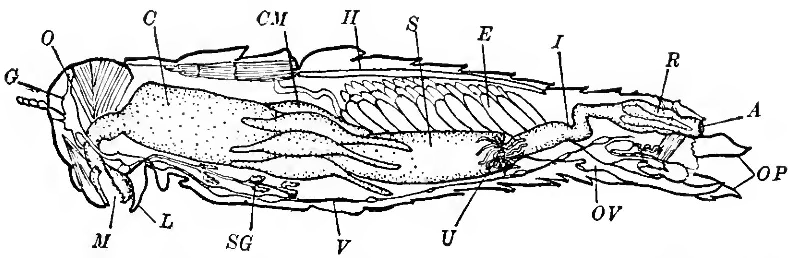


FIG. 53.—Internal anatomy of a grasshopper. *A*, anus; *C*, crop; *CM*, caecum; *E*, eggs; *G*, supresophageal ganglion; *H*, heart; *I*, intestine; *L*, labium; *M*, mouth; *O*, esophagus; *OP*, ovipositor; *OV*, oviduct; *R*, rectum; *S*, stomach; *SG*, salivary gland; *U*, Malpighian tubules; *V*, ventral nerve cord. (*After Packard, Textbook of Entomology.*)

Complete Alimentary Canal.—The digestive organs of an insect like the grasshopper display a considerable advance in complexity over the preceding forms, and have many features in common with the vertebrate type of system. The alimentary canal of the grasshopper is a tube open at both ends, beginning with a *mouth* and terminating in an *anus;* a type that is known as a complete alimentary canal (Fig. 53). The tube lies in a cavity of the body, the *hemocoel*, which is filled with blood. The mouth is provided with organs of mastication: a *labrum*, or upper lip; a *labium* or lower lip; and between them a pair of *mandibles* and a pair of *maxillae*. The mandibles are the principal chewing organs, and both they and the maxillae operate by a side-to-side movement, instead of up and down as with the jaws of man. The maxillae aid the lips in manipulating the food so that it can be chewed by the mandibles. The mouth leads to a narrow *esophagus* extending dorsally to about the center of the head, where it turns posteriorly to dilate into the *crop*. The latter is lined with a cuticular membrane armed with toothlike projections for completing the process of mastication begun in the mouth. Alongside the crop are branched salivary glands whose ducts run forward to empty into the mouth. Next comes the *stomach* surrounded by a set of six to eight double cone-shaped pouches, known as *caeca*, which secrete a digestive fluid. The posterior limit of the stomach is marked by a large number of *Malpighian tubules*, excretory in function, which enter the digestive tube at the junction of the stomach with the *intestine*. The latter passes back to terminate at the tip of the abdomen in an anal opening. The *rectum* is an enlargement in the intestine near the anus where fecal matter accumulates until excreted.

Digestion and absorption in the grasshopper take place in the stomach and intestine, whence the products of digestion pass into the body fluid filling the hemocoel. The body fluid and the blood in insects is the same, and is pumped by the heart to all parts of the body, supplying the tissues in this way with nutrition and at the same time ridding them of the waste products of metabolism. Undigested food and excretory products are expelled through the anus.

Vertebrate Alimentary System.—The alimentary canal of vertebrates begins with a mouth, opening into an oral cavity, continues as a tube, regionally differentiated, and terminates in a rectum that opens into a cloaca, as in the frog, or directly to the outside, as in the majority of mammals.

Oral Cavity.—The lining of the oral cavity as well as part of the rectum is ectodermal in origin, *i.e.*, it is derived from the primitive outer covering of the vertebrate embryo. The lining of the remainder of the alimentary canal is formed of endoderm, which for the present may be described as an internal germ layer. Briefly, the oral cavity develops as an invagination of the head ectoderm, producing an indentation, that deepens until it comes in contact with the wall of the pharynx. The ectoderm of the oral cavity fuses with the endoderm of the pharynx, after which the fused layers break down to form a passageway. The posterior opening of the alimentary canal is formed in a similar way. From this it follows that the lining of the oral cavity differs in its embryological origin from the lining of the pharynx, though in the frog or in the adult of any air-breathing vertebrate it is impossible to establish any sharp histological difference at the line of fusion of ectoderm and endoderm. In fishes the pharyngeal region is definitely distinguished from the oral cavity because it is provided with gill clefts and gills. In the frog gill clefts are present in the embryo and tadpole, but all of them except the first disappear during metamorphosis. Since the persisting first gill cleft is converted into the cavity of the middle ear, connecting with the pharynx by the Eustachian tube, the location of the opening of the Eustachian tube gives a rough idea of the anterior limit of the pharynx. Otherwise in the frog and in all higher vertebrates there is no simple way of establishing the line of demarcation between the oral cavity and pharynx. The oral cavity may be provided with teeth, a tongue and the openings of oral glands.

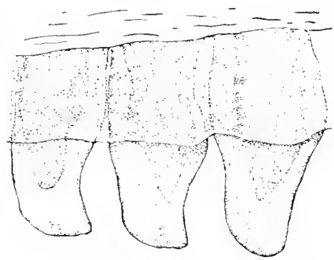


Fig. 54.—Maxillary teeth of *Rana pipiens*, shown in normal position, attached above to bone, below which transparent gum tissue is shown.

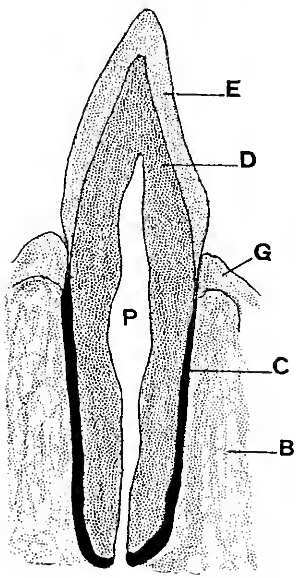


Fig. 55.—Diagrammatic longitudinal section of human tooth. B, bone of jaw; C, cement; D, dentine; E, enamel; G, gum; P, pulp cavity.

Teeth.—True teeth, such as human teeth, are hard bony structures found in the oral cavity of most vertebrates, notable exceptions being birds and some reptiles (turtles). The teeth of the frog consist of a single row attached to the inner edge of the premaxillary and maxillary bones of the upper jaw and a small group in the ventral surface of each vomerine bone. The tooth consists of a conical bony core of *dentine*, whose root is attached to the bone of the jaw by a *cement substance* and whose exposed crown is covered with *enamel* thickened at the apex (Fig. 54). The enamel in turn is covered with the *cuticula dentis*, a colorless membrane, highly resistant to the action of chemical reagents. The *pulp cavity* is a space in the dentine, open at the base of the root, and filled with blood vessels and *odontoblasts* (cells that produce dentine). Human teeth have the same general structure except that a cuticula dentis is absent, and the enamel is more evenly distributed over the entire crown (Fig. 55). The pulp also contains nerve endings. Each human tooth is inserted in a socket or *alveolus*, the dentine of the root of the tooth

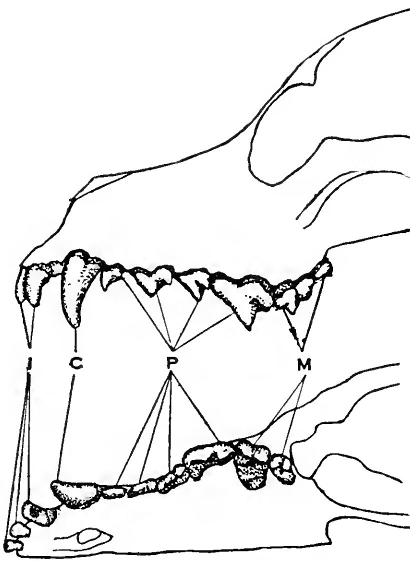


FIG. 56.—Upper teeth of the dog. C, canine; I, incisor; P, premolar; M, molar. The carnasial or flesh-cutting tooth is the fourth premolar.

being attached to the bone of the jaw by a cement substance. The dentine of the vertebrate tooth is formed of mesoderm, the same embryonic germ layer that gives rise to bones, while the enamel is a secretion of ectodermal cells of the oral cavity.

The vertebrate tooth evolved apparently from what is known as a *placoid scale*, such as is found in the skin and in a modified form, in margins of the jaws of the Elasmobranchii (sharks). The placoid scale consists of a curved spine projecting from the outer surface of a flattened base of dentine embedded in the skin (Fig. 25). The spine, which extends beyond the surface of the skin is covered with an enamel-like substance of ectodermal origin and is also provided with a pulplike cavity, open below. Near the jaws in sharks the scales pass by gradations into the teeth. Presumably teeth originated as placoid scales covering the surface of the body as well as the margins of the jaws, a condition that has persisted in sharks, accompanied by a certain amount of specialization in the jaw scales; while in higher forms the scales

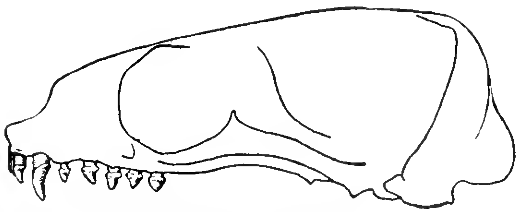


Fig. 57.—Side-view of the upper teeth of the sea-lion showing the peg-like character of all of them.

have become purely oral structures that have gradually taken on the form of typical vertebrate teeth.

Primitive vertebrate teeth, if one is to judge from their structure and from the manner in which they are used by the shark, were *prehensile* in function. That is to say, they were used for grasping, tearing and holding, and not for chewing. In the case of the frog the teeth are poorly adapted for anything but holding. The similarity in form and structure of the frog's teeth illustrates

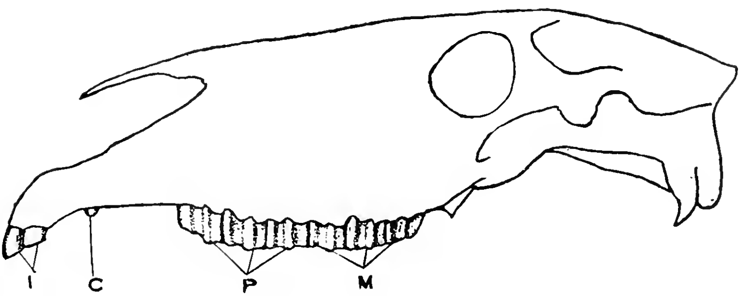


Fig. 58.—Side view of the upper teeth of the horse, *i*, incisors; *c*, canine; *p*, premolars; *m*, molars.

what is known as *homodont* dentition. The teeth of mammals, on the other hand, are with few exceptions *heterodont*, and may be differentiated or specialized in four ways: (1) as *incisors*, located at the front of the jaws and used for cutting or grasping; (2) as *canines* for grasping or tearing; (3) as *premolars* for shearing; or (4) as *molars* for grinding (Figs. 56, 57 and 58).

Mammals belonging to the order *Carnivora* have strong, recurved canine teeth, poorly developed incisors, and high crowned premolars and molars. In such animals the jaws have practically no side play, a condition which reaches its highest development in cats, in which the cheek teeth have a purely shearing action on food. In dogs, the premolars are shearing teeth, but the molars are adapted for grinding or crushing (Fig. 56). Omnivorous bears, such as the common black bear, lack shearing teeth but do have well-developed grinders. Carrion-

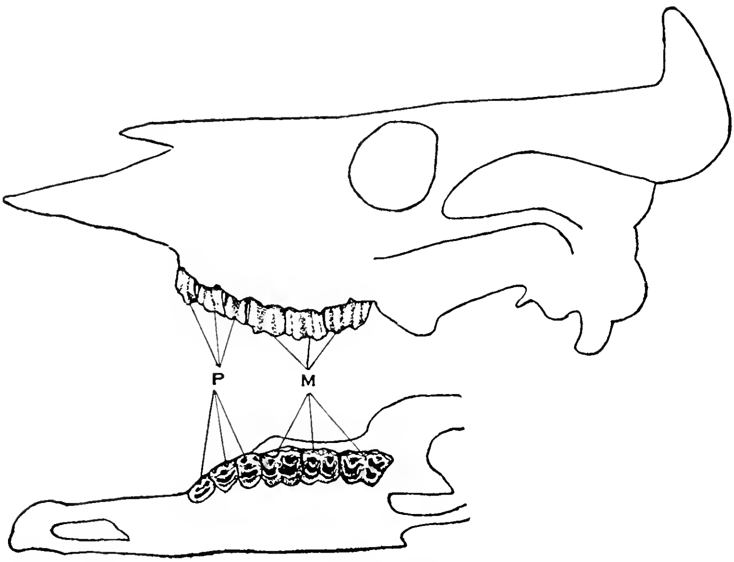


Fig. 59.—Side and ventral view of the upper teeth of the ox. P, premolars; M, molars.

eating forms have blunter teeth, while fish eaters such as the seal have teeth that are all pointed and prehensile in function (Fig. 57).

Some of the plant-eating animals belonging to the *Ungulata*, hoofed animals, illustrate a high degree of specialization which contrasts strongly with the conditions found in the teeth of typical Carnivora. Incisors may be present in both jaws and adapted for seizing or cutting as in the horse; but in ruminants, such as the ox, they are absent in the upper jaw, which, instead of teeth, is provided with a tough pad against which the incisors of the lower jaw bite (Fig. 59). The tusks of the elephant are highly modified incisors. Canine teeth as a rule are not well developed among ungulates unless used for defense or for digging as in swine. The premolars and molars of the ox represent a typical condition in which these teeth are adapted solely for grinding. In such animals the jaw is articulated so as to permit considerable side play, a motion that is familiar to anyone who has watched a cow chewing its cud.

Human teeth of the permanent dentition consist of four incisors, two canines, four premolars and six molars in each jaw. The incisors are spade-shaped with a cutting edge and occupy the front of the jaws. The canines are conical and bluntly pointed. The premolars and molars have flattened but not smooth biting surfaces that are adapted for grinding. Human teeth are adapted for an omnivorous diet.

Tongue.—The tongue of fishes is simply a fold in the floor of the mouth incapable of movement since it has no intrinsic muscles. In some fishes it bears teeth. Above fishes the tongue becomes a muscular organ appearing in a wide variety of morphological forms. The frog's tongue is attached at the margin of the lower jaw and its free end when at rest is folded back on the floor of the mouth. It is used in capturing food. In snakes the tongue is used as a tactile sense organ. The tongue of mammals, whales excepted, is a highly muscular organ capable of a variety of movements. Its dorsal surface may, as in cats, develop cornified, filiform *papillae* producing a rasping surface. The tongue also may contain *mucous glands* and at its posterior end, *gustatory* organs.

Oral Glands.—Glands are lacking in the oral cavity of most aquatic vertebrates. In air-breathing vertebrates glands are present in a variety of forms. Such glands produce a secretion that is poured into the oral cavity by means of ducts leading from the glands. The principal oral glands of the frogs are the *intermaxillary* glands, located chiefly between the premaxillary bones and the nasal capsule and opening in the fore part of the roof of the mouth by about 25 ducts. The secretion of this gland gives the tongue its adhesive properties.

The lining of the oral cavity consists of a ciliated columnar epithelium, containing *goblet* cells, which produce a mucous secretion.

Mammals, in addition to numerous mucous glands located in the oral epithelium, are provided with three kinds of salivary glands, *viz.*, the *parotid*, the *sublingual*, and the *submaxillary* glands (Fig. 60). The parotid gland lies beneath the skin of the side of the head near the ear and its duct (Stenson's duct) enters the oral cavity by piercing the cheek near the molars of the upper jaw. The sublingual gland lies between the tongue and the margin of the lower jaw and opens by several ducts in the floor of the oral cavity. The submaxillary gland lies inside the lower jaw and its duct (Wharton's duct) has its outlet near the lower incisor teeth. All of these glands are paired.

The secretions of the salivary glands vary. In man the submaxillary and sublingual glands produce most of the *mucin*, the substance that gives saliva its ropy, mucilaginous character; whereas the secretion of the parotid is more watery and contains *ptyalin* in larger amounts than the other two. Ptyalin is a digestive enzyme that acts upon starchy food.

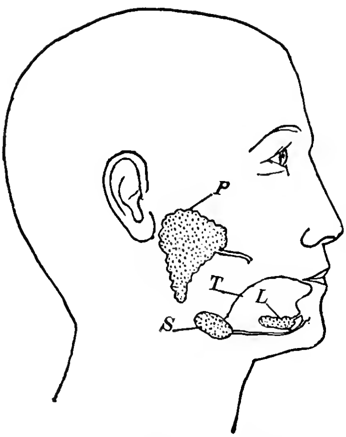


FIG. 60.—Diagram showing location of the salivary glands in Man. L, sublingual; S, submaxillary; P, parotid; T, tongue.

Pharynx.—The pharynx, so far as alimentation is concerned, is merely a passage connecting the oral cavity with the esophagus. Its importance is in connection with respiration, discussed in the following chapter.

Esophagus.—The esophagus is for the most part a tube connecting the pharynx with the cardiac end of the stomach. In the frog it is neither sharply marked off from the pharynx in front nor from the stomach behind. A cross section of the frog's esophagus shows the four layers that are typical of the wall of the vertebrate alimentary tract. These layers, beginning at the outside, are (1) *serous membrane* or *visceral peritoneum;* (2) the *tunica muscularis*, consisting of an outer longitudinal layer and inner circular layer of plain muscle, the longitudinal layer thinning out in the stomach region; (3) the *submucosa*, composed of connective tissue, nerves, blood and lymphatic vessels; and (4) the *mucosa*, an epithelium, supported by connective tissue (Fig. 61). Between the submucosa and mucosa of the stomach and intestine there is another muscular layer, the *muscularis mucosae*, which is composed of an inner circular and an outer longitudinal layer. Both are very thin. The inner surface of the esophagus is thrown into longitudinal folds. The mucosa consists of columnar goblet cells among which ciliated cells are found similar to those lining the oral cavity. The frog's esophagus is provided with tubular glands that secrete pepsin, which, however, does not function until it reaches the stomach.

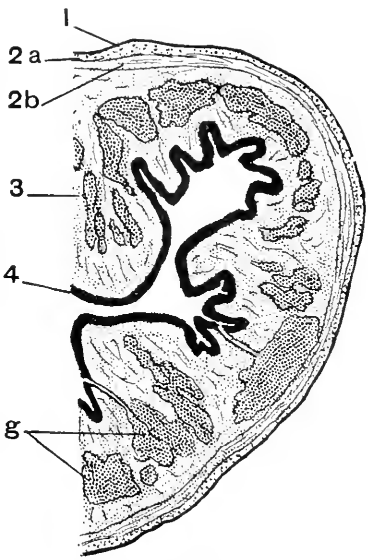


Fig. 61.—Diagrammatic cross section of half of lower esophagus of *Rana pipiens*. 1, serous membrane or visceral peritoneum; 2a, longitudinal muscle; 2b, circular muscle; 3, submucosa; 4, mucosa; g, glands.

The muscle tissue found in the walls of the vertebrate alimentary tract and also in the walls of blood vessels consists of mononucleated, spindle-shaped cells (Fig. 62), without the striations found in skeletal and cardiac muscle. It is known as plain or nonstriated muscle and, as already noted, is involuntary in its action.

The innervation of the esophagus as well as of the remainder of the alimentary tract is from branches of the *sympathetic* nervous system and the *vagus* nerve, that penetrate the tunica muscularis to form the *myenteric plexus* between the two layers of muscle and the *submucosal plexus* in the submucosa.

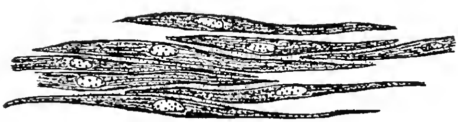


Fig. 62.—Plain muscle cells of the muscularis layer of intestine of *Rana pipiens*.

The crop or *ingluvies* of birds is a differentiated, saclike expansion on one side of the esophagus serving as a receptale for food. Sometimes its wall forms a secretion that moistens the food or starts its digestion. In pigeons the crop, consisting of a

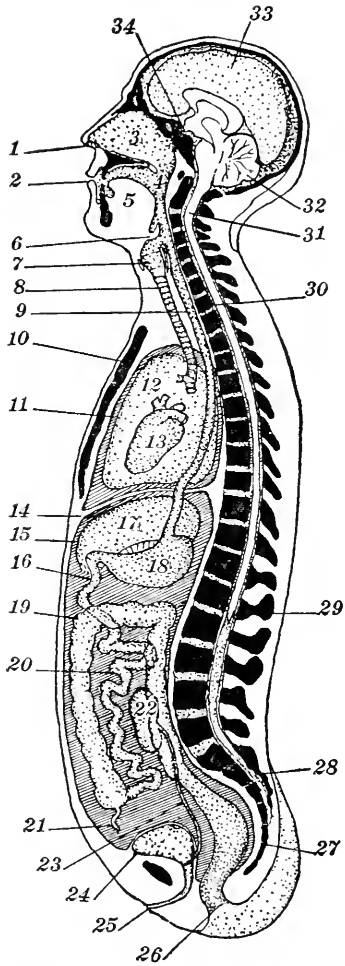


FIG. 63.—Median section of the human body showing the alimentary canal and other viscera diagrammatically disposed; bone is shown in solid black. 1, external nares; 2, mouth; 3, nasal passage; 4, pharynx; 5, tongue; 6, epiglottis; 7, larynx; 8, trachea; 9, esophagus; 10, sternum; 11, pleural cavity; 12, lung; 13, heart; 14, diaphragm; 15, abdominal cavity; 16, duodenum; 17, liver; 18, stomach; 19, large intestine; 20, jejuno-ileum; 21, vermiform appendix; 22, kidney; 23, ureter; 24, bladder; 25, urethra; 26, anus, 27, coccyx; 28, sacrum; 29, neural spine of first lumbar vertebra; 30, centrum of first thoracic vertebra; 31, spinal cord; 32, cerebellum; 33, cerebrum; 34, pituitary body.

median and two lateral pouches, produces during breeding season a thick fluid, called pigeon's milk, that is fed to the young.

The human esophagus is a tube of uniform diameter lined with a stratified epithelium which receives the openings of two types of glands, producing secretions having the properties of mucin and serving apparently for lubrication. The esophagus joins the stomach at the cardiac aperture (Fig. 63).

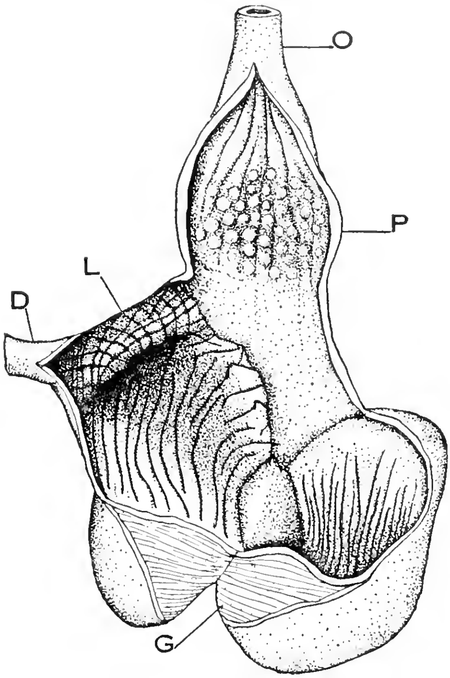


FIG. 64.—Stomach region of the domestic fowl, cut open. D, duodenum; G, gizzard, showing thickness of muscular wall; L, cornified lining of gizzard; deeply creased; O, esophagus; P, proventriculus, showing rounded elevations of its soft glandular lining.

Stomach.—The stomach of fishes and lower vertebrates is generally little more than a dilatation in the digestive tract, serving as a food reservoir in which a certain amount of digestion may take place. The stomach of the frog is widest at its anterior (cardiac) end, where it bends slightly to the left and then continues to the right in almost a straight line to the narrow pyloric end. Its union with the duodenum, at the pylorus, is marked by a well-defined constriction, where the circular layer of the muscularis is well developed. The mucosa receives the openings of tubular glands of two general types, cardiac and pyloric, of which the cardiac glands possess the greater number of *granular* cells. Experiments indicate that the pepsin content of the stomach wall is greatest in the cardiac portion, from which it is inferred that the pepsin is formed by the granular cells. Hydrochloric acid is produced in the stomach and gives its contents an acid reaction.

In a bird such as the domestic fowl the stomach consists of two distinct regions: an anterior glandular part, the *proventriculus*, and a highly muscular posterior part, the *gizzard* (Fig. 64). The glands of the proventriculus produce a digestive

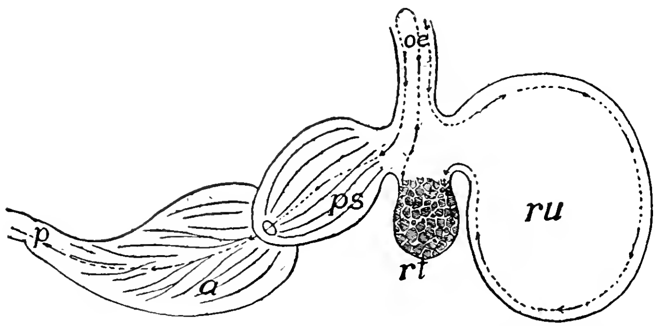


Fig. 65.—Diagram of ruminant stomach, the dotted line showing the course of the food. *a*, abomasum; *oe*, esophagus; *p*, pylorus; *ps*, psalterium (omasum, manyplies); *rt*, reticulum (honeycomb); *ru*, rumen (paunch). (*From Kingsley, Comparative Anatomy of Vertebrates, P. Blakiston's Son and Company. By permission.*)

secretion that is mixed with the food before it enters the gizzard where it is ground up. In the absence of teeth the gizzard of grain-eating birds serves as an organ of mastication, to which end it is adapted by having thick muscular walls lined with a tough, horny membrane. The process of trituration is facilitated in such birds by small pebbles or other gritty material, swallowed with the food. The gizzard is less well developed in purely carnivorous birds, whose food is of a softer consistency.

The stomach of a ruminant, like the ox, also shows rather striking departures from the common type of vertebrate stomach. In this case the stomach region consists of four parts; (1) the *rumen* or *paunch;* (2) the *reticulum* or *honeycomb;* (3) the *psalterium;* and (4) the *abomasum.* Of these, the first two divisions seem to be modifications of the lower end of the esophagus in which food is stored. Thus in feeding, vegetation is cropped by the incisors of the lower jaw and swallowed unmasticated into the rumen and reticulum. When the animal stops grazing, it seeks a quiet spot and begins to chew its cud. In this process food is regurgitated in small amounts from the reticulum to the mouth and then thoroughly ground up by the premolar and molar teeth. When the masticated food is swallowed, it passes

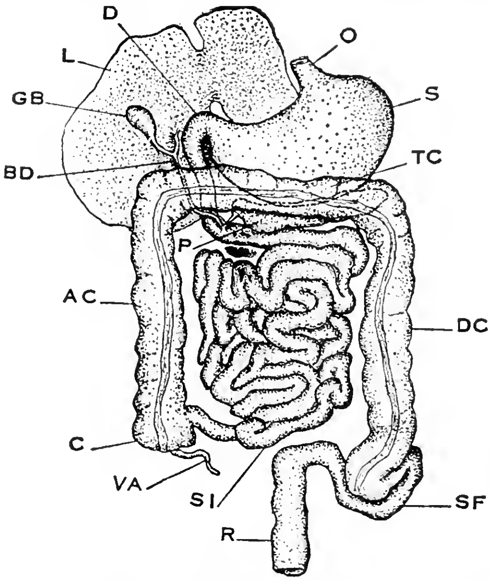


FIG. 66.—Human alimentary tract, diagrammatic. AC, ascending colon; BD, bile duct, extending from the liver to the duodenum; C, caecum; D, beginning of duodenum; DC, descending colon; GB, gall bladder; L, liver, turned up so as to show its under surface; O, end of esophagus; P, pancreas, whose duct connects with the duodenum near the end of the bile duct; R, rectum; S, stomach; SF, sigmoid flexure of descending colon; SI, small intestine; TC, transverse colon; VA, vermiform appendix.

into the psalterium and abomasum where it undergoes gastric digestion (Fig. 65).

The human stomach is sharply marked off from the esophagus at the cardiac orifice and from the intestine at the pylorus (Fig. 66). Between the cardiac and pyloric regions it is enlarged to form the fundus, which gives the stomach the shape of a pouch with a greater and lesser curvature. The actual shape of the human stomach varies considerably in different individuals and in the same individual at different times. When empty, its walls are collapsed and after a meal its outline is continually changed by waves of contraction, beginning at about the middle and extending to the pylorus. The epithelium of the mucosa consists of a single layer of cells, some of which are mucus-producing goblet cells. As in the frog, the surface of the mucosa is pitted with the mouths of glands whose epithelium is continuous with that of the surface. The glands of the fundus are believed to secrete pepsin and hydrochloric acid. No specific function is attached to the glands of the cardiac and pyloric regions.

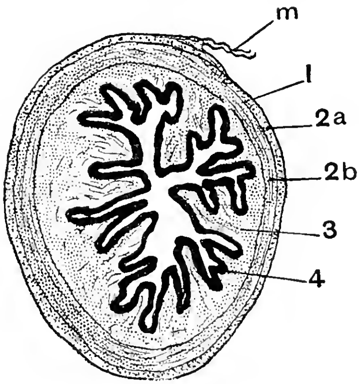


Fig. 67.—Diagrammatic cross section of the small intestine of *Rana pipiens*. 1, serous membrane or visceral peritoneum; 2a, longitudinal muscle; 2b, circular muscle; 3, submucosa; 4, mucosa; m, mesentery by which the intestine is attached to the body wall.

The tunica muscularis of the stomach is composed of a thin outer longitudinal layer and a thicker inner circular layer. What is sometimes referred to as a third and innermost layer, whose fibers run obliquely, is really a modification of a portion of the circular layer, resulting from the twisting of the stomach in the course of its development. At the pylorus the circular layer is enlarged to form a *sphincter* muscle which acts as a *pyloric valve.*

Intestine.—The superficial basis for the division of the intestine into large and small portions rests on a difference in diameter. More important differences are found in the function and structure of the mucosa of the two regions. The small intestine is primarily concerned with digestion and absorption, and the large intestine with absorption alone, principally the absorption of water. The *duodenum* is the first segment of the small intestine. In the frog it extends from the pylorus to the first bend in the intestine and receives the bile duct about midway. The distinction between the duodenum and the remainder of the small intestine, the ileum, or the jejuno-ileum, is largely based on histological structure. The liver and pancreas pour their secretions into the duodenum and these secretions play important parts in intestinal digestion. In the frog the bile duct collects the secretion of the pancreas and thus serves as a common bile and pancreatic duct. In the higher vertebrates the small intestine also produces digestive agents. This apparently is not true of the frog.

The mucosa of the small intestine of the frog is arranged in irregular folds, but there are no villi or tubular glands such as are found in mammals. The epithelium of the mucosa consists of columnar cells, some of which are goblet cells. The structure of the large intestine is much the same. In the rectum the folds of the mucosa are longitudinal (Fig. 67).

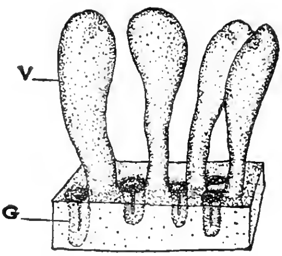


FIG. 68.—Diagram of surface of mucosa of small intestine of man. G, intestinal gland opening on the surface between the bases of the villi; V, villus.

In man the mucosa of both the large and small intestine is provided with numerous tubular glands. In the small intestine the mucosa between the mouths of the glands is raised in thin folds or finger-shaped processes called villi, which are important in absorbing the products of digestion (Fig. 68). A curious example of a simplification of a villus structure is seen in the spiral valve of the intestine of the dogfish (Fig. 69). This valve consists of a rather wide, thin, spiral fold of the mucosa which slows the movement of the contents of the intestine and also increases

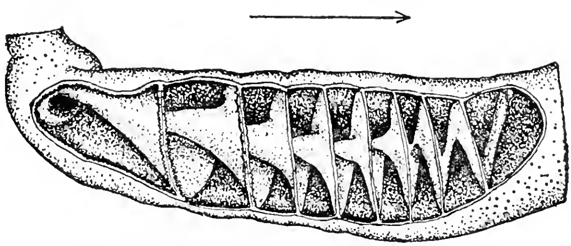


FIG. 69.—Spiral valve of *Raia*. The arrow indicates the direction in which the food passes. (*Modified after Mayer.*)

the absorbing surface of the relatively short intestine. In the higher vertebrates an increase in digestive capacity and absorbing area is achieved by an increase in the length of the intestine as well as by villiform elevations of the mucosa. Also, a correlation exists between the character of the food and the length of the intestine. The frog tadpole feeds on plants growing in the water and has an alimentary canal relatively and actually much longer than that of the adult frog, which is mainly carnivorous. The length of the alimentary canal of a ruminant mammal is from 20 to 28 times the length of the body while that of a meat-eating form is only five to six times the body length. This may be understood if it is remembered that plant eaters require a larger volume of food than carnivorous forms, because the bulkier vegetable food such as grass, hay, clover, etc., contains less nutriment and more of difficultly digestible material than an equal volume of meat.

The large intestine of the frog is simply the enlarged continuation of the small intestine. In mammals the small intestine joins the large intestine at right angles in such a way as to leave a blind end of the large intestine at one side of the union (Fig. 66). At this junction is a circular valve, the *ileocaecal valve.* The blind end of the large intestine, called the *caecum,* is highly variable in form and size, being best developed in herbivorous forms and least in carnivorous ones. Thus in the horse it measures about four feet in length and has a capacity of seven or eight gallons. In the cat it is practically absent. In man the caecum measures about $2\frac{1}{2}$ in. in length and $3\frac{1}{8}$ in. in width. The *vermiform appendix* is a diverticulum of the caecum about 3 in. long and about $\frac{1}{4}$ in. wide. The human large intestine is known as the *colon.* From its point of union with the small intestine in the lower right abdominal (pelvic) region, the colon passes anteriorly as the *ascending colon,* continues to the left beneath the anterior wall of the abdomen as the *transverse colon,* and then turns posteriorly as the *descending colon,* which takes an S-shaped turn, the *sigmoid flexure,* before joining the *rectum* which terminates at the *anus* (Fig. 66). The longitudinal layer of the tunica muscularis of the colon is arranged in three equidistant longitudinal flat bundles or bands between which the longitudinal layer is reduced to a thin sheet. These bands, known as *taeniae,* are shorter than the internal layers of the colon, and as a result, the colon is divided into pockets, called *haustra,* by transverse folds or *plicae semilunares.*

Liver.—The liver is a large gland whose duct, the *bile duct,* empties into the duodenum. The tributaries to the bile duct are the *bile capillaries,* which course between the liver cells and send lateral branches into the cells. *Bile* is a fluid secreted by the liver cells into the bile capillaries, which unite to form larger vessels leading to the bile duct. The *gall bladder* is a dilatation of the bile duct in which bile is stored. Bile consists of water, salts, pigment, bile acids, lipoidal substances such as cholesterin and lecithin, neutral fats and soaps, a nucleo-albumin, which gives bile a mucilaginous consistency, and traces of urea. It is partly excretory in nature but is also important in the digestion and absorption of fats. It has an alkaline reaction and is secreted continuously, and in those forms in which a gall bladder is present it is discharged intermittently into the duodenum. The liver, as already noted in an earlier chapter, in addition to secreting bile, performs other important functions in metabolism, such as the storage of sugar and the storage of fats, the production of urea and the formation of fibrinogen. In its development the liver is an outgrowth of the endoderm, forming the lining of the embryonic intestine. The liver is formed of the distal part of this outgrowth and the bile duct represents the proximal part.

Pancreas.—The pancreas is also a digestive gland. It contains two sorts of secretory cells: (1) *alveolar* cells, whose secretion is removed by ducts, and (2) *islet* cells having no connection with ducts and whose secretion is removed by the blood stream. The alveoli are spherical or tubular arrangements of cells surrounding a lumen, drained by the ducts. The epithelium of the ducts is simply the continuation of the glandular epithelium. The islet cells are isolated groups of cells scattered between alveoli at irregular intervals. The secretion produced by the alveolar cells is conveyed by ducts to one or more large trunks terminating in the duodenum at or near the mouth of the bile duct. In the frog the pancreatic ducts all open into the bile duct before the latter reaches the duodenum. In man the pancreatic duct joins the bile duct near the intestine, thus forming a short common hepatopancreatic duct, or there may be in a certain percentage of cases an additional pancreatic outlet into the duodenum. The pancreatic fluid produced by the alveolar cells of the pancreas contains important digestive agents, or inactive forms of these agents, that act upon proteins, fats, and carbohydrates in the alimentary canal (Fig. 70).

Digestion.—The absorption of nutritive substances from the alimentary canal is preceded by a process of digestion which renders food soluble, since only liquids can pass through the wall of the alimentary canal into the blood or lymph streams. Liquefaction is produced by breaking down the complex organic food substances into simpler compounds; but a chemical transformation is also undergone by a soluble substance like cane sugar. The diet of a frog or man consists of organic and inorganic substances. Of the latter, water is the principal one taken alone. Inorganic salts are of course present in meat, milk, vegetables bread, etc., but we ordinarily think of these articles of food as organic in nature. Since in the process of digestion inorganic salts are released from organic combination and absorbed or

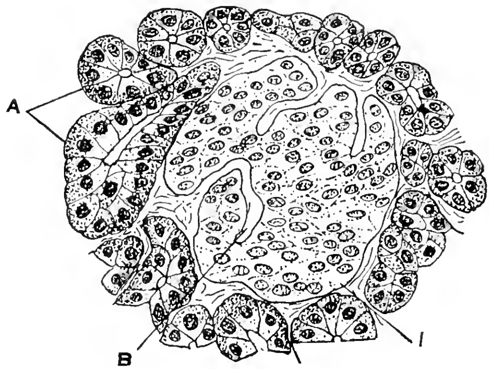


FIG. 70.—Section of an island of Langerhans surrounded by glandular alveoli of pancreas; diagrammatic. A, alveoli of glands drained by pancreatic duct; B, blood vessel; I, island of Langerhans (islet cells), having no connection with ducts. (*After Stöhr.*)

secreted without further change, digestion is primarily concerned with the changes undergone by the organic constituents of food. The organic foods, protein, carbohydrate, and fat, are distinctly different chemical substances, yet digestion in the case of each is brought about by the same sort of chemical process, known as *hydrolysis*, the essential feature of which is a preliminary union with water and a subsequent splitting of the combination into simpler products. An example of a relatively simple form of hydrolytic cleavage may be illustrated by the breaking down of a molecule of a polysaccharide, such as malt sugar, into two molecules of a monosaccharide, dextrose:

$$\underset{\text{malt sugar}}{C_{12}H_{22}O_{11}} + \underset{\text{water}}{H_2O} \rightarrow \underset{\text{dextrose}}{2C_6H_{12}O_6}$$

Digestion is not always completed by a single hydrolytic cleavage, the number of cleavages involved depending upon the composition of the food. What happens in the case of complex substances such as proteins, is a continuous separation of soluble fractions from a residue that becomes more and more soluble as its chemical composition is simplified, until the original complex molecule is converted entirely into simpler and more soluble molecules.

Enzymes.—The hydrolytic cleavages of foodstuffs in the alimentary canal are brought about by organic catalytic agents known as enzymes. A catalytic agent is a substance whose presence hastens chemical reaction. It does not initiate the reaction but greatly accelerates the rate of reaction. Thus, to use a common example, hydrogen and oxygen which do not combine in any appreciable degree at ordinary temperatures to form water, may be made to do so if exposed to spongy platinum. Since the catalytic agent, platinum, does not appear in the product of the reaction, a very small amount is capable of producing an infinite change. Similarly, digestive enzymes bring about changes in food without becoming a part of the product of digestion.

Enzymes are organic catalytic agents produced by cells from which they may be extracted by water, salt solutions, or by glycerin. From such an extract the enzyme may be obtained in a fairly pure state by precipitation with an excess of alcohol. The action of enzymes is destroyed by temperatures between 60 and 100°C. and greatly retarded by temperatures near 0°C. Enzymes are specific in their reaction; thus proteolytic enzymes act only on proteins, fat-splitting enzymes only on fat, etc. Enzymes are reversible in their reaction, the direction of the reaction being determined by whether or not the products of the reaction are removed. If the products are removed as rapidly as formed, the reaction may go to completion in one direction. This is what happens in all probability in the alimentary canal, where the products may be absorbed as soon as formed. If the products are allowed to accumulate, the reaction comes to equilibrium, under which conditions there is as much tendency for the reaction to go in one direction as the other, and thus, for all practical purposes, to come to a halt.

It has been shown that an enzyme may be secreted by the cell in an inactive form, to which the general term *zymogen* is applied.

Zymogen has been identified with certain granules in the cytoplasm of the cell producing it. To bring about its normal reaction, the zymogen must be activated by some agent encountered after it leaves the cell. Thus *trypsinogen*, the inactive form of trypsin, is a product of the pancreas that is converted into active trypsin by *enterokinase*, an organic substance secreted by the small intestine.

The enzymes concerned in the digestion of protein, starches, sugars, and fats all act by hydrolysis. Other kinds of enzymes are: (1) *coagulating* enzymes, such as the *rennin* of the stomach of young mammals, that produces the coagulation of casein in milk; (2) *oxidizing* enzymes, that bring about oxidizing processes in the body; and (3) *deaminizing* enzymes, that produce the separation of the NH_2 group from amino acids, of which an example is the formation of ammonia and lactic acid from alanine ($CH_3 \cdot CH(NH_2) \cdot COOH$).

Enzymes are sensitive to the hydrogen-ion content of the medium. Thus an enzyme normally acting in a neutral or alkaline medium becomes inactive in the presence of acid.

Digestive Enzymes.—The enzymes concerned in digestion and nutrition in the human body include the following:

1. *Proteolytic* enzymes, acting on proteins.

a. Pepsin, secreted by the glands of the stomach, acts in an acid medium; it converts proteins into peptones and proteoses. (In the frog pepsin is also secreted by the esophagus, but becomes active only after passing into the stomach.)

b. Trypsin, secreted in an inactive form as trypsinogen by the pancreas and activated by the enterokinase in the intestine; it acts in an alkaline, neutral, or slightly acid medium; converts proteins into polypeptides.

c. Erepsin, secreted principally by the mucosa of the small intestine and in small amounts by the pancreas. It also is found in the tissues generally. It acts in an alkaline or neutral medium and splits the products formed by pepsin and trypsin into amino acids. (In the frog no erepsin is produced by the small intestine.)

2. *Diastatic* enzymes, act on starches in an alkaline or neutral medium.

a. Ptyalin, secreted by the salivary glands, converts starch into sugar (maltose).

b. *Amylase*, secreted by the pancreas, converts starch into sugar (maltose). Ptyalin and amylase have a similar action on starch.

c. *Glycogenase*, produced in the liver, converts glycogen to dextrose. It is also found in muscle.

3. *Inverting* enzymes, secreted by the small intestine principally, act in an alkaline or neutral medium; they convert double sugars (disaccharides) into simple sugars (monosaccharides).

a. *Sucrase* secreted by the small intestine; converts cane sugar to dextrose and levulose.

b. *Maltase*, secreted by the small intestine, salivary glands, and pancreas, converts maltose to dextrose.

c. *Lactase*, secreted by the small intestine, converts lactose (milk sugar) into dextrose and galactose.

4. *Lipolytic* enzyme, acting on fat in an alkaline or neutral medium.

a. *Lipase*, secreted by the pancreas, acts in conjunction with bile to split neutral fats into fatty acids and glycerin, in the small intestine.

5. *Coagulating* enzyme.

a. *Rennin*, secreted by the stomach in an inactive form, *prorennin*, which is activated by the acid of the stomach, converts the casein of milk into an insoluble protein, the *curd*, which is then acted upon by pepsin.

Foodstuffs.—The useful constituents of food consist of the following foodstuffs: water, inorganic salts, proteins, fats, and carbohydrates. These substances are foods in the sense that they yield energy or serve as the raw material for the replacement of the losses involved in metabolism. The living state is accompanied by continuous physical and chemical changes in the cells of the body, as a result of which, energy, largely in the form of heat, is evolved along with carbon dioxide, water, inorganic salts, and other excretory products.

Calorimetry.—By means of a respiration calorimeter it is possible to demonstrate that the energy of heat and work is obtained from the potential energy of the food. The potential energy of foodstuffs can be determined by burning or oxidizing them in a calorimeter, which is an apparatus by means of which the heat liberated during oxidation may be accurately measured. Naturally only organic foodstuffs are involved in this consideration since the inorganic constituents of the diet are incapable of further oxidation. Organic foodstuffs contain potential energy in a chemical form in an amount equivalent to the amount of energy expended in the original synthesis of the foodstuff from simple elements, just as a bent spring possesses potential energy in proportion to the amount of work expended in bending it. If one end of the spring is released, it straightens out and in doing so its potential energy is converted into kinetic energy. In a similar way, when a complex organic substance, such as protein or carbohydrate, is oxidized, the complex spatial arrangement of the atoms in the molecule is destroyed in the formation of simpler molecules, in which process energy is released. Thus a molecule of carbohydrate possesses potential energy as long as the atoms of carbon, hydrogen, and oxygen maintain a certain structural and spatial relation to each other in the molecule. When this relation is disturbed by an oxidation process, the structure collapses, energy is liberated in the form of heat, and the carbon, hydrogen and oxygen emerge from the reaction as carbon dioxide and water.

The energy value of foods is measured in *calories*. A small calorie or *gram-calorie* is the amount of heat necessary to raise the temperature of 1 gm. of water 1°C. By means of the calorimeter it has been determined that, on the average, 1 gm. of fat yields 9,300 gram-calories, 1 gm. of carbohydrate 4,100 gram-calories, and 1 gm. of protein 5,778 gram-calories. Except for protein these values represent the actual energy values of these substances to the body. Owing to the fact that protein is not completely oxidized in the body (1 gm. of protein yielding ⅓ gm. of urea), to obtain the calorific value of 1 gm. of protein, it is necessary to subtract the energy value of ⅓ gm. of urea, which is 841 calories, from 5,778 calories, leaving 4,937 calories. Very likely this value is too high since all of the nitrogen of protein metabolism is not eliminated as urea. If allowance is made for nitrogen losses in forms other than urea, the actual calorific value of 1 gm. of protein is reduced to 4,100 gram-calories.

The energy requirements of a man can be determined by means of a respiration calorimeter. In its most complete and elaborate form the respiration calorimeter is a small room in which an individual may remain for long periods in comfort, and so arranged that the amount of oxygen consumed from the air supply can be determined as well as the quantity of carbon dioxide produced. It also permits the measurement of the amount of heat produced by the subject which, when supplemented by analysis of the urine and feces, gives the total carbon and nitrogen excretion along with the heat loss. Since the amount of protein, fat, and carbohydrate oxidized in the body may be determined from the carbon and nitrogen excretion, the amount of foodstuffs necessary to meet these requirements can be calculated; and since there is a close correspondence in the estimated and actual food requirements, a satisfactory proof is reached that the energy released as heat, or as heat and work, is derived from the potential energy of the food stuffs eaten.

The *basal metabolism* refers to the amount of heat produced when the body is at rest. On the average this amounts to about 1,600 calories for a man and about 1,400 calories for a woman, during a 24-hour period. If the subject in the calorimeter performs active work on a bicycle ergometer, the total energy produced as heat and muscular work may be increased to over 5,000 calories. The dietary requirements vary in proportion to the total energy requirements.

Foods.—Animals use food closely allied in chemical composition to animal tissues. Foodstuffs, except water, cane sugar, and sodium chloride, are not ordinarily used as separate articles of diet. Any single article of food, such as rice or meat, may contain all the foodstuffs, yet rice is thought of as a carbohydrate food and meat as protein food, because of the relative predominance of carbohydrate in rice and of protein in meat. Protein exists in various forms, such as the *myosin* of meat, *casein* of milk, *gluten* of bread, and *albumin* of eggs. Carbohydrate foods, such as rice or whole-wheat flour, contain a high percentage of starch. Carbohydrate in the form of sugar is obtained principally from fruits or in a pure form, usually as cane sugar. A variable amount of fat is found in meat, fruit, and vegetables. In diets this is usually supplemented by additional fat in the form of butter or vegetable oils. Water and inorganic salts are constituents of all foods.

Vitamins.—In addition to protein, fat, carbohydrate, water, and inorganic salts the animal body requires minute amounts of organic substances known as vitamins. A number—at least six—have been identified, though not completely isolated in a pure state, so that their chemical formulas are not known with any degree of certainty, at least in all cases. Their importance as essential constituents of a diet has been established beyond all question. They occur in milk, fruit, fresh vegetables, meat, and in the outer kernels of grain. Vitamins exist in such small quantities in foods that they are negligible as sources of energy. They are not enzymes. Their precise role is unknown, but there is some resemblance between them and hormones. Some authors designate them as *exhormones* to indicate their origin outside the body in contrast to the hormones of the endocrine glands which are formed within the body.

At the present time, five vitamins, known as A, B, C, D, and E, are recognized, with some evidence to indicate that vitamin B is a combination of two or more vitamins.

Vitamin A is fat-soluble and promotes growth. Rats on a vitamin A-deficient diet show in addition to stoppage of growth and loss of weight, inflammatory conditions in the conjunctiva and the cornea of the eye, as well as other effects. Cooking does not destroy it in fruits and vegetables.

Vitamin B or B_1 is water-soluble and its absence in food produces *polyneuritis* or *beriberi.* Fowls fed on polished rice (rice in which the reddish outside layer has been removed) develop in the course of a few days a weakness in the legs caused by a nervous degeneration which is known as polyneuritis. Such fowls soon die unless the diet is changed, or rice polishings added to it. Beriberi, a disease common among rice-eating peoples, shows similar symptoms and seems to be due to similar causes. In this case the vitamin involved is located in the cortex of the grain. It also occurs in yeast, milk, leafy vegetables, and fruit.

Vitamin C is alcohol-soluble and is *antiscorbutic.* Absence of vitamin C in the diet produces *scurvy,* a disease manifested by bleeding of the gums, tooth pulp, mucous membrane, and skin. It was particularly prevalent among sailors in the days of sailing vessels when voyages too frequently outlasted the available supply of fresh vegetables and meat. Scurvy results in bodily weakness and terminates in death unless checked by feeding vegetables and meat or by giving the juice of lemons, limes or oranges. *Ascorbic acid,* $C_6H_8O_6$, has the antiscorbutic potency of lemon juice, of which it is one of the constituents.

Vitamin D is fat-soluble and *antirachitic.* *Rickets,* a disease in which the bones and teeth are defective, may be prevented by administering cod-liver oil, which is high in vitamin D. Since rickets may also be controlled by ultraviolet radiation, it is thought that radiation liberates vitamin D from substances in the tissues that might be regarded as a kind of *provitamin.* This substance is *ergosterol,* an unsaturated fat. The active vitamin occurs in abundance in fish oils, butter fat, whole milk, and yolk of eggs. Administration of irradiated ergosterol shows the same antirachitic effects as the vitamin D of fish oils. Vitamin D is involved in regulating the concentrations of phosphorus and calcium in the blood and is concerned with the calcification of bones and teeth.

Vitamin E is fat-soluble and is necessary for fertility in reproduction. It is found in meat, cereal, lettuce, liver, and egg yolk. Its omission from a diet results in sterility.

Vitamin G or B_2 consists of two substances: (1) *lavine,* a yellow pigment, which seems to be essential for growth, and (2) a portion called B_6 that prevents and cures a dietary skin disease in rats somewhat similar to pellagra in man. These vitamins occur in yeast, whole cereals, milk, vegetables, and fruits.

Salivary Digestion.—In the frog, food is swallowed without mastication and salivary digestion is entirely lacking. In man and most mammals, the saliva contains a starch-splitting enzyme, ptyalin, secreted principally by the parotid gland. The flow of saliva is a result of reflex stimulation of secretory nerves. Thus the sight and odor of food cause a flow of saliva before the food enters the mouth. In the mouth the taste of food also stimulates salivary secretion. The action of saliva upon starch may be demonstrated in a test tube, or by holding a small quantity of boiled potato in the mouth for a short time. After a few minutes sugar is found in the solution. The conversion of starch into sugar is a step-by-step reaction, in which maltose is split off leaving residues that become progressively simpler in chemical structure until entirely converted into sugar. This may be illustrated as follows:

Starch ↗ maltose
Starch ↘ erythrodextrin ↗ maltose
erythrodextrin ↘ achroodextrin ↗ maltose
achroodextrin ↘ dextrin ↗ maltose
dextrin ↘ maltose

Chewing thoroughly mixes saliva with the food, but swallowing takes place before all the action of ptyalin can be completed in the mouth. The reaction of saliva is neutral or slightly acid, but its activity is stopped by concentrations of hydrochloric acid as low as 0.003 per cent and also by strong alkali. The gastric juice contains enough acid (0.50 per cent of HCL) to stop the action of ptyalin on food in the stomach; nevertheless the action of ptyalin may continue in the stomach because the food may remain undisturbed in the fundus for an hour or more and remain unmixed with acid. If a rat is fed with food of different colors, the stomach removed, frozen, and sectioned, it is found that the food is deposited in concentric layers, the first layer against the wall and each later layer inside the preceding one. Since time is required for the complete mixing of the food with gastric juice, ptyalin might well continue its action particularly on food swallowed toward the end of the meal.

Gastric Digestion.—The acidity of pure gastric juice, is about 0.5 per cent, while the acidity of the contents of the stomach during digestion is about 0.2 per cent. The drop in acidity during digestion is due to neutralization and dilution by the stomach contents and also apparently by regulated regurgitation of the alkaline contents of the duodenum during gastric digestion.

Gastric juice is secreted by the stomach in response to the stimulations of nerve endings of taste and odor, produced during the chewing and swallowing of food. This constitutes the *appetite secretion.* In addition there is evidence of a chemical stimulation of the gastric glands brought about by the action of food on the stomach mucosa, producing a substance, *gastric secretin,* which is absorbed by the blood and carried to the gastric glands, where it causes secretion of the gastric juice.

The principal enzyme of the stomach, pepsin, acts only in an acid medium, upon proteins, reducing them to simple and more soluble forms known as peptones. The curdling of milk brought about by rennin, the coagulating enzyme of the gastric juice, takes place in two steps: (1) the conversion of casein into *paracasein,* and (2) the reaction of the paracasein with calcium salts of the milk to form the *curd,* which is an insoluble protein. The latter then undergoes proteolytic digestion by pepsin. Digestion of protein is begun in the stomach and carried to completion in the intestine.

Gastric digestion is facilitated by movements of the pyloric half of the stomach. During these movements, which consist of rhythmic muscular contractions beginning at about the middle of the stomach and extending to the pylorus, the fundus remains quiescent. The stomach cavity is entirely shut off from the rest of the alimentary canal by the contracted sphincter muscles at the cardia and pylorus, except at certain intervals when the pyloric sphincter relaxes and allows a portion of the stomach contents to be pushed out into the duodenum. That portion of the food subjected to the rhythmic contractions of the stomach is gradually converted into a liquid mass known as *chyme;* and it is thought that the liquefaction of the food may be one of the factors involved in causing the relaxation of the pyloric sphincter, since observations have been recorded indicating that when liquid food alone is taken, it leaves the stomach in a few minutes. In other words, the pyloric sphincter remains contracted as long as the pyloric contents are solid, but relaxes when subjected to the pressure of chyme of a certain degree of fluidity. It has also been suggested that the chemical reaction of the chyme may be a factor, but agreement is lacking on this point. After the expulsion of a quantity of the chyme, a corresponding quantity of food is pushed out of the fundus, presumably by the tonic contractions of the fundic muscles.

Digestion in the Small Intestine.—In the intestine, the chyme from the stomach is subjected to the action of enzymes contained in the pancreatic juice and also enzymes produced by the small intestine itself. The alkaline secretion from the pancreas contributes four enzymes: two proteolytic enzymes, trypsin and erepsin; an amylolytic enzyme, amylase; and a lipolytic enzyme, lipase. From the intestinal mucosa comes a proteolytic enzyme, erepsin, identical with the erepsin of the pancreatic fluid; various inverting enzymes; and enterokinase, which activates trypsinogen. All of these enzymes act in an alkaline or neutral or faintly acid medium.

When the acid chyme from the stomach is discharged into the duodenum the pancreatic juice begins to flow into the duodenum. A substance, *pancreatic secretin,* is formed by the action of acid on the duodenal mucosa and is carried by the blood stream to the pancreas, where it causes active secretion. It has a similar effect on the liver, causing the secretion of bile. Pancreatic secretin, like gastric secretin, is an example of a *hormone*, a chemical agent that stimulates the activity of organs other than the one in which it is produced. The chemical control of pancreatic secretion provides an automatic mechanism for regulating the secretion of pancreatic juice.

The peptones formed by the gastric digestion of proteins are hydrolyzed by trypsin and erepsin into *amino acids*, the final product of protein digestion.

Amylase is similar to ptyalin in its action on starches. Thus the amylolytic action by ptyalin begun in the mouth and continued in the stomach until interrupted by hydrochloric acid, is renewed and carried to completion by amylase in the intestine. Maltose, the product of starch digestion is then converted by maltase into dextrose. Most of the maltase is produced in the intestine, but saliva also contains small amounts, so that some inverting action on maltose may take place before the food reaches the intestine. Cane sugar, taken in a pure form with food is converted in the intestine by sucrase into dextrose and levulose. Milk sugar or lactose is changed by lactase into dextrose and galactose. *Dextrose, levulose*, and *galactose* are all monosaccharides and represent the end products of carbohydrate digestion.

It is usually agreed that the digestion of fats takes place in the small intestine. The lipolytic enzyme involved is lipase, produced by the pancreas. Lipase is capable of hydrolyzing or saponifying neutral fats. Its action on beef fat, tristearin, may be illustrated as follows:

$$\underset{\text{tristearin}}{C_3H_5(C_{17}H_{35}COO)_3} + \underset{\text{water}}{3H_2O} \rightarrow \underset{\text{glycerin}}{C_3H_5(OH)_3} + \underset{\text{stearic acid}}{3C_{17}H_{35}COOH}$$

Since this reaction takes place in an alkaline medium, the free acid is at once neutralized to form a soap, sodium stearate, as follows:

$$\underset{\text{stearic acid}}{C_{17}H_{35}COOH} + \underset{\text{sodium hydroxide}}{NaOH} \rightarrow \underset{\text{sodium stearate}}{C_{17}H_{35}COONa} + \underset{\text{water}}{H_2O}$$

Or both steps may perhaps be combined in a single reaction as follows:

$$\underset{\text{tristearin}}{C_3H_5(C_{17}H_{35}COO)_3} + \underset{\text{sodium hydroxide}}{3NaOH} \rightarrow \underset{\text{glycerin}}{C_3H_5(OH)_3} + \underset{\text{sodium stearate}}{3C_{17}H_{35}COONa}$$

Glycerin and a *salt of a fatty acid*, or soap, constitute the final products of the digestion of fats.

Since lipase acts more rapidly and effectively when bile is present, it is thought that bile acids alone or with lecithin (a constituent of bile) functions as a coenzyme, which increases lipolytic action.

Gastric Absorption.—Relatively little absorption of substances takes place in the stomach. Water is not absorbed to any appreciable extent. One experiment with a dog showed that of 500 cc. of water given through the mouth 495 cc. entered the duodenum within a half an hour. Alcohol, on the other hand, is absorbed readily by the stomach. Sugars and peptones are not absorbed.

Absorption in the Small Intestine.—The products of digestion are absorbed principally in the small intestine. In this connection it is necessary to refer again to the structure of the intestinal villi. The mucous lining of the human small intestine throughout the greater part of its length is raised into permanent transverse folds, the *valvulae conniventes.* Both on the valvulae and between them the mucosa is in the form of closely packed cylindrical or club-shaped villi. In the duodenum villi are plate-shaped. Each villus is covered with columnar epithelium, beneath which is an incomplete layer of plain muscle. The core of the villus is formed of loose connective tissue, with a centrally located lymph capillary or lacteal, which communicates with larger lymphatic vessels in the submucosa. Peripheral to the lacteal is a network of blood vessels (Fig. 71).

Absorption and Metabolism of Protein.—The products of protein digestion, amino acids, are absorbed through the epithelium of the intestinal mucosa into the blood stream and carried by the blood to different parts of the body. They are stored temporarily, principally in the liver and muscles. Experiments show that with excessive feeding some of the products of protein digestion may enter the lymph stream. Apparently there is no circulating protein to provide the tissues with their protein requirements. Instead it is believed that this function is served by amino acids in the blood, each tissue using what is required to build up its own form of protein. Amino acids that are not used for tissue-building may undergo *deaminization.* This consists in splitting off a portion of the molecule as urea, leaving a nonnitrogenous residue which can be readily oxidized. Deaminization occurs principally in the liver, though there is evidence that it also occurs in the tissues generally. Urea, which has the formula $\mathrm{C}\begin{matrix}\diagup \mathrm{NH_2}\\ =\mathrm{O}\\ \diagdown \mathrm{NH_2}\end{matrix}$, is the chief end product of nitrogen metabolism in the body. The role of the products of protein digestion is

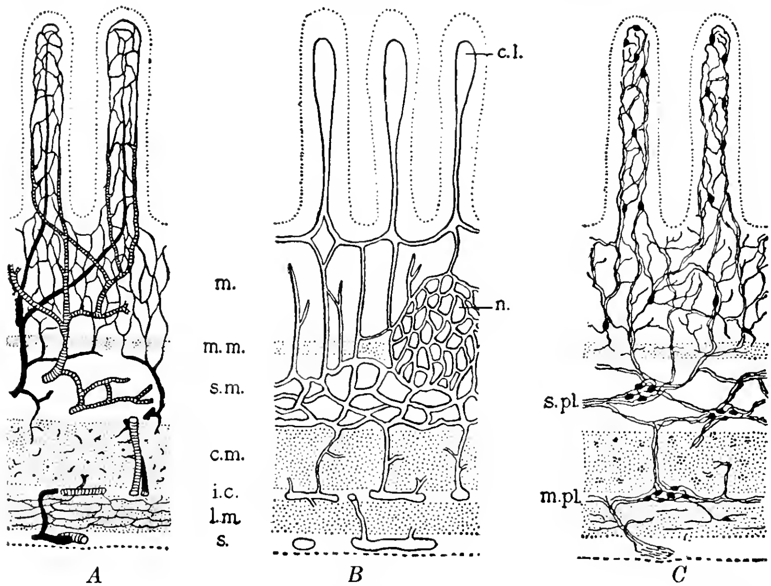


Fig. 71.—A, diagram of the blood vessels of the small intestine; the arteries appear as coarse black lines; the capillaries as fine ones, and the veins are shaded. (*After Mall.*) B, diagram of the lymphatic vessels. (*After Mall.*) C, diagram of the nerves. (*After Cajal.*) The layers of the intestine are m, mucosa; m.m., muscularis mucosa; s.m., sub-mucosa; c.m., circular muscle; i.c., intermuscular connective tissue; l.m., longitudinal muscle; s, serosa; c.l., central lymphatic; n, nodule; s.pl., submucous plexus; m.pl., myenteric plexus. (*From Stöhr, Textbook of Histology, by Lewis. P. Blakiston's Son and Company. By permission.*)

therefore twofold: (1) to *build tissue*, and (2) to provide *fuel*. Of the two the first is the more important. There is evidence that the liver is involved in the formation or in the mechanism of regulation of the blood proteins, especially fibrinogen.

It is possible to keep a dog in nitrogen equilibrium (in which intake and outgo of nitrogen are equal) and even with a plus balance of nitrogen if it is fed on certain amino acids without fats or carbohydrates. This means, of course, that some part of the amino acids can act as a source of heat or energy. Some of the non-nitrogenous product of deaminization may be converted to sugar and glycogen and then into fat, though most of the body fat comes from fat taken as such in the food and from carbohydrate.

Absorption and Metabolism of Carbohydrates.—Since carbohydrate food is taken mainly in the form of starch, the principal end product of carbohydrate digestion is *dextrose*. This passes through the walls of the villi into the blood capillaries, whence it is carried by the blood of the portal vein to the liver. In the liver a certain amount of sugar is removed and converted into *glycogen*, an insoluble starchlike substance, which is stored in the liver cells, leaving about 0.1 per cent of sugar in the blood. As sugar in the form of glucose is used up in the general circulation and tissues, glycogen is converted back into dextrose by the enzyme glycogenase, thus maintaining a fairly constant sugar content in the blood. Sugar may be absorbed in a form other than glucose, in which case it is converted into glycogen by the liver and released as glucose in the blood.

The islet cells of the pancreas produce a hormone, *insulin*, which plays an important part in sugar metabolism. Sugar is used in the body (1) to provide a source of energy for cells and for muscular work; (2) by oxidation to supply heat; and (3) excessive amounts may be converted into fat and stored as such. Energy is obtained from sugar by oxidation which may occur in the circulation or in the tissues, but in order for oxidation to take place, insulin must be present. If insulin is kept out of the general circulation in an experimental animal by removing the entire pancreas, the percentage of sugar rises, indicating that the normal amount of sugar is not being used. If the pancreatic ducts are ligated, all of the cells of the pancreas except the islet undergo atrophy. In such an animal the amount of the sugar in the blood remains normal. Thus the rise of sugar in the blood in the first case must have been due to the absence of something produced by the islet cells.

In the disease, *diabetes mellitus*, practically all the carbohydrate taken as food may be lost in the urine in the form of sugar and even if no carbohydrate is eaten, sugar, derived from stored-up glycogen, continues to be eliminated in the urine. That this condition is due to lack of insulin is indicated by the fact (1) that in such cases lesions have been found in some or all of the islet tissue of the pancreas, and (2) that the administration of insulin, a preparation containing the active principle of the islet cells, causes a return to normal sugar metabolism.

Absorption and Metabolism of Fats.—The end products of fat digestion are glycerin and soaps. These are absorbed as such but are apparently at once combined to form fats in the outer zone of the epithelium of the mucosa because fat droplets can be demonstrated in these cells in sections of tissue taken from an animal during absorption (Fig. 72). In absorption it is believed that the bile salts or other constituents of the bile dissolve the fatty acids or their soaps, thus enabling them to pass into the cells. Thus the bile is not only important in the digestion of fats but also in their absorption. Most of the synthesized fat passes from the epithelium of the mucosa into the lacteals, then into the larger intestinal lymphatics, the thoracic lymph duct, and finally into the blood stream at the point where the thoracic duct joins the right subclavian vein near the heart. During absorption the lymphatics of the intestine are distended with fat, which gives them a milky appearance. Fat in the form found in the lymphatics is known as *chyle*. A smaller quantity of fat enters the blood capillaries of the mucosa and thus passes to the liver through the portal vein, before entering the general

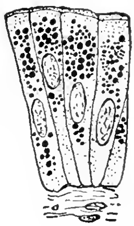


Fig. 72.

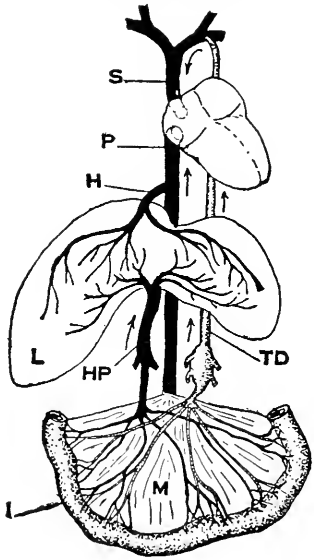


Fig. 73.

Fig. 72.—Intestinal epithelium of frog showing spherules of fat (in black) as they appear during absorption. (*After Krehl.*)

Fig. 73.—Diagram of the larger veins and lymphatic vessels of intestine. H, hepatic vein; HP, hepatic portal vein; I, intestine; L, liver; M, mesentery; P, postcava; S, superior cava; TD, thoracic duct, which conveys lymph to the subclavian vein.

circulation. Since liver cells show an accumulation of fat during absorption, it follows that some of the fat is taken out of the blood by the liver (Fig. 73). Chyle is removed from the lacteals by contractions of the musculature of the villi.

Fat is used by the tissues for *heat* production, the final products of oxidation being carbon dioxide and water. Fats like carbohydrates are energy producers. An excess may be stored in the body as adipose tissue, a reserve which may be drawn upon when needed.

Digestion and Absorption in the Large Intestine.—The mammalian large intestine does not produce specific digestive enzymes. The same is also true of the frog. The secretion of the human large intestine consists of mucus and is alkaline in reaction. However, since the contents received by the large intestine from the small intestine contain some undigested food together with enzymes and since the large intestine retains its contents for a long time, digestion and absorption continue there as in the small intestine. The outstanding function of the large intestine is the absorption of water as a result of which the contents are dried to the consistency of the feces.

Bacterial Digestion.—The intestine of man as well as that of other animals normally contains large numbers of bacteria. In the small intestine they cause fermentation of carbohydrates, which results in the production of carbon dioxide, water, alcohol, and acetic acid. These substances are probably absorbed and used by the body, but they could be used equally well if absorbed as unfermented sugar. In the large intestine the same thing may take place, but usually bacterial action in this part of the digestive tract is on undigested fragments of protein, causing *putrefaction*. Autointoxication results from the absorption in the large intestine of toxic substances formed in the process of putrefaction.

CHAPTER VI

CIRCULATION AND RESPIRATION

A circulatory system consists of a fluid, blood or lymph, driven by the contractions of one or more hearts to all parts of the body, usually through tubular blood vessels. If blood vessels are absent or poorly developed, as in insects, the blood shortly after leaving the heart flows through the tissues unconfined by vessels. The heart is a highly specialized region of a blood vessel. In the frog there is a single heart for moving the blood and a number of lymph hearts which maintain a flow of lymph from the tissues to the veins of the blood system. Lymph hearts are absent in mammals. The circulatory system serves to transport to the tissues nutritive substances, absorbed from the alimentary canal, and oxygen, absorbed from air or water by the respiratory organs. The blood collects from the tissue products of metabolism such as carbon dioxide, water, and various other substances, which are eventually eliminated. In warm-blooded animals the blood is important in controlling and regulating body temperature. The importance of the circulatory system in connection with these functions is not the same for all animals. Thus in insects, air containing oxygen is carried to blood-bathed tissues and carbon dioxide from them, by special tubes that function as respiratory organs (p. 426), the blood forming only a short link in the final phase of oxygen transport and the initial phase of carbon dioxide transport. Blood is a fluid tissue composed of a liquid *plasma* in which cells or cell-like bodies called *corpuscles* are suspended. Lymph has a somewhat similar composition.

Blood Vessels of Vertebrates.—*Arteries* are vessels that carry blood away from the heart. *Veins* carry blood toward the heart. The small arteries or arterioles terminate in still smaller vessels known as *capillaries,* which soon reunite to form veins. The arterial and venous vessels are connected centrally by the heart and peripherally by the capillaries, the whole providing a circular pathway through which the blood moves. Sometimes a capillary network is intercalated in the arterial system, as in the gill capillaries of a fish, to and from which blood is carried by arteries. A similar situation may also occur in the venous circulation. Thus the hepatic portal vein arises from capillaries in the intestine and terminates in capillaries in the liver, forming what is known as a *portal* circulation. Since the major functions of the blood are carried out in the capillary bed, arteries and veins serve principally as conduits for conveying blood to and from the capillaries. In the capillaries the important exchanges take place between blood and tissues upon which metabolism depends. The heart, the walls of the larger arteries and veins, as well as all other parts of the vertebrate body except some epidermal structures are provided with a capillary circulation.

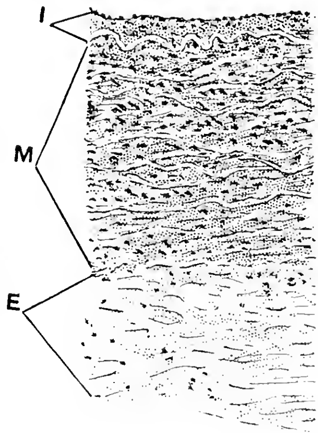


FIG. 74.—Section of wall of medium sized artery of cat. E, externa; I, intima; M, media.

Arteries.—A cross section of a large artery shows three regions: the *intima*, the *media*, and the *externa* (Fig. 74). The intima consists of a flattened layer of cells known as *endothelium*, lining the vessel. External to the endothelium, the intima contains a layer of white and elastic fibers forming a meshwork elongated in the direction of the length of the vessel. The media consists of a thick layer of circular, nonstriated or plain muscle fibers, spread through wide-meshed elastic tissue. The externa, the outer covering of the artery, is composed of somewhat denser connective tissue, part of which is elastic.

Veins.—The wall of a vein is thinner than that of a corresponding artery, but otherwise the plan of structure is the same for both. In larger veins the media is reduced or absent. Unless distended with blood, veins appear collapsed or wrinkled in sections. At the same level veins appear larger than corresponding arteries in sections because the arteries contract markedly when treated with a killing fluid such as is used in preparing sections.

Capillaries.—As arteries approach capillaries, the outer layers of the artery are lost, until only the endothelial layer with a few scattered muscle cells remain. These endothelial tubes are not the true capillaries, the latter having an even more simplified structure, the details of which are not completely known. According to some descriptions, the capillary is a noncellular membrane or *perithelium* which contains scattered contractile cells and nerve endings. The diameter of the smallest capillaries is so reduced that blood corpuscles are distorted in their passage through them. The wall of the capillary is therefore extremely thin which would seem to be of significance in connection with rapid exchanges by diffusion between blood and tissue.

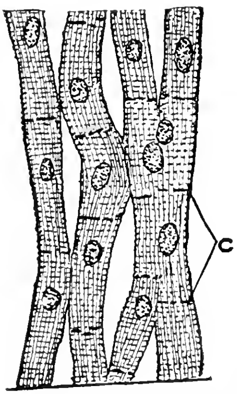


Fig. 75.—Cardiac muscle tissue of mammal. C, intercalated disks.

Heart of the Frog.—The pericardium, the sac enclosing the heart, bears the same relation to the heart as the peritoneum bears to the intestine. The pericardium is really a double-walled sac, whose inner or visceral wall is closely applied to the heart and separated from the outer or parietal wall by a space filled with pericardial fluid. The two walls of the pericardium are continuous about the heart where the large vessels are joined to it. The heart is an organ composed almost entirely of muscle. Cardiac muscle is striated and the structure of the myofibrils is similar to that found in skeletal muscle. Unlike skeletal muscle, whose fibers are usually straight, cardiac muscle fibers form a branching network (Fig. 75). The nuclei are located in the central axes of the fibers. In human cardiac muscle the fibers are crossed by irregular *intercalated disks*, located about midway between adjacent nuclei, which gives the appearance of a cellular structure. Though striated, cardiac muscle is involuntary in function.

The frog's heart is composed of a single *ventricle* and two *auricles* or *atria*. Viewed from the ventral side, the triangular ventricle forms the posterior half of the heart and is marked off from the atrial region in front by the *coronary sulcus*. The ventral face of the atrial region is traversed by the broad *truncus arteriosus* arising from the right anterior border of the ventricle and dividing into right and left branches at the anterior edge of the heart. On the dorsal side of the heart is a triangular sac, the *sinus venosus*, which communicates with the right atrium. The right and left atria are completely separated by an *interatrial septum.* The right atrium is larger than the left (Fig. 76).

The cavity of the ventricle is a single chamber but its thick muscular wall is indented by deep depressions which form numerous alcoves. The atria, on the other hand, have smooth thin walls. The blood which enters the right atrium from the sinus venosus is deoxygenated blood from the systemic circulation. Backflow of blood into the sinus venosus when the heart con-

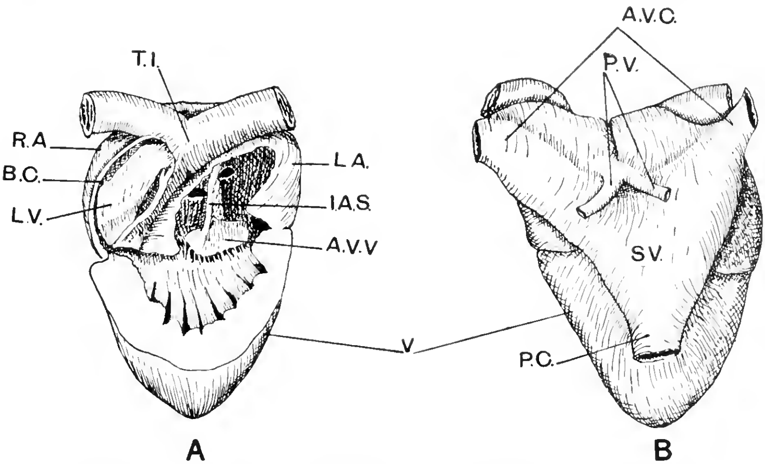


FIG. 76.—Heart of *Rana catesbeiana.* A, dissection from ventral side; B, dorsal view. A.V.C., anterior vena cava; A.V.V., atrioventricular valve (dorsal); B.C., bulbus cordis (proximal segment of truncus arteriosus); I.A.S., interatrial septum; L.A., left atrium; L.V., longitudinal valve; P.C., postcava; P.V., pulmonary veins; R.A., right atrium; S.V., sinus venosus; T.I., truncus impar (distal segment of truncus arteriosus); V, ventricle.

tracts is prevented by a pair of transverse lips or valves guarding the *sinu-atrial* aperture. The left atrium receives oxygenated blood from the lungs brought to it by the *pulmonary veins*, which enter the atrium at an acute angle so that when the atrium contracts, the mouth of the venous aperture is closed. Both atria open into the ventricle through the *atrioventricular* aperture, which, however, is divided into right and left portions by the interatrial septum (Fig. 76). The atrioventricular aperture is guarded by four valves, *viz.*, a large flap on the dorsal edge, a similar one on the ventral edge, and two smaller valves, one at the right and one at the left edge of the aperture. The free edges of the valves are prevented from being pushed back into the atria by small fibers, known as *chordae tendineae*, extending from the edges of the valves to the wall of the ventricle.

The truncus arteriosus takes its origin from the anterior margin of the right side of the ventral wall of the ventricle and then follows a diagonal course across the atria from right to left. It is composed of two regions: a proximal segment, the *bulbus cordis*,

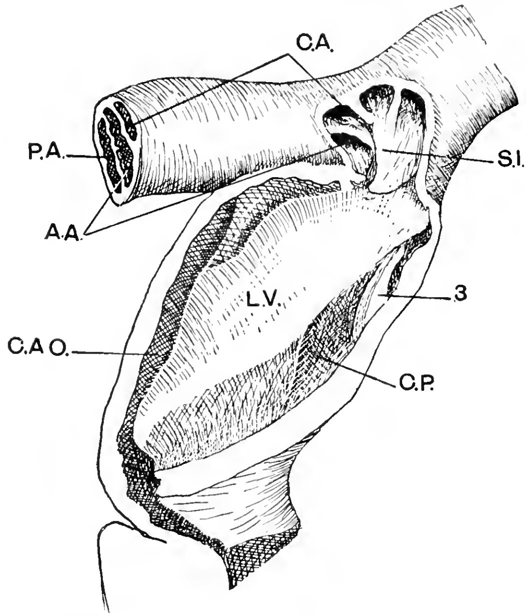


FIG. 77.—Dissection of truncus arteriosus of *Rana catesbeiana* from ventral side. A.A., aortic arch; C.A., carotid arch; C.AO., cavum aorticum of bulbus cordis; C.P., cavum pulmocutaneum of bulbus cordis; L.V., longitudinal valve; P.A., pulmonary arch; S.I., septum interaorticum; 3, valve.

marked off by a transverse constriction from a distal segment, the *truncus impar*, which almost immediately bifurcates into right and left trunks. Each of these trunks separates into three branches, known as *arterial arches*, of which the anterior one is the *common carotid artery*, the next, the *aorta*, and the posterior one the *pulmocutaneous artery*. Each common carotid artery divides almost at once into *internal* and *external carotid* arteries which supply the head. Each aortic arch curves outward and dorsally to join its fellow of the opposite side at about the level of the sixth vertebra, to form the *dorsal aorta*. Each pulmocutaneous artery divides into (1) a *great cutaneous artery,* which is distributed mainly in the skin of the dorsal and lateral regions, and (2) a *pulmonary artery* to a lung. One division of the great cutaneous artery, the *auricularis,* forms anastomoses with other arteries, such as the *occipital* and *carotid* (Fig. 81).

If the truncus arteriosus is opened by a ventral incision from its point of origin to the bifurcation, its bulbar region is found to contain a number of valves, of which the largest is the *septum bulbi* or *longitudinal valve* (Fig. 77). The septum bulbi is attached at its posterior end to the ventral wall of the proximal end of the bulbus, but as one traces the valve forward, its point of attachment spirals sharply to the left through an arc of 180 degrees to the dorsal wall of the bulbus, which it follows in a slight curve from left to right to the beginning of the truncus impar where it is united dorsally and laterally to the truncal walls. Since the ventral edge of the septum is free throughout the greater part of its length, a complete division of the bulbar channel into two can only occur when the free edge of the septum is pressed tightly against the ventral wall of the bulbus. The attached edge of the septum is broad and the free edge is thin and movable. The two channels formed in the bulbus by the septum are known as the *cavum aorticum,* on the right, and the *cavum pulmocutaneum,* on the left.

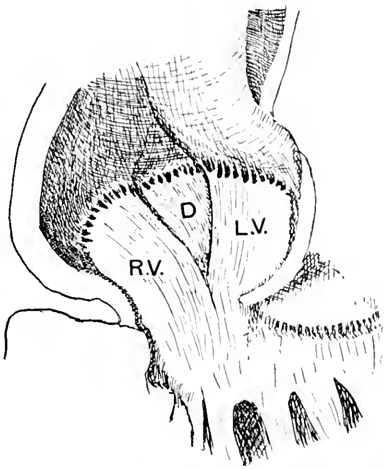


FIG. 78.—Dissection proximal end of truncus arteriosus of *Rana catesbeiana,* with walls spread apart. D, dorsal valve; L.V., left valve; R.V., right valve.

At the posterior end of the septum bulbi, where it is attached to the ventral and lateral wall of the bulbus, are three valves: (1) a *left ventral valve,* closely applied to the right lateral face of the septum; (2) a *right ventral valve,* attached to the right wall of the bulbus; and (3) a *dorsal valve,* very small and lying between the first two. These valves are connective tissue flaps, whose free edges are attached to the walls of the bulbus by chordae tendineae. Another set of three valves is found at the anterior end of the septum, as follows: (1) a large one, *valve* 3, on the left side of the septum, beyond which is an opening leading to the pulmocutaneous arteries; (2) another one, called *valve* 2, lying ventral and to the right of valve 3; and (3) a cup-shaped valve formed by the anterior end of the septum bulbi and known as *valve* 1 (Figs. 78 and 79).

The truncus impar is divided into dorsal and ventral channels by the *septum principale*, which, taking its origin from the anterior edge of the septum bulbi, divides the cup-shaped valve of the latter into dorsal and ventral portions, *valves* 1*a* and 1*b*. The dorsal channel, leading from the cavum pulmocutaneum of the bulbus, divides with the truncal arms of the truncus impar into right and left pulmocutaneous arches. The ventral channel of the truncus impar is divided into right and left portions by the *septum interaorticum*, which is at right angles to the septum principale. The two channels thus formed are the beginnings of the aortic arches. The carotid arches originate as two small openings in the septum interaorticum, leading from the right aortic branch of the truncus. Blood leaving the cavum aorticum of the bulbus enters the aortic and carotid arches.

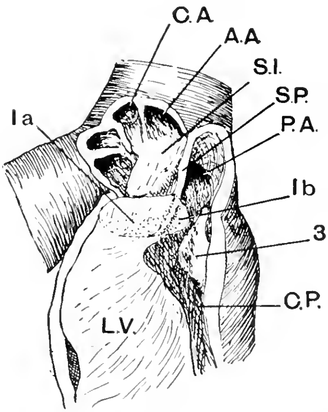


FIG. 79.—Dissection of distal end of truncus arteriosus of *Rana catesbeiana*. A.A., aortic arch; C.A., carotid arch; C.P., cavum pulmocutaneum; L.V., longitudinal valve of cordis bulbus; P.A., pulmonary arch; S.I., septum interaorticum; S.P., septum principale; 1*a*, 1*b*, 3, valves. (Valve 2, removed with the ventral wall of the truncus, is not shown.)

The sinus venosus, situated on the dorsal side of the heart, receives a right and left *anterior vena cava* (precava) in front, and an unpaired *postcava* behind. The blood brought to the sinus venosus is for the most part deoxygenated or venous blood, coming from the capillaries of all parts of the body except the lungs. Since the sinus venosus empties into the right atrium, the blood of the right atrium is venous in character. On the other hand, blood returned from the lungs to the heart by the pulmonary veins is usually oxygenated blood, and this blood enters the left atrium. The plan of the blood circulatory system of the frog provides for two circuits, a general systemic circulation and a pulmonary circuit, but these two circuits are not completely separated because they both make use of a single ventricle in passing through the heart.

Action of the Frog's Heart.—The study of the living heart shows that each atrium and the ventricle contract and dilate in a regular sequence. Contraction of a part of the heart is known as *systole*, and the dilatation which follows is *diastole*. The order of sequence of contraction is right atrium, left atrium, ventricle. Immediately after the ventricular systole, the bulbus cordis swells and then contracts to its normal size. Since both atria contract before the ventricle, the latter becomes filled with venous blood from the right atrium and oxygenated blood from the left. However, owing to the spongy internal structure of the ventricle and to the fact that ventricular systole follows almost immediately after the contraction of the left atrium, there is probably little mingling of the two kinds of blood in the ventricle. When the ventricle contracts, the blood is forced into the bulbus cordis, the atrioventricular valves preventing backflow of blood into the atria. The first blood to leave the ventricle is the venous blood since it occupies a position on the right side of the heart near the entrance to the bulbus cordis. This venous blood seems to enter the cavum pulmocutaneum and thence flows into the pulmocutaneous arteries for two reasons, *viz.*, (1) the relatively slight peripheral resistance in the pulmocutaneous trunks as compared with the pressure in the carotid and systemic arches, and (2) the contraction of the bulbus brings the free edge of the bulbar septum in contact with the bulbar wall, closing the cavum pulmocutaneum immediately after it is filled. Backflow into the bulbus is prevented by the anterior bulbar valves. The opening into the pulmocutaneous arteries is guarded by valve 1*b* on the dorsal side of the septum bulbi and by valve 3 which lies opposite on the wall of the bulbus. The aortic opening is guarded by valve 1*a*, on the ventral side of the septum bulbi, and by the large valve 2, which is attached to the ventral wall of the bulbus. In each aortic arch, just before turning posteriorly, are *semilunar valves*. Each carotid artery is provided with a *carotid gland* at the point of bifurcation into internal and external carotid arteries. The carotid gland is a spongy structure containing a network of small blood vessels through which the blood of the carotid artery passes.

There is still a difference of opinion as to the function of the valves in the bulbus. The present account is based on the morphological relations and also on experimental data. If India ink is injected into the postcava, the sinus venosus or the right atrium, much of the ink may appear in the aortic and carotid arches, but on the average, less in amount than in the pulmocutaneous trunks. Thus it would seem that there is a considerable separation in the bulbus of the two kinds of atrial blood but that the separation is not absolute. Such experiments support the idea that most of the blood from the right atrium enters the pulmocutaneous arches and that most of the blood from the left atrium enters the aortic and carotid vessels. It would also seem that the last blood to leave the heart, the least venous blood, enters the carotid system since the small openings of the carotid arteries are beyond the larger entrances to the aortic trunks.

This interpretation of the action of the frog's heart can have a functional significance only on the assumption that the blood returned to the heart from the lungs has a higher oxygen content than the blood in the right atrium. This point must be considered because the frog obtains a considerable portion of oxygen through buccal and cutaneous respiration. It would seem to be fairly obvious that the internal structure of the lung provides a mechanism for the absorption by the blood of oxygen from the alveolar air and for the release of carbon dioxide from the blood into the cavity of the lung. The pulmonary artery runs along the outer surface of the lung to the tip, giving off at right angles lateral branches forming a rich capillary network in the alveolar walls (Fig. 14). The pulmonary vein arising from this capillary network courses along the inner surface of the lung from the tip to the base. On the other hand, the great cutaneous veins from the skin of the dorsal and lateral regions of the body contain oxygenated blood which passes into the venous stream, but the volume of this contribution to the venous stream is relatively small, compared to the volume of the venous stream as a whole. Therefore, it would appear that the venous blood brought to the right atrium contains less oxygen than the blood entering the left atrium directly from the lungs.

The Blood Vascular System of the Frog.—The arterial system is made up of the arterial trunks leaving the heart and their subdivisions, which go to all parts of the body (Fig. 81). The carotid arteries supply the head. The remainder of the body except the lungs and some parts of the skin are supplied by the aortic arches and the dorsal aorta. The pulmocutaneous arteries lead to the lungs and certain regions of the skin. The arched form of these arterial trunks is a survival of a fish type of branchial circulation that is present in the frog tadpole.

In a fish such as the dogfish shark, a common marine form, the sinus venosus receives all the venous trunks of the body and

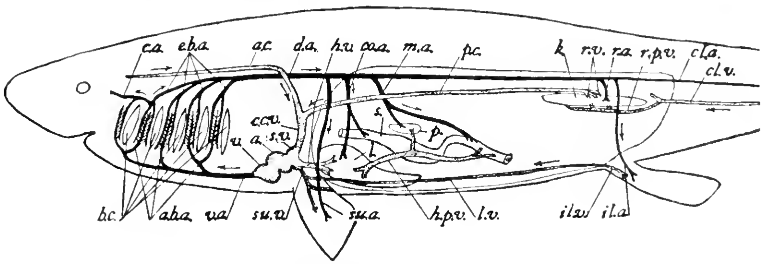


FIG. 80.—The circulatory system of the dogfish. *a*, atrium or auricle; *a.b.a.*, afferent branchial arteries; *a.c.*, anterior cardinal vein; *b.c.*, branchial clefts; *c.a.*, carotid artery; *c.c.v.*, common cardial vein; *cl.a.*, caudal artery; *cl.v.*, caudal vein; *co.a.*, coeliac artery; *d.a.*, dorsal aorta; *e.b.a.*, efferent branchial arteries; *h.p.v.*, hepatic portal vein; *h.v.*, hepatic vein; *il.a.*, iliac artery; *il.v.*, iliac vein; *k*, kidney; *l*, liver; *l.v.*, lateral vein; *m.a.*, mesenteric artery; *p*, pancreas; *p.c.*, post-cardinal vein; *r.a.*, renal artery; *r.p.v.*, renal portal vein; *r.v.*, renal veins; *s*, stomach; *su.a.*, subclavian artery; *su.v.*, subclavian vein; *s.v.*, sinus venosus; *v.* ventricle; *v.a.*, ventral aorta. (*Modified from Parker and Haswell.*)

pours its blood into a single atrium (Fig. 80). From the atrium the blood passes into a single ventricle. Thus all of the blood in the dogfish heart is venous blood. Leading forward from the ventricle is a short truncus arteriosus which divides right and left into afferent branchial arteries leading to the gills. After passing through the wide capillaries of the gills, during which the blood absorbs oxygen from water passing over the gills and gives off carbon dioxide to the water, the oxygenated blood is collected dorsally by efferent branchial arteries which unite to form a dorsal aorta that proceeds posteriorly to the tip of the tail. The carotid arteries are given off from anterior efferent arteries to the head. The arrangement of the branchial vessels is such that all of the blood leaving the heart passes through the gills. The gill capillaries are thus intercalated in the arterial system. In the frog a similar condition exists in the tadpole, but with the development of the lungs and other changes accompanying metamorphosis, the gills are resorbed, and the branchial arteries become the three pairs of arterial arches of the adult frog (Fig. 81).

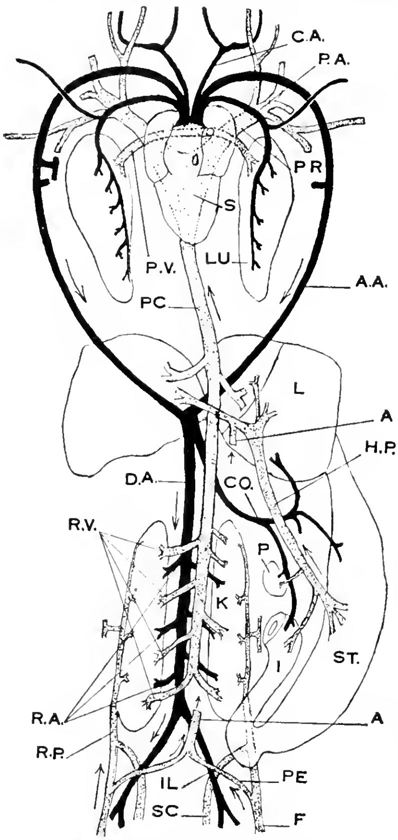


FIG. 81.—Diagram of the circulatory system of the frog from the ventral side. A, anterior abdominal vein; A.A., aortic arch; C.A., common carotid artery; CO., coeliac artery; D.A.; dorsal aorta; F, femoral vein; IL, iliac artery; K, kidney; L, liver; LU, lung; P, pancreas; P.A., pulmonary arch; P.C., postcava; P.E., pelvic vein; PR, precaval vein; P.V., pulmonary vein; R.A., renal artery; R.P., renal portal vein; R.V., renal vein; S, sinus venosus; SC, sciatic vein; ST, stomach.

Blood is returned to the sinus venosus of the frog's heart through three large venous trunks, *viz.*, a right and left precava or anterior cava, and a single postcava. The anterior cavae drain blood from the capillaries of the head and the anterior part of the body. The postcava has its roots in the segmental *renal veins* which collect blood from the kidneys. The principal venous trunks of each hindleg are the *sciatic* and *femoral* veins. At the juncture of the leg with the body each femoral vein bifurcates to form a *pelvic vein* and an *external iliac vein*. The two pelvic veins unite in the mid-line to form the *anterior abdominal vein* which proceeds forward in the mid-line of the abdominal wall to join one of the branches of the hepatic portal vein. The external iliac vein unites with the sciatic to form a *renal portal vein*, which terminates in capillaries in a kidney. Each kidney receives oxygenated blood from segmental *renal arteries*, given off by the dorsal aorta, and it also receives venous blood from the renal portal vein. The blood is drained from the kidneys by the renal veins. The renal portal veins and their tributaries begin in capillaries in the hindlegs and end in capillaries in the kidneys. A portion, therefore, of all the venous blood from the hindlegs must pass through kidneys before reaching the heart.

The *hepatic portal system* is made up of the hepatic portal vein, which originates in the capillaries of the stomach, intestine, spleen and pancreas and ends in capillaries in the lobes of the liver. The anterior abdominal vein, draining parts of the hindlegs, divides into two branches just before entering the liver. One of these branches usually joins a branch of the hepatic portal vein. Before it enters the liver, the anterior abdominal vein receives a small vein, the *cardiac vein*, from the bulbus cordis.

Human Heart.—The human heart consists of four chambers: two atria, or auricles, and two ventricles, making possible a completely double circulation (Fig. 82). A sinus venosus is not present in the adult. In the fish the heart cavities contain only venous blood; in the frog the right atrium contains venous blood, the left atrium arterial blood, while the ventricle contains both kinds imperfectly separated; in the mammal the right side of the heart carries only venous blood while the left side carries arterial. Each atrium is connected with the ventricle of the same side by an opening guarded by valves which allow the blood to pass from atrium to ventricle, but not in the reverse direction. The ventricles have much thicker walls than the atria and the left ventricle is much stouter than the right. The inner walls of the atria are relatively smooth, while those of the ventricle are raised into thick muscular ridges. The atrioventricular valves are thin, tough flaps, three (*tricuspid*) on the right and two (*bicuspid*) on the left side of the heart. The free edges of the valves are held in place by thin tendinous threads (chordae tendineae) attached by thick muscular pillars to the walls (Fig. 82). The contraction of the muscular pillars exerts a steady tension on the tendons, keeping the valves closed during ventricular contraction. Venous blood is returned from the head and anterior parts of the body by a single *superior vena cava* that enters the right atrium; from the posterior part of the body by the *inferior vena cava* (postcava) whose entrance into the right atrium is guarded by a large flaplike valve (Eustachian valve). The large veins of the extremities are provided with cuplike valves that allow the blood to flow toward the heart but not away from it (Fig. 83). From the right atrium venous blood passes into the right ventricle, whence it is pumped through the *pulmonary aorta* to the lungs. Backflow is prevented by a set of three *semilunar* valves located in the aorta a little beyond the ventricle. The pure, aerated blood is returned from the lungs by the pulmonary veins

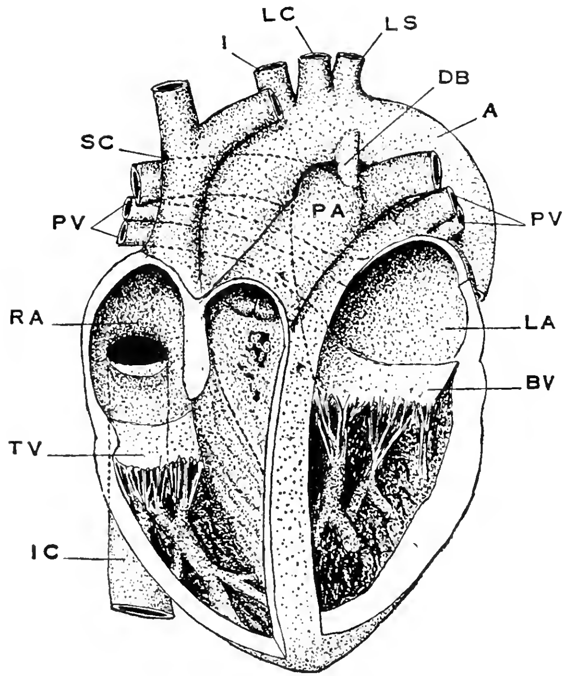


Fig. 82.—Human heart dissected from the ventral side, diagrammatic. A, aorta; BV, bicuspid valve; DB, Ductus Botalli, a solid cord, which in the embryo is a blood vessel connecting the pulmonary artery with the aorta; I, innominate artery; IC, inferior cava (postcava); LA, left auricle; LC, left carotid artery; LS, left subclavian vein; PA, pulmonary aorta which divides into right and left pulmonary arteries; PV, pulmonary veins; RA, right auricle; SC, superior cava; TV, tricuspid valve.

to the left atrium, from which it passes through the atrioventricular aperture into the left ventricle. The latter then pumps it through the *systemic aorta* to all parts of the body. The systemic aorta, like the pulmonary aorta, contains three semilunar valves that prevent backflow. Mammals have a hepatic portal circulation, but no renal portal system, except in embryonic stages.

Lymphatic System.—Among invertebrate animals the blood, lymph, and body fluids are in many cases the same fluid but in vertebrates lymph is distinct from blood and a portion of its circulatory pathway is composed of lymphatic vessels, which are distinct from blood vessels. Lymphatic vessels are best developed in mammals. In the frog the lymphatic system is characterized by numbers of large communicating lymph spaces, especially in the subcutaneous region. The *cisterna magna*, one of the largest lymph spaces, is formed in the subvertebral region, as a large sac in the dorsal wall of the body cavity. Lymph spaces are also found within and between the organs, the larger spaces being lined with flattened endothelial cells.

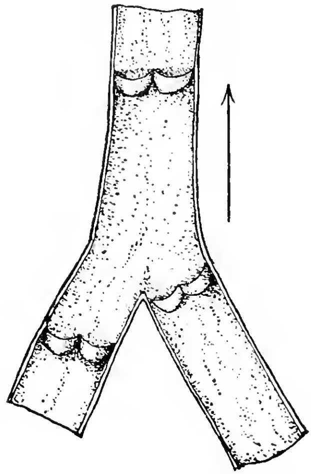


Fig. 83.—Diagram to show the position of the cup-like valves in an opened vein spread out flat. The arrow shows the direction of blood flow.

There are two pairs of *lymph hearts* in the frog. The two anterior hearts are located on the posterior side of the transverse processes of the third vertebra, each heart connecting with a vertebral vein, which in turn joins an internal jugular vein. The two posterior hearts lie one on either side of the tip of the urostyle, each heart connecting with the transverse iliac vein, which is a vein joining the sciatic and femoral veins near the hip joint. Each heart is provided with a pair of semilunar valves at its venous opening. The lymph hearts pulsate rhythmically and slowly pump the lymph into the blood. There is no relation between the beating of the heart and the pulsations of the lymph hearts. The action of the lymph hearts on opposite sides of the body is not correlated. Another connection between the lymphatic system and the blood stream is through ciliated openings (nephrostomes) from the body cavity into some of the tubules opening on the ventral surface of the kidney. The relation of these tubules to the blood system will be discussed in connection with the kidneys in the following chapter. The lymph entering the nephrostomes comes from the body cavity.

Human Lymphatic System.—In the human body there are well-developed lymphatic vessels, which originate in lymph capillaries in practically all parts of the body and end in openings into the large veins near the heart. The lymphatic vessels differ from blood vessels in two respects: (1) Their walls are more delicate in structure and (2) the free passage of the vessels may be interrupted from time to time by lymph glands, which are nodules of various sizes, composed largely of lymphocytes enclosed in capsules, through which the lymph slowly filters. The flow of the lymph, as in the frog, is from peripheral parts toward the heart. Since lymph hearts are absent in the human body, the movement of the lymph is brought about principally by movements of the surrounding parts exerting pressure on the thin-walled lymph vessels. Other factors are involved, such as the low pressure in the large veins near the heart, which would encourage flow toward the heart. Lymphatic vessels of the extremities are provided with valves, similar to those in the long veins, which allow the lymph to be squeezed past them toward the heart, but not in the reverse direction (Figs. 84 and 85).

Blood.—The blood of vertebrates consists of a fluid, the *plasma*, in which various kinds of cells or cell-like bodies, known as *corpuscles*, are suspended. The principal constituent of plasma is water, in which fats, sugar, and proteins are held in colloidal solution or suspension, along with a number of inorganic salts. In addition the plasma contains various decomposition products of metabolism, formed in various parts of the body. It also contains various endocrine substances, a discussion of which is set forth in Chap. X.

The principal proteins of the blood are *serum albumin*, *serum globulin*, and *fibrinogen*. The source of these proteins is probably from end products of protein digestion (amino acids) in the alimentary canal that are absorbed into the blood stream. Of these proteins, fibrinogen is of special interest because under certain conditions it forms a solid fibrous substance known as *fibrin* which entangles the blood corpuscles to form a blood clot. The fluid left after fibrin has been formed from plasma is called *serum*. Normally blood does not clot in the vessels, but clotting may occur in the vessels from the presence of air or foreign bodies produced as a result of injury or infection. There are a number of factors involved in the clotting process, not all of which are understood. That a certain amount of calcium is necessary for clotting can be demonstrated by adding oxalic acid to the blood, which precipitates the calcium and prevents coagulation. Blood drawn into an oil-coated vessel may be kept from clotting particularly if kept at a temperature near 0°C. Blood heated to near 100°C. loses its power to clot, owing apparently to the destruction of an enzyme, *thrombin*, which is necessary in addition to

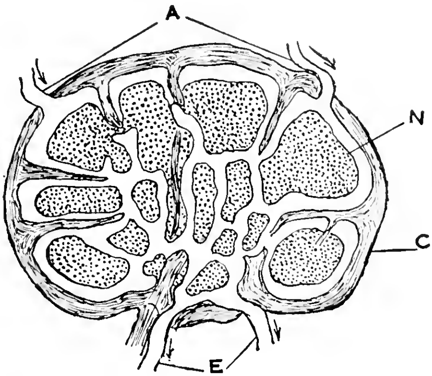


FIG. 84.—Diagram of a lymph gland. A, afferent lymph vessels; C, capsule, from which traveculae extend inward; E, efferent lymph vessels; N, nodule, composed mostly of lymphocytes. (*Modified after Stöhr.*)

calcium to produce clotting. However, if a calcium-free solution of fibrinogen is brought into reaction with a calcium-free solution of thrombin, a clot is formed, the fibrin of which is practically free of calcium. From this it would seem that calcium is not essential to the process of clotting after the thrombin is once

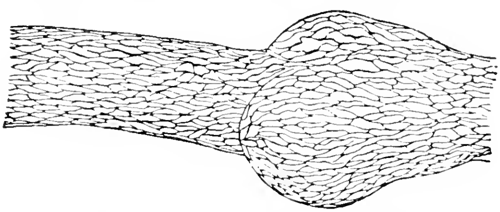


FIG. 85.—Silver nitrate preparation of a lymphatic vessel from a rabbit's mesentery, showing the boundaries of the endothelial cells and a bulging just beyond a valve. (*From Stöhr's Textbook of Histology, by Lewis. P. Blakiston's Son and Company. By permission.*)

formed and that, therefore, the role of the calcium is in the production of thrombin. *Thrombogen*, the inactive form of thrombin, is thought to occur in blood plasma and tissues.

Corpuscles of the Frog's Blood.—Three kinds of corpuscles can be distinguished in the frog's blood, *viz.*, *red corpuscles* or *erythrocytes, white corpuscles* or *leucocytes*, and *spindle cells* (Fig. 86). The red corpuscle is an elliptical disk measuring about 22.3 by 15.7μ, with a rounded edge and a bulged center in which a single nucleus is located. The red color of the blood is due to the presence of a chromoprotein known as *hemoglobin*, contained in the cytoplasm of the erythrocyte. However, if a thin film of freshly drawn blood is examined under the microscope, the hemoglobin appears yellow rather than red.

Leucocytes lack hemoglobin and are variable in form and size. Under the microscope, the outline of the leucocyte slowly changes in the manner of an amoeba. The cytoplasm of the living cells

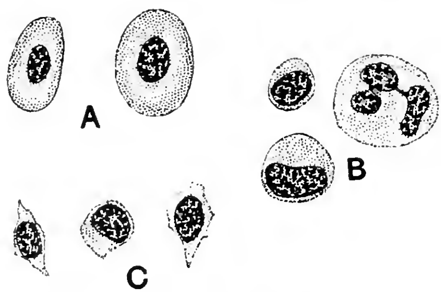


FIG. 86.—Blood corpuscles of *Rana pipiens*. A, erythrocytes; B, leucocytes; C, spindle cells. (*After Jordan.*)

is colorless, and staining brings out the presence of granules of various kinds.

The nucleus may be single and rounded or irregular in outline. In some cells the irregularity seems to lead to subdivision into several nuclei (larger cell of Fig. 86, B). The amoeboid movements of the leucocytes endow them with independent locomotion, which enables them to pass through capillaries, into surrounding tissues, without apparently rupturing the walls. They may actually leave the tissues and pass into the alimentary tract. Red cells may also leave through the capillary walls, though less frequently than leucocytes.

The spindle cells, the third type of blood corpuscle found in the frog, are colorless spindle-shaped cells about half the size of the erythrocytes. They are said to develop from small leucocytes and in the spring transform into erythrocytes. However, they may be found as a normal constituent of frog's blood at all times of the year. The fact that spindle cells collect in masses in clotting blood is believed to indicate that they play a role in clotting similar to that of the blood platelets of mammalian blood, described below.

Human Blood Corpuscles.—The erythrocytes of human blood are non-nucleated, biconcave circular disks (Fig. 87). They average about 5,000,000 per cubic millimeter of blood. Nucle-

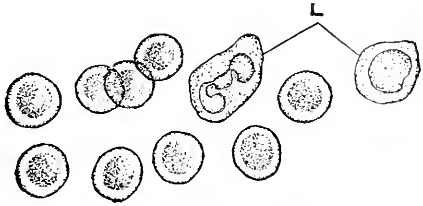


FIG. 87.—Group of red corpuscles and two leucocytes (L) as seen in a fresh human blood preparation. × 900.

ated erythrocytes are present in the blood stream of the human embryo but not in later life under normal conditions (Fig. 88). *Erythroblasts*, the cells which give rise to erythrocytes, are found during fetal life in the liver and the spleen, and in postnatal life, mainly in the red bone marrow. The erythrocyte of the adult is a cell that has lost its nucleus. Though incapable of amoeboid movement, erythrocytes do leave the blood stream under certain conditions, through the capillary walls. The duration of an erythrocyte in the blood stream is relatively short. Some determinations indicate that in the rabbit the life of a red blood corpuscle is about 8½ days; in the dog about 16 days. Their destruction and removal from the blood stream occur in different ways. They may be engulfed by phagocytes of the spleen or hemolymph glands, or they may first break down into small pieces which are taken up by certain leucocytes or by the endothelial cells of the liver. The bile pigments, formed principally by the liver, are derived from the hemoglobin of the erythrocytes.

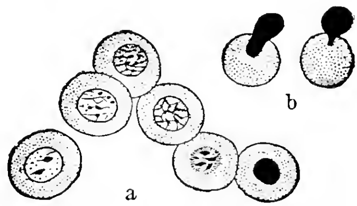


FIG. 88.—The development of red corpuscles in cat embryo. a, successive stages in the development of erythroblasts, b, the extrusion of the nucleus. (*From Stöhr, Textbook of Histology, by Lewis. P. Blakiston's Son and Company. By permission.*)

The leucocytes are nucleated and lack hemoglobin. The average number in a cubic millimeter of blood is 7,000. They may be divided into three classes: (1) *Lymphocytes*, forming about 23 per cent of the total; (2) *large mononuclear* leucocytes, 1 to 3 per cent; and (3) *polymorphonuclear* leucocytes, the remainder. The principal basis for this classification is the shape of the nucleus. In lymphocytes the nucleus is spherical and relatively large, the cytoplasm forming a narrow rim about it. Small lymphocytes measure from 4 to 7.5μ in diameter; large ones are twice this size. The mononuclear lymphocytes have a bean-shaped nucleus and may measure 20μ in diameter. They are phagocytic. The polymorphonuclear leucocyte has a nucleus consisting of a number of lobes, all connected by narrow strands. Polymorphonuclear leucocytes measure from 8 to 10μ in diameter. They are further subdivided according to the staining reaction of their cytoplasmic granules into *basophiles*, *eosinophiles*, and *neutrophiles*. All display amoeboid movement, particularly the neutrophiles, which are the most abundant form of leucocytes in the blood. They also emigrate from the blood vessels more readily than other types of leucocytes.

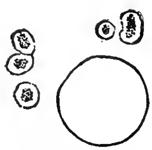


Fig. 89.—Blood plates beside a red corpuscle. (*From Stöhr's Textbook of Histology by Lewis. P. Blakiston's Sons and Company. By permission.*)

The blood *platelets* of human blood are non-nucleated fragments of the pseudopodia of the giant cells of the bone marrow. They have a circular or irregular outline, measuring from 2 to 4μ in diameter, and have centrally located granules and clear borders. They occur only in mammalian blood. When blood clots, fibrin is deposited in slender threads that radiate from disintegrating platelets; from this it is assumed that the platelets supply the clotting enzyme, thrombin, and accordingly, blood platelets are sometimes spoken of as *thrombocytes*. A similar function has been attributed to the spindle cells of the frog's blood (Fig. 89).

Functions of the Blood.—Blood is the nutritive stream that supplies the cells of the body with their requirements. The nutritive qualities of the blood are derived from digested food absorbed from the alimentary canal. The end products of digestion are: (1) sugar; (2) fat as such or in the form of its cleavage products, glycerin and fatty acids; and (3) amino acids. The sugar is absorbed by the capillary blood stream of the intestinal lining and is normally present in the blood plasma in a certain amount. Glycerin and fatty acids are synthesized into fat as they pass through the intestinal mucosa whence the fat is taken up mainly by the lymphatic system. Eventually this fat finds way into the blood and is found as a normal constituent of the plasma. Some fat is directly absorbed from the intestine by the blood. Amino acids, the end products of protein digestion, are absorbed as such by the blood from the intestine and are also normal constituents of plasma. Those portions of sugar, fat, and amino acid stored in the liver and muscles are later released into the blood stream. The blood also receives water and inorganic salts from the alimentary canal. It also carries oxygen and endocrines. In the case of the frog and certain other animals, a considerable amount of water may be taken through the skin into the blood. The blood also transports wastage.

Respiration.—In vertebrate animals and in some invertebrates too, the blood supplies the tissues with molecular oxygen. The source of oxygen is the air. The latter enters the body at the respiratory surface, which may be a gill, lung, or the body surface, from which it is then taken up, in the case of vertebrates, by the hemoglobin of the red corpuscles. Hemoglobin has a peculiar affinity for uniting with oxygen under certain conditions. If exposed to air, 100 cc. of blood plasma will, like an equal volume of water, absorb 0.56 cc. of oxygen at 20°C., at sea level. The amount of oxygen absorbed depends upon the partial pressure of the oxygen in the air, which is roughly one-fifth of the total atmospheric pressure. If the atmospheric pressure is increased, more oxygen will be absorbed; if decreased less. On the other hand, if defibrinated blood (blood from which fibrinogen has been removed, leaving corpuscles and serum) is exposed to air, it will absorb practically as much oxygen as it can be made to absorb under any higher pressure. Thus if the partial pressure of the oxygen is doubled, only as much additional oxygen is absorbed as the serum can take up, and this amount is very small. If the partial pressure of oxygen is reduced one-half, only a small amount is given off, and that comes from the serum. Since most of the oxygen of the blood absorbed under these conditions is unaffected by such pressure changes, it must be combined chemically in some way with something in the corpuscles. It has been shown that the substance in the corpuscles is the hemoglobin of the erythrocytes.

Oxyhemoglobin, the compound formed by oxygen and hemoglobin, is not stable at low pressures, for if the oxygen pressure to which it is exposed falls below 25 mm. of mercury, it dissociates completely and suddenly, all of the oxygen being given off. The pressure of oxygen in saturated arterial blood is equivalent to the pressure of 75 mm. of mercury, and since the oxygen tension of the tissues is zero, oxygen is readily given off to the tissues as the blood circulates through the systemic capillaries. Returning to the lungs with its oxygen tension reduced to 37.6 mm., the blood, in passing through the pulmonary capillaries, readily absorbs oxygen from the alveolar air, which has an oxygen tension of about 100 mm.

As a result of these properties the blood can absorb oxygen from the lungs and give it off to the tissues with great rapidity. At the same time, the absorption of oxygen is independent of small variations in atmospheric pressure.

The blood collects waste products of metabolism from the tissues and these leave the body through an excretory organ, such as the kidney, through skin as sweat (in mammals), and also through respiratory surfaces of the body and through the alimentary canal.

Carbon dioxide is an important gaseous waste product of cells. It is about 20 times as soluble in blood plasma as in oxygen. In the blood, part of it is held in solution in the plasma and the remainder in two forms of chemical combination: (1) in the form of sodium carbonate, and (2) in combination with blood proteins, including hemoglobin, forming a compound similar to oxyhemoglobin in the readiness with which it dissociates. The tension of carbon dioxide in the arterial blood entering the capillaries is about 35 mm., while that of the lymph and tissues is about 50 to 70 mm., so that there is a ready movement of carbon dioxide from the tissues to the blood. The carbon dioxide tension of the blood when it reaches the lungs is 42.6 mm. while that of alveolar air is 35 mm., as a result of which carbon dioxide leaves the blood.

The remaining excretory products are mostly in the form of solids in solution. In the dissolved state these substances are carried from the tissues by the blood to various excretory surfaces, the details of which will be discussed in connection with the general function of excretion.

Temperature Regulation.—About 90 per cent of the plasma of vertebrate blood is water. Some of the water that is excreted is water absorbed as such and some of it is metabolic water formed as a result of chemical reactions involved in metabolism. Water has greater solvent properties than any other substance, which is at least one of the reasons why it is important in cells. In mammals particularly, one of the functions of the blood is in connection with the regulation of body temperature, since, except under conditions of hibernation, normal metabolism requires that the body temperature be kept within rather narrow limits. A complicated mechanism is found in these animals for the maintenance of a fairly constant body temperature, only the broad outlines of which can be considered here. In the human body, a dilatation of peripheral blood vessels will increase loss of heat by radiation. Likewise, the activation of sweat glands covers the skin with perspiration, largely water, the subsequent evaporation of which appreciably lowers the body temperature. Contraction of the peripheral blood vessels tends to conserve body heat. Animals like dogs, when overheated, depend principally upon evaporation of water from the surface of the lungs. The same is true of birds.

Lymph.—Lymph consists of plasma, similar to blood plasma, and relatively few corpuscles, of which lymphocytes are the most abundant. Red corpuscles and polymorphonuclear leucocytes are usually absent. Strictly speaking lymph is the fluid contained in lymphatic vessels, though it differs but slightly from the body fluid found in spaces between the organs and body wall, or from the so-called tissue fluids occurring in microscopic spaces between cells. Except in the case of the contents of the lymphatics of the small intestine, which during digestion become gorged with fat, the lymph generally may be considered a part of the drainage system of the body, charged with excretory products, which eventually reach the blood system. Its movement is centripetal and thus comparable with the movement of the venous blood. Since the lymphatic vessels begin as capillaries in the tissues, the source of the fluid component of the lymph is from the blood.

In the human body, most of the lymphatic vessels are tributaries of the *thoracic duct*, which begins below the diaphragm by the confluence of the lymphatic vessels from the legs, abdomen, and viscera. It then passes anteriorly along the ventral side of the vertebral column, receiving branches from the thorax, left arm, and left side of the head, and empties into the *left sub-*

clavian vein near the heart. The right arm and shoulder, and the right side of the head are drained by a much smaller lymphatic trunk which opens into the *right subclavian vein.* Lymph nodes lie along the course of the lymphatic vessels, particularly those draining the neck, abdomen, axilla and groin. As the lymph filters through the nodes, lymphocytes from the nodes are added to the lymph stream. The nodes also act as checks to the spread of infection along the lymphatic channels.

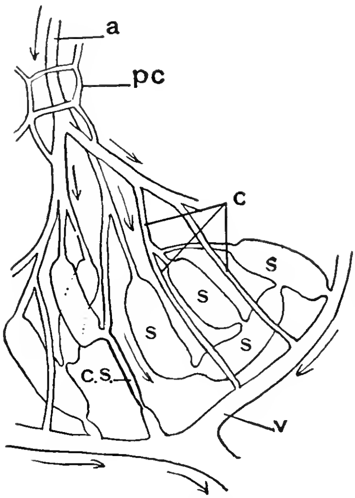


Fig. 90.—Diagram of vascular connections in spleen of rat. a, arteriole; c, capillaries passing directly to veins; c.s., conducting sinus, walls contracted; pc, peripheral capillaries (no sinuses); s, sinus, walls expanded by blood; v, vein; arrows indicate direction of blood flow. (*After Knisely.*)

From this it should be clear that the lymphatic and blood systems are merely parts of a general circulatory system. Each organ receives its primary blood supply from an artery. Most of this fluid leaves the organ by means of capillaries which unite to form veins. Some of it, however, mainly plasma, diffuses through the capillaries into tissue spaces and thence into lymph capillaries. Thus the lymph originates as an overflow of plasma from blood capillaries and accumulates cells as it moves along, in part, by immigration from the capillaries, but mostly from the lymph nodes. Since the cells are bathed by the lymph (tissue fluid), the lymph contributes nutritive material from the blood to the cells and at the same time takes from the cells metabolic products, part of which are carried away by the lymph and part by the venous blood.

Hemolymph Glands.—These glands resemble lymph glands, except that they have blood vessels in place of lymphatic vessels. Blood filters through the cells of the gland in much the same way as lymph filters through a lymph gland. During its passage through the gland blood loses red corpuscles, engulfed by phagocytic leucocytes, and gains lymphocytes, formed in the gland. Hemolymph glands occur in certain parts of the abdomen, thorax, and neck of mammals.

Spleen.—The spleen occurs as a distinct organ in all of the vertebrates except the Cyclostomata. In the frog it develops in the mesentery of the intestine; in man in the mesentery of the stomach. It has a rich blood supply but no lymphatic vessels, in which it resembles a hemolymph gland. The capillary circulation is peculiar in that in addition to the usual capillaries connecting arteries and veins there is also a series of venous sinuses in parallel with the capillaries. Thus arterial blood may reach the veins either through the capillaries or through the sinuses. The sinuses therefore serve as a by-pass to the capillaries, in which blood may accumulate in large quantities under certain conditions and be diverted from the general circulation (Fig. 90). In man the cells of the splenic tissue, known as the *spleen pulp*, consist of erythrocytes, lymphocytes, and phagocytic splenic cells resembling leucocytes.

The precise function of the spleen is unknown. It has long been thought to have to do with the normal destruction of red corpuscles, but agreement on this point is lacking. After a meal the spleen enlarges, reaches a maximum in five hours and then slowly contracts. The presence of venous sinuses accounts for the changes in volume, since these are brought about by the storage and release of blood from the sinuses.

CHAPTER VII

EXCRETION

Excretions are substances formed in the course of metabolism of cells. Such substances are in the nature of end products of chemical changes in the tissues and are useless as further sources of energy to the animal body. Not only are they useless but actually detrimental if allowed to remain in the body. A secretion differs from an excretion in that the secretion is of some definite use in metabolism, whereas the excretion is not. Gastric juice is a secretion of the glands in the stomach; urine is an excretion of the kidneys. Obviously undigested food, and inorganic salts and nitrogenous products of putrefaction absorbed from the alimentary canal, are not excretions. In man the major part of the solid excretions in solution, and certain substances occurring largely as by-products of digestion, absorbed from the alimentary canal by the blood, are excreted by the kidneys. On the other hand, the bile pigments, which are derived from broken-down erythrocytes and which are true excretory products, leave the body by way of the alimentary canal. Carbon dioxide, a gaseous excretory product, is eliminated by the respiratory organs—gills, lungs, or the surface of the body. In man some of the constituents of perspiration are excretory in character. Excretory substances are formed by and in the living tissues, from which they are collected by the blood and eliminated by various organs. A number of organs take part in excretion, but the kidney is unique in that the absorption of excretory products from the blood and the subsequent excretion of these products are its sole functions. The discussion of excretion therefore centers about the structure and function of the kidney.

Protonephridia.—One of the important functions of the blood is the collection or absorption of products of metabolism from the cells of the body and their transport to the excretory organ, which removes them from the blood stream. In some forms lacking a blood-circulating system, excretory products collect in the fluid of the body cavity from which they are removed directly by the kidney. In the group of flatworms (Platyhelminthes), in which neither a blood-circulatory system nor a coelomic cavity is present, a very primitive type of excretory organ is found consisting of numerous capillaries whose blind ends are formed of single cells, known as *flame cells* (Fig. 91). The flame cell is provided with irregular projections extending into the surrounding tissues and bears a bundle of cilia extending into the cavity of the capillary. The flickering movement of the cilia is like that of a flame. Leaving the flame cells, the capillaries unite to form large tubes, which eventually drain into one of two longitudinal ducts that open separately or by a single pore on the dorsal side of the posterior end of the body. Excretory products dissolved in water are absorbed from the surrounding tissues through the flame cells and the walls of the tubules, and are propelled through the tubes to the outside by the vibrations of the cilia. Such organs constitute a *protonephridial* system or a *water-vascular* system.

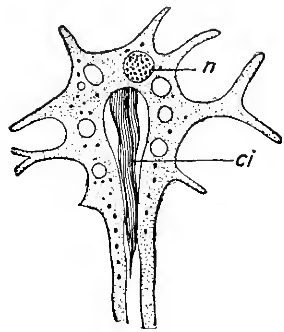


FIG. 91.—Flame cell of a protonephridium of a flatworm. *ci*, cilia within the funnel-shaped cavity of flame-cell; *n*, nucleus. (*From Hesse and Doflein after Lang.*)

Malpighian Tubules.—The hemocoel of insects is a poorly developed body cavity filled with blood. The Malpighian tubules of the grasshopper are a clump of fine hairlike tubules attached to the alimentary canal at the anterior end of the intestine, from which they extend into the hemocoel where they are bathed in blood (Fig. 53). They are blind at their free ends and open at their attached ends into the intestine. These tubes absorb nitrogenous and other excretory products from the blood and deposit them in the intestine, whence they pass out of the body with the feces. These products consist of urea, uric acid, urates of calcium, sodium and ammonia, as well as oxalates, carbonates and phosphates of calcium and potassium.

Nephridia.—The nephridial tubules of the earthworm are involved in connection with development of a coelomic cavity and a blood-vascular system, both of which are present in the earthworm. The earthworm is a segmented animal, which means that its body is made up of a linear series of more or less similar structural units called *segments*. The annulated form of the body is an external indication of segmentation. As a result, the body cavity instead of being a continuous space is subdivided by transverse septa, called *dissepimenta*, extending from the body wall to the intestine, in the planes of the annular

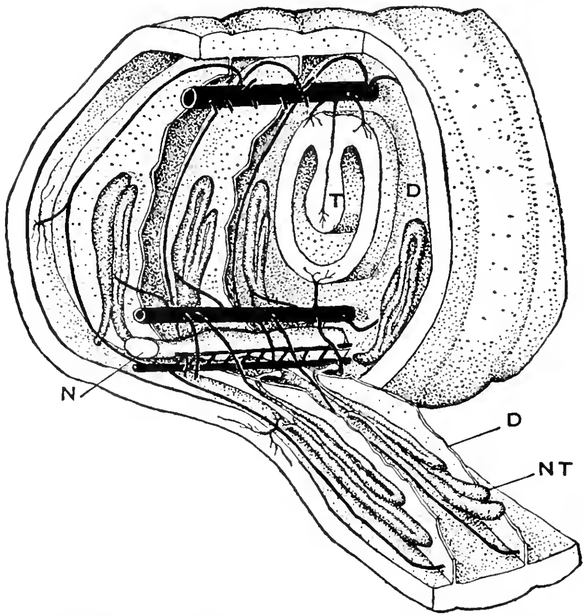


Fig. 92.—Stereogram showing the relations of organs in posterior segments of earthworm. The anterior end is to the right. A piece of the intestine has been removed and two dissepiments have been cut. Blood vessels are shown in black. The blood moves toward the anterior end (right) in the dorsal vessel and posteriorly in the subintestinal one. D, dissepiment; N, nerve cord; NT, nephridial tubule; T, typhlosole, a median longitudinal fold hanging from the dorsal wall of the intestine. (*After McGregor and Calkins.*)

grooves (Fig. 92). Thus each body segment has its own body cavity. In each of these cavities, except the first three and the last one, are two nephridial tubules, one on each side of the body. Five regions can be distinguished in each tubule, as follows: (1) a *ciliated nephrostome*, (2) a *ciliated neck*, (3) a *coiled narrow tubular* part, (4) a wide *glandular* portion, and (5) an *ejaculatory duct* opening to the outside by a *nephridiopore* (Fig. 93). The nephrostome, provided with a slit-shaped opening, projects through the anterior wall of the compartment in which the remainder of the tube lies, into the preceding compartment. Thus the nephrostome is in one segment and the nephridiopore in the following. Since the body cavities are filled with a colorless fluid or lymph containing corpuscles, excretory products dissolved in this fluid or in the form of solid particles can be drawn in by ciliary action through the nephrostome and eventually expelled to the outside through the nephridiopore. However, since the tubules as a whole are richly supplied with blood vessels, excretory material is probably also absorbed directly from the blood through the walls of the tubule.

Kidney of the Frog.—The kidneys of the frog lie against the dorsal wall of the posterior half of the body cavity, one on either side of the mid-line (Fig. 17). The ventral surface of the kidneys and their edges only are covered by the peritoneum, the dorsal surface being in direct contact with the body wall. The kidneys are therefore retroperitoneal. Each is flattened and oblong in shape and reddish in color. The yellow longitudinal band on the ventral face of the kidney is an *adrenal body,* which has nothing to do with the excretory function of the kidney. From the outer edge of each kidney a ureter passes back to open into the cloaca on its dorsal side near the mid-line. The functional unit of the kidney is the *uriniferous* or *renal tubule,* each of which bears a

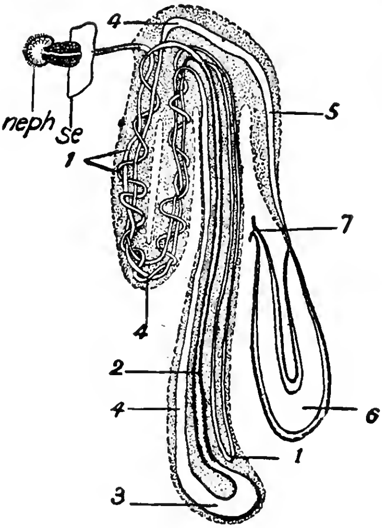


FIG. 93.

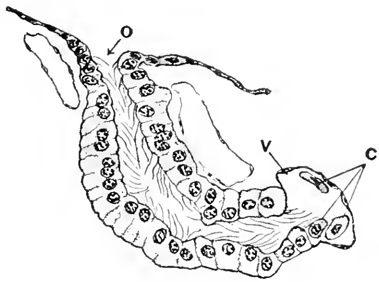


FIG. 94.

FIG. 93.—Nephridium of earthworm, schematic. *neph,* nephrostome; *se,* portion of septum; 1, neck and long narrow coiled part of tubule; 2, 3, 4, 5, includes two wide portions connected by narrow tube; 6, ejaculatory duct; 7, nephridiopore. (*From Hesse and Doflein after Maziarski.*)

FIG. 94.—Section of nephrostome of *Rana pipiens.* o, opening into nephrostome from ventral surface of kidney; v, vein, with contained blood corpuscles, c.

certain general resemblance to the nephridial tubule of the earthworm, in that both are segmental structures and both have nephrostomal connections with the body cavity, though in the frog this relation to the coelom is best shown in the embryo. The uriniferous tubules of the frog's kidney lack nephrostomes; but nephrostomes, no longer connected with tubules, are found as ciliated funnel-shaped openings on the ventral surface of the frog's kidney. These nephrostomes, strangely enough, have become secondarily connected with renal veins into which they

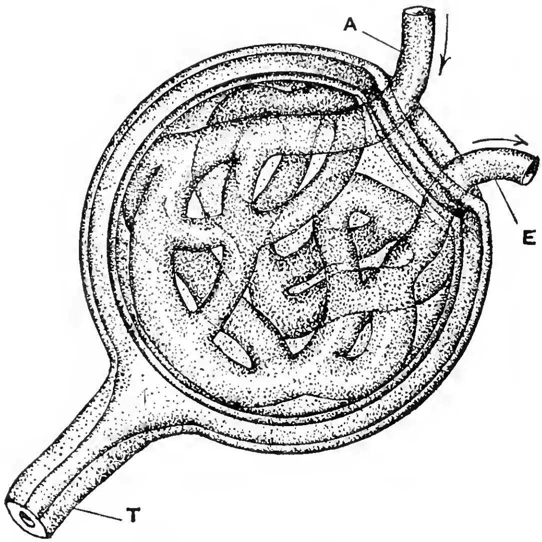


FIG. 95.—Diagram of glomerulus within capsule of uriniferous tubule, highly magnified. A, afferent artery; E, efferent artery; T, tubule. The arrows show the direction of blood flow.

draw body fluid from the coelom. This relation is found only in Salientia (Fig. 94). In other Amphibia and in the embryos of Salientia, the nephrostomes are connected with the renal tubules.

The blind nephrostomal end of the uriniferous tubule of the frog is provided with a double-walled capsule, enclosing a network of blood vessels, known as a *glomerulus*, in close contact with the inner wall of the capsule (Fig. 95). The outer wall of the capsule continues as a tubule, which after following a twisted course, during which it forms two loops, opens into a collecting duct, running transversely across the kidney, near the dorsal surface, from the inner margin to the ureter. The first loop of the tubule, lying in the dorsal region of the kidney is generally referred to as the *proximal convoluted tubule* and the second loop, the *distal convoluted tubule*. *Bidder's canal* is a longitudinal duct lying within the inner margin of the kidney roughly parallel to the ureter on the outer margin. The collecting ducts extend from Bidder's canal to the ureter. There are many collecting ducts and each duct has attached to it a number of uriniferous tubules. The capsular ends of the tubules are located in the ventral region of the kidney (Fig. 96).

The walls of the capsule are composed of thin flat cells which gradually pass over into a short columnar form in the tube proper. The first part of the tubule, next to the capsule, is the *neck*, so-called because its diameter is smaller than the rest of the tubule. The inner faces of the cells of the neck are provided with long cilia. Shorter cilia are also found in the cells of the tubule a short distance beyond the neck.

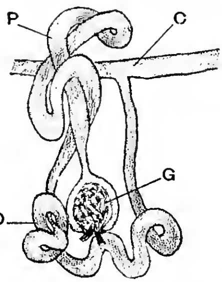


FIG. 96.—Uriniferous tubule and collecting tubule of frog's kidney. C, collecting tubule; D, distal convoluted tubule; G, glomerulus; P, proximal convoluted tubule. (*After Nussbaum.*)

The arterial blood supply to each kidney comes from four to six renal arteries. These enter the ventral surface of the kidney and send branches to both the capsular and the tubular portions of the renal tubules. Each glomerulus has an *afferent* and *efferent* artery. The kidneys also receive blood from the renal portal veins, which enter the dorsal surface of the kidney and form capillary networks about the tubules. The efferent arteries from the glomeruli join the capillaries from the renal tubules, from which the venous blood is drained by branches of the renal veins. The glomeruli therefore receive blood only from the arteries, but the tubular parts of the renal tubules receive blood both from the renal arteries and from the renal portal veins; mainly from the latter.

Excretory material is removed (1) by the capsule from the blood as it circulates through the glomerulus, and (2) by the remainder of the tubule as the blood flows through the capillary network about it. Opinion differs as to the manner in which the tubule functions, but subsequent observations tend to confirm the general conclusions reached by Nussbaum as the result of experiments made in 1875. Using *Rana esculenta*, Nussbaum cut off the circulation to the glomeruli by completely ligating the renal arteries. If a solution of a dye, indigo-carmine, is then injected into the venous system, the color is later found only in the loop of the tubule (proximal convoluted part) near the dorsal surface of the kidney, the other segments of the tubule remaining free of color. Practically no water is excreted. This shows that dyes are absorbed from the blood by the portion of the tubule supplied by the renal portal circulation. If a 10 per cent solution of urea is injected into the venous system instead of dye, the bladder becomes filled with urine in the course of two or three hours. This experiment shows that the uriniferous tubule, deprived of its glomerulus, is able to excrete urine under the stimulus of urea in the blood. Further, more recent work indicates that the urine is concentrated by the resorption of water in the distal convoluted tubule. Thus it would seem that the fluid absorbed from the glomeruli, largely water, as it flows down the tubule receives the specific excretion of the proximal convoluted region, the mixture being further modified by the resorption of water as it passes through the distal convoluted region.

Most of the nitrogen leaves the body in the form of urea, which is largely formed in the liver. Urine also contains inorganic salts such as sulphates, chlorides and phosphates of sodium, potassium, calcium and magnesium, as well as other substances in small quantities. There is evidence to show that in addition to most of the water, the glomeruli also excrete albumin, sugar, and inorganic salts.

The Bladder of the Frog.—The ureters open close together in the dorsal wall of the cloaca. The bladder arises as an evagination of the ventral wall of the cloaca, opposite the mouths of the ureters. In its fully developed state the bladder is attached to the cloaca at its point of origin by a narrow pedicle, beyond which it expands into a thin-walled, bilobed distensible vesicle (Fig. 17). It is lined with a stratified epithelium and contains plain muscle in its wall. The external opening of the cloaca is closed by a sphincter muscle. Urine passes from the ureters into the cloaca and collects in the bladder, from which it is expelled rather abruptly by the contraction of the muscles of the body wall.

The Human Kidney.—The human kidneys (Fig. 97) are bean-shaped retroperitoneal organs, attached to the dorsal body wall, opposite the last thoracic and the first two lumbar vertebrae. Each kidney is enclosed in a thin fibrous capsule, surrounded by loose fibrous tissue normally containing considerable fat. A ureter leaves each kidney from the concavity on the median side and proceeds to the bladder, a large saclike vesicle lying in the

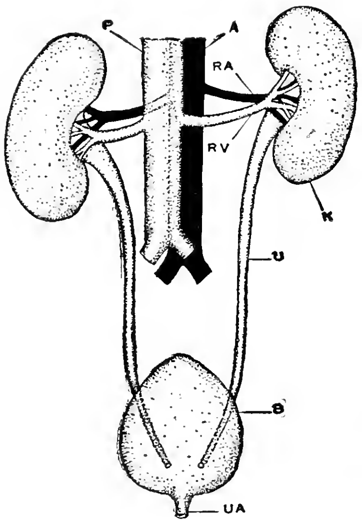


FIG. 97.

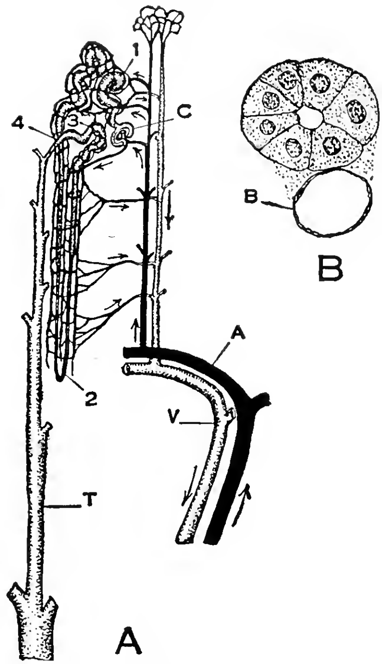


FIG. 98.

FIG. 97.—Excretory organ of Man, diagrammatic. A, aorta; B, urinary bladder; K, kidney (left); P, postcava; RA, renal artery (left); RV, renal vein (left); U, ureter (left), extends from the pelvis of kidney to the base of bladder; UA, urethra, a canal to the outside.

FIG. 98.—A. Diagram to show the relations between the blood vessels and the nephridial tubules of the human kidney. A, artery; C, capsule (glomerulus) 1 to 4, parts of tubule; T, straight collecting tubule which leads to the pelvis of the kidney; V, vein. The arrows indicate the direction of blood flow. B, section of the thick portion of a loop of Henle to show its relation to the blood capillary (B). (*Modified from Stöhr.*)

lower part of the abdominal cavity against the abdominal wall. A single duct, the *urethra*, leads from the bladder to the outside. A single renal artery brings blood to the kidney and a single renal vein drains it. There is no renal portal circulation. In the kidney the renal artery breaks up into smaller branches, some of which end in ordinary capillaries while others form glomeruli in the capsules of uriniferous tubules, before breaking up into capillaries about the loops of the tubules. Thus the blood supply to the tubule is entirely arterial. The tubule is somewhat more complicated in form and structure than in the case of the frog and consists of the following well-defined regions: (1) a *capsule* enclosing a glomerulus; (2) a *proximal convoluted portion;* (3) a U-shaped part composed of straight *descending and ascending limbs* of Henle's loop; and (4) the *distal convoluted portion* (Fig. 98). The distal convoluted portion is joined by an arched *collecting tubule* to a straight collecting tube, which leads to a *renal sinus* or *renal pelvis,* a chamber in the concave region of the kidney, drained by the ureter. The form of the tubule is such that the distal and proximal convoluted portions are very close to the capsule. The efferent arteries, after leaving the glomerulus, are distributed among the tubules, forming a capillary network leading to venous channels which eventually unite to form the renal vein.

Judging from experimental observations in rabbits, the mammalian uriniferous tubule functions in much the same way as the tubule of the frog's kidney. In the rabbit, excretion of solids in solution occurs in the proximal convoluted segment and in the descending limb of Henle's loop, and resorption in the ascending limb and in the distal convoluted segment. From the glomerulus water principally is excreted. It might also be added that in certain fishes, *Sygnathus* and *Hippocampus,* the uriniferous tubules lack glomeruli, yet urine is excreted containing dissolved substances in different concentrations than in the blood. All of this strengthens the idea that certain portions of the uriniferous tubule, exclusive of the capsule, excrete solids in solution and that other portions of the tubule modify the concentration of the solution by resorbing water.

It should be clear from what has been said that the organ of excretion, whether it be gill, lung, skin, or kidney, is merely a means of ridding the body of waste matter. The circulatory fluid transports excretory substances, formed by the body cells and to a certain extent in the circulatory fluid itself, conveying them to the excretory organ. The excretory organ is the eliminator. In the absence of a circulatory system, the excretory organ absorbs the metabolic products in a more direct manner from the cells.

CHAPTER VIII

MEANS AND METHODS OF REPRODUCTION

The reproduction of an individual organism begins with the separation from the parent of a part of its body, which is of course alive and continues to live as it progresses through developmental stages to the adult condition. Reproduction is a method of continuing life rather than one of creating life. It results in the production of generations of new individuals which, however, are derived from the preceding generations through living material. Single-celled animals, Protozoa, reproduce by the division of the entire animal. This also occurs in some of the lower metazoan animals. In all of the Metazoa, regardless of the occurrence or not of reproduction by simple division of the animal as a whole, there is a form of reproduction in which the development of a new individual starts in an egg that is usually fertilized by a spermatozoon. Both egg and spermatozoon are cells, so that the morphology of the elements out of which the new individual is produced is quite different from the morphology of the adult animal. The organism in all transformations undergone from the egg stage to the adult stage is a living thing. Life does not start at the hatching of the frog tadpole or at the birth of a human being. Life started in the far distant past and has continued in those kinds of organisms still alive at the present time. Extinct species are forms which for one reason or another ceased to produce descendants.

The organs of reproduction are the ovaries and testes, also known as *gonads*. In many invertebrates both ovary and testis are present in the same individual, in which case the animal is said to be *monoecious* or *hermaphroditic*. Other invertebrates and most vertebrates are *dioecious*, which means that two sexes are present and that ovaries are present only in the female and testes in the male. Sometimes, as in some of the Mollusca, there is a single gonad, the *ovotestis*, one portion of which produces eggs, the other spermatozoa; or the ovotestis may at one time function as an ovary, at another time as a testis, a condition known as *dichogamy*. Ova or eggs are produced in the ovary and spermatozoa or sperm cells in the testis. Ova and spermatozoa are spoken of generally as germ cells or *gametes*. In the method of reproduction known as *amphigony*, a spermatozoon (in some cases several) enters the egg and forms an *oosperm* or fertilized egg or *zygote*, which develops into a new individual animal. The details of the process of fertilization vary, but its essential feature is the union of a nucleus derived from the sperm cell with the egg nucleus. If more than one sperm cell enters the egg, as for example in the hen's egg, only one sperm nucleus combines with the egg nucleus. Fertilization may take place before or after the egg leaves the body of the female. In *parthenogenesis*, the egg develops without the intervention of the spermatozoon. Some eggs develop either parthenogenetically or in response to fertilization. Usually an egg requiring fertilization for its development does not develop parthenogenetically, under normal conditions. An *oviparous* animal is one in which the young are hatched from eggs laid by the female. A *viviparous* animal gives birth to its young. Both methods of producing young occur in both invertebrates and vertebrates.

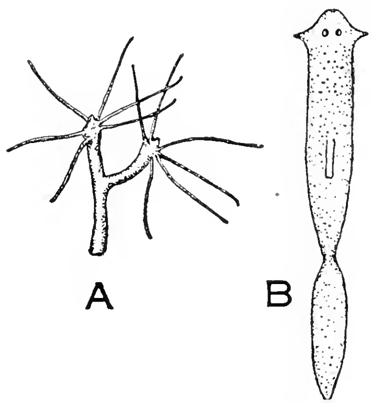


FIG. 99.—A, fission in Hydra by longitudinal division. (*After Koelitz.*) B, fission in Planaria. (*After Child.*)

Agamic Reproduction.—Some animals reproduce by *fission*, which consists in a division of the entire body into two parts of approximately the same size. Since no gametes or germ cells are involved, fission is an agamic or asexual form of reproduction. Another form of this type of reproduction is *budding*, which differs from fission in that the process starts with the formation of a bud on the surface of the body. The bud enlarges, differentiates, and finally detaches itself as a small fully formed new individual. Both fission and budding occur in Hydra. Fission takes place by a longitudinal splitting, beginning at the distal end and extending down through the basal disk, or by a transverse constriction across the middle of the body, the result in either case producing eventually two complete but smaller animals (Fig. 99). Budding in Hydra starts with the formation of a bulge in the body wall which takes on a cylindrical form with a circlet of tentacles developing at the free end of the cylinder. When fully grown, the bud is released as a new, free individual (Fig. 219). Euplanaria is another common laboratory animal in which fission occurs (Fig. 99).

Gamic Reproduction.—Gamic or sexual reproduction is repro-

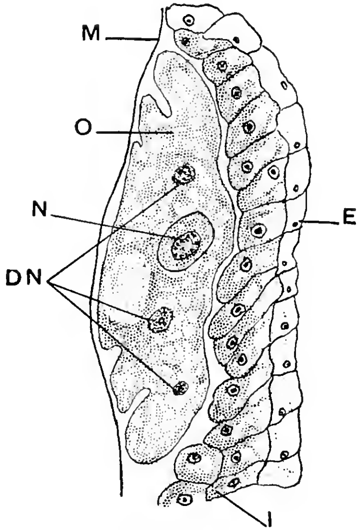


Fig. 100.

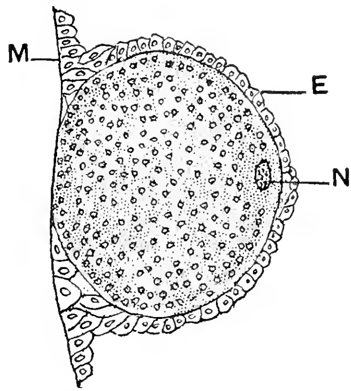


Fig. 101.

Fig. 100.—Section of mature ovum. DN, degenerating nuclei of interstitial cells contributing to formation of ovum; E, ectoderm; I, interstitial cells; M, mesoglea; N, nucleus of ovum; O, ovum. (*After Tannreuther.*)

Fig. 101.—Section of ovary of *Hydra*, showing developing ovum.

duction from an egg whether fertilized or not. It occurs in all metazoans, even in those that reproduce by fission or budding. Thus in Hydra, the gonads, which are not present at all times, develop as localized proliferations of the *interstitial* cells of the ectoderm. The spermaries or testes, containing numerous spermatozoa, form as round protuberances near the oral end, while the ovaries, somewhat similar in shape, are formed near the aboral end (Fig. 221). Within each ovary a single cell enlarges to form an egg by the rather unusual method of engulfing surrounding interstitial cells (Figs. 100 and 101). Thus a single cell becomes an egg at the expense of neighboring cells. Hydra is hermaphroditic, but since the ovary and testis of the same animal usually do not mature at the same time, the egg in most cases is fertilized by a spermatozoon from another animal. In this way the occurrence of self-fertilization is reduced to a minimum. When fully developed, the walls of the spermaries rupture, releasing free-swimming spermatozoa into the water. When the egg is mature, the wall of the ovary is partially ruptured, thus exposing a portion of the free surface of the egg, through which a spermatozoon may enter. The fertilized egg remains attached to the wall through the early stages of development, after which it is released and completes its development as an independent organism. In Hydra and other invertebrate animals of a relatively simple structure, the release of the germ cells from the gonads is accomplished by the rupture of the enclosing body wall, but in more complex animals, in which the gonads are located internally, ducts and other accessory structures are present for bringing the germ cells together or for conveying them to the outside of the body, either before or after fertilization. The female genital tract consists usually of a pair of *oviducts*, one for each ovary, through which the eggs pass to the outside and which, as in the frog, also provide the eggs with egg envelopes or capsules. In viviparous animals a portion of the oviduct is modified into a *uterus* in which the embryo develops until birth. The so-called uterus of the frog is merely an enlarged storage region in the oviduct in which eggs accumulate. In a true uterus nutrition is supplied to the embryo by the walls of the uterus. The *vas deferens* of the male corresponds to the oviduct of the female. It conveys spermatozoa from the testis to the outside. In the male there may also be a *penis*, an intromittent organ for introducing sperm cells into the genital tract of the female in those cases in which the eggs are fertilized internally. Internal fertilization occurs in all viviparous animals and in many oviparous ones as well. So far as development is concerned, the difference between oviparous and viviparous forms consists in the fact that in the former embryonic development takes place after the egg is laid, and in the latter embryonic development is completed before birth.

Among segmented worms, *Annulata*, and also among *Vertebrata*, there is a close relationship between the accessory parts of the reproductive system and the tubules and ureter of the excretory organs, both in embryonic development and in the adult state. Thus the vas deferens of vertebrates is a modified excretory duct (Wolffian duct) and some of the tubules of the testis are modified uriniferous tubules.

Reproduction in the Earthworm.—The manner in which reproduction takes place in the earthworm illustrates the process in a hermaphroditic animal, somewhat higher in the scale than Hydra. The testes of the earthworm consist of two pairs of organs lying

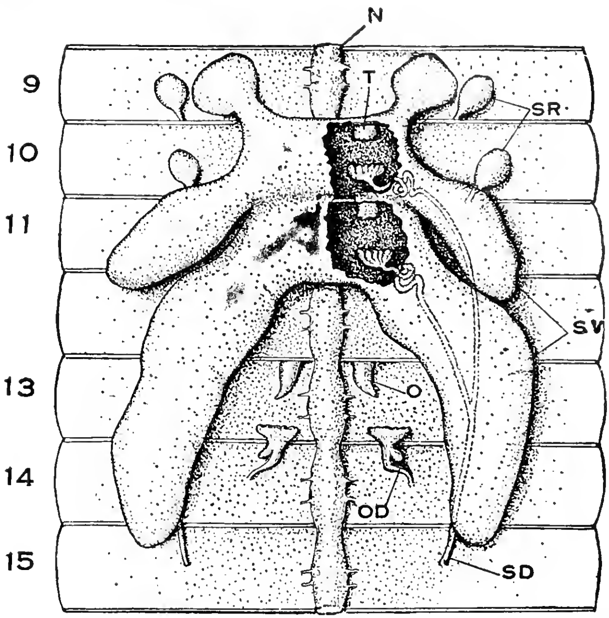


FIG. 102.—Diagram of the reproductive organs of earthworm. N, nerve cord; O, ovary; OD, oviduct; SD, sperm duct (vas deferens); SR, sperm receptacles; SV, sperm vesicle, with part of the roof removed to show the testes, T, and the funnels of the sperm ducts.

in the body cavity, one pair on the posterior side of the anterior wall of segment 10, and the other pair in a similar position on the anterior wall of segment 11. These same segments each contain a pair of ciliated funnel-shaped openings of the sperm ducts or *vasa deferentia.* Two ducts of the same side unite posteriorly to form a single duct or vas deferens, which opens externally on segment 15. Three pairs of *seminal vesicles,* communicating with each other, extend over segments 9 to 15. Those belonging to segments 10 and 11 enclose the testes and the mouths of the sperm ducts. When the sperm cells reach a certain stage of development, they are liberated from the testes and complete their development in the confines of the seminal vesicles. At the proper time they escape from the seminal vesicles through the four mouths of the sperm ducts (Fig. 102).

The ovaries of the earthworm are two in number, situated one on each side of the mid-line on the posterior surface of the anterior wall of segment 13. As the eggs mature, they burst from the ovaries and are conveyed to the outside through a pair of *oviducts*, each of which begins in a funnel-shaped opening located on the posterior wall of segment 13 and terminates in an opening on the outside of segment 14.

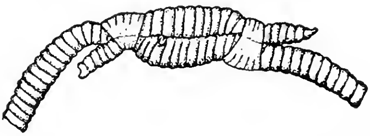


FIG. 103.—Copulation in *Helodrilus foetidus*. (*After Foot.*)

The *seminal receptacles* or *spermathecae* are two pairs of sacs in segments 9 and 10. At the reproductive period these sacs are filled with sperm from another worm in the manner to be described presently. Later the sperm cells are emitted to fertilize the eggs.

According to the observations of Grove on the common earthworm, *Lumbricus terrestris*, two worms oppose each other in a head-to-tail position in such a manner that segments 9 to 11 of one worm are opposite the ventral surface of the *clitellum* of the other. The clitellum is an enlarged region of the body composed of segments 32 to 37. At these points the worms become firmly bound together by bands of mucus secreted by the epidermal cells which soon hardens into a thin membrane (Fig. 103). There is also a slighter attachment between segment 15 of one and segment 26 of the other. A slime tube, composed of mucus, is then secreted about each worm, save at the ventral surfaces in intimate contact between segments 9 and 37. Seminal fluid containing spermatozoa then issues from the openings of the vasa deferentia in segment 15 and passes back through temporary grooves beneath the slime tube in the body wall to the clitellum. Emission of seminal fluid takes place in each worm

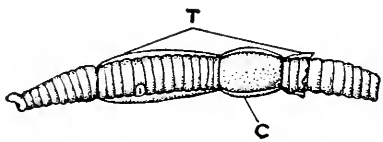


FIG. 104.—The formation of a slime tube by a single worm at some period after copulation. C, cocoon formed about the clitellum; T, slime tube. (*After Foot and Strobell.*)

though not always at the same time. The spermatozoa gradually accumulate between the clitellum and the lateral surface of segments 9 and 10, and then pass into the spermathecae. What takes place next is uncertain so far as the earthworm is concerned. In a related species, *Eisenia foetida*, the Brandling worm, according to Grove and Cowley, the worms separate after the spermathecae are filled and each worm forms a slime tube extending from segment 7 to some point beyond the clitellum; the portion enclosing the clitellum forming the cocoon (Fig. 104). Eggs are then discharged from the oviducts and pass back to the cocoon. It remains to be determined whether the spermatozoa also pass back to the cocoon while the slime tube is still in place or whether they are pressed into the cocoon when the worm wriggles out backward from the slime tube. At any rate, the eggs are fertilized in the cocoon, whose ends later contract to form a closed capsule as the worm withdraws. Apparently the supply of sperm is not exhausted in fertilizing the first batch of eggs, since single worms may form a number of slime tubes, with cocoons, a number of times after copulation. Each of these later slime tubes is shed after eggs and sperm have been deposited in the cocoon (Fig. 105).

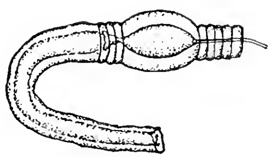


FIG. 105.—Appearance of slime tube after shedding. (*After Foot.*)

Reproduction in the Frog.—The frog is an example of an oviparous vertebrate whose eggs are fertilized externally. The testes of the frog are a pair of yellow ovoid bodies, each attached by a *mesorchium* to the dorsal body wall at the anterior border of the kidneys. Spermatozoa, formed in the testis, leave through a number of fine ducts, the *vasa efferentia*, extending from each testis to the inner border of the kidney. The vasa efferentia enter the kidney and open into Bidder's canal (Fig. 106), from which the passageway for the spermatozoa is continued through the collecting tubes of the kidney to the ureter. Near the termination of the ureter in the cloaca is an enlargement, the *seminal vesicle*, where the spermatozoa are stored until *amplexus*, the sexual embrace, takes place, when they are discharged through the cloaca. The ureter and some of the collecting ducts of the kidney in the male thus serve as genito-urinary passages. In the female these parts are urinary passages only.

The ovaries are a pair of lobulated organs, each of which is attached by a *mesovarium* to the dorsal body wall just in front of the kidney. The paired oviducts or Mullerian ducts are long convoluted tubes, each of which is provided with an opening or *ostium* at its narrow anterior end and a widened region or uterus near its posterior end just before it enters the cloaca. Since the ostia of the oviducts are located in the region of the pericardium, near the base of the lungs, they are separated by some distance from the ovaries. When the eggs formed in the ovary are mature, they escape into the body cavity through the rupture of the walls of the egg follicles and are carried by ciliary movement over the ciliated surface of the liver, body wall, and pericardium to the ostia where they are engulfed. In the upper parts of the oviducts the eggs receive a coating of thin albumen and then pass into the uterus where they are stored until spawned. Oviducts are developed in both males and females, but in the former they become reduced in size and remain functionless (Figs. 17 and 18).

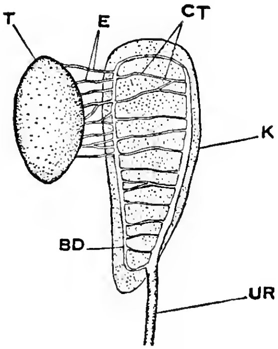


FIG. 106.—Diagram of urogenital organs of male frog, left side. BD, Bidder's duct; CT, collecting tubules of kidney, which also receive uriniferous tubules, not shown; E, vasa efferentia, through which sperm from testis reach Bidder's duct; K, kidney, shown in section T, testes; UR, ureter.

Fat Body.—At the anterior end of each of the gonads of both sexes of the frog is the fat body, a conspicuous mass of fatty tissue drawn out into finger-shaped lobes (Fig. 18). Its development is closely associated with the development of the gonad, in consequence of which the fat bodies are thought to represent degenerated segments of the embryonic rudiment from which the gonads develop. In temperate zones spawning takes place in the first warm days of spring that signalize the end of hibernation and the resumption of more active life. The fat bodies retain their full size throughout the period of hibernation but just before the beginning of the breeding season they undergo a reduction in fat content that continues until spawning is completed. The fat bodies thus serve to meet the energy requirements of the developing germ cells and of the bodily activities of the frog before active feeding is resumed. The fat may be drawn upon to meet metabolic requirements at other times, but the greatest demand arises in connection with breeding activities. Once these are completed, fat begins to accumulate in the fat bodies until by autumn they are restored to the maximum size.

Amplexus.—In amplexus the male embraces the female from the dorsal side, clamping its forelegs about the female just behind the latter's forelegs, firmly gripping the body of the female with the enlarged sexual pad of the first digit of each hand. Captured female frogs may lay eggs in the laboratory in the absence of males, but under natural conditions amplexus acts as a stimulus to spawning. Amplexus takes place in the water. Under its stimulus the female sheds its eggs and as the latter pass from the cloaca, the male emits sperm over them. The amplectant posture persists for three or four days until all the eggs are shed.

When the eggs leave the female cloaca, the thickness of the capsule of the surrounding jelly is less than one-half the diameter of the egg. A single spermatozoon now enters each egg, after which the capsule absorbs water and swells to two or three times its original thickness. At this time it can be readily seen that the capsule is really composed of three layers. The gelatinous capsule is comparable to the white of the hen's egg and serves as a protective covering. The jelly also serves another function in retaining heat absorbed from sunlight. The jelly seems to transmit the shorter rays but checks the loss by radiation of the longer heat waves from the egg.

Intrauterine Development.—The young of viviparous animals, whether invertebrates or vertebrates, are brought forth in a more or less fully developed state. What happens in the majority of cases, among invertebrates and among vertebrates below Mammalia, is that the large-yolked egg after fertilization remains in a specialized portion of the oviduct, known as the uterus, and develop there instead of outside the body. Thus in viviparous fishes and snakes, the yolk of the egg seems to be the main source of nutrition for the embryo, though an organic attachment of the egg to the wall of the uterus may occur in some cases, as in *Mustelus*, a common viviparous shark (Fig. 107). All mammals are viviparous with the exception of the lowest group, the *Prototheria*, which are oviparous. The uterus of viviparous mammals is a modified region of the oviduct whose walls are highly vascular and come into close enough contact with the egg, and later the tissues of the embryo, to supply the latter with nutrition and oxygen and to remove carbon dioxide and other waste products of metabolism. The eggs of such mammals are small in size and contain an insufficient amount of stored nutrition in the form of yolk to carry development beyond the very earliest stages.

Both the tissues of the uterus and the tissues of the embryo participate in the formation of a *placenta*, which is an organ that

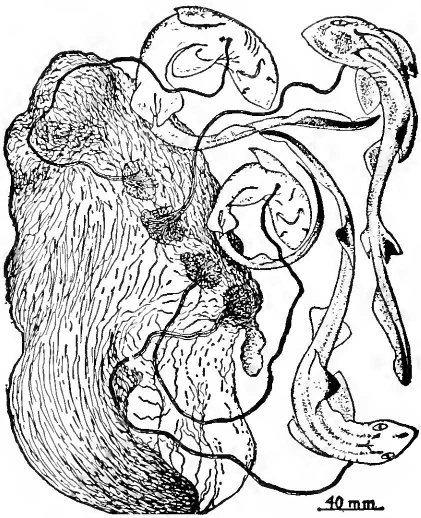


FIG. 107.—Embryo sharks of a viviparous species, *Mustelus mustelus*, attached to the walls of the uterus. The expanded end of each umbilical cord forms a placenta-like structure, resembling that of mammals, through which the young are nourished. (*From Shull, LaRue, and Ruthven, Animal Biology, after Fowler.*)

develops during the period of gestation. The placenta is thus a composite organ which differs in detail in different mammals. The maternal and embryonic blood streams are never confluent in the placenta, but they are brought close enough together to permit the diffusion of gases and substances in solution through the intervening tissue. The mammalian egg is released from the ovary by the rupture of the ovarian wall and enters the oviduct, in the upper part of which fertilization takes place. The fertilized egg begins to develop as it passes down the oviduct to the uterus where it becomes attached more or less firmly to the lining of the uterus. The placenta then begins to develop and with it the development of an *umbilical cord* through which blood vessels of embryonic origin pass from the embryo to the placenta. In some mammals, the pig for example, there is at birth a clean separation of the embryonic from the uterine portion of the placenta; in other mammals, as in Man, some of the uterine portion is shed along with the entire embryonic portion, the whole being known as the *afterbirth.* The uterine tissues, lost at birth or parturition, are soon restored by the uterus. The

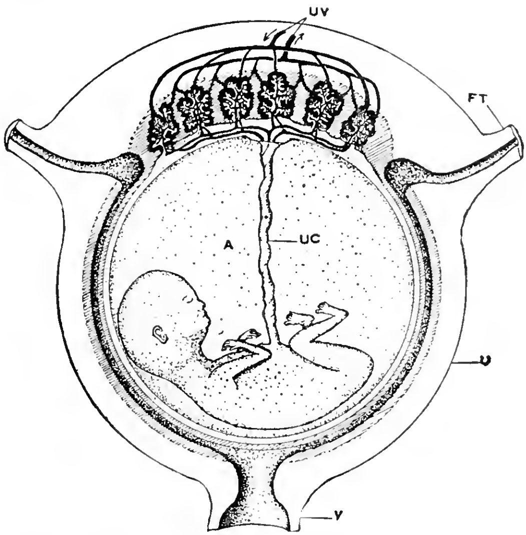


FIG. 108.—Diagram of gravid human uterus, anterior wall removed. A, amniotic cavity, filled with fluid in which the foetus (late embryo) rests; FT, Fallopian tube (oviduct); U, uterus; UC, umbilical cord, containing foetal arteries and veins through which blood circulates to and from the placenta, pumped by the foetal heart; UV, uterine vessels, carrying maternal blood to and from the placenta; V, vagina. The shaded portions of the uterus are shed at birth.

young are expelled by the contractions of the muscular walls of the uterus. In Man, the *navel* is the place on the abdomen where the umbilical cord was attached during intrauterine development (Fig. 108).

General.—The organs of reproduction, the ovary and the testis, as has been said before, are those producing germ cells, ova and spermatozoa, which, when united, are capable of reproducing a new animal. Both egg and sperm are merely detached portions of the parent body, possessing the capacity, when brought together under proper conditions, of developing a new individual. In parthenogenesis the ovum alone can do this.

Though a part of the body, the germ cells remain distinct from body cells, and when favorable conditions arise for the union of ovum with sperm, they proceed forthwith to display their remarkable developmental energy. Any other cell, such as muscle or liver cell, does not have this reproductive power, yet each, like the germ cell, has its origin in the fertilized egg. In becoming specialized body cells, it seems that the tissue cells lose the reproductive capacity, which must have been latent in them at the beginning. Germ cells, on the other hand, retain it because they do not differentiate into tissue cells. It would follow that once a cell has developed into a tissue cell, it can never afterward function as a germ cell. This is true in most animals, there being some apparent exceptions among invertebrates like the *Coelenterata*, where the germ cells develop from time to time from differentiated endoderm or ectoderm. Obviously, in such cases differentiation of body tissues even in the adult does not proceed so far that a return to an unspecialized state is impossible.

CHAPTER IX

THE NERVOUS SYSTEM

The nervous system is concerned with the perception of stimuli by *receptors,* the *coordination* of stimuli, and the *conduction* of nervous impulses to *effectors.* Receptors may be simple, unmodified nerve endings, such as occur in the lower layers of human epidermis, or nerve endings, sometimes highly specialized and intimately related with nonnervous structures, the whole forming a sense organ, such as the eye or the ear. Responses to sensory stimulation are manifested in movements of muscles or secretory activity of glands, both of which are the usual effectors. The coordination of the incoming sensory impulses and the responses is the function of nerve centers, such as the brain and the spinal cord. It should be noted that a chemical method of coordination also exists, examples of which were discussed in connection with the secretion of digestive fluids and of which further examples will be considered in the following chapter, dealing with the endocrine organs. *Sensation* is something produced in the central nervous system, dependent upon the nature of the connections of the nerve fibers carrying the afferent impulses. Afferent nerve fibers normally are stimulated by their receptors, but if a given afferent nerve is stimulated at any point the sensation is always the same. We know the nature of sensations in animals other than Man only by comparing their responses with our own, under similar conditions. Since sensations are entirely subjective, there must be considerable variation in both quantity and quality of sensations produced by the same sensory stimulation in different individuals.

Reduced to simple terms, the functions of the nervous system and sense organs are: (1) to bring about in the organism appropriate responses to external stimuli, and (2) to coordinate the functional activity of different parts of the body by nerve pathways. *Irritability* and *conductivity,* two properties manifested by all forms of protoplasm, are highly developed in nervous tissue, and all nervous phenomena are based primarily on these two fundamental properties. Since Protozoa respond to the same stimuli that activate the nervous system of Metazoa, it is clear that the action of the nervous system as a receptor-effector and coordinating mechanism involves nothing new in principle. Nerve cells may be regarded as cells that have become especially sensitive to stimulation of various sorts and that have also developed the capacity to conduct or transmit nervous impulses at a very rapid rate. A *stimulus* may be defined as any disturbing influence. A *nerve impulse* results from action of the stimulus. The impulse travels along the nerves by conduction, which is essentially a series or chain of chemical reactions running through the nerve, accompanied by the production of extremely small amounts of heat and carbon dioxide.

Neuron.—A neuron is a nerve cell. It is the anatomical and to a certain extent the functional unit of the nervous system. Neurons vary considerably in both size and shape in different animals and in different parts of the same animal, but in all cases the neuron consists of at least two regions: (1) a nucleated *cell body*, and (2) *processes* extending from the cell body. In higher forms the processes can usually be classified both on a structural and on a functional basis into two groups: (1) *dendrons* or *dendrites*, consisting of one or more processes, often branched, that convey nervous impulses toward the cell body; and (2) a single *axon*, that transmits impulses away from the cell body. Since the neuron as a whole under normal conditions carries impulses in one direction only, it is said to be polarized. Dendrons may be lacking in some neurons, and in others a single dendron may be present and so similar to the axon in form and structure as to be almost indistinguishable anatomically. The drawing of the neuron from the human brain, shown in Fig. 109, illustrates a highly complicated type. The cell body is the pear-shaped region in the center of the figure. The nucleus cannot be seen because the preparation only shows the entire nerve cell in silhouette. A number of dendrons with collateral branches are attached to the cell body, above and at the sides. The single axon leaves the cell body below and then divides into collateral branches, the main axis of the axon extending downward to join a bundle of nerve fibers. The term "nerve" refers to a bundle of axons or dendrons, or both, bound together by a connective tissue sheath. Axons or dendrons are also known as nerve

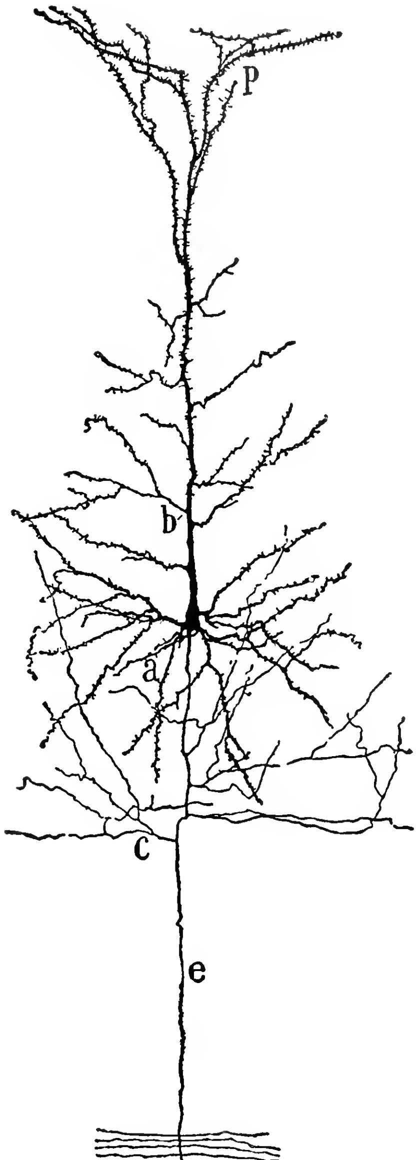


FIG. 109.—A nerve cell from the cerebral cortex. *a*, basal dendrons; *b*, apical dendron; *c*, collaterals of axon; *e*, axon; *p*, apical dendrons ending in branches near the surface of the brain. *(From Schäfer, Textbook of Microscopic Anatomy, Longmans, Green & Company, after Cajal. By permission.)*

fibers. An *afferent* or *sensory* nerve is one composed of dendritic fibers and one that conducts impulses from the surface of the body, or from some outlying point, to a centrally located nerve center, such as the brain or spinal cord. An *efferent* or *motor* nerve is made up of axons and transmits impulses in the opposite directions. Efferent nerves are called motor nerves because their stimulation commonly produces muscular contraction, which in turn produces movement of the body as a whole or in part. Experimentally the direction of the impulse through a nerve may be changed, though normally the direction is from dendron to cell body to axon.

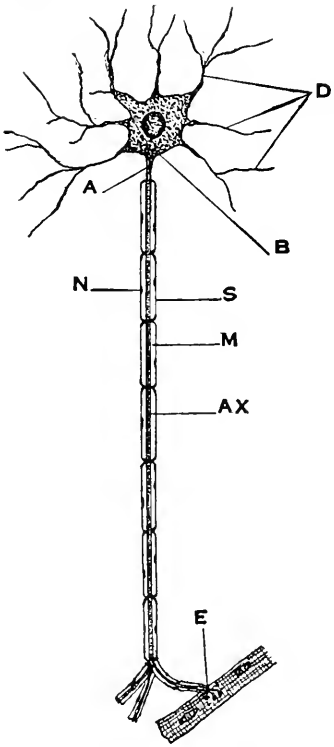
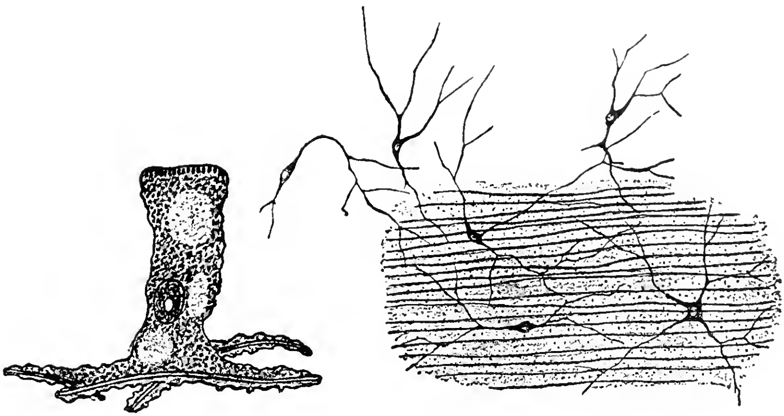


FIG. 110.—Diagram of a vertebrate motor neuron with a medullated axon. A, axon; AX, axis cylinder; B, cell body; D, dendrons; E, motor end organ in contact with muscle cells; M, myelin sheath; N, nucleus of sheath cell; S, one of the cells forming a sheath enclosing the myelin.

A *ganglion* is a mass of nervous tissue consisting largely of nerve cell bodies. In higher forms, nerve cell bodies are confined to ganglia, special nervous epithelia, and nerve centers such as the brain and spinal cord. Different levels of the brain and spinal cord are connected by nerve tracts, composed of nerve fibers, which are comparable to the peripheral nerves connecting the central nervous system with various parts of the body. Many of the connecting pathways of the brain and spinal cord consist of neurons lying entirely within the central nervous system.

A *medullated* nerve fiber is one provided with a sheath of white fatty material known as *myelin*. The axis cylinders of the spinal nerves of vertebrates in addition are provided with a *neurilemma* composed of delicate sheath cells surrounding the myelin (Fig. 110). Medullated fibers of the brain and spinal cord do not have sheath cells. Nerve fibers of the sympathetic system, to be discussed later, lack myelin but are provided with sheath cells. Finally, nerve terminations may consist of *axis cylinders* (naked axons) only.

The entire nervous system, including the sensory portions of the sense organs, develops from the ectoderm, with the possible exception of taste cells, which in some cases of vertebrates at least are said to be endodermal in origin. An ectodermal origin of the nervous system is what one would expect since the ectoderm is the primitive outer covering of the body and therefore the



A B

Fig. 111.—Nervous mechanism of Hydra. *A*, epitheliomuscular cell from ectoderm; *B*, ectodermal nerve plexus. The long fibrils in the background are the contractile parts of epitheliomuscular cells. They lie in the mesoglea. (*From Schneider.*)

portion of the body through which the environment is sensed. Neurons apparently are ectodermal cells that have gradually taken on a nervous function, accompanied by structural differentiation from other ectodermal cells.

Diffuse Nervous System.—A primitive form of nervous system is found in Hydra and related forms, consisting of nerve cells with branching processes, located in the ectoderm. The cells are arranged in a loose network, showing no marked tendency to be concentrated at any points to form nerve centers or ganglia. The nearest approach to centralization is about the mouth (hypostome) where the nerve cells are more numerous than elsewhere. The arrangement of the nervous system of Hydra suggests a crude mechanism for receiving stimuli and correlating responses, such as one might expect in the early stages of the evolution of the nervous system. The system has remained at its site of origin in the surface layer of the body (Fig. 111).

Primitive Ganglionic Nervous System.—The nervous system of a flatworm, such as *Euplanaria*, illustrates an early step in the process of centralization of a portion of the nervous mechanism. This has been brought about by the development of a pair of *cephalic ganglia*, in the anterior end of the animal, from which a pair of *nerve cords* extends posteriorly to the tip of the body. Both the ganglia and the nerve cords are completely covered over by the integument. From both ganglia and nerve cords, nerve fibers extend to various parts of the body. The anterior end of the body is provided with special *sense organs*, such as eyes, tactile organs, and organs of chemical sense. The concentration of sense organs at the anterior end is correlated with the presence there of the cephalic ganglion, the general result of which is to convert this region of the body into a "head end." When Euplanaria explores new territory, the part of the body that leads the way is the head end, which is the part best fitted with means of sensing the environment. Thus the cephalic ganglion may be regarded as a kind of brain that serves as a center for correlating the sensory and motor mechanism. As a result the head end assumes a position of dominance or control over the activities of the rest of the body. That the head end of Euplanaria is dominant in a physiological sense has been demonstrated by experiments that show that the rate of metabolism is higher in the head end than elsewhere. The evolution of a head end, *i.e.*, *cephalization*, is bound up with the evolution of the nervous system and sense organs (Fig. 52).

Ganglionic Nervous System.—A further elaboration of the type of nervous system found in flatworms occurs in a large number of invertebrates such as segmented worms (Annelida), and crabs, spiders and insects (Arthropoda). In these forms the general functional significance of the ganglia is the same as in the flatworms, but the arrangement and specific forms of the ganglia are influenced by a morphological factor, segmentation, that is absent in flatworms. A segmented worm, such as an earthworm, differs from a flatworm, among other things, in that the body of the earthworm is composed of a linear series of parts, called *segments* or *metameres*, of which mention was made in connection with the discussion of the excretory and reproductive systems of this form. Save for those at the anterior and posterior ends, the segments of the earthworm are practically alike. Some light on the significance of segmentation may be obtained from the manner in which segments originate. The first step consists in the constriction of the unsegmented embryo into anterior and posterior parts, of which the latter represents the posterior segment of the fully developed worm. New segments are budded from the posterior border of the anterior part until the full number is formed, which in *Lumbricis terrestris* is between 140 and 150. If segmentation be regarded as a sort of imperfect fission, a segmented animal really represents a string of individuals united end to end, an idea that is born out by the fact that each segment is provided with similar organs. Actually, of course, the segments are parts of a whole in which the individuality or independence of the segments is lost or obscured. That segmentation among annelids is a relatively primitive character is indicated by the fact that segments are strikingly similar. In an insect, such as the grasshopper, the primitive segmentation is obscured by a regrouping to form larger body divisions such as head, thorax, and abdomen. The type of segmentation found in annelids is called *homonymous* or *homodynamous* segmentation; that in insects *heteronymous* segmentation. Within limits, the greater the difference between the segments of the body of an animal, the less independence is retained by individual segments. Thus if an earthworm is cut in two through the middle, the anterior half is capable of living by itself and is able to regenerate some of the missing parts. If an insect is cut in two, both parts die.

The nervous system of the earthworm consists of two general regions, (1) a fused pair of relatively large *superior ganglia* located in segment 3 on the dorsal side of the pharynx and, (2) ventral *ganglionated nerve cord* extending backward from segment 4 through the length of the body (Fig. 112). The ventral nerve cord really consists of a series of ganglia, one to a body segment, joined together by a double nerve cord, partially fused. The superior ganglia are connected with the anterior ganglion of the ventral chain by a nerve cord on either side of the pharynx. The pharynx at this point is thus encircled by a nervous ring. The superior ganglion innervates the anterior three segments and the *prostomium*, an incomplete segment overhanging the mouth. Its large size is correlated with the higher development of the sensory field at the anterior or head end of the animal as compared with other portions of the body. The cephalic sensory field in some annelids, such as *Nereis*, a marine polychaete worm, is more highly developed by the presence of eyes, palps, etc. (Fig. 242). The ventral nerve cord with its ganglionic enlargements is primarily a segmental structure, in which correlation between segments is effected by longitudinal connections between the ventral ganglia (Fig. 113).

A pair of superior ganglia is a constant feature of the nervous system of invertebrate animals provided with a ganglionic nervous system. Where the segmentation is of the heteronymous

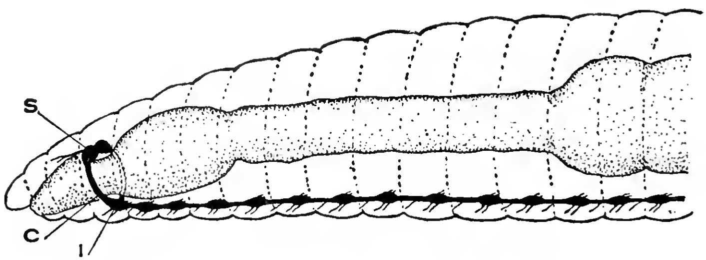


FIG. 112.—The nervous system of earthworm, diagrammatic. C, nerve commissure encircling pharynx; I, inferior ganglion; S, superior ganglion.

type, such as occurs in insects, the ganglia of the ventral chain become reduced in number and varied in size, in accordance with the extent of the modification of the primary segmentation. Thus in the grasshopper the head contains a superior ganglion (supraesophageal ganglion) and an infraesophageal ganglion, connected by nerve cords on either side of the esophagus. The infraesophageal ganglion is the anterior unit of the ventral nerve cord which is provided with three ganglia in the thorax and five in the abdomen (Fig. 53). The cord connecting these ganglia is double in the thorax and single in the abdomen. The total number of ganglia in the ventral chain is considerably less than the number of primary body segments of the region supplied by the ganglion. In such insects there is then a definite tendency toward centralization of nervous control. In other arthropods, such as certain crabs, this tendency is carried even farther, the entire ventral chain being represented by a single large ganglion.

Vertebrate Nervous System.—The central nervous system of vertebrates, consisting of the *brain* and *spinal cord*, is a hollow

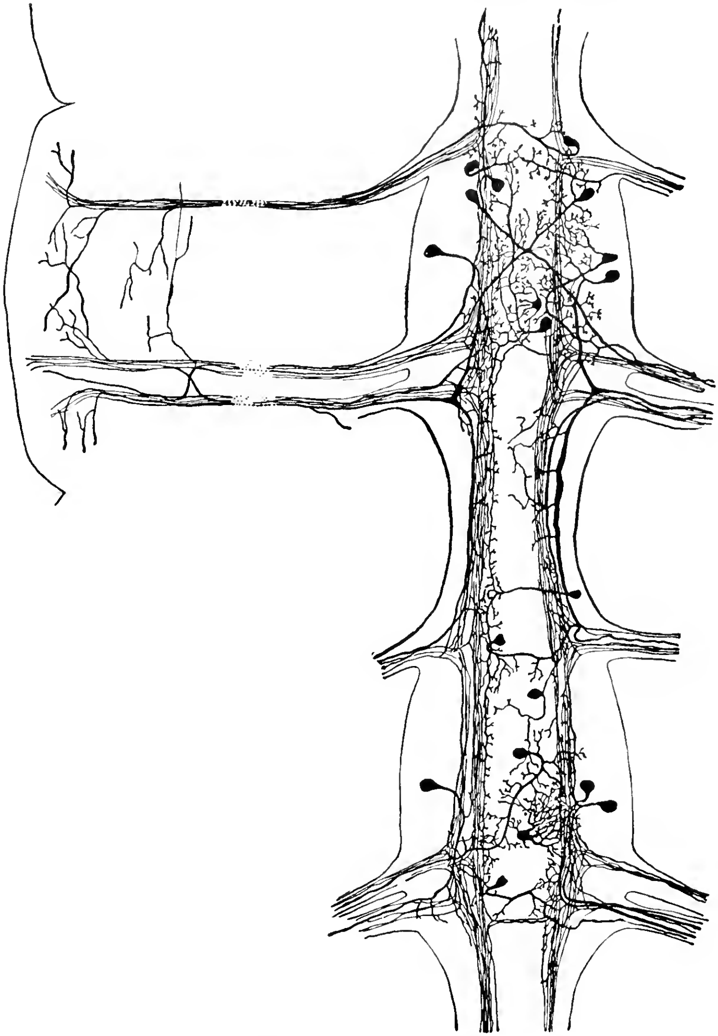


FIG. 113.—Portion of ventral cord of the earthworm with two ganglia and six pairs of lateral nerves. The sensory nerves end in terminal branches which connect with the dendrites of the motor and coordinating nerve cells of the cord. (*From Calkins, Biology, Henry Holt & Company, Inc., after Retzius. By permission.*)

structure that develops from an embryonic *neural tube*. The embryonic primordium of the vertebrate nervous system consists of a portion of the ectoderm covering the dorsal side of the embryo which is called the neural plate. In most vertebrates the first step in the conversion of the neural plate into a neural tube consists in the elevation of the lateral boundaries of the neural plate into approximately parallel folds or ridges. The crests of these ridges grow toward each other, meet, and fuse in the mid-line, thus forming a tube which soon separates from the under side of the reunited ectoderm (Fig. 114). A slight variation of this occurs in some of the lower vertebrates (cyclostomes, teleosts, and ganoids) in that the neural tube is derived

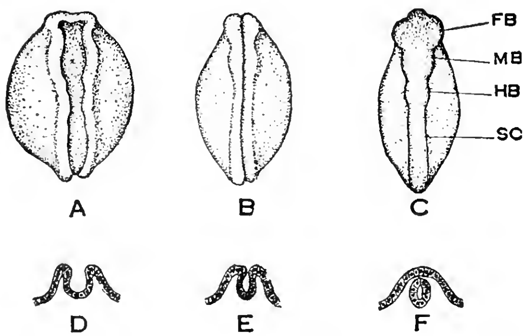


FIG. 114.—Three stages in the development of the nervous system of the salamander, *Ambystoma*. A, dorsal view of the embryo with open neural folds; B, edges of neural folds meeting in the mid-line; C, neural tube completely formed; D, cross section of open neural folds; E, cross section of closing neural folds; F, cross section of spinal cord of C, showing the cord as a tube pinched off from the ectoderm which has reunited above. FB, forebrain; HB, hindbrain; MB, midbrain; SC, spinal cord.

from a thickened keel formed in the mid-line of the neural plate on the under side. This keel acquires a lumen and becomes separated from the ectoderm above. In all cases, then, a neural tube is formed in vertebrates, and this neural tube develops into the brain and spinal cord. The neural tube also gives rise to all the neurons of the body except those of the olfactory nerve and some elements of the ganglia of cranial nerves V, VII, VIII, IX and X, that come from the ectoderm.

The walls of the anterior end of the tube thicken and differentiate into the embryonic *fore-*, *mid-*, and *hindbrain*, while the posterior portion of the tube becomes the spinal cord. The cavity of the neural tube in the region of the brain is represented by the *ventricles* and in the spinal cord by the *central canal.* Both ventricles and spinal canal are filled with cerebrospinal fluid, which resembles lymph but contains more water. Cross sections of fresh brain and cord show that they are composed of *white* and *gray matter.* The gray matter is made up largely of nerve-cell bodies, the white matter of myelinated or medullated nerve fibers.

Brain and Spinal Cord.—The three primary divisions of the embryonic vertebrate brain give rise to five regions of the adult brain as follows: (1) the *telencephalon,* composed of paired lobes, the *cerebral hemispheres,* are dorsolateral outgrowths of the fore-

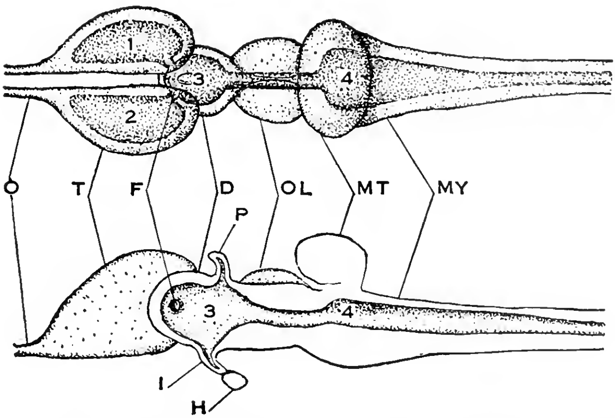


Fig. 115.—Diagram of vertebrate brain. Above, dorsal view showing ventricles; below, median view of right half of brain. D, diencephalon; F, foramen of Monro; H, hypophysis attached to infundibulum, I; MT, metencephalon; MY, myelencephalon; O, olfactory tracts; OL, optic lobes of mesencephalon; P, pineal body; T, telencephalon; 1 to 4, ventricles.

brain; (2) the *diencephalon,* or *twixt brain,* develops from the remainder of the forebrain; (3) the *mesencephalon,* whose walls form the *optic lobes,* is the fully developed midbrain; (4) the *metencephalon* or *cerebellum,* arises as a dorsal, unpaired outgrowth of the anterior end of the hindbrain; and (5) the *myelencephalon* or *medulla oblongata* forms from the remainder of the hindbrain (Fig. 115). The cerebellum of the frog is poorly developed and appears as a transverse ridge behind the optic lobes. In higher vertebrates there is a tendency for the cerebral hemispheres and the cerebellum to increase in size. In the adult vertebrate, the brain is enclosed in the cranium of the skull, and the spinal cord in the vertebral canal formed by the neural arches of the vertebrae.

The cavities of the cerebral hemispheres constitute the first and second ventricles, each of which is connected by a narrow passage, the *foramen of Monro*, with the third ventricle, which is the cavity of the diencephalon. A narrow channel, called the *iter* or *aqueduct*, extends through the mesencephalon, connecting the third ventricle with the fourth ventricle lying in the medulla. The roof of the fourth ventricle is very thin and is easily torn in dissecting the brain. The cavity beneath it is broad and shallow. In lower vertebrates the iter is expanded dorsally to form the *mesocoel* in the region of the mesencephalon.

Pituitary Gland.—The pituitary gland of the adult vertebrate is composed of two general regions, known as the *anterior* and *posterior lobes.* The anterior lobe, or *hypophysis,* develops as an evagination of the dorsal part of the embryonic oral cavity. The posterior lobe is formed from an evagination of the floor of the diencephalon known as the *infundibulum.* In all vertebrates except some of the cyclostomes the hypophysis loses its connection with the oral cavity and unites with the infundibulum, which remains connected with the brain throughout life. Thus the anterior lobe of the pituitary gland is derived from the oral epithelium and the posterior lobe from the neural tube. The *intermediate lobe* of the pituitary gland is proliferated from cells of the anterior lobe and forms a more or less distinct part between the anterior and posterior lobes.

Parietal Organ and Pinealis.—Two structures, varying considerably in different vertebrates, develop from the roof of the diencephalon. The more anterior of these, the *parietal organ,* is best represented in the lower vertebrates and lizards, in some of which it is provided with a lens and retina, though it has not been established that visual function is present. In other vertebrates, such as amphibia and mammals, the parietal organ is more rudimentary or lacking. The *pinealis* is a slender outgrowth in the mid-line, posterior to the parietal organ. In some of the lower vertebrates its structure is like that of an eye, but in the higher forms it takes on a glandular character. In the development of the pinealis of the frog, the distal end is cut off to form the brow spot. Apparently the parietal organ and the pinealis represent degenerated median unpaired eyes.

Meninges.—The brain and spinal cord of the frog are surrounded by two connective tissue membranes called the meninges.

Of these, the inner vascular layer corresponds to the *pia mater* and *arachnoid membrane* of higher forms. The outer tougher layer, the *dura mater*, consists of two sheets separated by an *interdural space* filled with lymph. The roof of the diencephalon in front of the pinealis, and also the roof of the medulla, is folded in by the invasion of blood vessels of the pia mater to form the anterior and posterior *choroid plexuses*, respectively. Such choroid plexuses occur in vertebrates generally and are probably the source of the *cerebrospinal* fluid, which fills the cavities of the brain and spinal cord. In man this fluid may leave the brain through minute passage ways in the roof of the medulla and join the fluid in the meningial space about the pia mater, thus providing a means for circulating the fluid. The cerebrospinal fluid is to be regarded as part of the circulatory mechanism of the brain and cord. In addition it also serves as a protective cushion of fluid.

Cranial Nerves.—The brain is connected with different parts of the head and adjacent regions by means of cranial nerves. In Amphibia and lower vertebrates there are 10 pairs of such nerves (Fig. 116), while the higher vertebrates (reptiles, birds, and mammals) have two additional pairs, making 12 in all. Some of the cranial nerves are composed of sensory fibers only, some of motor, and others of both sensory and motor. These nerves are known by name or by number, as follows:

I. *Olfactory nerve*, sensory in function, arising as axons of sensory cells located in the olfactory epithelium of the nose and terminating in the olfactory lobe of the telencephalon.

II. *Optic nerve*, sensory in function, arising in the retina of the eye, from which it extends across the ventral surface of the diencephalon in front of the pituitary gland to the optic lobes. In all vertebrates except mammals there is a crossing over of the fibers of the optic nerve at the optic chiasma, those from the left eye going to the right side of the brain and vice versa. In mammals the crossing is incomplete, some fibers remaining in the side of origin.

III. *Oculomotor nerve*, motor in function, arising from the ventral surface of the mesencephalon and supplying four of the extrinsic eye muscles: the superior, inferior, and internal recti and the inferior oblique muscles. A branch also goes to the *ciliary ganglion* of the eye.

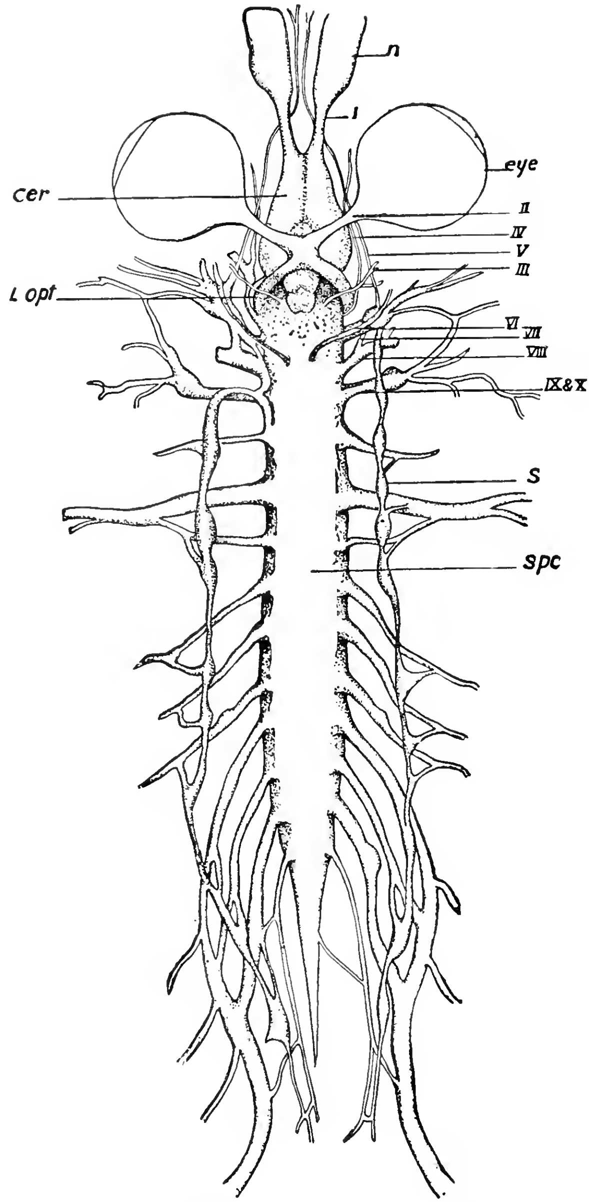


FIG. 116.—Nervous system of frog showing cranial and spinal nerves and sympathetic system, ventral view. *I* to *X*, cranial nerves; *cer*, cerebrum; *l.opt*, optic lobe; *n*, nasal sac; *s*, sympathetic system; *spc*, spinal cord. (*From Shull, LaRue, and Ruthven, Animal Biology, after Wiedersheim.*)

IV. *Trochlear nerve,* also motor, arising from the dorsal surface of the hinder margin of the mesencephalon and passing to the superior oblique muscle of the eye.

V. *Trigeminal nerve,* a large nerve arising from the antero-lateral angle of the medulla and dividing in the higher vertebrates into three main trunks: the *ophthalmic,* the *maxillary,* and the *mandibular.* The first two are sensory in function and supply the skin in the region of the eye, the roof of the mouth, the teeth of the upper jaw, etc., while the mandibular branch, composed of both sensory and motor fibers is distributed to the jaw muscles, the tongue, teeth of the lower jaw, and adjacent parts. Near the point where it leaves the brain the trigeminal nerve has a *semilunar* (Gasserian) ganglion.

VI. *Abducens nerve,* a motor nerve arising from the ventral surface of the medulla and innervating the external rectus muscle of the eye.

VII. *Facial nerve,* a mixed motor and sensory nerve, arising from the medulla posterior to the fifth nerve. In the lower vertebrates, it has two ganglia, the *geniculate* and the *lateralis,* but the latter in lung-breathing forms may disappear or unite with the geniculate or with the semilunar ganglion of nerve V.

VIII. *Auditory nerve,* sensory in function, consists in mammals of a *vestibular* branch from the utriculus and a *cochlear* branch from the cochlea, each from a separate ganglion, which unite to form a single trunk to the medulla.

IX. *Glossopharyngeal nerve,* a mixed motor and sensory nerve, extends from the medulla to the pharynx and tongue principally. It has a large *petrosal* ganglion near its junction with the brain.

X. *Vagus nerve,* also a mixed motor and sensory nerve, extending from the medulla to the esophagus, stomach, heart and other viscera. The *jugular ganglion* and, in gill breathers, a *lateralis ganglion,* occur near its origin. In higher forms the intestinal branch of the vagus has a *nodose ganglion.*

XI. *Spinal accessory nerve,* a motor nerve from the medulla, innervates the muscles of the pectoral region.

XII. *Hypoglossal nerve,* also a motor nerve from the medulla, is distributed in the muscles of the neck and tongue.

Long after the 12 cranial nerves were described and named, another pair was discovered at the anterior end of the brain. This nerve which should really be first in the series is known as the *nervus terminalis*. It has been found in all vertebrates but is easily overlooked because of its inconspicuous size which accounts for its remaining undiscovered until a relatively recent time. It extends from the brain near the olfactory nerve, to the olfactory epithelium. It is provided with a ganglion and is undoubtedly a sensory nerve, but nothing definite is known of its function.

The nerve cell bodies of the cranial motor nerves are located in the brain. The nerves themselves are composed of axons from their centrally located cell bodies. There is less uniformity in the location of the cell bodies of the sensory nerves. The cell bodies of the olfactory nerves lie in the olfactory epithelium, which morphologically is at the surface of the body. The olfactory nerves are composed of bundles of axons extending from the olfactory epithelium to the brain. The nerve cell bodies of the optic nerve are located in the retina of the eye from which axons pass to the brain. The sensory components of the fifth, seventh, eighth, ninth, and tenth nerves arise from cell bodies in the ganglia of these nerves. From the ganglia dendrons extend to the periphery and axons toward the brain.

Spinal Nerves.—The spinal cord is connected with peripheral regions of the body, below the level of the head, by paired spinal nerves. These pass from the cord through openings between the vertebrae. The total number of spinal nerves varies in different animals—10 pairs in the frog, 31 in Man, 42 in the horse, etc. Each spinal nerve is attached to the cord by two roots, a *dorsal root* provided with a ganglion and a *ventral root* without a ganglion. The ganglion is composed largely of nerve cell bodies whose axons pass into the cord and whose dendrons pass out to the periphery, as fibers from the dorsal root. The ventral root is composed of axons whose cell bodies lie in the cord. At their points of attachment to the cord each root splits up into smaller strands spread fanwise along the cord. The dorsal root, except in some of the lower vertebrates, is purely sensory in function. In the exceptional cases, efferent fibers arising from nerve cells within the cord pass out through the dorsal roots along with the sensory fibers. The ventral root in all cases is purely motor. The two roots unite to form a spinal nerve which almost at once divides into three divisions: (1) a *ramus dorsalis* to the skin and muscles of the dorsal region of the body; (2) a *ramus ventralis* to similar structures in the sides and ventral parts of the body; and (3) a *ramus communicans*, penetrating the coelomic cavity, but remaining retroperitoneal, just lateral to the attachment of the mesentery, where it forms connections with the autonomic nervous system (Fig. 117). The rami communicantes may be double, in which case one is a white ramus and the other gray.

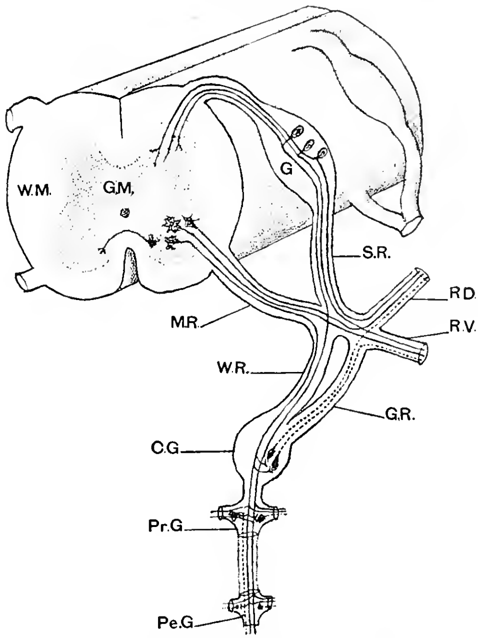


Fig. 117.—Diagram showing relations between spinal cord, spinal nerve and ganglia of autonomic nervous system. C.G., chain ganglia; G, spinal ganglion; G.M., gray matter of spinal cord; G.R., gray ramus communicans; M.R., motor root of spinal nerve; PE.G., peripheral ganglion; PR.G., prevertebral ganglion; R.D., ramus dorsalis; R.V., ramus ventralis; S.R., sensory root of spinal nerve; W.M., white matter of spinal cord; W.R., white ramus communicans; broken lines represent postganglionic fibers.

This difference is due to the fact that the fibers of the white ramus are medullated and those of the gray are nonmedullated. Both kinds of rami are not present in all spinal nerves. Thus in Man each spinal nerve has a gray ramus and nearly all except the cervical spinal nerves have, in addition, a white ramus communicans.

The functional significance of the dorsal and ventral roots of the spinal nerves of a mammal can be demonstrated by experiments. If a dog is anesthetized and the ventral roots of the spinal nerves supplying the forelimb are cut, the animal loses control of the muscles supplied by these nerves, though sensitivity to pain in the skin of the limb remains. If the dorsal roots are cut instead of the ventral, sensation in the limb is lost, but ability to move the muscles remains. If both dorsal and ventral roots of the limb nerves are cut, stimulation by an electric current of the distal end of the ventral root causes contractions of muscles in the limb, while stimulation of the central end of the cut ventral root produces no effect. Nor is any effect produced in the limb by stimulating the distal end of the cut dorsal root; but stimulation of the central end of the same root causes symptoms of pain. The dorsal root is therefore sensory in function and the ventral root motor.

Autonomic Nervous System.—The autonomic nervous system consists of (1) a pair of *ganglionated nerve cords*, one on each side of the mid-line of the dorsal wall of the body cavity and extending anteriorly into the cervical region; (2) a number of *outlying ganglia*, some of which are included within organs; and (3) *nerve fibers* forming connections between the ganglia and between the ganglia and the central nervous system. In Man the chain ganglia are composed of 3 cervical, 12 thoracic, 4 lumbar, and 4 sacral ganglia, though variations in these numbers are not uncommon. The white rami communicantes consist of both afferent and efferent fibers derived from dorsal and ventral spinal nerve roots, and extending from spinal nerves to the autonomic ganglia; some to the chain ganglia and others directly to more distal ganglia. Of these there is a *thoracolumbar* group from the first or second thoracic nerves to the second or third lumbar nerves and a *sacral* group from two or three of the sacral nerves. There is also a *cranial* group from cranial nerves III, VII, IX, and X. The thoracolumbar group connects with the chain ganglia and with the *coeliac*, *superior*, and *inferior mesenteric* ganglia. The sacral and cranial groups have no connections with the chain ganglia but pass directly to various organs and tissues. Nerve fibers arising in the central nervous system and passing to chain ganglia or to other ganglia of the autonomic nervous system are called *preganglionic* fibers because their terminations connect with other ganglia, whose fibers (*postganglionic*) innervate the tissue. Gray rami communicantes connect the chain ganglia to each of the spinal nerves. *Association cords*, made up of both white and gray fibers, connect each set of chain ganglia in a longitudinal direction.

The autonomic nervous system is composed of two parts; the *sympathetic* or *orthosympathetic* and the *parasympathetic* divisions (Fig. 118). The sympathetic division includes all of the chain ganglia, the coeliac, superior, and inferior mesenteric ganglia, the rami communicantes of the thoracolumbar group of spinal nerves, and their preganglionic and postganglionic continuations. The parasympathetic division is made up of the visceral branches of two or three of the sacral spinal nerves and visceral branches of cranial nerves III, VII, IX, and X, all of which pass directly to certain structures such as the *ciliary* ganglion of the eye, the *cardiac* ganglion of the heart, the *myenteric plexuses* of the gastrointestinal tract, etc., where they connect with postganglionic fibers that in turn innervate the tissue. Thus in both the sympathetic and parasympathetic divisions, the preganglionic fibers originate in the brain or cord and the postganglionic fibers in chain or peripheral ganglia. These are the efferent pathways. Afferent pathways to the central nervous system are provided by fibers from spinal-ganglion neurons that accompany the preganglionic fibers. The white rami communicantes are composed of efferent and afferent fibers originating in the spinal cord or the spinal ganglion. The fibers of the gray rami originate in chain ganglia of the autonomic system.

The autonomic system is concerned with the coordination and control of involuntary functions such as the beating of the heart and activities of the viscera in general, including blood vessels. With the exception of pain, fullness of the bladder or rectum, most of these activities do not enter consciousness to any extent. Actually the autonomic system is not completely independent of the central nervous system since all of its preganglionic fibers begin in the cord or brain and its afferent pathways end there. It is autonomic in the sense that most of its functional activity takes place without interference from the central nervous system.

Reflex Action.—A reflex action is an immediate involuntary response to a sensory stimulus. Such responses are invariable and can be predicted as a consequence of applying a definite stimulus at a certain point. The simplest kind of *reflex arc* accounting for such a result would consist of a sensory neuron leading to a motor neuron, passing in turn to the effector. Actually at least one or more intermediate neurons, between the

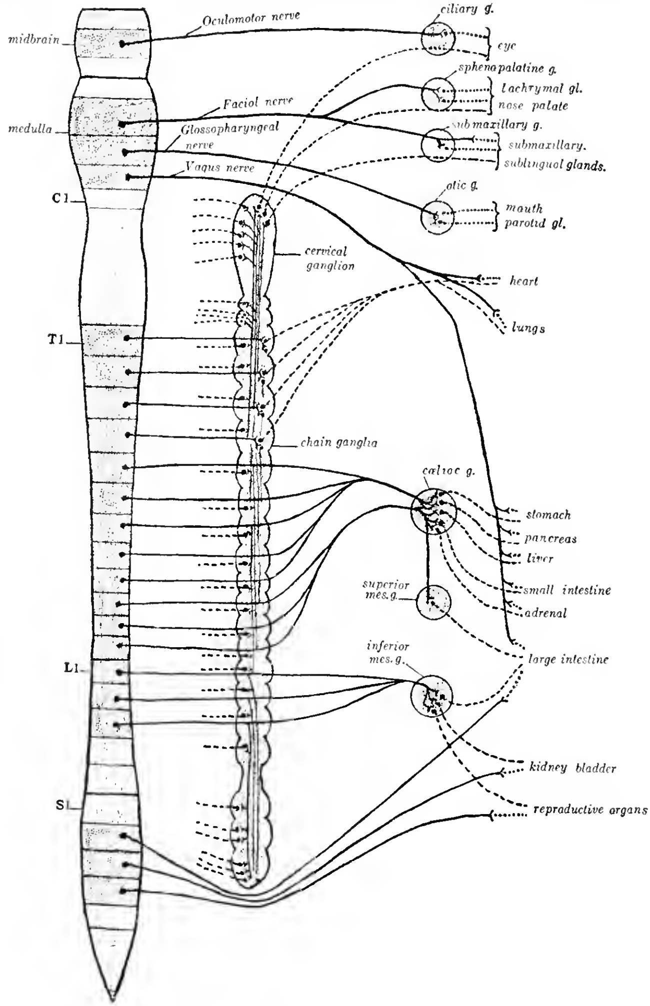


FIG. 118.—Diagram showing relations between central nervous system and autonomic nervous system. Postganglionic fibers of sympathetic system are represented by broken lines; those of the parasympathetic system by dotted lines. The short broken lines passing to the left of the chain ganglia represent postganglionic fibers passing to sweat glands and to arrector pili muscles. (*After Meyer and Gottlieb.*)

principal afferent and efferent neurons, are involved as well. An example of a simple type of reflex action is the knee jerk.

If the knees are crossed or if the leg is allowed to dangle freely from a chair or table, a tap on the patellar ligament, just below the knee cap, causes the foot to be jerked forward by the contraction of the quadriceps femoris muscle of the thigh. The peripheral nerve connections involved are the second and third lumbar spinal nerves, which provide the afferent pathways from the skin and ligament to the spinal cord, and also the efferent pathways from the spinal cord to the thigh muscle. In addition there are central pathways consisting of intermediate neurons in the spinal cord that form an integral part of the nervous circuit. The entire nervous pathway along which an impulse is transmitted to and from the central nervous system is a reflex arc. In the cord or brain a sensory neuron may connect with several motor neurons and its stimulation may thus bring about response in a number of effectors. Intermediate neurons connecting sensory and motor neurons of the same side are called *association fibers;* if they connect sensory neurons of one side with motor neurons on the opposite side, they are called *commissural fibers.* Thus through commissural and association pathways sensory impulses may affect motor neurons of the same or opposite side, or of different levels. Reflexes occur not only in the central nervous system but also in the peripheral ganglia of the autonomic system. The reflex is thus the functional unit common to all parts of the nervous system.

Synapse.—The axon of a neuron may terminate in an effector, such as muscle, or it may connect with the dendrites of another neuron. Whether the connection between two neurons is merely one of contact or actual fusion is a question about which much has been written. The term *synapse* refers to the functional connection between two neurons by means of which the impulse is transferred from one to the other.

Functional Significance of the Central Nervous System.—The cell bodies of the sensory neurons are located in the spinal ganglia, in the ganglia of the cranial nerves, in the olfactory epithelium, and in the retina of the eye. The sensory fibers make connections through intermediate neurons with motor neurons. The brain and spinal cord are composed of tracts or groups of neurons, all of the fibers of a tract usually having similar functions. In simple reflexes, the cord alone may be involved in distributing sensory impulses to motor neurons. In other cases the sensory impulses may be carried to the brain by ascending tracts and back by descending tracts to spinal motor neurons, the nature of the response being altered or controlled as a result of this special routing. Responses, under such conditions show the effect of past experience, as for example in *conditioned reflexes.* Shining a light into the eye causes a contraction of the pupil, but ringing a bell does not. If a bell is rung each time light is directed into the eye, after a while ringing the bell will cause the pupil to contract without the stimulus of the light. The spinal cord is composed principally of relatively simple reflex arcs and longitudinal tracts that connect these arcs with the brain.

Consciousness seems to be a function principally of the cerebrum as a whole. The reactions of a person to a pin prick may be the same when he is asleep as when he is awake, but when asleep the stimulus is not perceived. Intelligence, memory, interpretation of sensations are all general functions of the cerebrum. Localized areas, such as the "motor areas," are concerned with the control of individual muscle movements. Thus, if the area of the cerebrum controlling the movement of the foot and leg muscles is stimulated, the response is a coordinated movement, entirely unlike the uncoordinated movements produced by directly stimulating the peripheral nerves supplying these parts. There are many such "centers" in the cerebrum and also in other parts of the brain. The location of such "centers" in the brain is the principal difference between the brain and the cord.

Sense Organs.—Sense organs are specialized in their susceptibility to different kinds of stimulation and are classified accordingly. Since the matter of sensation also enters into the problem, more is known of human sense organs than of those of other animals, where one is limited to studying the responses—muscular or glandular activity—and where one can know but little of the sensation experienced by the animal. The best we can do is to compare their responses with our own under similar conditions. Similarity in the structure of the sense organs of vertebrates is fair presumptive evidence of similar function and of similar, though not necessarily identical, sensations. A classification of sense organs for animals generally is patterned on a classification of human sense organs. These include the following types of receptors: (1) tactile, (2) pain, (3) warmth, (4) cold,

(5) proprioceptive, (6) chemical (taste and smell), (7) sound, (8) light, and (9) gravitation (equilibrium).

Tactile Organs.—The sensitivity to touch that characterizes the integument of animals generally is brought about by the presence in the integument of tactile organs developed in connection with nerve endings. The tactile organ itself is usually composed of nonnervous tissue. Among invertebrates the commonest type of tactile organ is the *tactile hair*, examples of which are found in arthropods (Fig. 119). Such a tactile hair consists of a core formed of epidermal cells, covered by a thin cuticle, the distal end of which tapers to a delicate point. The base of the tactile hair is in contact with a nerve ending so that any movement of the hair serves as a stimulus for the nerve ending. In mammals, including man, the hair follicles are supplied with sensory nerve endings that are stimulated by movements of hairs. Where hairs are lacking, tactile corpuscles of *Meissner* serve as end organs of touch in the skin. These are elliptical structures composed usually of several nerve fibers enclosed by a capsule of nonnervous cells and are located in the subcutaneous tissue (Fig. 120). They are numerous in the finger tips, the soles and palms, the nipples of the mammary glands, the lips, and other hair-free areas of the skin.

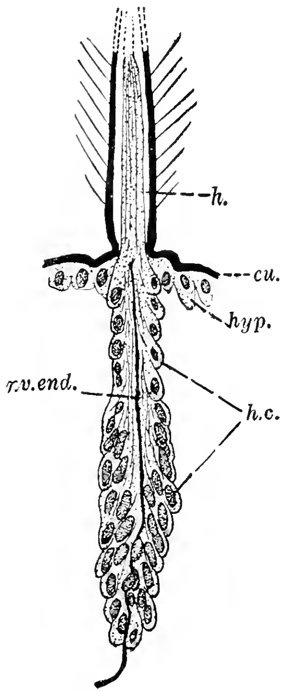


Fig. 119.—Tactile end-organ of a nerve fiber in the tactile hair of a shrimp, *Palaemonetes*. *cu.*, cuticle; *hyp.*, hypodermis, which is invaginated at (*h.c.*) into the hair cells. *h.*, outer structure of the hair; *nv.end.*, nerve ending in the lower part of the hair. (*From Dahlgren and Kepner, Principles of Animal Histology, copyright, The Macmillan Company. By permission.*)

Pain Receptors.—Sensation of pain can be aroused everywhere in the human skin by pricking with a sharp needle. The receptors for cutaneous pain are thought to be naked axis cylinders of sensory nerves distributed in the lower layers of the epidermis. The nerves involved are sensory components of cranial and spinal nerves. Some internal structures lack pain receptors. Thus surgical operations involving cutting through the skull and removing parts of the brain, can be performed under local anesthesia without causing pain. In such cases the anesthetic produces insensibility in the scalp but not in the deeper structures. Cutting or cauterizing the intestine causes no pain, though pain is produced in the peritoneum by the distention of intestine by gas or by the excessive contractions of the muscle in the intestinal wall. In general, since pain is a symptom of danger threatening life, the adaptive significance of the presence of pain receptors throughout the skin can be understood.

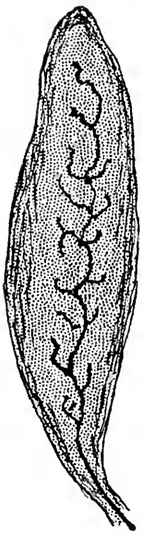


Fig. 120.—Corpuscle of Meissner, diagrammatic.

Warmth and Cold Receptors.—If the human skin is explored with warm or cold thin metal rods, it is found that some spots respond with a sensation of warmth and others with a sensation of cold. Evidence has been produced to show that the receptors for warmth and cold consist of two distinct types of receptors, *viz.*, the corpuscles of *Ruffini* for warmth and the corpuscles of *Krause* for cold. Human skin is composed of a great number of very small sensory areas, each of which is especially related to one or more of the sensations of touch, warmth, cold, and pain. Areas concerned with one sensation are everywhere mingled with areas concerned with others. It has been estimated that there exist in the skin of the trunk and limbs 30,000 warmth spots, 25,000 cold spots and 500,000 touch spots, with pain spots present everywhere.

Proprioceptors.—Corpuscles of *Pacini*, ovoid laminated bodies with a nervous core, resemble in their general structure the corpuscles of Meissner. They are found near joints and ligaments, and are thought to be receptors for proprioceptive sensations caused by movements of one bone upon another, such as accompany voluntary muscular movements. Other types of receptors, such as muscle and tendon *spindles*, composed of spirally coiled nerve endings, are also concerned in proprioceptive sense. Neuromuscular spindles must not be confused with the end plates of motor nerves which terminate in muscle fibers. The latter cause the muscle to contract when the motor nerve, of which they are the terminations, is stimulated. When the muscle contracts, the muscle spindle is stimulated and produces eventually the sensation of movement. In other words, the muscle and tendon spindles are the terminations of sensory nerves and the motor end plates of motor nerves (Figs. 121 and 122).

Taste Receptors.—A sense of taste is probably present in all animals, but since the end organs of both taste and smell are activated by chemical stimuli, it is often difficult in lower animals to differentiate between them. Thus, if a piece of crushed clam be placed near a burrow of *Nereis virens*, a marine annelid, the animal responds by thrusting its anterior end out of the burrow toward the food which it seizes, pulls back into the burrow, and devours. The animal is evidently stimulated by the meat juices, but whether by taste or smell or a combination of both, it is difficult to decide. Insects are provided with organs of taste located on the mouth parts and the antennae and in some cases at least on the legs. The taste receptors of vertebrates are known as *taste buds* (Fig. 123). Each consists of a number of taste cells provided with short bristles at their outer ends and a number of supporting cells, the whole forming a spherical body buried in the surrounding tissue except for a small area at the surface containing a pore. The outer ends of the taste cells converge at the pore. In fishes taste buds occur in the walls of the pharynx, on the gills, on the outside of the body, and in some (catfish) in the tail and the barbels. In higher vertebrates they are restricted to the oral cavity, where they are found in the tongue, soft palate, and epiglottis. The base of each taste cell is in contact with a nerve ending from which the sensory impulse is conveyed to the brain. In mammals the nerves involved in the sense of taste are a branch (chorda tympani) of the seventh cranial nerve and the lingual branch of the ninth.

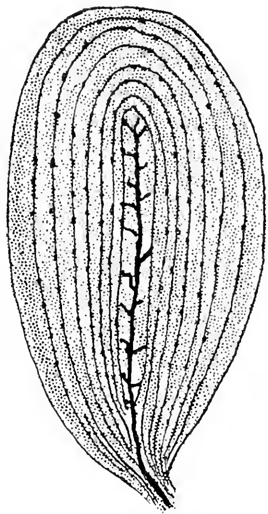


FIG. 121.—Pacinian corpuscle, diagrammatic.

Smell Receptors.—Olfactory organs are stimulated by chemical action, but the amount of the stimulating agent required is very much less than in the case of the taste receptors. Smell has been aptly described as "taste at a distance." It has been established that organs of smell occur in insects and in other invertebrates such as snails. In the case of insects the antennae and other parts of the body bear olfactory pits in which the receptors lie. In vertebrates, except Cyclostomata, the olfactory organ consists of paired sensory areas, which in fishes lie at the bottom of

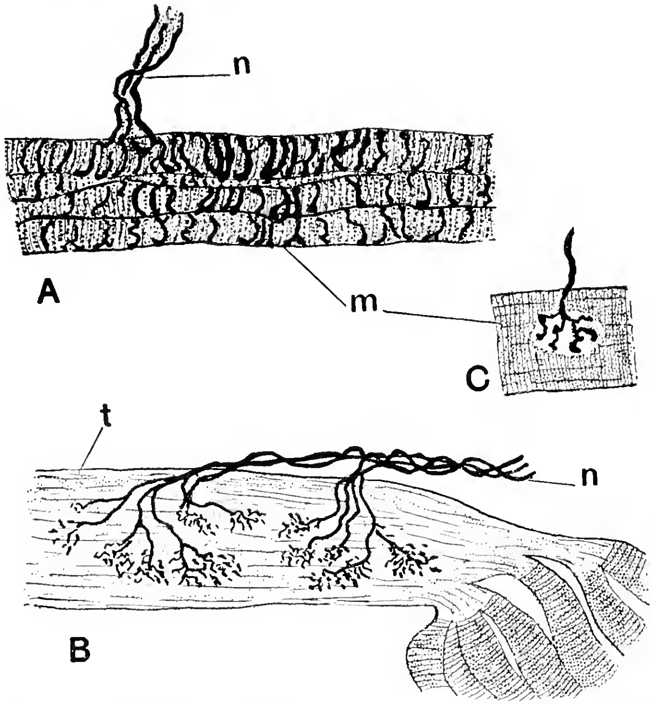


FIG. 122.—A, neuromuscular spindle. B, neurotendinous spindle; C, motor end plate. m, muscle; n, nerve; t, tendon. (*After Huber and De Witt.*)

ectodermal pits opening to the outside by nostrils, but having no connection with the pharynx. In air-breathing vertebrates these pits are continued backward as nasal passages, opening into the pharynx by internal nares. This condition exists in the frog and in Man. The sensory epithelium lining the passages consists of olfactory cells and supporting cells, the former bearing bristles at their outer ends, while their inner ends continue backward as nerve fibers to form the olfactory nerve. Since olfactory cells arise and remain in the ectoderm, the olfactory epithelium is said to be the most primitive nervous epithelium in the body (Fig. 124).

Light Receptors.—Sensitivity to light is a characteristic of protoplasm exhibited in its simplest form by organisms being attracted or repelled by light. *Phototaxis*, as this reaction is called, occurs even in forms that have no special organs for perceiving light stimuli, such as many Protozoa and some Metazoa, such as Hydra. Where special receptors exist, these in lower forms are often merely mechanisms for distinguishing

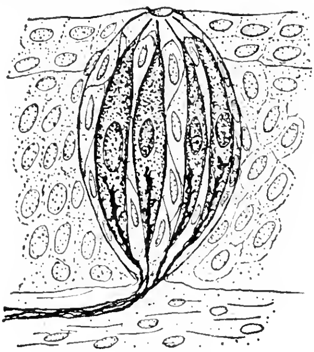


FIG. 123.

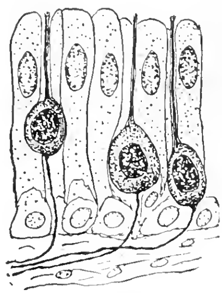


FIG. 124.

FIG. 123.—Section of a taste bud, diagrammatic. Four taste cells are shown with their outer ends converging toward the pit opening on the surface above. The inner ends of the cells are in contact with nerves entering the base of the bud. The pale cells within the bud are supporting cells.

FIG. 124.—Section of human olfactory epithelium, diagrammatic. The slender outer ends of the olfactory cells are ciliated. The process leaving the base of each olfactory cell is a nerve fiber.

between degrees of light. Such animals "see" only in the sense that they are capable of distinguishing light from dark. An example of such an eye is found in *Planaria gonocephala*. In this form the paired eyes are located in the head region, one on either side of the cephalic ganglion. Each eye consists of a cup-shaped structure lined with pigment, into which project the processes of 20 or more visual cells, each process being somewhat thickened at its distal end to form a *rhabdome* (Fig. 125). Proximally the visual cells are continued as fibers that form the optic nerves extending to the cephalic ganglion. The eye is sunk in the tissues and covered by a transparent epithelium, continuous with the ectodermal body covering. Light passes through the transparent epithelium and through the cell bodies of the visual cells until it strikes the rhabdomes, which are the receptors of the eye. The nervous impulse set up by the light stimulus then travels back through the visual cells to the central nervous system.

Compound Eye.—Invertebrates show a large variety of eyes which seem to have image-forming possibilities. Of these the most striking is the compound eye of arthropods. In the crayfish and other crustaceans these eyes are spherical in shape and are mounted on the ends of movable stalks. In an insect such as the

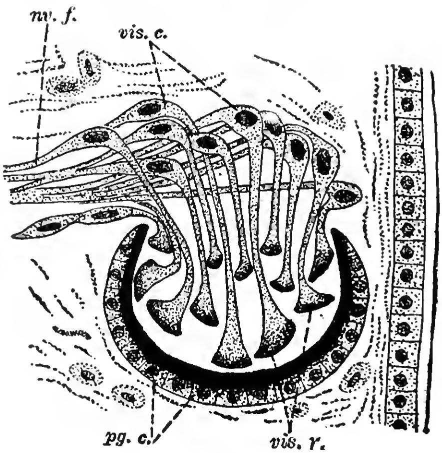


Fig. 125.

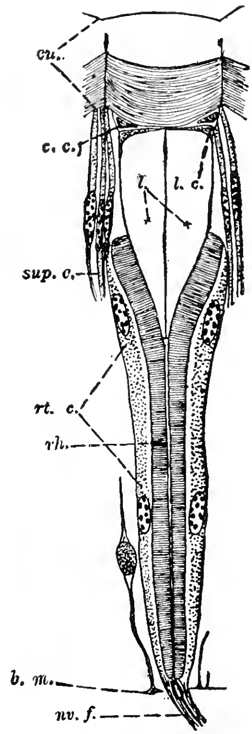


Fig. 126.

Fig. 125.—Axial section of the eye of *Planaria gonocephala*. *vis. c.*, visual cells; *vis. r.*, visual rods or rhabdomes; *nv. f.*, centripetal fibers of visual cells; *pg. c.*, pigment cells. (*From Dahlgren and Kepner, Principles of Animal Histology, copyright, The Macmillan Company, after R. Hesse. By permission.*)

Fig. 126.—Longitudinal section of a single ommatidium of a roach, *Periplaneta orientalis*. *b. m.*, basement membrane; *cu.*, cuticle divided into corneal areas; *rt. c.*, retinal cells; *rh.*, rhabdome or cell organ of light perception; *l.*, lens; *l.c.*, lens cells; *c. c.*, corneal cells; *sup. c.*, supporting cells; *nv. f.*, nerve fiber. (*From Dahlgren and Kepner, Principles of Animal Histology, copyright, The Macmillan Company, after R. Hesse. By permission.*)

grasshopper the eye forms a prominent rounded elevation on either side of the head. The outer surface of this type of eye consists of a transparent cornea divided into thousands of polygonal *facets*. In the crayfish the facets are quadrilateral in shape and in the grasshopper they are hexagonal. Each facet is the base of a narrow cone-shaped structure, the *ommatidium*, whose inwardly directed apex rests against a hemispherical basement membrane. Each ommatidium contains a pear-shaped lens supported by cells beneath the cornea. The remainder of the ommatidium is usually made up of seven elongated retinal cells, extending from the lens to the basement membrane. The surface of each retinal cell facing the cavity of the ommatidium is provided with rows of transverse plates or rods, which constitute a *rhabdome*. Since the plates or rods of the rhabdome project at right angles to the axis of each retinal cell, they are in a position to intercept light entering the ommatidium through the cornea. The lower or inner ends of the retinal cells are prolonged into nerve fibers to form an optic nerve leading to the central nervous system. Pigment cells occur between the cornea and the outer edges of the lens and also about the retinal cells so that the amount of light entering the ommatidium may be controlled (Fig. 126).

The compound eye is provided with all the elements necessary to produce an image of a mosaic type, each ommatidium in the proper location with reference to the object forming a portion of the total image. The number of ommatidia affected depends upon the degree to which the ommatidia are sheathed by pigment cells. When the pigment is extended about the ommatidia, only those ommatidia will be stimulated whose axes are in line with the source of light. When the pigment is withdrawn a larger number of ommatidia will be affected by a single source of light. Such an eye would seem to be especially adapted for recording a moving object, since a change in position of the object would affect in turn a larger number of ommatidia than would be the case if the object were stationary.

Human Eye.—The eyes of vertebrates are definitely image-forming organs, conforming to a common structural plan, though differing in details. The general plan of structure can be illustrated by the human eye. The shape of the human eye is roughly that of a sphere whose curvature in the region of the transparent part in front is somewhat greater than elsewhere (Fig. 127). The outer layer of the eye is made up of the transparent *cornea* in front and the tough, opaque *sclera* or *sclerotic* coat, forming the remainder. The visible portion of the sclera is the white of the eye. Beneath the sclera lies the vascular *choroid* layer, beneath which in turn lies the *retina.* The retina is composed of an inner nervous layer and a thin pigmented layer in close contact with the choroid. Neither the retina nor the choroid layer extends in front beyond the line of junction of the cornea and sclera. The lens is a doubly convex disk, composed of transparent cells, enclosed in a thin tough capsule, held in place by *suspensory ligaments* attached to the sclera along the line of the forward edge of the choroid coat. The *iris* is a pigmented muscular diaphragm with an opening, the *pupil,* in its center.

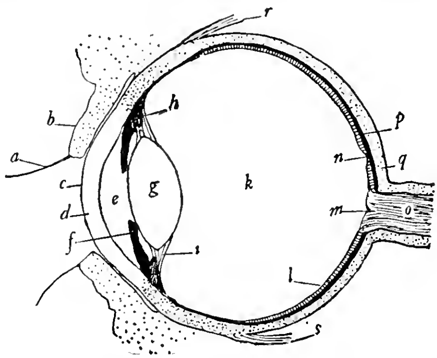


Fig. 127.—Diagram of a vertical section of human eye and eyelids. *a*, eyelash; *b*, lid; *c*, conjunctiva, a thin membrane continuous with the lining of the eyelid; *d*, cornea; *e*, anterior chamber filled with aqueous humor; *f*, iris; *g*, lens; *h*, muscles to ligament suspending lens; *i*, suspensory ligament of lens; *k*, chamber filled with vitreous humor; *l*, retina; *m*, blind spot; *n*, fovea centralis; *o*, optic nerve; *p*, choroid coat; *q*, sclera; *r*, superior rectus muscle of eyeball; *s*, inferior rectus muscle.

It lies in front of the lens and is attached at its outer edge to the *ciliary process,* which is a circle of plain musculature inserted in the sclera between the corneosclerotic juncture and the choroid layer. The lens divides the eye into an anterior region containing a liquid, the *aqueous humor,* and a posterior region filled with a jellylike *vitreous humor.* These two fluids keep the eye distended. The iris divides the anterior region into *anterior* and *posterior chambers* which are connected by the pupillary opening.

Retina.—The arrangement of the nervous elements of the retina is highly complicated and only the barest outlines of their histology will be considered. The light receptors of the retina are the *rods* and *cones,* which are cells lying in the outer zone of the sensory part of the retina and pointing toward the pigment layer of the retina. Under certain conditions processes from the pigment cells extend inward between the rods and cones. From the inner ends of the rods and cones processes extend to intermediate neurons which in turn form synapses with ganglion cells lying at the innermost surface of the retina (Fig. 128). Axons from ganglion cells all over the inner surface of the retina converge at the *blind spot* to form the *optic* nerve, which extends from the eyeball to the brain. The blind spot is not in the direct line of vision, being toward the nasal side of the center of the eye.

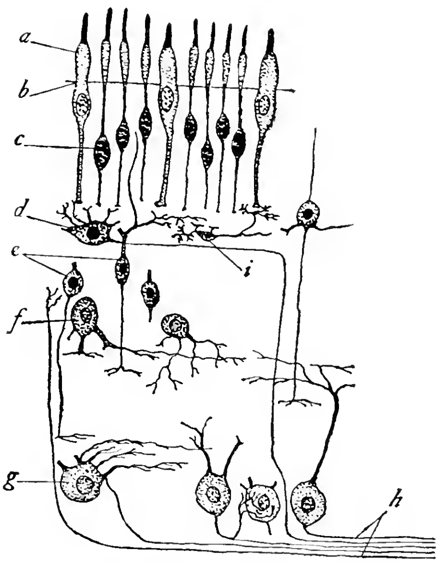


FIG. 128.—Diagram of human retina, *a*, cone cell; *b*, membrana limitans externa; *c*, rod cell; *d*, stellate ganglion cell; *e*, bipolar cell; *f*, amacrine ganglion cell (without axons); *g*, multipolar ganglion cell; *h*, nerve-fiber layer, at inner surface of retina; *i*, subepithelial ganglion cell. (*After Stöhr.*)

In a small area of the retina lying in the optical axis of the eye, rods are absent and the other retinal layers are greatly reduced. The slight depression at this spot is known as the *fovea centralis*, which is the point of most acute vision. In the fovea centralis cones alone are present. In other parts of the retina the rods far outnumber the cones.

Light Perception.—Light enters the eye through the cornea, which converges the rays, and then passes through the lens, where the rays are further converged and brought together at the focal point of the lens system. Before reaching the rods and cones, which are the percipient elements of the eye, it is necessary for the light to traverse the various layers of the retina lying between them and the inner surface of the retina. The rods and cones having been stimulated by the light, the nervous impulse set up passes in the reverse direction from the rods and cones to the fibers forming the optic nerve which convey the impulse to the brain. The cones are concerned in both chromatic and achromatic vision, while the rods function only in achromatic vision. Thus colors are perceived by the cones alone.

Accommodation.—The human eye resembles a photographic camera in many respects. The curved cornea, distended by aqueous humor, and the lens, provide a means for converging light rays, as in a camera, and the sensitive retina corresponds to the film or plate of the camera. Rays of light entering the eye from a luminous object, or from an object reflecting light, are brought to a focus at a point behind the lens, beyond which an image is formed on the retina. The human eye possesses a range of vision that makes it possible to see objects miles away or close at hand. The power of accommodation for objects at varying distances is due to the fact that the focal length of the lens can be changed. In the eye of some molluscs and in the eye of fishes, accommodation is brought about by altering the distance between the lens and the retina, as in a camera, where the lens is moved away from the film for near objects and in opposite direction for more distant objects. In these cases the focal length of the lens is fixed. In the human eye, the same end is achieved by changing the curvature of the lens rather than by moving the lens as a whole. Thus in viewing near objects the curvature of the lens is greater than when more distant objects are looked at. Increasing the curvature of the lens shortens the length of the focus, and decreasing the curvature lengthens it. According to the generally accepted explanation, this adjustment is brought about by the contraction of the ciliary muscles. When the eye is relaxed or unaccommodated, the suspensory ligament and the capsule containing the lens are taut, and the front surface of the lens is flattened, thus reducing its curvature, with the result that distant objects are seen without effort. In viewing near objects the lens becomes more convex as a result of the contraction of the ciliary muscles which pulls forward the region of attachment of the suspensory ligament to the eyeball, thus easing the tension on the ligament. The lens then thickens and increases its convexity until checked by the tension of the capsule. The response of the lens to changes in tension of the capsule and ligaments is due to its elasticity. Loss of elasticity is a natural accompaniment of old age and results in a loss of accommodation.

Acuity of vision also depends upon the amount of light entering the eye. This is controlled by the size of the pupil, which is contracted in a bright light and enlarged in a dim light. The "color" of the eye is determined by the amount and distribution of the pigment in the iris. Dark-brown and black eyes have pigment in the outer surface, through the stroma, and in the inner surface of the iris; light-brown, gray, and green eyes have less pigment in the outer surface; while blue eyes have pigment only in the inner surface of the iris. The pigment is the same substance in all cases.

Eye Muscles.—By means of six extrinsic eye muscles, the eyeball of vertebrates, including that of Man, can be moved about in the orbit in all directions through a considerable arc. The *internal* and *external recti* muscles move the eye from side to side; the *superior* and *inferior recti* muscles move it up and down; and the *superior* and *inferior oblique* muscles rotate it. These muscles have their origin in the wall of the orbit and are inserted on the sclerotic surface of the eyeball. They are innervated by cranial nerves III, IV, and VI. In the frog there are two additional eye muscles, the *retractor bulbi*, which pulls the eyeball into the orbit, and the *levator bulbi*, which raises the eye.

Visual Purple.—The change undergone by the rods and cones through which the nervous impulse is set up is generally believed to be photochemical in nature. By this is meant that light generates chemical changes in the rods or cones, similar in a general way to the effect of light on a photographic plate or film. This view is based on the fact that the outer segments of the rods contain a reddish pigment, called *visual purple* or *rhodopsin* that is bleached by light. This pigment is distinct from the pigment of the pigmented layer of the retina, though this layer seems to play some part in restoring the visual purple in the rods following its destruction by light. It would seem, however, that visual purple is not essential to vision since it is absent in the cones, which means that it is absent from the fovea centralis, the region of greatest visual acuity. It has been suggested that the visual purple increases the irritability of the rods in dim lights. The domestic fowl, the pigeon, and some reptiles lack visual purple. It is present in the eye of the frog.

Sound Receptors of Invertebrates.—Among invertebrates the only group in which organs of hearing are known with some degree of certainty are the insects. Since some insects are provided with structures for producing sounds, it is reasonable to assume that they also have means of perceiving sounds. Thus grasshoppers produce a sound by rubbing the femur of the last pair of legs against the anterior wings. (The femur is the large segment of the leg near the body.) In grasshoppers, the organs of hearing are thought to be the *tympanal organs,* located one on either side of the body where the abdomen joins the thorax. The tympanal organ consists of a thin chitinous membrane, stretched over a shallow cavity and provided with nerve endings. Sound waves impinging upon the membrane cause it to vibrate and stimulate the nerve ending. Similar organs are found on the anterior legs of crickets, katydids, and ants.

Gravitational Receptors of Invertebrates.—Gravitational receptors provide an animal with a means of maintaining its balance or equilibrium. Organs of this sort, known as *statocysts* or *lithocysts,* are found in Crustacea, such as the crayfish, lobster, shrimp, etc. The statocyst is a sac, located in the basal segment of each antennule, open to the outside, and lined with chitin. Projecting from the inner surface of the sac are sensory hairs among which are found a few grains of sand, called *statoliths.* Changes in position of the body displace the statoliths among the hairs, the differential stimulation of which gives the animal a sense of its position in space. This interpretation of the function of the statocyst is borne out by the fact that when the animal molts—a process in which the entire chitinous covering of the body, including the lining of the statocyst and the contained statoliths, is lost—the animal for a time lacks full power for maintaining itself right side up. The most convincing evidence regarding the function of the organ comes from an experiment in which shrimps newly molted and therefore without statoliths were placed in water containing iron filings. In the absence of sand grains to replace the discarded statoliths, the experimental animals placed iron filings in the statocysts. When an electromagnet of sufficient strength was brought near, the shrimp oriented itself with reference to the resultant of the lines of force of the magnet and the pull of gravity as it normally would to gravity alone. From this it would appear that under natural conditions the normal position of the animal is determined by the stimulation of certain sensory hairs in the statocyst by the weight of the statoliths. In the experiment, when these particular hairs are stimulated, so far as the animal is concerned, the resulting orientation is normal even though the animal is tilted at a considerable angle.

Inner Ear.—Among vertebrates the inner ear serves both as organ of hearing and as an organ of equilibration. It is present in all vertebrates. Vertebrates higher than fishes also have a middle ear, in addition to which mammals have an external ear. The middle ear and external ear are part of the sound-conducting apparatus employed in hearing.

The inner ear arises as an invagination of the ectoderm in the region of the embryonic hindbrain to form the otic sac, which later becomes embedded in the cartilage or bone of the skull and completely separated from the outside except in the case of elasmobranchs. Two regions develop in the otic sac; (1) the *utriculus,* bearing three semicircular canals, and (2) the *sacculus,* which in fishes is a rounded sac with a short appendage, the *lagena* (Fig. 129*A*). In the frog the lagena is short, but near it another outgrowth, the *basilar papilla,* is formed. In the higher vertebrates the lagena and the basilar papilla of the sacculus enlarge to form the *scala media* or *cochlear duct* which in mammals becomes a spirally coiled tube (Fig. 129*B*). The utriculus with its canals is concerned with equilibration, while the sacculus, the lagena, and its derivatives are concerned with hearing. Fishes are practically deaf so far as discrimination of pitch is concerned, which may be correlated with the slight development of the lagena. Goldfish respond to vibrations under water. By removing parts of the inner ear it has been shown that the utriculus is sensitive to vibration rates of 43 to 488 per second, and the sacculolagena to rates of 688 to 2,752 per second.

The utriculus and sacculus are connected by a *sacculo-utricular canal.* The *endolymphatic duct* is a slender tube, closed at its distal end, arising from the sacculo-utricular canal. In elasmobranchs it is lacking, but the cavity of the inner ear remains connected with the outside by a slender duct, the *invagination* *canal*, through which the inner ear is filled with sea water, which serves the same function as the endolymph of higher forms. The invagination duct is attached to the sacculo-utricular canal.

The various parts of the inner ear constitute what is known as the *membranous labyrinth*. It is filled with endolymph containing *otoconia*, which are microscopic crystals of calcium carbonate. The "ear stones" of fishes are really large otoliths. Areas of sensory epithelia consisting of large cells with long hairs, known

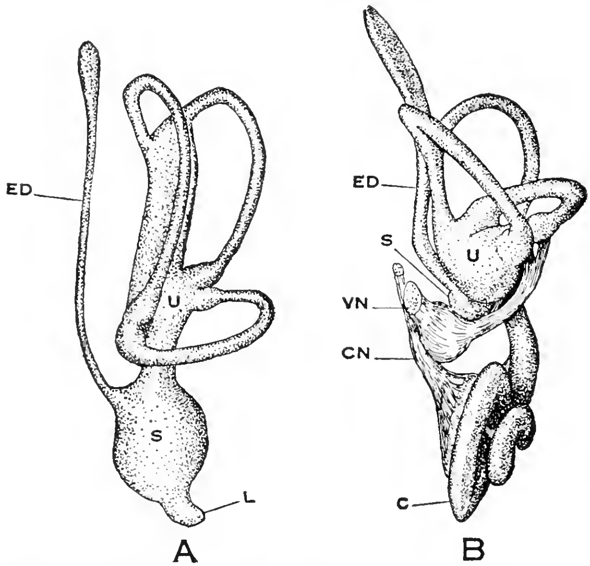
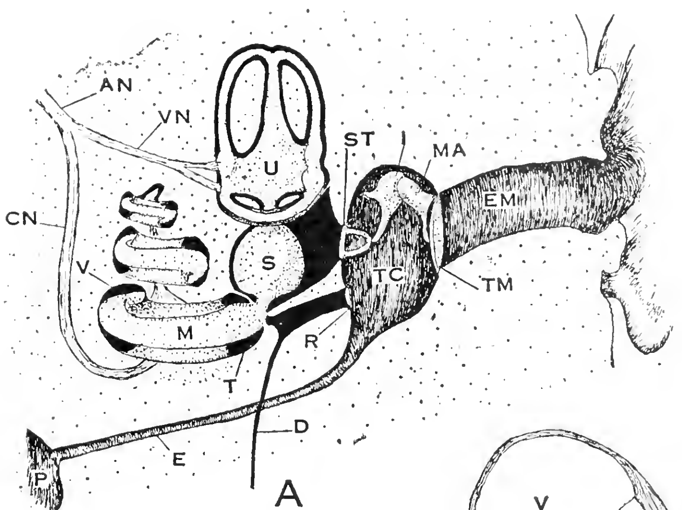


FIG. 129.—A, diagram of membranous labyrinth of lower vertebrate. B, membranous labyrinth of human embryo, 30 cm. in length. C, cochlea (scala media); CN, cochlear nerve; ED, endolymphatic duct; L, lagena; S, sacculus; U, utriculus; VN, vestibular nerve. (*B after Streeter.*)

as *cristae acusticae*, are located in the enlarged end (*ampulla*) of each semicircular canal, while other areas of cells with shorter hairs, called *maculae acusticae*, are found in the utriculus, sacculus, and scala media. In mammals, including Man, the *bony labyrinth* is the casing of bone closely following the outlines of the membranous labyrinth, but separated from the latter more or less completely by a perilymphatic space filled with lymphlike *perilymphatic fluid*. In the region of the spiral cochlea the perilymphatic space does not completely surround the scala media. Instead it is divided into two channels, one above and one below the scala media (Fig. 130), the two channels being connected with each other only at the distal end of the scala media. The upper channel is the *scala vestibuli* and the lower one the *scala tympani*. The terms "upper" and "lower" are used with reference to the cochlea, the apex of the spiral being "above" and the base "below." The bony labyrinth is pierced



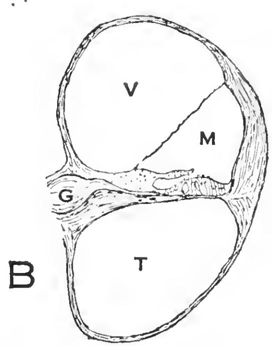


FIG. 130.—A, diagram of mammalian ear; B, cross section of one of coils of cochlea. AN, auditory nerve; CN, cochlear nerve; D, perilymphatic duct; E, Eustachian tube; EM, external meatus; G, spiral ganglion; I, incus; M, scala media; MA, malleus; P, pharynx; R, foramen rotunda; S, sacculus; ST, stapes; T, scala tympani; TC, tympanic cavity; TM, tympanic membrane; U, utriculus; V, scala vestibuli; VN, vestibular nerve. (*Modified from Kingsley, Comparative Anatomy of Vertebrates. P. Blakiston's Son and Company. By permission.*)

by two openings toward the middle ear: (1) the *fenestra rotunda*, located at the base of the cochlea where the scala tympani terminates, and closed by a membrane; and (2) the *fenestra ovalis*, in the region (*vestibulum*) of the sacculus, and closed by a bone of the middle ear, the stapes (Fig. 130*A*). The vestibulum is an enlarged perilymphatic space about the sacculus. The only passageway from the vestibulum to the fenestra rotunda is through the length of the scala vestibuli to the apex of the cochlea and then down through the scala tympani.

Scala Media.—The sound receptors are located in the scala media or cochlear duct, which in man is triangular in cross section (Fig. 130*B*). On its upper side the scala media is separated from the scala vestibuli by the thin vestibular membrane, also known as *Reissner's membrane.* The outer side of the scala media is firmly attached to the wall of the bony labyrinth by the spiral ligament. The floor of the scala media is formed by the *basilar membrane* which, with a narrow bony shelf extending from the axis of the bony cochlea, separates the scala media from the scala tympani. The *organ of Corti,* resting on the basilar membrane, is a complicated structure provided with sensory hair cells, which are the sound receptors through which nerve fibers of the cochlear branch of the auditory nerve are stimulated.

Middle Ear.—The middle ear is a chamber derived from the first gill cleft of fishes. It is connected with the pharynx by the Eustachian tube, by means of which air pressure within the chamber is kept constant. Its inner wall is in contact with the bony labyrinth at the fenestra ovalis and the fenestra rotunda. Its outer wall is provided with a circular tympanic membrane, which in the frog is visible externally at the side of the head. From the tympanic membrane a chain of small bones extends across the cavity to the fenestra ovalis. In the frog these consist of a rod-shaped *columella,* extending from the center of the tympanic membrane to a small cartilage lying in the fenestra ovalis. In man three bones are present: (1) the *malleus,* attached by an arm to the tympanic membrane; (2) the *incus,* extending from the malleus to (3) the *stapes,* a stirrup-shaped bone fitting into the fenestra ovalis. A middle-ear cavity is absent in snakes.

External Ear.—Mammals alone have external ears. The external ear consists of (1) the *pinna,* supported by cartilages and provided with muscles by means of which it may be moved, and (2) the *auditory meatus,* a canal leading to the tympanic membrane. The external ear increases the effectiveness of the ear by collecting and directing sound waves against the tympanic membrane.

Auditory Function.—Sound vibrations are transmitted from the tympanic membrane across the middle ear by the ear bones to the fenestra ovalis, where they are taken up by the perilymph in the vestibulum. Vibrations thus set up in the perilymph travel up the scala vestibuli to the apex of the cochlea, and then down the scala tympani to the fenestra rotunda, whose membrane moves in and out with the vibrations. In passing the scala media the vibrations in the perilymph are transmitted through the walls of the scala media, eventually stimulating the hair cells of the organ of Corti. Whether the vibrations reach the hair cells through the vestibular membrane and endolymph or directly through the basilar membrane remains an open question.

Equilibration.—The semicircular canals serve as organs of equilibration. Every movement of the head causes the endolymph and the contained otoconia to stimulate the cristae acusticae in the semicircular canals from which impulses are carried to the brain by the vestibular branch of the eighth cranial nerve. Since the three canals lie in planes at right angles to each other, movement in any direction is certain to affect one of them. The action of the fluid on the hairs can be illustrated by a simple experiment. If a glass of water is given a sudden rotary twist the glass moves, but the water tends to lag behind, so that if the glass had contained fine hairs extending from its sides into the water, these hairs would have been bent or otherwise disturbed by the water. In a similar way, when the head moves, the endolymph in the canal lying in the plane of motion tends to remain stationary while the sensitive hairs are dragged through it and stimulated. Thus means are afforded for recognizing the direction and components of any motion. At the same time sensory cells in other parts of the utriculus and sacculus are stimulated by the endolymph.

Integrative Action of the Nervous System.—The first appearance of the nervous system in the lower invertebrates, as has been already pointed out, does not involve the creation of a new functional activity so much as a specialization of the functions of excitation and transmission, which are common properties of all forms of life. Protozoa are sensitive to the same stimuli that affect higher forms, yet they lack a nervous system. The importance of the nervous system becomes more and more pronounced with increase in size and complexity of the animal body, because of the greater dependence on it as a means for providing rapid excitation and transmission. The significance of the ever-growing complexity of the central nervous system as the animal scale is ascended, lies in its function of *integration.* A large animal without an adequate nervous system would be merely a mass of protoplasm incapable of finely coordinated activities. The nervous system, with its ramifications connecting various parts of the body with each other and with the brain and spinal cord, provides a mechanism for coordination that brings about an integrative effect, so that activities of widely separated parts of the body function as parts of a whole.

CHAPTER X

THE ENDOCRINE SYSTEM

The internal secretion of an organ includes all substances formed in the organ as a result of metabolic activity and removed from the organ by the blood stream. In the case of glands provided with ducts there is an external secretion removed from the organ through the ducts. Thus the liver takes from the blood certain substances which, after undergoing various transformations, are secreted as bile through the bile duct into the intestine and utilized in part in the digestion of fats. At the same time the liver takes other substances from the blood and transforms them into glycogen and urea, which return as sugar and urea to the blood stream. Bile is the external secretion of the liver, while sugar and urea are its internal secretions. Similarly, the pancreas produces a substance that is necessary for the utilization, by oxidation, of sugar, but this substance instead of being poured through the pancreatic duct into the intestine along with the pancreatic juice—its external secretion—is absorbed by the blood as an internal secretion.

Endocrines or *hormones* are internal secretions, characterized by their capacity to stimulate metabolic activity in other organs or to influence the metabolism of the body as a whole in a rather specific manner. It should be clear, however, that while hormones are internal secretions, all internal secretions are not hormones. Urea is an internal secretion of the liver but is not a hormone, since it really represents one of the end products of nitrogen metabolism that is removed from the circulation by the kidneys.

Endocrines have been studied principally in vertebrate animals, particularly amphibians, birds, and mammals. In these forms it has been shown that normal metabolism of the body as a whole depends upon contributions to the blood stream of specific substances, endocrines, from various organs. Since the effects are produced through chemical means, the endocrine system represents a chemical method of coordinating and controlling metabolism. The fact that the various endocrine organs have definite functional relations with each other makes it impossible to define the functions of one type of endocrine organ without considering the functions of all of them. This interlocking relationship complicates the problem of understanding the system as a whole, since new discoveries may make it necessary to correct and restate what were seemingly well-founded conclusions. While this might be said to be true of all scientific work, it is particularly true of endocrinology because of the intense activity in this field of study at the present time. For this reason only a general outline of the subject will be presented in these pages, the discussion being confined to the known effects produced by the ductless glands individually and collectively. These glands include the pituitary, thyroid, parathyroid, thymus, adrenal, pancreas, and gonads. The pineal gland is also classified as a ductless gland, but since little is known of its function, it will not be considered here.

Anterior Pituitary Gland.—The pituitary gland, attached to the floor of the diencephalon, consists of two principal regions: (1) the *anterior lobe*, or *hypophysis*, derived from the embryonic oral epithelium, and (2) the *posterior lobe*, or *infundibulum*, derived from the floor of the forebrain. A third region, the *intermediate lobe* (Fig. 131), a band of tissue between the first two, is derived from the hypophysis. That the anterior lobe of the pituitary plays a dominant role in the endocrine complex is indicated by the fact that it produces at least five distinct endocrines or hormones, as follows: (1) *somatotropic* or growth-stimulating; (2) *gonadotropic*, or gonad-stimulating; (3) *thyrotropic* or thyroid-stimulating; (4) *lactogenic*, or milk-producing; and (5) *adrenotropic*, having a relation with the cortex of the adrenal gland. Reciprocal functional relations exist between the anterior pituitary lobe and the organs affected by its hormones.

Somatotropic Hormone.—The somatotropic hormone is necessary for the normal growth and development of the body, its absence or reduction resulting in some form of dwarfism. This has been demonstrated experimentally by causing an arrest of the growth of bones and other body tissues of mice and rats as a result of removing the anterior pituitary lobe.

Overproduction of the growth hormone of the anterior pituitary lobe in children produces *gigantism* and in adult life, *acromegaly*.

Gigantism is caused by an overstimulation of the growth of bones, particularly the long bones, during childhood, before the epiphyses (cartilaginous zones near the ends of the long bones) have ossified. A recent authenticated example of gigantism is that of a boy 19 years old, weighing 435 lb. and measuring 8 ft., 6 in. in height and still growing. Acromegaly also involves bone development, but since it arises in adult life, after the length of the bones has been fixed, the result is an increase in breadth of the bones, particularly noticeable in the bones of the face, hands, and feet. In both gigantism and acromegaly, post-mortem examinations show hypertrophy (enlargement) of the

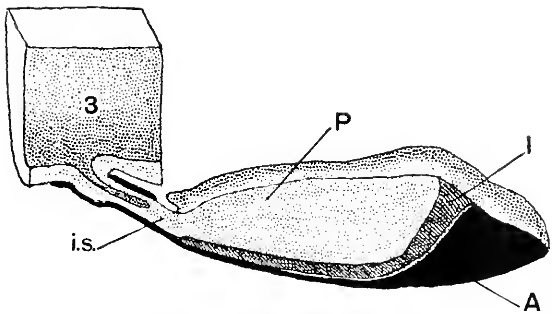


FIG. 131.—Cut surface of right half of pituitary gland and floor of diencephalon of rat, semi-diagrammatic. A, anterior lobe; I, intermediate lobe; i.s., infundibular stalk; P, posterior lobe; 3, third ventricle. (*From a preparation by L. B. Hobson.*)

anterior pituitary lobe. Gigantic rats and acromegalic dogs have been produced experimentally by the injection of extracts of the anterior pituitary lobe.

Gonadotropic Hormone.—One of the results of removing the anterior pituitary lobe of young mammals is the suppression of gonad development. Conversely, implantation of anterior lobe tissue under the skin or in the muscle of young rats causes a precocious development of the gonads. The ovary of the frog, *Rana pipiens,* is quiescent and does not produce mature eggs except during the breeding season, which occurs in the spring. However, ovulation can be induced at other times by implanting fresh frog pituitary tissue. As a result mature eggs may be obtained in the middle of winter. The testes of the male may be stimulated to produce mature spermatozoa by similar treatment. In fact, all the sexual responses, including amplexus, may be evoked out of season by implanting anterior lobe tissue. Ovulation may be produced by anterior lobe tissue from either male or female frogs.

Thyrotropic Hormone.—There is a close functional relationship also between the anterior pituitary lobe and the thyroid gland. If the anterior lobe of the frog tadpole is removed, metamorphosis fails to occur. The thyroid gland of such animals is highly atrophic, a condition that can be corrected by transplanting anterior pituitary tissue or injecting pituitary extract. In either case the thyroid gland is restored to normal condition and metamorphosis follows. Metamorphosis seems to require the presence of a normal thyroid gland in the tadpole. Thus removal of the thyroid gland in tadpoles prevents metamorphosis; feeding thyroid or thyroid extract to such tadpoles results in a completion of metamorphosis; and feeding thyroid gland to normal tadpoles hastens metamorphosis. The thyroid hormone is the immediate cause of metamorphosis, but the thyrotropic hormone of the anterior pituitary is necessary for its normal functioning.

Lactogenic Hormone.—An extract has been obtained from the anterior pituitary gland, which when injected into female rabbits, dogs, or pigs, causes a secretion of milk in the mammary glands, without increasing the amount of the mammary tissue. It is interesting that such extracts obtained from beef or sheep pituitary glands also stimulate the formation of "pigeon milk" in the crop glands of male or female pigeons. The crop glands of pigeons normally produce pigeon milk only when young are being reared.

Adrenotropic Hormone.—One of the effects of removing the anterior pituitary from rats is a degenerative change in the cortex (outer layer) of the adrenal glands, which can be restored by the implantation of pituitary tissue. An extract of the anterior pituitary lobe has been made that is high in adrenotropic activity. The relation of the adrenotropic hormone to the adrenal gland seems to be similar to the relation of the thyrotropic hormone to the thyroid. That is to say, both glands depend upon hormones from the anterior pituitary lobe for the performance of their normal functions.

In addition to these five well-known anterior pituitary hormones there is also evidence of endocrine relationship between the anterior pituitary lobe and the islet cells of the pancreas or their secretion, and therefore with carbohydrate metabolism. These results will be discussed in connection with the pancreas. Since removal of the anterior pituitary lobe also causes atrophy in the parathyroid glands, the presence of a *parathyrotropic* hormone is indicated.

Posterior Pituitary Gland.—Two substances, *pitressin* and *pitocin*, have been extracted from posterior lobe tissue, but since neither has been obtained entirely free of the other, there is some overlapping of the effects produced by them. Pitressin has effects on the heart, blood vessels, respiration, kidneys, and intestine. Pitocin causes the contraction of the muscles of the uterus. Pitressin produces at first a fall and then a prolonged rise in pulse rate, oxygen consumption, and heart output. An irregular quickening of the respiratory rate is a secondary effect of the circulatory disturbance. On the intestine, pitressin produces a muscular constriction. Pitressin has an *antidiuretic* effect, *i.e.*, it decreases the volume of urine. This may be the result of the resorption of water by the kidney tubules, or the retention of water by the tissues. Such results are obtained with patients having *diabetes insipidus* or with normal individuals, who have previously taken water by mouth. On the other hand, *diuresis* (secretion of urine) may be increased by pitressin in animals with a low urine volume. Pitressin thus has both a diuretic and antidiuretic action, depending upon the condition of the subject. The action of pitocin on the musculature of the uterus is more potent during the later stages of pregnancy and is sometimes used to induce parturition.

The Intermediate Lobe of the Pituitary.—A hormone called *intermedin* obtained from the intermediate lobe of the pituitary gland causes chromatophores (pigment-bearing cells) to expand. This can be demonstrated by producing a darkening of the skin of frogs as a result of injecting an extract of the intermediate lobe. In man there is evidence that intermedin has an antidiuretic action on patients suffering from diabetes insipidus, similar to the action of pitressin.

Thyroid Gland.—The thyroid gland of the frog consists of two lobes, completely separated, lying one on each side of the hyoid apparatus between the posterolateral and thyrohyoid processes. In man it consists of two lobes, joined usually by a narrow isthmus, the whole encircling the front and side of the trachea just below the larynx (Fig. 132). Histologically the thyroid gland is composed of a large number of follicles of a more or less spherical shape and filled with a viscous secretion known as *colloid*, in which the thyroid hormone is dissolved (Fig. 133). The thyroid gland has a very rich supply of blood vessels.

In the frog, removal of the thyroid glands of the tadpole prevents metamorphosis. In mammals, removal of the thyroid of the young results in a lowered rate of metabolism and a retarded physical, mental, and sexual development. When thyroidectomy is practiced on adult mammals, the main effect is lowered metabolic rate, manifested by a lowered heat production. Impaired functions and retarded growth can be restored to normal by implanting or feeding thyroid tissue.

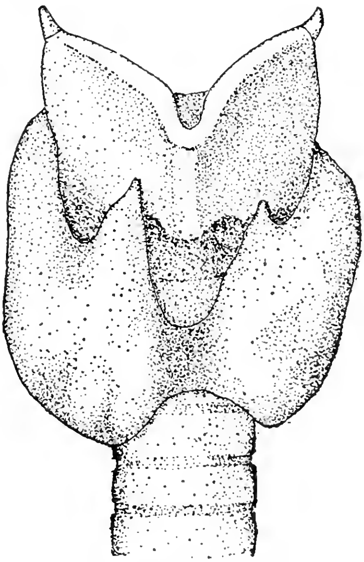


Fig. 132.—Diagrammatic view of human thyroid gland in position against anterior end of trachea.

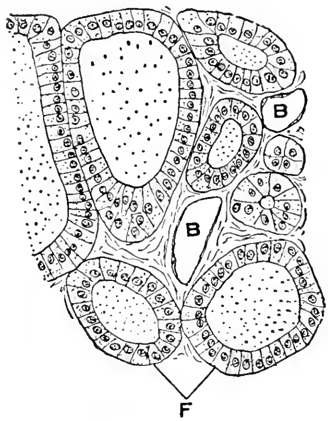


Fig. 133.—Section of human thyroid gland. B, blood vessels; F, follicles filled with colloid. (*After Stöhr.*)

The active principle of the internal secretion of the thyroid gland is *thyroxine*, whose formula is $C_{15}H_{11}O_4NI_4$. This compound has been synthesized and the synthetic substance has the same physiological action as natural thyroxine. Thyroxine fed to tadpoles results in a rapid loss of weight and the completion of metamorphosis in from four to five days. Thyroxine may be used effectively as a substitute for thyroid gland in cases of thyroid deficiency, natural or experimental.

Hypothyroidism or functional insufficiency of thyroid activity produces three pathological conditions that have been known for a long time, *viz.*, *endemic goiter*, *cretinism*, and *myxedema*. The thyroid gland is enlarged in endemic goiter, but the enlargement is due to an abnormal increase in number of the thyroid cells (*hyperplasia*) to compensate for a subnormal secretion of effective thyroid hormone; the diminished amount of effective thyroid hormone being the result of insufficient iodine in the food and water. Endemic goiter can be controlled by adding iodine in the form of iodides to food and water. Cretinism is a long-known pathological condition in human beings, marked by *atrophy* (degeneration) of the thyroid gland and retardation of growth in all parts of the body, including the nervous system and the reproductive organs. Myxedema results from a marked thyroid deficiency in adults and is characterized by reduced metabolism, and general ill health, mental and physical. Usually the skin is thick and dry and the hair falls out. Both cretinism and myxedema respond favorably to the administration of thyroid gland or thyroxine if continued throughout life.[1]

Hyperthyroidism refers to an increased functional activity of the thyroid gland, which, in exceptional cases only, may result in an enlargement, also called a goiter. In Graves' disease or *exophthalmic goiter*, metabolism, nervous irritability, rate of heart beat, and blood pressure are increased. The skin is moist and flaccid. Surgical removal of a part of the thyroid gland may correct the condition, though not always since nervous factors seem to be involved in addition to hyperthyroidism.

In general, the thyroid hormone serves to stimulate metabolic processes by maintaining the rate of oxidation at a certain level. Increased thyroid activity raises the level, and decreased activity lowers it. Removal of the thyroid, therefore, has some effect on every organ in the body. However, the functional activity of the thyroid seems to require for its full accomplishment the presence of the thyrotropic hormone from the anterior pituitary lobe.

The colloid content of the follicles of the thyroid gland varies in amount under different functional states. If anterior pituitary lobe is implanted in a normal animal, the contents of the follicles

[1] For a different view regarding the cause of goiter see H. M. Jones, The Cause of Goitre, Chicago, 1937.

disappear, the follicles shrink in size and the height of the follicle cells increases. Thus under the stress of pituitary stimulation the follicles are emptied and the additional secretion produced by the stimulated follicle cells is so rapidly removed from the glands that the follicles remain empty. This is also the picture one finds in cases of hyperthyroidism. On the other hand, in cases of endemic goiter (hypothyroidism) the follicle cells are low in height and the follicles are filled with colloid, which, however, is without the potency of the normal colloid because of insufficient iodine. In a normal individual, the colloid and the thyroid hormone contained in it seem to accumulate in the follicles under normal conditions of thyroid activity to produce a reserve supply of hormone. When the gland is stimulated, the colloid is resorbed by the follicle cells and passes into the blood. The height of the cells forming the walls of the follicles is a direct index of the activity of the gland.

Parathyroid Gland.—In man the parathyroid glands consist usually of two pairs of nodules attached to, or embedded in, the dorsal surface of the thyroid. They consist of corded masses of polygonal cells, with very little connective tissue. The follicles so characteristic of the thyroid gland are lacking in the parathyroid. Complete removal of the parathyroids in dogs is followed by death in four days, with the development of *tetany* (spasmodic muscular contraction) and a fall of calcium in the blood. Injection of calcium salts causes the tetany to disappear and partially restores the animal to normal conditions. Extracts of parathyroid gland when injected produce results similar to calcium salts. It is therefore concluded that the parathyroids produce a hormone which regulates calcium metabolism and maintains a normal calcium content in the blood. Since removal of the anterior pituitary lobe also produces disturbances in calcium metabolism, there is some evidence that a parathyrotropic hormone is produced by the pituitary which has a relation to the parathyroid similar to the relation of the thyrotropic hormone to the thyroid.

Thymus Gland.—The thymus gland of mammals extends down from the lower throat region into the thorax, overlying the pericardium. Like the thyroid and parathyroid glands, it is also a derivative of the embryonic pharynx. It increases in size until puberty, after which it undergoes atrophic changes so that in the adult it is reduced to fatty and fibrous strands. Histologically the thymus is quite different from the thyroid and parathyroid glands and shows a general resemblance to a lymph gland. It is distinguished by the presence in the medullary region of peculiar structures known as *thymic* or *Hassall's corpuscles*, consisting of rounded groups of degenerated cells bounded by flattened epithelial cells, whose function is unknown. The development and fate of the thymus would seem to imply some relation with the gonads. However, while removal of the gonads results in a hypertrophy of the thymus and thus seems to remove an inhibition to its continued growth, removal of the thymus in young guinea pigs has no effect on general body growth and fails to cause hypertrophy of the gonads. Feeding thymus to frog tadpoles stimulates growth and causes them to grow to unusual size before metamorphosis. Pigeons with defective thymus glands lay eggs deficient in shell, a condition that can be corrected by feeding dried thymus. Much uncertainty exists regarding the exact role of the thymus in the endocrine complex. The most recent work indicates that administration of an extract of thymus increases fertility in adult rats and that when given continuously through successive generations it produces marked precocity in growth and development.

Adrenal Glands.—The adrenal glands of mammals are paired and located near, or in contact with, the kidneys, with which, however, they seem to have no functional relation. In man, each adrenal is a triangular-shaped organ capping the anterior end of the kidney (Fig. 135). In the rat they are spherical in shape and are attached to the dorsal body wall just in front of the kidneys. Two general regions are recognized: a central, *medullary* region, and an outer, *cortical* region. These two regions differ in their embryological origins and also in their functions. In the frog (Fig. 134) the adrenal gland consists of a long narrow, orange-colored band embedded in the ventral face of each kidney. The cortical and medullary cells can be recognized, but they are intermingled.

The cells of the medullary region of the adrenal gland are stained by salts of chromium and are therefore referred to as *chromaffin* or *chromophile* cells. The staining reaction is due to the presence of a substance known as *epinephrine* or *adrenalin*, which has been prepared in a pure state and used in medicine many years. Its chemical structure is known and it has been prepared synthetically. Its formula is $C_6H_3(OH)_2CH{\cdot}OH{\cdot}CH_2{\cdot}$-$NH{\cdot}CH_3$. The principal action of epinephrine is on tissues innervated by the sympathetic nervous system. Its frequent use as a *styptic* (astringent) in minor surgery to control hemorrhage depends on its capacity to constrict arterioles. The vasoconstriction is, however, followed by a vasodilation, which makes the use of epinephrine as a styptic of questionable value. Subcutaneous injection of epinephrine also produces an increase of

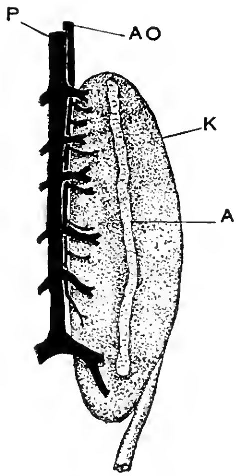


FIG. 134.—Adrenal gland of frog in position on ventral face of kidney. A, adrenal; AO, aorta; P, postcava; K, kidney.

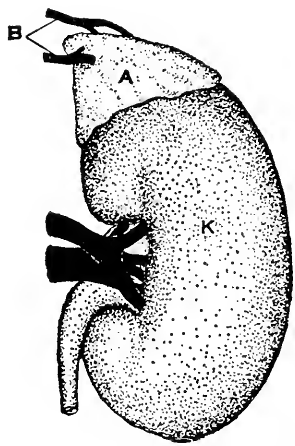


FIG. 135.—Human adrenal gland and kidney, somewhat diagrammatic. A, adrenal; B, adrenal blood vessels; K, kidney.

sugar in the blood (hyperglycemia) and loss of sugar through the kidneys (glycosuria), indicating that it stimulates *glycogenolysis* (conversion of glycogen into sugar) in the liver and elsewhere. It has been shown that in emotional excitement, such as is produced by fear or anger, there is an increased secretion of adrenalin which likewise increases the sugar in the blood. This has an adaptive significance since increased sugar means a ready source of energy. Secretion of epinephrine may be produced in an experimental animal by stimulating the splanchnic nerves to the adrenal glands. Injection of epinephrine in frogs causes contraction of chromatophores, an effect opposite to that produced by the hormone of the intermediate lobe of the pituitary gland.

An animal can get along without the medulla of the adrenal but not without the cortex. This is shown by the fact that while death follows the complete removal of the adrenal glands, death does not occur if only the medulla is destroyed. Death can be prevented in an animal whose adrenals have been removed if an extract of the cortex is given by injection. The extract of the cortex is known as *cortin.* Cortin has been used successfully in treating Addison's disease, which is an affection of the adrenal cortex. It is believed by some that the essential function of cortin is the regulation and maintenance of a normal circulating volume of fluid within the vascular system. In a dog whose adrenals have been removed the depletion of the volume of circulatory fluids seems to be due to a loss of sodium salts and water. The administration of sodium salts to such an animal has effects similar to those produced by cortin in restoring normal salt metabolism and circulatory volume, temporarily at least. *Ascorbic acid*, the crystalline form of vitamin C has been obtained from the adrenal cortex. It is generally believed that the high concentration of vitamin C in the adrenal cortex is the result of storage rather than of local synthesis.

The difference in properties of epinephrine and cortin are correlated with a difference in embryonic origin of the medulla and cortex. The chromaffin cells, which produce epinephrine, seem to be modified sympathetic nerve cells which retain close anatomical relations with the sympathetic nerves innervating the medulla of the gland of the adult. Isolated masses of chromaffin cells also occur in connection with sympathetic ganglia in various parts of the human body. In sharks, the chromaffin tissue exists in the form of numerous distinct organs, completely independent of what corresponds to cortical tissue of higher forms. In the frog, as already mentioned, chromaffin and cortical cells are intermingled. In mammals the cortical tissue is derived from what are known as *mesenchyme* cells, which enclose the chromaffin cells and sympathetic cells to form a single organ.

Pancreas.—The islet cells of the pancreas produce an internal secretion that is also important in the metabolism of sugar. Complete removal of the pancreas in a dog produces glycosuria, and an increased production of urine and of urea, accompanied by pronounced thirst and hunger. *Acetone* is also present in the urine. These symptoms are the same as those shown by human patients suffering from diabetes mellitus. That the symptoms in the case of the depancreatized dog are due to the loss of the islet cells is shown by the fact that the destruction of the alveolar cells alone does not produce them. This can be done by tying off the pancreatic ducts, which causes the degeneration of the alveoli but does not affect the islet cells. Then, too, there is the additional observation that lesions in the islet cells have been found in cases of diabetes mellitus.

Insulin is an extract prepared from islet cells which when injected into diabetic dogs or diabetic patients alleviates the symptoms. Injection of too much insulin into a normal rabbit produces a rapid fall in blood sugar to about 0.045 per cent, when convulsive seizures occur. These promptly disappear if glucose is injected. Obviously the function of insulin is concerned with the metabolism of sugar, though how it is brought about remains an open question. In general terms, insulin has the property of making dextrose available to tissues so that it may be oxidized.

Glycosuria and hyperglycemia can be produced in normal animals by injecting extracts of the anterior pituitary gland. The same symptoms often accompany acromegaly. Therefore the anterior pituitary gland produces a hormone which has the power to increase the amount of sugar in the blood. When insulin is absent, as in pancreatic diabetes, the sugar continues to rise in the blood as a result of the continued action of this hormone of the anterior pituitary which is known as the *diabetogenic* hormone. If the anterior pituitary is removed from a depancreatized dog, glycosuria and hyperglycemia are greatly reduced and the animal may survive for months, at any rate much longer than if its anterior lobe had remained in place. In a sense, then, the diabetogenic hormone is antagonistic to insulin, and this might also be said to be true of epinephrine and of thyroxine. The diabetogenic hormone is antagonistic to insulin in that the former tends to increase the sugar in the blood by promoting glycogenolysis, while the latter is active in consuming sugar. The action of epinephrine and thyroxine resembles that of the diabetogenic hormone in their power to increase the sugar in the blood.

Gonads.—Internal secretions of the gonads are necessary for the full development of *secondary sexual characters*, which are characters aside from the gonads that distinguish males and females, such as the comb, wattles, and spurs in the cock, or beard, voice, body size, and strength in a man. Removal of the gonads in young animals prevents or alters the full development of such characters in the adult. There is, however, no general rule for predicting the results of gonadectomy. Removing the testis of a young Brown Leghorn cock interferes with the complete development of the male type of plumage and of the head furnishings. Otherwise such birds, known as "capons," are large in size, have spurs, and look like cocks, though they lack the pugnacity and temperament of the normal male bird. The result of removing the ovary of the Brown Leghorn early in life is complicated by conditions peculiar to birds. In birds only the left ovary is functional, the right gonad being very rudimentary. If the functional ovary of the Brown Leghorn is completely removed, in a certain percentage of cases the rudimentary right gonad is changed into a testis, with the result that the spayed bird later develops all the pugnacious qualities and sexual instincts of a normal male. Such birds, however, retain their smaller size and develop a male plumage that is succeeded by a permanent typical hen plumage. The female in this case has the potentiality of both maleness and femaleness, the outcome in the normal cases being determined by the development of the left gonad and the suppression of the right.

In mammals extracts have been made from various parts of the ovary and their properties studied. *Theelin* has been made from the follicles in which the eggs develop. After an egg is discharged from a follicle, the cavity becomes filled with cells, forming what is called a *corpus luteum*, from which another hormone, *progestin*, has been extracted. Theelin has also been obtained during pregnancy from the placenta. It is also present in the blood of the female from puberty on. When injected into immature female rats, it causes the uterus and vagina to become mature. Theelin partially stimulates the proliferation of the uterine mucosa in anticipation of the implanting of the fertilized egg; and progestin holds the functioning of the ovary in abeyance until the birth of the young and also augments the action of theelin on the uterus. The production of both theelin and progestin is controlled by the gonadotropic hormone of the anterior pituitary. The latter is necessary for the normal growth of the follicles and the production of corpora lutea.

A hormone has been prepared from the testis which stimulates the growth of the accessory reproductive organs of the male. As in the case of the ovarian hormones, its secretion is under the control of the anterior pituitary.

General Significance of the Endocrine System.—The secretions of the endocrine organs furnish a chemical mechanism for the functional coordination of various parts of the body. The other general mechanism for this purpose is the nervous system with its nervous pathways, along which impulses are conducted to and from all parts of the body. Of the two, the chemical method is perhaps older phylogenetically, but practically it is difficult in the final analysis to draw a sharp line between them because the functional activity of the nervous system rests upon a chemical basis too. In the nervous system, however, the paths along which nervous impulses travel are separated and insulated from each other, while in the endocrine system the means of transporting the exciting agents is the blood, which is a common vehicle for all of them. In the nervous system some of the pathways have become specialized to perform a single function, as for example the optic nerve; in the endocrine system, specific substances are all mingled in the blood stream, where they may augment, counteract, or stimulate each other before reaching their functional destinations. Both systems, however, are closely related functionally and each loses its individuality in the correlation of the body as a whole.

CHAPTER XI

CELL DIVISION AND GAMETOGENESIS

The cell seems to be the smallest or simplest aggregate of matter capable of maintaining itself alone, or in combination with other cells, as a living thing over a period of time, and capable also of reproducing itself. A basic fact in the organization of the cell seems to be that it is always composed of two kinds of protoplasm, nuclear and cytoplasmic. In metazoans cell boundaries may be indistinct or lacking, but every cell region is provided with a nucleus. It is true, of course, that bacteria lack a morphological nucleus, but they do contain nuclear material, even though it is not segregated inside of a nuclear membrane. Mammalian erythrocytes are not nucleated, but these structures are really enucleated cells that survive for a relatively short time and are incapable of reproducing themselves. Since it has also been shown that under experimental conditions neither nucleus nor cytoplasm can survive long in the absence of the other, it appears that the chemicophysical system represented by the nucleus and cytoplasm combined as in a cell is the minimum for the production and continuation of the living state.

It is a dictum of biology that cells come only from preexisting cells by a process of cell division; and, on the other hand it is also said that the first forms of life, or the first cells, to appear on the earth were produced from nonliving matter (abiogenesis). No one can say what these first forms of life were like, or to what extent they resembled the simplest kinds of living things known today. Whatever may be the answer to that problem, it has been conclusively shown that known present-day species of living things come from preexisting species, or that the cells of which they are composed come from preexisting cells. Reproduction of organisms depends upon the reproduction of cells, which in turn is the result of cell division. Cell division is thus a very important phase of biological activity (Fig. 136).

The cells of the body of the metazoan animal fall into two general groups, *somatic cells* and *germ cells*, although these two groups are not distinguishable at all times, as in the case of some of the lower invertebrates. Somatic cells comprise the bulk of the body and include all cells except the reproductive cells, which are the germ cells. In the higher forms these two groups can always be recognized, often from very early stages in development. In lower forms, Hydra for example, germ cells are indistinguishable from somatic cells until the formation of the ovary and testis.

Somatic Mitosis.—The common method of cell division, known as *mitosis*, consists of a series of complicated changes which for convenience has been arranged in progressive stages as follows:

Resting Stage.—When a cell is not dividing, it is said to be in the resting stage, though as a matter of fact it may at the time be

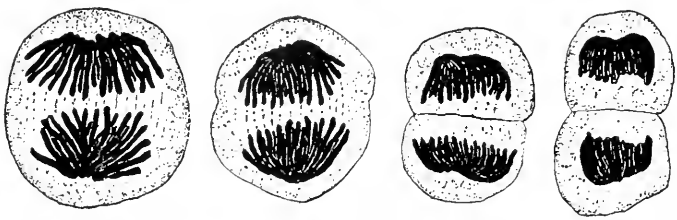


FIG. 136.—Mitotic figures in cells of larval salamander as they appear in an ordinary section of the skin. × 900.

actively engaged in the performance of its functional role in the body economy and be resting only in the sense that it is not dividing. Except in the basal layer of the epidermis, somatic mitoses are rare in the adult stage of vertebrates. For the study of somatic cell divisions embryonic stages are preferable since these abound in cell divisions. An embryonic vertebrate cell, say, of the skin or of the liver, consists of a cytoplasmic region in which usually a single nucleus is embedded. Cytoplasm and nucleus are each bounded by a membrane. In the ordinary fixed and stained section, the nucleus contains irregular faintly stained clumps of *chromatin* and usually one or more rounded bodies called *nucleoli.* If the cells are undergoing rapid cell division, a structure known as the *centrosome* may be seen in the cytoplasm, close to the nuclear membrane. The centrosome is a rounded area composed of compact cytoplasm, in the center of which are two rounded bodies called *centrioles.* Centrosomes and centrioles are usually not visible in sections of adult tissues. During rapid cell divisions they continue from one cell generation to the next, but there is evidence that they may be formed *de novo* from the cytoplasm.

Division Stages.—The following description is in the nature of a generalized account of the mitotic process as it occurs in somatic cells. There are many differences in detail in mitosis in different animals, which can be only touched upon here. The preparatory steps leading to cell division make up the *prophase* of the process, which is initiated apparently by the separation of the centrioles and the formation of a mitotic *spindle* between them (Fig. 137). This is often accompanied by the formation of *astral radiations* extending in all directions from the centrosomes. The chromatin of the nucleus meanwhile condenses into a number of thin threads, corresponding to the number of *chromosomes* characteristic of the species. In some forms the chromatin threads seem at first to be connected in a continuous thread, known as a *spireme*, which later breaks up into chromosomes; in others the chromatin threads appear separate from the beginning of their formation. In either case a definite number of chromosomes forms from the chromatin of the resting nucleus, regardless of whether a continuous spireme is formed or not. Chromosomes are frequently bent in V shapes, as shown in Fig. 137. The details of mitosis can be followed more readily in the latter type of chromosome, which for this reason has been used in the illustration.

As the chromosomes assume form, the centrioles move farther apart with an accompanying enlargement of the spindle which gradually shifts to the center of the cell. The nuclear membrane then gradually dissolves, releasing the chromosomes, which quickly assume places in the equatorial plane of the spindle. In some forms, the chromosomes appear as undivided rods, or each may show a longitudinal split that foreshadows the ensuing division, and which may appear in the chromosome while it is still within the nucleus. In the former case the undivided chromosomes become split shortly after reaching the spindle. The nucleolus melts away with the dissolution of the nuclear membrane and takes no part in the division process. When the chromosomes have become arranged in the equatorial plane of the spindle, the *metaphase* stage of mitosis has been reached

(Fig. 137, *D*, *E*, and *F*). In the case of the V-shaped chromosomes, shown in the illustration, the chromosomes are arranged with the

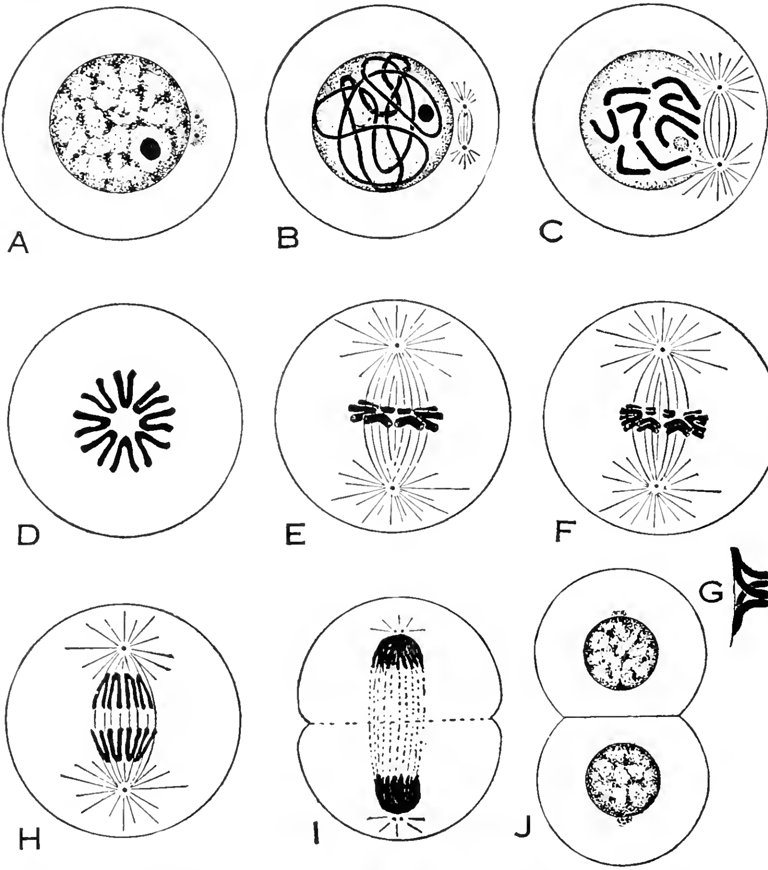


Fig. 137.—Diagram of karyokinesis. A, resting stage, two centrosomes in cytoplasm near nucleus; B, early prophase, spireme stage; *C*, later prophase, spireme segmented into eight chromosomes; D, polar view of chromosomes at metaphase; E, side view of spindle and chromosomes at metaphase, each chromosome undivided; F, metaphase, each chromosome shows a lengthwise split; G, side view of a single chromosome dividing, early anaphase; H, anaphase; I, telophase; J, two complete daughter cells.

apices of the V's pointed toward the spindle to which they become attached.

In the next stage, the *anaphase*, each chromosome, beginning at the apex of the V, is split longitudinally into halves, the result being the formation of two daughter groups of chromosomes, equivalent in every respect. The appearance of the mitotic figure at this point suggests that each half chromosome is being drawn toward a pole of the spindle, but nothing final is known as to the mechanics of the process. In favorable material, during the anaphase, each chromosome seems to be attached to a fiber extending from the chromosome to the pole of the spindle and known as a chromosome fiber or a *half-spindle fiber*. At this same stage, as the ends of the chromosome separate, one or two fibers stretch between the separated ends. These fibers are called the *interzonal fibers*. There is some evidence to show that chromosomal and interzonal fibers are formed by the chromosomes after they reach the spindle. The central or axial part of the spindle seems to be formed as a result of activity in the centrosomes. In endeavoring to understand the mechanics of mitosis it is necessary to remember that the separation of the chromosome into two halves is begun, in some cases at least, before the chromosome reaches the spindle. Thus there may be a repelling force operating to separate the chromosome halves, begun in the nucleus and continuing on the spindle. Some students of mitosis believe that both a "pulling" and a "pushing" factor are concerned in the process.

The anaphase includes stages following the metaphase up to the point where each of the two daughter groups of chromosomes forms a dense mass about each pole of the spindle. When this point is reached, mitosis is in the *telophase* or final phase of division. In the late anaphase or early telophase, the centriole at each pole of the spindle divides in two. A constriction in the cytoplasm in a plane at right angles to the spindle begins to appear at this time and gradually cuts the cell in two. The spindle fibers and astral radiations then fade and a typical nucleus forms in the region of the telophase chromosomes. The chromosomes become diffuse and a nucleolus reappears.

The most impressive feature of mitosis is the exact lengthwise division of each individual chromosome into two equal parts, resulting in each daughter cell receiving not only an equivalent *quantity* of chromosome material but also an equivalent *quality*, since each chromosome possesses qualities or characteristics that distinguish it from other chromosomes. It is true, of course, that the cytoplasm is also divided in equal amounts in mitosis, but in this case only a mass division takes place. The *achromatic* *structures* involved in mitosis are the spindle, the centrosomes, centrioles, and astral radiations, all of which together with the chromosomes may be involved in a final explanation of the mechanics of the process. Since tissues or cells ordinarily used for the study of mitosis consist of material that has undergone special treatment with reagents and stains prior to mounting on glass slides, it has been claimed that some of the structures seen in such preparations are possibly artifacts caused by coagulation or precipitation by reagents. These objections have been answered by demonstrating that chromosomes as well as a spindle and centrosome areas can actually be seen in living cells under proper conditions. When living cells undergoing mitosis are dissected, the spindle appears as a hyaline material to which the chromosomes adhere as jellylike masses. The spindle is not an artifact though the fibers may be. The centrosome areas are more viscous than the surrounding cytoplasm of dividing cells, showing that they too are actual structures in the cell.

Division of somatic cells occurs throughout the developmental stage of Metazoa. In the adult animal, cell division is confined to certain cells whose function is to replace loss. Thus the outer layer of the human epidermis is being continually rubbed off and replaced by cells pushing up from the deeper layers of the epidermis, in the lowest of which, cell reproduction takes place throughout life. The red blood corpuscles of mammals also have a short life in the circulation and are replaced by cells of the bone marrow. Mitotic divisions may occur sporadically among other tissue cells. It is said that the nerve cells of adult mammals never undergo cell division. The number of chromosomes appearing in somatic mitosis is a constant one for the species, although there may be a difference, also constant, between the sexes of the same species. This point will be discussed in connection with the germ cells.

Amitosis.—Though simple and more direct than the mitotic method of cell division, amitosis is a much rarer form of cell division. There has been much controversy about its occurrence and nature, which need not be entered into here. Amitosis has been described in various tissues under normal conditions, and in degenerating and pathological tissues, from which it seems clear that it is not the ordinary method of cell division. Figures of cells dividing amitotically show each constituent of the cell, beginning with the nucleus, dividing in two by simple constriction without the accompaniment of chromosome and spindle formation (Fig. 138).

Gametogenesis.—Reproduction in Protozoa may consist simply in the division of the animal as a whole into two parts, each of which then grows to the size of the original. In sexual reproduction among Metazoa, the egg and sperm (spermatozoon) are cells that have the power, when united in fertilization, of developing into a new organism by cell division, accompanied by growth and differentiation. Some Protozoa also produce germ cells and exhibit a primitive form of sexual reproduction. The asexual reproduction that occurs in some Metazoa does not involve the production of germ cells.

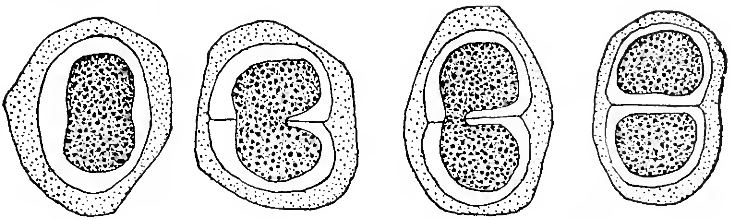


Fig. 138.—Amitosis in nurse cells of ovary of the potato beetle, *Leptinotarsa signaticollis*.

All of the cells of the metazoan body develop from the fertilized egg. That means that both somatic and germ cells have a common origin in the fertilized egg. The essential fact in fertilization, to be considered more in detail later, is the formation of a single cell, the fertilized egg, from the fusion of the egg nucleus with a nucleus brought in by the sperm. The number of chromosomes, the *zygotic* or *diploid* number, occurring in the somatic cells of the animal is thus determined at fertilization. The egg then undergoes cell division (cleavage) by the mitotic method, as described in the preceding pages, the cells or *blastomeres* thus produced containing the potencies of both somatic and germ cells. Then, after a number of cell generations have been produced, certain cells, called *primordial germ cells,* may be distinguished from the somatic cells. There is evidence in many animals that the appearance of the primordial germ cells marks an important and final differentiation of germ-cell material from somatic. In higher forms, it is generally thought that the functional germ cells are the descendants of the primordial germ cells and, as a corollary, that once the somatic cells have become differentiated as such, they never form germ cells at any subsequent period.

Gametogenesis is the production of gametes, or eggs and spermatozoa, from primordial germ cells. *Oogenesis* includes all

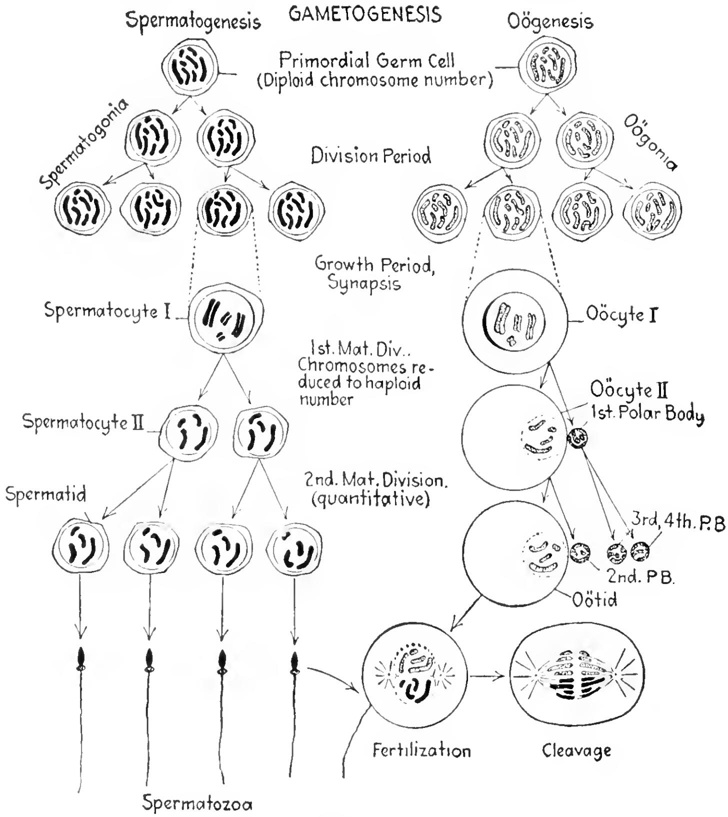


Fig. 139.—Diagram of gametogenesis, fertilization and cleavage.

stages involved in the development of eggs, and *spermatogenesis* is the process of producing spermatozoa from primordial germ cells. Oogenesis and spermatogenesis are essentially alike but differ in certain details.

Oogenesis.—In the female rapid cell division of the primordial germ cells leads to the production of a large number of *oogonia*, only a few of which are shown in Fig. 139. This period of cell multiplication is known as the division period, during which the rate of mitotic division is so rapid that practically no growth occurs between divisions. The growth period that follows the division period is characterized by cessation of mitosis and the enlargement of the oogonia by the storage of yolk in the cytoplasm. By this means oogonia are converted into *primary oocytes.* In insects (Fig. 140) some of the oogonia are converted into nurse cells and supply the growing oocytes with nutriment that enters the oocyte through the nutritive string, a temporary process of the oocyte. In Hydra, as mentioned in an earlier

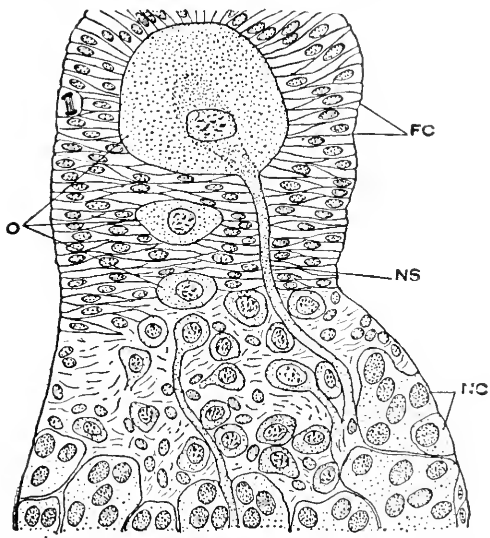


Fig. 140.—Longitudinal section of an ovariole showing how nutrition is supplied to the egg of the potato beetle, *Leptinotarsa signaticollis*, during the growth period. NC, nurse cells; NS, nutritive string; O, oocytes; FC, follicle cells.

connection (Chap. VIII) the oocyte grows by engulfing surrounding cells, some of which may have been potential oocytes. A similar engulfment of cells by the oocyte occurs in the growth period of the oocyte of flatworms. In vertebrates, the oocyte derives its nutrition from the blood vessels supplying the ovary. The fully developed oocyte is a cell of large size, in some cases, as in birds, of macroscopic proportions. Thus the yellow or yolk of the hen's eggs is the same size as the primary oocyte at the end of the growth period.

The oocyte at the end of the growth period now enters what is called the maturation period, characterized by two *maturation* *divisions.* During the first maturation division the oocyte divides into two cells of very unequal sizes, the larger called the *secondary oocyte* and the smaller the *first polar body* or *polocyte.* In the second maturation division the secondary oocyte divides into two cells, again of unequal size, the larger of which is the *ootid* and the smaller the *second polar body.* At the same time the first polar body may divide to form the *third* and *fourth polar bodies.* As a result of the two maturation divisions a primary oocyte may produce four cells: a single ootid, which is relatively very large and is the mature ovum, and three small polar bodies. The polar bodies may remain for a time attached to the egg at the point where they are extruded, but sooner or later they are lost and play no further part in development of the egg. It is generally supposed that the polar bodies have the same potentialities as ova but lack sufficient cytoplasm and yolk for development. This view is supported by experiments in which it was found that (in certain flatworms) abnormally large first polar bodies, when fertilized, develop to an early larval stage. Development up to a certain point is possible in this case because the polocyte contains a certain amount of yolk. In most animals it is very small and consists of little more than a nucleus (Fig. 141).

Spermatogenesis.—In the male, the division period produces a large number of *spermatogonia.* These then pass through a growth period, but the *primary spermatocytes* formed as a result are much smaller in size than the corresponding primary oocytes of oogenesis (Fig. 139), though greater in number. In the first maturation division each primary spermatocyte produces two *secondary spermatocytes* of equal size. Likewise, in the second maturation division each secondary spermatocyte divides to form two *spermatids* of equal size. Therefore each primary spermatocyte produces four spermatids. Each spermatid now undergoes a further development, called *spermiogenesis,* as a result of which it is transformed into a spermatozoon. In this transformation the nucleus of the spermatid is crowded into what is called the *head* of the spermatozoon, while the remaining parts of the spermatozoon, called the *middle piece* and *tail,* are formed of the cytoplasm. The tail is an organ of locomotion by means of which the spermatozoon propels itself through fluid. The spermatozoa of some animals lack a tail and are nonmotile.

Comparing oogenesis with spermatogenesis, the main differences are: (1) a more intensive growth period in oogenesis; (2) a larger total number of spermatozoa than of ova; and (3) the completion of oogenesis at the ootid stage.

Chromosomes in Gametogenesis.—What is perhaps the most striking feature of gametogenesis, *viz.*, the behavior of the chromosomes, may now be considered. Assuming that the

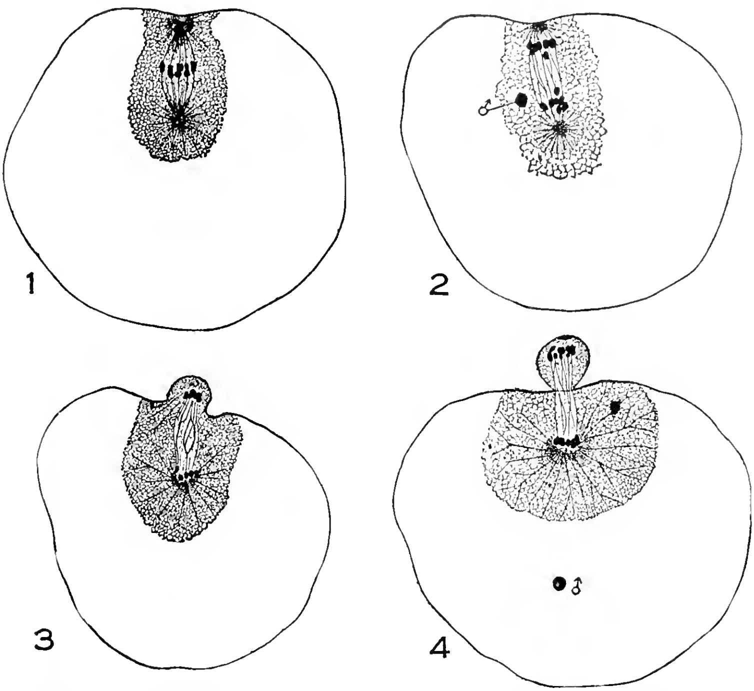


FIG. 141.—Four stages in the formation of the first polar body in the egg of *Planocera inquilina*. ♂, sperm nucleus. (*From Patterson and Wieman.*)

zygotic number of chromosomes of the fertilized egg is 8, both primordial germ cells and somatic cells exhibit 8 chromosomes at each mitotic division. So far as the somatic cells are concerned this condition prevails in all subsequent mitotic divisions. It also holds for the division period of gametogenesis, as indicated in the diagram (Fig. 139). During the growth period of the nucleus of the developing oocyte or spermatocyte, the chromosomes lose their identity in the resting nucleus. At the end of the prophases of the first maturation divisions, however, instead of the expected 8 chromosomes, only 4 appear, but each of the 4 is a double chromosome. This pairing of the chromosomes is known as *synapsis* and takes place in the prophase of the first maturation division.

Meiosis.—Owing to constant differences in form and size, it is possible to arrange the chromosomes of the presynaptic period, or of the cleavage period, or of any somatic cell, into two series of *homologous* chromosomes. In the hypothetical case represented in Fig. 139, the two series consist of 4 chromosomes each. During the prophase of the first maturation division these pair off according to form, size, or other characteristics to form double or *bivalent* chromosomes. As shown in Fig. 139, during the first maturation division, the members of the synaptic pairs undergo *disjunction* and pass as whole chromosomes to opposite poles of the spindle, so that each secondary spermatocyte or each secondary oocyte and the first polar body, receive 4 chromosomes. The reduction of the chromosome number from the diploid number 8 to the haploid number 4 is known as *meiosis.* It is also spoken of as a *qualitative division.* In the second maturation division, which follows, each of the four chromosomes divides in the usual way, with the result that each spermatid and each ootid and second polar body receive 4 chromosomes. The second division then is a *quantitative division,* such as takes place in any somatic mitosis.

If, as appears to be the case in some animals, the first maturation division is a quantitative one, each component of each synaptic pair being divided longitudinally, the second maturation division becomes a reduction division; but whether reduction occurs in the first or second maturation division, the final result is the same, *viz.,* the ootid, polocytes, and spermatids all receive the haploid number of chromosomes. The diploid or zygotic number is restored at fertilization by the union of the nuclei of the ootid and the spermatozoon. Since the cells of the embryo, and later the adult, are produced by cell division from the fertilized egg, it follows that each cell in the body is provided with the zygotic number of chromosomes, except the germ cells of the postreduction stages. It should also be clear that the zygotic chromosome complex consists of a maternal and a paternal series, which separate in meiosis. These facts are of utmost importance in understanding the mechanism of heredity, in which connection they will be referred to again in a later chapter.

Sex Chromosomes.—In the hypothetical example used to illustrate mitosis and gametogenesis, the zygotic number of chromosomes was assumed to be 8. Though constant for any

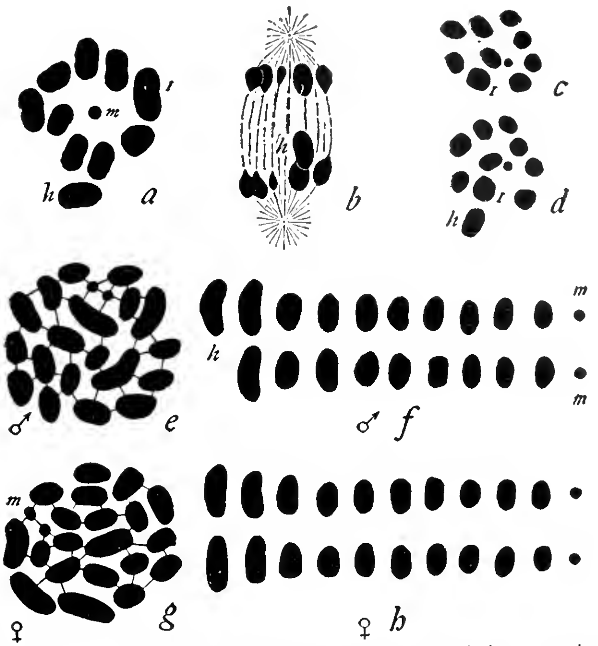


Fig. 142.—Chromosomes of the squash bug, *Anasa tristis*. *a*, polar view of equatorial plate, first spermatocyte; *b*, side view of anaphase, second spermatocyte; the heterochromosome (*h*) passes undivided to one pole of spindle; *c* and *d* show the results of the second spermatocyte division, ten chromosomes going to one cell (*c*) and eleven to the other (*d*), so that two classes of spermatozoa result; *e*, polar view of spermatogonium showing twenty-one chromosomes; *f*, diploid chromosome complex of male arranged in pairs according to size, and forming a biparental series; *g*, polar view of equatorial plate of oogonium showing twenty-two chromosomes; *h*, diploid complex of female, paired according to size. (*From Wilson, Journal of Experimental Zoology.*)

given species, the number may actually be from 2 to 100 or more. Thus in the nematode worm *Ascaris megalocephala univalens* the zygotic number is 2; in the frog, *Rana pipiens*, 26; in man, 48; etc. In some cases the number may be different in the male and female of the same species, an example of which may now be considered. *Anasa tristis* is the common squash bug. In this form the zygotic number of the female is 22, while that of the male is 21. During oogenesis the number is reduced to 11 in one of the maturation divisions, with the result that the ootid remains with 11 chromosomes, the gametic number of the female. The zygotic chromosomes of the female therefore consist of 11 synaptic pairs which undergo disjunction in one of the maturation divisions. In spermatogenesis, the prophases of the first maturation division show 11 chromosomes, 10 of which are synaptic pairs and the eleventh a single chromosome, known as the *odd chromosome* or the *sex chromosome.* It should be noted that the homologue of this chromosome is paired in the female zygotic series (Fig. 142). In the first maturation division, in the male, the 10 paired chromosomes undergo disjunction and the odd chromosome divides quantitatively, with the result that each secondary spermatocyte receives 11 chromosomes, one of which is an odd chromosome. In the second maturation division, the odd chromosome passes undivided to one pole of the spindle, while the remaining 10 chromosomes divide quantitatively. This results in the production of two kinds of spermatids (and later two kinds of spermatozoa), one containing 10 chromosomes and the other 11. Since the ootids all contain 11 chromosomes, a male is produced when a sperm containing 10 chromosomes fertilizes an egg (10 + 11 = 21), and a female when a sperm containing 11 chromosomes fertilizes an egg (11 + 11 = 22). In *Anasa tristis,* the presence or absence of the odd chromosome apparently determines the zygotic sex, and it is for this reason called the sex chromosome. It is also known as the X *chromosome* or as the *heterochromosome.* The remaining chromosomes, which are equally represented in the two sexes are known as *autosomes.*

An inspection of the spermatogonial chromosomes (Fig. 142) shows that the diploid complex of the male can be arranged into a series of 10 synaptic pairs of autosomes plus one X chromosome, which lacks a synaptic mate. The oogonia of the female consists of 10 synaptic pairs of autosomes, corresponding to those of the male, plus two X chromosomes. The difference in the zygotic chromosomes of the two sexes is the difference in the number of X chromosomes, of which the male has one and the female two.

X and Y Chromosomes.—Inequality of some sort in the chromosomes of the male and of the female seems to prevail in practically all animals. Frequently, as in *Anasa tristis,* the inequality consists of a difference in number of the X chromosomes, but in other cases it may consist in differences in size of one or more of the sex chromosomes. An example of such a condition occurs in the fruit fly *Drosophila melanogaster*, the zygotic number of which is 8 in both sexes (Fig. 143). In the female these 8 chromosomes are found to be made up of 3 pairs of autosomes plus 2 X chromosomes, and in the male of 3 pairs of autosomes plus one X and one Y chromosome, which is larger than X and is also hook-shaped. The difference in the chromosomes of the male and the female then becomes the difference between X and Y, which is a difference in form and size. At the end of the maturation divisions of the oocytes, each ootid receives 3 autosomes and one X chromosome. In the male two kinds of

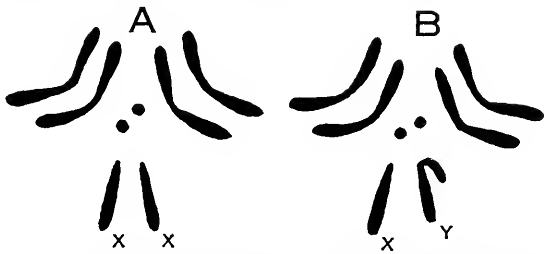


FIG. 143.—The diploid series of chromosomes of *Drosophila melanogaster*. A, female; B, male. (*After Morgan.*)

spermatids are produced, one receiving 3 autosomes plus one X chromosome and the other 3 autosomes plus one Y chromosome; resulting in the production of two kinds of sperm. An egg (3 + X) fertilized by a sperm carrying an X chromosome (3 + X) develops into a female (6 + 2X); fertilized by a sperm carrying a Y chromosome (3 + Y), it becomes a male (6 + X + Y). A similar condition prevails in man where the zygotic number is 48. In the female these 48 chromosomes are made up of 23 pairs of autosomes plus two X chromosomes, and in the male of 23 pairs of autosomes plus one X and one Y chromosome. X and Y combinations sometimes are found in reversed order so far as the sex is concerned, as in birds where the female has the XY combination and the male the XX.

Sex Determination.—The term *zygotic sex* refers to the sex, male or female, established at fertilization, presumably as a result of certain chromosome combinations. The *definitive sex* is the sex that finally develops. Under normal conditions it would appear that the zygotic sex is the same as the definitive sex. However, it has been conclusively shown that under abnormal or under experimental conditions, the zygotic sex may be altered, or completely changed. That amounts to saying that an animal determined as a female at fertilization may be changed to a definitive male or vice versa. Thus when the functional ovary of a Brown Leghorn is removed early in life, the rudimentary right gonad may develop into a testis and the bird takes on most of the characteristics of the male. This seems to indicate that the female in this case is *heterozygous* for sex, *i.e.*, that it has the potencies of both male and female sex organization. This is not true of the cock, where removal of the testes does not produce a female, but a kind of neutral condition known as the capon. In the female the presence of the normal ovary and, as a result, the presence of hormones secreted by the ovary, exercise a restraining influence on the development of inherent male potencies. Hens in their old age sometimes crow like cocks, a condition that also seems to be due to the removal of active ovarian tissue through atrophy. There is at least one authentic case on record of a hen, after having laid eggs that produced normal chicks, changing into a cock that became a functional male in all respects even to the point of "fathering" two chicks. In this case postmortem examinations showed that the ovary had been destroyed by tuberculosis.

There is nothing specific in the X or Y chromosome as sex determiners. Neither is endowed with what might be called exclusive qualities of maleness or femaleness. Some observations indicate that the result of normal XX or XY combinations seems to rest on the relative proportion of autosome to sex chromosome material. Thus the presence of XX or XY in Drosophila does not necessarily produce a female or male, respectively. Studies of flies in which abnormal chromosomal combinations had been formed as a result of nondisjunction in the maturation divisions, shows that flies with 2 X chromosomes but with 3 each of the autosomes, making a total of 11, are not females but intergrades between males and females. The tendency toward maleness in such cases would seem to be due to the fact that there is less X chromosome material in proportion to autosomes than is present in normal females. In other words, sex factors exist in the autosomes as well as in the "sex" chromosomes.

In pigeons, it has been found that the female-producing egg is not only larger than the male-producing egg but also contains a greater amount of chemical potential energy. Ordinarily pigeons lay eggs in clutches of two, one of which on the average develops into a male and the other into a female. It has been discovered that if eggs are removed from the nest as fast as laid, the female is stimulated to lay a greater total number of eggs than normally and that as a result the percentage of female-producing eggs is increased. Presumably the overstimulation caused by enforced egg-laying activity led to the production of eggs of greater metabolic capacity. The normal sex ratio of the offspring is changed by changing the metabolic rate of the mother.

Delaying fertilization in frog eggs for three or four days increases the number of males. Frog tadpoles reared at a temperature of 32°C. produce a preponderance of males. These and many other experiments might be cited to illustrate the fact that the zygotic sex may be changed by factors that in some way disturb the metabolic balance that normally accompanies, or is correlated with, a certain combination of chromosomes.

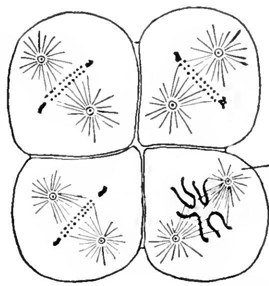


Fig. 144.—Third cleavage of egg of *Ascaris megalocephala*, semidiagrammatic. s.c., stem cell.

Chromatin Diminution.—As a general rule, the zygotic number of chromosomes, established at fertilization, continues to be the number found in the somatic cells of the embryo and later of the adult, and also the number occurring in the presynaptic stages of the germ cells. An exception to this generalization is the phenomenon of chromatin diminution, as it occurs in certain species of nematode worms belonging to the genus Ascaris. In *Ascaris megalocephala bivalens*, the zygotic number of chromosomes is 4. In the first and second cleavages of the fertilized egg, each of these large V- or U-shaped chromosomes is divided longitudinally in the usual way, so that each of the four cells receives 4 chromosomes. In the late prophase stages of the next cell division (third cleavage) in each of three cells the ends of the chromosomes are cast off into the cytoplasm and the chromosomes that actually appear later on the spindle are numerous small spherical bodies formed from the middle portions of the chromosomes. These divide as chromosomes and appear in succeeding cells descended from the three. Thus as a result of the process of *chromatin diminution*, the ends of the chromosomes are eliminated and the remainder of each chromosome breaks up into numerous smaller fragments. In the fourth cell, called the *stem cell*, the chromosomes appear in their usual form and are divided in the usual manner. In the fourth and fifth cleavage, chromatin diminution again takes place in one of the descendants of the stem cell. As a result, there are established two kinds of cells with regard to chromatin content, diminished and undiminished. In Ascaris the somatic cells are derived from embryonic cells in which chromatin diminution has occurred, and the germ cells from undiminished cells (Fig. 144).

CHAPTER XII

ONTOGENY

Ontogeny is the development of the individual; *phylogeny* is the development of the race. Since the history of a race is composed of a number of individual life histories, phylogeny and ontogeny are merely different aspects of the same process, *viz.*, development. The ovum and sperm are the basic elements from which the individual develops, while individuals in turn constitute the elements of the race. Ontogeny is the subject matter of embryology, the study of the development of the individual. In the study of organic evolution interest is focused on the origin and history of the larger unit, the race.

Germ Cells.—The egg and spermatozoon are alive by virtue of the fact that they are derived from living cells. Reproduction of an individual animal from germ cells is not a creation of life, but a continuation of life in the form of an individual animal body. New individuals are alive because they are produced from living germ cells. The egg is a relatively large cell, whose bulk is due to the presence in the cytoplasm of a greater or lesser amount of yolk stored there during the growth period of oogenesis; the amount of yolk being correlated with the conditions under which embryonic development takes place. Thus eggs scantily supplied with yolk, such as a human egg (Fig. 145), receive nutriment from maternal tissues during intrauterine development. Other eggs poor in yolk, such as the starfish egg, develop rapidly to a free-living larval stage capable of gaining food from the environment, which is sea water. Large-yolked eggs usually develop outside the body of the mother, the yolk serving as the source of nourishment. Exceptions to this are found in viviparous sharks and snakes, whose large-yolked eggs develop in the uterus. Eggs that are laid are provided with a shell of some sort to protect the developing embryo. The shell is not a part of the egg proper, but is secreted about the egg as it descends the genital tract. Physiologically the egg, before it is stimulated to develop by the sperm or by other means, is a cell whose metabolism has almost come to equilibrium. Eggs requiring fertilization die unless fertilized.

The spermatozoon is a very small fraction of the size of the egg, even if the egg has but little yolk. In sharp contrast with the immobility of the egg, the sperm is usually capable of ener-

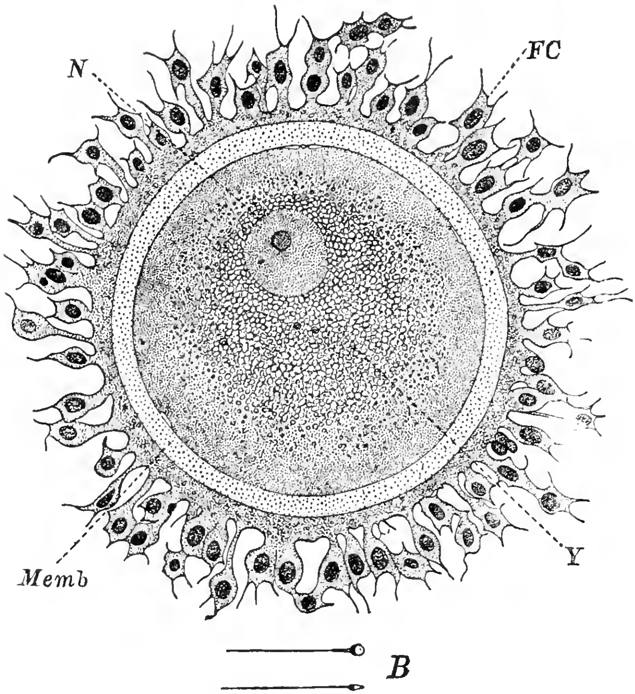


Fig. 145.—A nearly ripe human ovum in the living condition. The ovum is surrounded by follicle cells (*FC*) inside of which is the clear membrane (*Memb*) and within this is the ovum proper containing yolk granules (*Y*) and a nucleus (*N*) embedded in a clear mass of cytoplasm. Magnified 500. B, two human spermatozoa drawn to about the same scale of magnification. (*From Conklin, Heredity and Environment, Princeton University Press. After O. Hertwig; B after G. Retzius. By permission.*)

getic movements by means of its flagellum or tail. In some forms, such as nematode worms and crustaceans, a tail is lacking and the sperm is incapable of rapid locomotion (Fig. 146). Spermatozoa vary greatly in structure. In motile forms, the sperm consists of two general regions, (1) the *head*, which proceeds first in locomotion and which contains the chromatin, and (2) the *tail*, which is a stout flagellum, sometimes provided with a fin. Between the head and tail, a *neck* or *middle-piece* region may be recognized.

Fertilization.—If mature sea urchin or starfish eggs are placed in a shallow glass dish under a microscope and a drop of sea water containing ripe sperm from a male is added, one can readily see that almost at once each egg is surrounded by a vibrating fringe of spermatozoa, each of which seems to be doing its utmost to gain entrance into the egg (Fig. 147). The spermatozoa reach the egg

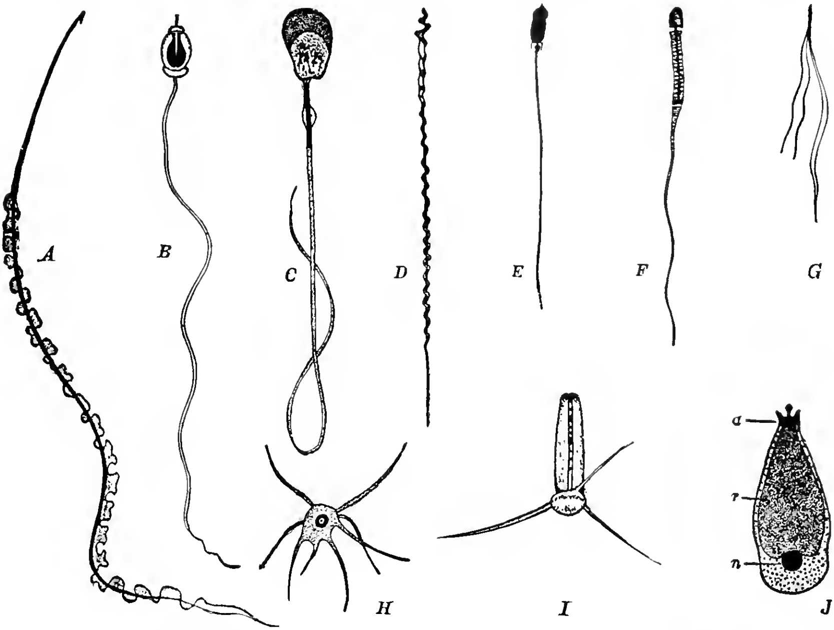


FIG. 146.—Types of spermatozoa. *A*, salamander. (*After Ballowitz.*) *B*, annelid (*Nereis*). (*After Lillie.*) *C*, guinea pig. (*After Meves.*) *D*, bird (*Phyllopneuste*). (*After Ballowitz.*) *E*, sturgeon. (*After Ballowitz.*) *F*, bat. (*After Ballowitz.*) *G*, turbellarian (*Castrada*). (*After Luther.*) *H*, crustacean (*Pinnotheres*). (*After Koltzoff.*) *I*, crustacean (*Homarus*). (*After Herrick.*) *J*, nematode (*Ascaris*). (*After Scheben.*) *a*, apical body; *n*, nucleus; *r*, refractive body. (*From Sharp, Introduction to Cytology.*)

by swimming movements executed by whiplike contractions of the tail, but these mechanical movements do not completely account for the results. Thus it has been shown that ripe eggs of a number of marine forms, when placed in sea water, give off a substance called *fertilizin*, which forms a necessary link in the fertilization process; for if this substance is removed from the eggs by repeated washings in sea water, the washed eggs are not fertilized when brought in contact with normal active spermatozoa. Fertilizin seems to sensitize the sperm and as a result of this the sperm is capable of inducing reactions in the egg, leading to engulfment of the sperm when the latter touches the egg. Penetration of the egg by the spermatozoon is not a mechanical boring process.

Entrance of the Sperm.—The ootid is the final stage of oogenesis, but in some cases the formation of the polocytes, which marks the completion of the maturation divisions, is not accomplished until after the egg (oocyte) has left the ovary. There is no general rule regarding the stage of development reached by the egg before it is laid or fertilized. In some species the egg is ready for impregnation or insemination by the sperm at the primary

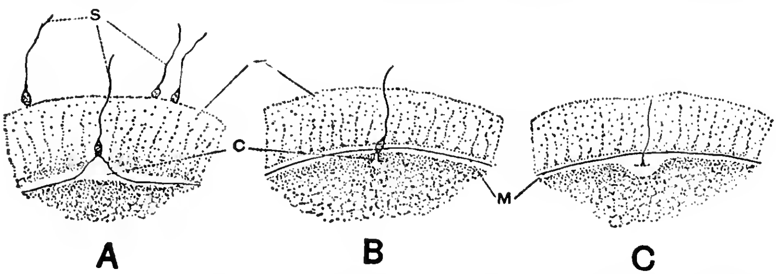


FIG. 147.—Entrance of the spermatozoon into the egg of the starfish, *Asterias*. (*After Fol.*) A, a single spermatozoon (S) has penetrated the jelly (J) and become attached to the fertilization (entrance) cone (C). B and C, succeeding stages in the engulfing of the spermatozoon. M, fertilization membrane.

oocyte stage, in which case the sperm enters before the polocytes are formed. In fact, unless the sperm does enter such an egg, no maturation divisions take place. In other cases, the sperm enters at the secondary oocyte stage, and in still others in the ootid stage.

Egg of Nereis.—The reactions of the egg that follow or result from the contact of the sperm with the egg are well illustrated in the case of the marine annelid, Nereis. When the egg of Nereis is deposited in the water, it is in the primary oocyte stage, neither polar body having been formed. The nucleus occupies a central position and the cytoplasm contains numerous yolk and oil globules. The egg is bounded by a thin vitelline membrane which is its only covering when it is laid. The spermatozoon consists of a flattened head, middle piece, and tail. The apex of the head is provided with a short spike, called the *perforatorium*, by means of which the sperm attaches itself to the egg membrane. The instant a sperm strikes the vitelline membrane, a jellylike substance begins to flow out from the cortical region of the egg and continues to flow until the egg is surrounded by a thick gelatinous envelope, except at the point where the sperm is attached to the egg. At this point there is a funnel-shaped depression in the jelly (Fig. 148). The jelly must not be confused with fertilizin, which is soluble in sea water and is given off from the egg independently. As the single sperm adheres to

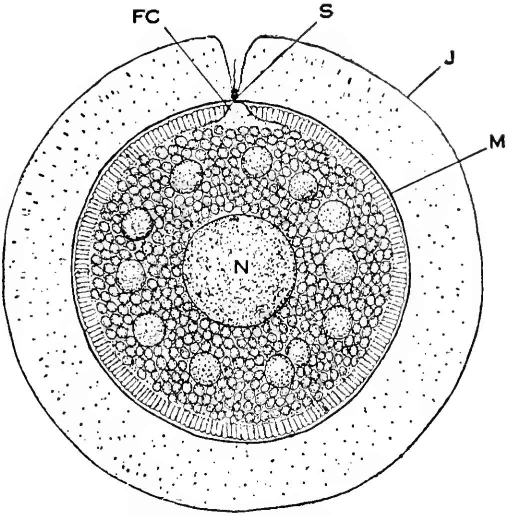


Fig. 148.—The egg of *Nereis* 12 minutes after insemination; the secretion of the jelly is completed, the walls of the emptied alveoli of the cortical layer appearing as radiating lines across the perivitelline space. The spermatozoon lies in the funnel-shaped depression in the jelly; the egg having formed a fertilization cone crossing the perivitelline space and touching the membrane beneath the spermatozoon. FC, fertilization cone; J, jelly; M, egg membrane; S, spermatozoon. (*After Lillie.*)

the egg by means of the perforatorium, the unsuccessful or supernumerary spermatozoa are pushed away from the vitelline membrane by the outflow of jelly. The jelly comes from alveoli in the cortical zone of the egg directly beneath the vitelline membrane and after the discharge of the jelly, a *perivitelline* space appears, traversed by delicate radiating strands. The impact of the sperm with the egg produces a small puncture in the vitelline membrane and evokes the formation of the *fertilization cone.* The fertilization cone arises in the cytoplasm opposite the point of attachment of the sperm and pushes out across the perivitelline space until it touches the vitelline membrane.

The next step is the retraction of the cone, as a result of which the sperm head is pulled into the egg, leaving the middle piece and tail outside. As the sperm head is drawn through the hole in the vitelline membrane, it is stretched into an elongated shape (Fig. 149), and as it is pulled away from the egg membrane

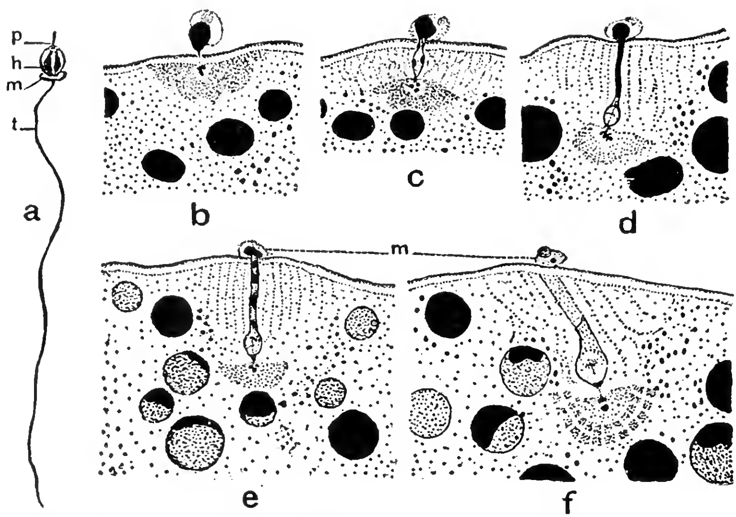


FIG. 149.—a, spermatozoon of *Nereis*. h, head; m, middle piece; p, perforatorium; *t*, tail. b-f, penetration of the spermatozoon into the egg. b, 37 minutes after insemination. The perforatorium is imbedded in the fertilization or entrance cone (closely stippled) which has withdrawn from the surface membrane. The tail of the spermatozoon is not shown. c, d, e, stages from eggs killed 48 minutes after insemination, showing the cone sinking into the egg and drawing the sperm head with it. f, 54 minutes after insemination, the sperm head is entirely within the egg, leaving the middle piece (m) outside. (*After F. R. Lillie.*)

deeper into the interior of the egg, it gradually becomes vesicular (Fig. 150). In the meantime the first and second polar bodies are formed and the primary oocyte is converted into an ootid. The nucleus of the ootid and the nucleus derived from the head of the sperm, the sperm nucleus, unite to form the *fertilization nucleus.* A spindle then forms, the nuclear membrane dissolves, and the egg is ready to undergo the first cleavage. The chromosomes of the first cleavage spindle consist of those contributed by the egg nucleus and of those contributed by the sperm.

Egg of the Frog.—The freshly laid egg of *Rana pipiens* is spherical in form and measures about 2 mm. in diameter; it is bounded by a thin membrane, which in turn is surrounded by the

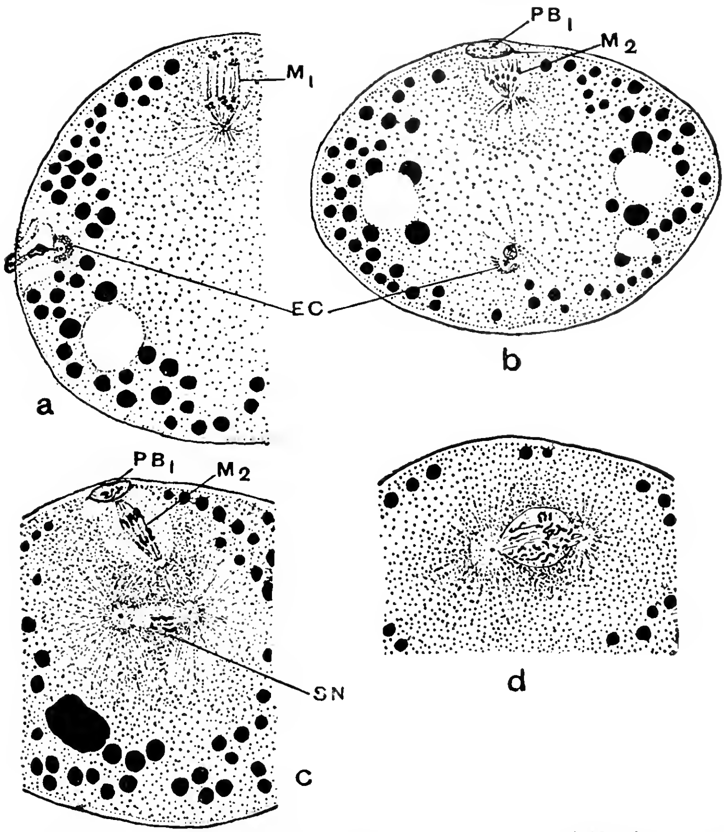


FIG. 150.—Penetration of the spermatozoon in the egg of *Nereis*. **a**, same stage as Fig. 149**f**, showing first maturation spindle; **b**, 54 minutes after insemination, showing rotation of sperm head and cone, and the origin of the sperm aster from the pole of the nucleus opposite the cone; **c**, 67 minutes after insemination showing the sperm nucleus between the unequal centrosomes and asters of the sperm amphiaster; **d**, later stage after insemination showing the fused egg and sperm nucleus lying between the cleavage centers which seem to be a further development of the sperm amphiaster. EC, entrance cone; M_1, M_2, first and second maturation spindle; PB_1, first polar body; SN, sperm nucleus. (*After F. R. Lillie.*)

jellylike egg capsule. More than half of the egg is colored by a dark pigment located in the outer portion of the cytoplasm, leaving a much smaller, cream-colored area on the opposite side.

The color of the dark portion fades out gradually at its edge toward the light area. The cream color of the light area is the color of the yolk seen through the egg membrane. Since the yolk is concentrated in the light-colored or *vegetal* half of the egg, the dark or *animal* half is relatively free of yolk. The egg is *radially symmetrical,* its principal axis being a line connecting the *animal pole,* a point in the center of the dark area, with the *vegetal pole,* a point in the opposite half in the center of the light area (Fig. 151, *A*).

When the egg is released from the ovary, it is in the primary oocyte stage, the nucleus lying in the animal half of the egg near the animal pole. The first polocyte is formed after the egg reaches the oviduct and then, without an intervening resting stage, the mitotic spindle of the second maturation division develops as far as metaphase, beyond which under normal conditions it does not proceed until the egg is fertilized. The first polocyte is extruded near the animal pole. Just before the formation of the spindle, the pigment thins out in the region of the animal pole to form what is known as the *fovea* of the egg. The fovea is also marked by a slight flattening in the surface of the egg.

Fertilization of the Frog's Egg.—During amplexus, eggs and sperm are deposited in the water simultaneously and the eggs are at once fertilized. In this process a single spermatozoon makes its way through the jelly of the capsule and penetrates the egg at a point about 40 degrees from the animal pole. The entrance of the sperm acts as a stimulus for the secretion of fluid from the egg which raises a *fertilization* or vitelline membrane from the egg surface and creates a perivitelline space within which the egg orients itself with the dark animal pole up. A second result of the entrance of the sperm is the formation of a *gray crescentic area* on the surface of the egg in the equatorial region opposite the point of penetration (Fig. 151). A third result is the completion of the second maturation division and the formation of an egg nucleus.

Usually the entire spermatozoon enters the egg, but the tail quickly disintegrates and plays no further part in fertilization. As the head and middle piece move through the egg, with the middle piece foremost, the penetration path is marked by a trail of pigment, which enables one to determine that the entrance path lies in a plane of a meridian of the egg that bisects the gray crescent. As a result the egg now has a *bilateral symmetry*. The entrance path also determines the bilaterality of the future embryo, since in the majority of cases the plane of the entrance path coincides with the median plane of the embryo.

The middle piece of the sperm as it moves through the egg forms a centrosome which soon divides into two. The egg and

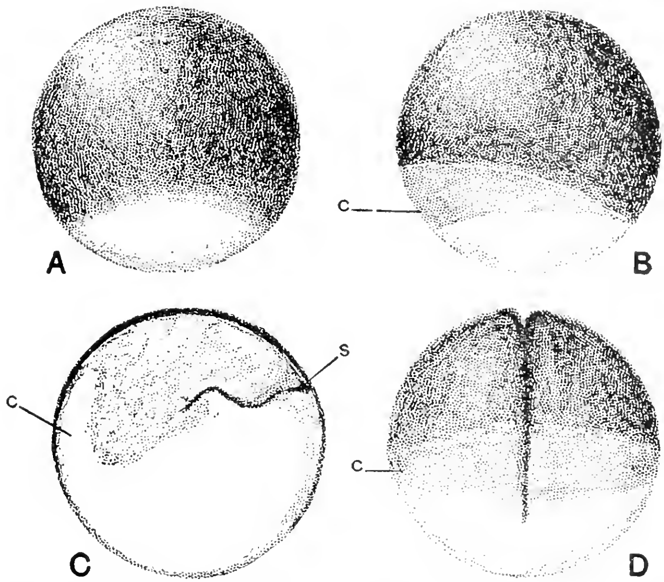


FIG. 151.—A. Unfertilized frog's egg, drawn without the capsule. B. Fertilized frog's egg showing gray crescent (c). C. Section of frog's egg in the plane of the first cleavage, showing the bisected gray crescent (c); s, penetration path of spermatozoon. D. Surface view of frog's egg during first cleavage. (*C and D after Schultze.*)

sperm nucleus come together near the center of the egg; a spindle develops between the centrosomes; chromosomes are formed in each nucleus; the nuclear membranes dissolve and the egg is ready for the first cleavage. The diploid number of chromosomes of *Rana pipiens* is 26, of which 13 are furnished by the egg nucleus and 13 by the nucleus derived from the head of the sperm.

Mature, unfertilized eggs of the frog can be made to develop by pricking them with a needle. Since under these conditions no additional chromosomes are brought into the egg by a spermatozoon, one would expect embryos developing from such eggs to have the haploid number of chromosomes, if it may be taken for granted that the second maturation division is completed. As a matter of fact, many of the larvae produced this way are haploid in chromosome number; but in addition others are diploid and a few triploid and tetraploid. How chromosome numbers greater than the haploid are produced in these embryos is a matter of speculation, but it is interesting that only diploid animals metamorphose into frogs of both sexes. It would seem that in the frog the diploid complement of chromosomes is necessary for normal development.

Cleavage.—Cleavage is a period in development following fertilization, marked by rapid mitotic cell divisions, in each of which the diploid number of chromosomes is present. An exception to this so far as the chromosomes are concerned is in cases of chromatin diminution, such as occurs in Ascaris, referred to in a previous chapter; but in the majority of animals it is generally believed that the diploid number of chromosomes appears on each cleavage spindle. This seems to be the case in the frog. The cells produced in the course of cleavage are known as *blastomeres*. Some of these produce primordial germ cells, which later participate in gametogenesis, and the remainder become somatic cells.

The manner in which cleavage takes place depends upon the quantity and distribution of the yolk in the egg. The frog's egg is called a *telolecithal* type of egg because the yolk is concentrated about one pole of the egg. The first cleavage plane (the plane separating the first two blastomeres) passes through the principal axis of the egg, and therefore through a meridional plane, and bisects the gray crescent. The furrow separating the blastomeres begins in the animal pole and gradually cuts through to the vegetal pole, forming two complete cells adhering to each other on their adjacent faces (Fig. 152). Since the entire egg is divided, the cleavage is spoken of as *holoblastic*. In contrast to this, in a *meroblastic* cleavage, such as takes place in the hen's egg, cleavage is confined to a small yolk-free area at the animal pole, the yolk remaining undivided. In the frog the first cleavage plane in the majority of cases coincides with the median plane of the future embryo. In such cases the first two blastomeres represent the right and left sides of the embryo. The second cleavage plane is also meridional, at right angles to the first. The third cleavage plane passes about 60 degrees from the animal pole, cutting the planes of the first two at right angles and for that reason is called *equatorial*. The 8 blastomeres formed at the end of the third cleavage consist then of an upper quartet of cells about the animal pole smaller in size than the four cells of the lower half of the egg. From this point on the rate of cleavage is retarded in cells located in the vegetative region of the egg.

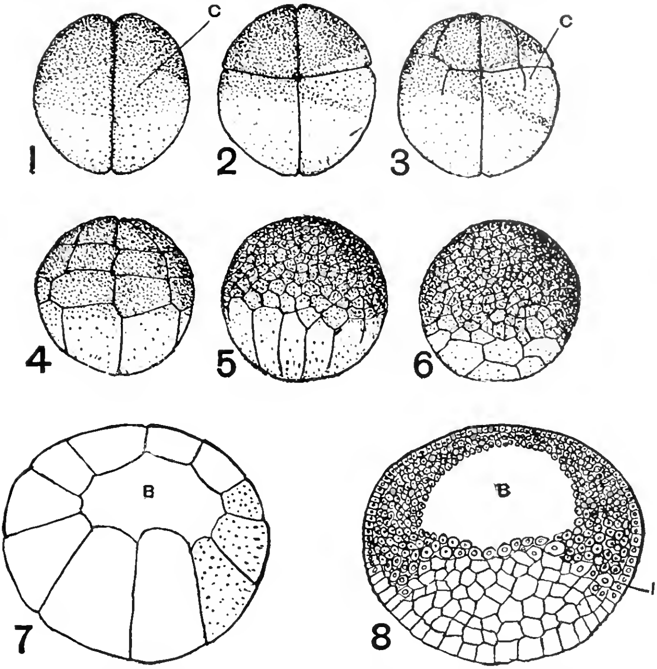


FIG. 152.—Cleavage in the frog's egg. 1, 2-cell stage, 1st cleavage plane bisecting gray crescent, C. 2. 8-cell stage. 3. 8-cell passing into 16-cell stage. 4. 32-cell stage. 5-6. Later cleavage stages. 7. Section of egg in early stage of blastocoel, B, or segmentation cavity; approximate position of gray crescent material shown by stippling. 8. Section of later blastula; I, point where invagination takes place.

Since the dark pigmented cells formed of animal-pole material divide more rapidly, they soon become smaller in size than those containing yolk. The cleavage thus becomes unequally holoblastic.

Blastula.—A section of a developing egg at the end of the third cleavage shows that the inner surfaces of the 8 blastomeres are rounded off so as to produce a space or cavity between them. This space is called the *segmentation cavity* or *blastocoel* and marks the beginning of the *blastula* stage in development. The walls of the blastula bounding the blastocoel become several cell layers in thickness as cleavage progresses. The cells forming the roof and sides of the blastula are derived from animal pole cells and are accordingly smaller than the yolk-laden cells forming the floor of the blastula. The blastocoel becomes filled with fluid absorbed from the outside or produced by metabolism of the cells of the blastula (Fig. 152, *7*, *8*).

Gastrulation.—Cleavage at first merely produces a number of cells in the dark and light areas, respectively, so that for a time the distribution of pigment is similar to that of the egg before cleavage. Gradually the pigmented area encroaches on the light area as the result of an overgrowth of the small pigmented cells. The advancing edge of the pigmented cells, known as the *germ ring*, slowly covers the vegetative cells, until the latter are completely hidden, except in a very small area, known as the *yolk plug*. At the beginning of the overgrowth a short horizontal notch forms at the margin of the germ ring in the region of the gray crescent and gradually extends around the entire margin of the ring. Thus the advancing margin of the germ ring is marked by a shallow groove which is more pronounced at its point of origin. The germ ring may now be considered as a *blastopore* whose dorsal lip lies in the region of the gray crescent. At the dorsal lip an active invagination of cells takes place principally from the animal-pole region, though yolk-laden cells are also lifted from the floor of the blastocoel. As the germ ring is reduced in size, the invagination becomes active throughout its extent, but only in the region of the dorsal lip is a large cavity, called the *gastrocoel* or *archenteron*, formed (Fig. 153). As this cavity pushes into the interior of the gastrula, the blastocoel is gradually obliterated. Externally the cells forming the yolk plug are finally covered up by the complete closure of the blastopore and gastrulation is completed. The region of the blastopore may now be referred to as the posterior end of the embryo.

Germ Layers.—The gastrocoel, produced largely as a result of the invagination of the dorsal-lip region of the blastopore, lies in the animal half of the egg. Its roof and side walls are derived mainly from animal-pole cells and its floor is made up of yolk cells. These cells represent the *endoderm* of the embryo except for some cells lying in the mid-line of the roof which separate to form the rod-shaped *notochord*. The cells covering the outside of the gastrula may now be called *ectoderm*. The rudiment of the notochord thus extends from the blastopore region forward under the ectoderm and above the roof of the endodermal

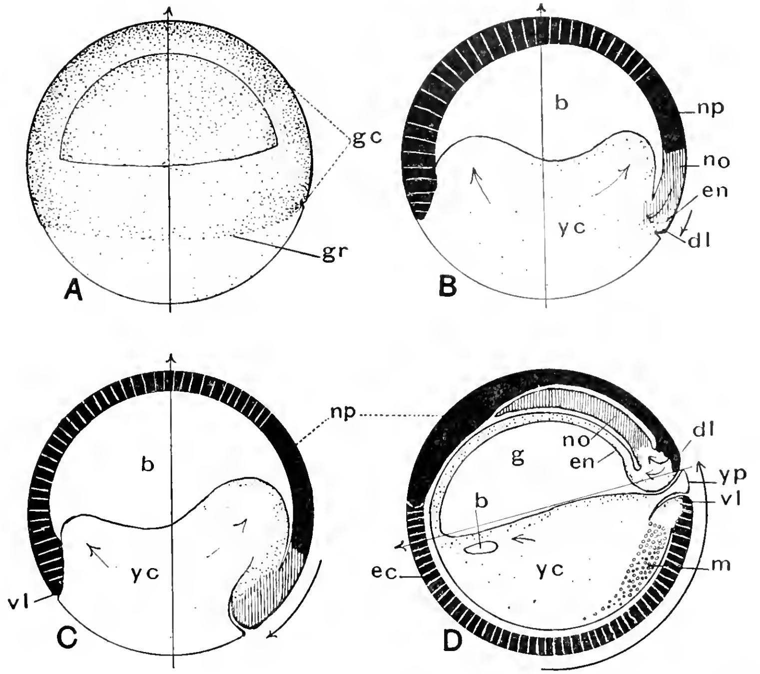


FIG. 153.—Schematized diagrams of gastrulation in the frog. A. optical section of blastula from left side showing the location of the gray crescent, **gc**, and the edge of the germ ring, **gr**, encroaching upon the yolk. B. beginning of gastrulation showing the hypothetical composition of the gray crescent substance, according to various interpretations. C. showing downward movement of the dorsal lip of the blastopore, **dl**, and the appearance of the ventral lip, **vl**, on the opposite side of the gastrula. D. formation of gastrocoel, separation of notochord from endoderm. **b**, blastocoel; **dl**, dorsal lip; **ec**, ectoderm; **en**, endoderm; **g**, gastrocoel (archenteron); **gc**, gray crescent; **gr**, lower edge of germ ring; **m**, mesoderm of ventral lip; **no**, notochord; **np**, neural plate; **vl**, ventral lip; **yc**, yolk cells; **yp**, yolk plug. Curved arrows outside figures; clockwise show movement of dorsal lip; counter-clockwise show rotation of embryo. Other arrows indicate direction of cell movements.

cavity. The third germ layer, the *mesoderm*, originates from cells lying between the ectoderm and endoderm, just within the lip of the early blastopore; and as the blastopore closes, mesoderm is formed throughout the extent of the blastopore. From this region mesoderm grows forward on either side of the notochord between the ectoderm and endoderm. On either side of the notochord the mesoderm becomes segmented to form a row of boxlike structures called *somites;* but lateral to each series of somites, the mesoderm extends as a sheet of cells between the ectoderm and endoderm. Later this sheet splits into two layers, one applied to the endoderm and the other to the ectoderm, the space between the two forming the coelom or body cavity. The somites later are transformed into muscle and connective tissue.

The ectoderm of the frog produces the epidermis of the skin, cutaneous glands, the entire nervous system, the lens of the eye, the lining of the oral and cloacal cavities, the enamel of the teeth, and some muscle. In other vertebrates the ectoderm also produces mammary glands, sweat glands, hair, horns, hoofs, nails, scales (of reptiles and birds), and feathers. The mesoderm, in addition to producing most of the muscle tissue, forms the corium of the skin, connective tissue, blood and lymph vessels, most of the organs of the excretory and reproductive systems, peritoneum, and skeleton, including the dentine of the teeth. The endoderm forms the inner layer of the alimentary canal, the epithelium of the liver, the pancreas, thyroid and thymus glands, and the respiratory tract. It also forms the lining of the Eustachian tube and middle ear.

Neural Tube.—At the end of gastrulation, the ectoderm over the entire surface is divided into an outer and inner layer of cells. As the blastopore is closing, a groove, the *neural groove,* is formed in the ectoderm, extending forward for about 90 degrees from the blastopore. This groove is flanked on either side by low ridges in the ectoderm called *lateral neural folds,* which are connected anteriorly by a curved *transverse fold,* the whole forming a continuous low wall enclosing the medullary plate in front and at the sides. The inner layer of the ectoderm of the medullary plate is several cell layers in thickness, and a similar thickening of the inner ectodermal layer is present in the outer slope of each of the lateral neural folds. These lateral thickenings of the inner layer of ectoderm, known as *neural crests,* lie one on either side of the medullary plate, to which each is connected along its inner edge (Fig. 154). The neural folds increase in height, grow toward each other, and fuse along their edges, thus converting the medullary plate into a *neural tube.* In the formation of the tube, the neural crests are carried up with the neural folds but are not included in the neural tube. After the fusion of the neural folds, the outer layer of ectoderm becomes continuous over the neural tube which is thus cut off from the outside. The closure starts in the region of the future hindbrain and then proceeds forward and back, the anterior end being the last to close. Posteriorly the neural tube connects with the blastopore by the *neurenteric canal,* which later disappears. The neural crests at first are continuous strands of cells one on each side of the neural tube. Later these strands break up into segments from which develop spinal and parts of cranial nerve ganglia.

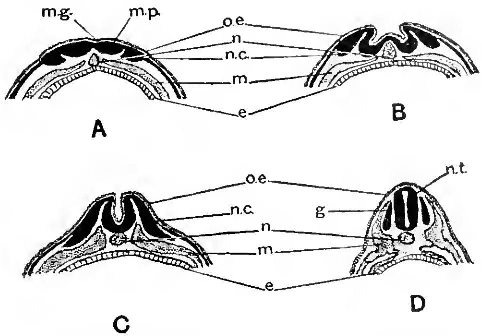


Fig. 154.—Semidiagrammatic cross sections illustrating four stages in the development of the neural tube and spinal ganglia of the frog. e, endoderm; g, spinal ganglion; m, mesoderm; m.g., medullary groove; m.p., medullary plate. n, notochord; n.c., neural crest; n.t., neural tube; o.e., outer ectoderm. Inner layer of ectoderm and structures derived from it are shown in solid black.

The neural tube is the rudiment of both the brain and spinal cord. *Sensory axons* arising in the neural-crest ganglia grow back to the neural tube to form sensory roots of cranial and spinal nerves. The motor roots of both cranial and spinal nerves originate from nerve cells located in the neural tube. The anterior half of the neural tube becomes constricted into three regions known as the forebrain, midbrain, and hindbrain, which in turn give rise to the five divisions of the adult brain. The ventricles of the brain are derived from the cavity of the neural tube. In the spinal cord this cavity is the *central spinal canal.* The sympathetic nervous system develops from cells that migrate from the spinal ganglia. Cranial portions of the neural crests in addition to forming ganglionic cells also produce considerable quantities of nonnervous mesenchyme which later give rise to connective tissue structures. Figure 155 is a longitudinal section of an early frog embryo.

Ganglia.—*Placodes* are thickened areas in the inner layer of the head ectoderm which give rise to sensory epithelia and to varying portions of the ganglia of certain cranial nerves. Thus the ganglia of cranial nerves V, VII, IX, and X are formed of placodal cells as well as of cells derived from the neural crest. The ganglion of the auditory nerve (VIII) is formed entirely from placodal material. The ganglia of spinal nerves, as already noted, are derived entirely from the neural crests. The ganglia

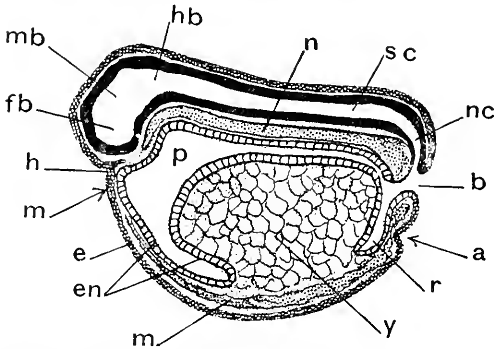


FIG. 155.—Diagrammatic longitudinal section of early frog embryo. a, anus; b, blastopore; e, ectoderm; en, endoderm; fb, forebrain; h, hypophysis; hb, hindbrain; m (arrow), mouth; m, mesoderm; mb, midbrain; n, notochord; nc, neurenteric canal; p, pharynx; r, rectum; sc, spinal cord; y, yolk.

of the sympathetic and parasympathetic systems are formed later from cells that migrate out from the central nervous system.

Notochord.—The notochord develops from cells forming part of the roof of the archenteron, derived by invagination from the dorsal-lip region of the blastopore. These cells, at first inseparable from those forming the lining of the archenteron, soon become organized or differentiated into a rod-shaped form lying directly beneath the medullary plate and, later, the neural tube. This rod of cells is the rudiment of the notochord which histologically is classified as a form of connective tissue. It becomes completely separated from the endodermal cells of the archenteron. The notochord is developed in all animals belonging to the phylum *Chordata*, which includes the subphyla *Enteropneusta*, *Tunicata*, *Cephalochorda*, and *Vertebrata*. The notochord evolved apparently as a skeletal axis and serves as such in the embryonic or adult stages of all chordates. In some of them such as Cephalochorda and some vertebrates (Cyclostomata) it persists in the adult animal. In most vertebrates, however, including the frog, the embryonic notochord is replaced by the centra of the vertebra, developed from tissue derived from the somites. As pointed out in an earlier chapter, in many fishes the notochord persists in the adult in spaces between the ends of vertebrae and to a slighter degree in the axial portions of the centra. In cyclostomes it persists in the adult in a fully developed condition as a long, flexible, tough rod, tapered at the ends, extending from about the middle of the brain to the opposite end of the body and lying directly below the central nervous system. It functions primarily as a supporting structure, is nonnervous in character, and should not be confused with the neural tube (Fig. 155).

Alimentary Canal.—The cells lining the archenteron after the separation of the notochord from its roof, represents the *definitive endoderm* of the frog and later forms the lining or *mucosa* of the alimentary canal, except that of the mouth and of the cloaca. Since the lungs, liver, and pancreas, as well as the thyroid and thymus glands, originate as outgrowths of the embryonic alimentary canal, all of these structures are endodermal in origin. The remaining parts of the wall of the alimentary canal, *viz.*, submucosa, muscularis, and serous membrane (visceral peritoneum) are derived from the lateral unsegmented mesoderm that grows down between the endoderm and ectoderm. About two weeks after fertilization, the tadpole hatches, *i.e.*, it leaves the egg capsule and swims about. By this time the animal has an elongated form with a short tail but no mouth or anal opening. On the underside of the head is a curved sucker, by means of which the tadpole attaches itself to solid objects. The mouth is formed by an invagination of the ectoderm just in front of the sucker to form a pit which deepens until it touches and fuses with the endoderm; the fused layers shortly after become perforate. An anal opening is formed in a similar way at the posterior end of the body. With the formation of the mouth, the sucker begins to atrophy and eventually disappears. Until a mouth is formed the embryo is dependent for nutrition upon yolk stored in the large endodermal cells, particularly those forming the floor of the alimentary canal. After the mouth is formed, the yolk rapidly disappears and the tadpoles gain sustenance from food taken in at the mouth. The alimentary canal lengthens and becomes spirally coiled. A peculiar larval feature of the mouth is the development of *horny sheaths* on the jaws which function as rasping organs. The lips are also provided with horny *papillae* which aid in obtaining food (Figs. 156 and 157).

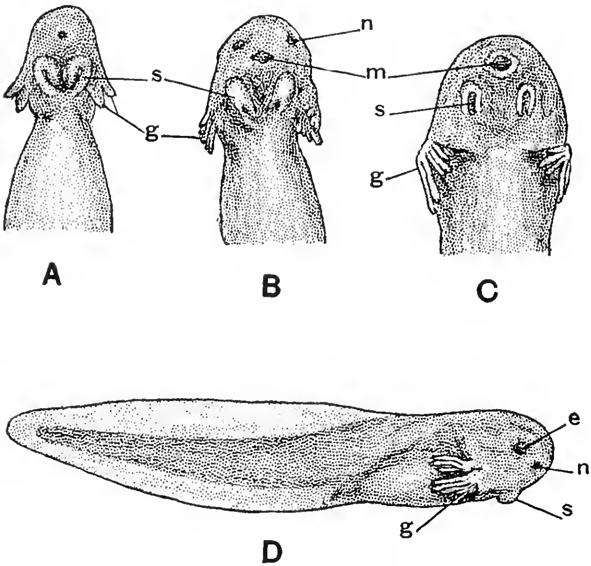


FIG. 156.—A, B, and C, three stages in the development of mouth, suckers and gills of *Rana arvalis*. D, side view of stage B. e, eye; g, gill; m, mouth; n, nasal pit; s, sucker. (*After Lieberkind.*)

Branchial Structures.—In addition to the notochord, another important distinguishing feature of the phylum Chordata is the presence of *gill clefts* and of gills (in aquatic forms) in the pharyngeal region. At the time of hatching the rudiments of the external gills can be seen on either side of the body just behind the head as a pair of small conical projections. Later these are joined by a third rudiment on each side. All three rudiments grow rapidly, though the third remains smaller than the other two, until they form a tufted mass on either side of the body (Fig. 156). Each gill develops finger-shaped lobes and is supplied with blood vessels, much as in a fish. Meanwhile four gill clefts develop on each side, one in front of the first pair of gills, one behind the last pair, one between the first and second and another between the second and third. The clefts are narrow slits connecting the pharynx with the outside of the body. The gill slits develop from *gill pouches*. These are lateral outpocketings of the pharynx, separated from each other by *gill arches*. A total of six pouches are formed, of which the first and last remain rudimentary. Each of the remaining four on each side enlarges until the endodermal lining comes in contact with the ectoderm when the tissue breaks down to form a vertical slit. The external gills now become enclosed in a branchial chamber by the *operculum*, which is formed of two folds of skin, one on each side, from the region in front and above the first pair of gills. These two folds grow backward over the gills, meet, and fuse with each other ventrally and with the body wall posteriorly, forming a common chamber communicating with the outside by a small opening, the *spiracle*, on the left side. The external gills are now resorbed and replaced by internal gills developed from the borders of the gill clefts. The internal gills are aerated by water taken in the mouth and passed through the gill clefts into the branchial chamber and out through the spiracle. The gills and skin are the principal organs of respiration during the larval period (approximately three months). The lungs develop as outgrowths from the floor of the pharynx and are ready to take over the respiratory function by the end of the larval period (Fig. 158).

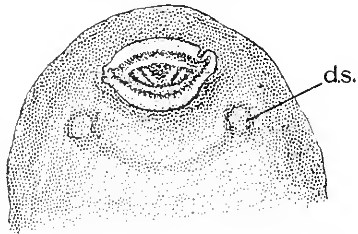


FIG. 157.—Larval stage of *Rana arvalis*, ventral view, in which the suckers (d.s.) are degenerating and the mouth is provided with horny jaws. (*After Lieberkind.*)

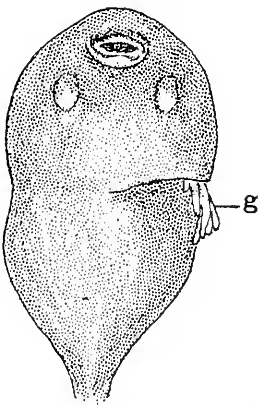


FIG. 158.—Larval stage of *Rana arvalis*, ventral view, showing gills (g) still visible beyond operculum on left side. On the right side the gills are enclosed in the branchial chamber formed by the operculum. (*After Lieberkind.*)

Paired Appendages.—During the larval period the caudal region of the tadpole increases in size and is provided with a well-developed vertical fin. The development of the legs begins at about the end of the first month. Both pairs of legs are formed from the body wall, but the forelegs develop within the branchial chamber which makes them invisible externally until metamorphosis sets in. The hindlegs develop from the lateral body wall at the base of the tail, and their development can be readily followed from the beginning. Actually the forelegs start to develop before the hindlegs.

Olfactory Organs.—The olfactory passages develop from a pair of ectodermal pits on either side of the head just above the oral invagination of the early larva (Fig. 156). These pits deepen and eventually connect with the pharynx to form the internal nares. The olfactory nerve develops from cells lining the olfactory passages. These cells are the *olfactory cells,* from which axons extend back to the forebrain to form the olfactory nerve. The passages themselves are enlarged to form the nasal cavities.

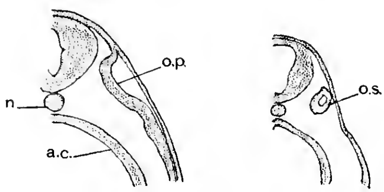


Fig. 159.—Cross sections illustrating two stages in the early development of the inner ear of *Rana sylvatica.* a.c., alimentary canal; o.p., otic pit; o.s., otic sac, developed from the pit and which in later stages forms the membranous labyrinth. (*After Pollister and Moore.*)

Ear.—The inner ear develops at about the same time as an *otic pit* in the inner ectoderm of the skin at the level of the hindbrain (Fig. 159). The pit becomes cut off from the surface and later differentiates into the *membranous labyrinth.* The *middle ear* develops later through an enlargement of the vestigial first (hyomandibular) gill pouch. This gill pouch, which in fishes is provided with a cleft opening to the outside and serves as a respiratory passage, in the frog never breaks through to the outside. It may therefore be regarded as an incomplete gill cleft. In the frog as the gill pouch enlarges, it encroaches on the surface until its outer wall is reduced to a thin membrane, the *tympanic membrane.*

The enlargement forming the tympanic cavity is connected with the gill pouch by a narrow channel, which is the *Eustachian tube* of the adult frog. The *columella* of the middle ear is derived from the dorsal wall of the tympanic cavity from which it becomes separated by excavation to extend freely from the tympanic membrane to unite with a small cartilage plugging the foramen ovale.

Eye.—The *optic vesicles* are paired evaginations of the ventrolateral walls of the forebrain which grow out toward the ectoderm. Each optic vesicle becomes constricted at its point of attachment to the brain to form the *optic stalk*. As the vesicle approaches the ectoderm, its outer surface invaginates to form a double-walled *optic cup* (Fig. 160). The invagination is continued along the ventral side of the cup to form the *choroid fissure*. In the meanwhile a thickening in the ectoderm opposite the mouth of the cup is pinched off the inner surface of the ectoderm to form the *lens*. The choroid fissure now closes down to the optic stalk where an opening persists, through which blood vessels and nerve fibers enter the optic cup. When the choroid fissure is closed, the optic cup is a double-walled hemisphere whose cavity is largely occupied by the lens (Fig. 160). The ectoderm overlying the lens becomes transparent to form the outer layer of the *cornea*. The inner layer of the latter is formed of mesodermal cells (mesenchyme). The *iris* develops from mesoderm at the edge of the optic cup and also perhaps from ectoderm derived from the cup. The inner layer of the optic cup becomes thicker than the outer layer early in its formation. It gives rise to the sensory part of the *retina* in which the rods and cones develop. The outer layer of the optic cup develops into the pigmented layer of the retina. The *choroid* and *sclerotic* coats of the eye are derived from mesoderm formed over the pigmented layer of the retina. The fibers forming the *optic nerve* arise from cells lying in the inner surface of the retinal layer of the optic cup. This passes out of the eye

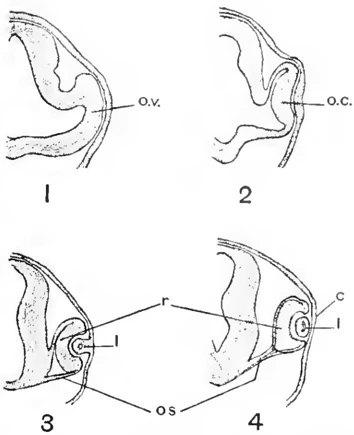


Fig. 160.—Cross sections illustrating four stages in the development of the eye of *Rana sylvatica*. 1, optic vesicle stage; 2, optic cup stage; 3, formation of the lens; 4, separation of lens from ectoderm. c, cornea; l, lens; o.c., optic cup; o.s., optic stalk; o.v., optic vesicle; r, retina (inner layer of optic cup). (*After Pollister and Moore.*)

through the lower (inner) end of the choroid fissure and then along the ventral side of the optic stalk to the brain. The optic stalk itself gradually extends around the optic nerve to produce a sheath for the latter.

Metamorphosis.—The tadpole of *Rana pipiens* undergoes metamorphosis, *i.e.*, transformation into a frog, toward the end of the third month of development. As the time nears, the tadpole frequently comes to the surface and gulps air, which is drawn into the lungs. The principal changes occurring during metamorphosis are: (1) the final stages in the development of the lungs, accompanied by the atrophy of the gills and the closure of the gill slits; (2) the freeing of the forelimbs by the rupture of the operculum, which disappears, and a marked lengthening of the hindlimbs; (3) the enlargement of the stomach and the shortening of the intestine; (4) the shedding of the larval epidermis together with the horny jaws and the labial papillae; and (5) the resorption of the tail.

Law of Biogenesis.—The embryos of higher vertebrates often display certain features, mainly anatomical, which seem to represent some sort of recapitulation of structures found in lower forms. Thus the structure and functions of the gills of the tadpole and the plan of branchial circulation have their prototypes in the corresponding organs of the fish. From this it is not to be inferred that these organs are structurally identical, because they are not; but the similarity in the general structural plan of these organs in the two cases is very marked and the function so far as the gills are concerned is the same in both. These resemblances may not seem unusual since both the fish and the tadpole live in an aquatic habitat and for that reason require somewhat similar respiratory organs. However, the fact that the embryos of the higher air-breathing vertebrates, such as reptiles, birds, and mammals, which have no aquatic larval period in development, also pass through stages in which the branchial region resembles that of the fish in its general anatomy, calls for some other explanation than that of environmental requirements.

To take the chick embryo of 72 hours' incubation for an example (Fig. 161), the heart lies in an anteroventral position in the body cavity and pumps the blood forward through a ventral aorta (truncus arteriosus), from which it passes right and left dorsally through aortic arches to a pair of dorsal aortae. The latter convey the blood to all parts of the body and to the yolk sac, from which it is returned to the heart by cardinal veins and vitelline veins (from the yolk sac). The yolk-sac circulation

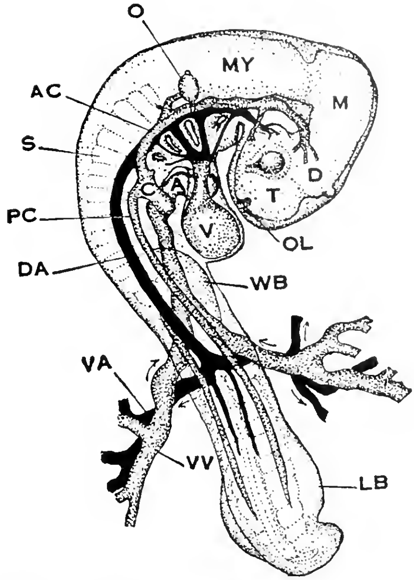


FIG. 161.—Circulatory system of chick embryo of 72 hours incubation; embryonic membranes not shown. Starting at the ventricle (V) the blood is pumped forward through the ventral aorta to the aortic arches of which the four of the right side are shown (in solid black). The gill clefts lie between the arches. Above, the aortic arches unite to form a dorsal aorta each of which sends a carotid artery (right one shown) to the head. Posteriorly, the aortae unite to form the dorsal aorta (DA) which in the middle of the trunk region gives off a right and left vitelline artery (VA) carrying blood to the yolk capillary circulation to be aerated and charged with food from the yolk. The blood returns to the embryo by right and left vitelline veins (VV) which unite and join the sinus venosus of the heart. Blood is collected from the embryo by right and left anterior and posterior cardinal veins (AC and PC) which form on each side a common cardinal (C), also joining the sinus venosus. The mingled venous blood from the cardinal veins and the aerated blood from the vitelline veins passes from the sinus venosus to the atrium (A) and then to the ventricle. D, diencephalon; LB, leg bud; M, mesencephalon; MY, myelencephalon; O, otic vesicle; OL, olfactory pit; S, somite (muscle); T, telencephalon; WB, wing bud.

serves to aerate the blood and to supply the embryo with nutrition. The blood in passing through the gill arches is not aerated, since that is done in the yolk sac at this stage of development. The resemblance of the aortic arches to the afferent and efferent branchial arteries of the fish or of the tadpole is merely anatomical and not complete at that, because no gill capillaries are present. Since the gill clefts of the chick later on disappear, accompanied by changes in the branchial circulation, it would seem that the only reason for their development at all in the chick is that the chick in its development is merely following the path along which its evolution from lower forms took place. The fact that the chick develops gill clefts and aortic arches seems to mean that the chick is descended from ancestors in which these structures had a functional significance. Hence the appearance in an embryo of a higher form of morphological relationships characteristic of lower forms is taken as an indication of relationship between the higher and lower forms. A more accurate picture of this relationship is obtained if corresponding embryonic stages are compared. Thus the resemblance in the branchial region is much closer between the chick embryo and the fish embryo than between the chick embryo and the adult fish.

No animal in its development repeats every step in its racial history or phylogeny—many are slurred over and omitted, and new ones interspersed among the old—so that a general conclusion must be limited to the statement that ontogeny is, to a *certain extent* only, a repetition of phylogeny. This generalization, known as the *law of biogenesis*, seems to hold throughout the animal kingdom and has been useful in many cases in throwing light upon phylogenic relationships.

Homology.—A practical difficulty in applying the biogenetic law as a criterion for determining the origin of embryonic conditions is that in the embryo old (*palingenetic*) characteristics are intermingled with new (*cenogenetic*) ones, so that an embryonic structure is never a perfect recapitulation of an ancestral structure. Thus the circulation of the vertebrate embryo only approximates the fish type of circulation; but the inference is implied that the fish type of circulatory system is near to the primitive type from which the circulatory systems of the higher vertebrates have evolved. The wings and legs of birds and the limbs of quadrupeds and of man all develop from the same sort of embryonic limb rudiment, which in its inception is an outgrowth of the body wall. The development of vertebrate limb buds may be said to be practically the same for all vertebrates up to a certain point, beyond which the path of development diverges in various directions. Vertebrate limbs are said to be *homologous*, by which is meant that they conform to a general structural type because they were differentiated by evolution from the same or corresponding part of an ancestral organism. Similarity of development of parts is taken as an indication of similarity in origin. *Analogy* refers to similarity in function. The wings of a bird and the arms of a man are homologous but not analogous; the eyes of a squid and those of man are analogous but not homologous; while the arms of an ape and the arms of man are both homologous and analogous.

CHAPTER XIII

HEREDITY

A fertilized frog's egg develops into a frog, rather than into a salamander or some other kind of animal, because it is endowed with certain inherited qualities, which under proper environmental conditions bring about development. Development is accompanied or caused by an interaction of internal factors, present in the egg, with external factors present in the environment. A certain sort of environment is required for the development of the frog's egg, but since the eggs of other species may develop in the same pool along with those of the frog, the factors determining the difference in results in each case must be internal rather than external. There is specificity in different kinds of eggs just as there is specificity in the animals developing from them. Each kind of egg is characterized by its own particular kind of developmental potencies which, however, are realized only when provided with the proper environment. The same environment may evoke the potencies of different kinds of eggs; but the same kinds of eggs require the same kind of environment for their development.

In the intrauterine development of mammals there is a similar relation between the egg and environment, the environment in such cases being the uterine tissue surrounding the egg. The uterus is the means through which the metabolic needs of the developing egg, and later the embryo, are met; and thus provides an environment in which the potentialities of the hereditary factors present in the egg can be expressed in the form of developmental activity. Theoretically, therefore, a mammalian egg should develop equally well in the proper sort of artificial culture medium outside the body; and, as a matter of fact, this has been accomplished with rabbit ova through early cleavage stages. As in the frog, the mammalian offspring inherits from its parents only those qualities that are represented by factors of some sort in the fertilized egg.

The fact that in parthenogenesis the egg develops without the intervention of a sperm shows that the egg alone may possess all of the internal factors for development and for heredity. However, since it is common knowledge that paternal characters are inherited in cases where the egg requires fertilization, it is clear that hereditary factors are contributed by the sperm as well as by the egg. The problem of heredity centers in explaining the nature and location of herditary potencies of the germ cells and, if possible, how the hereditary characters of the adult are controlled or produced by them.

We are accustomed to think of heredity as the cause or reason for the reproduction in children of characters similar to those of their parents; but while it is true that the reproduction of similarities is due to heredity, it is also true that characters in children differing from those of the parents are also the result of heredity. Thus the fact that blue eyes as well as brown eyes may be inherited from brown-eyed parents, means that blue eyes and brown eyes, though classified as dissimilar hereditary conditions, are really genetically related, and that the production of blue eyes from brown-eyed parents is a result of this relationship. Heredity may be defined as the production in successive generations of conditions not necessarily similar or identical, whose specific character is determined by factors located in the germ cells. The term *hereditary factor* or *gene* may be defined as a substance or a condition in the germ cells that determines the development of a hereditary character in the adult. Each hereditary character presumably is represented by a factor or set of factors in the germ cells.

Chromosome Theory of Heredity.—The germinal factors of heredity are generally thought to be located in the chromosomes or chromatin rather than in the cytoplasm of the germ cells for a number of reasons, some of which may be considered. The basic argument for this view is that, since the chromatin of the fertilized egg is the only substance contributed in practically equal amounts by the parents to the fertilized egg, and since in the long-run offspring inherit equally from the parents, it follows that the chromatin must be the hereditary substance. The cytoplasm of the fertilized egg is entirely maternal in origin, save for the slight addition to its bulk made in those cases where more than the head of the sperm enters the egg; yet the heredity of the animal developing from the egg is on the average as much paternal as maternal. The chromosome theory of heredity finds additional support in the fact that the biparental character of the nuclei of the cells derived from the cleavage nucleus provides an equal opportunity for both maternal and paternal genes to produce a biparental hereditary effect.

The disjunction of homologous chromosomes that occurs in the reduction division of gametogenesis may be interpreted in this connection as the mechanism which is directly responsible for the constancy in the total number of chromosomes, since without the reduction there would be an ever increasing number produced at each fertilization. In cases where disjunction fails to occur, or is incomplete, it can be shown that definite hereditary effects are produced. Change in the ratio of autosomes to sex chromosomes produces a definite effect in the characters of the offspring, because of a change in the normal number and relations of factors or genes. A further reason for assuming that the factors of hereditary characters are located in the chromosomes is that such an assumption provides the only known explanation of the results of animal and plant breeding, some of which will be discussed presently. The science of genetics is in fact postulated on this assumption.

Cytoplasm in Heredity.—The chromosome theory of heredity relegates the cytoplasm to a secondary role in development. To students of heredity, the cytoplasm is rather superfluous except as a source of nutrition or as a background for gene action. The facts warrant the assumption that genes or factors account for the inheritance of those characters that serve as material for genetic study; but these characters, such as eye color, body color, hair color, shape of legs and wings, etc., are largely superficial characters and genetic studies as a rule fail to deal with more fundamental characters such as those determining body axes or body plan. The cytoplasm of the egg can be shown in many cases to possess a certain amount of organization that foreshadows axial relationships in the later embryo, and this must be taken into account in a complete explanation of heredity. It will be recalled in this connection that in the frog's egg the entrance of the sperm results in the formation of the gray crescent and that in the majority of cases the future plane of bilateral symmetry of the embryo is established by the entrance plane of the sperm. The cytoplasm of the egg responds to the stimulus produced by the entrance of the sperm by a rearrangement of its substance to produce the gray crescent, which is the first indication of bilateral symmetry. Certainly the cytoplasm is organized and this organization is inherited, but for reasons to be considered later it is difficult to express the basis of this organization in terms of hereditary factors. In general terms it might be said that the cytoplasm of the egg is concerned with the determination of the groundwork on which the chromosomal factors operate. It is to be noted that there is no contribution from the sperm comparable to the cytoplasm of the egg. The latter is a purely maternal contribution to the development of the embryo. The conclusion is justified that there is in the egg cytoplasm a

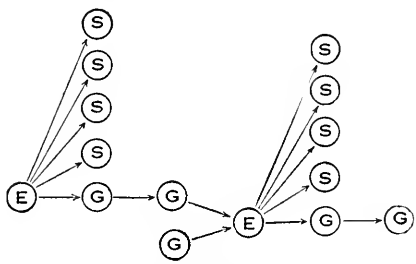


FIG. 162.—Diagram to illustrate Weismann's germ track. E, fertilized egg; G, germ cell; S, soma.

specific and highly organized substance, which with the chromosomes constitutes the material basis of development and heredity.

Inheritance of Acquired Characters.—In many animals the primordial germ cells are segregated from the somatic cells at a relatively early stage in ontogeny. Both germ cells and somatic cells are derived from the fertilized egg, but the germ cells retain the reproductive potency of the egg while the somatic cells lose it, presumably because the latter become differentiated into the various tissues of the body. It is generally believed that in higher forms the germ cells of the individual come only from the primordial germ cells and not from somatic cells. The reproductive potencies are therefore retained by the germ cells simply because they do not undergo differentiation into tissue cells. The somatic cells die with the individual, but descendants of the germ cells live on in following generations forming a line of germinal continuity or *germ track* (Fig. 162) connecting generations. This idea is the basis of the theory of the continuity of the germ plasm which was developed vigorously by the German zoologist, August Weismann (1834–1914). According to this view, the developmental and hereditary qualities of the germ cells are derived from antecedent germ cells, the somatic cells of each generation serving in a purely vegetative capacity as a means of protection and of supplying the metabolic needs of the germ cells, but contributing nothing to the hereditary qualities of the germ cells. The facts of development support this idea in many cases of animal embryogeny but not in all.

From the Weismannian point of view, on purely *a priori* grounds, one should expect that *acquired characters* (*i.e.*, peculiarities acquired by the somatic cells through special training or experience) would not be inherited, because there is no conceivable way in which changes in somatic cells, caused by environmental factors, could induce changes in the germ cells of such a nature that the latter would reproduce the somatic condition in the absence of the original cause. This does not mean that genes cannot be disturbed by external causes acting directly on the germ cells or indirectly through the somatic cells, but that a specific somatic effect, produced by external causes, does not produce a corresponding hereditary effect. One difficulty in dealing with this question in a limited space is that the term "acquired characters" includes a large category of conditions that are not all comparable. Every one knows that if a man loses his legs as the result of an accident, his children are not born legless. All such mutilations are not inherited. Neither is there any ground for the belief that maternal impressions produce specific effects on the unborn human young. The uterus is a place in which the fertilized egg develops—the kind of individual developing from that egg depends upon the kind of parents that produced it or more accurately upon the kind of ancestral germ cells preceding it. Experimentally it has been impossible to produce an inherited defect following an alteration in the somatic tissue. Observation and experiment over a wide field fail to demonstrate satisfactorily the inheritance of an acquired condition. On the other hand, had no characters been acquired by primitive protoplasm, there would have been no evolution, and consequently no great variety in life. A partial answer to this question is that the hereditary material of the germ cells does change—though the causes may be obscure—that environment also changes; and that either or both kinds of changes may affect development over a long period of time. Many experiments, some of which are described in the following paragraphs show that the genes can be affected by external causes.

Direct Action of External Factors on Germ Cells.—Stockard and Papanicolaou have succeeded in producing defects in the eyes and skeleton of the limbs in guinea pigs whose parents had been subjected to the inhalation of alcohol fumes. Since the defects were inherited in succeeding generations without further treatment with alcohol, it is clear that the germ cells of the treated parents must have been affected by the alcohol. However, since the treated parents showed no ill effects from the alcohol, the effect on their germ cells must have been direct rather than through the somatic cells. There is in this case no inheritance of acquired characters because the defects of the offspring were not present in the somatic tissues of the treated parents.

Muller and others have produced hereditary effects by treating fruit flies (Drosophila) with X rays. Here also the germ cells were affected directly and the genes were sufficiently modified to produce hereditary changes in the characters of the offspring.

Parallel Induction.—It is conceivable that under certain conditions both germ cells and somatic cells might be altered by environmental or external causes and result in hereditary effects. Such a result is known as *parallel induction*, which may be illustrated by the experiments of Guyer and Smith. These investigators injected into the blood stream of fowls the pulped lenses of rabbit eyes, for the purpose of producing an antilens substance in the fowl's blood. The serum from such an immunized fowl would therefore possess antilens properties. When such antilens serum was injected into the blood vessels of pregnant rabbits, the offspring showed a number of eye defects of which the most common were opaque lenses, small eyes, and abnormally rotated eyes. The defects, though not confined to the lens of the eye, were inherited through the female lines and occasionally through the male. These results are regarded as due in the first instance to the simultaneous effect of the antilens serum, circulating in the blood of the pregnant mother, on the eyes and germ cells of the developing embryos.

Somewhat similar eye defects were produced by Little and Bagg on young mice whose mothers were exposed to X rays during pregnancy. The defects in this case were also inherited.

It is probably significant that the same parts, *viz.*, the eyes, and to a certain extent the brain, were affected by such different harmful agents as alcohol, X rays, and antilens substance. Thus in all cases the head region of the embryo seemed most sensitive to these destructive agencies, which in view of the fact that the work of C. M. Child and others has demonstrated that the head end of an embryo is the region most susceptible to the action of harmful agents, such as potassium cyanide, suggests that the results obtained were due to a general effect on the most susceptible part of the body. Since alcohol, antilens serum, and X rays, under the conditions of the experiments, all seem to produce similar results in mammals, particularly in regard to the eye, the idea of specificity of effect, so far as the antilens serum is concerned, is rather difficult to maintain. The skeleton defects noted especially by Stockard and Papanicolaou may well be secondary results following the primary injury to the region of highest metabolism, *viz.*, the head.

Germ Track.—The failure of efforts to produce changes in the hereditary material or germ plasm through the somatic cells is in keeping with the idea of a germ track or lineage of germ cells connecting generations of individual animals, more or less distinct from somatic cells. Somatic cells undoubtedly influence the germ cells physiologically but not genetically, so far as known. Weismann regarded the germ track as a device for conserving the hereditary potencies of the chromosomes, but since somatic cells receive the same assortment of chromosomes as the germ cells, he believed that the chromosomes of the somatic cells during cleavage and differentiation underwent a kind of differential treatment, which he considered to be the cause or basis of differentiation. Something of this sort is indicated in the process of chromatin diminution of Ascaris, but since this is not of general occurrence in other species, it cannot be accepted as the general cause of differentiation. If it is generally true that as a result of cleavage both somatic and germ cells receive the same kind and number of chromosomes present in the fertilized egg, every somatic cell receives the same complement of genes from the egg. Differentiation of somatic cells presumably results from an interaction of the genes in the chromosomes with the cytoplasm and other environmental factors. The genes of the germ cells, because they are shielded in some way from these influences, fail to enter into differentiating processes and thus retain their full potencies as reproductive cells. It is true, of course, that in many animals, notably Coelenterata and Platyhelminthes, the evidence of a germ track from embryology is very unsatisfactory. And it is also true that in plants germ cells may be produced from *meristematic* cells, which are embryonic plant cells, also present in growing regions of mature plants. However, if the general thesis is true that the genes are the important hereditary material, and that they are located in the chromosomes, it might be maintained that even in these exceptional cases—since every cell in the body possesses the full complement of genes—any cell might become a germ cell. Why this does not ever happen to a definitive somatic cell of higher animals is another matter; but it is probably due to the irreversible nature of the differentiation accompanying normal development, an irreversibility that seems to increase with ascent in the animal scale.

Mendelian Heredity.—In 1866, Gregor Mendel, an Augustinian monk, published the result of experiments with the common garden pea conducted in the monastery at Brünn in what was then Austria. His work remained practically unnoticed until 1900 when conclusions similar to his were reached independently by three men, De Vries, Correns, and Tschermak. For this reason Mendel's work does not figure in the literature until about thirty-five years after it was published. His work is important because it demonstrated experimentally the fundamental laws governing the distribution of hereditary characters in offspring, and because it complements in an extraordinary way the chromosome theory of heredity, which was evolved independently of Mendel's work. The chromosome theory deals with the internal mechanism of heredity, while Mendel's work showed the externally visible results of the operation of this mechanism. A definite step in the direction of a more complete understanding of the working of the mechanism of heredity was made when it was realized that the results of Mendel's experiments and many others since can be readily explained by assuming that the genes for so-called Mendelian characters are located in the chromosomes.

Mendel's experiments dealt with the heredity of what are known as *allelomorphic* conditions of a hereditary trait or character. The traits studied by Mendel were such things as stature, color of seed, contour of seed, etc., each of which existed in allelomorphic or alternative forms. By this is meant that in the case of stature, for example, some plants were tall, others dwarf, but none intermediate; seeds were either yellow or green in color, smooth or wrinkled, etc. Mendel tested the heredity of these allelomorphic conditions of the same character by crossbreeding them and then breeding the hybrids and their progeny. In a typical experiment Mendel found that when he crossed a plant having yellow-colored seed coat with one having green-colored seed coat, the hybrid or first filial generation (F_1) produced only yellow-colored seeds. In the next generation (F_2), produced by the F_1, both yellow- and green-seeded plants were obtained in the proportion of 3 yellows to 1 green. The green, when inbred, gave only green from this point on. Of the yellows, one-third proved in subsequent breeding to be pure yellow, while the remainder behaved like the F_1, producing 3 yellows to 1 green. In this experiment, yellow is said to be the *dominant* character and green the *recessive.*

Purity of Gametes.—Mendel explained the results of this experiment by assuming that the gametes are pure with regard to the genes or factors responsible for producing yellow or green color in the seeds. A single gamete carries a yellow gene or green gene, but never both. In the first part of the experiment when yellow and green genes are brought together in the fertilized egg or zygote of the F_1, yellow is dominant to green. In the formation of the gametes of the F_1, the genes for yellow and green are segregated into different germ cells (law of segregation), with the result that two kinds of gametes are formed, one bearing the yellow gene and the other the green gene. Since this is assumed to occur in both male and female gametes, the F_2 results from the chance combinations of two kinds of male and female gametes, as illustrated in the following diagram:

	Parents	Gametes	F_1 Zygotes	F_1 Gametes	F_2 Zygotes
Yellow.......	YY →	Y Y	Yy →	Y y	
		╳	=	╳	= YY : 2Yy : yy
Green........	yy →	y y	Yy →	Y y	

From this it can be seen that of the four possible combinations, there is one chance for a pure or *homozygous* yellow, one for a pure or homozygous green and two for a mixed yellow and green or *heterozygous* combination. A *homozygote* or homozygous individual is one that has received from its parents like genes for a given character, and a *heterozygote* one that has received unlike genes for a character. The gametes produced by an individual that is homozygous for a given character will be alike with regard to the genes for the character. On the other hand, an individual that is heterozygous for a given character will produce two numerically equal classes of gametes with regard to the genes.

Independent Assortment of Genes.—It seems clear, then, that the results of crossing a single pair of allelomorphic conditions find a rational explanation in the assumption that the two kinds of genes of the F_1, and of similar hybrids, are segregated in different gametes, according to what Mendel called the *law of segregation.* Mendel determined further that when more than two pairs of allelomorphic conditions are hybridized simultaneously, each allelomorphic pair follows the law of segregation, each allelomorphic pair of genes being assorted independently of other pairs. If a plant bearing peas that are both yellow in color and smooth in contour is crossed with one whose seeds are green and wrinkled, the seeds of the F_1 plants are yellow and smooth. Yellow, as before is dominant to green, and smooth is dominant to wrinkled. If these plants are inbred, the F_2 from them are produced in a ratio of 9 yellow smooth: 3 green smooth: 3 yellow wrinkled: 1 green wrinkled. All the yellows taken together are to the greens as 3:1, all the smooths taken together are to the wrinkled as 3:1; but some of the yellows are wrinkled and some of the greens are smooth. In other words, while the results for each pair of allelomorphic characters are in accord with the law of segregation, a recombination of characters has been brought about as a result of an *independent assortment* of the genes in the formation of the gametes of the F_1. That the actual composition of the F_2 in this experiment is in accord with the principles of segregation and independent assortment is shown in the accompanying diagram (Fig. 163). If one arranges the F_1 gametes in a horizontal and vertical series, along two sides of a square, the points of intersection of imaginary lines from any pair of gametes will give the gene composition of the resulting zygote.

Chromosome Basis of Mendelian Inheritance.—A knowledge of the principles of segregation and independent assortment enables one to predict the result of hybridizing one or more pairs of allelomorphic conditions. The operation of both of these principles can be understood if one assumes that the genes for hereditary characters are located in the chromosomes, since the disjunction of homologous chromosomes in the reduction division of maturation meets all of the requirements of a mechanism to bring about segregation and independent assortment of genes.

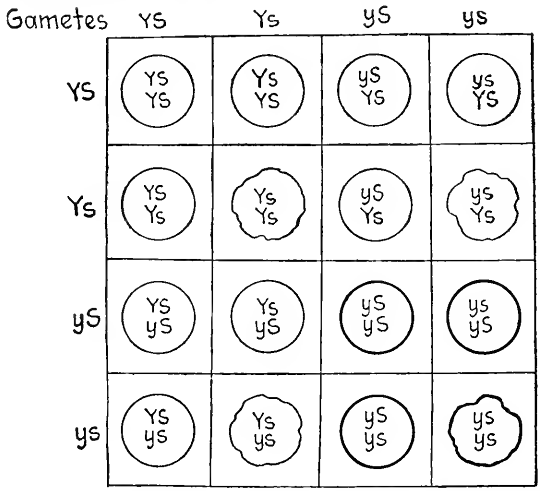


FIG. 163.—Diagram showing composition of the F_2 in a dihybrid cross. The light circles represent yellow smooth peas; the heavy circles green smooth; the light irregular circles yellow wrinkled; the heavy irregular circles green wrinkled. YSYS (yellow smooth) is an extracted dominant; ysys (green wrinkled) an extracted recessive; these with YsYs and ySyS are homozygous; the remainder are heterozygous. Summary: Nine yellow smooth; three yellow wrinkled; three green smooth; one green wrinkled.

In the diagram (Fig. 164) this mechanism of segregation is illustrated by using a single pair of homologous chromosomes (synaptic mates), each of which carry a gene for character *A* or its allelomorph *a*. To illustrate the law of independent assortment for two pairs of characters, it would be necessary to use two pairs of chromosomes, since there must be as many pairs of chromosomes as there are independently assortable pairs of characters. Thus, if we are dealing with two pairs of characters, *A*, *a*, and *B*, *b*, the zygotic composition of the F_1 would be *AaBb*. In the formation of the gametes of the F_1, *A* separates from *a*, and

B from b in the reduction division of the chromosomes carrying them. But since the synaptic mates, Aa and Bb, may arrange themselves on the spindle independently of one another, there is the possibility of four kinds of cells resulting from the division, depending on whether or not chromosome carrying A goes to the same pole of the spindle as the chromosome carrying B. Thus one result of the reduction division would be a separation of Aa, Bb combination into A, B and a, b; the only other into A, b and a, B; yielding in all four possible gene combinations. If three pairs of characters are hybridized and if they are independently

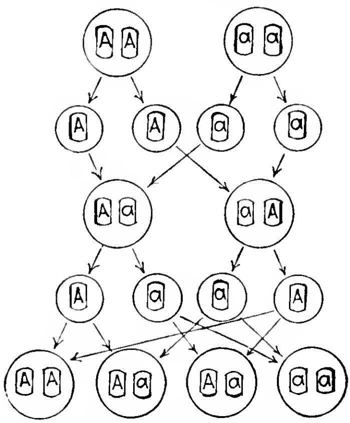


FIG. 164.—The behavior of a single pair of chromosomes in a Mendelian cross. Only the reduction division of maturation is shown. A, dominant; a, recessive.

assorted, three pairs of chromosomes are required to explain the breeding results. In such a case, if the third pair of characters be represented by C, c, there would be the possibility of eight different kinds of F_1 gametes, as follows: ABC, abc, AbC, aBc, ABc, abC, Abc, and aBC. From this it should not be inferred that a chromosome carries only one gene. A chromosome may carry many genes but only one of an allelomorphic pair.

Dominance.—In Mendel's experiments one character of an allelomorphic pair is dominant and is always expressed in heterozygous individuals to the complete exclusion of the recessive character. In later work and with other material it has been found that dominance is often incomplete, and the question as to whether or not one character is dominant to its allelomorph is a matter of no theoretical importance to the principle of segregation. Often the F_1 shows a condition intermediate between the parental characters and sometimes an entirely new character is formed. Correns, one of the rediscoverers of Mendel's laws, showed that when the white variety of the four-o'-clock, *Mirabilis jalapa*, is crossed with the red variety, the F_1 is pink. Inbred the pink-flowered plants produce in the F_2 a ratio of 1 red: 2 pink: 1 white, a modification of the 3:1 ratio, resulting from the fact that the heterozygotes are all pink. If a black Andalusian fowl is crossed with a white-splashed-with-black fowl, the F_1 is slaty blue. These inbred produce in the F_2 on the average a ratio of 1 black: 2 blue: 1 white-splashed-with-black. In cases of incomplete dominance the heterozygotes are distinguishable externally from the homozygotes.

Universality of Mendelian Heredity.—The basic principles brought to light by Mendel's experiments have been found to apply to the heredity of animals and plants generally, which means that all heredity, except cytoplasmic heredity, is Mendelian heredity. On this basis it becomes possible to analyze the heredity of an organism in terms of genes, which on the whole remain remarkably stable from generation to generation as a result of their immunity from the effects of disturbing environmental conditions of various sorts. They may, however, be affected by certain external influences under experimental conditions, as has been shown, and they may also change spontaneously to produce what are called *mutations*, some examples of which will be discussed presently.

A common human trait whose inheritance follows along the usual Mendelian lines is eye color. Difference in eye color is due to difference in amount and distribution of pigment in the iris and not to difference in the color of the pigment. In dark-brown and black eyes the pigment is present in the outer and inner surface of the iris and in the region (stroma) between the two surfaces. Light-brown, gray, and green eyes have less pigment in the outer surface. Blue eyes have pigment only in the inner surface of the iris. These various grades of eye color represent allelomorphic conditions. Thus brown is dominant to blue; so that if one parent has homozygous brown eyes and the other blue, the children will all have heterozygous brown eyes. If one parent has heterozygous brown eyes and the other blue, there is one chance out of two for blue eyes in the children. If both parents have heterozygous brown eyes, there is one chance out of four for blue-eyed children.

Sex Inheritance.—It has been pointed out in a preceding chapter (XI) that there is a correlation between the sex of the individual and the kind and number of sex chromosomes present. In *Anasa tristis*, the female condition is accompanied by the presence of 2 X chromosomes in the body cells, while the cells of the male possess only 1 X chromosome. It was also brought out that in other animals where the number of chromosomes in the two sexes is alike there are differences in form, size, or behavior of certain members of the chromosome complexes of the two sexes. It can therefore be accepted that under normal conditions there is a constant relation between the determination of sex and the kind and number of sex chromosomes present in the fertilized egg. Sex may be regarded as an inherited condition whose genes are located, in part at least, in the sex chromosomes. In dichogamous animals the sex of the individual may be male at one time and female at another.

In the fruit fly, Drosophila, 2 X chromosomes in an individual do not necessarily establish femaleness if there are irregularities in the number of autosomes. In Drosophila the zygotic or diploid complex is normally composed of 4 pairs of chromosomes consisting of a pair of sex chromosomes, known as group I, and 3 pairs of autosomes, known as groups II, III, and IV, in order of decreasing size. The difference between the male and female diploid groups is that group I in the male is composed of an X and a Y chromosome, while in the female it consists of 2 X chromosomes. The autosome groups II, III, and IV are the same in both sexes. Therefore under normal conditions in the female the ratio of X chromosomes to sets of autosomes is 2:2 (2 X chromosomes to 2 of each of autosomes II, III, and IV). In the male the normal ratio is 1:2. A fly having a ratio of 3:3 is still a female; but one having a ratio of 2:3 is a sex intergrade, combining qualities of both sexes.

From such facts it would appear that the genes for sex are present in autosomes as well as in the sex chromosomes and that maleness or femaleness depends upon the proportions of these two kinds of chromosomes. Since, however, under normal conditions the fertilized egg contains a double set of autosomes, the sex of the individual developing from such an egg is determined by whether, in addition to the autosomes, 1 or 2 X chromosomes are present. Under normal conditions, if only 1 X chromosome is present, there is also present a Y chromosome. Such an egg develops into a male. If 2 X chromosomes are present, the presence of a Y chromosome is excluded, and such an egg develops into a female.

Sex-linked Inheritance.—The results obtained by Mendel in his experiments with peas were the same in the F_1 and F_2 generations regardless of the parental origin of the allelomorphic characters. In the yellow-green cross, for example, yellow gene may be supplied by the egg and green by the pollen, or vice versa—the result is the same. The genes for these characters are common to both sexes and do not seem to be related in any way with the genes for sex. A *sex-linked character*, on the other hand, is one whose genes are linked in some way with the genes for sex. The eye color of wild Drosophila is red. Flies with white eyes appeared in cultures grown in the laboratory. White eye color is an example of what is known as a mutation, *i.e.*, a sudden and spontaneous variation, the cause of which is unknown. That the cause of the mutation is due to a change in the chromosomes or genes is indicated by the fact that the character is inherited. White-eyed flies breed white-eyed flies. The gene for white eye seems to be the result of a change in the gene for red eye, which is its allelomorph. If a normal red-eyed female of Drosophila is bred with a white-eyed male, the F_1 generation is red-eyed, males and females alike. If males and females of the F_1 are bred, there are produced in the F_2 red-eyed females, red- and white-eyed males, but no white-eyed females. If the reciprocal cross is made by starting with a white-eyed female and a red-eyed male, the F_1 consists of red-eyed females and white-eyed males. These produce in the F_2 red- and white-eyed males and females in equal numbers. The fact that the results differ, depending upon the parental origin of the characters, suggests that there is some connection between the genes for sex and those of eye color.

A simple explanation for the results may be reached by making the following assumptions: (1) that red eye is dominant to its allelomorph, white eye; (2) that the genes for both are located in the X chromosome; (3) that 2 X chromosomes produce a female; and (4) that the Y chromosome does not carry a gene for

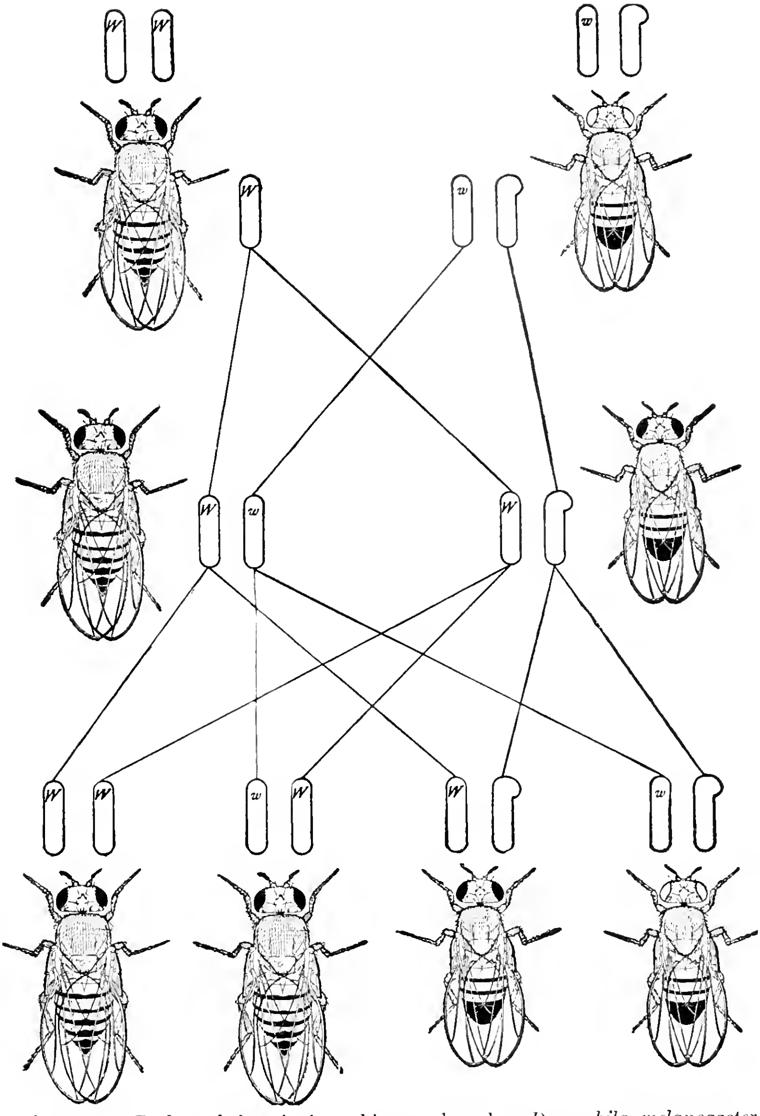


FIG. 165.—Red-eyed female by white-eyed males, *Drosophila melanogaster*. The factors for these characters are carried by the X chromosomes. Y chromosome shown with a knob. In this diagram red is indicated by the symbol W and white by w. The history of the chromosomes is shown in the middle of the diagram. (*From Morgan, Physical Basis of Heredity, J. B. Lippincott Company. By permission.*)

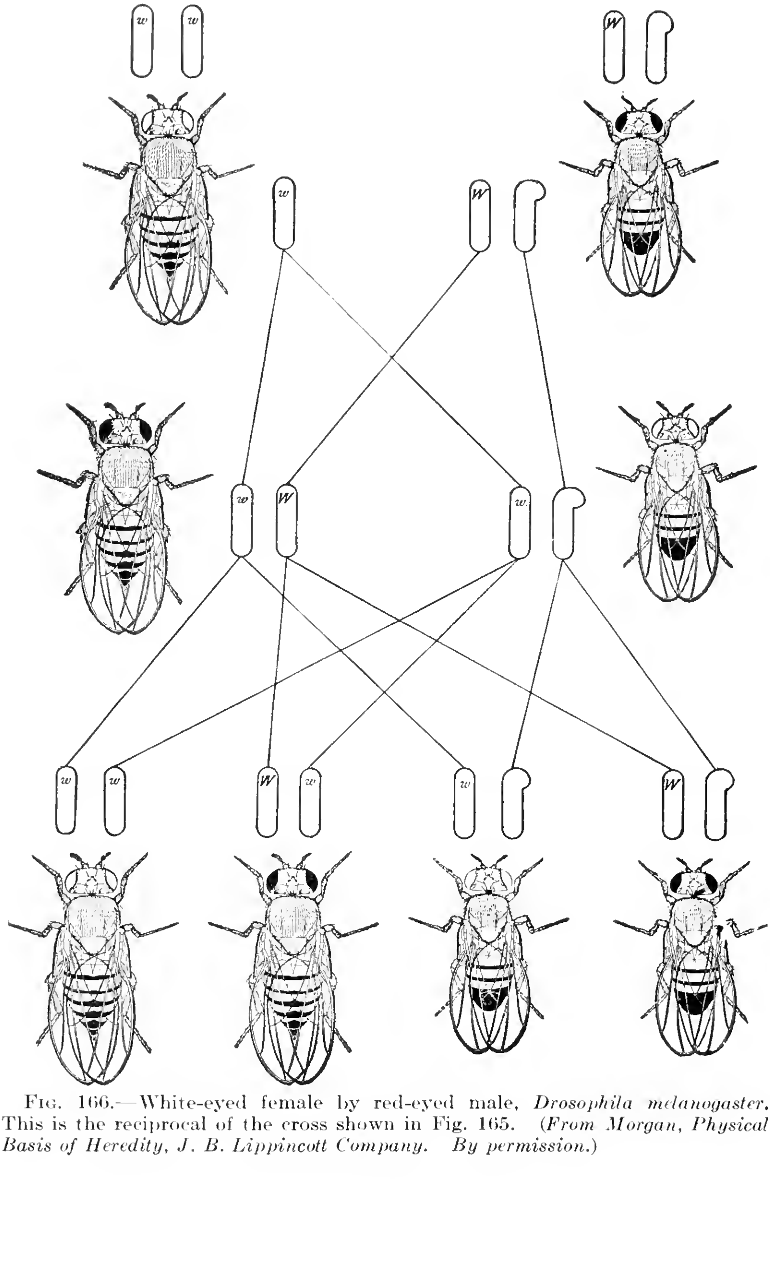


FIG. 166.—White-eyed female by red-eyed male, *Drosophila melanogaster*. This is the reciprocal of the cross shown in Fig. 165. (*From Morgan, Physical Basis of Heredity, J. B. Lippincott Company. By permission.*)

eye color. In the diagrammatic explanation of the results of crossing red-eye and white condition shown in Figs. 165 and 166, only the distribution of the X and Y chromosomes is considered, since the autosomes are not involved in the explanation and are common to both males and females.

Color blindness in man is inherited in a similar way. That color blindness is sex-linked accounts for the well-known fact that color blindness is more common in men than in women; since, according to the explanation, color blindness occurs in

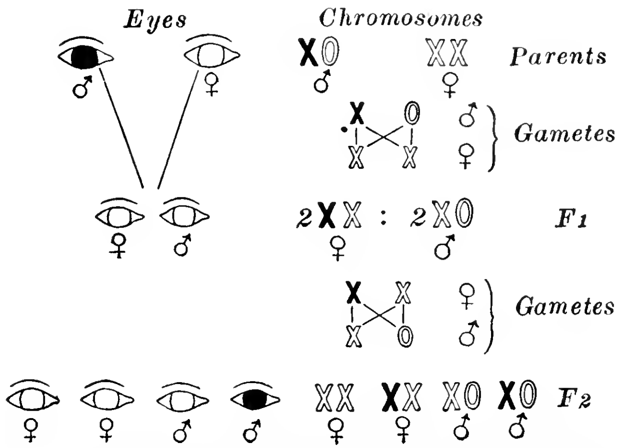


Fig. 167.—Diagram of the inheritance of color blindness through the male. A color-blind male (here black) transmits his defect to his grandsons only. The corresponding distribution of the sex chromosomes is shown on the right, the one carrying the factor for color blindness being black. The Y chromosome is shown as an O. *(From Conklin, Heredity and Environment, Princeton University Press, after Morgan. By permission.)*

women only when both X chromosomes carry the gene for color blindness. Heterozygous women are not color-blind, because color blindness is recessive to normal vision. In the male, on the other hand, a single gene in the X chromosome produces color blindness. The Y chromosome is not concerned in color blindness. As shown in the diagram (Fig. 167), the children of a color-blind father and normal mother are not color-blind. In the next generation, one-half of the sons of F_1 daughters may be color-blind, if mating is with a normal male. If such heterozygous F_1 daughters were mated with color-blind males, one-half of the daughters would be color-blind as well as one-half of the sons. Figure 168 shows the results of the mating of a color-blind mother and a normal father.

Crossing Over.—Many other sex-linked characters have been discovered and their heredity has been intensively studied in Drosophila. One should expect that if two sex-linked characters are present in the same animal, these two characters would remain associated in a single individual in subsequent generations, since according to the theory, the genes for both characters are

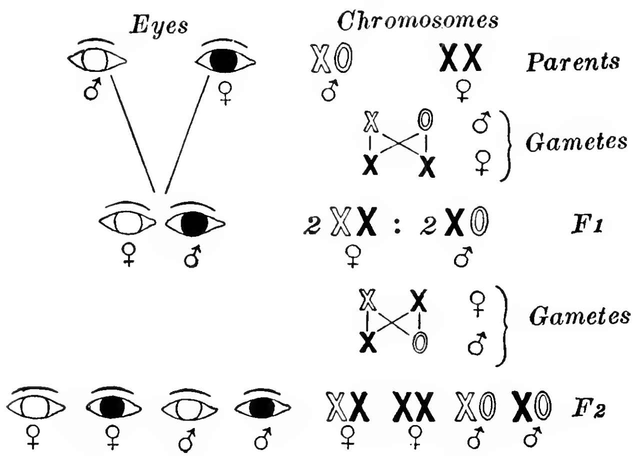


FIG. 168.—Diagram of the inheritance of color blindness through the female. A color-blind female transmits the defect to all her sons, to half of her grand-daughters and to half of her grandsons. Corresponding distribution of sex chromosomes on the right. (*From Conklin, Heredity and Environment, Princeton University Press, after Morgan. By permission.*)

located in the same chromosome. This, however, is only partially true, as may be illustrated by the following experiment. Yellow wing is a sex-linked character which, when crossed with its dominant allelomorph, gray wing, exhibits the same hereditary relationship as when white eye color is crossed with red eye. Its gene like that of white eye must therefore be located on the X chromosome, and the same must be true for the gene for gray wing. If a female having both white eyes and yellow wings is crossed with a male having red eyes and gray wings, the males of the F_1 have yellow wings and white eyes, and the females have gray wings and red eyes. Breeding the F_1 flies produces in the F_2 four classes as follows:

1. *Yellow wings* and *white eyes*, male and females	}	99 per cent
2. *Gray wings* and *red eyes*, males and females		
3. *Yellow wings* and *red eyes*, males and females	}	1 per cent
4. *Gray wings* and *white eyes*, males and females		

In the first and second classes, which make up 99 per cent of the total of the F_2, the characters have remained in their original combination or linkage, a result that should have applied to all of the F_2 flies, had the genes for yellow wing, white eye and gray wing, red eye remained in their original locations in their respective chromosomes in all cases. But since in 1 per cent of the total F_2 flies, represented by classes 3 and 4, new combinations of characters are present, the conclusion would seem to be that an exchange of parts of chromosomes must have taken place, provided, of course, the original premise that chromosomes are the bearers of these genes is true. In Fig. 169, which portrays these results, the first pair of flies represent the parent generation, the next pair, the F_1, and the last two groups the F_2. It will be noted that in the formation of the gametes of the F_1 female the assumption is made that an interchange of genes between the 2 X chromosomes has taken place, giving the possibility of four kinds of eggs instead of the expected two. Such a recombination of genes is known as *crossing over* and is thought to take place as a result of a twisting of the X chromosomes about each other during synapsis, with a subsequent reciprocal translocation or formation of composite chromosomes, as illustrated in Fig. 170. The result is 2 chromosomes, equivalent in size but differing from the originals in their gene content. If one assumes that such a recombination of genes occurred in 1 per cent of the cases, the experimental results are explained. Crossing over does not take place in the male. To detect and determine the amount of crossing over between two characters one must cross a heterozygous female with a recessive male.

Crossing over of non-sex-linked characters has also been studied in Drosophila. The genes for such characters are borne on the autosomes and therefore presumably are inherited from both parents regardless of sex. The wild Drosophila has a gray body and long wings. Black body and vestigial wings occur as mutations. If a female having a gray body and long wings is mated with a male having a black body and vestigial wings, the

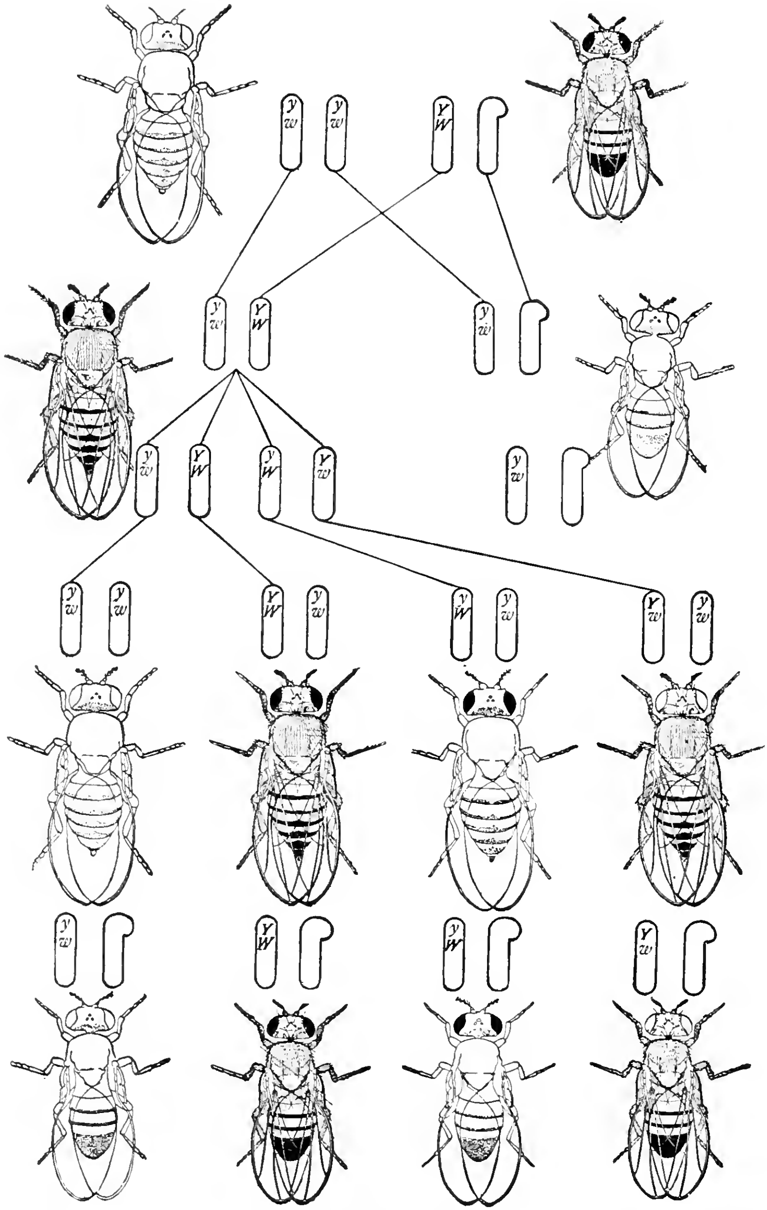


FIG. 169.—Diagram to illustrate the result of crossing a white-eyed yellow-winged female with a red-eyed gray-winged male. Y, gray wing; y, yellow wing; W, red eye; w, white eye. Y chromosome knobbed. (*From Morgan, Physical Basis of Heredity, J. B. Lippincott Company. By permission.*)

F_1 flies all have gray bodies and long wings. Since the reciprocal cross gives the same results, these characters are not sex-linked. Gray body is dominant to black, and long to vestigial wings. If a heterozygous gray-long female is mated with a recessive (homozygous) black-vestigial male, the following four classes of flies are obtained:

1. *Black body, vestigial wings,* males and females 2. *Gray body, long wings,* males and females	83 per cent
3. *Black body, long wings,* males and females 4. *Gray body, vestigial wings,* males and females	17 per cent

The first two classes show the characters in their original combinations which held for 83 per cent of the progeny. The new combinations, present in classes 3 and 4 and representing 17 per cent of the total, are the result of crossing over of genes in the formation of the germ cells of the heterozygous female parent. That crossing over takes place only in the female is shown by the fact that if the reciprocal cross is made (black-vestigial female × heterozygous gray-long male), only the first two classes are obtained, *viz.*, gray-long and black-vestigial. Limitation of crossing over to the female, though true of Drosophila, does not hold generally, since many forms exhibit crossing over in both sexes.

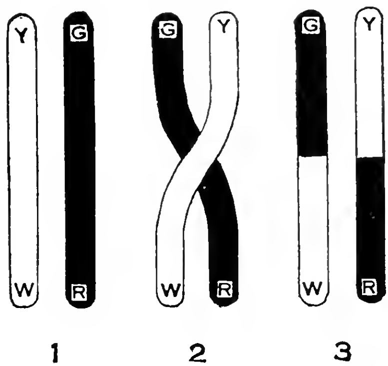


Fig. 170.—Diagram illustrating recombination of characters in crossing over.

Chromosome Maps.—The percentage of crossovers differs in the two examples just cited. Other characters whether sex-linked or not show different crossover percentages, but the same percentage under the same conditions is obtained from the same pair of characters. This has been interpreted to mean that the genes for different characters occupy different positions along the length of the chromosome and that the nearer together the genes are, the less the chance of their being separated in the crossover process. The percentage of crossovers obtained in any given case then becomes a measure of the distance separating the genes concerned. The strength of linkage tending to keep genes in the same chromosome is in inverse proportion to the distance separating the genes. What these distances actually are is unknown—the conclusions drawn from crossover data merely indicating relative locations of genes in a linear order.

Exhaustive breeding experiments have demonstrated that in Drosophila four linkage groups occur, and only four, which, fortunately for the theory correspond with the four pairs of chromosomes. Characters belonging to different linkage groups are independently assorted in breeding experiments because their genes are located in different chromosomes. Of the four groups, the sex-linked group may be assumed to have its genes in the sex chromosomes, the locations being determined by the crossover percentages obtained when the genes are tested in combinations of two and two. The assignment of the genes of the non-sex-linked groups to the autosomes is more difficult, since there is no simple way of determining why a character should be assigned to any particular autosome, except that there may be a correlation in the size of the linkage groups and the size of the chromosomes. A more accurate basis for answering this question is found in what is known as *translocation* or transport of a part of one chromosome to another, aside from that occurring in crossing over. This sometimes occurs spontaneously, but may be induced by heat and X rays. The alterations produced in the linkage groups, when correlated with the cytological conditions, enable one to arrive at a fairly accurate conclusion as to the chromosomal distribution of the linkage groups. Figure 171 illustrates such a chromosome map for Drosophila. The numerals opposite each character indicate the relative distances of the genes from the tops of the chromosomes. Similar maps have been prepared for other forms, including plants.

The Gene and Development.—The gene concept provides an internal mechanism governing the inheritance of characters that distinguish members of the same species. In the fertilized eggs these genes are present in a biparental series, the entire complement of which is distributed to every somatic cell by quantitative mitotic divisions. Since the nucleus of each body cell contains all the genes for the heredity of the entire body, the actual differentiation of the body cells would seem to be the result of an interaction between genes and environmental factors,

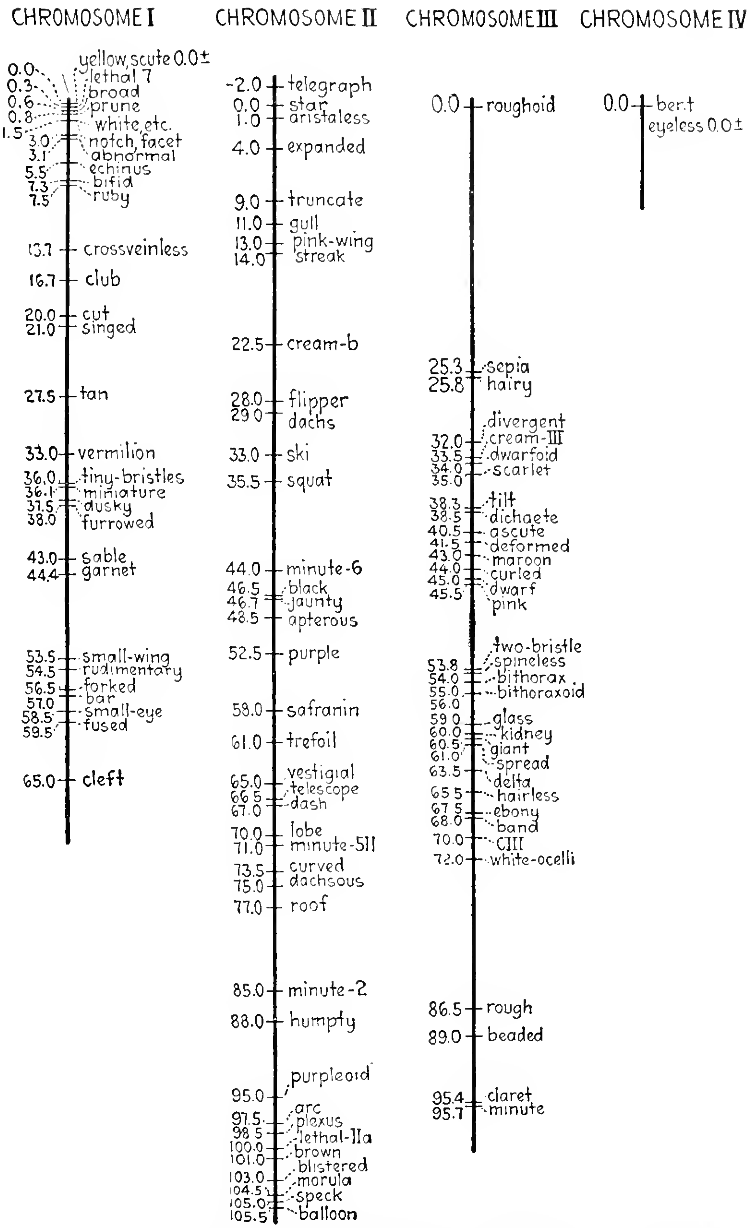


Fig. 171.—Chromosome map of *Drosophila melanogaster*. (*From Sharp, Introduction to Cytology, after Morgan.*)

represented largely by the cytoplasm. If the cytoplasm provides a necessary condition for the realization of the hereditary potencies of the genes, it becomes highly important in heredity. There is always a cytoplasmic inheritance from the egg, but its analysis into specific factors is difficult because its organization is not expressed in easily recognized morphological forms. The organization of the egg cytoplasm is a property of the *hyaline ground substance* of the egg, rather than the visible formed structures such as yolk, fat, mitochondria, etc. Unfortunately for purposes of microscopic analysis, the ground substance of the cytoplasm is optically homogeneous and contains no units comparable to chromosomes. Nevertheless, it is organized and an understanding of this organization is essential to an understanding of the action of genes in development. An animal inherits a certain protoplasmic organization permeating cytoplasm as well as nucleus; the final outcome of development being a result of the reaction of the organized plasm with the environment.

Some biologists regard the gene as the ultimate unit of life. It is thought to be protein in nature, capable of reproducing itself and carrying on the usual metabolic activities ordinarily associated with life. The cell is a medium in which its properties can be manifested. Within recent years it has been possible to obtain in a pure crystalline form the *virus* causing mosaic disease in tobacco plants. This virus is also protein in nature and is capable of reproducing itself. It has been suggested that the virus and the gene are possibly of the same general nature and that they represent a simple form of living system. If so, the first form of life evolved from nonliving nature may have been a system of this sort. The thought is suggestive in that it aids in partially bridging the gap between nonliving chemicophysical systems and typical cellular living systems.

Human Heredity.—Inheritance in man obeys the same laws of heredity that hold for other forms of life. Eye color, hair color, morphological peculiarities and physiological traits of various sorts are inherited. From the standpoint of their value to human society the inheritance of some human traits are far more important than others. The science of the improvement of the human race by better breeding, or as Francis Galton, the author of the term, put it, "the science which deals with all influences that improve the inborn qualities of a race," is known as *eugenics.* The argument of the eugenicist is simply this: If man has succeeded through artificial selection or controlled breeding in improving domestic animals and plants, it should also be possible by similar means to improve the *inborn qualities* of the human race, since man is no exception to the laws governing the heredity of other animals. A few of the characters of obvious importance to the human race are discussed in the following paragraphs.

Mental Ability.—There is good evidence that mental ability, or the lack of it, is inherited; but it is difficult to measure it in absolute units, such as can be applied to characters like stature or weight. Education and training do not create mental ability so much as provide opportunity for its development and expression. Environment plays an important part in providing suitable opportunity for the fullest realization of mental ability. Therefore, the actual accomplishments of two persons of equal mental ability may differ because of differences in opportunity for mental development. On the other hand, environment alone, however favorable, cannot make up for low-grade ability, for the simple reason that heredity in such cases establishes fixed limits to accomplishment. Thus, in the case of Charles Darwin, the author of the theory of evolution by natural selection, we have an example of marked mental ability, exhibited consistently through a number of generations as a result of heredity. Darwin's own accomplishment was of a very high order and marks him as one of the greatest biologists. His paternal grandfather, Erasmus Darwin, was a physician, naturalist, and poet. He was interested in the problem of evolution, to which he made interesting contributions and to other subjects as well. His maternal grandfather, Josiah Wedgwood, was the originator of Wedgwood pottery. His own father was a successful physician and his sons have achieved eminence in science. It is true, of course, that Darwin was favored in the enjoyment of desirable environment, which enabled him to pursue his work in relative comfort, though he was an invalid throughout the greater part of his life. It is therefore possible that his books on evolution might never have been written had he been poor and his time crowded with the duties of earning a livelihood. On the other hand, he might have spent his life in invalid ease, had he not inherited the ability and the urge to make the most of his opportunities.

In sharp contrast to cases of inherited mental ability, there are numerous records of marked mental defectiveness, which in the extreme conditions becomes feeble-mindedness or idiocy. The feeble-minded breed feeble-minded. At best they are helpless in competing with normal individuals, and at worst they are depraved and irresponsible. Criminal tendencies of a common sort, often associated with feeble-mindedness, form a prominent feature of the so-called Juke family of New York, whose ancestry has been traced as far back as 1772. In five generations of 1,200 individuals, including those who married into it, and who were of the same social stratum, only 20 learned a trade, and of these, 10 received their instruction in a state prison.

Disease.—In order that a disease caused by a microorganism may develop, infection by a specific organism must take place. Such diseases are not inherited. That children of tuberculous parents often develop *tuberculosis* is due in part to an inherited physiological resistance of a low order, which makes infection more likely than in children of sound healthy parents. A healthy individual may carry the germs of tuberculosis in his mouth, respiratory passages, including the lungs, and yet not develop symptoms of the disease. Disease in parents resulting from infection by pathogenic organisms does not affect their germ cells in such a way as to produce the same disease in their children, in the absence of infection through the usual channels. Theoretically, therefore, and for the most part practically too, it is possible by proper precautions against infection and by providing proper food and living conditions, to rear such children to healthy adults.

Syphilis, another disease whose control is important for human society, is also caused by an organism, though the statement is frequently heard that it is hereditary. Practically the latter is true, to the extent that the children of syphilitic mothers almost invariably are or become syphilitic. But here again it is not the germ cells that are responsible but the environment, because the opportunities for infection either before, during, or after birth are so great that the offspring rarely escapes.

Environment.—Attempts to improve the human race by means that fail to take the environment into consideration will not meet with much success. It could be maintained that Darwin owed much of his accomplishment to his education, his surroundings, and his private means, the last permitting him to pursue his life-long studies unhampered by the necessity of earning a living. Likewise it might be truly said that a large part of the misfortunes of the Juke family could be laid to the miserable environment in which they lived. But admitting that environment plays a large part in the achievement of success in life, it must not be forgotten that all the evidence points to the fact that heredity plays a greater part in one's destiny because it fixes limitations. All men are not born equal in a biological sense. A Juke would never make a Darwin.

Program of Eugenics.—In animal breeding man establishes an arbitrary standard, in the selection of which the animal has no part. In human breeding such a procedure is impossible except to the extent of legally preventing reproduction of the least desirable members of human society. A eugenics program at the present time can have no particular individual in mind as an ideal type for whose attainment human breeding should be controlled and regulated, but it can aim at the general adoption of a policy that will gradually eliminate the hereditarily unfit. Practical steps toward this end seem to be:

1. The promotion of eugenic marriages, *i.e.*, marriages between persons of sound mental and physical stock.

2. The forbidding of marriages between persons suffering from diseases such as gonorrhea and syphilis.

3. The prevention of reproduction among the mentally and socially unfit. At the present time (1938) some 27 states of the Union legalize the sterilization of social offenders of low mentality by the performance of simple surgical operations. In the male, *vasectomy* is performed by removing a small section of each *vas deferens*, thus preventing the egress of spermatozoa. In the female, by a similar operation known as *tubectomy*, a small piece of each *Fallopian tube* (oviduct) is excised, so that eggs cannot reach the uterus or be fertilized.

The ultimate adoption of a eugenics program rests largely upon education. Ignorance of facts forms the bulwark of resistance to such a program, which on mature consideration proves to be merely an honest attempt to raise the general physical and mental level of society as a whole and with it the individual happiness of its members.

CHAPTER XIV

EVOLUTION

The different kinds of animals and plants, their number and distribution, are all thought to be the results of natural causes collectively known as evolution. Evolution is a process of change that affects everything in the universe. All matter, living and nonliving, is changing continuously. In biology, evolution implies descent in living things; that the living animal and plant population is descended from a more primitive population; that higher forms have evolved from lower forms. This does not mean that the lower forms living today are in direct line of ancestry of higher forms, but that they have departed to a lesser degree from ancestral types common to both. Evolution is in direct conflict with the idea that the various forms of life known today were created as such in the beginning of the living world. The theory of evolution teaches that life evolved from nonliving matter, as a result of a universal process of change in matter, guided or controlled to a certain extent by environment, and that the first living things were relatively simple in form and structure and in all probability quite unlike the living things of the present time. Possibly the first living matter was not cellular at all but something of the nature of a so-called living virus, such as is the cause of mosaic disease in tobacco plants, referred to in the previous chapter. Such hypothetical primitive forms of life are thought to have gradually given rise to the various types of life known today. Diversity in living things is thus the result primarily of a fundamental law or condition of *change.*

From the broad view of evolution not only are all animals genetically related, but animals and plants as well, since the differences between the lowest animals and the lowest plants are bridged more or less by certain intermediate forms that combine animal and plant qualities. The community of origin is recognized in the employment of the term *Protista* to include all unicellular forms, both plant and animal. Protista, presumably, represent living forms that have deviated least from the first living things to be evolved from nonliving matter.

The evidence supporting the doctrine of evolution consists of a body of facts derived from morphology, embryology, physiology, ecology, and paleontology, for which evolution seems to be the most plausible explanation. This evidence is largely circumstantial but so convincing as to meet with acceptance among biologists and others who give the matter serious thought. At the same time the truth of the evidence is not experimentally demonstrable because it has not yet been possible to change one species into another, *i.e.*, to bring about experimentally the evolution of a lower form into a higher one. Failure to demonstrate species change experimentally detracts very little from the value of the principle of evolution as a practical means of interpreting biological phenomena, inasmuch as an evolutionary interpretation gives meaning to otherwise inexplicable facts of biology and is the basis of the scientific organization of the subject.

Variation.—Animals are classified into different species largely on a basis of morphological characters. A *species* is composed of organisms that resemble each other more closely than they do other organisms. It is a group of similar individuals. Similar species form a *genus*, similar genera a *family*, and so on, up to the *phylum*, which is the largest subdivision of either the plant or animal kingdom. The species is the basic unit in classification, but actually it is a variable unit because its members, though closely resembling each other, are rarely identical. This variability is the basis of evolution and because of it there is often difficulty in deciding whether extreme variants belong to the same or to different species. This is a familiar experience of any one who has collected sea shells and then arranged the shells of each species into a graded series according to color or structural differences. Often the extremes of such a series are so different that had none of the intermediate forms been found, there might have been some question as to whether they really belonged to the same species or not. Such *lability* in species characters suggest that a species is not a permanently fixed unit and, as a corollary, that evolution or change has taken place in the past and may be taking place in the present as a result of the instability of the species unit. Difficulties arising in connection with the classification of similar animals in the same or different species result sometimes in arbitrary decisions, which must be changed later when additional specimens become available for study. On a basis of special creation, every species should be distinct from every other species, without wide variation within a species and without overlapping between species. On the other hand, variability within and among species is a natural predisposing cause or accompaniment of an evolutionary process. To the degree, then, to which plasticity can be demonstrated as a property of species, presumptive evidence of an evolutionary process may be said to exist.

The mutant conditions appearing in Drosophila and used as a basis for numerous breeding experiments are examples of variations of a greater degree than normal. Little or nothing is known as to the cause of mutations, but their occurrence provides a basis for further evolutionary change. Since mutations occur naturally, the condition cannot be attributed to the abnormal laboratory conditions under which the flies are bred. A fuller discussion of the subject of variations will be considered presently in connection with the work of Darwin and De Vries.

Homology.—The concept of homology in parts or organs of different animals implies a common evolutionary origin of corresponding parts. A study of the comparative anatomy of any animal group, such as the vertebrates, reveals a basic pattern of structure occurring throughout the group, modified in various ways in the different subgroups, but always referable to a single structural type. Thus the skeleton of the forelimb of the bird, bat, whale, ox, horse, and man show the same parts of a common type of structure, though in some cases the parts are distorted almost beyond recognition (Fig. 172). The hand region of the bird consists only of rudiments of three digits and three metacarpal elements. In the bat the digits are enormously elongated, exceeding in length the remainder of the forelimb skeleton. In the whale the forelimb is greatly shortened in all its parts to form a paddlelike structure. In the ox there is a reduction of parts in the hand region to two fused metatarsals and two digits. This reduction is carried even farther in the horse. Curiously enough the human forelimb is the least modified of the lot. Such limbs are said to be homologous because they are believed to be derived by evolution from a common type of ancestral limb, such as that represented by the forelimb of Amphibia. In the case of vertebrate limbs and also other so-called homologous structures, the facts of comparative anatomy do not, of course, prove evolutionary relationship any more, perhaps, than a collection of automobiles including all types from the earliest one-cylinder motor to the latest multicylinder type proves that there is a genetic relationship between them. However, in the case of biology there is another line of evidence from embry-

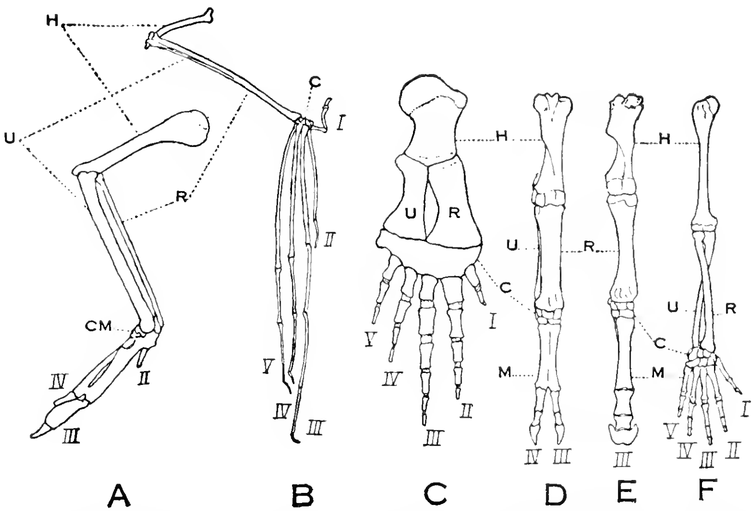


Fig. 172.—Skeleton of the right forelimb of several vertebrates to show the fundamental similarity of structure. A, bird (raven); B, bat; C, whale; D, ox; E, horse; F, man. c, carpals; cm, carpometatarsal; h, humerus; m, metacarpals; r, radius; u, ulna; i to v, digits. (*Modified from Scott, The Theory of Evolution, copyright, The Macmillan Company. By permission.*)

ology which warrants an evolutionary interpretation of facts of comparative anatomy and which justifies the use of the term homology.

Development.—The law of biogenesis holds that an animal recapitulates to a certain extent the history of its race. Actually ontogeny presents such a mixture of old (palingenetic) and new (cenogenetic) characters that the facts of development in any given case must be interpreted with proper care. Nevertheless there are cases where a knowledge of embryogeny has been useful in determining the relationship between two or more animals. Thus the subphylum *Tunicata* of the phylum *Chordata* includes animals that in the adult state resemble molluscs rather than chordates. A sessile tunicate, such as *Ciona,* is tubular in form and is provided with an incurrent and excurrent siphon through which water passes in and out as in a clam. There is no trace of a notochord and the central nervous system is represented by a ganglion lying between the two siphons (Fig. 264). About the only definite chordate character recognizable in the adult animal is the presence in the pharynx of gill clefts, but even these are highly specialized when compared with the gill clefts of other chordates. The question as to the position of the group Tunicata in the classification is settled by the presence in the motile, free-swimming, tailed larval stage of a well-developed dorsal neural tube and of a notochord lying between the neural tube and the alimentary canal. In metamorphosis the tail is lost, and with it the notochord, while the central nervous system is reduced to a ganglion embedded in the body wall between the two body apertures.

Aside from such special instances where embryology sheds light on problems of classification and therefore on problems of evolutionary origins, there is in all of the Metazoa a common plan of development followed by all of them. Thus the egg, a cell, is the starting point in metazoan embryogeny. Cleavage, a period of cell division following fertilization of the egg, occurs in all Metazoa, and leads in turn to the formation of the blastula, gastrula, and differentiation of the germ layers. Coelenterates go very little beyond the development of two germ layers. Hydra in its adult stage is but little more than a tube of ectoderm, lined with endoderm, with just the beginning of a trace of a third germ layer, represented by the mesoglea, between them. It might be said that the development of Hydra is arrested at the two-germ-layer stage. Higher forms, on the other hand, pass through and beyond the diploblastic condition and add a third layer, the mesoderm; the three germ layers serve as the point of departure for the differentiation of the tissues and organs of the embryo and later of the adult. Gastrulation is a fundamental process in the development of all Metazoa.

One of the characters distinguishing Vertebrata from other subphyla of the Chordata is the presence of the vertebral column, which in its embryonic origin and general development is the same in all of them. Since similarity in embryonic origin of the vertebral column is taken to mean evolution from a common ancestral structure, embryogeny becomes a criterion for homology. The embryonic record in a given case is regarded as an evolutionary record, but one that is often blurred and incomplete, and must therefore be interpreted with great care. The embryos of all vertebrates develop pharyngeal pouches, which in many cases fuse with the ectoderm and break through to form gill clefts. These are visible externally in early human embryos as

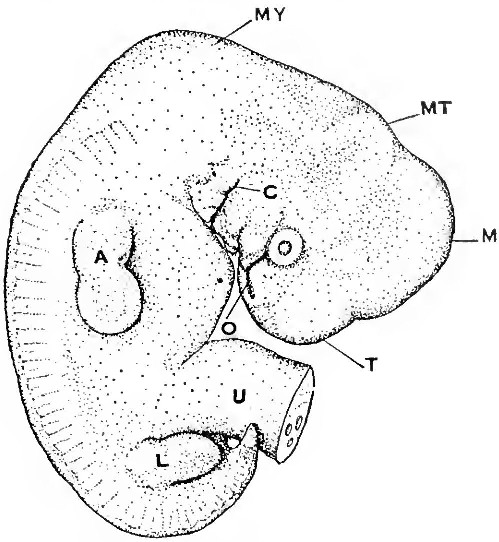


FIG. 173.—Human embryo of about thirty days in age. A, arm bud; C, gill cleft (hyomandibular); L, leg bud; M, mesencephalon; MT, metencephalon; MY, myelencephalon; O, olfactory pit; T, telencephalon; U, umbilical cord. (*After Keibel and Mall, Human Embryology, J. B. Lippincott Company.*)

grooves (Fig. 173), but no actual clefts are formed. Nor are gills developed. Obviously these incomplete gill clefts cannot be compared with the gill clefts of a fish which function as passageways for water, but they may be compared with a corresponding stage in the fish embryo. On this basis they may be also compared with the gill clefts of the embryo of the chick, of a reptile, or of an amphibian. The only plausible explanation of gill clefts in the human embryo would seem to be an evolution from an ancester whose embryo possessed gill clefts. In the fish the embryonic gill clefts continue developing, together with gills, to form a functional respiratory organ. In man or the chick the gill clefts never become functional parts of a respiratory system. Long before the adult stage is reached they disappear or, as in the case of the first gill cleft, enter into the formation of entirely different structures. Embryonic rudiments in higher forms must always be compared with embryonic rudiments of lower forms and not with the corresponding organs of the adults of the latter. Facts of development of this sort are none the less significant as evidences of evolutionary relationships.

The homology assumed to exist between various types of vertebrate limbs, previously referred to, on a basis of the comparative morphology of the adult limbs, is supported by development to the extent that in each case the limb arises from a

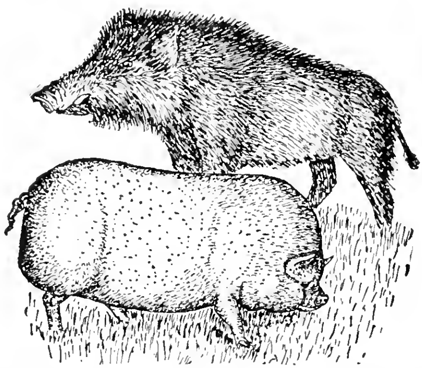


FIG. 174.—Domestic pig with its wild-boar ancestor. (*After Romanes, Darwin and after Darwinism, Open Court Publishing Company.*)

similar rudiment. Vertebrate limb rudiments are strikingly alike, particularly those of a single group, such as the mammals. Soon, however, each type of limb develops along its own particular lines into the type characterizing the adult. Thus the human limb does not pass through stages found in adults of lower mammals—instead it develops from a limb-bud stage, common to all of them, into a human limb. The origin of the limb in all cases from the same sort of rudiment is interpreted as indicating a common evolutionary origin. Enough of the common plan of structure survives in the adults to make the community of origin recognizable. The facts of comparative anatomy find their explanation in the facts of development.

Artificial Selection.—It has been pointed out that the members of the same species are not identical. Animal and plant breeders have known for a long time that by careful selection, certain chance differences or variations in a species of animal or plant can be perpetuated. The criterion by which the breeder decides which variations are desirable is in most cases utility. Thus the breeder of horses for running races selects for sires stallions that have established good records themselves or that are descended from good racing stock. Improvements in animals from the standpoint of their usefulness as food as in the case of the pig (Fig. 174) have been brought about as the result of perpetuating

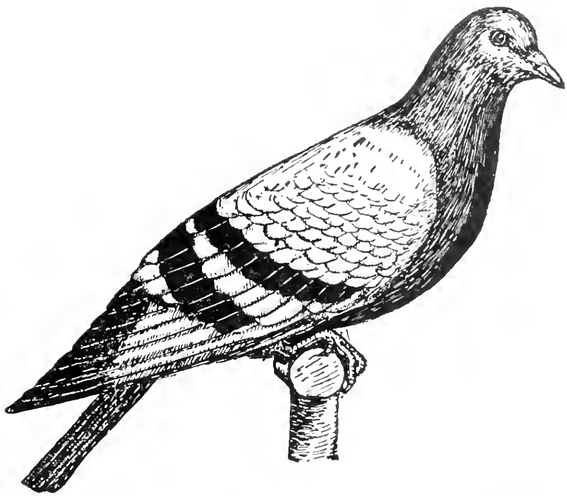


FIG. 175.—*Columba livia*, the ancestor of 150 or more varieties of domestic pigeons. (*After Whitman, Carnegie Inst. Pub.*)

desirable qualities, that arose originally as chance variations. In the case of the fancy breeds of dogs, characters other than utilitarian ones, have become the standards of the various breeds. In general the various breeds and varieties of our domestic animals and plants have been developed by artificially controlled breeding from relatively few primitive natural or wild species. Anyone unacquainted with the history of the various breeds of domestic pigeons would say that the breeds were at least as distinct as different species; yet, as Darwin first pointed out, they have in all probability been derived by selective breeding from a single wild species, *Columba livia*, the rock pigeon (Fig. 175). A common breed, the fantail, possesses something like 40 tail feathers, whereas the ordinary pigeon has but 16. In all probability the former was derived from the latter by taking advantage of chance variations in tail feathers and selecting for breeding

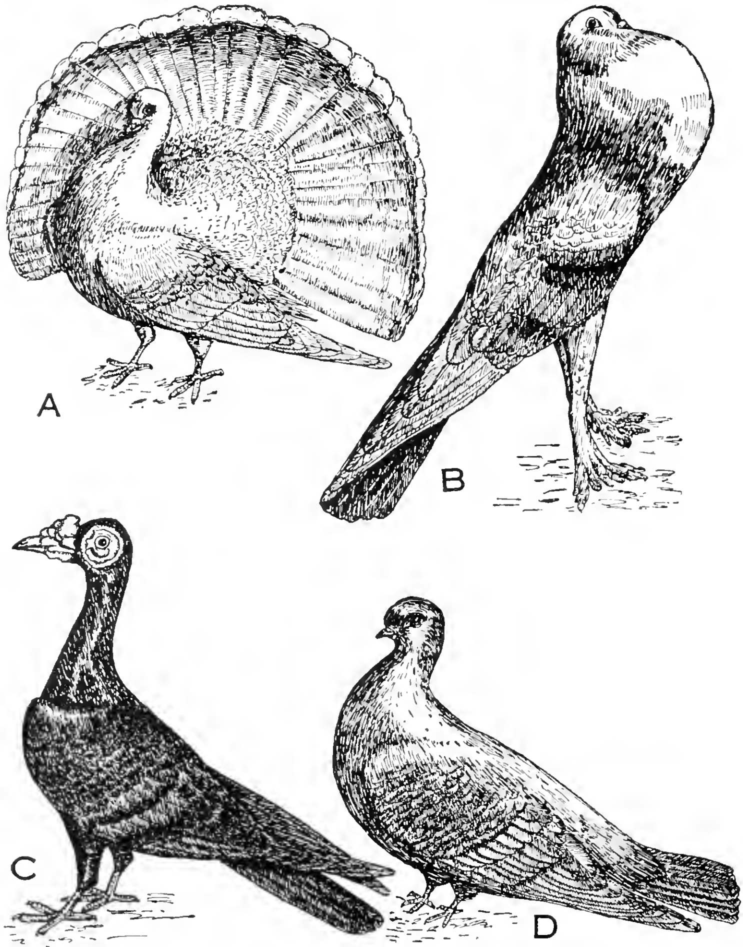


Fig. 176.—A few of the domestic varieties of pigeons. A, English Fantail; thirty to forty tail feathers, small feet. B, English Pouter; short beak, upright posture, inflated crop. C, English Carrier; elongated beak, neck, and body, corrunculated skin surrounding the eyes. D, short-faced English Tumbler; small beak, feet, and body; tumbling habit (tumbles backward, involuntarily, during flight). *(Redrawn from Darwin, Animals and Plants under Domestication. D. Appleton-Century Company. By permission.)*

only those birds showing abnormally large numbers, until the present fantail was produced (Fig. 176). The same principle has been followed in developing the various other breeds.

Wild species maintain species standards even in the face of promiscuous cross-breeding. Breeds developed by artificial selection can be maintained at a constant level only by breeding from selected stock. Promiscuous or uncontrolled breeding results in loss of breed characters and a tendency to revert to the unimproved natural or wild type. Among pigeons an occasional rock type will appear in an otherwise standard brood. Such tendencies to revert to primitive types indicate that the distinctive breed characters are not firmly fixed and that they would not in all probability survive long in the wild state. Indeed if domestic breeds are allowed to run wild they soon lose their distinctive breed characters and tend to become similar to, though not necessarily like, the original wild forms from which they were derived.

The results achieved by artificial selection in animal and plant breeding show that the protoplasm of a species has a certain amount of plasticity or capacity for modification, which can be directed or controlled to a certain extent. Heredity is a conservative mechanism—it tends to keep species constant. Evolution is possible because the heredity mechanism permits a certain amount of variability to appear in the offspring of similar parents. Variability provides a background for evolutionary change. Experience has shown that there are limits to the use to which variations can be put in selective breeding, as will be pointed out in later pages.

Serum Tests.—The accuracy of the evolutionary relationships of the members of a phylum or of any of its subdivisions, as portrayed in the taxonomic system on the basis largely of morphological data, may be put to a further test by means of certain blood reactions. If human blood serum, *i.e.*, blood minus corpuscles and fibrinogen, is injected in small quantities at repeated intervals into the blood vessels of a rabbit, there are developed after a while in the blood of the rabbit antibodies which, when brought into contact with normal human blood serum, cause the precipitation of the human blood proteins. Serum from the blood of such an immunized rabbit may be called *antihuman serum.* Blood sera of man, chimpanzee, gorilla, and monkeys, at a certain dilution, all produce precipitates when mixed with antihuman serum. At a higher dilution no precipitation is obtained with monkey sera; and at still higher dilution only with chimpanzee and human sera. If the sera are diluted still more, a point is reached when the antihuman serum reacts only with human serum. Thus on a basis of the susceptibility of the blood proteins to precipitation by the antihuman bodies, the chimpanzee ranks next to man, the gorilla next to the chimpanzee and the monkeys farthest from man, all of which is in keeping with the morphological findings. In general the precipitin tests confirm the generally held view that apes are more closely related to man than monkeys.

Similar tests show that lizards and snakes are more closely related to each other than to turtles, which in turn are more closely related to crocodiles. When reptilian sera and bird sera are tested, birds show a closer relationship to crocodiles. In general when the serum reactions of two animals are tested with the antiserum of a third, that animal whose serum in the higher dilution produces a precipitate with the antiserum of the third is more closely related to the third. From such experiments the important fact emerges that the degree of relationship as ascertained by ordinary methods of classification is borne out by blood reactions. In some cases the precipitin tests have established relationships between species when the usual morphological criteria have failed or proved uncertain.

Blood Groups.—Within a species, the blood of different individuals may be classified into groups, depending upon the conditions under which the serum of one individual will cause the *agglutination* or clumping of the red blood corpuscles of another. An understanding of the individual differences in properties of human blood has become important in connection with blood transfusions, because agglutination leads to the destruction of the injected corpuscles and thus makes the transfusion ineffective. When the blood of one individual is transferred into the blood system of another, in some cases agglutination occurs and in other cases not. Since agglutination is to be avoided, studies have been made leading to the classification of human beings into four blood groups known as 0, *A*, *B*, and *AB*. The designation of the groups depends upon the presence or absence of one or both of two substances *A* and *B*, located in the red corpuscles and which are necessary for agglutination. Group 0 contains neither *A* nor *B* in its corpuscles. Group *AB* has both. The principle underlying the agglutination reaction is simply this:

The serum of a given group or type will agglutinate whichever of *A* or *B* is absent in the red corpuscles of its own group. Serum of a group 0 individual will agglutinate red cells of *A*, *B*, or *AB* individuals; *A* serum will agglutinate *B* or *AB* corpuscles; *B* serum will agglutinate *A* or *AB* corpuscles; while *AB* serum will not agglutinate corpuscles of any of the other types. An *AB* type is a universal recipient; an 0 type, a universal donor.

Similar blood groups have been discovered in lower mammals, but only in the apes do the groups correspond with those of man; thus adding one more link in the closeness of the relationship between man and the apes. The blood-group characteristic is permanent throughout life and is also inherited. If a mother belongs to the 0 group and her child to the *B* group, the father could be of *B* or *AB* but not 0 or *A* group.

Paleontology.—Paleontology deals with the distribution of animals in time. Its material consists of remains of hard parts, such as bone or shell, or imprints of bodies and tracks made in soft mud, later hardened and preserved. A fossilized bone is a bone whose organic constituents have been completely replaced by mineral matter without destroying the original form of the bone. Bones do not survive long if left exposed to the weather on the surface of the ground. Fossilization resulted from the embedding of dead animals in silt and soil at the bottoms of streams, lakes, and oceans, where slow chemical changes transformed the harder parts into minerals. It therefore is very seldom that the entire bodies of extinct animals are preserved. It is true, of course, that complete skeletons of prehistoric men and of various animals have been found in limestone caverns, and that there are unusual instances where insects have been found in amber and where whole bodies of mammoths have been exposed by the erosion of the covering layers; but these are in the nature of exceptions rather than the rule. The value of paleontology, as evidence for evolution, ranks high because fossils definitely prove that animals (and plants, too) have actually changed and that when the fossils are arranged in proper chronological order, they form a more or less progressive series from low to high forms of life.

The data of paleontology must be interpreted in terms of age as well as in terms of comparative morphology. A paleontologist must be a good comparative anatomist and at the same time have a good working knowledge of geology in order to arrive at a correct estimate of the age of any given fossil-bearing geological stratum. Fossils are found in what is known as *sedimentary rock*, produced by the solidification of fine particles eroded from the earth's surface and eventually washed into lakes, streams, and oceans. It is possible to measure the amount of erosion at the present time over a given surface of land, from which the time required to form a layer of a certain thickness can be estimated. Thus the thickness of a geological formation gives an indication of the approximate time required for its formation. If all of the different kinds of strata occurring in all parts of the world could be piled on top of one another, the total thickness of the superimposed layers would be about 100 miles. Knowing the approximate rate of formation of the series, the total time for its formation may be computed. All of the components of the geological series are not found in one place because more recent rocks are formed in valleys from material eroded from materials of more ancient layers, which at the time constituted the hills and mountains. When all of the strata of sedimentary rocks are arranged in order of their formation, the age of contained fossil remains must correspond to the age of the strata in which they are found. Another method of determining the age of the earth depends upon measuring the rate of the decomposition of radioactive ores contained in igneous rocks, from which the amount of time required to form the decomposition products occurring in a given sample can be estimated. Igneous rocks have been formed at various times in the history of the earth, but since they contain no fossils, their age in terms of geological eras and periods must be determined largely from their relations to fossiliferous strata. The total elapsed time since the beginning of the formation of sedimentary rocks, based on a combination of purely geological data and measurements of the decomposition of radioactive ores, is about 1,800 million years.

A plan of the distribution of life in time is shown in Table 1, in which the latest time is at the top and the earliest at the bottom. "Eras" are intervals separated from one another by marked changes in the earth's plant and animal life. "Periods" are distinguished by geological changes principally. "Epochs," which are subdivisions of periods, are not shown. The figure opposite each era is the duration of time for the era in millions of years. The percentage following this figure is the percentage of the whole of geological time. The bracketed figures give time durations of the periods. The table is based on a total of 1,800 millions of years of geological time.

TABLE 1.—THE DISTRIBUTION OF LIFE IN TIME

Eras and periods	Time	Fauna and flora
Psychozoic era	Postglacial	Historical time
Recent period		Cro-Magnon man
Cenozoic Era	60—3 per cent	Age of mammals
		Neanderthal man, Sinanthropus man
Quaternary period	(1)	
Tertiary period	(59)	Primates, birds
Mesozoic Era	155—9 per cent	Age of reptiles
		Archaic mammals, flowering plants
Cretaceous period	(75)	
Jurassic period	(40)	Archaeopteryx, insects
Triassic period	(40)	Cycads (fernlike palms), reptiles
Paleozoic Era	410—23 per cent	Age of amphibia, primitive reptiles
Permian period	(30)	
Carboniferous period	(90)	Ferns and other early plants
Devonian period	(50)	Age of fishes
Silurian period	(40)	Early land plants
Ordovician period	(110)	Ostracoderms, bryozoans, crinoids
Cambrian period	(90)	Cephalopods, brachiopods, corals, trilobites (crustacean-like arthropods)
Proterozoic era		Simple forms of life
Archeozoic era	1,175—65 per cent	Indirect evidence of life
Azoic era		No evidence of life

It will be noted from Table 1 that prior to the Cambrian period only the more primitive forms of life have been found. Thus the sedimentary rock of the Azoic era is entirely without fossils. During the Archeozoic and Proterozoic eras life was beginning, but in all a total of something over 1,000 millions of years passed before the record shows the existence of invertebrates in any numbers. The lack of fossils in these early rocks may be due in part to the fact that the conditions for fossilization preclude the possibility of the preservation of many forms, particularly soft-bodied forms. This, of course, holds true for all succeeding strata and accounts for gaps in our knowledge of the ancient history of soft-bodied progenitors of modern groups of animals. Beginning with the Paleozoic rocks the material becomes richer in fossil content and reveals the gradual emergence of higher forms as time goes on. The predominant forms of the Paleozoic era are higher invertebrates, fishes, amphibians, and toward the end of the era, primitive reptiles. The Mesozoic era is spoken of as the age of reptiles, because during this period they achieved a greater size and abundance than during any time before or since. During this era also birds and mammals made their first appearance. The Cenozoic era is characterized by a fuller development of mammals and the Psychozoic by the later stages in the evolution of man.

On an evolutionary basis, the relationships of the various animal groups can be represented graphically in the form of a tree, whose terminal twigs alone represent the living fauna. The rest of the tree structure represents the paths leading to the evolution of the living forms. All of the tree except the twigs therefore represents generations of ancestral forms that have become extinct as species. The proof that such ancestral forms actually existed in the past is furnished by paleontology. But since many ancestral forms have left no record, and since the record of those preserved is often fragmentary, the task of reconstructing ancestral series of any single species with any degree of completion is a very difficult one. Nevertheless, this is being accomplished in an ever-increasing number of instances, of which one of the best known is the case of the ancient history of the horse.

Evolution of the Horse.—The earliest known ancestor of the horse lived in the Eocene (epoch) of the Cenozoic era of North America and is known as *Hyracotherium* or *Eohippus*. It had four toes and a rudiment of digit I on its forefeet, and three toes and a splint of digit V on its hindfeet. In later strata of the Eocene were found the remains of *Protorohippus*, somewhat larger than Hyracotherium, with four toes on the forefeet and three on the hindfeet. *Mesohippus*, the size of a sheep and found in the Oligocene epoch, had three toes and the splint of

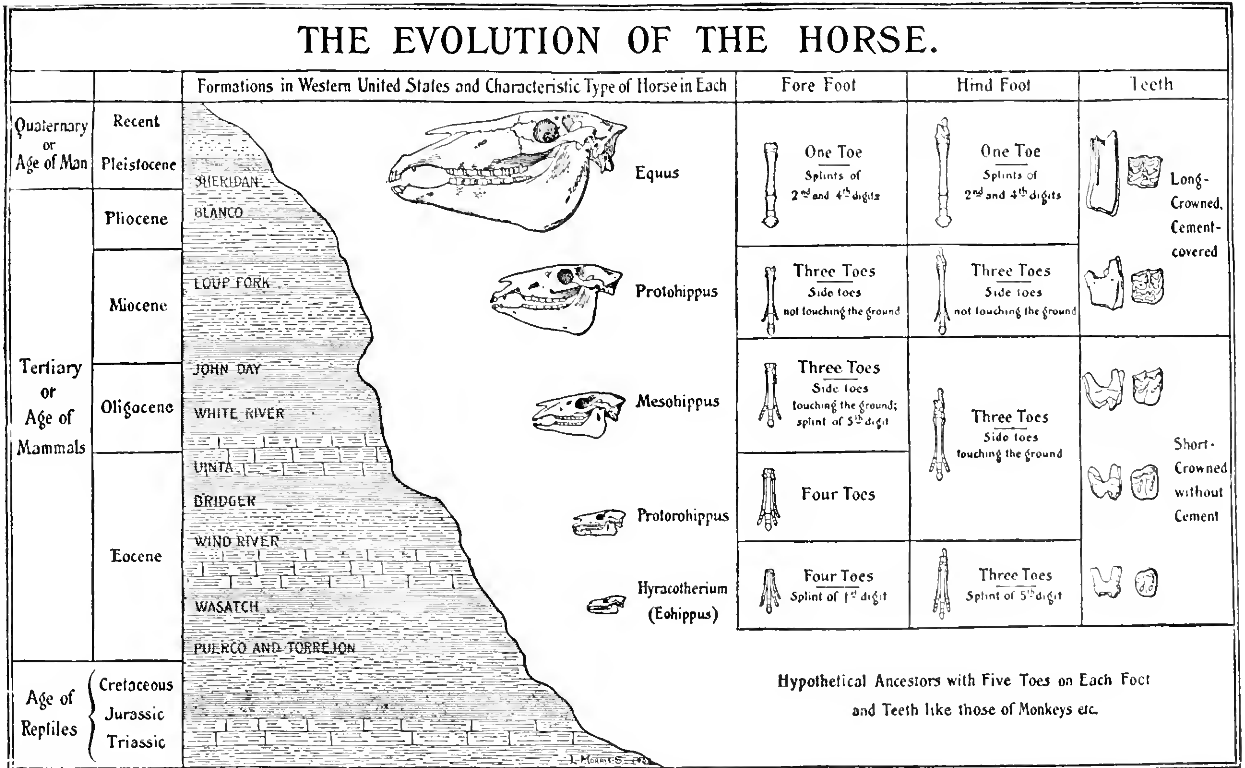


FIG. 177.—Graphic outlines of the evolution of the horse. (*From Osborn. By permission of author and the American Museum of Natural History.*)

digit V on the forefeet, and three on the hindfeet; all the toes of all feet touched the ground. *Protohippus*, about the size of a donkey, lived in the Miocene epoch and had one large toe (III) and two smaller ones (II and IV) on each foot; only the larger one touched the ground. The earliest remains of the modern horse *Equus* date from the Pleistocene epoch. It had a large, well-developed, single digit and two very rudimentary splints on each foot. This fossil series demonstrates the changes undergone in the morphology of the body of the horse, particularly the steps by which the single-digited foot of the modern horse has been arrived at. The teeth also show interesting transitions (Fig. 177). The evidence indicates that the horse was not created as such in the beginning, but arrived at its present state after a series of changes extending over millions of years from Hyracotherium, prior to which other forms, not completely known, push the ancestry of the horse still farther into the past. As for the horse, so for other forms of life.

Evolution of Man.—The evidence for evolution in man is similar to the evidence for the evolution of other animals. If the principle of evolution is accepted for the animal kingdom generally, it must also be accepted for man, since he is part of the phyletic series of animals. The structure of the human body is that of a mammal, without doubt the most intelligent mammal, but neither more nor less than a mammal. Taxonomically, man belongs to the Class *Mammalia*, Order *Primates*, Suborder *Anthropoidea*, Family *Hominidae*, Genus *Homo*, and Species *sapiens*. The oldest known member of the human race, the Peking man or *Sinanthropus pekinensis*, lived in the early Pleistocene epoch at the onset of the Great Ice Age in the northern hemisphere, which occurred between 500,000 and 1,000,000 years ago. The site in which the remains were found was a limestone cave, located 40 miles southwest of Peiping, China, and filled with sand and debris, along with the remains of other mammals, such as the rhinoceros, elephant, saber-toothed tiger, horse, etc., all dating from early Pleistocene times. The first complete cranium was found in 1929 and since then parts of at least 11 individuals have come to light. The skull is apelike with heavy brow ridges and receding forehead (Fig. 178). The lower jaw is heavy and without a chin. The Peking man could build a fire and make tools. The Java man, *Pithecanthropus* *erectus*, was discovered near Trinil, Java, in 1891 (Fig. 179). The remains consisted of a skull, a jaw bone, a few teeth, and a femur, from which it has been possible to reconstruct the entire skull. The straight femur indicated that he walked erect. The Java man is dated at a little less than a million years in age. The Piltdown man, *Eoanthropus dawsoni*, found in 1911 at Piltdown, England, lived about 500,000 years ago. His cranium in front was broader and steeper than that of the Java man, and his brain was nearly as large as that of modern man. The Heidelberg man, represented by a jaw bone found near Heidelberg, Germany, in 1907, was contemporary with the Piltdown man.

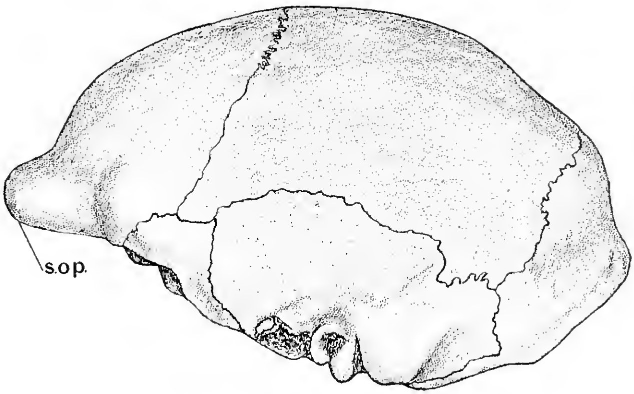


FIG. 178.—Cranium of *Sinanthropus pekinensis*. s.o.p., supraorbital process. (*After Black.*)

The Neanderthal man, *Homo neanderthalensis*, is a type of man prevalent in Europe about 200,000 years ago. He is named from a skull found in the Neander Valley, in 1856, though a similar skull had been unearthed in Gibraltar, in 1848. Parts of other skeletons discovered since provide a very complete series of bones of this particular species of prehistoric man. Neanderthal man, who is thought to be descended from Heidelberg man, may have become extinct during the latter part of the Great Ice Age when the glaciers covering half of Europe were beginning to retreat; though some anthropologists believe that he survived and that Australoid and negroid races are descended from him. Another opinion holds that modern human races sprang from men originating in Asia about 40,000 years ago and represented in Europe by the Cro-Magnon Man of the Paleolithic or Old Stone

Age. A considerable amount of material of the Cro-Magnon man is available for study, and this material shows that human morphology has changed very little during the last 40,000 years.

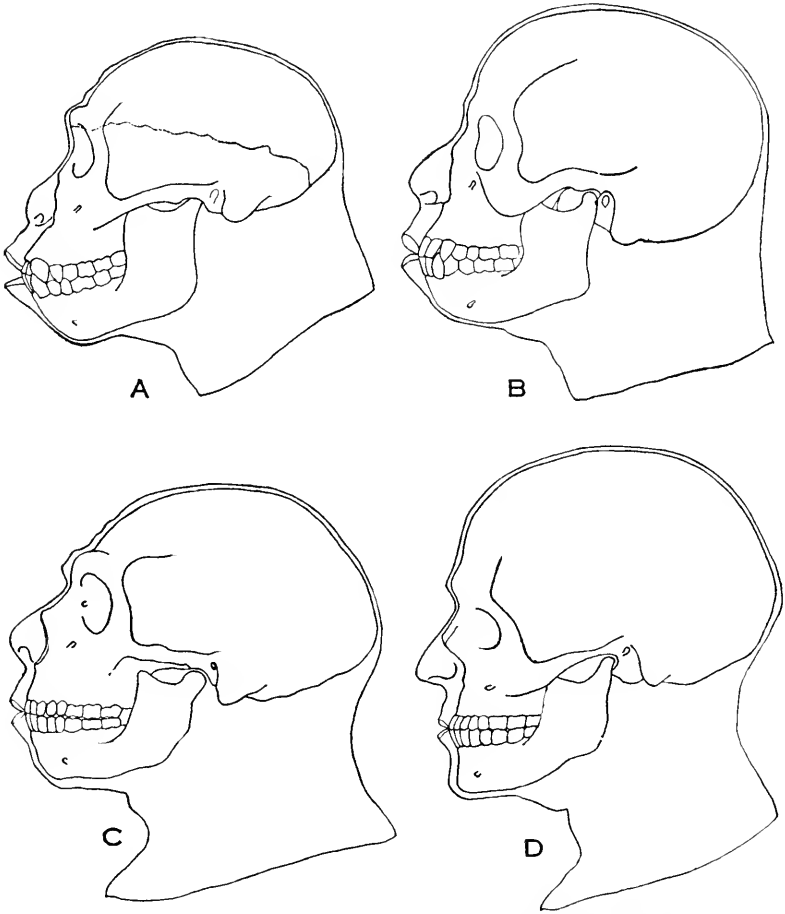


FIG. 179.—Prehistoric men. A, Java Man, *Pithecanthropus erectus*, lived approximately 1,000,000 years ago. Portion below irregular line restored. B, Piltdown Man, *Eoanthropus dawsoni*, 400,000 to 500,000 years old. C, Neanderthal Man, *Homo neanderthalensis*, 200,000 years old; probably an offshoot not in the direct line of human ancestry. D, Crô-Magnon Man, *Homo sapiens*, 40,000 years old. (*After Lull, The Evolution of Man, Yale University Press.*)

The evidence from paleontology indicates that the older prehistoric men were apelike and that, in all probability, men and apes sprang from a common ancestor. Many of the species of apelike men became extinct and left no living descendants. Such failures have been recorded time and again in other lines of descent and are therefore not unusual. Finally in the human lines, the Neanderthal and the Cro-Magnon types were evolved and one or both survived and left living descendants. The apelike skulls of prehistoric men, characterized by prominent orbital ridges over the eyes, sloping foreheads, and heavy jaws, are present to a certain extent in modern primitive races of men. The close resemblance between the human skeleton and the skeleton of the gorilla may be noted in Fig. 180. Other apelike characters, such as ears pointed above, and the presence of unusual quantities of hair about the ears and over the entire body, are also seen in some modern men. There seems to be a closer resemblance between the young of man and the adult ape than between the young of man and adult man. In the human infant the great toe stands out and the foot is almost prehensile; the abdomen protrudes, the arms are longer in proportion to the legs; and the grip in the hands is so great that if a three-weeks old infant is permitted to grasp a stick, it can be lifted from the ground by raising the stick.

Man's advance over other animals has been due to the exercise and development of ingenuity and intelligence rather than physical strength, although the human body as a machine is probably the most efficient mechanism known. The high degree of adaptability of the human race, shown by its ability to live in any climate and to move about over land, water, or through the air is in keeping with the relatively unspecialized morphology of the human body. In comparison with man, most mammals show a greater degree of structural adaptation to special habitats, as for example, the form of the body of the whale for an aquatic habitat, the forefeet of the mole for digging, or the hoofs of the ungulates for locomotion over a hard substratum, all of which in each case restrict the animal in varying degrees to a certain environment. Man has supplemented his rather meager natural equipment for obtaining food and for providing protection from destructive factors in the environment, by learning to use fire and tools, to manufacture weapons and clothing, to build suitable shelter, and to store food. These with the ability to speak, and later to write, are the manifestations of an intellectual development brought into being with the human brain. The superiority of the human brain as a mechanism through which action can be suited to requirement, distinguishes man from all

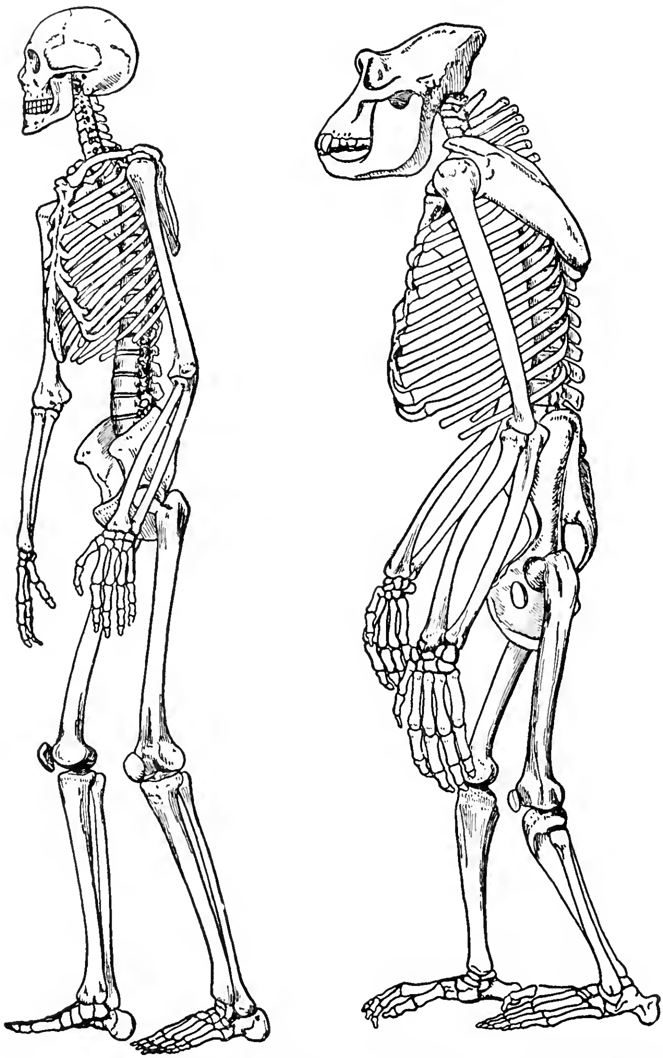


Fig. 180.—Skeletons of Man and Gorilla. *(From Lull, Organic Evolution, copyright, The Macmillan Company. By permission.)*

other animals. Superior intelligence enables man to control his environment to the extent that he is able to withstand its onslaughts and to bend to his own uses phenomena exhibited by it. Man's superiority over other animals rests upon his greater success in controlling the forces of environment.

Pre-Darwinian Theories.—The essential features of evolution as a process were understood by the ancient Greek philosophers, but prior to the time of Charles Darwin theories advanced to explain the process were too feebly supported by facts to carry much conviction. Several of Darwin's immediate predecessors contributed ideas which were important in the later development of the subject. Comte de Buffon (1707–1788), supported the teaching of the Greek philosopher Aristotle (384–322 B.C.), that species form a single ascending series from the lowest to the highest, and that higher forms evolved from lower ones. He emphasized the importance of variations as the basis of evolutionary change and believed that the larger differences between species resulted from the building up of smaller differences or variations between the members of the same species, under the direction or guidance of environment. He accepted the principle of the inheritance of acquired characters, a principle that was stressed by his successors, particularly Lamarck. Buffon pointed to the results achieved by animal and plant breeders in developing new varieties from a common wild stock as an example of the effect of environmental conditions or stimuli on the plastic nature of organisms. This idea was also supported by Erasmus Darwin (1731–1803), poet and physician, and the grandfather of Charles Darwin. In connection with the question of the effects produced by environment, Erasmus Darwin emphasized the importance of the inheritance of functional responses of the organism to external stimuli.

The French biologist, Jean Baptiste Lamarck (1744–1829), discarded the idea of a single evolutionary series from the lowest to the highest forms and formulated instead the modern concept of the origin of all forms of life from a common stock by diverging lines of ascent, similar to the formation of limbs and smaller branches from the trunk of a tree. Thus the treelike arrangement of the scheme of classification was originated by Lamarck. In his later years Lamarck was a staunch evolutionist, yet he failed to produce a completely worked-out theory to explain the process. His ideas may be summarized as follows: (1) The environment has a direct effect in modifying plants and an indirect effect, through functional responses, in modifying animals. (2) Organisms develop new structures and parts as a result of need or necessity, *i.e.*, new parts evolve to meet certain requirements. (3) Use or exercise develops an organ, while disuse results in atrophy. (4) All characteristics or changes, whether caused by environmental effects, habits, use or disuse, are inherited. Lamarck's emphasis and elaboration of the principle of the inheritance of acquired characters have resulted in this principle being often referred to as the Lamarckian factor in evolution, though as a matter of fact the idea was also held by a number of his predecessors.

Darwin.—Appointed naturalist of a British naval surveying expedition, Charles Darwin, an Englishman, at the age of 22 sailed from Plymouth on H.M.S. Beagle for a round-the-world voyage that lasted five years. Most of this time (nearly four years) was spent in coasting the Eastern and Western shores of South America and it was in South America that Darwin first became interested in evolution. There is every reason to believe that Darwin left England firm in the conviction that species were created separately and that he was converted from that view by "certain facts in the distribution of organic beings inhabiting South America, and in the geological relations of the present to the past inhabitants of that continent." Darwin is outstanding in the field of evolution because he was the first properly to evaluate the data of morphology, embryology, and paleontology, and to utilize the derived principles in the elaboration of an explanation of evolution that anyone could understand. Save for minor details, that have proved to be incorrect, Darwin's theory of evolution has withstood the tremendous surge of adverse criticism with remarkable success, all of which is a tribute to the fundamental soundness of his work. Darwin neither affirmed nor denied the possibility of the inheritance of acquired characters. On the other hand, he appreciated the greater importance of congenital variations and heredity in evolution, and stressed them accordingly. Alfred Russel Wallace, Herbert Spencer, Patrick Mathew, and others had also recognized the importance of these factors, but none achieved Darwin's success in welding these factors into a constructive theory. Darwin published the results of his studies in a series of books of which the first, "Origin of Species," appeared in 1859, over 20 years after his return to England.

Natural Selection.—In 1838 Thomas Malthus published an article on the Law of Population to the effect that since man reproduces in a geometrical ratio, the world would soon be over-populated were it not for checks such as war, famine, disease, etc., which keep down the total numbers. Darwin's theory of natural selection is the doctrine of Malthus applied to the whole animal and vegetable kingdom. The argument of the theory of natural selection may be outlined as follows:

1. *Overproduction.*—Animals and plants tend to reproduce more offspring than can possibly grow to maturity.

2. *Struggle for Existence.*—Overproduction brings about a struggle for existence, which is largely a struggle for food.

3. *Variation and Heredity.*—Offspring of the same parents vary from each other and from the parents; and variations are inherited.

4. *Natural Selection or Survival of the Fittest.*—As a result of propositions 2 and 3, the fittest in each generation survive and, in consequence of the gradual accumulation of favorable variations growing out of a slow process of natural selection, a gradual change in species is brought about.

Overproduction.—That living things reproduce in a geometrical ratio is a self-evident fact that will be admitted by everyone. If an annual plant produced only two seeds—and there is no plant so unproductive as this—in 20 years there would be a million plants. There are numerous cases of a single fish producing millions of eggs in one year. Darwin pointed out that even the slow-breeding elephant, which, beginning at 30 years of age and ending at 90 brings forth 6 young on the average, would at the end of 740 to 750 years produce nearly 19,000,000 elephants. If human breeding were to continue unchecked for say 1,000 years, there would not be standing room on the earth for the progeny.

Struggle for Existence.—An important limiting factor controlling the total population of animals and plants from year to year is food. Doubtless other factors, difficult to evaluate, are also involved. However, since the food supply, under natural conditions, remains practically constant from year to year, a definite limit is set to the numbers of animals and plants that can be supported in a given area. Darwin, however, used the term struggle for existence in a larger sense to include such things as the dependence of one organism on another and the success in leaving offspring. In times of scarcity, two animals of the same species may be truly said to struggle with each other to get food and live. On the other hand, a plant on the edge of a desert struggles for life against dryness. Mistletoe is parasitic on certain trees and therefore dependent upon them, but cannot be said to struggle with the tree host, since too many parasites on the same tree would kill it. But two seedling mistletoes on the same branch may be said to struggle with each other. Since mistletoe seeds are disseminated by birds, the mistletoe plant is dependent on birds. The struggle for existence is a struggle against various factors of environment, including other organisms.

Survival of the Fittest.—Darwin believed that "variation is generally related to the conditions of life to which each species has been exposed during several successive generations," and "that changed conditions act in two ways, directly on the whole organization or on certain parts alone, and indirectly through the reproductive system." Variations, favorable or otherwise, are inherited. Darwin was uncertain as to what extent changed conditions or food, climate, etc., acted in a definite manner to produce variations, but he believed that "the effects have been greater than can be proved by clear evidence." Success in the struggle for existence over a period of time is heightened or diminished according to whether favorable or unfavorable characters are inherited. The fittest of each generation survive as a result of the inheritance of favorable variations.

Changes in environment alter the conditions determining fitness. Thus the food supply of a large area, while averaging constantly from year to year, may not be uniform throughout the entire area, with the result that animals in the pursuit of food migrate from famine zones to regions of plenty. Such immigration of a foreign species introduces a competitive factor for the native species that in extreme cases might cause its extinction, unless necessary readjustments in "fitness" were accomplished. As Darwin notes, "when a variation is of the slightest use to any being, we cannot tell how much to attribute to the accumulative action of natural selection and how much to the definite action of the conditions of life."

Geographic changes such as are known to have occurred in the past have been potent factors in modifying the struggle for existence and therefore the characters of the survivors. When islands are separated from continents, the problem of living becomes changed for those left on the island and may result in the development or preservation of unique characters. Thus the peculiar fauna of Australia is attributed to the fact that Australia was cut off from Asia at the beginning of Cenozoic times. In this case isolation fostered the preservation of egg-laying mammals comparable to those alive in times immediately preceeding the Cenozoic era. Such Australian mammals presumably failed to survive in other parts of the world because of inability to meet competition of more favorably endowed forms. Changes of consequence to the inhabitants occur when a continent is cut in two, or when two continents or smaller bodies of land become joined by an isthmus. The formation of mountain ranges by eruptions in the earth's surface results in barriers as effective as water for some animals and may bring in its wake changes in climate. When new conditions of living arise, animals must meet them or perish. Granted that the proper variations materialize at the proper time to enable living things to overcome new obstacles to existence, the fittest of each generation will in the course of time come to differ so much from the original stock as to be distinct species. Evolution results from the survival of the fittest which in turn results from the accumulation of favorable variations in each generation.

Variation.—Darwin's stand on the question of the inheritance of acquired characters was uncertain, but the acceptance of this principle is not vital to the theory of natural selection. Natural selection is the "preservation of favorable individual differences and variations, and the destruction of those which are injurious." Darwin offered no explanation for variability—variability is axiomatic. The minimum amount of variation between two human individuals is found in identical twins, which are twins that have developed from a single egg. Identical twins are of the same sex and show a striking correspondence in physical and mental traits. Fraternal twins, each of which develop from a single egg, may be as unlike as any brothers or sisters born at different times. Variation among individuals of the same species, developing from different eggs, is a fact many times verified.

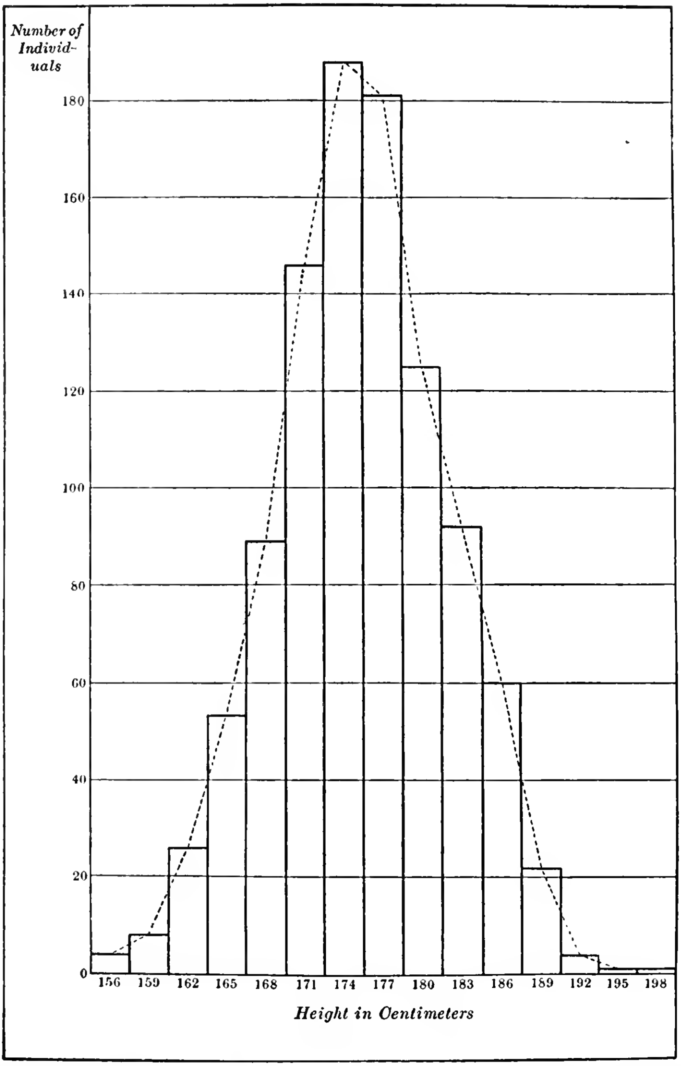


FIG. 181.—Frequency polygon and curve showing variation in height of 1,000 college students of ages 18 to 25. Modal class 174 centimeters; average height 175.33 centimeters. (*From Castle, Genetics and Eugenics, Harvard University Press. By permission.*)

Two general kinds of variations are recognized: (1) continuous or fluctuating or Darwinian variation, and (2) discontinuous or sport variation or mutation. Fluctuating variation may be illustrated by stature. If the individual heights of 1,000 college men are grouped into classes, and the results plotted on right-angled coordinates, a graph such as shown in Fig. 181 is obtained. A class contains all the individuals within certain limits of height. Thus the first class (from the left in the figure) contains all whose height is from 155 to 157 cm., the next class, those who measure from 158 to 160 cm., etc. The size or frequency of each class is measured in a vertical direction on the ordinate, and the value of each class is recorded on the horizontal base line or abscissa. The height class containing the largest number of individuals is the mode, in this case, class 174. The average height, 175.33 cm., is somewhat greater than the modal height, because, as compared to the modal height, there are more taller individuals than shorter. The curve produced by connecting the height polygons is a smooth curve showing gradations between classes. This is a general type of distribution found in fluctuating variations.

A discontinuous variation in stature would be one falling outside the normal limits of variation and not connected with the normal variation range by intermediate conditions. Thus, if the group measured had included individuals of, say, 150 or 210 cm. in height, their position in the group would be outside the limits of the range of the rest of the group, to which they would not be related or connected by intermediate groups.

Darwin attached more importance to fluctuating variation as the basis of evolution because he believed discontinuous variations occurred too rarely in nature to be of any considerable value in bringing about the origin of new species. To illustrate his interpretation of the action of natural selection, if we assume that the plus variations of any given character, *i.e.*, variations greater than the mode, tend to improve the equipment of an animal in the struggle for existence, there is a premium on "plus" characters which makes them more valuable than "minus" characters. If plus individuals reproduce more of their own kind and less of undesirable kinds, *i.e.*, if the variations are inherited, the minus variants would as a result of the struggle for existence tend to be reproduced in smaller and smaller numbers, so that the mode of the variation graph would in the course of time gradually shift in a plus direction (Fig. 182). Thus, through the partial or complete elimination of minus individuals in each generation, the variation of Graph 1, representing the original distribution of the character, would shift in a plus direction to position 2, position 2, then to 3, and finally to 4, which represents a variation range entirely beyond the upper limit of the original. The character would have undergone a complete change as a result of the natural selection of the more favorably endowed individuals in each generation.

If the same argument held for the sum total of the variable parts, there would result in later generations an entirely different sort of animal from the original one. According to Darwin,

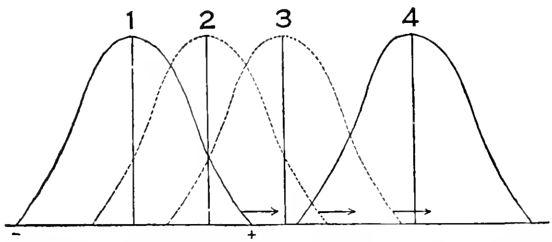


FIG. 182.—The hypothetical effect of selection on a single character.

the origin of a new species results from such a gradual accumulation of slight variations under the guidance of natural selection.

On the other hand, discontinuous variations, provided they are favorable, would hasten the process of change, since a discontinuous variation represents a greater difference from the mode than the most extreme fluctuating variation. Darwin understood this but refused to attach much importance to discontinuous variations as a basis for species change, because he believed they occurred too infrequently to be of selective value.

Darwin assumed that all variations are inherited, which of course simplified his explanation of the action of natural selection. It is now known that many fluctuating or continuous variations are not inherited and while this fact does not destroy Darwin's theory, it limits the action of natural selection to the role of an eliminating agent rather than that of a creative factor in the evolution of new species—natural selection determines whether or not a character shall survive after it has appeared; but the causes leading to its appearance are independent of natural selection. The work of De Vries has been important in establishing this point of view.

The Mutation Theory.—In 1886 Hugo de Vries, a Dutch botanist, found a number of evening primroses, *Oenothera lamarckiana*, growing wild in an abandoned potato patch at Hilversum, Holland. The peculiar feature about these plants was that in addition to the usual fluctuating variants there were some discontinuous variants which De Vries called mutations. On transplanting some of the typical *lamarckiana* plants to a garden where he could keep them under observation, he found that in the course of 7 generations, involving a total of some 50,000 plants, 5 or 6 different mutations, totaling about 800 plants, were produced from the parent stock (Table 2). Since

TABLE 2.—AN EIGHT-GENERATION PEDIGREE CULTURE OF LAMARCK'S EVENING PRIMROSE

Generation	Gigas	Albida	Oblonga	Rubrinervis	Lamarckiana	Nanella	Lata	Scintillans
1	..	..	..	..	9			
2	..	..	..	..	15,000	5	5	
3	..	..	..	1	10,000	3	3	
4	1	15	176	8	14,000	60	73	1
5	..	25	135	20	8,000	49	142	6
6	..	11	29	3	1,800	9	5	1
7	..	..	9	..	3,000	11		
8	..	5	1	..	1,700	21	1	

The giant mutant was obtained only once, but all the others, in at least three different generations, from lamarckiana parents. (*From Castle, "Genetics and Eugenics," Harvard University Press.*)

the characters of the mutations were markedly different from those of the typical *Oenothera lamarckiana* that produced them, and since the mutant characters were inherited, De Vries believed that he was witnessing the formation of new species at one single step.

De Vries was so impressed with the importance of mutation as the method of evolution that he discounted Darwin's view of the gradual accumulation of fluctuating variations under the guidance of natural selection in the building up of new species. De Vries believed that fluctuating variations are of no importance in this connection because they are not inherited. Mutations, according to De Vries, are due to changes of unknown cause in the germ plasm, the hereditary substance of the germ cells, while fluctuating or Darwinian variations are due to variations in the somatic cells caused by environmental conditions.

The work of De Vries gave great impetus to the search for mutations and their study in animals and plants. The sport variations of Darwin, which correspond to mutations, have been observed in many forms, though not in great abundance, nor under the conditions found in Oenothera. The mutations appearing spontaneously and also produced by radiation in Drosophila, black sheep in an otherwise white flock, albinos (individuals lacking pigment in the skin, hair, and eyes), hornless cattle, mule-footed pigs, six-fingered hands and six-toed feet in man, are all common examples of mutations. It has been established that these conditions are hereditary, which means that they are germinal rather than somatic in origin. Many mutations are abnormal in nature, but it is possible that some of the more favorable characters might have survival value and serve as a basis for species change. So far as Darwin's theory is concerned, the occurrence of mutations would hasten the process of evolution for the reason that mutation provides abrupt and quick changes in place of the slower changes resulting from the accumulation of smaller fluctuating variations.

It is rather curious that the mutations in Oenothera, discovered by De Vries and others since, differ in their origin from mutations in other forms. According to some investigators, *Oenothera lamarckiana* is not a pure stock but some sort of complex hybrid whose heterozygous character is shown from time to time by the production of so-called mutations. It cannot be an ordinary Mendelian hybrid because the mutations are not produced in Mendelian ratios. In some cases it has been shown that mutations breed true, not because they are true (new) species but because they are heterozygotes that do not produce viable homozygous offspring. In another case, that of *Oenothera gigas*, distinguished by its large size, the mutant condition is accompanied by a doubling of the chromosomes. Even though mutation may be an important factor in evolution, the mutations of the primrose cannot be regarded as incipient species, unless, as some maintain, hybridism plays a part in the evolution of species. Though mutations occur in many forms in the absence of any visible changes in the chromosomes, it is generally thought that mutations result from minute invisible changes in the chromosomes or genes.

Efficacy of Selection.—Selection, natural or artificial, of itself cannot bring about an enlargement of variability. In self-fertilized plants both egg and pollen gametes develop in the same parent individual. A parent individual, homozygous for all genetic factors, should presumably produce descendants in which the same genetic factors are reproduced. Johannsen found that when the progeny of single beans of a common self-fertilizable garden variety, of different weights, were raised, pure lines could be sorted out by selection (Fig. 183), each pure line varying about its own mode. A pure line was defined as "the descendants from a single homozygous organism exclusively propagating by self-fertilization." Selection within a pure line failed to shift the mode of the variation curve in either a plus or a minus direction. The only result of selection in the general population was the isolation of pure lines, which were beans of similar germinal constitution. The difference between pure lines rests upon a hereditary basis; the variations within pure lines upon non-heritable, environmental factors. Selection within a pure line failed to produce larger or smaller beans because such size differences were the result of environmental factors. New types of variants within a pure line can only be produced by mutation.

The term *phenotype,* first used by Johannsen, is now generally applied to a group of individuals having similar external features. A *genotype* includes individuals having the same germinal composition. Put in another way, the genotype refers to the fundamental genetic constitution of an organism, including all the genes; while the phenotype includes all of the characters appearing in the individual, regardless of genes, which though present, do not produce visible effects. The general population of beans, or the phenotype, is made up of a number of genotypes. In an ordinary monohybrid Mendelian cross involving a dominant and a recessive character, the 3:1 ratio of individuals in the F_2 is composed of two phenotypes, one showing the dominant trait and the other the recessive. The dominant individuals (comprising a single phenotype) consist of two genotypes, one homozygous and the other heterozygous. The recessives are homozygous and of the same genotype.

Tests of the pure-line idea by other workers seem to show that in the protozoan, *Difflugia*, selection within a pure line may be effective in increasing the number of spines on the shell, the number of teeth on the mouth of the shell, and the dimensions

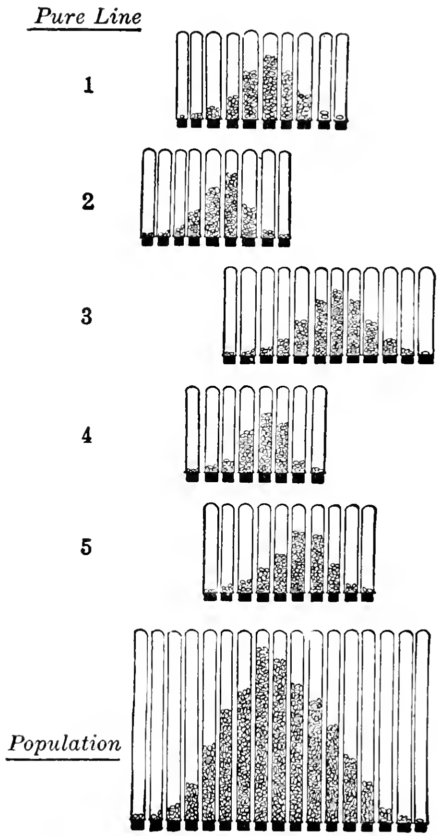


Fig. 183.—Diagram to illustrate five pure lines derived from a population of beans assorted according to weight. Tubes containing beans of the same weight are placed in the same vertical view. (*From Walter, Genetics, copyright, The Macmillan Company, after Johannsen. By permission.*)

of the shell as a whole. The differences in these results and those of Johannsen may be due to a difference in the organisms as to the frequency of variation. It would seem that if an organism is in a period of active mutation, selection of maximal individuals will extend the variation range at its maximal end. The outcome of selection, in any given case, all boils down to whether or not the organism is relatively quiescent or active in producing mutations.

Present Status of Darwin's Theory.—Darwin explained evolution by the gradual accumulation of small variations under the direction of natural selection. De Vries emphasized mutations because they were hereditary and also because they represented larger steps in evolution. For a while many geneticists favored the mutation idea and made use of mutations in the study of heredity. Now as a result of intensive study it has been learned that small mutations are more numerous than large ones, which in fact wipes out the distinction between continuous and discontinuous variation. If mutations occur in small steps as well as in large, we return once more to Darwin's view that the origin of species involves the accumulation of small heritable variations. It may be fairly said that on the whole the work of three-quarters of a century since the publication of Darwin's "Origin of Species" has tended to support and verify his theory of evolution by the natural selection of heritable characters. Natural selection offers the only scientific explanation of the coordinated adaptation detectable in living things.

CHAPTER XV

ADAPTATION

Every animal seems to be fitted at least moderately well to its environment. A certain amount of harmony, between the anatomical structure and functions of organisms and the environment, is evident to even the casual observer. The common grass frog, *Rana pipiens*, for example, possesses structural and functional features that can be understood if interpreted with reference to an amphibious habitat. Its well-developed hindlimbs, provided with webbed toes, and its shorter forelimbs enable it to move about in water or on land with equal facility. It has lungs with which it can obtain oxygen by breathing air; but in addition a considerable amount of oxygen can also be absorbed through the skin. It can remain for a long time under water. Its protective coloration renders it inconspicuous. The young develop from eggs laid in the water. The tadpoles upon hatching are capable of living entirely in water until sufficient time has elapsed for organs to develop to the point where the animals can live on land as well. The adults can survive a considerable range of temperatures. A frog may be frozen in a block of ice and, when the ice is thawed, resume its normal activities none the worse for the change. The frog is more or less specialized for the conditions under which it lives, but this specialization in turn imposes limitations. Thus a frog requires a moist environment. Because its skin cannot prevent a loss of water in a dry atmosphere, a frog left overnight in a warm dry room may be dead in the morning, its body shrunken to a fraction of its normal size.

There are various views about the origin and significance of adaptation. The old traditional view of adaptation, such as was held by Georges Cuvier (1769–1832), the greatest comparative anatomist of his time, looked upon adaptation as a universal property of living matter. The adaptive relation of organisms to environment is an expression of a plan of nature ruled by Providence. It is an *a priori* established harmony in living things and between them and their environment. It is the work of Providence whose foresight extends to every minute detail of creation. Cuvier actively combated all attempts to explain life as the result of evolutionary processes and this attitude is reflected in his conception of adaptation. Such a dogmatic view of life finds little support in scientific circles today.

Lamarck also believed in the reality of adaptation, but his interpretation was entirely different from Cuvier's. These men were contemporaries and on opposite sides on the question of evolution. Lamarck emphasized the importance of environment in shaping the development of adaptive features. To him the organism is plastic with reference to environmental influences, and is always responding to environmental stimuli, the stimulus and response gradually bringing about a state of adaptation in the organism. Environment induces needs, needs induce habits, and the use and disuse of organs play prominent parts in giving directions to adaptation. Useful organs improve with use, useless ones degenerate and finally disappear. According to Lamarck, adaptation is an *a posteriori* fact. Organs are created by function. Lamarck assumed further that the effects of use and disuse are inherited, the inheritance of acquired characters becoming the immediate cause of the evolution of new species from old. He offered no proof of the inheritance of acquired characters, *i.e.*, characters acquired by the organism as the result of special training, education, or experience directly due to environmental influences; and proof is still lacking, yet the idea that organisms are molded more or less by environmental factors is one that today is given serious consideration in the problem of adaptation and evolution. The main value of Lamarck's writings on this subject lies in calling attention to the probable importance of environment in developing adaptive conditions in the organism.

Charles Darwin, in building up his theory of evolution by natural selection, used variations as the basis of adaptation. Those individuals whose variations best fit them for the struggle for existence survive, the others perish. The survival of the fittest is the survival of the best adapted. Adaptation is recognized as a real condition. The adaptation begins as a chance variation, the environment determining whether or not the variation will survive. Darwin did not throw any light on the origin and source of variation. He accepted variations as facts and analyzed the manner in which they are continued or eliminated.

A more modern point of view (Cuenot) maintains that variations arise independently of any utilitarian value, but after their appearance they may or may not become useful. Organisms are *preadapted*. In the struggle for existence the new variations become useful if the bearer can find an "empty place" in nature where its new variations are of real service in the struggle for existence. The bearer of the new variations is fully adapted. There is no slow process of "fitting" into the new environment. In other words, the organism does not develop characters adapted to its environment, but chooses or finds an environment that is compatible with whatever equipment it has. The skin of the frog is adapted to a moist environment; but the nature of the skin also acts as an effective bar to living in a dry atmosphere. The nature of the skin makes it necessary for the frog to live in a moist environment.

Some deny that structure has any adaptive meaning. For example, most aquatic birds have webbed toes, but the moor hen (*Gallinula chloropus*), a bird of distinctly aquatic habits, has toes without webs. There are also some terrestrial birds with interdigital membranes. Many other cases might be cited in which well-developed structures seem to be without adaptive value. How can these apparent exceptions be reconciled to what appear to be adaptive structures in other forms? In biology as in other sciences no law has an absolute and uniform value. "The laws are the common resultant of a large set of particular facts not identical, but statistically compensatory" (Caullery). The webbed toes of aquatic birds occur in sufficient frequency to be of statistical value and are certainly correlated with aquatic life, regardless of exceptions. "It is not likely that pure chance had resulted in such a statistical uniformity of conformation."

What, then, is the relation of adaptation to environment? Lamarck's idea of direct effect of the environment lacks support and cannot be accepted in its original form. On the other hand, the environment does play a part in the development of certain characters in some animals. An often cited example is that of the European cave salamander, *Proteus anguinus*. Under natural conditions in the dark, the body is pale, but if kept in the light, the pigment appears. The basis for pigment formation is present in the skin, but it requires light for its development. In surface-dwelling salamanders, pigment develops in the skin even in the dark. Therefore, something in the skin of Proteus was lost as a result, presumably, of residence in caves. The eyes of Proteus under cave conditions develop to a certain stage, stop, and then degenerate. If Proteus is reared in an alternating combination of white and red light, the eyes develop almost to a normal state.

The American blind salamander, *Typhlotriton spelaeus*, spends its larval (tadpole) period near the mouths of caves and during this period has functional eyes. During metamorphosis (when the gills are lost and other changes take place) the animal migrates into caves and as a result, the eyelids become partially fused and the rods and cones, the sensory cells of the retina, degenerate completely. That the degenerative effect on the eyes is the result of cave life is indicated by the fact that the eyes fail to degenerate when the animals are raised in the light. In the case of both Proteus and Typhlotriton the reactions of the animals to external conditions must be due to the cumulative effect of cave life on the ancestors, induced by darkness. It does not seem to be a direct and gradual effect as Lamarck pictured it, but a complex and indirect effect involving the loss of factors that are necessary for the full development of the pigmentation of the skin and the complete development of the eyes in the absence of light.

It should be clear from what has been said that there is a difference of opinion as to the significance of adaptation. Assuming that structural adaptation is a fact and not an illusion, it is entirely reasonable to admit that in some cases preadaptation has played an important part in bringing about what are called adaptive relations in organisms; but it must also be admitted that environmental influences have also played a part in modifying preadapted structures and, in some cases at least, have been a potent influence in shaping the course of adaptation independently of a preadapted origin. That an interplay of internal protoplasmic factors and external environmental stimuli, though not clearly understood and difficult to demonstrate, should exist, is a logical conclusion; but to translate this interplay into terms of structural adaptation is another matter. It must be borne in mind that environment determines the conditions under which organisms live and that organisms must be adapted to these conditions.

An animal must be able to meet the conditions of environment at any given time and to meet new conditions when the environment changes. The alternative is extinction. Man is independent of his environment only to the extent that he can control it by profiting by experience, a faculty that has been slowly acquired. Adaptations center about certain activities which are common to all forms of animal life. These are:

1. Preservation of self, which consists in gaining sustenance from the environment and in the protection of self from destructive agents both animate and inanimate.

2. Preservation of race, which depends on each kind of organism reproducing its own kind in sufficient numbers to assure the continued existence of the race.

The examples of adaption discussed in the following paragraphs have been chosen largely because of their obviously adaptive nature. They illustrate states of fitness of a structure or function for the accomplishment of certain ends. All of them center in the two main activities of animals: self-preservation and race preservation.

Weapons.—Structures, such as claws, teeth, horns, etc., are familiar examples of weapons, some of which may be used in capturing food. An unusual weapon of highly specialized type is the sting of the honeybee, *Apis mellifica*. The sting, located in the sting chamber at the tip of the abdomen, consists of right and left basal arms which curve toward each other in the mid-line and then continue as a pair of lancets or darts, each of which is barbed near the end (Fig. 184). The sheath, lying above the darts also consists of two arms, paralleling the course of the arms of the darts. The two arms of the sheath meet in the mid-line to form a median bulb, beyond which the sheath tapers to form a slender shaft. The sheath is hollowed on the side next to the darts, the channel between the sheath and the darts thus forming a poison canal, which in the region of the bulb expands into a large cavity. The darts can be moved separately or together along the lateral edges of the sheath. A large poison sac opens into the enlarged region of the sheath. Arising from the free end of the sac is a narrow tubular gland, which consists of two highly coiled branches. The liquid produced by this gland is principally formic acid, and the gland is known as the acid gland. In addition there is an alkaline gland opening into the base of the sac. The secretions produced by these two types of glands form the "poison" of the bee's sting. The two substances are mixed in the bulb at the base of the sting and, when the sting is used, are forced through the channel formed by the shaft of the sheath and the two darts, by a pump located within the bulb. The darts are moved along the edges of the sheath by the contraction of abdominal muscles.

The damage to a victim of a bee's sting is caused by the action of the poisonous fluid injected into the wound. The effect of this poison on insects like houseflies and blowflies is fatal; on man it produces a very painful result. There is some question as to which of the constituents of the poison sac is the effective toxic agent. If the sting remains in the wound, the poison sac and the adjacent organs in the tip of the bee's abdomen are torn out with the sting and the bee loses its life. The adaptive value of the sting might be questioned, since its use frequently causes the death of the user; but this objection disappears when one understands that the activities of the members of the colony of bees center about the welfare of the colony rather than the individual. The honeybee is a social insect, and the protective adaptations in such organizations are directed toward safeguarding the social unit, the colony, rather than the individual. In such a colony, worker bees, which are abortive females, and the queen, the sexually active female, have stings. The drones or males have no stings. The workers use the sting indiscriminately on enemies of all kinds; the queen reserves her sting for use on other queens.

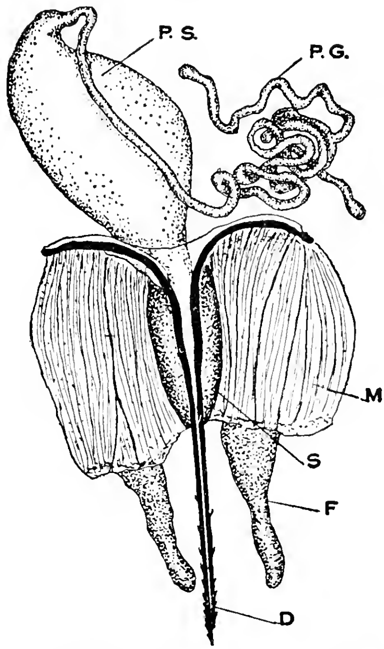


FIG. 184.—Sting of the honeybee, *Apis mellifica*, dissected. D, serrated darts; F, feelers provided with tactile sense organs; M, muscles, attached at the lower edge to the body wall, whose contractions force the darts into the wound; P.S., poison sac with a duct leading to the darts; P.G., poison gland; S, sheath into which the darts can be withdrawn. Alkaline gland not shown.

The queen's sting is larger than that of the worker, with fewer and smaller barbs on the darts. The poison sac is large.

It is well established that the sting of the honeybee is a modified ovipositor and is an example of a complete change in function of an organ. An ovipositor is a structure developed at the end of the abdomen of the female of many insects. It is used for making holes in leaves or in stems, in which the eggs are laid. Grasshoppers make holes in the ground for the eggs. Among the *Hymenoptera*, the group to which the honeybee belongs, it is only forms like bees and wasps that are provided with stings. The females of other Hymenoptera have ovipositors which closely resemble those of such insects as the katydids, crickets, cicadas, and the grasshoppers. Figure 185 shows the ovipositor of a common grasshopper. Since the queen honeybee deposits her eggs in wax cells prepared by the worker, it can be understood why the ovipositor should no longer function as such. That it develops into a piercing organ is in keeping with the fact that the parasitic Hymenoptera use the ovipositor to insert eggs into the bodies, eggs, or nests of other insects. The absence of a sting in drones is understandable since the forerunner of the sting was primarily a female organ.

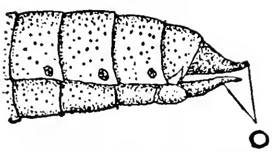


Fig. 185.—Abdomen of the grasshopper showing the ovipositor, o.

The fangs of a rattlesnake are another example of a weapon, quite different from the sting of the bee in structure and development and yet functionally of the same general significance. The timber rattlesnake, *Crotalus horridus*, is provided with a pair of erectile fangs surrounded by a fleshy sheath and located in the front of the upper jaw. Each fang is hinged at its base to the maxillary portion of the jaw, so that it can be folded back into the sheath when the mouth is closed. The fang is a hollow tooth, the channel extending from the base of the tooth to a point near the sharp end. At the base of the tooth, the channel connects with the duct of a poison gland, located at the side of the upper jaw (Fig. 186). In striking, the fangs are buried in the victim and the poison is injected into the wound. A rattlesnake does not always coil and rattle before it strikes, although the power of the blow is undoubtedly increased when delivered from the coiled position. The poison of the timber rattlesnake is highly potent and kills a small animal in a few minutes. It may also cause the death of a human being. Rattlesnakes are not immune to their own poison. In captivity they sometimes bite themselves and die as a result. On the other hand, the rattlesnake suffers no ill effects from eating prey killed by its venom. The rattle consists of a series of cornified shells on the end of the tail which produce a shrill note when vibrated. This "warning signal" is a protective adaptation for the snake, since its use in most cases serves to keep its enemies at a distance. The rattle itself is harmless and receives an additional segment after each molt. Since molting occurs at irregular intervals the number of rattles is not an exact indication of the snake's age.

The skin secretion of some amphibians is highly poisonous in nature. Various species of *Bufo* (toads), which are otherwise defenseless, produce in their skin highly toxic substances, which render them inedible. One of these substances is *bufotalin,* which has the formula $C_{34}H_{46}O_{10}$. Another is *bufogin,* $C_{18}H_{24}O_4$. Both these substances when tested on experimental animals have an action similar to digitalis. They stimulate the heart muscle, eventually stopping its action. The secretions of the *parotoid glands* of the skin in the region of the ear and the side of the body have been found to contain adrenalin, which in other animals is a secretion of the adrenal gland. The secretions of a tropical toad, *Dendrobates,* is said to be used by the Indians of Colombia as a source of poison for their arrows.

The electric organ of certain fishes is a rather remarkable example of an organ that is capable of producing an electric current, which in the case of the electric skate, *Torpedo,* or the electric eel, *Gymnotes,* is great enough to be considered of value as a means of protection. The electric organ is built on the general principle of a voltaic pile. A voltaic pile consists of a column of alternating disks of dissimilar metals, such as copper and zinc, separated by pieces of cloth or paper moistened with dilute acid. When the top and bottom disks, or any two neighboring disks, are connected by a wire, an electric current flows from the zinc disk to the copper disk. In *Torpedo marmorata,* a Mediterannean skate, the electric organ consists of rows of *electroplaxes* (Fig. 187) forming a considerable mass of tissue on either side of the head. Each electroplax consists of an inner striated layer covered above and below by a gelatinous layer.

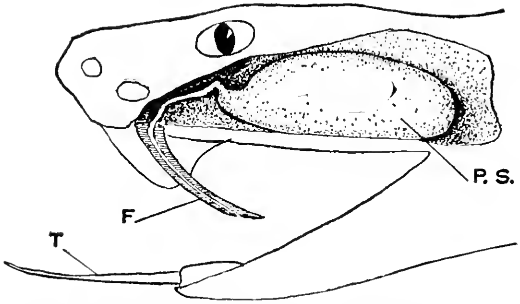


FIG. 186.—Head of the rattlesnake, based on a dissection to show the poison apparatus. F, hollow fang, shown in vertical section, is hinged above to the maxillary bone of the skull, so that it can be folded back when the mouth is closed; P.S., poison sac, a modified salivary gland, whose duct conveys the secretion to the fang; T, tongue, which is harmless and serves principally as a tactile sense organ. As in the bee, the damage or injury is caused by the highly toxic venom injected into the wound.

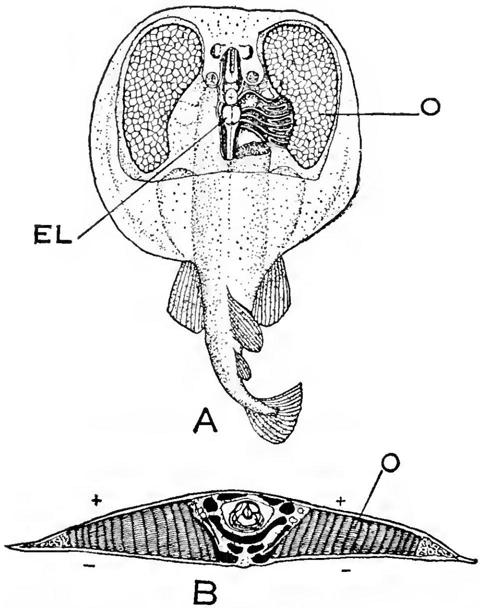


FIG. 187.—Electric organs of *Torpedo marmorata*. A, dorsal view of entire animal, the upper surface being partially dissected away to show the electric organs, O, and the brain with its electric lobes, EL, from which nerves pass to the electric organs. B, Transverse section through the entire body at the level of the electric lobes of the brain, showing the electric organs composed of flat disks, electroplaxes, arranged in vertical columns. The polarity of the current generated in the organ is indicated by plus and minus signs. (*Redrawn from Dahlgren, Carnegie Inst. Pub., after Fritsch.*)

Nerves are distributed principally to the upper layer. The electroplax, which represents the electric unit in the organ, seems to be modified striated muscle tissue. The discharge is brought about by nervous stimulation, the quantity of the discharge varying with the size of the organ and its state of fatigue. If a small Torpedo is grasped by the thumb and fingers in the upper and lower surface of the body, respectively, a slight pressure brings forth a distinct shock, which produces a tingling sensation in the hand. Electric organs are relatively rare among animals. If the electroplax be regarded as a modified muscle fiber, the relationship between the nervous stimulation and the electrical discharge can be understood when it is remembered that the contraction of a muscle occurs through nervous stimulation and that the contraction is accompanied by minute electrical discharges. In the case of the electroplax, the conditions seem to be reversed to the extent that the major result of nervous stimulation is the production of an electric current rather than motion. The outstanding features of the electric organ can thus be explained as the result of a change in the functional response of what in other animals is a contractile tissue.

Protective Coloration.—A general harmony in the coloration of an animal and its surroundings is a common condition in many animals. The coloration of the animal is rarely an exact duplication of a part of its natural surroundings; often it is merely a neutral tint which blends with the surroundings when the animal is at rest. Thus the fur of the rabbit, *Sylvilagus floridanus*, is a shade of gray which makes the animal inconspicuous against almost any natural background. This same color tone is often found in many small and some large fur-bearing animals. In other cases there is a closer correspondence between the coloration of the animal and its surroundings. Among amphibians for example, tree frogs, such as *Hyla andersonii*, which are found in leafy trees, are bright green. *Hyla arenicolor*, another species, is found on rocks and is gray. *Rana pipiens*, the grass frog, is greenish in color with spots and stripes which adapt it to a meadow environment. The value of interpretation of coloration comes into question when forms with conspicuous color patterns are found living side by side with inconspicuous forms. Thus *Ambystoma maculatum*, a common salamander which has a black body with brilliant yellow spots, lives in the same habitat with

A. jeffersonianum which lacks the spots. If one adopts the view that in the case of Hyla the green color is protective, one must also admit that in other cases the coloration is of no particular protective significance. That does not necessarily destroy the value of protective coloration to some animals.

Arctic mammals such as the polar bear, *Thalarctos maritimus*, and some other arctic mammals, are white in conformity with the general character of the background. Green-colored birds abound in the tropics but are rare elsewhere. The flounder, *Rhomboidichthys podas*, a bottom-feeding fish, is white underneath and mottled above. The color pattern of the upper surface can be changed to harmonize with the sea bottom to such an extent as to render the fish practically invisible from above. Some remarkable examples of protective coloration are the seasonal variations such as are found in the ptarmigan, *Lagopus lagopus*, the otter, *Lutra canadensis*, the northern fox, *Alopex lagopus*, and the varying hare, *Lepus americanus*, whose color in each case is white in winter and varying shades of brown, or gray during the rest of the year.

Among birds, as a rule the male has far more gorgeous and more conspicuous plumage than the female. The plumage of the male may not have any special significance, but the role of the inconspicuous coloration of the female as a protective adaptation during the breeding season seems evident. The young of either sex are protectively colored to an equal degree until sexual maturity when the characteristic adult types of plumage develop. The immediate cause of the two types is an internal secretion produced by the ovary in the female and by the testes in the male. The effect of this secretion in the plumage of the female is the production of a protective type of plumage; in the male the testicular substance seems to produce a result without adaptive meaning.

Mimicry.—The protective value of coloration is greatly enhanced when the animal possesses in addition a bodily structure bearing a close resemblance to surrounding objects. Such a combination of color and structural resemblances is called mimicry, of which the best examples are found among insects. The dead-leaf butterfly, *Kallima inachis*, an Asiatic species, when at rest with the wings brought together in a vertical plane over its body, looks remarkably like a dead leaf not only because of the brown color of the underside of its wings but also for the even more striking reproduction there of minute details of leaf structure in the form of stalk, mid-rib, and veins. Even worm holes are present. The gaudy color of the upper side of the wings is also significant. Rendered conspicuous by these colors during flight, the insect practically drops out of the field of vision when it alights and changes into a dead leaf (Fig. 188). Similarly, *Phyllium*, the green-leaf insect of South America, is pro-

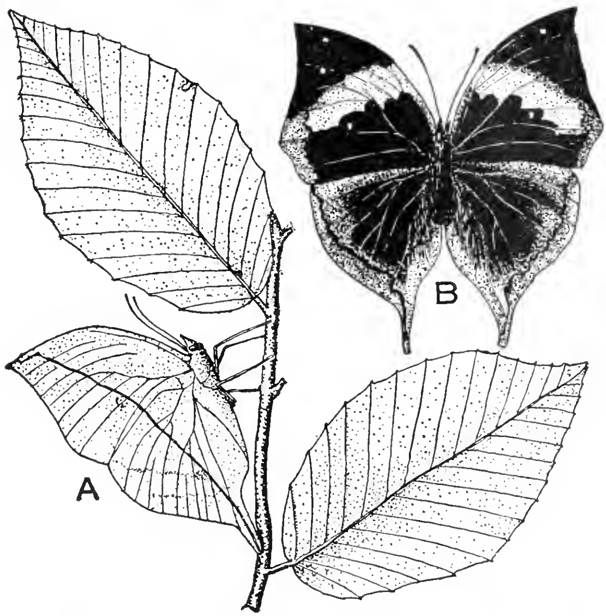


Fig. 188.—*Kallima inachis*, the Indian leaf butterfly. *A*, at rest with its wings folded; B, with the wings spread.

tected by a broad leaflike body and a bright-green color (Fig. 189). The common American insect, *Diapheromera femorata*, the walking stick, gets its name from its resemblance to a branched twig, its long greenish-gray body and slender legs making it almost indistinguishable from the plant structure (Fig. 190). Mimicry sometimes is found between two animals, a harmless or defenseless one deriving a certain advantage from its resemblance to a noxious one. Bees and wasps which have dangerous weapons in the form of stings are mimicked by a whole host of harmless flies and moths.

A very common example of this type of mimicry is the case of the resemblance of the viceroy butterfly, *Basilarchia archippus*, to the monarch butterfly, *Danaus menippe* (Fig. 191). Both are rather large butterflies of a warm-brown color, with black lines.

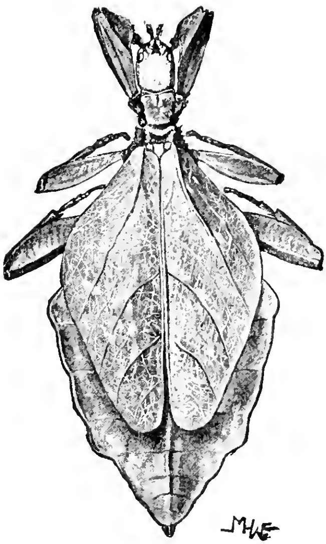


Fig. 189.

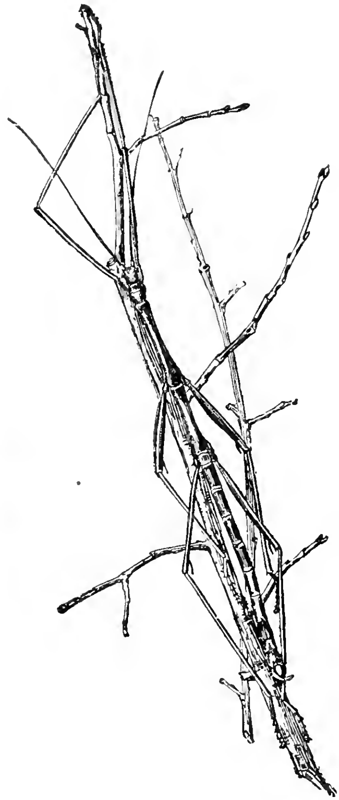


Fig. 190.

Fig. 189.—*Phyllium*, the green-leaf insect, a South American form. (*From Jordan and Kellogg, Evolution and Animal Life, D. Appleton-Century Company. By permission.*)

Fig. 190.—The walking stick, *Diapheromera*, on a twig. (*From Jordan and Kellogg, Evolution and Animal Life, D. Appleton-Century Company. By permission.*)

The monarch butterfly is distasteful to birds, and therefore escapes, to a certain extent, from being eaten by birds. The viceroy, on the other hand, is edible but is in all probability frequently unmolested because of its resemblance to the inedible monarch. In these and other cases of mimicry the condition is not to be regarded as a conscious act on the part of the imitator. The steps by which the resemblance has been brought about are unknown, but their history is doubtless similar to that of other adaptations.

Warning Adaptations.—Many animals provided with stings, poison glands, or other effective means of defense, such as inedi-

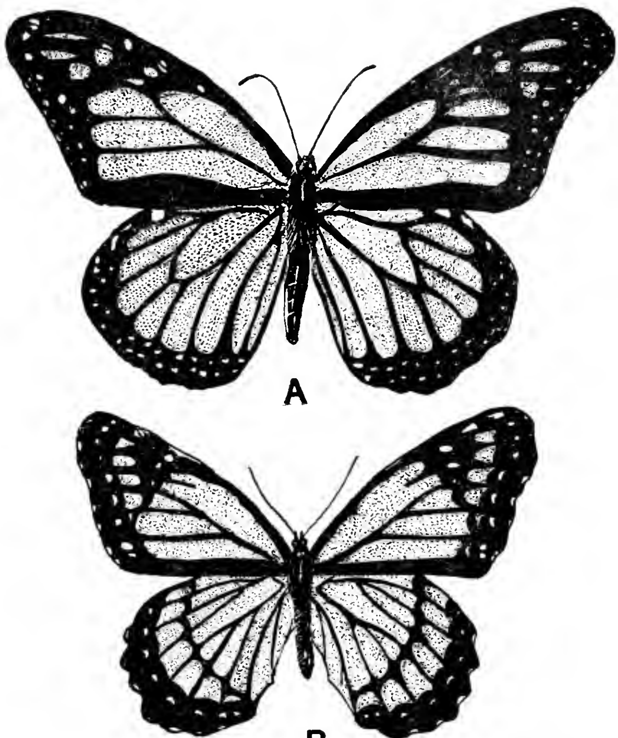


Fig. 191.—Mimicry. A, the monarch butterfly, *Danaus menippe;* B, the viceroy butterfly, *Basilarchia archippus.*

bility, are often conspicuously marked by what is known as warning coloration. The orange- and black-banded coloration of hornets and wasps are examples of this. Some brightly colored caterpillars are avoided by birds because they are distasteful. The distinctive black and white of the fur of the skunk is associated, in the minds of the experienced, with its powerful scent glands. Poisonous amphibians and snakes are sometimes gaudily colored or distinctively marked, but not always. *Den-*

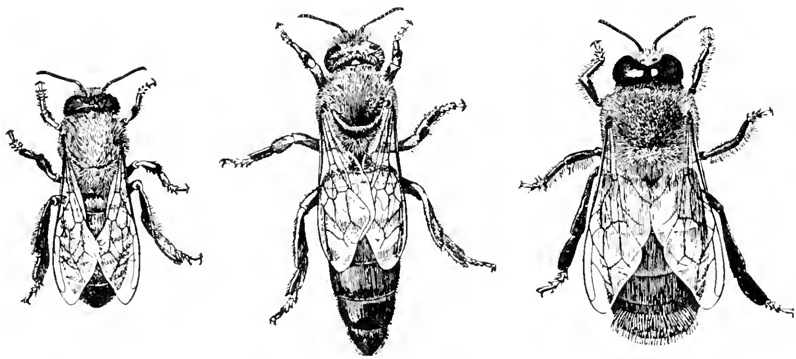
drobates, the tropical toad whose secretions are used for arrow poison, is bright green or pink, spotted with a dark color. On the other hand, one of the most poisonous toads, *Bufo marinus*, found widely distributed in the American tropics is drab-colored. The rattlesnake, whose color pattern is well defined but not particularly conspicuous, is provided with a warning mechanism in the shape of its rattle. The copperhead snake, *Agkistrodon mokasen*, colored an inconspicuous yellowish brown, is also poisonous but lacks a rattle. It would seem to be entirely lacking in any sort of warning adaptation.

Warning adaptations may or may not be present in animals that are provided with some noxious means of defense. Where present, warning adaptations are to be regarded as primarily for the protection and benefit of the possessor rather than its enemies. While it is true of course that the lack of a warning rattle makes the copperhead snake in some ways more dangerous to man than the rattlesnake, a harmful animal is benefited by announcing its presence, because it may thereby be relieved of the necessity of risking battle. One or two experiments probably teach a bird to avoid unpalatable insects, with the result that the latter as a whole are benefited, though some are killed. This interpretation is supported by experiments showing that hungry animals discriminate between palatable caterpillars and other varieties.

Signals.—It is thought that signals may play a part in the protective mechanism of some animals, though there is considerable difference of opinion among biologists on this point. The American antelope, *Antilocarpa americana*, an inhabitant of open country in Western North America, has white hairs on the rump which when spread flash a signal. The "cottontail" of the rabbit *Sylvilagus floridanus*, which is so conspicuous when the animal is running, is supposed by some to serve as a beacon for the young to enable them to follow the parent in escaping from danger.

Feint.—Some animals, particularly insects and spiders, when touched or held in the hand, become motionless. The death-feigning posture is held for a short time and then the animal resumes its usual activity. Several species of toads when suddenly disturbed respond by bending back the head and twisting both pairs of legs over the back of the body, leaving the animal resting on its belly on the ground. In this position the animal remains completely quiet, the deathlike immobility being heightened by the closing of the eyes and a slowing down of respiratory movements. The newly hatched young of the common tern, *Sterna hirundo hirundo,* can be handled without exciting fear, but later when about a third grown and not yet able to fly, the same birds will feign death by lying perfectly quiet in the grass when one approaches them. If a bird is picked up, it maintains its lifeless attitude even when feathers are pulled out. Its patient indifference to such treatment does not last long, however, and comes to an end abruptly, with the bird struggling frantically to escape. This death feint is not shown by terns after they have learned to fly. Feigning a broken wing or lameness is a device employed by a number of ground-nesting birds during the breeding season to direct the attention of intruders away from the young or the nest. The tactics of the opossum, *Didelphis virginiana,* in shamming death when uncovered in its nest is an example of the same general sort of behaviorism that is displayed by a number of other smaller mammals. Feigning death or injury is widespread in different groups of animals. The tonic immobility produced in many animals may merely be the result of fear and have no especial adaptive significance. They may be "scared stiff." If the temporary immobility aids in concealing the animal, as in the case of young terns, there results a certain benefit which may be considered adaptive. The simulation of bodily injury by adult birds would certainly seem to be directed toward protecting the young.

Animal Associations.—Certain kinds of animals are ordinarily found in groups of individuals. Such animals are gregarious—they live in flocks or herds. The horse, antelope, elk, buffalo, elephant, etc., illustrate this mode of existence. The herd is made up of individuals of the same species. The leader of the herd, in the case of horses, is a male and the same is true of other groups. In the buffalo (bison) herd the leader is a female. Sometimes two or more species are associated as in the presence of flocks of white herons with elephants, or of the ostrich with the zebra and gnu. All domestic animals except the cat are gregarious in habit. Herding in mammals is confined almost entirely to herbivorous forms. Such animals subsist on plant food and require a relatively large amount which must be gathered from more or less open country. The usual natural defenses of such animals are speed and kicking ability, to which herding has come to be an additional measure of protection. Carnivorous animals such as the wolf occasionally hunt in packs, but the pack is seldom large and its organization is purely temporary in character. Wolves hunt in packs only when food is scarce. The members of the pack are competing against each other to obtain food. In a herd of antelope the benefit of association comes from the increase in power to sense danger. Instead of depending on one set of sense organs each member of the herd receives the benefit



Worker Queen Drone
FIG. 192.—Honeybee. × 2. (*From Phillips, U. S. Dept. Agr. Farmers' Bulletin 447.*)

of the sense organs of every other member in perceiving danger. Escape depends upon individual effort. In some cases of gregarious animals, however, the herd acts as a unit in defending its members. A herd of musk oxen held at bay by dogs forms a circle, with the calves in the center, the adults having their heads toward the outside. The protective value of herding in such cases consists in multiplying the individual weapons of defense by the number in the herd.

Communalism.—In herding, all members of the group are alike except for differences in sex. By communalism is meant a social condition in which a species of animals lives in a group of a permanent character, distinguished by a marked division of labor among the members, and often accompanied by a physical differentiation of the members. Such forms of social organization have reached the highest degree of perfection among the social insects, such as the honeybee and the ant.

A honeybee colony can be understood by regarding it as a *compound organism*, in which the various and specialized activities of the individual members are to be interpreted in terms of the colony as a unit. A colony normally consists of a single queen bee, the mother of the colony, thousands of sexually undeveloped females, called workers, and, during part of the year, some hundreds of drones or males. The queen alone is capable of laying eggs. The workers, though genetically females, have no part in reproduction. They build the wax comb, gather food, keep the hive clean, feed the young, ventilate the hive—in short take care of the entire colony. The function of the drone is to inseminate the queen, a single insemination providing the queen with sufficient spermatozoa to last her lifetime. These three forms differ in size and structure (Fig. 192), the worker being the smallest of the three. Under natural conditions, the colony inhabits a hollow tree or similar cavity, but it thrives equally well in an artificial hive. The comb of the hive is formed of wax secreted by the workers. It is slab-shaped and consists of a double layer of tubular cells, hexagonal in cross section and open at their outer ends (Fig. 193). The cells of the two sides of the comb are separated by a septum running through the center of the comb parallel to its two faces. The cells are pitched at a slight angle, the bottom of the cell being slightly lower than the opening. They serve as brood chambers for developing bees and as storage places for pollen and honey. Those used for rearing workers are about $\frac{1}{5}$ in. in width, and those for rearing drones and storing honey measure about $\frac{1}{4}$ in. across. These make up the majority of the cells. At certain times, the worker bees enlarge some worker cells for rearing queens (Fig. 194).

With the coming of warm weather in the spring, the queen begins to lay eggs in the worker cells, one egg to a cell. The eggs develop into white grubs or larvae which are fed by the workers. At the end of the larval period the grub completely fills the cell, which is then capped by the workers. During the quiescent stage that follows the larva is gradually transformed into a pupa and then into an imago, or adult stage, after which it emerges as a worker bee. The first activities of the workers are inside the hive where they engage in secreting wax, caring for the new brood of young (developing in the meantime from eggs laid by the queen) and in cleaning the hive. Later they join the outside

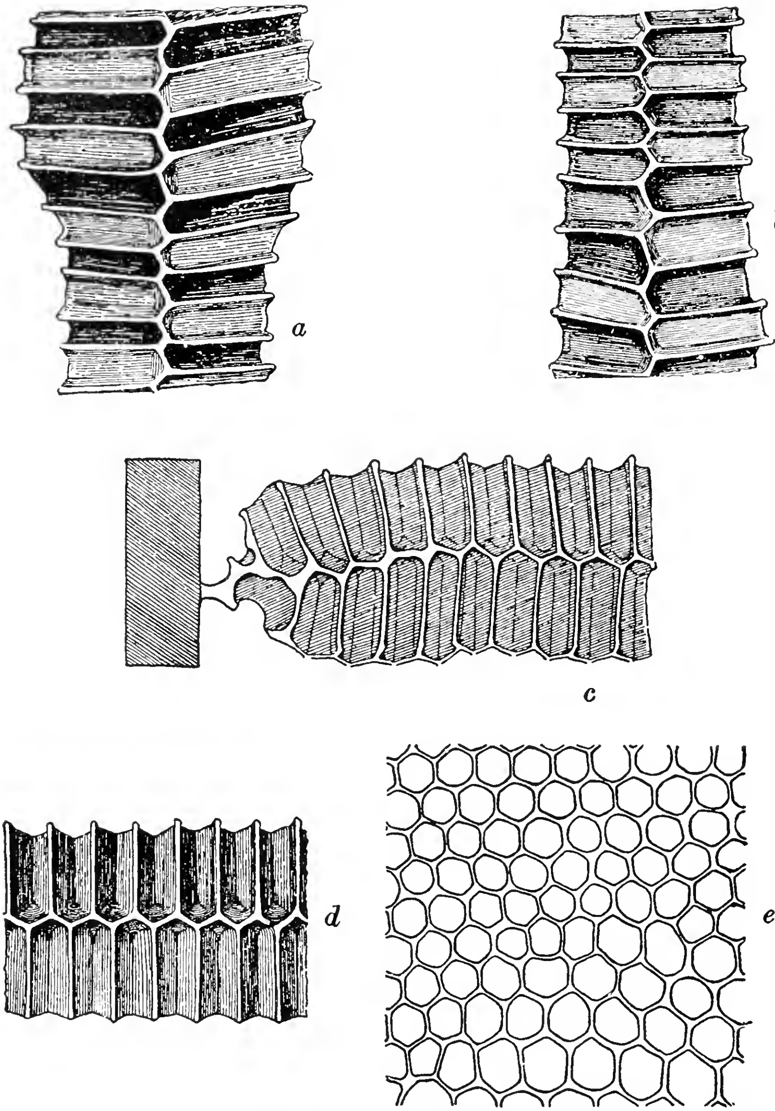


Fig. 193.—Structure of the comb of the honeybee, *Apis mellifica*. *a*, vertical section at top of comb; *b*, vertical section showing transition from worker to drone cells; *c*, horizontal section at side of comb showing end bar of frame; *d*, horizontal section of worker brood cells; *e*, diagram showing transition cells. Natural size. (*From Phillips, U. S. Dept. Agr., Farmers' Bulletin* 447.)

force in collecting food. The varied activities of the workers under normal conditions follow each other in a regular sequence. This process goes on until the hive is nearly full of bees and stored food, when the queen begins to lay eggs in the drone cells prepared by the workers. Several hundred drones develop from these eggs. The queen then lays eggs in four or five specially prepared queen cells. The royal larvae are provided with food composed of a rich mixture of digested honey and pollen mixed with glandular secretions. When the queen larvae have com-

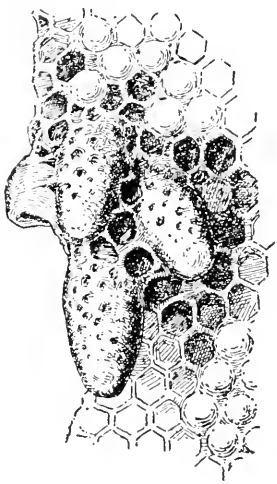


Fig. 194.

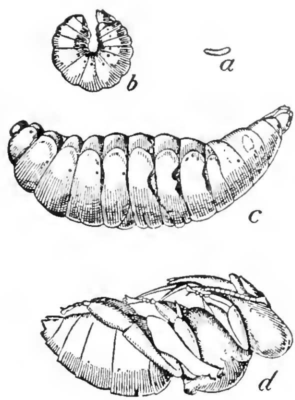


Fig. 195.

Fig. 194.—Queen cells. Natural size.

Fig. 195.—Stages in the development of the honeybee. *a*, egg; *b*. young larva; *c*, old larva; *d*, pupa. × 3. (*From Phillips, U. S. Dept. Agr., Farmers' Bulletin* 447.)

pleted their development, the queen cells are capped and the colony is now ready for swarming (Fig. 195).

The first swarm from the colony consists of the original queen and hundreds of workers which pour out of the hive and fly away in a dense mass and finally settle down in a new location. What ordinarily happens at this time under artificial conditions is that the beekeeper gathers the swarm and places it in a prepared hive. Under these conditions, the bees start in and gradually build up the conditions of a typical hive.

Meanwhile in the old hive, from which the swarming took place, activity goes on as usual until a queen emerges from one of the queen cells. If the colony is not too populous, the first queen to emerge tears down the other queen cells and kills the developing queens. If a second swarm is imminent, the workers see to it that the other queen cells are protected. In about a week after emerging, the first queen flies from the hive and mates with one of the drones in the air. Mating usually occurs but once, after which the mating drone dies. The mated queen returns to the hive and after about two days starts laying eggs, repeating the routine of her predecessor. The spermatozoa received from the drone are stored in the spermatheca, which is a small sac opening into the oviduct. As the eggs pass the opening of the spermatheca, spermatozoa may be released or not. Fertilized eggs, those which have been penetrated by spermatozoa, develop either into workers or queens depending upon the kind of food given during the larval period. If a virgin queen is lost on her flight, or if the colony for any reason becomes queenless, it may happen that a worker will start to lay eggs, though normally workers do not lay eggs. Such eggs develop into drones, just as the unfertilized eggs laid by the queen do under normal conditions. Queens that have exhausted their supply of spermatozoa lay only drone eggs. The average number of eggs laid daily during the breeding season by a single queen is about 900. The maximum on any single day may reach 2,000.

Life in a colony of honeybees is ordered along rather definite lines. The function of the queen is to lay eggs, of the drones to produce spermatozoa for fertilizing the eggs, while to the workers falls the burden of caring for the entire colony, including the rearing of the young and the building and guarding of the nest. If the colony as a whole be compared with an organism in the ordinary sense, the queen and drones represent the germ cells of the organism, and the workers the somatic or body cells, which carry on the routine metabolic activities of the body.

The length of life of the queen is bound up with her ability to lay eggs for the reason that when she stops laying she is superseded by a young queen reared by the workers. The queen lives on the average from three to four years. Drones make their appearance in a hive after a considerable number of workers have been produced and conditions become crowded. Drones begin to fly about a week after emerging. The drone mating with a young queen in the nuptial flight dies after copulation. Other drones may return to the hive with the queen and remain there. Drones may be present in a colony up to the end of the honey flow, after which they are carried off by the workers to some distance from the hive, 100 ft. or more, and left to die. The life of a drone thus extends over a variable number of weeks. The life of the worker is determined by the amount of work it does. When food is abundant, it is actively employed in collecting it and under these conditions lives for about six weeks. With less work the life span is lengthened. The bees which survive the winter are those which emerged in the early autumn. In their case the length of life extends over several months.

There are also many varieties of such colonial organization among ants, such as *Atta*, a genus of leaf-cutting ants found in tropical America. A typical colony is made up of a queen, some drones, and numerous sterile females, which in this group are found in three types, known as the *maxims*, *mediums*, and *minims*. As in the case of the honeybee, the function of the queen is to lay eggs, the drones to supply spermatozoa for fertilizing the eggs, and of the workers to rear the young and to provide for the colony generally. The maxims are large in size and have powerful biting jaws with which they defend the nest. The mediums are smaller and their duties are largely domestic. They bring into the nest small pieces bitten out of a leaf which are handed over to other mediums who thoroughly chew the leaf tissue. The triturated tissue is then taken over by the minims who form it into balls on which a certain fungus (*Rozites gongylophora*) is cultivated. The fungus is used as food by the entire colony.

Commensalism.—Commensal animals, literally, are those that eat at the same table. In biology, commensalism refers to an association between two different species of animals partaking of the same food. The benefit of such an association in many known cases seems to be one-sided rather than mutual. A common example of commensalism is found in the association of suckfishes, members of the genus *Remora*, and sharks. The suckfish has a slender body about 18 in. in length, provided with a peculiar sucking disk on the top of the head, by means of which it attaches itself to the side of the shark's body (Fig. 196). The shark carries the suckfish about and apparently suffers no harm from its passenger; but neither does it benefit. The suckfish, on the other hand, probably picks up scraps of the shark's food. It will leave the shark to seize a baited hook and is frequently caught in that manner. All the benefit of the association seems to be in favor of the suckfish. *Sycotypus canaliculatus* is a large, marine, gasteropod mollusc, common on the New England coast. In the respiratory chamber of this animal one frequently finds one or more flatworms, *Planocera inquilina*, about ½ in. in length. They can be readily picked off the surface of the respiratory chamber and so far as is known cause no injury to the host. The benefit is again one-sided and in favor of the flatworm, which gains food and shelter by the association and gives nothing in return. Commensal associations occur frequently and may represent a step toward a parasitic association,

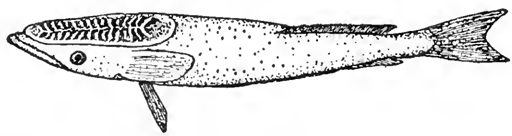


Fig. 196.—*Remora*, the suckfish. The dorsal fin is modified into a sucking disk by which the fish attaches itself to a shark. (*After Jordan and Kellogg.*)

in which the host definitely pays for the entertainment of the guest.

Symbiosis.—The living together of two different kinds of organisms may develop to the point where the union becomes very close without either suffering harm from the presence of the other. This is known as symbiosis. Usually there is a mutual benefit from the association. The hermit crab, *Eupagurus*, is always found inhabiting an empty gasteropod shell, its abdomen having become modified and slightly crowded to conform with the spiral passage of the shell. In feeding or walking, only the head and thorax protrude from the mouth of the shell. It can retract into the shell and block the opening with an enlarged claw (Fig. 197). When the shell becomes too small, the crab seeks a larger one, sometimes killing and removing the original inhabitant. In some species the surface of the shell is covered with sea anemones or hydroid polyps which serve to conceal the crab and also to protect it from fishes, because the polyps are armed with stinging cells that make them unpalatable. When the crab feeds, the polyp shares the food, capturing fragments as they float upward or bending over the edge of the shell to reach them. Evidently each animal benefits by the association. If the polyps are removed from the shell, the crab makes an effort to replace them, showing that the association between the crab and the polyp is by no means an accidental one. This tendency for disguisement is shown by other species of crabs. The spider crab, *Libinia emarginata,* is often provided with a covering of sea weed, sponges, hydroids, etc. Kept in aquaria, spider crabs have been observed to tear off bits of sea weed with their claws and fasten them on their backs among the stiff hairs which

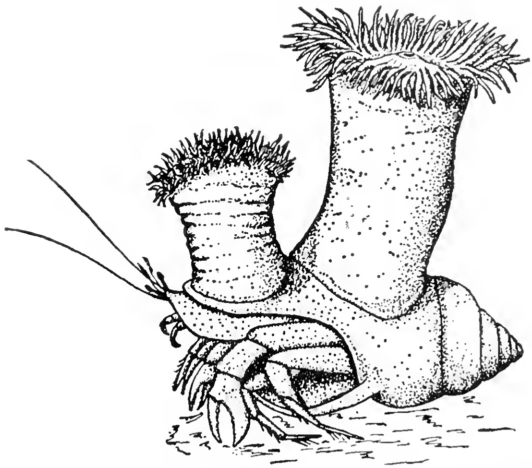


Fig. 197.—Hermit crab and sea anemones. Usually the gasteropod shell inhabited by the crab is completely covered by sea anemones, but only two of the latter are represented for the sake of clearness.

occur there. The transplanted plants and animals often grow and provide an effective covering.

An example of a closer symbiotic relationship is found in the green hydra, *Chlorohydra viridissima,* which owes its green color to the presence of microscopic green plants embedded among its cells. The plants utilize the carbon dioxide given off by the animal cells and in return yield oxygen which is readily absorbed by the cells. The same sort of relations is found in some Protozoa that contain numbers of unicellular plants.

A rare symbiotic relationship between a mammal and algae is illustrated by conditions found in the hair of the two-toed sloth, *Choloepus didactylus,* a South American form. This animal is largely arboreal in its habits, moving about in the trees, suspended in an upside-down position from the branches by its strongly curved claws. It assumes other postures when climbing vertical stems or when asleep. It is a good swimmer but is incapable of assuming a standing position on the ground. All of its movements are extremely slow, and active means of defense seem to be entirely lacking; its fur and hide and its habit of rolling up into a tight ball serve as its principal protection. This passive means of defense is heightened by the presence of algae in the fur. This is made possible by the structure of the hairs, which are distinctly fluted, with four ridges and three grooves on each side, the grooves offering a lodging place for the algae. The algae, which are said to be always present in the long hairs, change color under different degrees of moisture. When the fur is dry, the algae produce a dirty brown color pattern; when wet, the pattern turns green. Such a protective coloration would seem to be of value against enemies flying overhead. There is no reason to suppose that there is a mutual respiratory benefit such as is present in Chlorohydra and algae.

A common symbiotic condition exists in the alimentary canal of vertebrates in the presence there of bacteria, which appear to be not only harmless but actually beneficial to the host to the extent that they aid in digestion of the host's food. The bacteria benefit by being provided with food and protection.

Parasitism.—When the association between two different kinds of organisms becomes such that one of them, the *parasite*, receives food and protection from the other, the *host*, without giving anything in return, the condition is known as parasitism. The effect on the host is usually detrimental, and if fatal, the death of the host as a rule takes place only after the parasite has developed to the point where the host is no longer needed. Judging from the great frequency of the condition, parasitism must be a very successful way of living and reproducing, though often it is the most complicated. The adjustments necessitated by this mode of existence have resulted in remarkable states of structural and functional adaptations on the part of the parasite, producing in many cases a distinct specificity in the host or hosts invaded by the parasites. Parasites may occur in practically any organ of the host's body, but the most common location is the alimentary canal. *Taenia solium*, the pork tapeworm, is found as an adult in the human intestines where it reaches a length of 4 to 10 ft. The head or scolex (Fig. 231) is very small and is provided with hooks and suckers by means of which it attaches itself to the intestinal wall. The body behind the head consists of a series of segments or proglottids. The parasite has no mouth or alimentary canal of its own, the host's food being absorbed directly through the body wall. The more posterior proglottids become filled with eggs, which are probably fertilized by spermatozoa from the same proglottid. As the proglottids become laden with embryos, they break off and pass out of the alimentary canal of the host. If the proglottids are eaten by a pig, the embryos are released and bore through the walls of the pig's alimentary canal, whence they make their way to voluntary muscles where they encyst. Here the embryo develops into an oval *cysticercus*, or bladder worm, and remains as a cyst until the infected muscle is eaten (Fig. 233). When the wall of the cyst is dissolved by the human gastric juice, the scolex is protruded from the inverted position occupied in the cyst, in the manner of a finger of a glove. The scolex then attaches itself to the intestine, and with the development of proglottids the bladder worm is transformed into the adult. From this it is seen that in the usual life history of the pork tapeworm two hosts are involved. Neither host is killed by the presence of the parasite in the ordinary course of events.

In other cases of parasitism the host is killed as a result of the parasitic association. Thus, the *chalcid* flies deposit their eggs in the bodies of caterpillars. The eggs hatch into larvae which devour the caterpillar. Similarly the *ichneumon* flies lay their eggs in caterpillars and other insects, which are destroyed by the developing parasitic larvae.

Regeneration.—Many animals have the power to replace or regenerate new parts if old ones are lost. *Euplanaria* is a genus of the free-living flatworms occurring in fresh-water ponds. If such an animal is cut transversely, the head end will regenerate a new tail and the tail end a new head. If a crab loses a leg, a new one is regenerated. The same is true of the cockroach before the final molt. If one or more arms are torn from a starfish, they are replaced by new ones (Figs. 198 and 199). Regeneration, which enables an animal to survive the loss of considerable portions of the body, is common among lower invertebrate animals. Regeneration of lost parts is present in the larval stages of lower vertebrates. Thus the limbs of amphibian tadpoles if cut off are replaced. If a limb bud is removed from a mammalian embryo, regeneration does not occur. Regeneration in the adults of vertebrates is confined almost entirely to wound healing. This

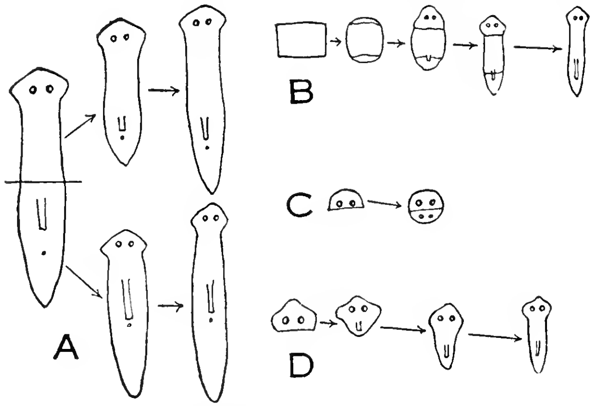


FIG. 198.—Regeneration in *Euplanaria*. A, regeneration of the anterior and posterior ends following transverse section. B, regeneration in piece taken from the middle. C, regeneration of new head on piece from head region. D, regeneration of a larger head piece. (*After Morgan.*)

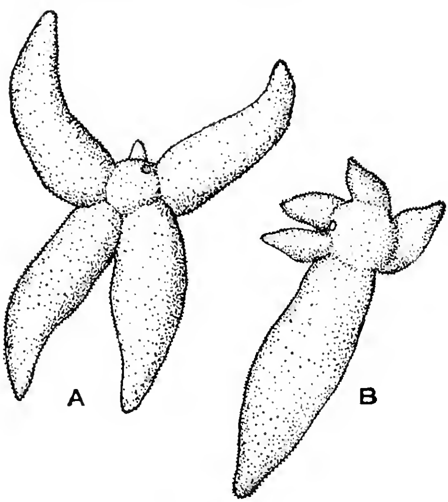


FIG. 199.—Regeneration in the starfish, *Asterias*. In A a single arm is regenerating, in B four arms. Both are young animals.

also has a protective significance since wounds caused by injuries of whatever sort, unless promptly closed, may lead to serious results not only because of the primarily traumatic effect but more particularly because the broken integument opens the way for invasions of bacteria.

Immunity.—By slowly increasing the dosage, the tolerance of the body for certain poisons can be gradually increased. An animal can acquire an immunity to bacterial diseases by having the disease itself. In either case there is a functional response to the action of the toxic substance of the pathogenic agent which results in an improvement of the defense mechanism of the body. The usual explanation of what happens during the recovery from a bacterial infection is that substances known as *antitoxins* are formed and that these substances counteract the effects of the bacterial toxins, with the result that the patient for some time afterward is immune to further attack by the particular organism concerned. Immunity against smallpox, for example, may be established by having the disease or by submitting to vaccination with virus of a mild form of the disease. In other cases, the practice of giving antitoxin as a prophylactic or preventive measure is based upon the fact that an animal such as a rabbit, guinea pig, or horse, if inoculated with disease-producing organisms, reacts by producing a substance, antitoxin, which tends to neutralize the injurious effect of the organisms. Serum, the clear fluid obtained from clotted blood taken from such an animal, contains the antitoxin, which if injected into another animal or a human being, is capable of establishing immunity in the latter against the particular pathogenic organism involved. Immunity reactions and the power to regenerate lost parts are excellent examples of purely physiological adaptation.

Temperature.—The rate of metabolism varies with the temperature of the animal body, within a range that is not the same for all forms of life. The so-called cold-blooded animals have a body temperature that is slightly higher than that of the surrounding medium. Fluctuations in body temperatures follow fluctuations in outside temperature, a condition described by the term *poikilothermous.* All invertebrate animals and the lower vertebrates, including fishes, amphibians, and reptiles, with the possible exception of the turtle, are poikilothermous. Such animals lack a mechanism for maintaining a constant body temperature and a constant rate of metabolism. Some kinds of goldfish can be frozen stiff in icy water and be recovered unharmed if the warming is done gradually. In the "frozen" state the temperature of the body is only a little above 0°C. The integument of such animals is without any insulating mechanism for preventing loss of heat.

Birds and mammals are warm-blooded or *homoiothermous.* In such animals the range of body temperature compatible with living is much more limited and must be maintained in the neighborhood of 39°C. for birds and 37°C. for mammals, except in a hibernating animal. Most homoiothermous animals are provided with feathers or hair which, in addition to serving as a protection from mechanical injury, also aid in conserving body heat. Secretion of sweat and evaporation of water from the lungs are important means for preventing overheating. Feathers, heavy fur, or hide constitute good protections against cold. Aquatic mammals, such as whales, are provided with a layer of fat or blubber beneath the skin. A thick hide is also effective as a protection from the heat of the sun, as in the case of the hide of the elephant and rhinoceros. The human body in its natural state is poorly adapted for living in cold climates. The problem has been met by the use of artificial covering in the form of clothing.

Hibernation.—Many of the invertebrate animals such as snails, crustaceans, insects, spiders, and myriapods undergo hibernation. Among vertebrates hibernation also occurs during the winter in most amphibians, and in terrestrial reptiles such as lizards, tortoises, and snakes, and also in some mammals, particularly many rodents and some carnivores. Hibernation in mammals occurs in holes, hollow trees, caves, dens, etc., where the animal is protected from cold and enemies. During hibernation the animal is in a deep torpor resulting from a greatly lowered rate of metabolism. In some cases there are records to show that the hibernating animal awakes from time to time to take food from a supply previously stored in the nest. The time spent in hibernation varies roughly from three to six months, depending upon the kind of animal and also upon the latitude of its habitat.

The decline in metabolic rate of a hibernating animal is indicated by the rates of respiration and heart beat, body temperature, and loss in weight. The respiratory rate of a species of ground squirrel, *Citellus tridecemlineatus,* during hibernation ranges from ½ to 4 per minute as compared with 100 to 200 per minute under conditions of normal activity. The heart beat during hibernation averages 17.4 beats per minute as compared with 200 to 300 per minute under normal conditions. The body temperature, which under normal conditions varies from 32 to 41°C., during hibernation may drop as low as 2°C. The loss of body weight may total 40 per cent; it occurs principally in stored fat.

When the hibernating animal awakes, the resumption of normal activities is gradual, but the rise in body temperature is abrupt. Observations on the European dormouse record a rise from 13.5 to 35.7°C. in 1 hour and in the case of a bat, a rise from 17 to 34°C. in 15 minutes.

Among warm-blooded animals hibernation occurs only in some mammals and never in birds. It is relatively common in amphibians and reptiles and also occurs in some fishes (lungfishes). The lack of a delicately adjusted temperature-regulating mechanism in the lower vertebrates fits them for the hibernating habit; in fact, if a frog is chilled in cold water, it takes on the characteristics of a hibernating animal. In birds and mammals, the normal range of fluctuation of body temperature is rather limited, particularly in forms that do not hibernate. In man a few degrees' rise in body temperature produces a fever condition with deleterious results, while a subnormal temperature beyond a very limited range interferes with metabolism. Hibernating mammals, on the other hand, have a temperature-regulating mechanism that maintains a fairly constant value under conditions of normal activity but which ceases to function when the animal hibernates. In such animals the fluctuation of body temperature under nonhibernating conditions, 32 to 41°C., is much greater than in the case of man. The hibernating habit of certain mammals is possible because of the absence of a rigid temperature-regulating mechanism which in turn may be a survival from cold-blooded ancestors.

Light.—Animals are sensitive to light and react to it by moving toward or away from it, or by developing anatomical features of an adaptive significance. A light-sensitive organ, such as the red eyespot of the protozoan, *Euglena viridissima*, by increasing the light absorption makes the region of the body in which it is located more sensitive to light than other regions. The various types of eyes found in different groups of animals, climaxed by the highly complex vertebrate eye, all represent specialized end organs for the perception of light stimulation. In the lower forms these organs do not form images of external objects but serve simply as light receptors which distinguish intensities of light. The image-forming function of eyes of higher forms is an acquisition that came with the evolution of the lens and accompanying structures, which in the case of the vertebrate eye is a cameralike organ capable of projecting images of external objects on a sensitive retina.

There is undoubtedly a relation between light and the formation of pigment in the skin, but there are difficulties involved in reaching a clearcut conclusion regarding the relationship, as has been indicated in the discussion of the pigment of cave salamanders. In addition to the facts brought out in that discussion, it might be noted that light, in some cases at least, is necessary for the complete development of pigment in the skin. Thus, if frogs or young salamanders are allowed to develop in the dark, the formation of pigment is retarded. Flounders are normally pigmented above and are white on the undersurface of the body, which ordinarily is not exposed to the direct action of light. If young flounders are allowed to develop in tanks illuminated from below, it has been found that pigment develops on the undersurface as well as above. Human races native to tropical regions have deeply pigmented skin and dark-brown or black-colored eyes, which certainly act as protective adaptations against the intense illumination of the sun. The dark eye of the Eskimos similarly is a protection from the intense reflection of a snow-covered environment. White-skinned races developed in regions of less intense light. Skin color seems to be a purely environmental phenomenon, not necessarily correlated with other traits such as intellectual vigor.

Moisture.—Metabolism requires that the concentration of the body fluids be maintained at a certain value. If an undue amount of water is lost through the integument or in other ways, death follows. Aquatic and semiaquatic animals, such as fishes and amphibians, are so highly adapted to a moist environment that they cannot live for any length of time in a medium of dry air because under these conditions there is no check on the loss of water through the integument. Such uncontrollable loss does not occur in terrestrial animals because of a difference in the nature of the integument. Animals living in a desert must be adapted to an environment in which there is a scarcity of water. Many of the smaller desert forms of mice and lizards never take water in the free state and are able to derive sufficient amounts from their food to meet their needs. The stomach of the camel is provided with water reservoirs in the form of small flask-shaped cavities, each with a constricted mouth. When the stomach is filled with water, the muscles at the mouths of the cavities relax automatically, allowing the cavities to be filled. Water is absorbed from the stomach but not from the reservoirs. As the demand for water arises it is released from the reservoirs into the stomach.

Pressure.—Animals are adapted to conditions of atmospheric or hydrostatic pressure under which they live. This is strikingly brought out when the animal is subjected to a considerable change in pressure conditions. Deep-sea fishes brought to the surface from depths of 10,000 to 16,000 ft. are unable to survive the transition for any length of time. At high altitudes bleeding at the nose may occur in human beings owing to the diminished air pressure. Since there is less oxygen, per unit volume, in high altitudes than at lower ones, the reduced amount of oxygen taken with each lungful of air also causes respiratory distress.

Adaptations for Race Preservation.—In many animals there is no such thing as parental care of the young. Marine forms, such as the starfish, sea urchin, and many fishes, deposit the eggs in water, where they are fertilized, after which all parental responsibility ceases. The development of starfish is so rapid that in 24 hours it has advanced to the stage where free-swimming larvae are produced which are fully able to care for themselves. In fishes developing outside of the body, the egg is provided with a quantity of yolk which serves as a source of nutrition until the young fish is able to shift for itself, but even here the rate of development is very rapid. Among other fishes and among amphibians the eggs are deposited with some attempt at concealment, so that they do not become too easy prey, but on the whole the parental supervision and protection are rather scanty. Naturally, an enormous number of eggs and embryos are destroyed, but since the rate of reproduction is so great in such cases—a cod is said to produce 6 million eggs—there is under ordinary conditions but little danger of the extermination of any given species. Most birds protect and feed their young as long as the young are weak and unable to care for themselves. Bird nests are in most cases temporary homes, built primarily for the protection of the young, and therefore occupied only during the breeding season.

Among other animals the protection, care, and rearing of the young seem to be the principal business of life. The meticulous care which the honeybee bestows upon the young in all stages of development is an example. The food of the developing larvae is not only collected but is partially digested by the workers before being administered to the young. The character of the food is changed to suit the change in requirements of the larva at different stages of its development. The care and the guardianship exercised by the worker do not cease until the young reaches its fully developed condition when it is relinquished with a few final touches. The remarkable part of it all is that the progeny are not the offspring of the workers, but of the queen. Parental care is exercised only by the foster parents.

The method employed by the digger wasp of the genus *Ammophila* for providing the young with food during the larval period has some points of seeming refinement about it that merit notice. The food, consisting of caterpillars which the wasp overcomes by stinging, is sealed in the burrow with the wasp's eggs. A discriminating surgical skill has been ascribed to the wasp because in many cases the caterpillar is not killed by the sting but only paralyzed, and this has been interpreted as an adaptation to keep the food alive until the larvae of the wasp are ready to feed upon it. Unfortunately for this idea it has been shown that in cases where the wasp has killed the caterpillars, the larvae feed upon the dead bodies with as much satisfaction as upon the paralyzed ones. It seems to be largely a matter of chance whether the stinging of the caterpillar causes death or paralysis, and so far as the larvae are concerned it makes no difference whether the food provided is dead or kept in live storage.

One of the most curious habits in guarding and rearing the young is found in a species of marine catfish, the gaff-topsail catfish, *Felichthys felis*, a subtropical form common along the South Atlantic coast of the United States, the male of which carries the eggs in its mouth until they hatch. The number of eggs found in a single individual male varies from 2 to 55 in observed cases. The eggs are held loosely in the mouth and are subjected to effective aeration by the water streaming over them and out through the gill clefts at either side of the mouth. So far as known the male does not feed during the time the eggs and the developing young are in its mouth, which may be 70 days.

The actual time required for the development of *mammals* to the adult state is considerably longer than for other animals. In general, mammals that depend primarily upon speed for escape from danger do not have helpless or unprotected young, and in such cases either the young are able to move rapidly as soon as born, or they are brought forth in some secluded spot. Thus, the young of the ox or deer are capable of running or walking shortly after birth. Of course, the young are dependent upon the mother's milk for food—as is the case with all mammals—but in times of danger they are capable of fleeing with the mother. In the opossum and also in the kangaroo, the young are born in an extremely immature condition but are at once transferred into a large pouch formed by a fold of the skin of the abdomen in which they are carried (Fig. 200). According to the observations of Hartman, in the case of the opossum the newly born animal reaches the pouch by its own efforts. In the pouch the young grasps the nipple of the mammary gland, from which milk is forced into the mouth by mammary muscles, strangulation being prevented by the prolongation of the larynx into the naso-pharynx. Even after the young kangaroo runs about, it often retreats to the pouch. Rodents and carnivores also bear their young in a relatively immature state of development. Newly born rabbits or kittens are blind and remain so for days, during which time they are dependent on the parent for both food and protection. In each case the young are brought forth in a secluded place.

A consideration of adaptations emphasizes the fact that living demands an adjustment between the organism and its environment. Without its environment the organism does not exist. It has been said that "evolution is no more than adaptation of organisms to environment" (Osborn). The debate as to the origin and method of development of adaptation is of minor consideration in comparison with the importance of the fact of adaptation. As to their general character, adaptations "are primarily for the good of the species; they are beneficial to individuals only so far as these individuals are essential to the welfare

FIG. 200.—Black swamp-wallaby of Australia carrying young in the marsupium. (*From Shull, La Rue, and Ruthven, Animal Biology.*)

of the species; and they often are injurious or destructive to the individual, but since the welfare of the species is usually identical with that of the constituent individuals, the destructive or injurious effect is not obvious unless the good of the species demands the sacrifice of individuals" (W. K. Brooks).

CHAPTER XVI

ENVIRONMENT AND DISTRIBUTION

The environment of an animal includes biological factors, mainly breeding and feeding conditions, as well as physical factors, such as temperature, moisture, light, altitude, etc., all of which are reflected in its adaptations. Darwin, in discussing the nature of the struggle for existence, illustrated the complicated interplay of biological factors involved in the production of red clover (*Trifolium repens*). The fertilization of red clover depends upon the visits of bumblebees, which in their search for nectar unwittingly carry pollen from one flower to another. The number of bumblebees in any district is controlled in part by the number of field mice, which destroy the combs and nests of the bees. The number of field mice in turn is regulated by the number of cats or other enemies of the field mice. Hence the number of cats may become an important factor in determining the size of the clover crop. Every living thing is beset with biological hazards which it must surmount in order to survive. The background for the interplay of biological forces is the physical environment, some aspects of which will be briefly summarized in the following paragraphs. The two major physical environments are water and land.

Water.—The most obvious adaptive features found in animals living submersed are means of obtaining sufficient oxygen for respiration and means of locomotion in a fluid medium. The source of oxygen available for respiration is air dissolved in the water and oxygen generated by aquatic chlorophyll-bearing plants. The water of a well-aerated stream contains from 9 to 10 cc. of oxygen per liter, which is about $\frac{1}{20}$ of the amount of oxygen in an equal volume of air. However, the amount of oxygen available to aquatic animals may be greater than this if the water contains green plants. Aquatic animals are adjusted or adapted physiologically to a relatively low supply of oxygen because they are poikilothermous, which eliminates the necessity of maintaining a body temperature higher than that of the water.

The organ, by means of which oxygen is absorbed from the water and carbon dioxide is excreted into it, is some sort of gill, the fundamental structure of which is the same for both invertebrate and vertebrate aquatic animals. Very small forms lack gills and are capable of respiring through the body surface. Aquatic mammals, such as the whale, seal, porpoise, and manatee, have taken to an aquatic existence secondarily and obtain oxygen from the air above the water. The same is true of aquatic reptiles and some aquatic insects.

Locomotion is simplified for an aquatic animal because the density of water is great enough to support partially or completely the body weight. Movement is accomplished by pushing against the water, and resistance to forward motion is reduced by the shape of the body. It is interesting that aquatic mammals have evolved a fish-shaped body with degenerated limbs.

Land.—Terrestrial animals are enveloped by air from which oxygen is absorbed by means of lungs, the buccal cavity, the surface of the body, or by a tracheal system. Locomotion over the ground is accomplished as a rule by means of limbs, which in many cases raise the body clear of the ground. The weight of the body, whether carried or dragged, is a factor that does not figure in aquatic locomotion. There is therefore a correspondingly greater energy requirement involved in terrestrial as compared with aquatic locomotion which is reflected in the greater oxygen (and food) requirement of the terrestrial animals as a whole. Both oxygen and food requirements are increased for flying animals since the density of air is very much less than that of the body. The requirements for flying are met by a heightened basal metabolism and, particularly in the larger flying forms such as birds, by a lightening of the body. The form of the body also is such as to reduce friction to a minimum during flight. The streamlining of both fishes and birds has the same significance.

Animal Communities.—Animals whose needs are met by similar conditions, or who have become adapted to similar conditions, form an animal community. The members of the same community, though often unlike and belonging to widely separated taxonomic groups, are capable of living together because their responses to the environment are similar. Less specialized and therefore less rigidly adapted forms may live in two or more communities. The classification of communities is primarily a classification of physical environments of which there are three subdivisions: (1) that of the ocean (*halobios*); (2) that of the fresh water (*limnobios*); and (3) that of the land (*geobios*).

Ocean Communities.—Animals found in the ocean are capable of living in an aqueous medium containing certain concentrations of inorganic salts, oxygen, and some organic matter, as well as plant life. Some marine animals are so completely adapted to the salinity of the ocean that they die when placed in fresh water. The ocean offers a variety of aquatic environments differing in depth, salinity, oxygen content, light, temperature, etc.

Littoral Animals.—The water lapping the shore of the ocean forms the littoral zone. Owing to its slight depth, it has the greatest amount of light and wave action and is subject to maximal variations in temperature. Since the ocean tides vary from a few inches to many feet, great changes in depth of the shore water are common. When the tide is out, many marine animals are uncovered for hours. The community of shore animals includes coelenterates, echinoderms, worms, arthropods, and molluscs. At low tide some of these lie buried in sand, while others such as oysters, barnacles, some echinoderms, and corals remain exposed to the air.

Animals of the open ocean may be divided into three groups, *viz.*, (1) those of shallow water, (2) those living at the surface, and (3) those at great depths.

Shallow-water Animals.—Shallow water includes depths of 450 to 500 ft. At these depths in addition to those animals found in the littoral zone, free-swimming stages of littoral animals occur. Such forms are never uncovered by the tide, are less subject to wave action, and are adapted to a greater pressure.

Pelagic Animals.—This group includes the free-swimming forms such as fishes, and also floating forms such as jellyfishes, small Crustacea, many larval forms, and Protozoa. The transparency of the bodies of some of these plankton animals makes them almost invisible. The Portuguese man-of-war is a common floating type provided with a large gas-filled sac (pneumatophore).

Animals of Great Depths.—Animals living at great depths of the ocean, 5,000 to 15,000 ft., bathybic animals, are adapted to enormous pressures, low temperature, and varying degrees of darkness. Fishes taken from a depth of 1 mile show no visible structural adaptation to temperature, which is not surprising since fishes are poikilothermous and even shallow-water forms can withstand freezing temperatures. As to pressure, some withstand the transition from a depth of 1 mile to the surface without disintegrating. Adaptations to darkness, however, can be recognized and these take two general forms: (1) the development of long attenuated, highly sensitive tentacles, or (2) the development of luminescent organs. The most abundant forms of deep-sea life are shrimps, prawns, and related crustaceans, particularly copepods. Many are luminescent.

Fresh-water Animals.—Fresh-water communities are classified according to the form of the body of fresh water, *viz.*, pond, lake, or stream. Fresh-water environment differs from the ocean in a greater variability in temperature, lower salt content, and greater liability to contamination arising from erosion. Many of the common marine forms such as echinoderms, barnacles, and oysters are not found in fresh water. There are fresh-water sponges, some coelenterates (Hydrozoa), and a few species of polychaete worms. The common fresh-water forms are fishes, amphibians, oligochaete worms, leeches, arthropods, molluscs, and protozoa. These, as in the case of marine forms, may be divided into swimmers, floaters, and bottom dwellers.

Land Communities.—Terrestrial animals may be divided into two general classes: (1) those that live in the soil or in caves, and (2) those that live above ground.

Subterranean Animals.—The habitats of subterranean animals resemble aquatic habitats in that sudden changes in temperature and moisture do not occur. Oxygen is less abundant than on the surface. Common soil-dwelling forms include protozoans, earthworms, arthropods, amphibians, reptiles, rodents, and moles. Darwin found earthworms at a depth of 6 ft.; the burrows of prairie dogs may reach a depth of 8 or 9 ft.; but the majority of soil animals are found nearer the surface. Temperature and moisture are remarkably constant throughout the year in caves. The common terrestrial cave dwellers include spiders, insects, and salamanders. Owing to the uniformity of temperature and moisture in caves, hibernation is rare among permanent cave dwellers. Cave animals in general have degenerated eyes and pigment, and highly developed tactile sense organs. Since caves may contain pools of water or streams, the cave population is increased by a number of aquatic forms.

Surface Animals.—Many animals having their habitat primarily on the surface may at times enter the soil, and likewise some burrowing forms may come to the surface. The surface habitat, in sharp contrast to the subterranean, exposes animals to wide variations in temperature, light, and humidity. Surface animals may be divided into three general classes: (1) those living on the ground, (2) those associated with plants, and (3) those able to fly or glide through the air.

Ecological Succession.—The physical environment, particularly of land and fresh-water forms, is constantly changing and this change for the most part takes place in an orderly manner. Lakes change to ponds, ponds to marshes, and marshes to dry land, on which forests grow, or which becomes a treeless prairie. Each change in physical environment is accompanied by changes in the animal communities affected. Aquatic communities in the usual course of events are succeeded by land communities. *Ecology* is concerned with the study of all factors involved in the determination of animal communities. It consists largely in the study of the reactions of animals to environmental conditions which result eventually in a balance or equilibrium between the individual members of a community and their environment. Actually such balances or equilibria are unstable and change with conditions. Then too, major geographical changes, such as are known to have occurred in the past, may completely destroy the balances established in the usual course of ecological successions.

Distribution.—Zoogeography is the study of the geophysical distribution of animals. As might be expected, such studies show that representatives of the same group of animals are found living under similar conditions in different parts of the world, ecological relations being what they are. However, a review of the natural, geographical distribution of animals in modern times shows areas devoid of animals that are capable of living in those areas. Thus the introduction into Australia of the rabbit by man has resulted in the rabbit becoming established completely as a member of the Australian fauna. Similarly the horse introduced into the American continent by Spaniards has been able to thrive in the plains of North and South America. Many animals show a discontinuous distribution in that members of the

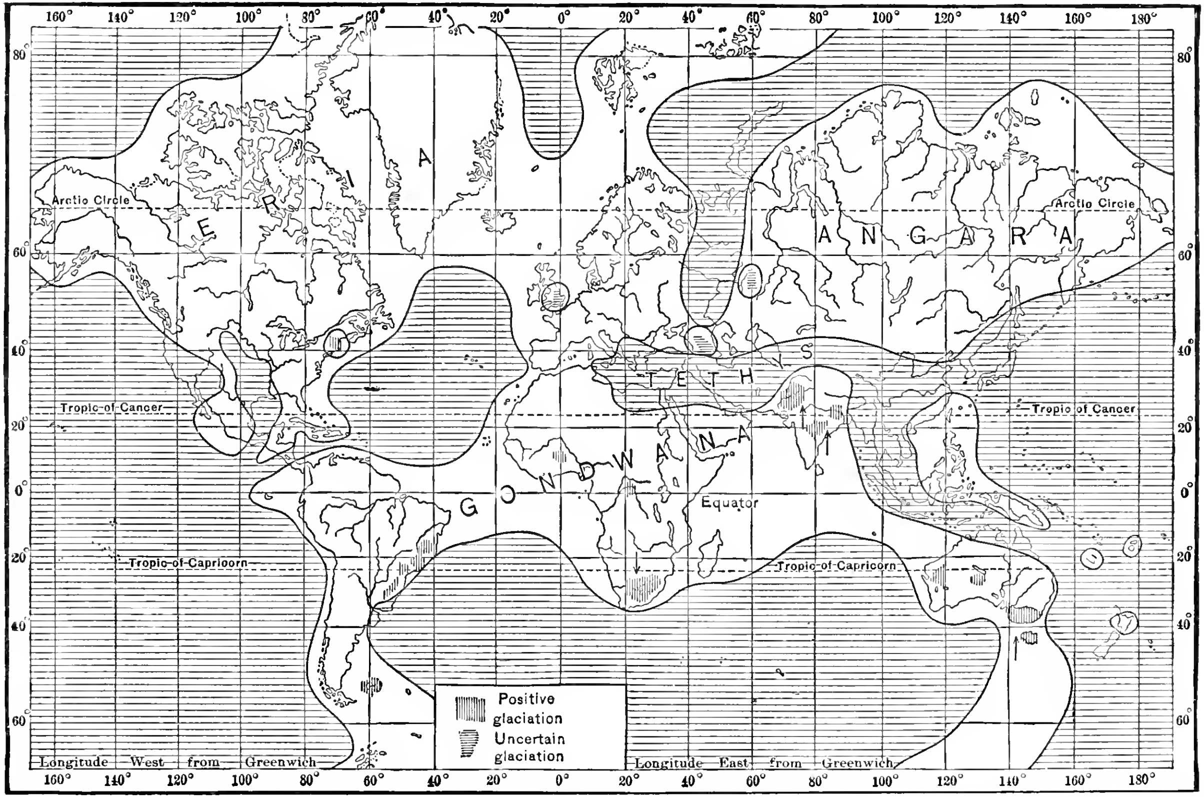


FIG. 201.—Map of the world in early Permian time showing a connection between all continents including Australia. (*From Shull, et al., Animal Biology, after Schuchert.*)

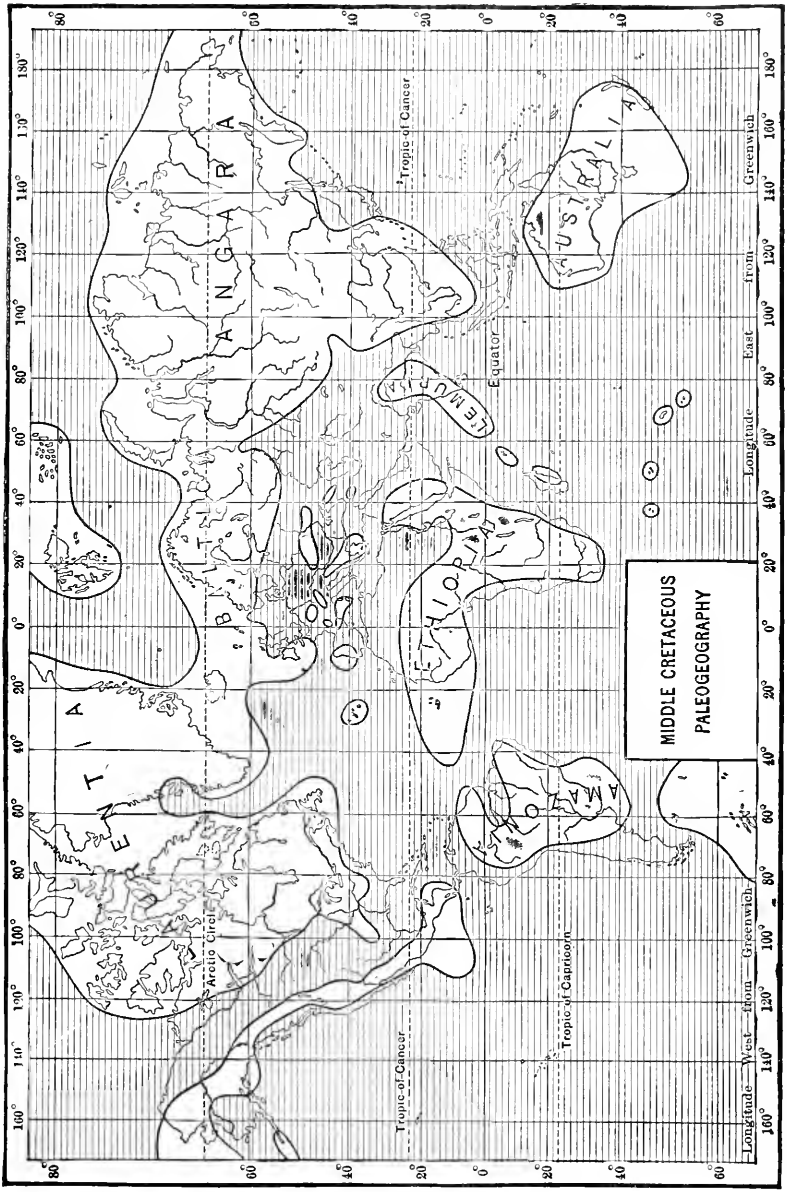


FIG. 202.—Map of the world in middle Cretaceous time showing the separation of continents. (*From Shull et al Animal Biology, after Schuchert.*)

same group have their natural habitats in widely separated parts of the world. Thus the tapir is found in Central and South America and in Southern Asia; and alligators occur in central China and Southeastern United States. Why have many animals failed to occupy certain regions favorable for their support and why are other groups found in widely separated regions?

In answering these questions, in addition to the usual factors operating in relatively stable communities and in ordinary ecological succession, the effects of major geographical changes, dealt with in geology and paleontology, must be considered. Paleontology demonstrates that animal groups often originated in localities far removed from the present habitats of the living descendants. Fossils show that members of the camel family formerly ranged North America as well as Asia, a fact that can be readily understood when it is pointed out that these two continents were formerly connected where Bering Strait now separates them (Figs. 201 and 202). Ancestral camels became extinct in North America but survived in Asia, whence they spread to Africa. In South America they are represented by the llama. The horse is not indigenous to North America. It arose there, spread to the Old World, but became extinct in the place of its origin during the Quaternary period. In the Old World it survived and gave rise to modern horses. Paleontology discloses the wandering of many animals from place to place, in all probability in search of food and shelter, until the paths of these various migrations have become a complicated network, which has been interpreted in relatively few cases by fossil remains.

Discontinuous distribution in many cases is the result of the creation of barriers isolating animal communities in whole or in part in various ways. The peculiar fauna of Australia is undoubtedly due to the fact that this continent has been separated from other continents from the beginning of Cenozoic times, with the result that its egg-laying mammals are entirely different from mammals found in continental Asia. Accordingly, prior to the coming of civilized man much of its fauna remained mesozoic in character. Apparently the higher types of mammals never evolved in Australia. In addition to water, other barriers such as mountains, hills, deserts, temperature, climate, etc., have been equally effective in bringing about a checker-board distribution of many animals of similar species.

CHAPTER XVII

THE ANIMAL KINGDOM

The animal kingdom may be subdivided into 17 phyla, only about 10 or 12 of which are ordinarily studied by the beginning student. The present account includes all the phyla and usually the major subdivisions, but detailed descriptions are confined to animals commonly studied in the laboratory. Since there is still uncertainty as to the proper systematic position of some animals, the grouping followed here must be regarded as a tentative one and not necessarily the ultimate arrangement. In citing examples of animals typical of a phylum or its subdivisions, there is given either the *scientific name*, consisting of the name of the genus followed by that of the species, or the *generic* name alone. A common name is mentioned also where a common name is in use.*

PHYLUM 1—PROTOZOA

Knowledge of the existence of the group of animals now known as Protozoa dates from 1674, when they were observed and described by the Dutch microscopist, van Leeuwenhoek, whose pioneer work with the microscope led to the discovery of many organisms of minute size. The term Protozoa was applied to the group by Goldfus in 1820. Protozoa (first or primitive animals) may be defined as single-celled animals living singly, or in colonies in which the members are attached to one another. The apparent simplicity of their organization is largely a matter of minuteness in size of the individual organisms. Visible evidence of differentiation consists in the presence of *organelles*, which to all intents and purposes are functionally comparable to

* In the preparation of this chapter numerous sources were drawn upon, particularly the following: H. S. Pratt: "A Manual of the Common Invertebrate Animals," Philadelphia; H. S. Pratt: "A Manual of Land and Fresh-water Vertebrate Animals," Philadelphia; H. H. Wilder: "The Pedigree of the Human Race," New York; C. L. Metcalf and W. P. Flint: "Destructive and Useful Insects," New York.

the organs of metazoans. Examples of such structures, not all of which are present in every protozoan, are the following: one or more *contractile vacuoles*, by means of which a rudimentary circulation is maintained; a mouth or *cytostome*, where food enters; a number of *food vacuoles*, where food is digested; an *eyespot* that is sensitive to light; and organs of locomotion, such as *pseudopodia*, *cilia*, and *flagella*. Protozoa occur practically everywhere—in water, soil, air, and in or on the bodies of other animals. In the air they are carried in an encysted form that prevents desiccation and permits them to be distributed by air currents. As parasites they cause a number of diseases in man and other animals.

SUBPHYLUM 1. PLASMODROMA. Includes Protozoa having *pseudopodia*, or *flagella*, or entirely without organs of locomotion. A pseudopodium is a finger-shaped or filamentous extrusion of the cytoplasm, usually of a temporary nature. A flagellum is a permanent, threadlike, and vibratile process of the cytoplasm.

CLASS I. MASTIGOPHORA. Protozoa whose motile organs consist of one or more flagella, which by whipping movements draw or propel the animal through water.

SUBCLASS 1. PHYTOMASTIGOPHORA. PLANTLIKE FLAGELLATES.

Examples: *Volvox globator*, a colonial form (Fig. 203); *Euglena viridis*, a common pond form; *Ceratium*, an armored form, found in fresh and salt water; *Noctiluca*, a luminescent marine form (Fig. 204).

Euglena viridis has a fusiform body, colored green by masses of chlorophyll (*chromatophores*) and is provided with a long flagellum at its anterior end. The body is enclosed in an elastic pellicle which permits contractile movements but otherwise holds the body in a more or less definite shape. Near the anterior end of the body is a light-sensitive organ, the eyespot, or *stigma*, which contains red pigment. The nucleus is single, oval in shape, and centrally located. The presence of chlorophyll indicates that photosynthesis is possible, but there is also a gullet or *cytopharynx*, a small depression at the base of the flagellum, through which food particles are probably taken. Thus Euglena seems to utilize the nutritional methods both of plants (*holophytic nutrition*) and of animals (*holozoic nutrition*). It is also thought that Euglena may to a certain extent be

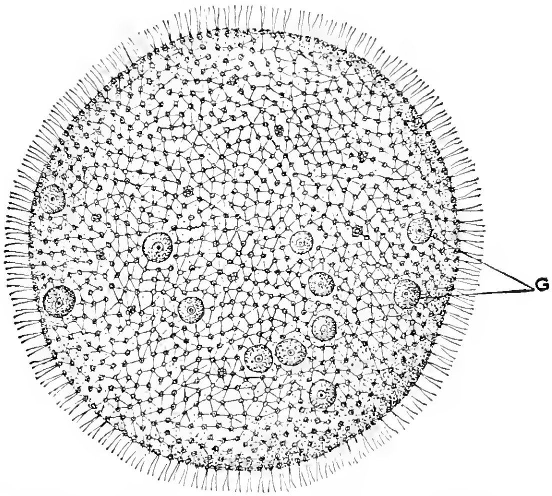


Fig. 203.—*Volvox globator*, containing developing germ cells, G. Volvox is made up of thousands of flagellated cells arranged in a gelatinous matrix in the form of a hollow sphere. The individual cells are connected by cytoplasmic extensions which give the sphere a reticulate appearance. Daughter colonies develop within the cavity of the sphere.

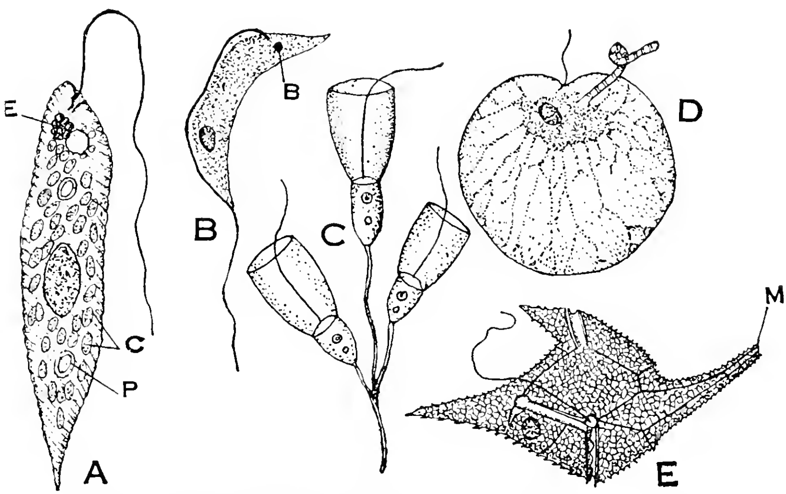


Fig. 204.—A, *Euglena viridis*, a flagellate, showing the striated cuticle. C, chromatophores; E, eyespot; P, pyrenoid body. (*After Bourne.*) B, *Trypanosoma lewisi*, from rat's blood. B, blepharoplast, a nuclear structure. (*After Laveran and Mesnil.*) C, *Codosiga*, a choanoflagellate. (*After Kent.*) D, *Noctiluca miliaris*, a cystoflagellate. (*After Cienkowski.*) E, *Ceratium cornutum*, having an armor of cellulose plates. (*After Stein.*)

saprophytic, i.e., capable of living on dead or decaying organic material. The cytoplasm consists of a clear outer layer, the *ectosarc*, and an inner region, the *endosarc*, in which lie the nucleus, chromatophores, and contractile vacuoles. The nature and action of the contractile vacuole are considered in connection with Amoeba, in which it can be more readily studied (p. 372). During encystment Euglena secretes a thick gelatinous envelope about itself and assumes a spherical form. Euglena may reproduce (1) in the free state by longitudinal fission; (2) by conjugation, a method described in detail in connection with paramecium (p. 382); and (3) during encystment by binary or multiple fission.

SUBCLASS 2. ZOOMASTIGOPHORA. ANIMAL-LIKE FLAGELLATES, lacking chromatophores and living as solitary or colonial forms under holozoic, saprozoic, or parasitic conditions.

Examples: *Trypanosoma gambiense*, a blood parasite, the cause of sleeping sickness among human beings in Western and Central Africa. It is transmitted by the bite of a tsetse fly, *Glossina palpalis*. *T. lewisi*, another species, is transmitted to rats by fleas. *Codosiga*, a colonial form, each member of the colony being provided with a collarlike ridge surrounding the base of the flagellum (Fig. 204).

CLASS II. SARCODINA. Protozoa whose body lacks a firm pellicle, in consequence of which change of body shape is possible. Some have shells.

SUBCLASS 1. RHIZOPODA. CREEPING FORMS WITH ROOTLIKE PSEUDOPODIA.

Order 1. Amoebida. Naked forms found in fresh and salt water, soil, and as parasites in the alimentary canal of Metazoa. Contractile vacuoles are present except in salt-water forms.

Examples: *Amoeba proteus*, a common fresh-water form; *Endamoeba histolytica*, parasitic in the human colon, causing dysentery and ulcers in the liver.

Amoeba proteus, examined on a slide under the microscope, appears as an irregular, jellylike mass of protoplasm, slowly changing its outline by projecting pseudopodia (Fig. 205). Its size varies from about 127 to 340 μ in diameter. The action of the pseudopodia in bringing about movements can best be understood if the amoeba is viewed from the side instead of from above. To do this, the amoeba is placed in water in a narrow glass chamber which is mounted on the stage of a microscope, tilted into a horizontal position. In this position the bottom of the chamber is horizontal and the amoeba can then be watched as it moves over the bottom to the observer's right or left. Under these conditions it can

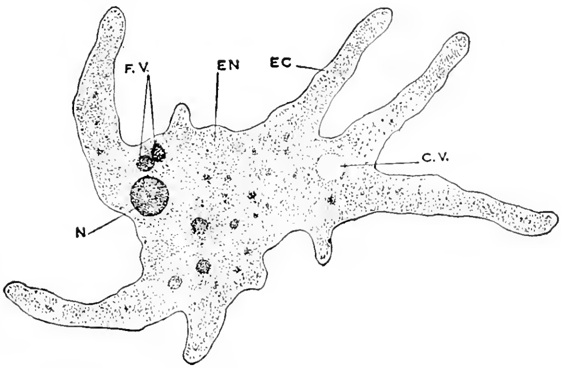


FIG. 205.—*Amoeba proteus* with pseudopodia extended. EC, ectoplasm; EN, endoplasm; F.V., food vacuole; C.V., contractile vacuole, expanded; N, nucleus.

be determined that the amoeba moves by extending and attaching a pseudopodium to the bottom and then drawing the rest of the body toward the attached pseudopodium (Fig. 206).

The nucleus has a rounded outline but is not unalterably fixed in position in the cytoplasm. Two general regions are

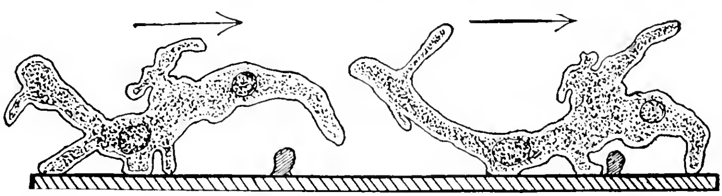


FIG. 206.—Side view of *Amoeba proteus* moving over a solid substratum by attaching the extended pseudopodia and then drawing itself forward. (*Adapted from Dellinger, Jour. Exp. Zool.*)

recognized in the cytoplasm: an inner portion, the endosarc or endoplasm, and an outer bounding layer, the ectosarc or ectoplasm. The endoplasm, in which the nucleus is located, has a granular appearance caused by the presence of embedded particles of various sizes, some of them food particles, others crystals and grains of sand. The ectoplasm is flexible and transparent but somewhat tougher and denser than the endoplasm. The larger granules in the endoplasm represent food substances that have been engulfed and that are in the process of digestion. The spaces occupied by the food, the food vacuoles, are temporary digestive organs which disappear when the food is digested. Near the surface of the body is a clear circular area, which disappears and reappears at regular intervals. This is the contractile vacuole. Careful observation shows that when the vacuole contracts, the contents are expelled through the ectoplasm. The vacuole then fills from the confluence of streams of fluid drawn from the cytoplasm, and accumulating at the site of the contractile vacuole. The fluid is water containing small amounts of metabolic products dissolved in it. Water in regulated amounts probably enters the amoeba through the surface, though this cannot be demonstrated by direct observation. The vacuole seems to be the focal point where metabolic products dissolved in water accumulate before being expelled.

There are no special respiratory organs in Protozoa for absorbing molecular oxygen and giving off carbon dioxide; such respiratory changes are functions of the surface of the body. In this respect the amoeba behaves in the same way as a cell in the body of a metazoan, with the difference that in the latter oxygen is absorbed from the blood and carbon dioxide is given off into the blood, while in the amoeba, the water in which the animal lives supplies it directly with oxygen and absorbs carbon dioxide from it. A nervous system and sense organs are lacking in amoeba, yet the animal reacts to stimulation of touch, light, heat, etc., by movements toward or away from the source of stimulation, thus indicating that irritability and contractility are present as properties of the animal as a whole. There is no indication of differentiation in the cytoplasm to account for the conduction of nervous impulses or the contractions that characterize the active animal. The semifluid character of the animal precludes the development of rigid structural features. Even in the case of the contractile vacuole, which has the appearance of stability, microscopic examination fails to reveal any structure that might account for its functional activity.

There is no mouth through which food passes into the interior of the animal. Food is obtained by means of the pseudopodia, the method used varying with the type of food. In securing nonmotile food such as certain plants (desmids) and encysted protozoans, the pseudopodia surround the object in a tight embrace and gradually engulf it. In attacking a larger object such as a mass of *bacterial glea*, two pseudopodia surround a portion of the mass and gradually pinch it off. As a rule rapidly moving objects cannot be captured, though motile Protozoa such as *Paramecium* or *Chilomonas* (Fig. 207) may be secured when they are relatively quiet. Thus a paramecium

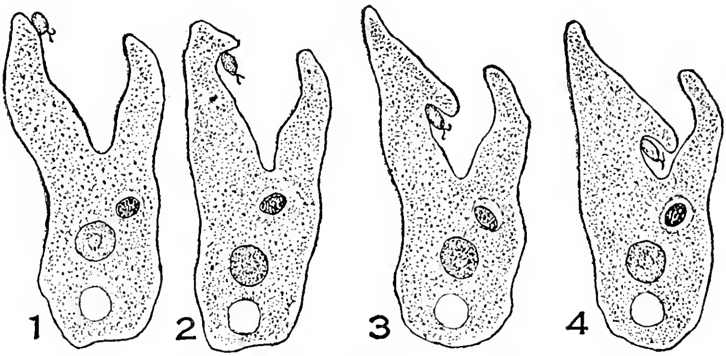


FIG. 207.—*Amoeba proteus* capturing *Chilomonas para*, another protozoan, by means of its pseudopodia. Sketched at successive stages. (*After Kepner and Taliaferro, Biol. Bull.*)

may be cornered by an amoeba against a solid object and trapped in a pocket formed by two pseudopodia, or the amoeba may send pseudopodia about the paramecium and confine it to an enclosed space before disturbing it. Sometimes the amoeba advances upon a paramecium and holds it fast by gripping it with the ends of the pseudopodia, after which a portion of the prey is "bitten" off (Fig. 208). Smaller objects are engulfed entirely. Within the body of the amoeba the food is broken up into small particles and digested in the food vacuoles. Undigested remains are cast out through the body wall. It may be inferred from this that the taking of food is not a haphazard process, for the amoeba does not engulf everything that it happens to meet; this means that it is capable of distinguishing between food and inedible objects.

An amoeba is protected to a certain extent by its ectoplasm, which has the characteristics of a thin elastic membrane; but since it often overcomes its enemies, if small enough, by engulfing them, securing food and gaining protection are in such cases accomplished by the same operation.

Amoeba proteus reproduces by simple fission, during which an *intranuclear spindle* and chromosomes are formed. According to some observations the nuclear membrane persists

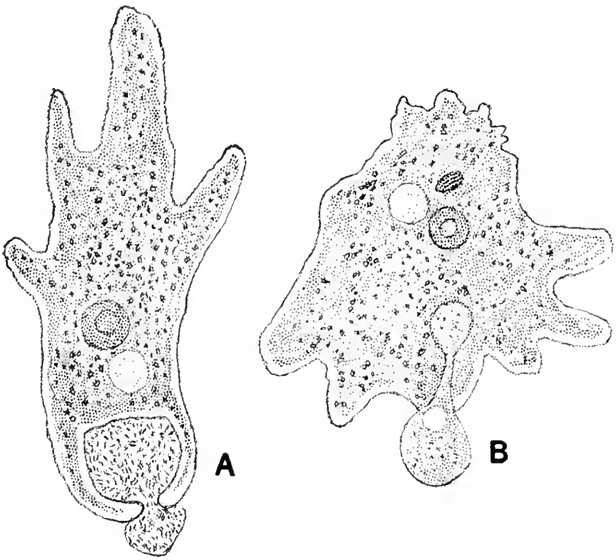


FIG. 208.—Reactions of *Amoeba proteus* to food. A, ingesting a portion of nonmotile bacterial glea; B, ingesting a paramecium, which has been constricted into a dumbbell shape. (*After Kepner and Whitlock.*)

throughout the mitotic process, surrounding the spindle. During the telophase it constricts into two parts, within each of which nuclear reorganization then follows.

Order 2. Proteomyxa. Protozoa with filamentous and often branching pseudopodia.

Example: *Nuclearia simplex,* common on Spirogyra and other fresh-water plants.

Order 3. Testacea. Body enclosed in a single-chambered shell provided with a single opening through which the pseudopodia can be thrust.

Example: *Difflugia urceolata,* a fresh-water form (Fig. 209).

Order 4. Foraminifera. Body enclosed in a single or many-chambered shell of siliceous or calcareous material, through the numerous pores of which delicate pseudopodia extend.

Example: *Globigerina bulloides,* a marine form, both pelagic and bathybic down to depths of 18,000 ft. Chalk beds are composed largely of the discarded shells of this species.

Order 5. Mycetozoa. Large amoeboid forms, multinucleated, with numerous contractile vacuoles and often colored red, orange, yellow, or green. Reproduce by spores and regarded as border-line forms between animals and plants.

Example: *Mucilago spongiosa* and other slime molds, found on decaying wood. Some colonies may be several inches in diameter.

SUBCLASS 2. ACTINOPODA. Floating forms with radiating unbranched pseudopodia.

Order 1. Heliozoa. A spherical body with fine raylike pseudopodia and often a siliceous skeleton. Cytoplasm is divided into an outer *cortex* and an inner *medulla,* the latter containing one or more nuclei. Mostly fresh-water forms.

Example: *Actinospherium eichhorni,* common in fresh water (Fig. 209, C).

Order 2. Radiolaria. Marine forms, usually with a siliceous skeleton. The spherical body is divided by a perforated chitinous central capsule into an extracapsular cortex and an intra capsular medulla containing one or more nuclei.

Example: *Acanthometra elastica* (Fig. 209, D).

CLASS III. SPOROZOA. Endoparasites in the cells and tissues of many animals. No vacuoles. Body is covered by a thick pellicle through which food is absorbed. Reproduction by spores.

SUBCLASS 1. TELOSPORIDIA. Intracellular parasites whose life history terminates in spores.

Order 1. Gregarinina. Intestinal parasites of arthropods and annelids.

Example: *Gregarina blattarum,* found in the digestive tract of roaches. The body of the gregarine (*trophozoite stage*) is divided by a transverse partition into an anterior *protomerite* and a posterior nucleated *deutomerite* (Fig. 210). The *epimerite* is an additional segment in front of the protomerite which is well defined during only a part of the life cycle. In reproduction two trophozoites, also known as *gametocytes*, unite and become encysted (*pseudoconjugation*) within a single envelope,

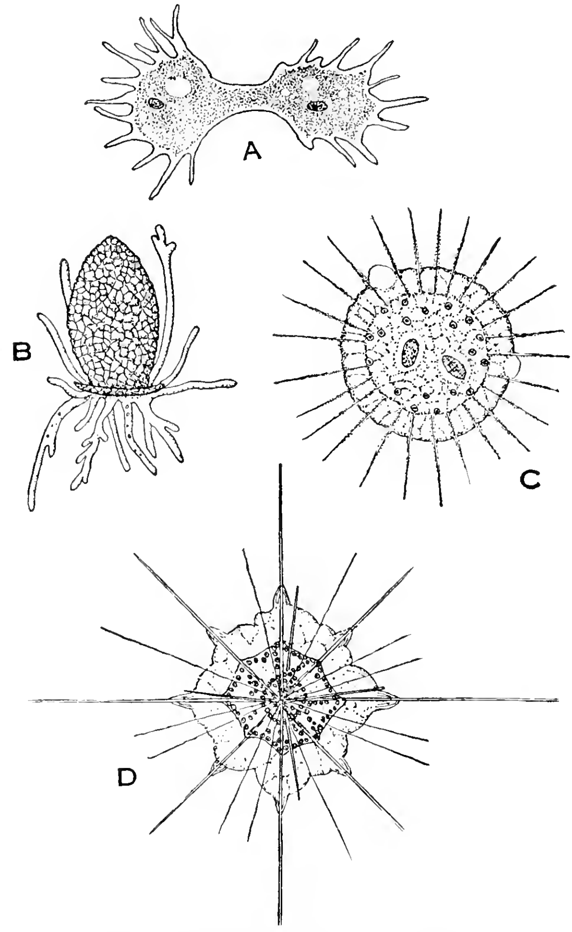


FIG. 209.—A, *Amoeba polypodia*, dividing. (*After Schulze.*) B, *Difflugia urceolata*, having a shell composed of grains of sand held together by chitin. (*After Leidy.*) C, *Actinosphaerium eichhorni*, a multinucleated heliozoan without a skeleton; the oblong objects in the medullary region are food particles; two contractile vacuoles are shown in the cortex. (*After Hertwig.*) D, *Acanthometra elastica*, a radiolarian with a spiny skeleton; the central capsule contains a large number of small rounded nuclei. (*After Hertwig.*) (*A, C, and D redrawn from Hertwig, Manual of Zoology, by Kingsley, Henry Holt & Company.*)

the *gametocyst*. Each conjugant then forms gametes, those from one individual uniting with those from the other to form

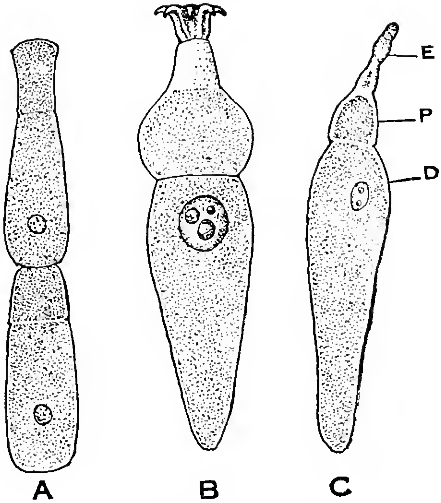


FIG. 210.—Gregarines. A, *Gregarina blattarum*, showing a chain of two individuals. (*After Cuenot.*) B, *Corycella armata.* (*After Leger.*) C, *Stylorhynchus longicollis.* (*After Schneider.*) E, epimerite by means of which the parasite is attached to tissues of the host; P, protomerite; D, deutomerite.

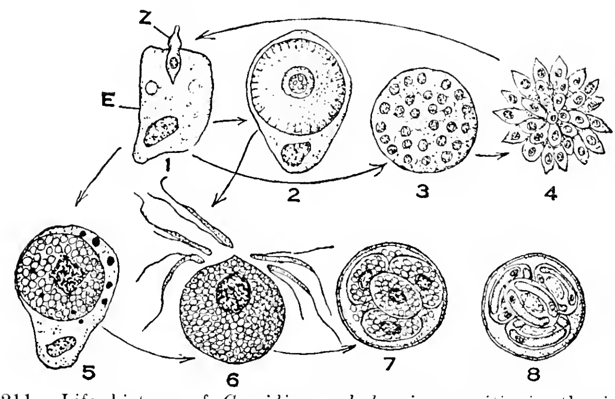


FIG. 211.—Life history of *Coccidium schubergi*, parasitic in the intestinal epithelium of the centipede, *Lithobius forficatus.* (*After Schaudinn.*) Cysts (8) swallowed with food are dissolved by digestive fluid. Each cyst contains four spores each of which in turn contains two sporozoites. The sporozoite attacks the intestinal cell (1), enlarges to form a schizont (3) which undergoes a rapid nuclear division eventually forming merozoites (4). The latter reinfect other cells, repeating the cycle. Sooner or later schizogony is replaced by sporogony which leads to the formation of microgametocytes (2) and macrogametocytes (5). Figure 6 shows a macrogamete surrounded by a number of microgametes. The fertilized macrogamete becomes encysted, forming four sporoblasts (7) each of which develops two sporozoites (8). The latter remain encysted until favorable conditions arise for their development in another host. E, intestinal cell; Z, sporozoite.

a large number of *zygotes*. Each zygote divides to form a large number of *sporozoites*, which penetrate the epithelial cells of the host's intestine and grow into trophozoites. Only a single host is necessary for the completion of the life cycle. The trophozoite eventually emerges from the epithelial cells but remains attached for a time by the epimerite. The latter disappears when the parasite becomes free in the intestine.

Order 2. Coccidiomorpha. Parasitic in many invertebrates and vertebrates.

Examples: *Coccidium schubergi*, an intestinal parasite of the centipede (Fig. 211); *Plasmodium vivax*, a blood parasite causing tertian malaria in man. The sexual phase of the life cycle is passed in the body of the female of a species of mosquito belonging to the genus *Anopheles*. An asexual phase, including preparatory steps for the sexual phase, is passed in the human blood stream (Fig. 212).

The salivary glands of a mosquito capable of infection carry *sporozoites*, which are spindle-shaped cells, 10 to 12 μ in length. These are introduced into the wound when the mosquito bites a human being. In the human blood stream the parasite bores into a red blood corpuscle, where it takes on an amoeboid shape known as the *trophozoite* stage. On reaching its full growth, the trophozoite undergoes segmentation or *schizogony*, as it is called, to form spores or *merozoites*, which are liberated in the blood stream by the rupture of the corpuscle, about 48 hours after infection. The free merozoites attack fresh corpuscles and the cycle is repeated; each time the corpuscles break down, the *chill* characteristic of malaria occurs. After several generations of merozoites have been produced, two kinds of gametocytes are formed, *macrogametocytes* and *microgametocytes*. The factors determining the development of the merozoites into gametocytes instead of trophozoites are unknown. For further development and complete differentiation, the gametocytes must pass into the stomach of the mosquito, a transfer readily brought about when a mosquito bites a patient containing them. The macrogametocyte undergoes certain nuclear changes somewhat akin to polar-body formation and is thus transformed into a *macrogamete*. Each microgametocyte, on the other hand, produces from six to eight whiplike *microgametes*. A single microgamete enters a macrogamete, with which it fuses to form the *zygote*. The zygote in the course of 24 hours is transformed into an active

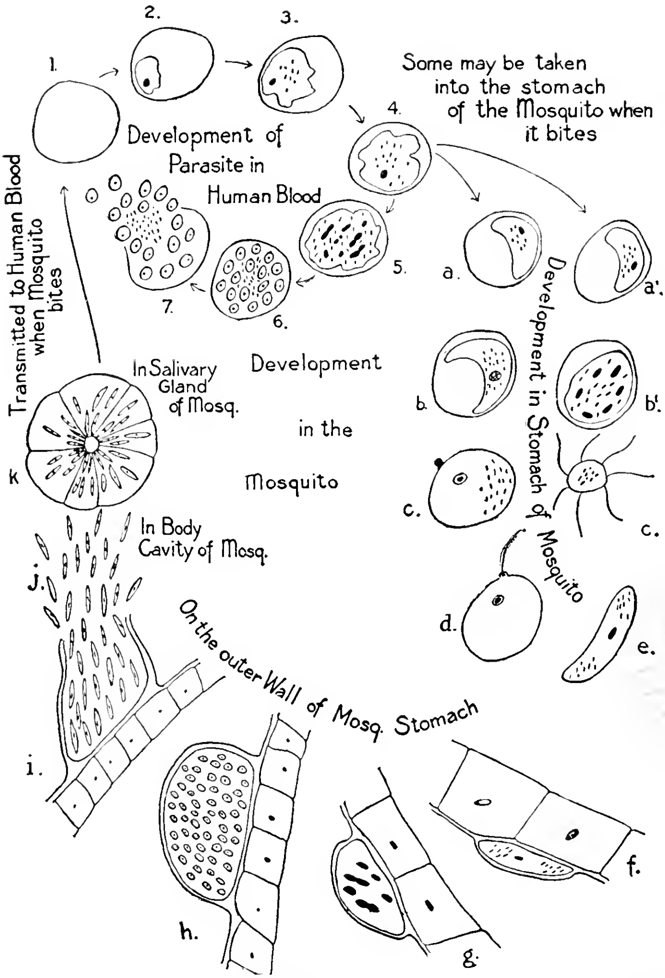


FIG. 212.—Diagram illustrating the life history of malarial parasite. 1, red blood corpuscle; 2 to 7, schizogony; *a*, *b*, *c*, *a'*, *b'*, *c'*, development of gametocytes; *d*, zygote; *e*, ookinete; *f*, *g*, *h*, development of oocyst; *i*, liberation of sporozoites; *k*, section of salivary gland. (*From Doane, Insects and Disease, Henry Holt & Company. By permission.*)

ookinete, which bores into the stomach wall, in the outer layers of which it forms the *oocyst*. The latter grows in size and then divides to form sporoblasts, each of which, in turn, forms a number of sporozoites. The oocyst bursts, liberating the sporozoites in the body cavity, whence they find their way via the body fluids to the salivary glands (Fig. 212).

Tertian malaria is so called because the chill comes at the end of 48 hours, *i.e.*, on the third day. Other forms of malaria have a different incubation period and are caused in each case by a different species of parasite. The life histories are all similar to that of *P. vivax* given above, though differing in details.

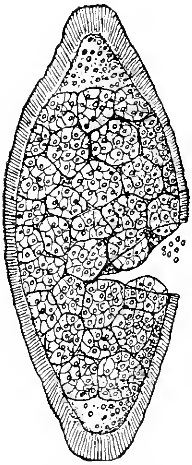


FIG. 213.—*Sarcocystis miescheriana*, from the pig's diaphragm. The organism, enclosed in a cyst, has divided into numerous alveoli, each containing a number of spores some of which are shown free where the cyst has been cut open. (*After Manz.*)

SUBCLASS 2. CNIDOSPORIDIA. AMOEBOID MULTINUCLEATED FORMS, undergoing continuous spore formation. Spores characterized by thread capsules.

Example: *Myxobolus lintoni*, occurring in the subcutaneous tissue of the carp.

SUBCLASS 3. ACNIDOSPORIDIA. PARASITIC in invertebrates and vertebrates. Reproduction continued through vegetative life.

Example: *Sarcocystis miescheriana*, parasitic in the muscles of the pig (Fig. 213).

SUBPHYLUM 2. CILIOPHORA. PROTOZOA PROVIDED WITH CILIA THROUGHOUT LIFE OR IN EARLY STAGES. Cilia are short processes resembling hairs, located on the surface of the body (Fig. 2, B).

CLASS I. CILIATA. Ciliated protozoans with a firm pellicle. A macronucleus and one or more micronuclei are present, except in parasitic species. A mouth (cytostome) and gullet (cytopharynx) are usually present, along with food vacuoles and contractile vacuoles. The ectoplasm or ectosarc may contain *trichocysts*, which are small sacs containing poisonous fluid that is discharged, with the sacs, for purposes of offense or defense. In the water the trichocysts are converted into long, thin threads. The cytoplasm may also contain contractile fibers called *myonemes*. *Cirri* and *membranelles* may be present. A cirrus is formed by the fusion of a small tuft of cilia; a membranelle by the fusion of two or more transverse rows of cilia. Cirri are used in creeping over the substratum. Membranelles are vibratile membranes found in the region of the cystostome.

SUBCLASS 1. PROCTOCILIATA. Parasitic in the large intestine of a number of amphibians. No cytostome; a single type of nucleus; reproduce by binary fission.

Example: *Opalina ranarum,* intestinal parasites of frogs and toads.

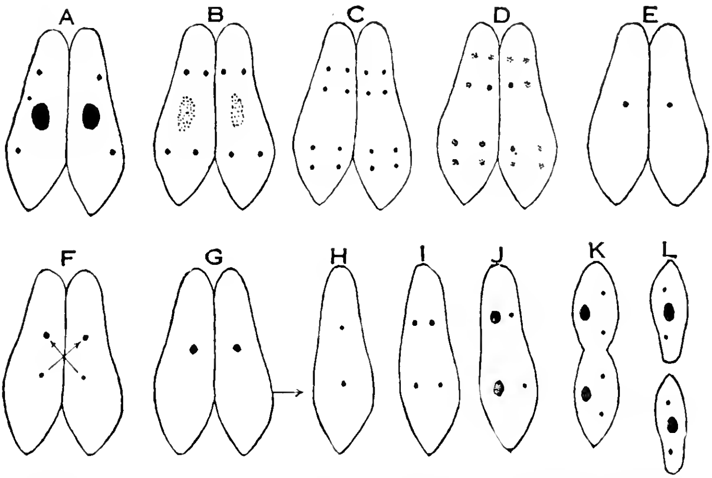


Fig. 214.—Diagram of the nuclear changes in *Paramecium aurelia* during conjugation. A, union of conjugants; B, degeneration of macronuclei and first division of micronuclei; C, second division of micronuclei; D, degeneration of seven of the eight micronuclei in each conjugant; E, each conjugant with a single micronucleus, which in F has divided into a stationary and micronucleus; G, each conjugant with a synkaryon formed by the fusion of the migratory nucleus of one with the stationary nucleus of the other conjugant; H, first reconstruction division of the synkaryon to form two micronuclei (takes place in each of the conjugants which now separate); I, second reconstruction division of the micronuclei; J, two micronuclei transformed into two macronuclei; K, division of two micronuclei and division of cell; L, two complete new individuals. (*After Woodruff, Foundations of Biology, copyright, The Macmillan Company. By permission.*)

SUBCLASS 2. EUCILIATA. Macronucleus and one or more micronuclei present and usually a cytostome.

Order 1. Holotrichida. Cilia rather uniform in size and distribution, and usually arranged spirally in parallel lines. The longest cilia are about the mouth. Trichocysts are common.

Example: *Paramecium aurelia,* found in fresh water has a cytostome, gullet, and cytopyge; contractile and food vacuoles; a large macronucleus and two small micronuclei. If samples from a culture of this protozoan are kept under continuous observation, it is found that at fairly regular intervals *binary fission* takes place and a single individual divides into two daughter cells. Each of the latter grows and in about 10 hours attains the size-limit characteristic of the species, when division again occurs. A large number of binary fissions may take place after this fashion; but sooner or later, under ordinary conditions in a laboratory culture, an entirely different sort of phenomenon, known as *conjugation,* occurs. In this process two individuals touch, at first in front, and then along the entire surface of one side, so that the cytostomes come together; the *macronucleus* swells and breaks up, the fragments eventually dissolving; and the *micronuclei* by two successive divisions produce *eight* nuclei in each conjugant. *Seven* of these nuclei disintegrate while the *eighth* divides, forming a *stationary* micronucleus and a *migratory* micronucleus. Each migratory micronucleus then passes into the opposite cell and fuses with the stationary micronucleus to form a *synkaryon* or fertilization nucleus. The conjugants now separate and in each the synkaryon divides twice, producing *four micronuclei,* two of which are transformed into macronuclei. The two remaining micronuclei each divide again, accompanied by a division of the cell, so that two complete individuals, each provided with a macronucleus and two micronuclei are derived from each of the conjugants (Fig. 214).

Woodruff has shown that if the medium in which isolated paramecia are living is kept fresh by constant changing, conjugation does not occur for thousands of generations (12,000, in the period from 1907 to 1921). It was found, however, that every 40 or 50 generations the macronucleus degenerates and is replaced by chromatin from the micronucleus, a process known as *endomixis.* The nuclear changes, as may be seen from the figure, are similar to those occurring in conjugation, except that there is no exchange of nuclear material between two individuals; *i.e., reciprocal fertilization* does not occur (Fig. 215). The common feature of both conjugation and endomixis, *viz.,* the periodic replacement of the macronucleus with material from the micronucleus, would seem to have some significance as a means of *rejuvenescence.* However, it is generally believed, in view of experiments with other species of Protozoa, that the prevention of death in Protozoa is due less to the environment than to the nature of the organism—in the case of Paramecium, to the process of endomixis.

Order 2. Heterotrichida. Membranelles about the oral zone. Cilia uniform over the rest of the body.

Example: *Stentor*, common in fresh water (Fig. 216, A).

Order 3. Oligotrichida. Cilia limited almost entirely to the oral zone.

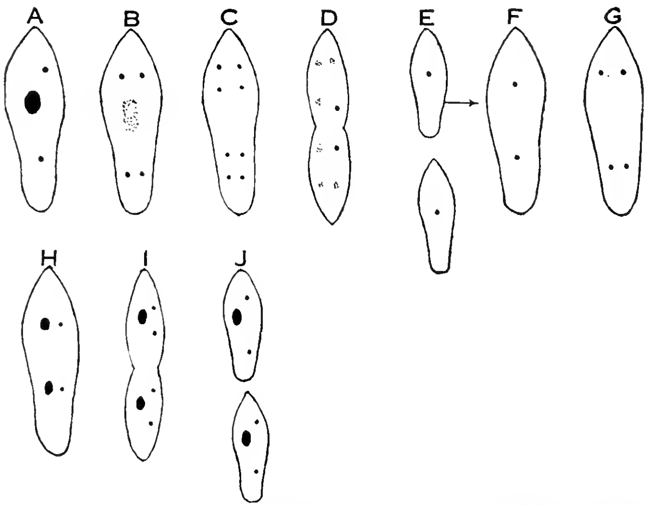


Fig. 215.—Diagram of the nuclear changes in *Paramecium aurelia* during endomixis. A, typical nuclear condition; B, degeneration of macronucleus and first division of micronuclei; C, second division of micronuleci; D, degeneration of six of the eight micronuclei; E, cell division; F, first reconstruction division of micronuclei; G, second reconstruction division; H, transformation of two micronuclei into two macronuclei; I, division of micronuclei and cell division; J, two complete new individuals. (*After Woodruff, Foundation of Biology, copyright, The Macmillan Company. By permission.*)

Example: *Halteria*, a fresh-water form that moves in leaps by means of cirri.

Order 4. Hypotrichida. A flattened body, as a rule with cilia, cirri, and membranelles on the ventral surface.

Example: *Stylonychia* (Fig. 216, D).

Order 5. Peritrichida. Cylindrical or cup-shaped body, usually free of cilia except in the adoral zone; and usually provided with a contractile stalk.

Examples: *Vorticella* (Fig. 216, C); *Carchesium*, a branched colonial form.

CLASS II. SUCTORIA. SESSILE PROTOZOANS WITHOUT CILIA EXCEPT IN EARLY STAGE OF DEVELOPMENT. They are parasitic forms provided with tentacles for piercing or sucking.

Example: *Tokophrya* (Fig. 216, B). One species is frequently found attached to fresh-water copepods, which are small crustaceans.

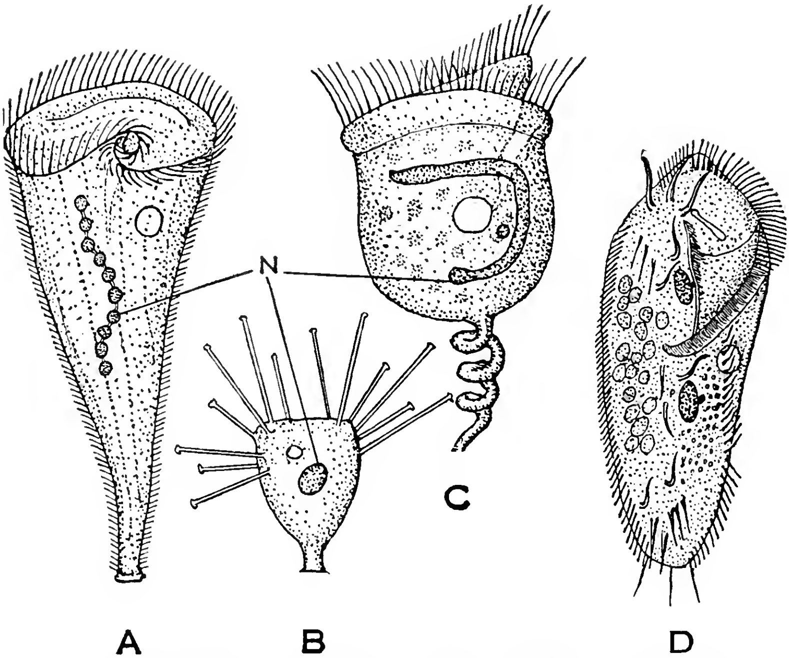


FIG. 216.—A, *Stentor*. B, *Tokophrya*. (*After Hertwig.*) C, *Vorticella*. D, *Stylonychia mytilus*. (*After Stein.*) N, macronucleus.

METAZOA

The group Metazoa includes all animals above Protozoa and therefore has the rank of a *subkingdom*. On this basis Protozoa is both a subkingdom and a phylum. The general features that distinguish Metazoa from Protozoa are as follows:

1. The body of the Metazoan is composed of many cells that may be divided into two general classes: somatic cells and germ cells.

2. The somatic cells are differentiated into tissues and organs, in which there is specialization of structure and function.

3. The germ cells are the reproductive cells, which in many forms are segregated from the somatic cells early in ontogeny.

4. Though asexual reproduction by fission or budding occurs, there is always sexual reproduction from a fertilized egg or, less commonly, an unfertilized egg.

5. The developing egg undergoes cleavage; the cells or blastomeres thus formed adhere to one another to produce a multicellular complex.

6. At least two germ layers develop: an ectoderm, forming the external covering, and an endoderm, lining the alimentary canal and its outgrowths. Between these, in the majority of metazoans, a third germ layer, the mesoderm, is formed from which muscles, vascular and other tissues and organs develop.

The distinction between Metazoa and Protozoa is not sharp since colonial protozoans, such as *Volvox*, consist of groups of different kinds of cells, organically connected with one another. Colonial Protozoa to a certain extent bridge the gap between solitary Protozoa and Metazoa, but in the latter there is a greater degree of interdependence among the cells of the individual organism than there is between the individual members of a protozoan colony.

PHYLUM 2—PORIFERA

Porifera (pore bearers) or sponges are lowly organized Metazoa that do not seem to lie in the direct line of ancestry of the higher forms. They are sessile, aquatic animals, most of which live in the sea. The body of the simplest sponges (*Ascon* type) is tubular in form and is attached at its closed basal end to the substratum. The free end is provided with an opening, the *osculum.* The thin walls are pierced with smaller openings called *pores* (Fig. 217A). The principal cavity of the tube, the *gastral cavity,* is lined with *flagellated collar cells* (Fig. 218), known as *choanocytes,* which bear a striking resemblance to certain flagellated protozoans such as Codosiga. The food of sponges consists of small animals and plants and organic matter in the water, which with its contents is drawn in through the pores by the action of the flagella of choanocytes into the gastral cavity, where the food is ingested and digested by the choanocytes, the water leaving the gastral cavity by the osculum. In the *Sycon* type of sponge the gastral cavity consists of numerous outpocketings of the main cavity, called flagellated chambers or *ampullae*, which alone contain choanocytes. Water enters the ampullae through pores and passes into the central cavity, now called the *cloacal cavity*, from which it leaves by the osculum (Fig. 217B). The *Leucon* type of sponge (Fig. 217C) results from a separation of the ampullae from both external and cloacal surfaces by an increase of mesodermal tissue, the ampullae retaining their connections with both surfaces by means of narrow canals. Both the incurrent canals (the original pores), leading to the ampullae, and the excurrent canals, leading away from them to the cloacal cavity, may be enlarged to form *subdermal* and *sub-*

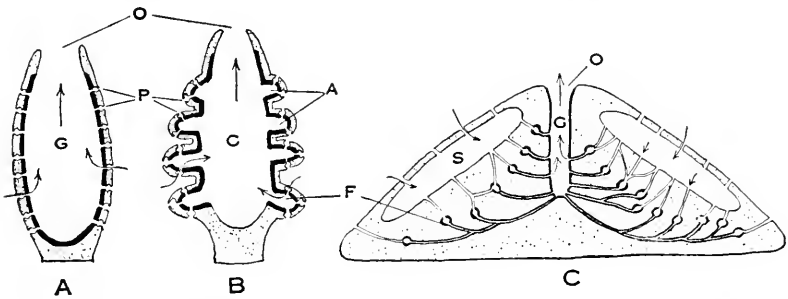


Fig. 217.—Diagrams of three structural types of sponges. A, *Ascon* type; B, *Sycon* type; C, *Leucon* type. The dermal epithelium is indicated in light line, the gastral epithelium in heavy black. Since the outer layer of the sponge larva becomes the inner layer of the adult, there is some difficulty in applying the terms ectoderm and endoderm. As it is, the dermal epithelium corresponds in position to the ectoderm of other forms and the gastral epithelium to the endoderm. C, cloacal cavity; F, flagellated chamber; G, gastral cavity; O, osculum; P, incurrent pores; S, subdermal cavity.

cloacal spaces. In any case the choanocytes are confined to the ampullae.

The outer layer of the body of the sponge is composed of a single layer of flattened cells. The gastral cavity and the ampullae are lined with choanocytes. The remaining cavities are lined with a smooth epithelium. The middle layer, or mesoderm, lying between the dermal layer and the gastral layer or the derivatives of the latter, varies in thickness and contains a variety of structures, some of which are skeletal parts, such as the hard *calcareous* or *siliceous spicules*, or the softer horny fibers of *spongin*. Both spicules and spongin are present in many sponges, though some contain neither. Some spicules are narrow rods, pointed or rounded at the ends, others are tri- and tetra-actinal and various other shapes. The cells of the mesoderm or more properly, the *mesenchyme*, consist of (1) *scleroblasts*, which secrete the spicules, and spongioblasts, which produce the spongin; (2) *stellate connective tissue cells;* (3) *myocytes*, which are contractile and are found at the pores and osculum, where they function as sphincters; and (4) *archeocytes.* The last are amoeboid cells that share with the choanocytes the ingestion and digestion of food and also give rise to germ cells and to

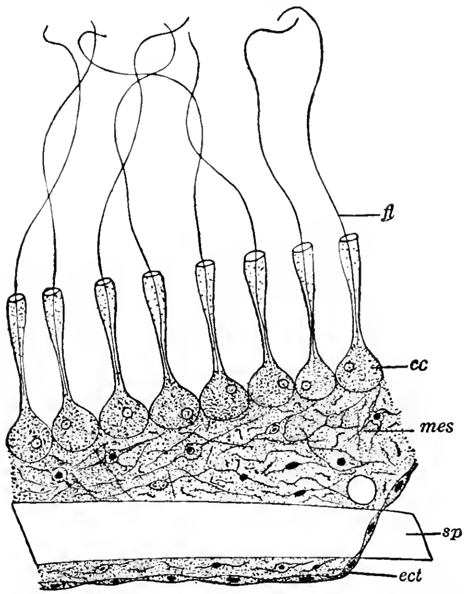


FIG. 218.—Portion of cross section of *Grantia*, a Sycon type of sponge. *cc*, choanocytes; *ect*, dermal epithelium; *fl*, flagellum of choanocyte; *mes*, mesoglea; *sp*, portion of spicule. (*From Shull, LaRue, and Ruthven, Animal Biology.*)

gemmules. Reproduction occurs asexually by budding, sexually from fertilized eggs and by the formation of gemmules. Gemmule formation, which is more common in fresh-water sponges, seems to be an adaptation for surviving low temperature or lack of water. This is accomplished, in the case of the fresh-water sponge during summer and fall by the formation of capsules of archeocytes in the mesenchyme. The gemmules, composed of encapsulated archeocytes, fall to the bottom if the sponge dies and remain there until the following spring, when they develop into sponges. All fresh-water sponges do not die in the winter, even though gemmules are formed.

Separate sexes occur in some species of sponges; others are hermaphroditic. The fertilized egg develops into a two-layered, ciliated, motile larva. The gastral cavity and its derivatives develop from the outer layer of the larva; and the dermal layer and mesenchyme come from the inner layer of the larva. Thus there is in sponges what is called an *inversion* of the germ layers, since in other metazoa the outer layer of the gastrula gives rise to ectoderm and the inner layer to endoderm. At metamorphosis the ciliated sponge larva becomes attached to the substratum and is transformed into a sponge.

Sponges lack the usual organ systems found in higher Metazoa. There is no nervous system. The flagella of the collar cells beat independently and not in unison, as do the cilia of ciliated epithelia of other metazoans. The currents created in the water by the flagella bring in food and oxygen and remove waste. There is no other circulatory or excretory system. The myocytes located about the pores and the osculum represent a very primitive form of contractile tissue which combines the properties of nerve and muscle, since it responds normally to direct stimulation. In keeping with their low degree of organization, sponges display a remarkable power of regeneration. If sponges, of certain species, are crushed to a pulp and pressed through fine bolting cloth, the dissociated cells collect in small masses, some of which eventually develop into normal sponges.

CLASS I. CALCAREA. Marine sponges, small in size, tubular in shape, solitary or colonial, with calcareous spicules.

Example: *Grantia canadensis*, a common species of the Sycon type.

CLASS II. NONCALCAREA. Marine and fresh-water forms with siliceous spicules or spongin, or both, or neither.

Examples: *Euplectella aspergillum*, Venus flower basket, a "glass" sponge; *Spongilla lacustris*, a common fresh-water sponge; *Hippospongia gossypina*, an American species of commercial sponge.

PHYLUM 3—COELENTERATA

There are two morphological types among the Coelenterata: (1) the *polyp* or *hydroid* form, which is sessile, and (2) the *jellyfish* or *medusoid* form, which is free-swimming. The polyp type is illustrated by *Hydra*, whose body is a double-walled, tubular sac provided with a fringe of usually six tentacles around its open, free oral end. Its body wall consists of two layers of cells: the outer one, *ectoderm,* and the inner one, *endoderm.* Between these two layers is a thin noncellular, supporting tissue, the *mesoglea.* The endoderm lines the *gastrovascular cavity* and the tentacles. Thus each tentacle is a double-walled tube, whose cavity, reduced in size, is a continuation of the gastrovascular cavity (Fig. 219A). The medusa type is illustrated in a simple form by *Gonionemus,* the convex side of whose bell-shaped body, the *exumbrella,* corresponds to the attached blind end of the

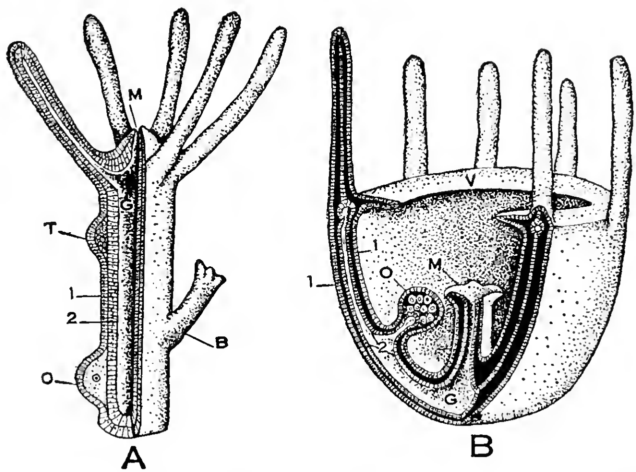


FIG 219.—Diagrams for comparing the *polyp* type, A, with the *medusa* type, B. 1, ectoderm; 2, endoderm; B, bud; G, gastrovascular cavity; M, mouth; O, ovary; T, testis; V, velum. Mesoglea is shown in solid black.

polyp; while the open end of a tube, the *manubrium,* leading from the concave surface of the bell, corresponds to the oral end of the polyp (Fig. 219B). In jellyfishes, which are large medusoids, the mesoglea is a thick jellylike layer containing cells that have immigrated from the ectoderm and endoderm. Both polyp and medusa types are radially symmetrical. The term "Coelenterata" (hollow-intestined) refers to the presence of the gastrovascular cavity in these animals.

The ectoderm of Hydra is composed of *epitheliomuscular* cells, *interstitial* cells, and *nerve* cells. The epitheliomuscular cell of the ectoderm has the form of a short column whose inner end is drawn out at right angles to the main axis of the cell and contains contractile fibers. These fibers run parallel to the long axis of the hydra, so that when they contract, the body of the hydra shortens. The interstitial cells produce egg and sperm cells and also give rise to *nematoblasts*, which are stinging cells capable of discharging a threadlike tube, the *nematocyst*, and usually a

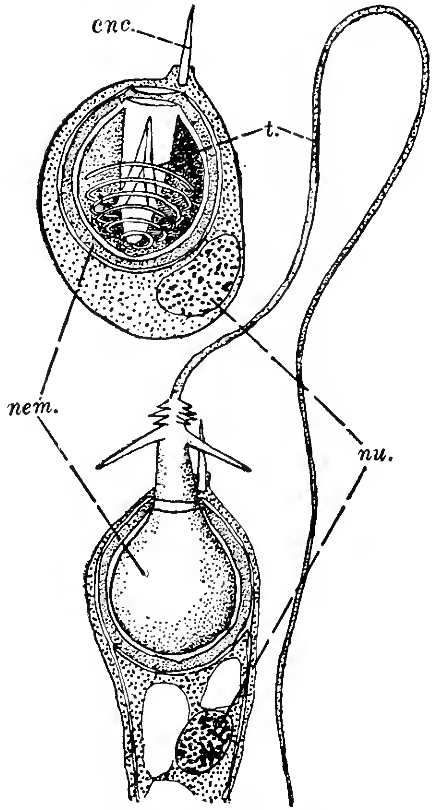


FIG. 220.—Nematocysts of *Hydra* before and after discharge. *cnc*, cnidocil; *nem*, nematocyst; *nu*, nucleus of nematoblast; *t*, threadlike tube. (*From Dahlgren and Kepner, Principles of Animal Histology, copyright, The Macmillan Company, after Schneider. By permission.*)

poisonous fluid. Discharge of nematocysts can be produced in a living hydra on a slide in water by the addition of dilute acetic acid or methyl green. The function of the *cnidocil*, a short projection at the free end of nematocyst, is unknown. Once a thread has been discharged the nematoblast from which it came disappears and a new one takes its place from the interstitial cells. The thread of a *penetrant* type of nematocyst is capable of piercing the integument of small animals. In the *volvent* type the thread forms a coil about objects when discharged. In a third type, the *glutinant* type, the discharged thread adheres to objects by means of a sticky secretion. All three types are probably used in capturing food (Fig. 220).

The nerve cells of Hydra are in the form of a loose network extending throughout the ectoderm and also in the endoderm. In medusoid forms there is a *nerve ring* in the outer rim of the umbrella, which also contains sense organs (simple eyes or pigment spots, with or without a lens).

Hydra attaches itself by a basal disk to the substratum by means of an adhesive substance secreted by the ectodermal cells. In *Hydra oligactis*, these cells, under certain conditions, secrete a gas, which, confined in a bubble of mucus, serves as a float from which the hydra hangs downward in the water (Fig. 221).

The mouth of the hydra is a star-shaped opening in a rounded elevation, the *hypostome*, about which the tentacles are arranged. The tentacles with the aid of the nematocysts capture food and bring it to the mouth. The single layer of cells composing the endoderm is thicker than the ectoderm. Its principal cells are epitheliomuscular cells and *gland* cells. Most of the epitheliomuscular cells of the endoderm bear several flagella on their free surfaces. They are digestive in function, ingesting and digesting food after the manner of an amoeba (intracellular digestion). The gland cells are also flagellated but are without contractile fibers at their bases. They secrete a digestive fluid, by means of which food is digested in the gastrovascular cavity (extracellular digestion). Undigested material is ejected through the mouth. The peristomal (about the mouth) gland cells and the gland cells of the basal-disk region differ in appearance from the remainder and may have special functions. Interstitial cells are also found in small numbers in the endoderm near the mesoglea. A few nerve cells also occur in the endoderm.

The contractile fibers of the endodermal epitheliomuscular cells run transversely to the main body axis of the hydra and thus form a circular muscular band. This, with the longitudinal band formed by the fibers of the ectodermal epitheliomuscular cells, accounts for the active and varied movements of the hydra.

Hydra attaches itself by means of the basal disk, but it can move by a creeping motion of the disk. It also moves by a head-over-

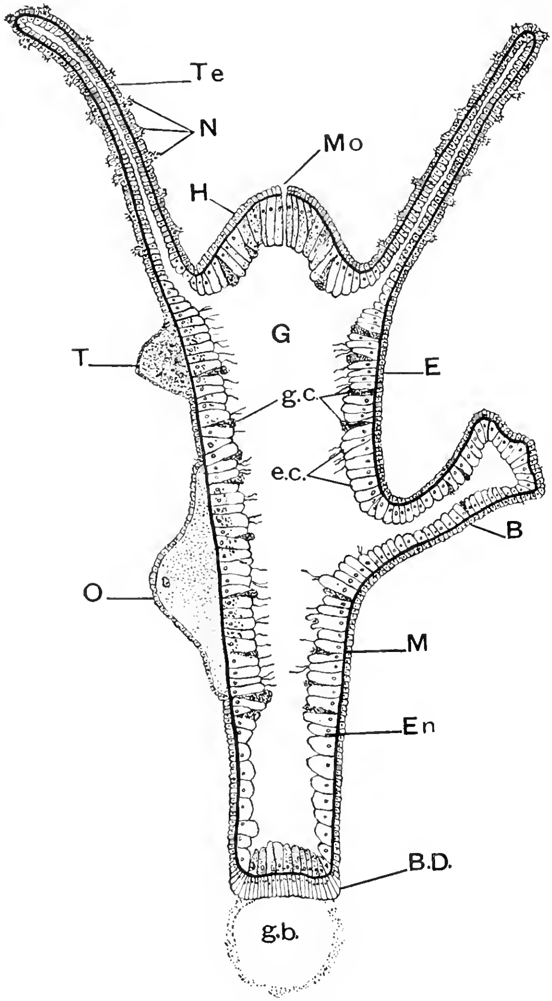


FIG. 221.—*Hydra oligactis*, semidiagrammatic longitudinal section. B, bud; B.D. basal disk; E, ectoderm; En, endoderm; e.c., epitheliomuscular cells of endoderm; G, gastrovascular cavity; g.b., gas bubble; g.c., gland cells; H, hypostome; M, mesoglea (solid black line); Mo, mouth; N, nematocysts; O, ovary; T, testis; Te, tentacle. (*After Kepner.*)

heels movement by arching the body until the ends of the tentacles can grasp the substratum and then, releasing the basal disk, swinging the latter to a new position for attachment. Letting go the hold by the tentacles, the hydra rises to an upright position. In strong contrast with sponges, the hydra is capable of quick energetic movements of its body and tentacles. As already noted, it may in some cases detach itself and float about by means of a mucus-enclosed gas bubble formed at its base.

Reproduction in Hydra, referred to in an earlier connection (p. 155), may be asexual (budding or fission), or sexual. The germ cells of Hydra and the lower coelenterates are said to arise from interstitial cells of the ectoderm. In the higher coelen-

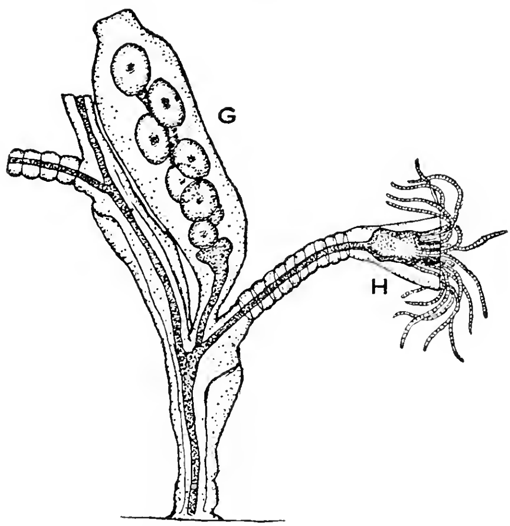


FIG. 222.—*Obelia.* G, gonosomes and gonotheca; H, hydranth and hydrotheca.

terates they come from similar cells in the endoderm. In the face of these facts, it is difficult to hold that a line of germinal continuity or a germ track of cells as distinguished from the somatic cells, exists in these animals, unless one assumes that the interstitial cells are undifferentiated cells that have retained the reproductive potencies of the egg. In Hydra the testis develops as a swelling in the ectoderm of the body wall just below the tentacles; the ovary develops as a similar swelling near the base (Fig. 221). A single testis develops numerous spermatozoa; a single ovary produces a single egg. The egg is fertilized in the ovary and undergoes development as far as gastrulation within the ovarian epithelium, after which it escapes and grows into an adult hydra. In many of the Hydrozoa there is metagenesis in the life cycle, *i.e.*, an alternation of polyp with medusoid generations. The polyp, developing from fertilized egg, reproduces asexually by budding the medusae, which are male and female.

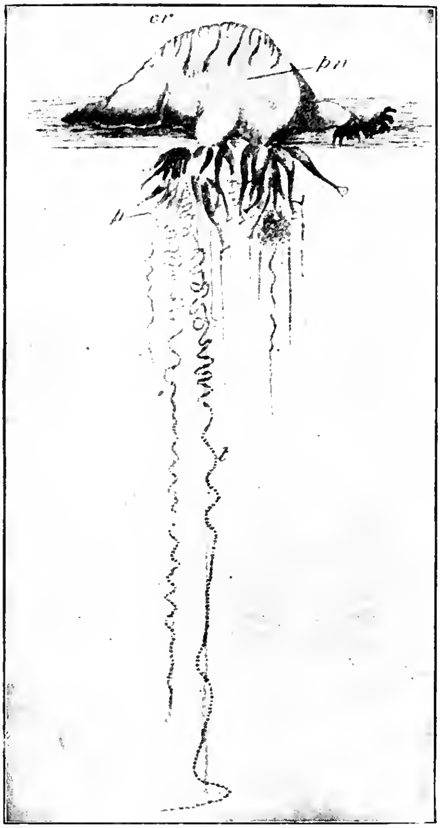


FIG. 223.—*Physalia*, the Portuguese man-of-war, a pelagic colonial hydrozoan. *cr*, crest; *p*, polyp; *pn*, pneumatophore. (*From Parker and Haswell, Textbook of Zoology, copyright, The Macmillan Company. By permission.*)

Regeneration is marked in Hydra. Grafting of parts can also be experimentally accomplished without difficulty.

CLASS I. HYDROZOA. Radially symmetrical, sessile, polyp forms, and free-swimming sexual medusae; both sometimes occurring in the life history of a single species. Without going into the intricacies of classification, these different conditions may be illustrated by the following:

Chlorohydra viridissima, also known as *Hydra viridis,* the common fresh-water hydra, colored green by algae in the endodermal cells, has a *polyp* stage only. *Gonionemus murbachi,* a marine, *craspedote medusa* (*i.e.,* having a velum extending inward from the edge of the subumbrella), has practically

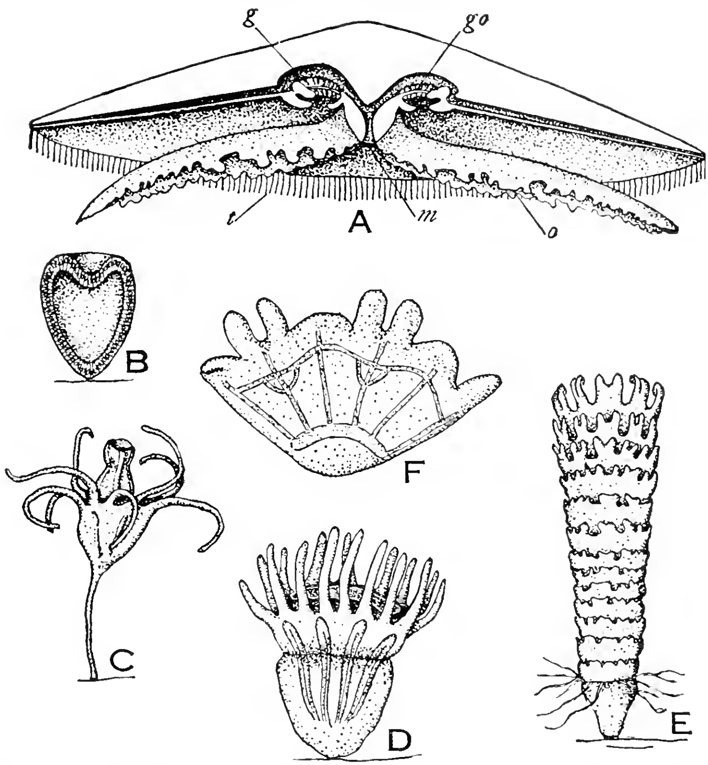


FIG. 224.—*Aurelia,* a jellyfish, and stages in the life history. A, vertical section of adult; B, vertical section of gastrula; C, polypiform larva with eight tentacles; D, scyphistoma with sixteen tentacles, in beginning of strobilation; E, strobila; F, ephyra, which develops into a jellyfish. *g,* gastral cavity; *go,* gonad; *m,* mouth; *o,* oral lobe; *t,* tentacles. (*After Leuckart-Nitsche wall chart.*)

a medusa stage only, its polyp stage being minute and of short duration. *Obelia dichotoma,* a marine form, has a definite *alternation of generations,* the colonial polyp producing sexual buds (*gonosomes*) that develop into free-swimming male and female medusae. The fertilized egg develops into a polyp (Fig. 222). *Physalia pelagica,* the Portuguese man-of-war is a free-swimming colonial form, the individual, highly *polymorphic* members of which are in communication with one another by means of the common gastrovascular cavity. The colony is attached to a float (*pneumatophore*) containing gas that can be released through a pore, and later regenerated, enabling the animal to drop below the surface and rise again. There is an *alternation of generations* (Fig. 223).

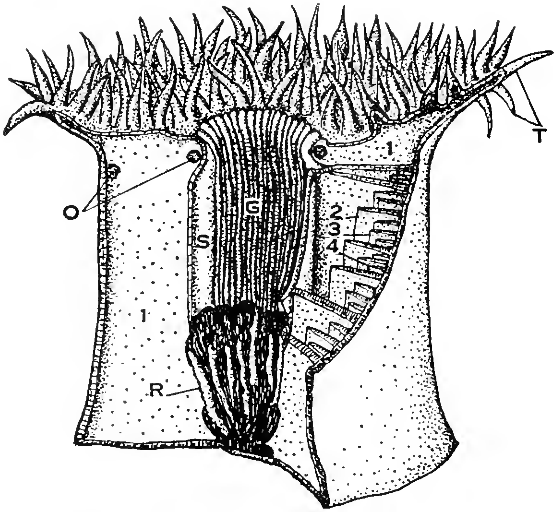


FIG. 225.—Dissection of *Metridium marginatum*, a sea anemone, showing the internal structure. 1, 2, 3, and 4, primary, secondary, tertiary, and quaternary mesenteries extending inward from the body wall, only the primary reaching the gullet, G. The gullet opens into a common basal gastrovascular cavity. O, ostia, pores through which water passes from one chamber to the other through the primary mesenteries. R, reproductive organs; S, scyphonoglyphe, a ciliated groove in either side of the gullet; T, tentacles. (*Modified from Lineville and Kelly, Textbook in General Zoology, Ginn and Company.*)

CLASS II. SCYPHOZOA. JELLYFISHES. Radially symmetrical, usually with an alternation of generations, although the medusoid or the hydroid generation alone may be present in some. In general, the medusoid stage is more prominent in the group than the polyp. The latter, known as the *scyphistoma,* differs from Hydra in the following points: (1) the attachment of its *aboral* end in a cup; (2) the presence of four endodermal *mesenteries* projecting into the gastrovascular cavity; (3) the possession of an ectodermal *gullet.* The medusae are *acraspedote* (lacking a velum), and are produced from the scyphistoma by terminal budding (*strobilation*).

Example: *Aurelia*, a large jellyfish, common on the Atlantic coast (Fig. 224).

CLASS III. ANTHOZOA. SEA ANEMONES AND CORALS. The body is cylindrical and attached at the aboral end by the foot or pedal disk. The mouth is oval, giving the animal a *biradial* symmetry, and is surrounded by from six to several hundred tentacles. An ectodermal *gullet* leads from the mouth to the gastrovascular cavity, which is subdivided by six or more longitudinal *mesenteries* composed of mesoglea and endoderm. The ectoderm secretes, in corals, a *skeleton* of calcium carbonate, and in other forms a hornlike substance called *ceratine*. All are marine and dioecious.

Examples: *Metridium marginatum*, a sea anemone (Fig. 225); *Epizoanthus americanus*, a sea anemone often attached to a hermit crab; *Porites porites*, a common West Indian coral.

PHYLUM 4—CTENOPHORA

These beautiful marine animals are sometimes included in the Phylum Coelenterata, which they resemble very closely (Figs. 226 and 227). The *biradially symmetrical* body is almost transparent and may be round, oval, or ribbonlike in outline. Its outer surface is soft and bears eight longitudinal rows of *combs* whose teeth are composed of transverse plates of fused cilia. Ctenophore means "comb bearer." In many, branched *retractile tentacles* arise from pits near the aboral pole (Fig. 227). They are provided with *adhesive cells*, which are used in capturing prey. The slit-shaped *mouth* opens into a widened *stomach* region, to which is connected a system of tubes opening to the outside by minute pores. This complicated gastrovascular space is lined with endoderm. Between the latter and the ectoderm is a thick jellylike mesenchyme, which differs from the mesoglea of coelenterates in that it represents a true third germ layer. It also contains muscle fibers of mesodermal origin. The animals, therefore, are *triploblastic*.

Lying in a pit at the aboral pole is a *statocyst*.

Ctenophores are *hermaphroditic*, and pass through a complicated *metamorphosis* before reaching the adult stage. *Paedogenesis*, reproduction in the larval stage, occurs in some species.

CLASS I. TENTACULATA. Characterized by a pair of long tentacles or a pair of oral lobes which, however, may appear only in the larva.

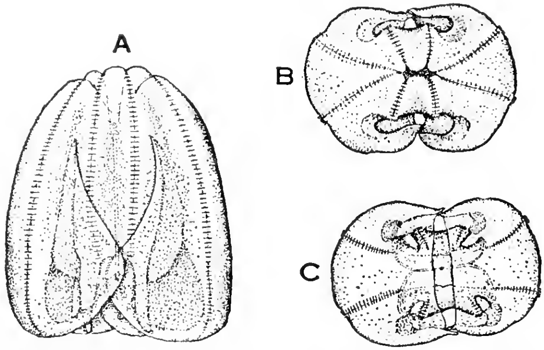


FIG. 226.—*Mnemiopsis*, a ctenophore with lobes in place of tentacles. A, side view; B, aboral side; C, oral side, showing the mouth as a small opening in the center.

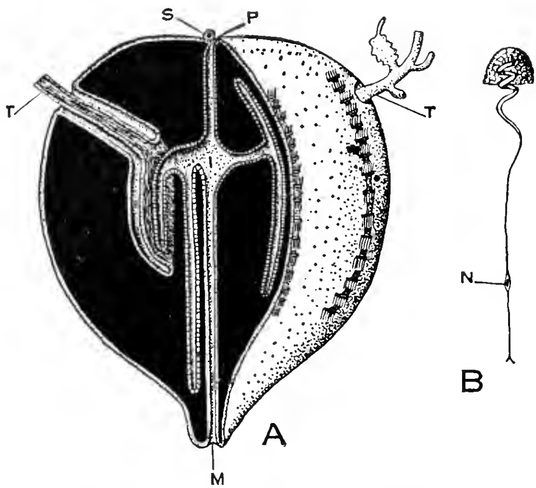


FIG. 227.—A diagrammatic dissection of *Hormiphora*, a ctenophore; the ectoderm is dotted, the endoderm striated, and the mesoderm solid black. I, infundibulum, the stomach region, which is connected with eight meridional canals one of which is shown beneath the more central row of combs. The infundibulum also gives off two stomodaeal canals and two tentacular canals, one of each being shown in the figure. The stomodaeal canal is close to the stomodaeum, the tube leading from the mouth (M) to the infundibulum. P, excretory pore; S, statocyst; T, tentacle, the one on the left, in longitudinal section, shows the muscular core by which the tentacle may be retracted into the sheath. (*Based on Parker and Haswell.*) B, adhesive cell from a tentacle. The convex surface is sticky, and the coiled filament acts as a spring to prevent the cell being pulled out when it is attached to prey. The spiral thread is attached at its base to the muscular axis of the tentacle. N, nucleus. (*After Hertwig and Chun.*)

Examples: *Pleurobrachia pileus*, sea comb; *Cestus veneris*, a flattened, ribbonlike form; *Mnemiopsis leidyi*, the sea walnut (Fig. 226).

CLASS II. NUDA. Tentacles and oral lobes absent.

Example: *Beroe ovata.*

PHYLUM 5—PLATYHELMINTHES

Platyhelminthes (flatworms) are the first forms in which a definite "head end" is present. The process of cephalization as pointed out in a preceding chapter (p. 170) involves the concentration of sense organs at the anterior end of the animal and a corresponding concentration of nervous control mediated through cephalic nerve ganglia. Usually the body in cross section is an oval, flattened dorsoventrally. Flatworms occur in water, moist earth, and as parasites in animals and plants. The body is *triploblastic, unsegmented* and covered by a ciliated epithelium or by an unciliated cuticle. An alimentary canal may be present but not a body cavity, the space between the alimentary canal and the body wall being filled with a loose connective tissue known as *parenchyma*, of mesodermal origin. The alimentary canal like that of coelenterates is usually a blind tube lacking an anal opening. The excretory system consists of numerous *flame cells* connected with tubes opening by single or paired excretory pores to the outside of the body (Fig. 91). There is no blood circulatory system, nor a respiratory system. The nervous system consists of a pair of *cephalic ganglia* from which nerves pass to various parts of the body. Reproduction is sexual, but fission and budding are also common. Hermaphroditism is the rule. The ovaries and testes are well-developed internal organs provided with ducts leading to the outside.

CLASS I. TURBELLARIA. Ciliated, free-living forms, living in fresh or salt water, or in moist soil. In most cases the ciliated glandular epidermis contains *rhabdites*, very small rodlike bodies, produced by the epidermal gland cells or by the parenchyma. They are discharged in the slimy secretion of the ectoderm. Functional nettle cells, nematoblasts, are sometimes found, but these have been shown to have been acquired from coelenterates taken as food. *Adhesive suckers* are present in some. The mouth is an opening at the end of a pharynx, which usually can be thrust from the mouth as a movable muscular proboscis (Fig. 228).

SUBCLASS 1. ACOELA. A mouth, with or without a proboscis, is present, but the remainder of the alimentary canal is absent. Eyes are usually lacking. There is a statocyst in the dorsal surface over the cephalic ganglia.

Example: *Childia spinosa,* marine form, 1.4 mm. in length.

SUBCLASS 2. COELATA. An intestine is present.

Order 1. Rhabdocoelida. The intestine is an unbranched tube, in some cases, slightly lobulated. Found in marine and fresh water and on land (Fig. 228, A and B). Some reproduce asexually by terminal budding (Fig. 228, B).

Examples: *Dalyellia,* a fresh-water American form; *Microstomum,* both fresh- and salt-water genus.

Order 2. Tricladida. Commonly known as planarians and characterized chiefly by an intestine with three main branches, one extending forward and two backward from the pharynx. Each main trunk gives off diverticula with separate branches. A pair of eyes are usually present (p. 192) in the head end. On either side in front of the eyes is a sensitive lobe or *auricle.*

Example: *Euplanaria maculata,* a fresh-water form (Fig. 228, C).

Order 3. Polycladida. The intestine has many branches ramifying to all parts of the body. Eyes, otocysts, tentacles, and tactile organs are well developed (Fig. 228D).

Example: *Planocera inquilina,* found as a commensal form in the branchial chamber of a large marine snail, *Busycon.*

CLASS II. TREMATODES. FLUKES. Exclusively *parasitic.* Cilia are absent, or present only in larval stages. Usually the mouth is subterminal and the intestine is bifurcated. *Hooks* and *suckers* are found in *ectoparasites* for attachment to the host, but *suckers* only in *endoparasites.* The name of the class, Trematodes, refers to the presence of suckers (*trema,* hole). *Eyespots* occur in ectoparasites, but only in the larva of endoparasites.

Order 1. Monogenea. For the most part are *ectoparasites* on aquatic animals, but some change to endoparasitism. There is but *one host.* The organs for attachment, at the ends of the body, are well developed. Some have small pores.

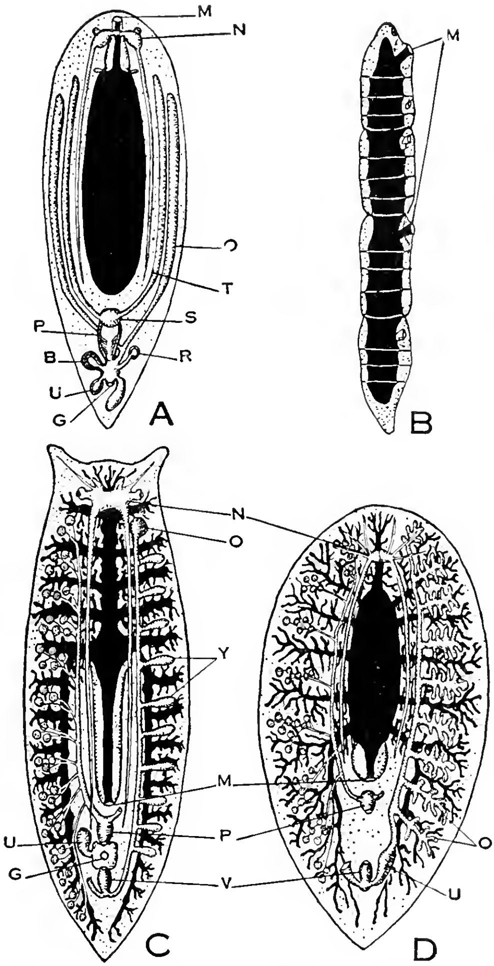


Fig. 228.—Types of Turbellarians. (*Based on von Graff.*) A and B, Rhabdocoeles; C, triclad; D, polyclad. The alimentary canal is represented in solid black. B shows strobilation or division taking place in a chain of four individuals of *Microstomum*. Division begins in the alimentary canal by the formation of septa which reach to the body wall. The chain really consists of sixteen partially formed zooids. B, bursa copulatrix; G, genital aperture; M, mouth; N, nervous system; O, ovary; P, penis; R, receptaculum seminis; S, vesicula seminalis; T, testis; U, uterus; V, vagina; Y, yolk glands; in C and D, the testis and its ducts are shown on the left side of the animal and the ovary and oviduct on the right.

Examples: *Tristoma coccineum*, parasitic on the gills of the swordfish; *Polystoma integerrimum*, as a *larva*, parasitizes the gills of the frog tadpole, but when the gills are absorbed at *metamorphosis*, it passes into the pharynx, through the alimentary canal to the urinary bladder, where it is found in the adult frog as an internal parasite.

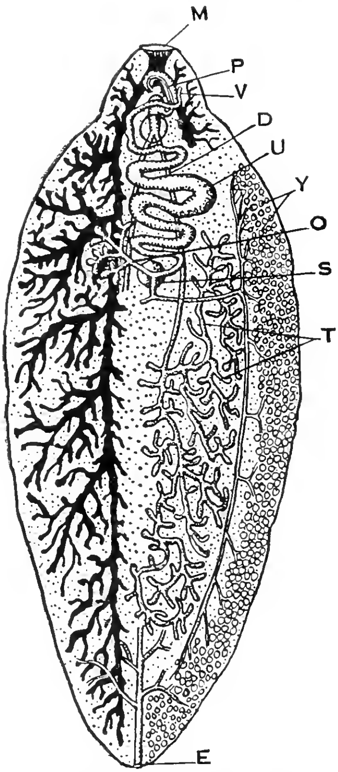


FIG. 229.—*Fasciola hepatica*, diagrammatic from the ventral side. The digestive tract in solid black is shown only in the left of the figure. The reproductive system is complete only in the right side of the figure. D, sperm duct; E, excretory pore and a small portion of the terminal excretory tubes; M, mouth; O, ovary; P, penis; S, shell gland; T, testis; U, uterus; V, vagina; Y, yolk glands. The ventral sucker is indicated by a circle below the penis.

Order 2. Digenea. *Endoparasites* living in two or more hosts, to which they attach themselves by one or two median suckers, of which the anterior one is the mouth, and the second one, when present, is for attachment only (Fig. 229).

Example: *Fasciola hepatica*, the *liver fluke*, lives as an adult in the liver of sheep, cattle, man, and other animals, where sexual reproduction takes place. The young embryos pass down the bile duct into the intestine, and out of the sheep's body into water, where they develop into a ciliated *miracidium* larva. Its intermediate host is a water snail of the genus *Limnaea*, whose tissues it enters by boring, and inside of which it forms a *sporocyst*. Eggs contained in the sporocyst develop parthenogenetically into *rediae*, which leave the sporocyst and enter the tissues. A number of parthenogenetic redia generations may be produced, followed, finally, by different larvae known as *cercariae*. These resemble the adult, except that they have a tail, which serves as an organ of locomotion until the animal encysts on a water plant, when the tail is lost. Sheep are infected by eating plants bearing cysts, the contents of which find their way to the liver, where the young animals grow to maturity. *Liver rot*, the disease produced by this parasite, is often fatal (Fig. 230).

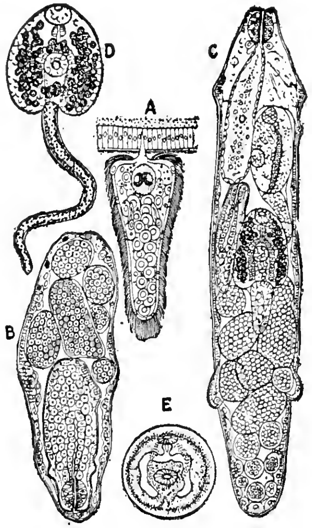


FIG. 230.

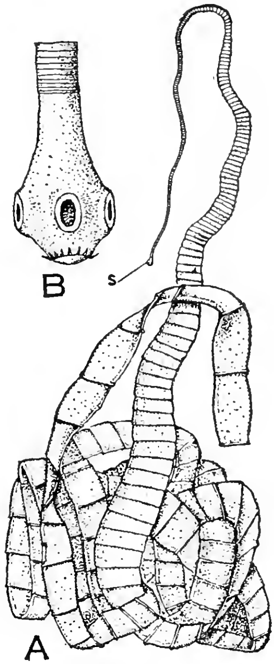


FIG. 231.

FIG. 230.—Stages in the development of *Fasciola hepatica*. A, miracidium; B, sporocyst, with rediae developing internally; C, rediae with second generation of rediae and cercariae; D, free cercaria; E, encysted cercaria. (*From Van Cleave, Invertebrate Zoology, after Thomas.*)

FIG. 231.—A, *Taenia solium*, the pork tapeworm. s, scolex. B, scolex, magnified. (*After Leuckart-Nitsche wall chart.*)

CLASS III. CESTOIDEA. TAPEWORMS. *Endoparasites* with two body regions: (1) the *scolex*, or head, containing hooks or suckers for attachment to the host; (2) the *strobila*, which is a series of segments, called *proglottids*, each of which is provided with both male and female reproductive organs. A mature proglottid is practically filled by the enlarged gonads. Tapeworms inhabit the intestine of vertebrates and live as larvae in the tissues of another animal used as food by the *principal host*.

There is no digestive tract, nutrition being absorbed through the body wall. The outer covering is a *nonciliated* cuticle capable of resisting the action of digestive juices (Fig. 231).

Example: *Taenia solium*, the pork tapeworm, is found as an adult in the human intestine, where it reaches a length of from 4 to 10 meters. It attaches itself by means of hooks and suckers. A small *six-hooked larva* develops from the fertilized egg and is expelled. The larva must then enter the stomach of the pig, where it bores through the stomach wall, and finds its way to the skeletal muscles. Here the larva develops into an oval *cysticercus* (9 by 5 mm.) and remains as a cyst until the infected tissue is eaten by man. In the cavity of the cysticercus the scolex is developed in an inverted position, and when the cyst wall is dissolved by the gastric juice, the scolex is protruded like the finger of a glove. In the intestine the scolex attaches itself and develops proglottids from its posterior end (Figs. 231, 232, and 233). *Taenia saginata*, the beef tapeworm, has a similar life history, except that the intermediate host is the ox. It is the commonest tapeworm in the United States.

PHYLUM 6—NEMERTEA

Nemertea (from *Nemertes*, one of the sea nymphs of Greek mythology) is the name of a group of ciliated, unsegmented worms, mostly marine, often included in the Phylum Platyhelminthes. The body is wormlike, ovoid, or circular in cross section and varies in length in different species from a few millimeters to 6 meters or more (30 meters in the case of *Lineus longissimus*). The alimentary canal, beginning with a mouth on the ventral surface near the anterior end, is a pouched tube, extending the length of the body and terminating in an anal opening. There is no body cavity, the space between the intestine and the body wall being occupied by a gelatinous parenchyma. A simple blood circulatory system is represented by two or more longitudinal vessels, connected with each other and with blood sinuses in the tissues. At the anterior end is a four-lobed cephalic ganglion above the alimentary canal, from which nerves extend to various parts of the body. The excretory system consists of flame cells, connected by tubules with two longitudinal canals opening on the surface of the body. Numerous simple eyes, ocelli, occur, sometimes along the sides of the body. Some also have auditory vesicles. The body wall contains several layers of circular and longitudinal muscles. They are dioecious as a rule, though a small number are hermaphroditic.

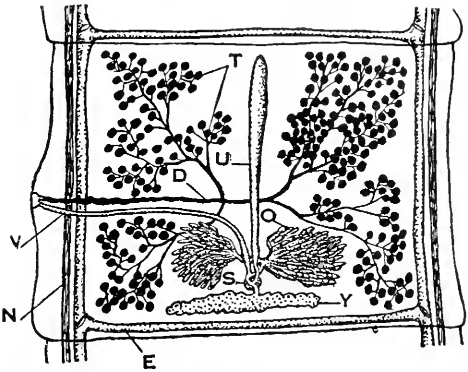


Fig. 232.—Diagram of a proglottid, showing organs of reproduction (*Based on Leuckart.*) D, sperm duct; E, excretory duct; N, nerve cord; O, ovary; S, shell gland; T, testis; U, uterus; V, vagina; Y, yolk gland.

One of the striking features of nemerteans is the proboscis, a muscular organ that can be extended from a pocket in front of the mouth to a distance almost as great as the length of the body. It seems to be primarily a tactile organ, though the fact that it is armed with dartlike stylets indicates an offensive or protective function also. Another feature is the contractility of the body. A specimen of *Cerebratulus lacteus*, capable of extending itself to 5 meters, can shorten to less than a meter. Many are brightly colored.

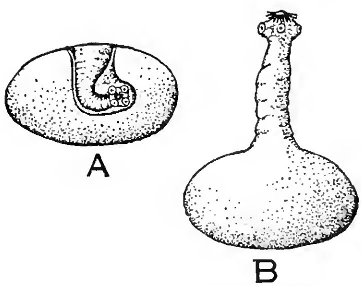


Fig. 233.—A, cysticercus (bladderworm) with inverted scolex. B, cysticercus with everted scolex. (*After Leuckart.*)

Most nemerteans are nonparasitic.

Examples: *Cerebratulus lacteus*, a marine form, found on the New England coast in the sand near low-water mark. Length of body is from 2 to 6 m.; width, 25 mm. *Prostoma rubrum*, breeds in fresh-water aquaria; reddish in color and about 18 mm. in length. *Carcinonemertes carcinophila*, parasitic on the gills and eggs of crabs.

PHYLUM 7—NEMATHELMINTHES

Nemathelminthes (threadworms or roundworms) are nonciliated, unsegmented worms circular in cross section, elongated and threadlike in form; some are free-living in water or moist earth and others parasitic in animals and plants. They lack paired appendages, though bristles, hairs, and suckers may be present. Most are dioecious.

CLASS I. NEMATODA. A smooth firm cuticula, overlying a softer subcuticula, forms the body covering. The mouth is at the dorsal side. The alimentary canal is a slightly differentiated tube lying loosely in a body cavity and provided with an anal opening near the posterior end of the body. The body cavity is a hemocoel and lacks a peritoneum. The subcuticula on each side projects into the body cavity, forming two longitudinal ridges (lateral lines) each of which contains an excretory tubule connected with the body cavity by a ciliated funnel or nephrostome. The two excretory tubules open to the outside by a single pore on the ventral side behind the mouth. A dorsal and ventral band of the form of longitudinal muscle fibers bulges into the body cavity. Each band of muscle is divided into right and left portions by a longitudinal nerve trunk. There are no circular muscle fibers. The nervous system consists of a ganglionated ring encircling the esophagus, and of a number of longitudinal nerves. Simple eyes and sensory papillae are present in some. Most nematodes are parasitic and dioecious. A few are viviparous. They are very widespread and the number of species has been estimated at over 100,000.

Examples: *Trichinella spiralis*, the cause of *trichinosis*, lives as an adult (male 1.5 mm. in length, female 3 to 4 mm.) in the small intestine of *man*, the *pig*, *rat*, *dog*, and *mouse*, where they reproduce sexually. The female after copulation penetrates the mucosa and gives birth to from 1,500 to 10,000 young. The latter migrate via the blood and lymph to the muscles of the thorax, neck, and jaw, in which they become encysted, thereby injuring the muscles to such an extent that death of the host may ensue. Man is infected by eating undercooked pork containing cysts from which the young worms are liberated by the action of the gastric juice (Fig. 234).

Necator americanus, the *American hookworm*, is found in the intestine of *man* and the *gorilla*, where it lives on the blood of its host, after first making a wound with its cutting lips and teeth. The adult male is 9 mm. in length, and the female 11 mm. After copulation, the female deposits numerous eggs, which do not complete development until discharged with the feces. Development then proceeds, the embryo molting twice and remaining inside of the loosened skin after the second molt. There are two general modes of *infection:* (1) through the *mouth*, in which case the larva passes directly to the intestine; (2)

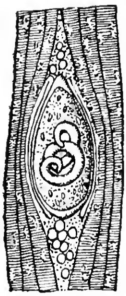


FIG. 234.

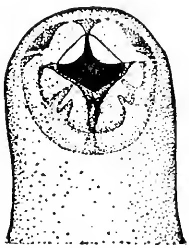


FIG. 235.

FIG. 234.—*Trichinella spiralis*, encysted in the muscle of the pig. (*After Leuckart.*)

FIG. 235.—Enlarged view of the dorsal side of the anterior end of the hookworm *Necator americanus*, showing the quadrangular shaped mouth opening through which two of the flat, platelike teeth can be seen. (*After Stiles.*)

through the *skin* of the feet and hands, from which it is carried by the blood to the lungs. Considerable damage is then caused by the animal boring through the lungs, heart, trachea, etc., to the intestine (Fig. 235).

The hookworm is a serious menace in the South, especially in localities where precautions are not taken to avoid soil and water pollution.

Ascaris lumbricoides is an intestinal parasite, especially common in *children*. The male averages about 20 mm. in length by 3 mm. in diameter, and the female 30 by 5 mm. The eggs pass out with the feces and develop directly to the larval stages in water or moist soil. Infection is by mouth from water, soil, and the skin of raw fruits (Fig. 236). The larvae bore through the walls of the intestine of the host, migrate through the lungs, liver, or heart, and then return to the intestine where they complete their development.

CLASS II. NEMATOMORPHA. Hairworms. In the adult state they resemble thick horsehairs. The integument consists of a thick cuticula, beneath which is a single layer of epidermal cells (hypodermis). The mouth and esophagus are closed in the adult state in some species. The body cavity is lined with a peritoneum and is provided with dorsal and ventral mesen-

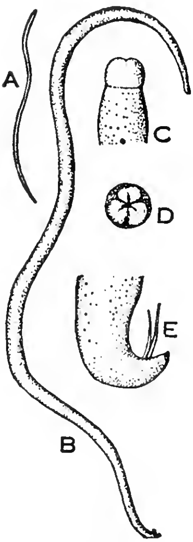


Fig. 236.

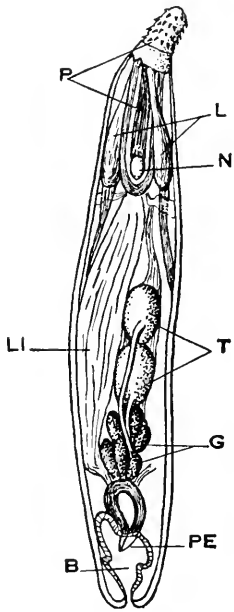


Fig. 237.

Fig. 236.—*Ascaris lumbricoides.* (*After Beneden.*) A, male three-fourths natural size; B, female, three-fourths natural size; c, head, enlarged, ventral side showing excretory pore; d, head, front view, three lobes surrounding the mouth; e, posterior end of the body of male greatly enlarged showing penial setae.

Fig. 237.—*Acanthocephalid*, male. (*After Leuckart.*) b, bursa; g, cement glands; l, lemnisci, two saccular organs of unknown function; li, ligament; n, nerve ganglion; p, proboscis and sheath; pe, penis; t, testes.

teries. A pair of eyes and a number of tactile bristles are present. The animals are dioecious and the fertilized eggs are deposited in the water, where the larvae develop and later parasitize aquatic insect larvae. If the host is eaten by a predaceous insect, or if the host dies, the larva may enter the body of a grasshopper or other insect. In either case, development is completed in the second host, from which the adult escapes through the body wall and eventually reaches water.

Example: *Gordius robustus*, a common horsehair worm, about 28 cm. long and 1 mm. wide; found in fresh water.

CLASS III. ACANTHOCEPHALA. There are *three body regions:* (1) the *proboscis*, armed with hooks, (2) the *neck*, (3) the *trunk*. The proboscis contains a ganglion from which two nerve cords pass backward. There are no special sense organs. There is a body cavity, but no alimentary canal. A pair of nephridia opens into the reproductive duct. These animals are *parasitic* in the intestine of vertebrates, attaching themselves by the hooked proboscis. The larval stage occurs in another host. Infection is by mouth from water containing the intermediate host (Fig. 237).

Examples: *Echinorhynchus gadi*, parasitic in the cod and other fishes; *Macranthorhynchus hirudinaceus*, parasitic in the intestine of the pig; larval stage in beetle grubs.

PHYLUM 8—TROCHELMINTHES

Trochelminthes (wheelworms) are very small aquatic animals, often microscopic in size, unsegmented, and with cilia, if present, confined to the anterior end or to the ventral surface of the body.

CLASS I. ROTATORIA. Rotatoria (rotators), or rotifers (wheel bearers), the best known members of the phylum, are extremely small aquatic animals, discovered by Leeuwenhoek in 1703. A common species, *Hydatina senta*, measures only 0.6 mm. in length. Other species are even smaller. The body of the rotifer is composed of three regions: *head*, *trunk*, and a *postanal tail* or *foot*, depending upon whether the animal is free-swimming or fixed. Free-swimming forms may attach themselves temporarily by means of cement secreted by a gland in the tail (Fig. 238). The cuticle covering the body is secreted by the epidermis (hypodermis). The head is provided with a ciliated disk (*corona*), in the center or ventral edge of which is the mouth. The cilia serve as organs of locomotion and also direct food into the mouth. The alimentary canal is a straight or slightly curved differentiated tube provided with an anal opening. The muscular pharynx (*mastax*) contains on its inner surface hard jaws (*trophi*). A pair of excretory tubes, connected with flame cells, opens into the hinder end of the intestine, on either side. Sometimes they open into a pulsating *bladder*, which in turn empties into the intestine (Fig. 238, v). The central nervous system consists of a cephalic (cerebral) ganglion from which nerves extend to the periphery. There are one or two dorsal antennae, located over the ganglion, and two lateral antennae, one on each side of the trunk. One or more rudimentary eyespots are usually present. They are dioecious, though there are a few species in which males are unknown. Both oviparous and viviparous types of reproduction occur.

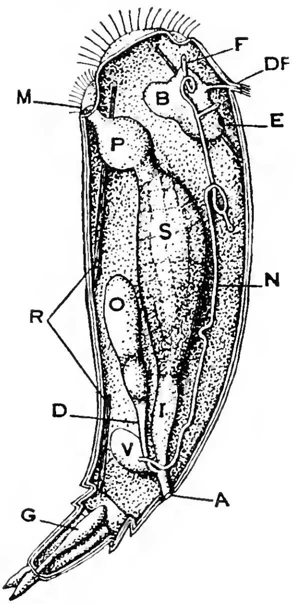


Fig. 238.—Diagram of a Rotifer. A, anus, B, brain; D, oviduct; DF, dorsal feeler; F, flame cell; G, cement gland, by the secretion of which the animal attaches itself temporarily; E, eyespot; I, intestine; M, mouth; N, nephridial tube; O, ovary; P, pharynx, containing masticating organs; R, retractor muscles; S, stomach; V, contractile vesicle (bladder). *(After Parker and Haswell.)*

The life history of a typical rotifer is interesting. There are two kinds of eggs: (1) a thick-shelled "winter" or "resting" egg, which can survive drought or cold; and (2) a thin-shelled "summer" egg. There are two types of females, externally alike, but differing in the kinds of eggs they produce. *Amictic* females produce eggs that cannot be fertilized. *Mictic* females produce eggs that may develop parthenogenetically but are also capable of fertilization. The fertilized winter eggs develop into amictic females. These in turn produce eggs that develop parthenogenetically into females, both mictic and amictic. The eggs of mictic females develop parthenogenetically into males, which produce sperm that may fertilize other eggs of mictic females. Thus the same eggs that produce males, if unfertilized, produce females if fertilized.

Whitney has shown that feeding *Hydatina senta* with *Polytoma*, a colorless flagellated protozoan, results in the production of a larger number of female-producing (amictic) daughters; while feeding with *Chlamydomonas*, a green flagellate, increases the number of male-producing (mictic) daughters. It will be noted that the effect of diet on sex potencies does not appear until the second generation following special feeding.

Physiologically, rotifers have remarkable powers of resistance to heat and drying. Some species when slowly dried on a slide, secrete a protective covering that enables them to survive lack of water and extremes of temperature. Such animals can be revived if placed in water after a year or more of desiccation. Under natural conditions this property enables them to survive drought and unfavorable conditions of temperature.

Example: *Hydatina senta,* a fresh-water species.

CLASS II. GASTROTRICHA. Gastrotichs are common aquatic forms but less well known than rotifers, from which they differ principally in possessing cilia on the flattened ventral surface of the body. The head is characteristically marked off from the trunk by a narrow neck region. They are both dioecious and monoecious. Some of them measure only 1.5 mm. in length.

Example: *Lepidoderma rhomboides,* a fresh-water species.

CLASS III. KINORHYNCHA. Very small marine trochelminthes measuring from 0.18 to 1.0 mm. in length; lacking cilia but provided with spines and bristles. Locomotion characterized by a peculiar invagination and evagination of the head. Sexes are separate.

Example: *Trachydemus mainensis,* found on tidal flats, Maine coast.

PHYLUM 9—BRYOZOA

Bryozoa (moss animals) are small, usually colonial animals, found on the surface of rocks, plants, and other objects in salt or fresh water. Externally some of them bear a resemblance to compound hydroids, but internally the resemblance ceases; for the individual zooids have a body cavity and a complete alimentary canal, bent so that the anus lies near the mouth (Fig. 239). There is usually a central nervous system between the mouth and the anus, and in some a pair of nephridial tubes with flame cells. The *lophophore* is a characteristic horseshoe-shaped ridge about the mouth, bearing hollow, ciliated tentacles. The epidermis (hypodermis) secretes a calcareous cuticle, the *ectocyst,* which protects the soft parts of the animal. In some the tentacles can be completely withdrawn into the ectocyst. These animals are either monoecious or dioecious. They are very ancient forms of life, fossils having been found in the Cambrian and all subsequent formations. The great majority of the species is marine.

Examples: *Plumatella princeps*, common in American ponds and streams; *Bugula flabellata*, Vineyard Sound; *Cristatella mucedo*, in ponds; colony, an elongated jellylike mass, 3 to 25 cm. in length.

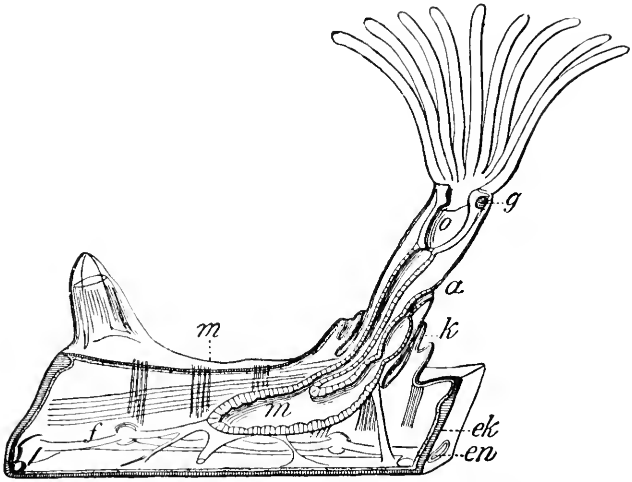


FIG. 239.—*Flustra membranacea* (*after Nitsche*), a single animal. *a*, anus; *ek* ectocyst; *en*, entocyst; *f*, funiculus; *g*, ganglion; *k*, collar, which permits retraction; *m*, stomach, also dermomuscular sac; *o*, esophagus. (*From Hertwig's Manual of Zoology by Kingsley. Henry Holt & Company. After Claparede.*)

PHYLUM 10—BRACHIOPODA

Brachiopods are characterized by a *bivalve* shell, which suggests a relationship to a mollusc, such as a clam or oyster; but the valves of the brachiopod are dorsal and ventral instead of right and left as in molluscs. As a rule, the animal is attached by a muscular stalk, the *peduncle*, which is a prolongation of the body, passing out between the valves or through an opening in the ventral valve (Fig. 240). The animal is attached to the valves by means of thin sheets of tissue called *mantles*. Within the space between the dorsal and ventral mantles are the lophophores, a pair of hollow coiled tentacles attached at either side of the mouth. Each lophophore has a ciliated groove, along one side of which are small ciliated tentacles. The lophophore gives the name to the group (Brachiopoda—arm-footed) and serves as a sensory-respiratory organ and also to direct food to the mouth. The mouth is a simple opening into a digestive tube, differentiated into esophagus, stomach, and intestine. An anal opening may or may not be present. There is a circulatory system consisting of a heart, blood vessels, and lacunar spaces. The body cavity is represented by a space in each mantle, connected with the cavities of the lophophores. Nephridial tubes, one or two pairs, connect the body cavity with the space between the two mantles. Usually dioecious, there is a *trochophore* larval stage resembling a similar stage in annelids (p. 415). Like bryozoans, brachiopods are very ancient animals, of which fossils are known from the Cambrian to

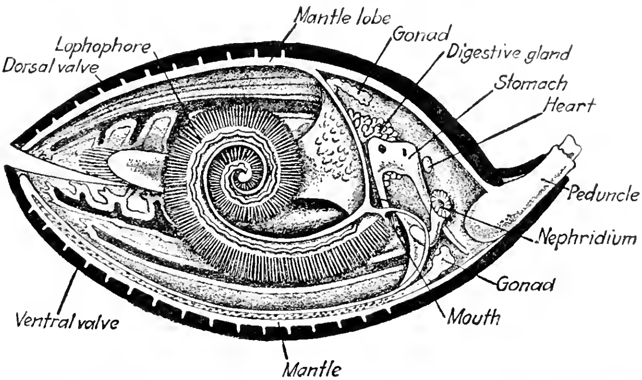


FIG. 240.—Semidiagrammatic sagittal section of a brachiopod, *Magellania lenticularis*. (*From Van Cleave, Invertebrate Zoology, after Parker and Haswell.*)

the present time. According to Pratt, there are about 2,500 fossil species and about 120 living species known at the present time.

Examples: *Terebratulina septentrionalis*, off Cape Cod; *Laqueus californicus*, California coast.

PHYLUM 11—PHORONIDEA

The Phoronidea are a small group of animals of uncertain systematic position but showing some resemblance to bryozoans and brachiopods. They are marine worms living in chitinous tubes within which the body can be completely withdrawn. A lophophore, consisting of a horseshoe-shaped ridge, bearing tentacles, is present at the anterior end of the body and can be thrust out of the tubes. The tubes frequently form tangled masses but do not communicate with one another. Each animal develops from a fertilized egg and there is no asexual generation formed by budding. The mouth, located in the center of the lophophore, opens into a U-shaped digestive tube terminating in an anus, also located in the center of the lophophore but separated from the mouth by a small lobe, the *epistome*, overhanging the mouth. The digestive tube is supported in a body cavity by longitudinal mesenteries. The body cavity is divided by a transverse portion into two parts, of which the anterior one is continuous with the cavities in the epistome and the lophophore. There is a blood circulatory system and also a nephridial system consisting of a pair of tubes leading from the body cavity to the outside. The nervous system consists of a ring about the anterior end of the alimentary canal and nerves extending from it to the tentacle and other parts of the body. The animals are monoecious. Development includes a larval stage (*actinotrocha*). There are only a single genus and about 11 species (Pratt).

Example: *Phoronis architecta*, lives in a straight tube, about 12 cm. in length. Coast of North Carolina.

PHYLUM 12—CHAETOGNATHA

The Chaetognatha (bristle-jawed) are free-swimming, unciliated, and unsegmented marine worms. The group gets its name from a fringe of prehensile, hooklike bristles and one or two rows of small spines on either side of the mouth. The digestive tract is a straight tube lying in a body cavity to which it is attached by dorsal and ventral mesenteries. An anus is present. The body cavity is divided into three parts by transverse septa. Special organs of circulation, excretion, and respiration are absent. A large dorsal nervous ganglion is located anteriorly above the mouth and a ventral ganglion under the intestine. There are a pair of eyes and an unpaired olfactory organ. These animals are monoecious and their development is interesting because the coelomic cavity is formed by the longitudinal fusion of a pair of diverticula of the lining of the archenteron, much as in annelids and chordates.

Example: *Sagitta elegans*, the arrowworm, about 3 mm. in length and common in the North Atlantic.

PHYLUM 13—ANNELIDA

The Annelida (ringed or annulated forms) are the *segmented worms*, which are found in fresh and salt water and in the earth. They differ from other worms in the fact that the body is made up of a number of similar (homodynamous) segments or metameres, united end to end. The body wall is covered on the outside by a cuticle, secreted by a single layer of underlying cells, the epidermis (hypodermis). Beneath the epidermis are an outer circular and an inner longitudinal layer of muscle. The inner surface of the body wall encloses a coelomic space and is usually lined by a peritoneum. As a rule, the coelomic cavity is subdivided by transverse septa (*dissepimenta*) into as many compartments as there are complete body segments. Paired appendages, when present, are not jointed. The subterminal mouth is overhung by a lobe, the *prostomium*, which represents the anterior end of the animal. The prostomium may bear eyes, tentacles and *palps* (tactile organs). The region about the mouth, the *peristomium*, may bear tentacles, also known as *cirri*. The mouth leads to a straight, differentiated digestive tract, sometimes lobulated, terminating in an anus. A circulatory system, approximating a closed type, is present. The excretory system consists of a segmentally arranged series of paired nephridial tubes, described in the case of the earthworm in an earlier connection (p. 146). Likewise a description of the reproductive system of the earthworm and the manner in which it functions has already been given (p. 157). The central nervous system consists of a *circumpharyngeal* ring, connecting ganglia above and below, the latter joined with a *ventral ganglionated nerve cord*, extending posteriorly the length of the body. Annelids are monoecious (earthworms) and dioecious (marine worms). In the dioecious annelids, the eggs, fertilized externally, develop into *trochophore* larvae. The trochophore larva of the marine worm *Polygordius* is unsegmented and is provided with an alimentary tract having a right-angled bend in it. The exterior of the larva is at first ciliated everywhere, but later the cilia become restricted to one or more bands of epithelium, the ciliated bands, of which the *preoral band* is shown in Fig. 241. The latter encircles the body, marking off a prestomial area in front (above in the figure), which contains an *apical plate*, beneath which is the rudiment of the supra-esophageal ganglion. The larva also contains nephridial organs opening to the outside. Most of the larva seems to represent the head end (*prosoma*) of the fully developed worm. The segmented trunk (*metasoma*) of the worm grows from the posterior edge of the prosoma by the formation of segments one after the other.

In some annelids the head of the adult later increases in size by taking up trunk segments. In monoecious annelids such as the earthworm, the egg develops directly into a worm, but the prostomium shows such a close resemblance to the trochophore larva that the two structures are thought to be homologous. The trochophore larva is important in connection with the evolution of the annelids, since it bears a rather striking resemblance to a rotifer and an even closer resemblance to the larva of the Brachio-

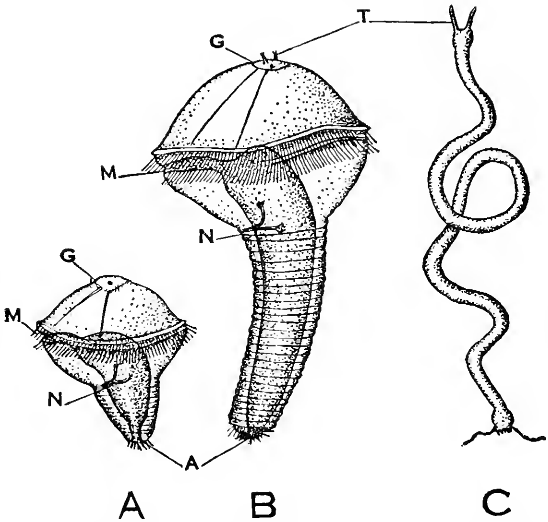


FIG. 241.—*Polygordius.* A and B, two stages in the development of the trochophore (trochosphere) larva which grows by the addition of segments to the posterior end. C, dorsal view of the adult. A, anus; G, rudimentary supra-esophageal ganglion; M, mouth; N, protonephridium, provided with flame cells; T, tentacles. (*After Hatschek and Fraipont.*)

poda and the Phoronidea and also to the veliger larva of the Mollusca (p. 433).

CLASS I. ARCHIANNELIDA. PRIMITIVE MARINE ANNELIDS. Setae (locomotor bristles) absent or scanty. Head may bear ciliated bands or a pair of tentacles. External segmentation often indistinct. A trochophore larval stage occurs. All dioecious.

Example: *Chaetogordius canaliculatus,* has setae on its posterior segments. Common at Woods Hole.

CLASS II. POLYCHAETA. Mostly marine annelids, with a few fresh-water species. They are free-swimming or tube dwellers. The body is distinctly segmented, the head with sense organs being well developed in the free-swimming forms. A characteristic structure of the latter is the *parapodium.* This is a fleshy outgrowth of the body wall usually consisting of two

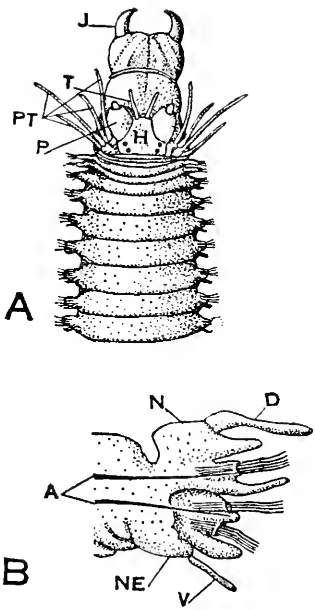


Fig. 242.

Fig. 243.

Fig. 242.—A, Anterior end of *Nereis*, with proboscis extended. (*After Ehlers.*) B, enlarged view of parapodium from posterior aspect. (*After Quatrefages.*) A, acicula (large bristles embedded in parapodium); D, dorsal cirrus; H, head (prostomium) bearing four simple eyes; J, jaw; N, notopodium; NE, neuropodium; P, palp; PT, peristomal tentacles; T, tentacles; V, ventral neuropodium.

Fig. 243.—Diagram of alimentary canal of leech. A, anal opening; G, nerve ganglia; H, head with eyespots; P, muscular pharynx; S, stomach; SU, sucker.

lobes: a dorsal *notopodium* and a ventral *neuropodium* (Fig. 242), both of which may bear cirri and setae, and are supported internally by heavy bristles called *acicula.* Parapodia are reduced or lacking in the sedentary forms. They are used in locomotion and in aerating the body by producing a flow of water over it when the animal is in its burrow or in a tube.

Filamentous external gills are present in some. The pharynx of the free-swimming predaceous forms is provided with a pair of sharp, pointed chitinous jaws and may be protruded as a proboscis in capturing food. The sedentary forms live in tubes of a slimy material, secreted by the integument and usually encrusted with bits of sand and shell. As a rule, polychaet annelids are dioecious.

Examples: *Nereis virens*, the clamworm, a free-swimming marine form about 25 cm. in length; *Nereis limnicola*, a fresh-water California species about 45 mm. in length; *Chaetopterus pergamentaceus*, a marine form, living in a U-shaped tube buried in the sand.

CLASS III. OLIGOCHAETA. Fresh-water or terrestrial annelids, lacking parapodia and cephalic appendages. The head region consists of the prostomium, a lobe projecting dorsally over the mouth, and the peristomium, containing the mouth. The setae, mounted in pits in the body wall, are few in number and may be absent. Aquatic forms may have gills. Oligochaete worms are monoecious and development is direct, there being no larval stage. Some also reproduce asexually by transverse fission.

Examples: *Enchytraeus albidus*, milk white in color, and about 25 mm. in length. Used as food for aquarium fishes. *Lumbricus terrestris*, an earthworm, about 10 in. in length. An Australian species reaches a length of 3 to 4 ft.

Earthworms are found in temperate and tropical countries at depths down to 6 ft. They live in burrows in the soil and in decaying vegetation, and obtain nourishment by passing soil with organic matter through the alimentary canal. Burrows are made by pushing the soil aside or by swallowing it. After swallowing the earth, whether for food or burrowing, the earthworm returns to the surface and ejects the earth through the anus. Charles Darwin, in his book "The Formation of Vegetable Mold" (1881), calculated that the weight of the castings of all earthworms present in an acre of soil during the course of a year averaged between 7.56 to 18.12 tons. Earthworms are important agents in preparing the ground for the growth of fibrous rooted plants and seedlings of all sorts. Incidentally, earthworms play a part in the burial of stones and parts of buildings.

The mouth of the earthworm is without teeth. It leads to a muscular pharynx, which seems to be the principal agent in drawing food into the mouth. Food or earth passes from the pharynx to a narrow esophagus into which the secretions of two pairs of *calciferous glands* is discharged. This secretion contains calcium carbonate and serves to neutralize the strongly acid condition of the food. From the esophagus the food passes to a muscular *gizzard*, where it is pulverized, and then into a stomach-intestine, where it is digested and absorbed. The digestive fluid contains proteolytic and lipolytic enzymes. Earth and other indigestible material taken into the alimentary canal are eliminated at the anus.

CLASS IV. GEPHYREA. Marine worms without parapodia; unsegmented in the adult stage. The body cavity is undivided and the nephridia are reduced to a single pair. A few setae may be present. They are dioecious and there is a trochophore stage in development.

Example: *Thalassema melitta,* found on the coast of North Carolina.

CLASS V. HIRUDINEA. The Hirudinea, or leeches, lack parapodia, tentacles, and setae, but have sucking disks: one surrounding the mouth and another at the posterior end of the body. The body is flattened dorsoventrally and is marked externally by two or more grooves to a segment. The body cavity is partially filled with a vacuolated parenchyma. In some leeches there are three sharp chitinous plates in the pharynx that are used in drawing blood. Others, lacking jaws, can pierce the integument by means of a proboscis that can be thrust out of the pharynx. The salivary glands of leeches produce a substance called *hirudin,* which prevents coagulation of the blood. It acts apparently by preventing the action of thrombin upon fibrinogen and may therefore be considered an antithrombin.

In many leeches the crop and stomach are provided with capacious pouches that become greatly distended after a meal. The food consists principally of the blood or body fluids of various animals. Leeches live in the water or in moist ground and vegetation. They completely devour small aquatic worms, insect larvae, etc.; and from larger animals, such as fishes, amphibians, turtles, and mammals, they draw blood. A full meal of blood may suffice for a year. Eyes and other sense organs are present upon the head. Leeches are monoeeious and development is direct (Fig. 243).

Examples: *Hirudo medicinalis*, the medical leech, a European form used in blood letting, is now found in ponds and streams in this country. *Macrodella decora* is one of the larger fresh-water species.

PHYLUM 14—ARTHROPODA

Arthropods, like annelids, are segmented externally, and the arrangement of the nervous system, muscles, heart, and other organs shows evidence of internal segmentation. On the other

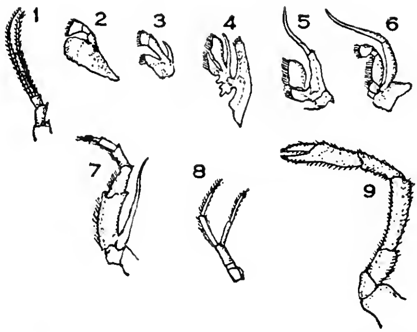


Fig. 244.—Appendages of crayfish of left side, ventral view, three-fourths natural size. 1, first antenna; 2, mandible; 3 and 4, first and second maxillae; 5, 6 and 7, maxillipeds; 8, pleopod; 9, first walking leg (biramous).

hand, arthropods differ from annelids in that (1) the segmentation is *heteronomous*, which means that the primitive segments are fused to form larger segments, such as the *head*, *thorax*, and *abdomen;* (2) the paired appendages are *jointed;* and (3) the *body cavity* is almost eliminated. The possession of jointed appendages is the most important feature and gives the name to the phylum; Arthropoda means jointed feet. These appendages were primarily *locomotor* and *sensory* in function, functions which some of them have retained, while others have evolved into (1) *mandibles* and *maxillae*, chewing organs; (2) *maxillipeds*, intermediate between legs and jaws; (3) *pleopods*, the *swimmerets* of Crustacea; (4) *spinnerets*, the spinning organs of spiders; and (5) the *ovipositor* of insects, etc. (Fig. 244).

The chitinous *exoskeleton* is a seeretion of the epidermis and serves as a protective covering to which muscles and other organs are attached. The alimentary canal is a *complete* tube, highly differentiated into various regions. The muscular system is well developed; all of the muscles are striated. The nervous system is of the *ganglionic type*, like that of annelids, but as a result of condensation, or concentration, the number of ganglia in the ventral chain is reduced and often does not correspond in number with the body segmentation. There are two types of eyes, simple *ocelli* and *compound* eyes. Except in the small crustaceans, there is a blood circulatory system, but the degree of development of the vessels depends upon the character of the respiratory system. Thus, vessels are practically absent in forms that have a diffuse organ of respiration, like the tracheal system of insects, but are well developed in gill breathers, like the crustaceans. The heart is tubular and lies in the mid-dorsal line. Both *nephridia* and *Malpighian tubules* occur as organs of excretion.

The eggs as a rule contain a large amount of yolk, which is enclosed in a thin layer of yolk-free cytoplasm. The union of the male and female nuclei takes place in the center of the yolk. Cleavage in large-yolked eggs is of the *superficial* type which means that the yolk-free cytoplasm is organized into a blastoderm by the immigration of cleavage nuclei arising in the yolk. Hermaphroditism is rare. Alternation of amphigony with parthenogenesis (*heterogony*) occurs. Sometimes parthenogenetic reproduction in these cases takes place in the larval stage (*paedogenesis*). *Metamorphosis* is common.

Over 600,000 species of arthropods are known, which is five-sixths of the total number of known species of animals.

CLASS I. CRUSTACEA. Mostly *aquatic*, breathe by means of gills, have *biramous* appendages, and two pairs of antennae. The presence of large amounts of calcium carbonate in the exoskeleton makes it thick and hard, and gives the name to the group. The first two body regions are usually fused into a *cephalothorax*. Many of the smaller Crustacea are parasitic. Barnacles are the only sessile forms.

SUBCLASS 1. ENTOMOSTRACA. These are small in size, with a variable number of segments. Head, thorax, and abdomen are distinct in some.

Examples: *Eubranchipus vernalis*, the fairy shrimp; *Daphnia pulex*, a fresh-water cladoceran; *Temora longicornis*, a copepod, marine; *Cyclops viridis*, a fresh-water copepod; *Eucypris virens*, a fresh-water ostracod; *Balanus balanoides*, the rock barnacle.

SUBCLASS 2. MALACOSTRACA. Usually with 20 *body segments:* head 5, thorax 8, and abdomen 7; and 19 pairs of *appendages:* head 5, thorax 8, and abdomen 6. Head and thorax generally combined in a cephalothorax.

Examples: *Porcellio scaber*, a sow bug, terrestrial; *Palaemonetes vulgaris*, a common shrimp, marine; *Homarus americanus*, American lobster; *Cambarus bartoni*, American crayfish; *Cancer irroratus*, a common New England crab; *Libinia emarginata*, a spider crab (Fig. 245).

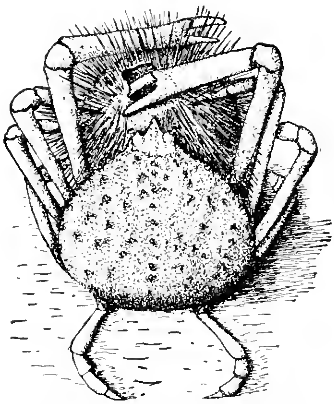


Fig. 245.—*Libinia*, a spider crab, sketched devouring a sea urchin.

CLASS II. ARACHNOIDEA. *No* antennae are present. There are two body divisions, the cephalothorax, with six paired appendages, and the abdomen, *without* appendages, except in the horseshoe crab.

SUBCLASS 1. XIPHOSURA. A horseshoe-shaped cephalothorax, six platelike paired appendages on the abdomen, and a spikelike tail.

Example: *Limulus polyphemus*, the American horseshoe crab.

SUBCLASS 2. ARACHNIDA. The cephalothorax bears six pairs of appendages: the mandibles or *chelicerae*, the *pedipalps*, and four pairs of walking legs. The last three pairs of abdominal appendages of spiders are modified into *spinnerets*. Mostly terrestrial and breathe by modified gills known as lungs. Some have a tracheal system.

Examples: *Diplocentus whitei*, a scorpion of the Southwestern United States; *Argiope aurantia*, an orb-weaving spider (all spiders belong to the Arachnida); *Phalangium opilio* (daddy-long legs). Has a tracheal system with a single pair of spiracles. Does not spin a web. *Sarcoptes scabiei*, one of the itch mites, causing itch in man and mange in pigs. *Margaropus annulatus*, the Texas cattle tick. The bite of the tick inoculates cattle with *Babesia bigemina*, a sporozoan which causes *Texas* *fever. Trombicula irritans*, chigger; *Macrobiotus hufelandi*, a water bear, .7 mm. in length.

CLASS III. ONYCHOPHORA. The head bears a pair of simple eyes, a pair of segmented antennae, and a mouth with a pair of hooked jaws. The wormlike trunk is *unsegmented* and provided with numerous annulated legs (14 to 43 pairs). The body cavity is hemocoel through which the alimentary canal passes as a straight tube. A tracheal respiratory system and a nephridial excretory system are present. There is an opening of a nephridium at the base of each leg. The sexes are separate. In *viviparous* forms the egg is poor in yolk and is totally divided in cleavage. The embryo in such cases is nourished by the walls of the *uterus*, forming a very primitive sort of *placenta*. The animals are terrestrial and feed on insects and other small forms. From the point of view of evolution, they are important as a connecting link between annelids and arthropods (Fig. 246).

Example: *Peripatus eiseni*, a viviparous species; habitat, central South America.

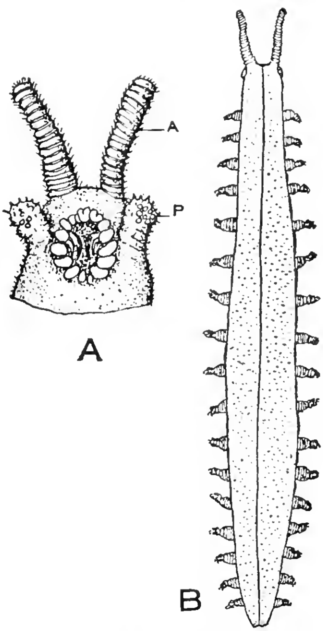


FIG. 246.—A, ventral view of the head of *Peripatus capensis*, showing the mouth surrounded by lips raised into large white papillae. B, dorsal view of entire animal. A, antenna. P, oral papilla at the base of which a gland ejects a sticky slime used in capturing food. (*After Leuckart-Nitsche wall chart.*)

CLASS IV. MYRIAPODA. The head bears a pair of segmented antennae, a pair of mandibles, and one or two pairs of maxillae. The trunk is segmented (11 to 173 segments) and each segment has *one* or *two pairs* of legs with claws. The sexes are separate and all are oviparous. Development is direct. There are four orders, of which the Diplopoda (millipedes) and Chilopoda (centipedes) are the more important.

Order 1. Diplopoda. A cylindrical body with usually two pairs of legs to a segment. A single pair of maxillae. An anterior genital pore.

Example: *Julus virgatus*, a common millipede.

Order 2. Chilopoda. A flattened body with *one pair* of legs to a segment. Two pairs of maxillae. The first pair of legs are maxillipeds, provided with *poison glands*. Reproductive openings are posterior.

Example: *Scolopendra morsitans*, a common southern centipede.

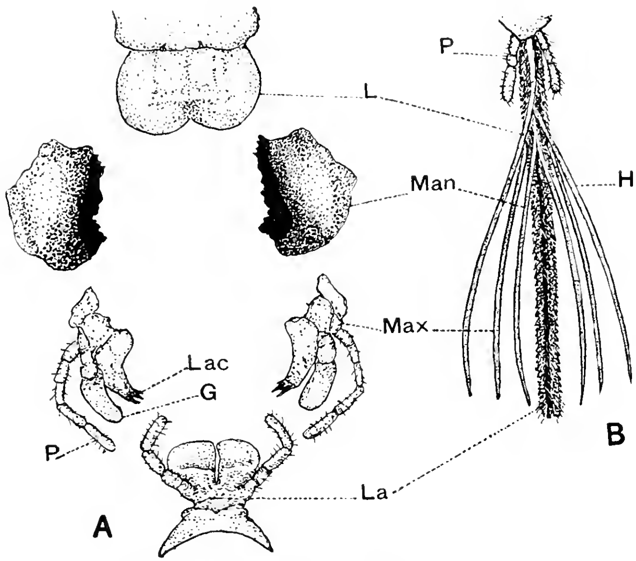


FIG. 247.—A, chewing type of mouth parts as found in grasshopper; B, piercing-sucking type as found in female mosquito. G, galea; H, hypopharynx (a tonguelike prolongation of the floor of the mouth, attached to the inside wall of the labium); L, labrum; La, labium; Lac, lacinia; Man, mandible; Max, maxilla; P, palp. (*After Metcalf and Flint: Destructive and Useful Insects.*)

CLASS V. INSECTA. INSECTS. Insects are characterized by three body divisions, head, thorax, and abdomen, and by three pairs of legs. The head bears four pairs of appendages; *antennae, maxillae, mandibles,* and lips or labia (*labrum* and *labium*). The trunk is composed of three segments, *prothorax, mesothorax,* and *metathorax,* each of which bears a pair of legs. The mesothorax and metathorax may each bear in addition a pair of wings. Respiration is carried on by means of a tracheal system. Insects are dioecious and the reproductive openings are at the end of the body. A metamorphosis in development is common.

The mouth parts conform to two general types, *viz.*, biting and sucking. In the biting type there is an upper lip or labrum and a lower lip or labium, each of which is a chitinous plate. The labium bears a pair of palps. Inserted laterally between the lips are a pair of maxillae and a pair of mandibles (Fig. 247). Each maxilla consists of a forked *lacinia* and a spoon-shaped *galea*, and also bears a single palp. The palps are not only tactile but also contain organs of taste and smell. Typical mandibles are hard resistant plates of irregular outline and edged with sharp points. Both maxillae and mandibles operate with a side-to-side motion. The mandibles are the chewing organs, the maxillae serving with the lips to hold and manipulate the food. In sucking insects such as the mosquito the mouth parts are shaped to form a slender beak (Fig. 247B). The elongate maxillae and mandibles lie in a sheath formed by the labium, the labrum being reduced to a small plate at the upper side of the base of the beak. There are variations of these two types, combining features of both.

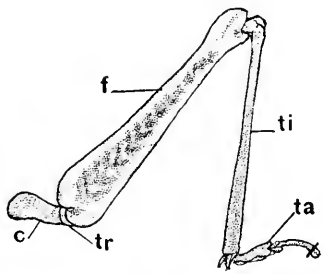


FIG. 248.—Parts of metathoracic leg of grasshopper. c, coxa; f, femur; ta, tarsus; ti, tibia; tr, trochanter.

On the head there are usually two kinds of eyes, simple and compound, and a pair of segmented antennae. The compound eye has been described (p. 192). The simple eye or ocellus is much smaller and consists of a spheroidal mass of light-sensitive cells covered externally by a lens-shaped thickening of the integument.

Each leg, beginning at the proximal end, consists of five parts: (1) a short *coxa*, (2) a short *trochanter*, (3) a long, broad *femur*, (4) a slender *tibia*, and (5) a foot or *tarsus*, composed of several segments (Fig. 248). The insect wing is without a forerunner in the preceding groups of animals. Since primitive insects are wingless, the insect wing must be a structure that originated in the insect group. The insect wing is a chitinous plate, usually very thin and flexible, and reinforced by "veins" composed of branches of the tracheal system. In beetles the anterior wings are thickened and serve as a protective covering for the posterior pair when the insect is not flying. In butterflies and moths the wings are covered with small scales. There are two general views as to the origin of insect wings: (1) that they are modified gills, or (2) that they have developed from chitinous thoracic plates.

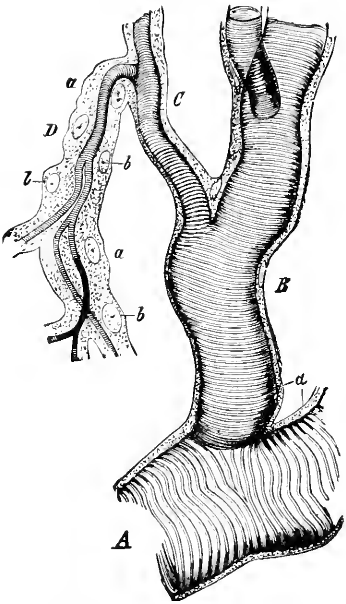


Fig. 249.—*A*, portion of trachea of caterpillar with its branches, *B*, *C*, *D*. *a*, peritracheal membrane; *b*, nucleus. (*From Packard, "Text book of Entomology," The Macmillan Company. By permission.*)

The tracheal system of respiration, though present in certain other arthropods, is best developed in insects. It consists of tubes called tracheal tubes, which beginning at openings (*spiracles*) arranged in a row on each side of the body penetrate to all parts of the body, branching as they go and terminating in *trachioles* in the tissues. The wall of the tracheal tube consists of a single layer of cells lined with a chitinous membrane. Under the microscope the larger tubes have a ringed appearance caused by transverse folds in the chitinous lining arranged in a close spiral that prevents collapse of the tubes (Fig. 249). In flying insects, the tracheal tubes near the

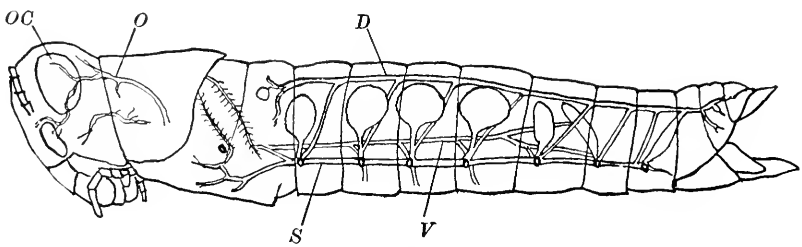


Fig. 250.—The distribution of tracheae and air sacs in a grasshopper. *D*, left dorsal trachea; *O*, left cephalic trachea; *OC*, ocular trachea; *S*, left stigmatal trachea with stigmata (spiracles); *V*, ventral trachea. (*After Packard, Textbook of Entomology.*)

spiracles are expanded into thin-walled air sacs, which are compressed and expanded by contractions and expansions of the body wall (Fig. 250). Air enters and leaves through the spiracles. In the grasshopper it has been shown that the two thoracic spiracles and the first two abdominal spiracles are inspiratory and that the last six pairs of abdominal spiracles are expiratory. Oxygen is carried directly to the tissues by the tracheal system and carbon dioxide is removed by the same system. The blood plays a minor role in the respiratory exchange, but since the tissues are bathed in blood, the latter serves as a medium through which oxygen passes from the trachioles to the tissues and carbon dioxide in the opposite direction.

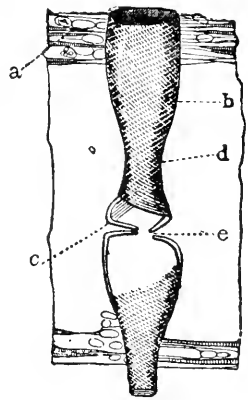


FIG. 251.—Part of heart of a beetle, *Dytiscus marginalis*, showing spiral arrangement of fibers. *c*, closed valve; *e*, open valve; *a*, muscular and connective tissue sheet lying ventral to the heart; *b*, arrangement of fibers. (*From Packard, Textbook of Entomology, copyright, The Macmillan Company, after Grober. By permission.*)

Blood vessels, poorly developed in insects, are practically absent except near the heart. The heart of the grasshopper is a delicate muscular tube lying directly in the mid-line of the dorsal region of the hemocoel. It is closed at its posterior end, open at its anterior end, and perforated along its sides by apertures called *ostia*, guarded by valves (Fig. 251). Anteriorly, blood vessels extend a short distance from the heart. When the heart contracts, the ostia are closed so that the wave of constriction, beginning at the posterior end and passing forward, forces the blood out of the anterior end. As the heart relaxes, blood reenters the heart through the ostia from the pericardium, a space about the heart, incompletely separated from the rest of the hemocoel. In some insects the heart reverses the direction of its beat at regular intervals, propelling the blood first in one direction and then in the other. The blood distributes nourishment to the tissues and collects waste material other than carbon dioxide.

There are two general types of metamorphosis: complete (*holometabolous*) and incomplete (*hemimetabolous*). When metamorphosis is complete, the egg hatches as a worm-shaped larva, such as the *maggot* of flies, the *grub* of the beetle, or the *caterpillar* of moths and butterflies. The larval period is characterized by voracious feeding, in the course of which the larva passes through stages known as *instars*, separated by periods of molting or *ecdysis*, the number varying in different insects. Loss of the chitinous covering of the body permits growth of the larva from the first to the last instar. The last larval instar is succeeded by the stage of the *pupa*, during which feeding ceases and a reorganization of the body takes place. In many insects the pupal period is passed in the ground, in others in a cocoon formed of silky fibers secreted by special glands. At the end of the pupal period, which in extreme cases may extend over a number of years, the insect emerges as an *imago* or adult.

If the metamorphosis is incomplete, the larva or *nymph* resembles the adult in its general morphology, except that it lacks wings, as, for example, in the case of the larval grasshopper, where the nymph undergoes successive molts and gradually takes on the adult form.

Of the many orders of insects those listed in the following paragraphs include only the more common ones.

Order Collembola (Glue Bar). SPRINGTAILS. The order is named from the presence of a *collophore*, a ventral tube on the first abdominal segment that is provided with a pair of eversible sacs, by means of which the insect adheres to smooth surfaces. These insects are wingless and are believed to have descended from ancestors in which wings were never evolved. The fourth abdominal segment usually bears a forked appendage that folds under the body and is used as a spring in propelling the insect. There is no metamorphosis in development.

Examples: *Papirius maculosus*, the spotted springtail; *Achorutes nivicola*, the snow flea, which is remarkable in that it is found in winter on snow.

Order Ephemeroptera. MAYFLIES. The delicate wings, triangular in outline, are held vertically above the body when at rest. The tip of the abdomen bears a pair of long slender cerci, and in addition a median caudal filament. The adult mayfly takes no food, the alimentary canal being inflated with air, which gives buoyancy to the body. It lives only a day or two as an adult. The eggs are laid in water, where the larval stage is passed. Metamorphosis is incomplete. The entire life history may extend over several years. So far as known, these are the only insects that undergo a molt after attaining functional wings.

Example: *Ephemera simulans*, occurs in large numbers, usually late in June in the Great Lakes region.

Order Orthoptera (Straight-winged). CRICKETS, GRASSHOPPERS, ROACHES, KATYDIDS, ETC. The wings, when well developed, consist of a thickened anterior pair, straight and narrow in outline, and a thin posterior pair, which when at rest is folded in plaits under the anterior pair. The mouth parts are for chewing. Metamorphosis is incomplete. Most of them feed on vegetation and their destruction of plant life causes enormous damage. Some, cockroaches, for example, are more general feeders.

Examples: *Gryllus domesticus*, the house cricket, an old world species that has been introduced into this country; *Melanopus differentialis*, a large grasshopper, common in Eastern United States; *Periplaneta americana*, the American cockroach; *Diapheromera femorata*, the walking stick, lacks wings; *Stagmomantis carolina*, the praying mantis, feeds principally on other insects and therefore has a positive economic value.

Order Odonata (*odous*, tooth). DRAGONFLIES AND DAMSEL FLIES. There are two pairs of membranous wings with marked veining, the posterior pair as large as, or larger than, the anterior. The mouth parts are for chewing and the metamorphosis is incomplete. The eggs of American species are laid in water. The maxillae and mandibles of the larva are provided with sharp teeth. The labium of the larva is enlarged, jointed, armed with hooks, and can be thrust out in front of the head to seize prey.

Examples: *Anax junius*, a common dragonfly; *Agrion maculatum*, a common damsel fly.

Order Isoptera (Equal-winged). TERMITES. These are social insects, comprising a number of castes, each caste including males and females. They may be distinguished from ants, which they greatly resemble, by the fact that the abdomen is joined to the thorax by a broad connection. (In ants this connection is slender.) There are usually two pairs of long narrow wings which are shed by the adult sexual males and females after the nuptial flight. The intestine of some termites contains flagellated Protozoa that are capable of rendering digestible the cellulose of wood eaten by the termites. It has been shown that without the flagellates termites are unable to digest cellulose. The mouth parts are for chewing, and metamorphosis is gradual. Some tropical species build nests 10 or 12 ft. in height. In the United States they live in mines in the earth and in wood. They cause considerable damage to the wooden structure of buildings.

Example: *Reticulitermes flavipes*, a common termite of Northeastern United States.

Order Hemiptera (Half-winged). BUGS. The proximal halves of the anterior pair of wings are thick and the extremities, which overlap, are very thin. The posterior wings are membranous. The mouth parts are for piercing and sucking. Metamorphosis is incomplete. Many have stink glands located on the abdomen.

Examples: *Anasa tristis*, the squash bug; *Lygaeus kalmii*, the milkweed bug; *Lethocerus americanus*, the giant water bug or electric-light bug; *Gerris remigis*, the water strider; *Cimex lectularius*, the bedbug; *Blissus leucopterus*, the chinch bug; *Arctocorixa alternata*, the water boatman.

Order Homoptera (Same-winged). CICADAS, APHIDS, AND GALL INSECTS. There are usually two pairs of wings of uniform thickness. Some are wingless and in one family (*Coccidae*) the posterior pair of wings is reduced to a pair of club-shaped *halteres*. The mouth parts are for piercing and sucking. Metamorphosis is incomplete.

Examples: *Tibicen linnei*, the "dogday" cicada; *Magicicada septemdecim*, the 17-year cicada, whose larval stage lasts 17 years; *Aphis gossypi*, the melon aphis, one of the plant lice; *Phylloxera vitifoliae*, forms galls on grape leaves; *Aspidiotus perniciosus*, the San José scale insect.

Order Anoplura. LICE. These are wingless parasitic insects whose mouth parts are in the form of a tubular proboscis provided with sharp stylets. Recurved hooks in the base of the proboscis serve to anchor the proboscis after it has been inserted in the skin of the host. Metamorphosis is incomplete.

Examples: *Pediculus capitis*, the head louse; *Pediculus corporis*, the body louse or "cootie"; *Phthirius pubis*, the crab louse.

Order Coleoptera (Sheath-winged). Beetles. When at rest the thickened anterior pair of wings, known as *elytra*, form covers for the posterior membranous wings. Mouth parts are for chewing, and metamorphosis is complete.

Examples: *Dytiscus marginicollis*, diving beetle; *Coccinella novemnotata*, ladybird beetle; *Photinus scintillans*, firefly; *Leptinotarsa decemlineata*, potato beetle; *Calosoma scrutator*, a common ground beetle with conspicuous iridescent coloring; *Tenebrio molitor*, mealworm beetle.

Order Lepidoptera (Scale-winged). Moths and butterflies. The two pairs of membranous wings are covered with overlapping scales. Scales also cover the body, legs, and appendages. Mouth parts are for sucking. Metamorphosis is complete. Usually moths have feathered or threadlike antennae and hold the wings horizontally or wrapped around the body when at rest. Most moths are nocturnal. The antennae of butterflies and skippers as a rule are threadlike and knobbed at the ends. At rest the wings are held together in a vertical position over the body. They fly in the daytime.

Examples: *Samia cecropia*, the large cecropia moth; *Actias luna*, luna moth; *Protoparce quinquemaculata*, a hawk moth, whose large green larva is known as the tomato or tobacco worm, depending upon which plant it is feeding; *Porthetria dispar*, the gypsy moth; *Bombyx mori*, the silkworm moth; *Papilio polyxenes*, common swallowtail butterfly; *Pieris rapae*, cabbage butterfly; *Epargyreus tityrus*, silver-spotted skipper.

Order Diptera (Two-winged). Flies. The anterior wings are large and membranous; the posterior wings are reduced to a pair of knobbed threads, the *halteres*. Anterior wings are sometimes lacking. Mouth parts are for sucking, and metamorphosis is complete.

Examples: *Anopheles quadrimaculatus*, a mosquito, the female of which transmits malaria; *Glossina palpalis*, tsetse fly that transmits African sleeping sickness; *Musca domestica*, housefly; *Braula caeca*, bee louse, a wingless form parasitic on the thorax of queens and drones of the honeybee; *Melophagus ovinus*, the sheep tick, wingless.

Order Siphonaptera (Tube, Wingless). Fleas. Wingless insects with the body compressed laterally; mouth parts for piercing and sucking; legs for leaping. Metamorphosis is complete.

Examples: *Pulex irritans,* human flea; *Ctenocephalis felis,* cat flea; *Ctenocephalis canis,* dog flea; *Xenopsylla cheopis,* rat flea, carries the germ of bubonic plague.

Order Hymenoptera (Membrane-winged). BEES, WASPS, ANTS, SAWFLIES, AND ICHNEUMON FLIES. Two pairs of wings with reduced venation; the anterior pair larger than the posterior. Mouth parts are for chewing or for both chewing and sucking. Ovipositor of the female may be modified into a sting, piercing organ or saw. Complete metamorphosis.

Examples: *Apis mellifica,* honeybee; *Bombus pennsylvanicus,* a bumblebee; *Vespa maculata,* a social wasp, builds large papier-maché nests; *Trypoxylon albitarsis,* mud-dauber wasp; *Vespa maculifrons,* yellow jacket; *Monomorium pharaonis,* red ant, common about houses; *Megarhyssa,* a genus of ichneumon flies, the females of which drill through the wood of trees to parasitize wood-boring insect larvae; *Cimbex americana,* a sawfly. The ovipositor of the female is composed of two sharp plates, the saws, flanked on either side by saw guides and is used in depositing the eggs in the bark of maples, elms, and other trees.

PHYLUM 15—MOLLUSCA

Molluscs are *soft-bodied, bilaterally symmetrical, unsegmented* animals, with only a remnant of a coelom, and usually enclosed in a *shell.* In well-developed molluscs, like the snail, four body parts can be distinguished: (1) the *visceral sac,* containing the viscera and forming the bulk of the body. This is continuous in front with (2) the *head,* bearing the mouth, tentacles, and eyes. (3) The *foot,* the organ of locomotion, lies ventral to the visceral sac. (4) The *pallium,* or *mantle,* is a dermal fold, forming between it and the sac a mantle cavity which is provided with gills or lungs, and receives the openings of the intestine, reproductive ducts and excretory organs. The outer surface of the mantle secretes the shell (Fig. 252).

The *nervous system,* typically, consists of three pairs of ganglia connected by cords: (1) The *cerebral ganglia* lie dorsal to the esophagus and supply the sense organs of the head. (2) The *pedal ganglia* lie in the foot, and supply statocysts and muscle. (3) The *visceral ganglia* lie in the viscera, which they supply, and also send nerves to the *osphradia,* organs of chemical sense located in the mantle cavity.

The mouth opens into a muscular pharynx, usually provided with a *radula*, a toothed, chitinous ribbon, used for rasping. Attached to the stomach is a large liver. Paired or single

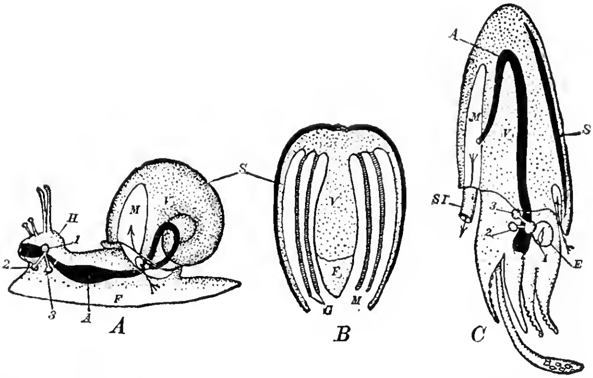


FIG. 252.—Diagrams of three types of molluscs. A, Gastropod; B, Pelecypod (clam), cross section; C, Cephalopod. A, alimentary tract; E, eye; F, foot; G, gills; H, head; M, mantle cavity; S, shell; SI, siphon; V, visceral mass; 1, cerebral ganglion; 2, pedal ganglion; 3, visceral ganglion.

nephridial tubules drain the *pericardium*, which represents the coelom, and open into the mantle cavity. The circulatory system is composed of a heart with a *ventricle* and one or two *auricles*, arteries, and veins. The ventricle drives the blood through the arteries to the lacunar spaces in the tissues, from which veins take it to the kidneys and gills, and then to the heart. The blood in the heart is, therefore, always pure. Both dioecious and hermaphroditic forms occur. A *veliger-larva* stage is common in development (Fig. 253).

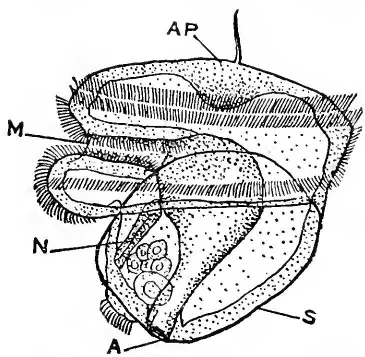


FIG. 253.—Veliger larva of *Toredo*. (*After Hatschek.*) A, anus; AP, apical plate bearing a cilium; M, mouth; N, nephridial tube; S, shell. (Compare with Fig. 241, A.)

Molluscs are classified as follows:

CLASS I. AMPHINEURA.

The nervous system consists of an esophageal ring and four longitudinal nerve cords. Those without a shell are wormlike in appearance. A radula is usually present. All are marine.

Examples: *Chaetopleura apiculata,* rock sucker; *Chaetoderma nitidulum,* lacks a shell.

CLASS II. SCAPHOPODA. Have *tubular shells.* A radula is present. Sexes are separate. All marine.

Example: *Dentalium entale,* tooth shell.

CLASS III. GASTROPODA. *Snails* and *slugs.* Asymmetrical body with four parts well developed; a creeping foot; an unpaired mantle, nephridium, and gonad. The shell is usually coiled spirally. A radula is present. Aquatic forms breathe by gills, the land forms with lungs. The shell is reduced or lacking in slugs.

Examples: *Lymnaea palustris,* a fresh-water snail; *Polynices duplicata,* a marine snail (Fig. 254); *Busycon canaliculatum,*

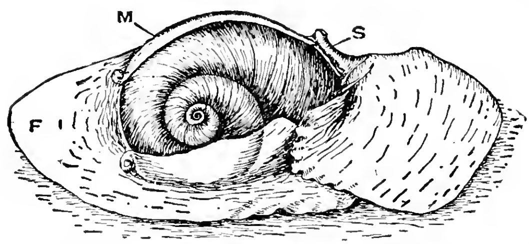


Fig. 254.—*Polynices,* a marine snail with a highly developed mantle and foot. F, foot; M, mantle; S, syphon.

a whelk, marine; *Helix pomatia,* French snail, edible; *Limax flavus,* a land slug; *Dendronotus frondosus,* a sea slug.

CLASS IV. PELECYPODA. Lack a head and cephalic appendages. Have a *bivalve shell* consisting of right and left halves; with paired mantle, gills, nephridia, and gonads. Frequently the hinder edges of the mantle are modified to form incurrent and excurrent *siphons.* The sense organs are poorly developed. Sexes are usually separate.

Examples: *Anodonta grandis,* a fresh-water clam; *Ostrea virginica,* the American oyster; *Venus mercaneria,* the hard-shelled or little-neck clam; *Mya arenaria,* the soft-shelled or long-necked clam (Fig. 255).

CLASS V. CEPHALOPODA. Active, carnivorous, marine forms, including the largest and most highly organized molluscs. As a rule, eight or ten *tentacles* surround the mouth which with the *siphon* represent the foot region. A pair of sharp *chitinous jaws* lie just back of the lips in the mouth. The siphon is an excurrent tube from the mantle cavity. The mantle is unpaired. A shell may or may not be present. The highly developed paired *eyes* strongly resemble those of vertebrates. *Statocysts* and *osphradia* are also present. Except in *Nautilus*, there is a glandular *ink sac* opening near the end of the rectum that secretes a brown or black fluid. The ink is expelled from the mantle cavity through the siphon and affords protection by clouding the water. The sexes are separate.

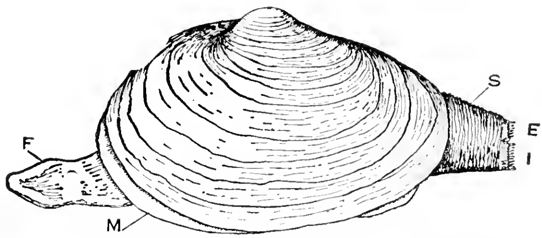


FIG. 255.—*Mya*, the soft-shelled clam. E, excurrent opening of syphon; F, foot; I, incurrent opening of syphon; M, mantle; S, syphon.

Examples: *Loligo pealei*, the common squid, its shell (cuttlebone) being embedded in the tissues; *Octopus bairdi*, a common devilfish (no shell); *Architeuthis princeps*, a squid, the largest mollusc, having a body about 6 meters in length and tentacles up to 10 to 12 meters long. *Nautilus pompilius*, pearly nautilus, which has a shell divided into compartments. It has about 90 tentacles about the mouth. *Argonauta argo*, the paper nautilus, has a spiral shell without septa.

PHYLUM 16—ECHINODERMATA

The term Echinodermata (hedgehog-skinned) was originally applied to sea urchins, for which it was very appropriate, but the term is now used to include in addition to sea urchins all forms related to them, such as starfishes, sea lilies, brittle stars, and sea cucumbers, some of which lack spines and are not in the least "hedgehog-skinned." Echinoderms are marine animals having a radial symmetry, usually of a five-radiate plan. The larva is *bilaterally* symmetrical, indicating that the radial symmetry of the adult is secondary. *Calcareous plates*, with or without spines, are developed in the mesoderm, and may form a hard exoskeleton. An *ambulacral* water-vascular system is present. In the starfish this system begins on the aboral surface with a porous plate, the *madreporite*, through which water enters a *stone canal*, leading to a *ring canal* encircling the mouth (Fig. 256). From the ring canal, five *radial canals* extend into the arms, and from each of these are given off at right angles paired *ambulacral canals*. Each of these, in turn, joins a tubular muscular sac, the *ambulacrum*, expanded at one end into an *ampulla*, and terminating in a *sucker disk* at its longer free end, which can be extended or retracted through the ambulacral groove on the oral surface of each arm. The system is filled with a fluid, mostly water, but containing lymph and blood corpuscles supplied by *glands* (Polian vesicles, Tiedemann bodies) attached to the system at various points. The ambulacra are used in loco-

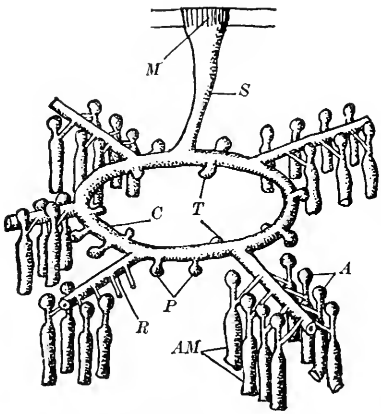


Fig. 256.—Water-vascular system of the starfish, diagrammatic. A, ampulla; AM, ambulacra; C, ring canal; M. madreporite; P, Polian bodies; R, radial canal; S, stone canal; T, Tiedemann bodies.

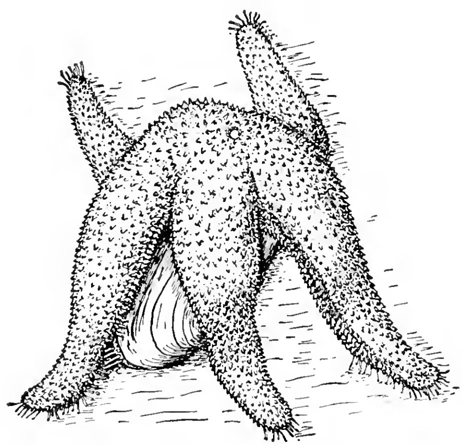


Fig. 257.—*Asterias* feeding on a clam. The valves of the clam are pulled apart by the ambulacra and the stomach of the starfish is then everted about the soft parts of the clam. The stomach juices of the starfish may aid in causing the valves of the clams to open.

motion by extending and attaching the sucking disks to the substratum, a muscular contraction of the appendage then pulling the animal along. The ambulacra are also used in capturing and holding prey (Fig. 257). They are important as tactile organs. The fluid in the ambulacral system is moved by cilia on the inner surface of the stone canal and by the contractions of muscles in the walls of the ampullae and the ambulacral feet. In addition to the ambulacral system there is also a blood circulatory system in which blood is circulated by cilia lining the vessels.

The radial symmetry is impressed on all of the internal organs. The body cavity is a complicated system of spaces, some of which are cut off from the rest, and all containing a fluid similar to that of the ambulacral system. The alimentary canal is usually a complete tube and lies in the largest of these spaces. The nervous system consists of (1) a *superficial nerve ring* around the esophagus, with *radial cords* extending into the arms; (2) a deeper *oral ring* and *radiating nerves;* (3) an *apical* system in the aboral wall but not present in all echinoderms. Respiration and excretion are carried on at the surface of the body, which is usually ciliated. Some brittle stars reproduce asexually by *fission*, but otherwise reproduction is *sexual*. The sexes are usually separate. While the eggs normally require fertilization, it has been found that they can be stimulated to develop by artificial means, *artificial parthenogenesis;* for this reason they have been favored material for experimental work along these lines. Ripe echinoderm eggs, when subjected to the effects of *hypertonic sea water*, certain *acids*, *temperature changes*, or *mechanical shock*, will develop without the intervention of a sperm.

CLASS I. CRINOIDEA. SEA LILIES AND FEATHER STARS. Have a nonciliated, cup-shaped body, the *calyx*, usually attached by a *stalk* on its aboral side. The oral surface is pointed upward, and contains the mouth, and also the anal opening. The arms, 5 or 10 in number, are usually *branched* and *feathery* in appearance, and bear ambulacral grooves on the aboral surface. Crinoids were more abundant in paleozoic times than now, about 2,100 fossil species being known (Pratt).

Example: *Hathrometra tenella*, a feather star. Atlantic Coast, at 150 to 3,000 ft.

CLASS II. ASTEROIDEA. STARFISHES. Usually have five arms, with open *ambulacral grooves* on the oral side, through which the ambulacra are extended. Gastric pouches and hepatic caeca extend into the arms. Spines, pincerlike *pedicellariae*, and tubercles project on the surface. At the tip of each arm is an eyespot. Starfish possess a remarkable power of regenerating lost parts.

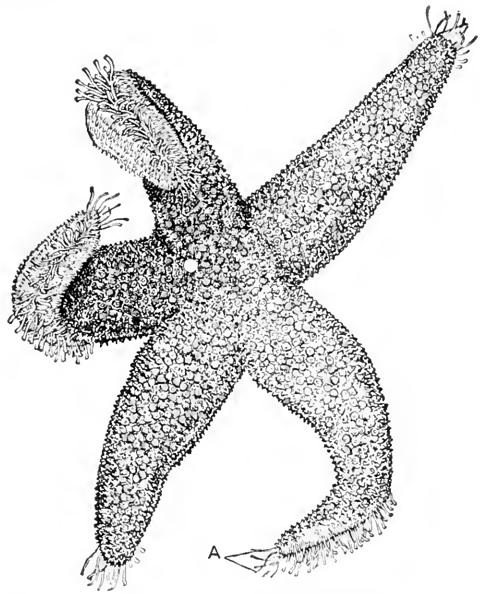


FIG. 258.—*Asterias*, a starfish, viewed from the aboral side. The pale circular area to the left of the center is the madreporite. The ambulacral grooves through which the ambulacra extend can be seen on two of the upturned arms.

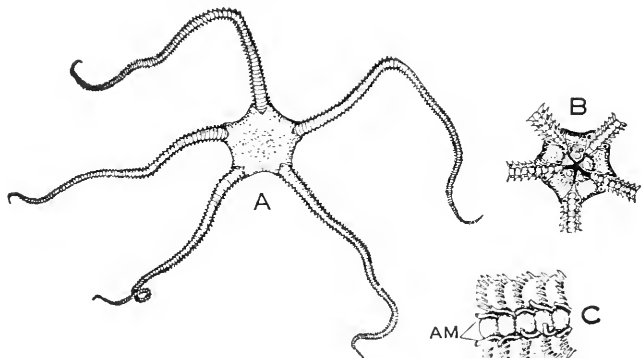


FIG. 259.—A, *Ophiura*, a brittle star, aboral view; B, oral view of central disk; C, oral side of portion of arm, magnified, showing ambulacra, AM.

Example: *Asterias forbesi*, a common starfish, Cape Cod region (Fig. 258).

CLASS III. OPHIURIOIDEA. BRITTLE STARS. The arms are sharply set off from the central disk and are *without* ambulacral grooves. The ambulacra are tactile, respiratory and excretory in function. The external surface is not ciliated. Hepatic caeca are absent and the intestine lacks an anal opening.

Example: *Ophiura robusta*, a Cape Cod form (Fig. 259).

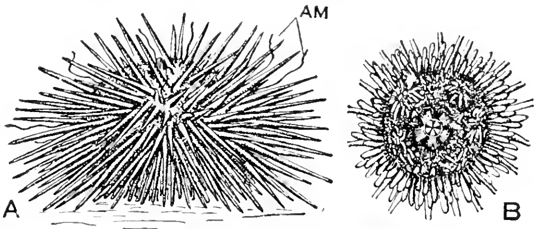


FIG. 260.—A, *Arbacia*, a sea urchin, side view. AM, ambulacra. B, oral view showing mouth region surrounded by shorter ambulacra and blunter spines.

CLASS IV. ECHINOIDEA. SEA URCHINS AND SAND DOLLARS. A subglobular or disk-shaped body *without* arms. Usually, five calcareous teeth project from the mouth. The calcareous exoskeleton is well developed and is often provided with long movable spines. The surface of the body is ciliated.

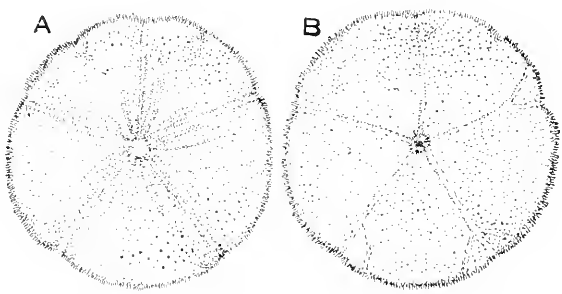


FIG. 261.—A, *Echinarachnius*, a sand dollar, aboral view; B, oral view.

Examples: *Arbacia punctulata*, a sea urchin common on the Atlantic coast (Fig. 260); *Echinarachnius parma*, the sand dollar (Fig. 261).

CLASS V. HOLOTHURIOIDEA. An elongated, *wormlike shape*, with a *leathery integument*, the exoskeleton being much reduced. There is a partial bilateral symmetry. The madreporite is usually internal, the fluid filling the ambulacral system coming from the body cavity. The external surface is not ciliated and lacks both spines and pedicelluriae. Regeneration is well marked.

Examples: *Holothuria marmorata*, trepang, used as food by the Chinese; *Cucumaria frondosa*, sea cucumber of the Maine coast; *Thyone briareus* a common Woods Hole species of sea cucumber (Fig. 262); *Leptosynapta inhaerens*, a wormlike form, without ambulacral feet. Atlantic Coast.

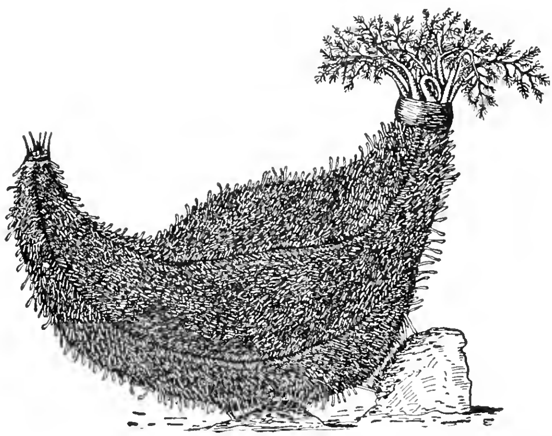


FIG. 262.—*Thyone*, a sea cucumber. The branched tentacles (at the right) are alternately drawn into the mouth, wiped off and extended. Ambulacra are present over the surface of the body.

PHYLUM 17—CHORDATA

The Chordata are characterized by (1) the presence at some time in the life history of a notochord, a flexible fibrous elastic rod, lying between the central nervous system and the digestive tract; (2) a tubular central nervous system lying dorsal to the digestive tract; and (3) a pharynx with gill slits, which may or may not function as repiratory organs in the embryo or in the adult.

SUBPHYLUM 1. ENTEROPNEUSTA. Unsegmented wormlike animals with three body divisions: (1) *proboscis*, (2) *collar*, and (3) *trunk* (Fig. 263). A blind tubular extension from the pharynx into the proboscis is taken to represent the notochord. The nervous system consists of (1) a dorsal tubular portion lying in the collar, and (2) a layer of nerve fibers beneath the entire ectoderm. The dorsal portion develops from a tube, as in vertebrates. The mouth is ventral and in front of the collar. The pharynx, perforated with gill slits, leads to the intestine, which terminates in an anus at the posterior end of the body. Dorsal and ventral mesenteries support the intestine and divide the coelomic cavity into two pouches. There are dorsal and ventral blood vessels, a portion of the dorsal one being contractile. The sexes are separate and there is a metamorphosis in development. Usually a *tornaria* larva, resembling the larvae of echinoderms, is present. In colonial forms, in addition to sexual reproduction, asexual reproduction by budding also occurs. All are marine.

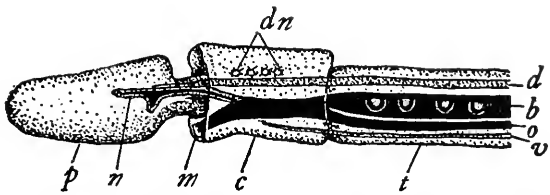


FIG. 263.—Diagram of the anterior end of *Balanoglossus*. *b*, branchial region of alimentary tract with gill clefts; *c*, collar; *d*, dorsal blood vessel; *dn*, dorsal nervous system; *m*, mouth; *n*, notochord consisting of a tube of cells connected with the alimentary canal; *o*, esophagus; *p*, proboscis; *t*, trunk; *v*, ventral blood vessel.

Examples: *Balanoglossus aurantiacus*, about 15 cm. long, occurs in sand and mud of shallow water of the Carolina coast. It lacks a tornaria larva. *Dolichoglossus kowalevskyi*, in the sandflats, Atlantic Coast; *Rhabdopleura sp.*, a deep-sea colonial form without gill slits.

SUBPHYLUM 2. TUNICATA. The presence in many tunicates of a *mantle cavity*, with incurrent and excurrent siphons, gives them a superficial resemblance to molluscs (Fig. 264). The mantle is covered by a *tunic* composed largely of *cellulose*. The *incurrent opening* is the mouth, which leads to the wide pharynx through whose gill slits the water passes either directly to the outside, or into a peribranchial or cloacal space, which opens to the outside by the *excurrent syphon*. In the mid-ventral line of the pharynx is the *endostyle*, a glandular ciliated groove, whose cilia move entangled food masses forward to the ciliated *peripharyngeal band*, from which it passes to the *dorsal lamina*, another ciliate tract in the mid-dorsal line, whence it reaches the esophagus. The latter is followed by a stomach and intestine, the intestine opening into the cloacal cavity. The heart has the peculiar property of periodically *reversing* the direction of its beat, driving the blood toward the gills for a certain interval and then driving it in the opposite direction to the viscera, etc. The central nervous system develops from a tube and is entirely dorsal to the alimentary canal. In the adult it is represented by a simple *dorsal ganglion*, located in the mantle near the mouth. Close to it is the *subneural* ganglion, thought by some to be homologous with the hypophysis of vertebrates. Tunicates are generally hermaphroditic. The tailed larvae of the sessile tunicates show unmistakable evidence of relationship to Amphioxus and the lower vertebrates. Some of these larval characters are retained in the adult stage by free-swimming forms. In some colonial tunicates (*Salpa*) there is an alternation of generations between a solitary asexual form and a sexual chain form. All tunicates are marine.

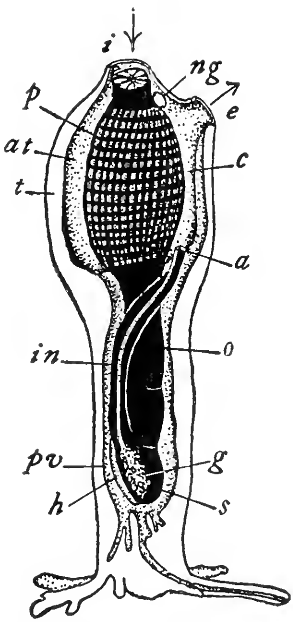


FIG. 264.—Diagram of a Tunicate, one-half of the tunic removed. *a*, anus; *at*, atrium; *c*, cloaca; *e*, excurrent siphon; *g*, gonad whose duct following the intestine opens into the cloaca; *h*, heart; *i*, incurrent siphon; *in*, intestine; *ng*, nerve ganglion; *o*, esophagus; *p*, pharynx; *pv*, perivisceral cavity; *s*, stomach; *t*, tunic. (*Based on Leuckart-Nitsche wall chart.*)

Examples: *Oikopleura flabellum*, pelagic, retains larval characters; *Ciona intestinalis*, the sea squirt, about 7 cm. in length, a common New England form: *Salpa democratica*, about 2 cm. in length, a free-swimming form; *Amaroucium stellatum*, known as sea pork, a colonial tunicate common in the Cape Cod region.

SUBPHYLUM 3. LEPTOCARDIA.

The body is fish-shaped but lacks a clearly defined head (Fig. 265). The mouth, encircled by numerous cirri, lacks jaws and is located slightly behind and under the anterior end of the body. The pharynx, into which the mouth opens, is provided with numerous gill slits that connect externally with a *branchial chamber*, from which water taken in through the mouth leaves by the *atriopore*. The atriopore is a median, ventral opening at the posterior end of the branchial chamber. Above the dorsal ends of the gill slits are numerous paired nephridial tubes opening into the branchial chamber. In the mid-dorsal line and also in the mid-ventral line of the pharynx is a ciliated groove, thought to be homologous with the endostyle of tunicates. Back of the pharynx the intestine continues as a straight tube to an anal opening near the posterior end of the animal, but to the left of the mid-line. The liver is a diverticulum from the anterior end of the intestine, extending forward to the right of the pharynx. Its walls are said to produce a digestive fluid. The digestive tract lies in a body cavity lined by coelomic

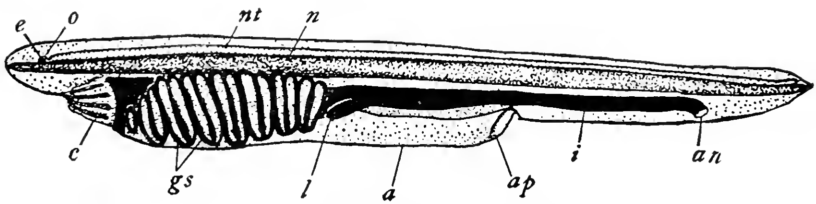


FIG. 265.—Diagram of young *Amphioxus* shortly after metamorphosis. *a*, atrium; *an*, anus, opening asymmetrically on the left side; *ap*, atropore; *c*, oral cirri, surrounding mouth; *e*, eyespot; *gs*, gill septa; *i*, intestine; *l*, liver; *n*, notochord; *nt*, neural tube; *o*, olfactory pit. (*Based on Leuckart-Nitsche wall chart.*)

epithelium. The musculature of the trunk is conspicuously segmented into V-shaped somites as in fishes.

The ventral surface of the body is flattened in the region of the branchial chamber, with slightly projecting edges on each side, known as *metapleural folds.* A dorsal fin runs the length of the body and connects posteriorly with a caudal fin around the tail. Ventrally the caudal fin is joined with the ventral fin, which extends forward to the atriopore.

There is no heart, auditory organ, skull, or vertebral column. The notochord is a well-developed rod, tapered at the ends, lying between the neural tube above and the digestive tract below, and extending the entire length of the body. The anterior end of the neural tube is slightly enlarged into a region corresponding to the brain of vertebrates. The remainder of the neural tube is the spinal cord. A median olfactory pit, located at the anterior end of the neural tube, opens externally on the dorsal surface just back of the tip of the snout. Nerves extend from the neural tube to all parts of the body.

The spinal cord gives off a pair of dorsal and ventral nerves to each segment of the body, the dorsal and ventral nerves arising independently from the cord. The blood circulatory system consists of (1) a longitudinal vessel dorsal to the alimentary canal and divided into right and left forks over the branchial region; (2) a longitudinal vessel lying ventral to the alimentary tract; and (3) lateral connections between the longitudinal vessels, those passing between the gill clefts functioning as branchial vessels. The blood is circulated by the contractions of the anterior end of the ventral longitudinal vessel and parts of other vessels. The blood moves forward in the ventral vessel and backward in the dorsal one.

The sexes are separate. All are marine.

Example: *Branchiostoma virginiae*, one of the lancelets, also known as Amphioxus, lies buried in the sand up to the mouth in an upright position. About 5 cm. in length, it is found on the southeastern Atlantic Coast. There are also numerous other species.

SUBPHYLUM 4. VERTEBRATA. A notochord develops in the embryo and, in some cases, persists as a rod-shaped structure in the adult. In most of the fishes, including the sharks, and in all higher vertebrates, it is partially or totally replaced by the centra of the vertebral column. The skeleton of vertebrates is an endoskeleton composed of cartilage or bone, or a combination of both. The integument consists of two well-defined layers: the epidermis and the corium, supplemented by (1) epidermal modifications such as the scales of reptiles, the feathers of birds and the hair of mammals; and (2) modifications in the corium, such as the scales of most fishes, and dermal bone of certain reptiles and mammals. The body is fundamentally bilaterally symmetrical and is made up of at least three body parts: head, trunk, and tail (postanal region). There are usually two pairs of locomotory appendages: the paired fins of fishes and the fore- and hindlimbs of other forms. Paired appendages are lacking in the lowest vertebrates (Cyclostomata), some Amphibia (Apoda), snakes, and some lizards. Dorsal, ventral, and caudal median unpaired fins are found in aquatic adult and larval forms. The segmental character of the vertebrate body is shown by the metameric arrangement of the vertebrae, the nerves, and the body muscles. The body cavity is a coelom in which the alimentary canal is attached by mesenteries (Fig. 266). The pharynx is concerned with respiratory function (1) by serving as a respiratory surface, (2) by developing gill slits and gills, or (3) by developing lungs. The presence of gill slits in the pharynx is a constant feature of the vertebrate embryo regardless of the type of respiration found in the adult. The central nervous system is tubular and lies entirely dorsal to the alimentary canal. Its anterior end is enlarged to form a brain composed of five regions: (1) telencephalon, (2) diencephalon, (3) mesencephalon, (4) metencephalon, and (5) myelencephalon. The remainder of the neural tube is the spinal cord. The special senses of taste, smell, sight, hearing, and equilibration are highly developed, though not to the same degree in all forms. The blood circulatory system is of the closed type. Hermaphroditism is rare.

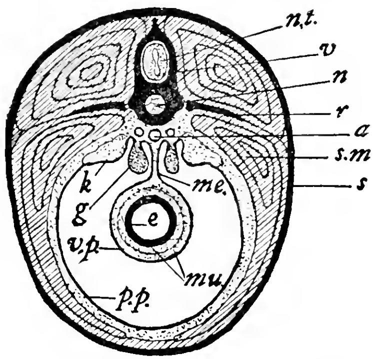


FIG. 266.—Diagram of a cross section of vertebrate body. *a*, aorta; *e*, mucosa, the endodermal lining of the alimentary tract; *g*, gonad; *k*, kidney; *me*, mesentery supporting the alimentary canal; *mu*, muscularis coats of alimentary canal; *n*, notochord; *n.t.*, neural tube; *p.p.*, parietal peritoneum; *r*, pleural rib; *s*, skin; *s.m.*, body musculature; *v*, vertebra; *v.p.*, visceral peritoneum.

CLASS I. CYCLOSTOMATA. Jawless vertebrates with a cylindrical body, lacking paired appendages, ribs, scales, and true teeth. The notochord persists as the axial skeleton throughout life (Fig. 267). Above it lies the neural tube, supported by rudimentary cartilaginous neural arches. The brain is enclosed in an imperfect skull, which is firmly attached to a cartilaginous basketwork of cartilage supporting the branchial region. There is a median fin supported by cartilaginous rays. The mouth is suctorial and is provided with sharp cuticular spines, which with similar spines on the end of the tongue are used as boring or rasping organs. There is no pancreas, spleen, or swim bladder. The olfactory organ is unpaired and median. The heart has one ventricle and one atrium. All are destructive to fishes.

Order 1. Hyperotreta. HAG FISHES. These are the most primitive vertebrates and are practically parasitic in their habits. There is a single cornified spine or tooth in the roof of the mouth which, with the rasping lingual teeth on the end of the tongue, is used in boring into the bodies of fishes. There are from 6 to 14 pairs of gills, which in some have but a single orifice on each side of the body. The hypophysis connects with the nasal sac in front and with the pharynx behind, forming a channel through which water enters and passes out through the gill slits behind. All are marine.

Examples: *Myxine glutinosa*, a North Atlantic species, reaching a length of 2 ft., has six pairs of gills with a common

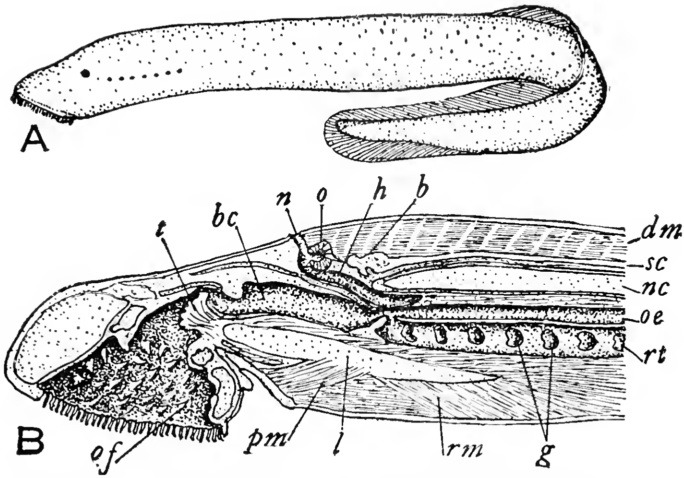


Fig. 267.—A, *Petromyzon marinus*. B, median section of anterior end of body. *b*, brain; *bc*, buccal cavity; *dm*, dorsal musculature; *g*, internal openings of gill pouches; *h*, hypophysis; *l*, lingual cartilage; *n*, nasal opening; *nc*, notochord; *o*, olfactory sac; *oe.*, esophagus; *of*, oral funnel; *pm*, protractor muscle of tongue; *rm*, retractor muscle of tongue; *rt*, respiratory tract; *sc*, spinal cord; *t*, tongue.

aperture on each side of the body. It is thought to be *protandrous* hermaphroditic (male and female alternately). The pronephros of the embryo is retained in the adult. *Bdellostoma stouti*, of the California coast, has 6 to 14 pairs of gills, each with a separate opening to the outside. A peculiar fact is that the number of gills may differ on the two sides of the body of the same individual.

Order 2. Hyperoartia. Lampreys. The nasal sac opens posteriorly into the hypophysis, but the latter does not communicate with the pharynx. The mouth is at the apex of a cornified buccal funnel, armed with sharp cuticular teeth

(Fig. 267). The tip of the tongue is also provided with similar teeth. These animals attach themselves to fishes; and feed by sucking the blood and shredded tissues from the rasped surfaces. There are seven pairs of gill pouches, opening separately on the outside and communicating internally with a median respiratory canal, located ventral to the esophagus and opening from the mouth in front. When the animal is attached to prey or to a stone, both inspiration and expiration of water take place through the external gill openings.

Example: *Petromyzon marinus*, the sea lamprey, reaches a length of 3 ft. and is found in the North Atlantic and also in fresh water.

CLASS II. ELASMOBRANCHII. SHARKS AND RAYS. These have a cartilaginous skeleton, in which the notochord is partially replaced by the centra of the vertebrae; a skull with jaws; a ventral subterminal mouth and ventral paired nostrils; paired and median fins; a spiral valve in the intestine; and a *heterocercal* tail (one in which the axis of the tail curves dorsally). The skin is invested with dermal denticles or scales of the *placoid* type. On the margins of the jaws the scales are enlarged into teeth. The placoid scale is thought to be the forerunner of the vertebrate tooth. The first gill cleft or *spiracle* has only rudimentary gill filaments and with the mouth serves as an incurrent respiratory passage. An operculum covering the gill slits is usually lacking. There is no swim bladder. All are marine.

Examples: *Mustelus canis*, a dogfish shark, 2 to 3 ft. in length; *Carcharias taurus*, the sandshark, 10 to 12 ft. long; *Pristis pectinatis*, the sawfish of Florida and the Gulf of Mexico, 16 to 18 ft. long; *Raji erinacea*, a common ray or skate, 1 to 2 ft. long. Rays and skates have gill slits on the ventral surface of the body. The spiracle or first gill cleft through which water enters is located on the dorsal surface just back of the eye. *Torpedo marmorata*, an electric ray.

CLASS III. PISCES. TRUE FISHES. These have a more or less ossified skeleton; a skull with membrane bones, and usually distinct maxillary and premaxillary bones; paired nostrils; median fins; and usually two sets of paired fins.

SUBCLASS 1. TELEOSTOMI. Cartilaginous or bony skeleton. Breathe principally by gills, which are usually covered by an operculum (Figs. 268 and 269). A swim bladder is usually present.

Series 1. Ganoidei. Skeleton cartilaginous or bony, with heterocercal or *homocercal* (outwardly symmetrical) tail fin. Scales may be (1) the *ganoid* type (rhomboidal bony plates covered with enamel or *ganoin*), (2) the *cycloid* type (bony plates with evenly curved borders), (3) the *ctenoid* type (free edge of scale spiny), or (4) the *scute* type (bony plate with enameled spines and articulating with one another to form a stiff armor. A swim bladder is present with an open duct connecting with the pharynx or esophagus. There is a spiral valve in the intestine.

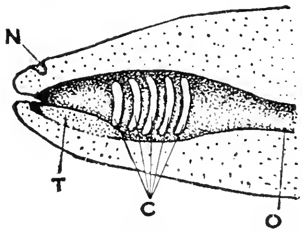


FIG. 268.—Diagram of one side of the mouth and pharynx of a fish, split lengthwise. C, gill-clefts, separated by gill arches; N, nasal pit; O, esophagus; T, tongue.

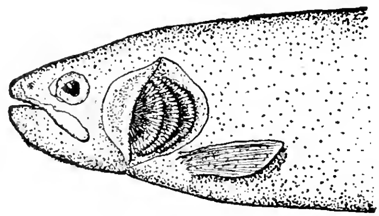


FIG. 269.—*Trutta irideus*, the rainbow trout, with the gill cover bent back to show the gills. (*After Jordan and Kellogg, Animal Life and Evolution.*)

Order 1. Crossopterygii. Jointed pectoral fins; continuous median fin; ganoid scales; and paired swim bladder. Mostly extinct.

Example: *Polypterus bichir*, a living species found in the River Nile.

Order 2. Chondrostei. Cartilaginous skeleton; persistent notochord; heterocercal tail; body naked or covered with bony plates.

Examples: *Acipenser fulvescens*, lake sturgeon, length up to 6 ft.; *Acipenser oxyrhynchus*, common sturgeon found in the North Atlantic and tributary streams, length up to 9 ft.; *Polyodon spathula*, the spoon bill or paddle fish of the Mississippi Valley, skin naked, length up to 6 ft.

Order 3. Holostei. Bony skeleton; ganoid or cycloid scales; terminal mouth provided with teeth; lunglike air bladder connected with the esophagus.

Examples: *Lepisosteus osseus*, common garpike, in fresh water, length up to 4 ft.; *Amia calva*, fresh-water dogfish or bowfin, length up to 2 ft.

Order 4. Teleostei. Bony skeleton; homocercal tail; cycloid or ctenoid scales; gills covered by an operculum; intestine without spiral valve. There is usually a swim bladder. The majority of fishes belong to this order.

Examples: *Coregonus clupeaformis*, whitefish of northern lakes; *Oncorhyncus tschawytscha*, Chinook or king salmon of Pacific Coast; *Trutta irideus*, rainbow trout; *Carpiodes carpio*, carp sucker of Ohio Valley southward; *Ictalurus furcatus*, channel catfish, has no scales; *Ameiurus nebulosus*, common bullhead, no scales.

SUBCLASS 2. DIPNOI. Lungfishes. A paired or unpaired swim bladder opening into the esophagus functions as a lung, though gills are also present. The nasal passages are respiratory and connect with the pharynx. The notochord persists as an unsegmented rod. The skeleton is partly ossified cartilage. The pectoral fins are lobate and jointed; the scales are cycloid. To a certain extent lungfishes represent a transition from fishes to amphibians. There are only a few living species.

Examples: *Neoceratodus forsteri*, the Australian lungfish, lives in brackish water and frequently comes to the surface to breathe air; *Protopterus annectans*, one of three African species, aestivates in the dry season by burrowing in the mud, where it forms a slimy cocoon about itself and remains in a state of suspended animation until the return of the rainy season; *Lepidosiren paradoxa*, a South American species that also aestivates.

CLASS IV. AMPHIBIA. Salamanders, frogs, and toads. These are both terrestrial and aquatic animals, provided usually with two pairs of pentadactyl limbs, lacking claws or nails on the digits. Limbs and limb girdles are absent in the Apoda. The integument is usually without scales. The eggs develop in water or damp earth into swimming larvae (tadpoles), provided with a tail and breathing by integumentary gills (Fig. 270). The heart has a single ventricle and two atria except in the case of lungless salamanders, in which there is a single atrium. None is marine.

Order 1. Apoda. Blind burrowing forms, without limbs. The skin contains small bony scales.

Example: *Ichthyophis glutinosus*, about 1 ft. in length. Found in India and Ceylon.

Order 2. Caudata (Urodela). SALAMANDERS AND RELATED FORMS. An elongate body with a well-developed tail; usually two pairs of limbs; teeth may be present on the maxillary and premaxillary bones, the vomer, pterygoid, parasphenoid, and mandible; gills are permanent in some, lost in others at metamorphosis. There is no tympanum.

Examples: *Necturus maculosus*, the mud puppy, is completely aquatic and has permanent gill slits and external gills, and also lungs. Length about 1 ft. Common in rivers and lakes of Eastern United States. *Cryptobranchus alleganiensis*, the hellbender, has internal gills and lungs. Length about $1\frac{1}{2}$ ft. It is aquatic and is common in Eastern United States. *Ambystoma maculatum*, the spotted salamander (black body with large bright-yellow spots), is terrestrial but returns to water to lay its eggs. The adult has lungs but no gills. *Ambystoma opacum*, the marbled salamander, lays eggs on land in the fall. Rains wash the eggs into water where larvae are hatched and complete their development. *Eurycea bislineata*, a common lungless salamander, has neither gills nor lungs in the adult state. *Siren lacertina*, the mud eel, an aquatic form, breathes by gills, and lacks hindlegs. Length about $2\frac{1}{2}$ ft. Found in Southeastern United States. *Proteus anguinus*, a blind salamander about 1 ft. in length, found in caves in Austria.

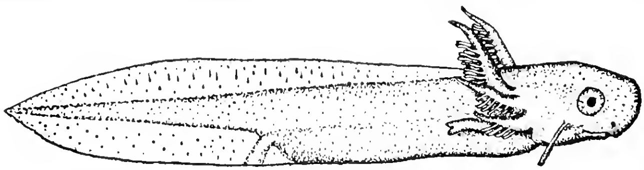


FIG. 270.—*Ambystoma maculatum*, with external gills which disappear at metamorphosis.

Order 3. Salientia (Anura). FROGS AND TOADS. A tail is absent, the caudal vertebrae being transformed into the urostyle. The posterior pair of legs modified for leaping; a tympanum is present, level with the surface of the head; males frequently have vocal sacs. There is usually a marked metamorphosis.

Examples: *Rana pipiens*, the grass or leopard frog; *Rana catesbeiana*, the bullfrog; *Bufo americanus*, a common toad.

CLASS V. REPTILIA. REPTILES. The skeleton of reptiles is well ossified; the body is covered by epidermal scales or ossified dermal plates; there are claws on the digits; breathing by lungs; no gill respiration at any time in the life history; the heart has two incompletely separated ventricles and two atria. Most reptiles are oviparous, though viviparous forms also occur. The egg in either case is large, resembling a bird's egg, and in the oviparous forms the egg is laid on the ground. There is no metamorphosis in development.

Order 1. Crocodilia. ALLIGATORS AND CROCODILES. The teeth are set in sockets (*thecodont*); there are bony plates in the skin; two pairs of legs, and a laterally flattened tail. A tympanum is present. All are oviparous.

Examples: *Alligator mississippiensis*, the common American alligator has a broad head, blunt snout and its length may reach 15 ft. *Crocodylus acutus*, the American crocodile, has a long head, pointed snout and reaches a length of 20 ft. Both occur in Southeastern United States and tropical America.

Order 2. Lacertilia. LIZARDS. The body is elongate and is covered with scales, which are periodically shed and renewed. The teeth are either attached to the edge of the jaws (*acrodont*) or laterally to the walls of a groove (*pleurodont*) in the jaw. The tongue is usually well developed and is protractile. Most lizards are oviparous.

Examples: *Sceloporus undulatus*, the common fence lizard; *Phrynosoma cornutum*, the horned toad; *Sphenodon punctatum*, a New Zealand lizard remarkable for the presence of a well-developed pineal eye: *Rhineura floridana*, the legless lizard of Florida, about 8 or 9 in. in length.

Order 3. Serpentes. SNAKES. The elongate body is limbless and covered with *scales*, which are periodically shed and renewed. The teeth are *acrodont* and the jaws are loosely articulated to the skull. The tongue is long and forked. There is no middle ear. The eyelids are not movable. Locomotion is brought about by the lateral bending of the body and by movements of the ribs, which are attached at their lower ends to the abdominal scales or scutes. Snakes are either oviparous or viviparous.

Examples: *Coluber constrictor*, the common blacksnake; *Thamnophis sirtalis*, the common garter snake; *Agkistrodon mokasen*, the copperhead, poisonous; *Crotalus horridus*, the common rattlesnake, poisonous.

Order 4. Testudinata. Turtles. The body is enclosed in a dorsal *carapace* and a ventral *plastron*, each of which is usually composed of epidermal plates, internally supported by bone. Toothless jaws are covered with horny sheaths. The eyes have upper and lower lids and a nictitating membrane. The skin is usually covered with scales. The limbs are pentadactyl with clawed toes. In marine turtles the limbs are modified into flippers with reduced numbers of digits. Eggs of both aquatic and terrestrial forms are deposited on land.

Examples: *Chelydra serpentina*, the snapping turtle; *Terrapene carolina*, the box turtle; *Malaclemys centrata*, the diamond-back terrapin; *Chrysemys picta*, the painted turtle; *Amyda spinifera*, the soft-shelled turtle, lacks horny plates or scales and has fleshy lips; *Eretmochelys imbricata*, the tortoise-shell turtle, marine; *Caretta caretta*, the loggerhead turtle, is also marine.

CLASS VI. AVES. Birds. A modern bird is a homoiothermous animal, whose body is covered with feathers and scales, whose anterior limbs are modified for flight, and whose jaws lack teeth. The heart has two ventricles and two atria and the circulation is completely double. The stomach consists of two regions: a glandular *proventriculus* and a muscular *gizzard*. There are usually two *caeca* at the junction of the ileum and colon. The lungs are attached to the walls of the coelom and are provided with long sacs that extend among the viscera and into some of the bones. Sense organs are well developed. A middle ear is present. The carpals of the forelimb are reduced by fusion and the rudimentary digits correspond to digits II, III, and IV of the pentadactyl hand. In the hindlimb as a result of fusions, *tibiotarsal* and *tarsometatarsal* bones are formed. The elements of the pelvis are fused to form a rigid structure. The sternum of flying birds is provided with a deep keel for the attachment of the wing (pectoral) muscles.

The caudal vertebrae are fused to form a *pygostyle*. Birds are oviparous. The egg is large and is incubated by the parents. The left oviduct and left ovary only are functional.

That birds are undoubtedly descended from reptilian ancestors is indicated by embryogeny and by the anatomy of extinct and modern birds as well. *Archaeopteryx* (Fig. 271), a prehistoric

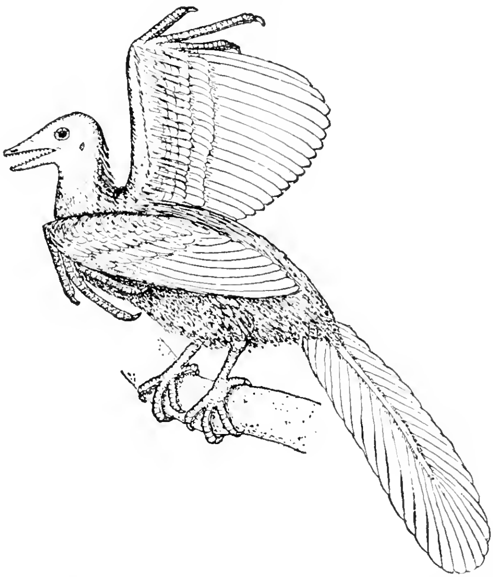


Fig. 271.—*Archaeopteryx macura*, restored. The fossil remains of this link between reptiles and birds was found in the Jurassic of Bavaria. The jaws do not have a beak but are provided with teeth. The tail consists of about twenty separate vertebrae to which feathers are attached on either side. Each wing has three clawed fingers. Feathers are well developed on the wings and tail but the head and other parts of the body are naked. The bones are without air sacs. (*After Romanes, Darwin and after Darwinism, Open Court Publishing Company.*)

bird, had toothed jaws, a vertebrated tail (instead of a pygostyle), and three clawed fingers on the wing, all of which are reptilian rather than avian in character. In modern birds the fingers are so reduced and modified as to be practically nonexistent, yet in the young of the *hoactzin*, a South American bird, the forelimbs are provided with fingerlike claws which, with the feet, are used in climbing about the branches of trees in a lizardlike fashion before the bird learns to fly.

SUBCLASS 1. ARCHAEORNITHES. Extinct birds.

Example: *Archaeopteryx*.

SUBCLASS 2. NEORNITHES. Includes four orders of extinct birds as well as all existing birds.

CLASS VII. MAMMALIA. MAMMALS. A mammal is a homoiothermous animal, covered more or less with hair and provided with mammary glands on the ventral surface of the body which in the case of the female are used in suckling the young. The teeth are thecodont and are of four kinds: *incisors*, *canines*, *premolars*, and *molars*. Except in certain aquatic mammals, an external ear, in addition to a middle and inner ear, is present. The middle ear contains three ossicles: malleus, incus, and stapes. A muscular *diaphragm* divides the body cavity into a thoracic cavity containing the heart and lungs in front and an abdominal cavity containing the rest of the viscera behind. Each lung lies freely in a pleural cavity. The heart consists of two ventricles and two atria, and the circulation is completely double. The red corpuscles of the blood lack nuclei.

SUBCLASS 1. PROTOTHERIA. EGG-LAYING MAMMALS. These have a single cloacal opening for both the urinogenital and alimentary systems. The mammary glands have no distinct nipples. The egg is large, contains much yolk, and resembles the reptilian or avian egg. As in birds, the left ovary and left oviduct only are functional.

Examples: *Ornithorhynchus anatinus*, the Australian duck-bill or platypus, is about 20 in. in length. It has a duck-like bill, webbed feet, and is covered with fur. *Echidna aculeata*, the spiny ant eater, also found in Australia. These with a few other species are the only representatives of the entire subclass. They occur only in Australia and the neighboring islands.

SUBCLASS 2. METATHERIA. MARSUPIALS. These are viviparous mammals whose young are born in an immature state and are usually carried for a period after birth in a *marsupium* or pouch, located on the abdomen of the mother. A cloaca is absent and the urinogenital and anal openings are distinct. The mammary glands are within the marsupium and are provided with teats. The vagina is partially or completely double.

Examples: *Didelphys virginiana*, the Virginia opossum; *Macropus giganteus*, the giant kangaroo of Australia.

SUBCLASS 3. EUTHERIA. Placental mammals. The vagina is single and the embryo is nourished by a placenta formed from the *allantois* of the embryo and the lining of the uterus. The allantois is an embryonic membrane. Eutheria are called placental mammals, but as a matter of fact a placenta is also present in some marsupials.

Section A. Omnivorous Forms. Five digits on hand and foot; clavicle well developed.

Order 1. Insectivora. Typically, walking feet with dorsal surface often scaly; first digit not opposable; radius and ulna separate, but tibia and fibula often fused.

Examples: European *hedgehog*, *shrews*, and *moles*.

Order 2. Primates. Primitive dentition; first digit opposable on fore or hind limb or both; hands and feet for grasping. Large cranium; reduced jaws and nasal cavities; orbits directed forward. Semierect or erect posture.

Examples: *Monkeys*, *apes*, and *Man*.

Order 3. Rodentia. Two chisel-shaped incisor teeth (four in rabbits) in each jaw, modified for gnawing. Radius and ulna separate; tibia and fibula some times fused. Clavicle absent in guinea pigs.

Examples: *Mice*, *rats*, *rabbits*, *guinea pigs*, *beavers*, and *porcupines*.

Order 4. Galeopithecoidea (Dermoptera). On each side a lateral fold of skin including limbs and tail, when spread acts as a parachute, enabling the animal to make long leaps. Primitive dentition. Ulna, fibula, and clavicle rudimentary.

Example: *Galeopithecus*, the *flying lemur* of India and the Malay Archipelago, the only representative of the order.

Order 5. Chiroptera. Greatly lengthened arm bones and fingers supporting a membranous wing used in flying.

Example: *Bats*.

Order 6. Edentata. Incisors and occasionally all of the teeth lacking.

Examples: *Anteaters*, *sloths* and *armadillos*.

Order 7. Tubulidentata. Body covered with bristlelike hairs; five prismatic molars in each jaw; four toes in front, five behind.

Example: *Orycteropus,* the South African *aardvark,* the only representative of the order.

Order 8. Pholidota. Body scaly with scattered hairs; teeth lacking.

Example: *Pangolin,* the *scaly anteater.*

SECTION B. CARNIVOROUS FORMS.

Order 9. Carnivora. Strong recurved canine teeth; molars more or less modified for cutting. Four- or five-toed feet which may be plantigrade, semiplantigrade, or digitigrade; toes usually clawed. Some are omnivorous and some may live largely on a vegetable diet.

Examples: *Wolves, dogs, cats,* and *bears.*

Order 10. Pinnipedia. Pentadactyl webbed feet for swimming; feed on fish.

Examples: *Walrus* and *seals.*

Order 11. Cetacea. Fore limbs paddlelike; hindlimbs lacking; usually a dorsal fin; a caudal fin composed of two lobes or flukes. There is no neck owing to fusion of the cervical vertebrae. Rudimentary pelvic bones and, in some, vestiges of the skeleton of the hindlimbs occur embedded in the flesh. Skin may be entirely naked.

Examples: *Porpoises, dolphins,* and *whales.*

SECTION C. HERBIVOROUS FORMS. Terminal digits encased in hoofs. Ungulata.

Order 12. Hyracoidea. Plantigrade, three toes in front and four behind.

Example: *Hyrax,* the *coney* of the Bible. Most primitive living ungulate, found in Western Asia and South Africa.

Order 13. Proboscidea. Pentadactyl; long proboscis with nostrils at the tip; never more than two incisors (tusks) in each jaw; no canine teeth; no clavicles.

Examples: *Elephants.*

Order 14. Sirenia. Pentadactyl, finlike forelimbs; hindlimbs lacking. Skin naked or sparsely haired. Harmless aquatic animals of huge size, feeding on seaweed and river grasses.

Examples: *Manatee* or *seacow* of tropical America and Africa; *Dugong* of the Indian ocean.

Order 15. Artiodactyla. Even number of digits (four or two), the axis of the foot passing between the third and fourth digits.

Examples: *Swine, hippopotamus, deer, sheep, oxen, and camels.*

Order 16. Perissodactyla. Odd number of digits (five, three, or one) the axis of the foot passing through the middle of the third digit.

Examples: *Horse, zebra, tapir,* and *rhinoceros.*

Man.—The *Primates*, the order to which man belongs, are, from the standpoint of general anatomy, the most primitive mammals with the exception of the *Insectivora*, and for that reason occupy a position among the lowest orders. When compared with Primates, most other mammals show considerably more departure from the original type, as for example, in the general form of the body of the whale or manatee, the specialized fore arm of the bat or the mole, the hoof of the ungulate, or the teeth of the rodent. The primitive characters of the Primates are best seen in the skeleton, which aside from the skull has retained the original elements of the class with but little modification. Thus, in Man the clavicle is present, both radius and ulna occur in the forearm and the tibia and fibula in the leg; the arrangement of bones of the wrist is primitive, the elements being distinct and showing only slight modification. On the other hand, the ankle region is modified as a result of the elongation of the foot which anatomically is more highly specialized than the hand; the tail, highly developed in some Primates, is absent in apes and Man, being represented by the coccyx, composed of reduced caudal vertebrae and not visible externally.

The important feature which makes the Primates a superior group is the brain and this reaches its highest development in Man. The enlargement of the brain has been accompanied by modifications in the cranium and secondary modifications in the face, such as the forward-directed orbits, the reduction of the nasal region with a corresponding loss of olfactory sense, the shortening of the jaws and the retreat of the teeth, the latter causing the formation of the chin in the lower jaw. Very likely the shortening of the face developed as the hand with its opposable thumb came to be used more and more to bring food to the mouth, thus relieving the latter of seeking and grasping food.

Primates were, and some of them still are, essentially arboreal animals. Man is a terrestrial animal, descended in all probability from arboreal ancestors. The change from arboreal to terrestrial habitat is thought for many reasons to have taken place in Central or Southern Asia as a direct result of an increase in bulk too great for arboreal life, or because of geological or geographical changes which compelled the larger Primates to seek the ground for shelter and food. Since Primates long before this event had become widely scattered, only those living in the disturbed region modified their mode of living, with the result that monkeys and apes, the gorilla excepted, surviving in other parts of the world are largely arboreal to this day. The subsequent progress of the human race is undoubtedly the result of this change in habitat, whatever the cause, since an arboreal existence has rather limited possibilities for human development. If the interpretation of the geological record is at all correct, specialization and increase in size without a corresponding development of the brain have spelled disaster for many animals in the past. Man is fortunate in that his specialization has been in the direction of greater brain power while the rest of his body has retained a certain flexibility by remaining relatively unspecialized, a combination which enables Man to make use of past experiences and to suit action to requirement to a greater degree than any other animal.

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GLOSSARY

ABIOGENESIS. The spontaneous generation of living things from nonliving matter, a theory held but not experimentally demonstrated.

ABORAL. A pole of the body opposite the mouth.

ABSORPTION. The passage of a fluid into living cells by osmotic or capillary action.

ACHROMATIC. Uncolored. Free of color.

ADAPTIVE. Having the quality of fitness; favorable to life processes.

ADORAL. A point of the body near the mouth.

AGAMIC. Without gametes. Asexual.

ALBINISM. The absence of pigment in the skin, hair, feathers, eyes, etc.

ALBUMIN. One of the blood proteins; found also in milk, muscle, and other animal substances.

ALBUMINOID. A substance having many characteristics of true proteins.

ALIMENTARY CANAL. Same as digestive tract.

ALLELOMORPH. One of a pair of alternative characters in Mendelian inheritance; said also of the genes which represent these characters in the chromosomes.

AMINO ACID. An organic acid in which one or more of the nonacid hydrogen atoms is replaced by the NH_2 group. *Glycine* ($CH_2 \cdot NH_2 \cdot COOH$); *Lysine* ($CH_2 \cdot NH_2 \cdot CH_2 \cdot CH_2 \cdot CH_2 \cdot CH \cdot NH_2 \cdot COOH$).

AMITOSIS. Direct cell division, in which the formation of a spindle and chromosomes is lacking.

AMOEBOID. Having a flowing movement, such as occurs in *Amoeba*.

AMPHIGONY. Reproduction from a fertilized egg. Sexual reproduction.

ANABOLISM. The constructive or reintegrative phase of metabolism.

ANALOGOUS. Similar in function.

ANASTOMOSIS. A joining or communication between vessels.

ANATOMY. The structure of organisms as determined by dissections.

ANIMAL POLE. The yolk-free region of the egg.

ANKYLOSIS. Abnormal immobility and consolidation of a joint.

ANTENNA. One of a pair of jointed appendages of the head of an insect, or crustacean.

ANTERIOR. Toward the head or front end of an animal.

ANTITOXIN. A complex compound, probably protein in nature, formed in the blood serum and capable of neutralizing the effect of a specific poison or toxin, especially such as is produced by pathogenic bacteria.

ANUS. The terminal opening of the digestive tract.

APICAL. Pertaining to or located at the apex.

ARCHENTERON. The cavity of the gastrula; gastrocoel.

ARTERIAL BLOOD. Oxygenated blood. It may be carried by either arteries or veins.

ARTICULATE. To join; to unite by means of a joint.

ARTIFICIAL PARTHENOGENESIS. The development of an egg following artificial stimulation without the intervention of a sperm.

ASSIMILATION. The transformation of digested and other absorbed food products into living substance, or into material that can be utilized by living substance.

ASYMMETRY. An arrangement of parts incapable of being divided by a plane into halves which are mirrored images of each other.

ATOM. The smallest particle of a chemical element which can exist either alone or in combination with other similar atoms or with atoms of another element; the smallest particle of a chemical element which enters into the composition of a molecule.

AUTONOMIC, AUTONOMOUS. Self-governing; said of the sympathetic and parasympathetic nervous systems.

AXIAL. Pertaining to an axis. The backbone is the axial skeleton of vertebrates.

AXON. Process of a nerve cell conducting impulses away from the cell body.

BACTERIA. A group of microscopic plants, some of which are the causative agents in the production of certain diseases. They exist in three general forms as follows: *cocci*, which are spherical; *bacilli*, rod-shaped; and *spirilla*, spiral filaments.

BARBEL. A slender tactile process on the lips of certain fishes.

BICONCAVE. Hollow on each side or end.

BILATERAL SYMMETRY. An arrangement of parts capable of being divided by a plane into right and left halves.

BINOMIAL NOMENCLATURE. The method of designating organisms by two names, one for the Genus and the other for the Species. Example: *Rana pipiens*, the leopard frog.

BIOGENESIS. The generally accepted principle that all living things are derived from living things; that only life reproduces life (see Abiogenesis).

BIOGENETIC LAW. In its modern form, the doctrine that an animal in its development repeats to a certain extent the history of its race. Also known as the *law of recapitulation.*

BIPARENTAL. Derived from two parents, male and female.

BIPED. An animal which walks on two feet.

BLASTOCOEL. The segmentation cavity within the blastula.

BLASTOMERE. One of the cells formed in cleavage of the egg, fertilized or parthenogenetic.

BLASTOPORE. The opening of the archenteron or gastrocoel.

BLASTULA. The stage during cleavage, when the cells are arranged in the form of a hollow sphere.

BUCCAL CAVITY. Mouth cavity.

CARBOHYDRATE. Sugars, starches, and cellulose. Organic compounds consisting of carbon, hydrogen, and oxygen, the hydrogen and oxygen being in the same proportion as in a molecule of water (H_2O).

CARNIVORE. A mammal belonging to the order *Carnivora.*

CARNIVOROUS. Flesh-eating.

CATABOLISM. The disintegrative phase of metabolism.

CATALYSIS. The acceleration in rate of a chemical reaction by an agent which itself remains unchanged.

CAUDAD. Toward the tail.

CAUDAL. Pertaining to the tail.

CELL. A small mass of protoplasm containing one or more nuclei.

CELL DOCTRINE. That all organisms are composed of cells and the products of cells; that the cell is a functional and structural unit of the organic body.

CELLULOSE. A carbohydrate found in the walls of plant cells. Its occurrence in animal tissues is rare.

CENTIGRADE THERMOMETER. One in which 0° is the freezing point and 100° the boiling point of water.

CENTIMETER. A unit of linear measurement in the metric system. Abbreviation: *cm.;* (2.54 centimeters = 1 inch).

CEPHALAD. Toward the head or anterior end.

CEPHALIC. Pertaining to the head.

CERCUS. Either of a pair of appendages at the posterior end of the body of arthropods.

CERVICAL. Pertaining to the neck.

CHARACTERS OF CHARACTERISTICS. Physical, mental, and physiological traits.

CHLOROPHYLL. An important plant pigment, concerned in photosynthesis.

CHONDROCRANIUM. A continuous cartilaginous structure incompletely enclosing the brain. It occurs in the embryos of all vertebrates and in the adult sharks and lampreys.

CHORDATE. An animal in which the notochord is or represents the skeletal axis during some period of its life history. All vertebrates are chordates.

CHROMATIC. Pertaining to color.

CHROMATIN. The deeply staining substance of the nucleus which forms into chromosomes when the cell divides.

CHROMATOPHORE. A cellular organ containing pigment.

CHYLE. The fatty contents of the lacteals of the intestines.

CHYME. Partly digested food as it occurs in the stomach and intestine.

CILIA. Hair-like processes of Protozoa and ciliated epithelial cells.

CIRCULATION. The movement of the blood or body fluid through a more or less complete system of vessels.

CIRRUS. A soft tentaclelike appendage.

CLASS. One of the principal subdivisions of a phylum in the system of classification.

CLEAVAGE. The period of cell division following fertilization, during which the egg is converted into a blastula. Parthenogenetic eggs also undergo cleavage.

CLOACA. A common cavity into which open the urogenital ducts and the alimentary canal, in fishes, amphibia, reptiles, birds, and the lowest group of mammals (*Prototheria*).

COCOON. A case in which eggs are deposited and in which larvae may develop; a protective covering of mucus secreted by the integument.

COELENTERON. A saclike body cavity in which digestion and absorption of food take place. Same as gastrovascular cavity.

Coelom. The body cavity of the vertebrate type, lined with mesothelium and containing the viscera attached by mesenteries. It is entirely distinct from the digestive cavity of the alimentary canal.

Collagen. A gelatinlike protein.

Colloid. A state of matter consisting of a dispersed system of molecular aggregates.

Colony. A group of individuals of the same species, often organically connected, forming a unit of a higher order than the individual.

Commensalism. The association of two or more individuals of different species, often for mutual benefit.

Concave. Curved inward.

Conjugation. A temporary union of two Protozoa during which an exchange of nuclear material takes place.

Convex. Curved outward. Bulging out.

Copulation. The sexual act during which spermatozoa are transferred from the male to the female; or the sexual act of two monoecious animals.

Cortex. The outer region of a cell or organ.

Cranial. Pertaining to the cranium, the portion of the skull enclosing the brain.

Cretinism. A condition characterized by subnormal mental and physical development, caused by thyroid insufficiency.

Cuticle. The outer layer covering the surface of the organic body. It may be a secretion product of underlying cells, as in many invertebrates, or it may be composed of dead cells, as in the stratum corneum of human skin.

Cytoplasm. The extranuclear part of a cell; the cytosome.

Cytozoic. Parasitic in a cell.

Darwinism. The explanation of evolution by the theory of *Natural Selection* as set forth by Charles Darwin.

Deaminization. The process in the body by which nitrogenous radicals are removed from amino acids, thus liberating nonnitrogenous portions capable of oxidation and energy production.

Differentiation. In embryogeny the transformation of blastomeres into tissues and organs. In general, a change from *homogeneity* to *heterogeneity*.

Digestion. The result of the action of digestive agents on food which reduces food to a liquid condition capable of absorption and assimilation by living cells.

Dioecious. A condition in which the male and female organs, testis and ovary, are borne by different individuals.

Diploblastic. Having two germ layers.

Diploid. The unreduced number of chromosomes.

Distal. Remote from point of origin or attachment.

Diuresis. Free or excessive secretion of urine.

Dorsal. Pertaining to the back.

Ductless gland. A gland whose secretion is poured directly into the blood stream. An endocrine gland.

Dynamic. Pertaining to change or process. Characterized by energy or action.

Ecology. The study of the relation of organisms to their environment, both animate and inanimate.

Ectoderm. The outer layer of the gastrula.

Ectoparasite. External parasite.

Egg. The female germ cell, either before or after fertilization.

Embryo. An animal in the early stages of its development before it is liberated from the egg membranes.

Embryogeny. The formation of the embryo and the course of its development. Embryogenesis. Embryology is the study of embryogeny.

Encystment. The formation of a protective covering about an organism. particularly Protozoa.

Endocrine gland. See Ductless gland.

Endoderm. The germ layer forming the lining of the gastrula and bounding the archenteron or gastrocoel; lining of the alimentary canal.

Endomixis. A nuclear reorganization occurring in Protozoa without conjugation and therefore without synkaryon formation (fertilization).

Endoparasite. Internal parasite.

Endoskeleton. An internal living skeleton such as is present in vertebrates.

Entelechy. A word adopted from Aristotle by Hans Driesch to designate the "vital force," which he believes is necessary as an additional factor outside the range of known forms of energy to explain life. Entelechy and the "soul" of Descartes are practically the same concept, except that Descartes entertained the fanciful notion that the soul resided in the pineal gland, which is a dorsal outgrowth of the roof of the forebrain and in all probability represents an ancestral eye.

Enzyme. An organic catalytic agent which accelerates chemical reaction in the body.

Epigenesis. The idea that an organism in its development starts as a relatively homogeneous initial plasma which becomes heterogeneous as a result of the action of external factors upon it. The opposite of preformation in development.

Epithelium. A layer of cells covering an external or internal surface of the body.

Eugenics. The science of improving the inborn qualities of the human race by better breeding.

Eustachian tube. A duct connecting the middle-ear cavity with the pharynx. It is a survival of the first gill cleft of the fish.

Eutheria. A subclass including the viviparous mammals.

Evagination. The outgrowth of a pocket of cells from a surface.

Evolution. The doctrine that organisms of today are derived by *descent* from those of the past; that organisms have *changed* from time to time; that, in general, higher organisms are *descended* from lower ones.

Excretory. Pertaining to waste substances formed in metabolism.

Exoskeleton. The lifeless external cuticle forming the protective covering and supporting framework of arthropods. An external skeleton.

EXTERNAL RESPIRATION. The passage of oxygen from the air or water into the blood.

EXTRACELLULAR. Outside of cells.

FACTOR. Any causative agent. Its effect is called response.

FAMILY. A subdivision of an order in classification.

FAT. An organic compound consisting of carbon, hydrogen, and oxygen, in the form of a glyceric ester of a fatty acid.

FAUNA. The animal organisms occurring in a given region or place.

FECES. The excrement or undigested food residue discharged from the alimentary canal.

FERMENTATION. The decomposition of organic compounds, usually through the action of enzymes (*ferments*).

FERTILIZATION. The culmination of the series of events following the entrance of the sperm into an egg, ending in the union of a male and of a female nucleus to form the first cleavage nucleus.

FETUS. The mammalian embryo in later stages of development when the body regions are well defined.

FLAGELLUM. A greatly enlarged cilium occurring in Protozoa, and frequently as the tail of a spermatozoon.

FLUCTUATING VARIATION. A relatively slight variation of somatic origin which is not heritable.

FOSSIL. The remains of a prehistoric organism or its tracks, etc., found usually embedded in the earth's crust.

GAMETE. Male or female germ cell; sperm or egg.

GANGLION. A tissue mass composed principally of nerve-cell bodies.

GASTRIC. Pertaining to the stomach.

GASTROCOEL. The cavity of the gastrula.

GASTRULA. In embryogeny, the double-walled sac resulting from the invagination of the single-layered blastula. The outer layer is ectoderm and the inner endoderm. Gastrulation is a fundamental process in development.

GEL. A more or less rigid colloidal state.

GENE. The germinal representative of a character.

GENOTYPE. The factor or gene complex of an organism or a group of organisms. The germinal complex as contrasted with somatic.

GENUS. A group of related species. A subdivision of a family in classification.

GERM LAYER. One of the primary embryonic tissues, ectoderm, endoderm, or mesoderm, from which the tissues and the organs of the adult develop.

GESTATION. The period of development in viviparous animals between fertilization and birth.

GILL. A platelike or filamentous appendage of an aquatic animal bathed by water and serving as an organ of respiration.

GILL CLEFTS. Paired openings leading from the sides of the pharynx to the exterior. Present in all Chordates. In fishes gills are attached to the septa separating the clefts.

GLAND. An organ whose cells secrete one or more substances that may be used by the organism (as in secretions of the glands of the alimentary tract), or that may be excretory in character (as in the metabolic products excreted by the kidney).

GLOMERULUS. A complicated network in the course of an arteriole of the kidney.

GLOTTIS. A slitlike opening in the floor of the pharynx leading to the respiratory tubes and the lungs.

GLYCOSURIA. The presence of excessive amounts of sugar (dextrose) in the urine.

GONAD. The organ in which germ cells develop. Ovary or testis.

GUSTATORY. Pertaining to the sense of taste.

HABITAT. The natural abode of an organism; the kind of environment in which it lives.

HAPLOID. The reduced number of chromosomes.

HEMOCOEL. A body cavity which contains blood. A type of body cavity found in many invertebrates.

HERBIVOROUS. Plant eating.

HEREDITY. The occurrence or production in offspring of parental traits or characteristics; the transmission of genes through the germ cells.

HERMAPHRODITE. An organism provided with both male and female gonads.

HETEROCERCAL. Said of the type of fish tail in which the terminal part of the vertebral column takes an upward bend, making the tail fin asymmetrical, the ventral portion much smaller than the dorsal.

HETEROGONY. The alternation of amphigony with parthenogenesis.

HETEROZYGOTE. An organism which has received from its parents two unlike genes for a given character and which, in turn, produces two numerically equal classes of gametes with respect to the genes.

HOMOLOGOUS. Said of organs having a similar origin in evolution though not necessarily a similar function.

HOMOIOTHERMAL. Having a practically constant body temperature.

HOMOZYGOTE. An organism which has received from its parents two like genes for any given character. Its gametes are, therefore, all alike with respect to these genes.

HORMONE. An internal secretion of a gland which activates other organs, or the body as a whole, in a specific manner.

HOST. An organism which harbors a parasite.

HYALINE. Glassy, translucent.

HYBRID. The offspring of parents, differing from one another in at least one heritable character.

HYDROID. Colonial coelenterate made up of individuals resembling *Hydra*. A polyp.

HYDROLYSIS. A double chemical decomposition reaction into which water enters.

HYDROSTATIC. Relating to the pressure and equilibrium of liquids.

HYPERGLYCEMIA. The presence of excessive amounts of sugar (dextrose) in the blood.

HYPERTONIC. Having a higher osmotic pressure than normal, or than another substance.

Hypothesis. A tentative supposition provisionally adopted for explaining certain facts and serving as a guide for further investigation. A stage in the development of a theory.

Hypotonic. Having a lower osmotic pressure than normal.

Immunity. The resistance of the body to infection by pathogenic organisms, natural or acquired, through the production of antitoxins.

Infection. Implantation of disease, pathogenic organisms, or parasites from without.

Insemination. The addition of sperm to eggs. The introduction of sperm into a female.

Integrative action. Said of the function of the nervous system as a coordinating mechanism for unifying bodily activities.

Intercellular. Between cells.

Internal respiration. The interchange of oxygen and carbon dioxide between tissues and the circulatory fluid. *True* respiration.

Internal secretion. Usually the product of a ductless gland that is absorbed by the blood. Hormone. Endocrine.

Intracellular. Within a cell.

Intussusception. Growth by the intercalation of substances throughout the cells of an organism, as contrasted with growth by accretion—deposits of particles on the outside—such as occurs in crystals.

Invagination. The ingrowth of a pocket of cells from a surface.

Invertebrate. An animal without a backbone.

Ion. An atom or group of atoms bearing an electrical charge. *Hydrogen-ion concentration* refers to the number of free hydrogen ions in a solution, which determines whether the solution is "acid" or "basic" in reaction.

Irritability. The power of protoplasm to respond to stimuli.

Isotonic. Having the same osmotic pressure.

Karyokinesis. The indirect method of cell division; mitosis.

Kinetic energy. Energy possessed by a body by virtue of motion. Manifested by heat production in chemical reactions.

Lacteal. A lymph vessel of the intestine.

Lacuna. An intercellular space.

Lamellated. Arranged in layers.

Lamellibranchiate. Belonging to a group of molluscs having platelike gills, such as the clam, oyster, mussel, etc.

Larva. A usually active stage in the development of an animal marked by the presence of larval organs and by the absence of adult ones. An immature but free-living stage in development.

Lateral. Pertaining to the side.

Law. A statement of an order or relation of scientific facts which, so far as known, is invariable.

Lesion. A wound or local degeneration.

Linear. Arranged in a line or row.

Lumbar. Pertaining to the region of the back posterior to the thorax.

Lumen. Cavity or passageway of a tubular structure.

Lymph. In vertebrates a circulatory fluid similar to blood but lacking red corpuscles. Same as blood in many invertebrates.

Macroscopic. Large enough to be seen with the unaided eye.

Mammal. A vertebrate having hair and mammary glands.

Mandible. A biting mouth part of invertebrates. The lower jaw of vertebrates.

Maternal. Pertaining to or derived from the female parent.

Matrix. The intercellular material of cartilage and bone. Intercellular substance.

Maxilla. A mouth part of an invertebrate. The upper jaw of vertebrates.

Mechanism. The hypothesis supported by many facts that the phenomena of life are inherent in the physical and chemical properties of the constituents of protoplasm. It does not admit "vital force" as a factor in explaining life processes.

Mendelism. A universal type of inheritance based on the fact that genes of inherited characters separate and combine as units in the germ cells.

Mesoderm. The embryonic germ layer formed between the endoderm and ectoderm.

Mesoglea. A noncellular layer lying between the ectoderm and endoderm of *Hydra* and related forms.

Metabolism. The chemical processes of protoplasm which are made up of disintegrative and reintegrative phases, catabolism and anabolism, respectively.

Metagenesis. The alternation of sexual and asexual generations in the life history of an organism. The alternation of sexual medusa and asexual polyp in *Obelia*.

Metamerism. The repetition of parts or segments in a linear series, as in the segmentation of the earthworm, or the arrangement of vertebrae in the vertebral column.

Metamorphosis. The more or less sudden change of the larva into the adult. The transformation of a tadpole into a frog; or of a caterpillar into a moth.

Metazoa. Animals whose bodies consist of more than one cell. All animals above Protozoa.

Millimeter. One-tenth of a centimeter. Abbreviation: *mm.*

Mitosis. The ordinary form of cell division. Also called karyokinesis.

Molecule. A group of atoms. The smallest particle of a substance that possesses the properties of the substance.

Monoecious. Having both ovary and testis in one individual.

Motor neuron and nerve. One carrying impulses away from the central nervous system and causing muscular contraction or glandular activity. Efferent neuron.

Mucosa. The layer of cells lining the digestive tract of vertebrates.

Mutation. A heritable variation of a discontinuous type caused by some sort of change in the germplasm.

Myotome. One of the segments in the body musculature of vertebrates.

Natural selection. The natural process of eliminating the unfit. The survival of the fittest in nature.

Nephridium. A tubular type of excretory organ such as occurs in the earthworm and which is the forerunner of the tubules of the vertebrate kidney.

Nerve. A bundle of nerve-cell processes, axons, or dendrons, or both.

Neural canal. The cavity in the vertebral column containing the spinal cord.

Neural tube. The embryonic ectodermal tube from which the brain and spinal cord develop.

Neuron. A nerve cell, including cell body, axon, and dendron.

Nitrogen equilibrium. A condition in which the animal body is receiving from food as much protein nitrogen as it is metabolizing and eliminating.

Notochord. A structure characterizing the phylum Chordata consisting of a cylindrical rod lying ventral to the neural tube. In all vertebrates except *Cyclostomata* it is replaced in varying degrees by the centra of the vertebral column.

Nucleolus. A usually spherical body within the nucleus taking an acid stain. Chromatin takes the basic stain.

Nucleus. One of the two principal components of a cell, usually occupying a central position in the cytoplasm.

Olfactory. Pertaining to the sense of smell.

Ontogeny. The development of the individual.

Oocyte. The developmental stage of the egg during the growth period.

Oogenesis. The development of a mature egg from a primordial germ cell.

Oogonium. One of the products of division of the female primordial germ cell.

Oosperm. A fertilized egg.

Ootid. The final product of oogenesis, the mature egg.

Order. A subdivision of a class in classification.

Organ. A tissue complex which performs a definite function.

Organelle. A protozoan organ; an organ within a cell.

Organic. Of or pertaining to organisms.

Organism. A living thing.

Organology. The study of organs.

Osmosis. The slow passage or diffusion of fluids through semipermeable membranes. Osmotic pressure results from the difference in behavior of solvent and solute with respect to the membrane, the latter not being equally permeable to both. The surfaces of cells constitute the membranes through which substances must pass in and out of cells, the direction being determined by conditions within the cell with reference to the surrounding medium.

Osseomucoid. A glycoprotein found in bone.

Ovary. The organ in which eggs develop.

Oviparous. Egg laying.

Ovum. Egg, female gamete.

Oxidation. The chemical combining of a substance with oxygen, partial or complete. Combustion.

Paedogenesis. Reproduction in the larval state.

Paleontology. The science of prehistoric organisms.

Parasitism. An animal association in which one member, the *parasite*, derives nourishment from the tissues of the other, the *host*, to the detriment of the latter.

PARTHENOGENESIS. Development of an egg without fertilization.

PARTIAL PRESSURE. The pressure exerted by one component of a mixture of gases. The pressure of each component is proportional to its quantity.

PARTURITION. Act of bringing forth young.

PATERNAL. Pertaining to, or derived from, the male parent.

PATHOGENIC. Disease-producing.

PELAGIC. Said of the habitat of organisms living at or near the surface of large bodies of water.

PELVIS. The posterior region of the abdomen in vertebrates. The pelvic girdle. A region in the kidney.

PENIS. An intromittent organ of the male by means of which spermatozoa are transferred to the vagina of the female.

PERICARDIUM. In vertebrates the peritoneal sac surrounding the heart.

PERISTALSIS. The rhythmic contraction of the intestinal wall.

PERITONEUM. The membrane lining the coelom of vertebrates.

PHAGOCYTE. A cell which ingests and destroys waste and harmful material, bacteria, etc., in the body.

PHARYNX. The region of the alimentary tract between the mouth and esophagus.

PHENOTYPE. The somatic complex of an organism or a group of organisms regardless of the potential germinal possibilities.

PHOTOSYNTHESIS. The synthesis, or building up, of complex organic compounds from relatively simple inorganic substances through the agency of sunlight in the presence of pigments like chlorophyll. A natural process in plants.

PHYLOGENY. The developmental history of the race.

PHYLUM. A main subdivision of a plant or animal kingdom.

PLACENTA. A composite maternal and fetal organ of the mammalian uterus which serves to attach the embryo, to supply nourishment and oxygen from the maternal blood, and to remove waste products. It is shed in whole or part at birth.

PLACOID SCALE. Consists of a rhombic basal plate of dentine (bone) from the middle of which a spine projects. In the spine is a pulp cavity with blood vessels. Characteristic of *Elasmobranchs.* Forerunner of vertebrate tooth.

PLASMA. The liquid part of the blood. Blood *minus* corpuscles.

PLEXUS. A union of several nerves to form a network.

POIKILOTHERMAL. Having a body temperature slightly higher than that of the environment.

POLAR BODY. One of the minute cells formed in the maturation divisions of the egg.

POLARITY. Differentiation at the two ends of an axis.

POLYMORPHISM. Several forms. The existence of two or more types of individuals in a species, as in the honeybee.

POLYP. A Hydralike coelenterate.

POTENTIAL ENERGY. The energy a body possesses by virtue of its position. A lifted weight has potential energy in proportion to the kinetic energy expended in lifting it. An organic compound possesses potential energy in a chemical form in proportion to the energy expended in establishing a certain spatial relation between atoms in the molecule.

PREFORMATION. In its original form, the idea that development consisted in the unfolding of adult structures already preformed in the germ; which, of course, can no longer be accepted. In a modified sense the term can be applied to the organized ground substance of the egg and to the orderly arrangement of genes in a chromosome.

PROBOSCIS. A tubular process or prolongation of the head or oral region.

PROTANDRY. A condition in monoecious animals in which the testis becomes functionally mature before the ovary.

PROTEIN. An organic compound of large molecules made up of carbon, hydrogen, oxygen, nitrogen, and sulphur with sometimes phosphorus and iron which upon hydrolysis yields amino acids. A very important constituent of protoplasm and one which has not yet been synthesized.

PROTOPLASM. Living matter.

PROTOTHERIA. The lowest group of mammals, which are oviparous.

PROTOZOA. Unicellular animals.

PROXIMAL. Next or nearest, as to a point of attachment.

PSEUDOPODIUM. A temporary fingerlike extension of the cytoplasm of *Amoeba* and related forms.

PULMONARY. Pertaining to the lung.

PUPA. The quiescent stage following the larval period in an insect, during which the adult organs are developed.

PURE LINE. All the offspring of a homozygous self-fertilized parent. A group of individuals having an identical germinal constitution.

PUTREFACTION. The decomposition of proteins as brought about by enzymes or bacteria.

RADIAL SYMMETRY. Symmetry that is referable to a circle. Two or more planes passing through a common axis will in each case produce halves that are mirrored images of each other.

RECEPTOR. A sensory-nerve ending or end organ.

RECTUM. The terminal portion of the alimentary canal in vertebrates and in many invertebrates.

REDUCING AGENT. A chemical agent which causes a loss of oxygen in a substance.

REDUCTION DIVISION. One of the two maturation divisions in gametogenesis during which synaptic chromosome mates separate, reducing the number to one-half.

REFRACTIVE. Having power to turn from a direct course. Said of the effect of certain substances on light.

RESPIRATION. The absorption of gaseous oxygen and the excretion of carbon dioxide by protoplasm.

RESPONSE. Any change in protoplasmic activity resulting from a stimulus.

RETICULUM. A network.

RUMINANT. A herbivorous animal that chews its cud.

SACRAL. Pertaining to the region of the vertebrate axial skeleton to which the pelvic girdle is attached.

Salivary glands. Glands whose secretion is discharged into the mouth and usually has some digestive property.
Sebaceous glands. Oil-secreting glands present in hair follicles.
Secondary sexual characters. Traits other than the gonads that distinguish sexes.
Secretion. The substance produced by a gland. The activity of a gland.
Segmentation. See Metamerism.
Sensory. Pertaining to sensation. Said of a neuron carrying impulses from the periphery toward the central nervous system.
Septum. Partition.
Serum. The clear fluid remaining after blood has clotted.
Sessile. Fixed; not free-swimming.
Sex-linked characters. Characters whose genes are linked with those of sex.
Sol. A more or less fluid colloidal state.
Solute. The substance dissolved in a liquid.
Solvent. The liquid in which a substance is dissolved.
Somatic. Pertaining to the soma or body as distinguished from germ cells.
Species. A group of individuals derived from similar parents, or practically alike in all important characters.
Sperm. Male gamete. Spermatozoon.
Spermatid. The male germ cell after the second maturation division but before its transformation into a spermatozoon.
Spermatocyte. The developmental stage of the male germ cell during the growth period.
Spermatogenesis. The development of a mature sperm from a primordial germ cell.
Spermatogonium. One of the products of the division of the male primordial germ cell.
Spontaneous generation. Same as abiogenesis.
Static. Pertaining to a body at rest or in equilibrium.
Stimulus. Any disturbing influence producing a reaction in an organism.
Stratum. A layer.
Striation. Striping, such as the cross marks of skeletal muscle.
Symbiosis. The association of two species of organisms for mutual benefit.
Synkaryon. The fertilization nucleus formed by the union of male and female germ nuclei.
Systematist. A student of taxonomy. An expert in classification.
Tactile. Pertaining to the sense of touch.
Taxonomy. The science of classification.
Theory. A general principle serving as a plausible explanation of phenomena, supported by facts and by relevancy of reasoning.
Thorax. In mammals, the anterior division of the coelom separated from the abdomen by the diaphragm and containing the heart and the lungs. In arthropods, the middle body region.
Thyroidectomy. The surgical removal of the thyroid gland.
Tissue. A group of histologically similar cells.
Traumatic. Due to a wound or injury.

Triploblastic. Having three germ layers.

Umbilical cord. A ropelike connection between the mammalian embryo and the placenta carrying embryonic blood vessels, by means of which the nutritive and respiratory needs of the embryo are supplied. The umbilicus or navel on the abdomen of the adult marks the point of attachment of the cord.

Unguiculate. Provided with claws.

Ungulate. Provided with hoofs.

Unit character. A hereditary trait that maintains its integrity from generation to generation.

Ureter. The duct leading from the kidneys to the cloaca, or to the urinary bladder.

Urethra. The duct leading from the urinary bladder to the exterior.

Urine. The secretion of the kidney consisting of water and other catabolic products.

Urinogenital. Pertaining to the excretory and reproductive systems.

Uterus. In mammals, a specialized portion of the oviduct or oviducts in which the placenta forms and the embryo develops. In the frog, a portion of the oviduct in which eggs are held before deposition.

Vacuole. A small cavity or space in a cell containing fluid or other substances.

Vagina. The terminal portion of the female genital tract leading from the uterus or oviducts to the exterior.

Vascular. Pertaining to blood vessels, or blood supply.

Vas deferens. A duct in the male leading from the testis to the exterior.

Vasoconstriction. The constriction of blood vessels brought about by the contraction of muscles in the walls of the blood vessels.

Vegetal, vegetative. Nutritive. Said of the pole of the egg in which the yolk is concentrated.

Venous blood. Deoxygenated blood.

Vertebrate. An animal with a backbone or vertebral column.

Viscera. Internal organs. In mammals, the contents of the abdomen.

Vitalism. The doctrine that living phenomena can only be explained by assuming the presence in protoplasm of a "vital" factor of some sort in addition to the factors made up of the chemical and physical properties of protoplasm.

Viviparous. Reproduction by birth.

Voltaic pile. A vertical series of alternating disks of two dissimilar metals, as zinc and copper, separated by disks of paper moistened with acid water. When the top and bottom are connected by a wire, a current of electricity is produced.

Zooid. One of the members of a hydroid colony.

Zygote. The fertilized egg, or the individual produced from the egg. Exconjugants are also zygotes.

INDEX

Names of genera and species are printed in italics; names of higher ranks, such as families, orders etc., in capitals and small capitals; all other terms and proper names in roman type. Numbers refer to pages.

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