ESSENTIALS OF ZOOLOGY

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ZOOLOGY

EMPHASIZING PRINCIPLES OF ANIMAL BIOLOGY

BY

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SECOND EDITION

With 224 Text Illustrations

DEDICATED TO

the late

PROFESSOR W. B. WILSON

Ottawa University

my former teacher and inspiration in biology

PREFACE TO SECOND EDITION

The present edition represents a complete editing of the previous edition with some revision and addition of material at certain points. The general form and content of the book have been retained. A number of condensed and pertinent tables have been added to the chapter on Physiology, and a new section dealing with the snail has been included in the chapter on mollusca. The author makes acknowledgment here for many valuable suggestions which came from Dr. C. J. Goodnight of Purdue University. Also, appreciation is expressed to Betty Ann Potter for her valuable assistance with the index of this book.

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PREFACE TO FIRST EDITION

There has come into being a considerable number of relatively short but fundamental zoology courses. Often they are given in a single semester. Such courses usually involve rather intensive laboratory study of the systems of one or two vertebrate forms, a few selected invertebrates, and a number of special relationships as parasitism, reproduction, development, etc. The recitation or theory portion of such a course is ordinarily concerned with some coordination and summary of the selected materials treated in the laboratory, but perhaps more particularly with the lessons in principles which may be drawn from them.

It is the presence of this type of course in a number of different zoology or biology departments which has prompted the organization of the present book. It is the purpose of the author to bring into the book the essential fundamentals which every zoology student should have, regardless of the length of the course he happens to take.

It is likely true that the majority of the students taking elementary zoology will have only that one course in the field and for that reason some emphasis is placed on the economic aspect, on the human relation, and on the principles involved. It is assumed that the teacher will elaborate upon the details of particular topics of interest to the class beyond the limitations of detailed information contained in this volume.

The arrangement of the chapters has been placed in an order which seems logical. However, the chapters are written in such a way that the teacher may change the order with no difficulty. Since this is true, the teacher has some option in the possibility of striking a workable combination of "types" and "principles" material as well as balance in laboratory-lecture program.

The author is indebted to, and extremely grateful for the cooperation of, the following who have contributed to the manuscript:

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CHAPTER I

INTRODUCTION

The question, What is Life? is the greatest riddle in the biological world. The term *life* is an abstraction with no objective reality except as it is a phenomenon related to the activities of living units. The following statement has been given and is probably as nearly a definition as can be found: Life is a continuous series of reactions in a complexly organized substance, by means of which the organization tends to adjust itself to a constantly varying environment. Numerous attributes of living material may be given. Living material has the ability to carry on active chemical reactions without losing its body form. It is responsive to changes in the environmental conditions; therefore, it is said to be adaptive. Living material is able to sustain and reproduce itself under favorable conditions.

Biology is a word derived from two Greek words, *bios*, life, and *logos*, discourse, and is the name universally applied to the study of living organisms and life processes. Since living things fall largely into two general categories, plants and animals, such a study deals with the forms and phenomena exhibited by both.

Nature is ever inviting investigation; her forces are in constant operation about us, but she hides the truth. The biologist looks upon himself as a seeker after truth, as one striving to get a glimpse into the mysteries of life. As he succeeds in obtaining these glimpses, he soon realizes the existence of certain fundamental features common to the structure and function of all living forms. He soon recognizes the oneness of all life, and himself as a part of one great organic system, each unit of which has some relation to the whole. A biological concept may rest upon observations, which may be changed from day to day by the discovery of new facts, but the biologist, like the chemist or physicist, is justified in holding to a theory or hypothesis as long as it provides a true working basis for further investigation.

"Trained and organized common-sense" was the definition of science given by Thomas H. Huxley, an eminent English biologist

who lived from 1825 to 1895. That was his way of saying that scientific knowledge is simply an extension and organization of the knowledge based upon common observation and experiment concerning the facts of nature. Facts are indispensable building stones of science. Facts must be gleaned from careful observations and experiments which have been rigidly checked and will yield identical results with frequent repetition and by numerous observers.
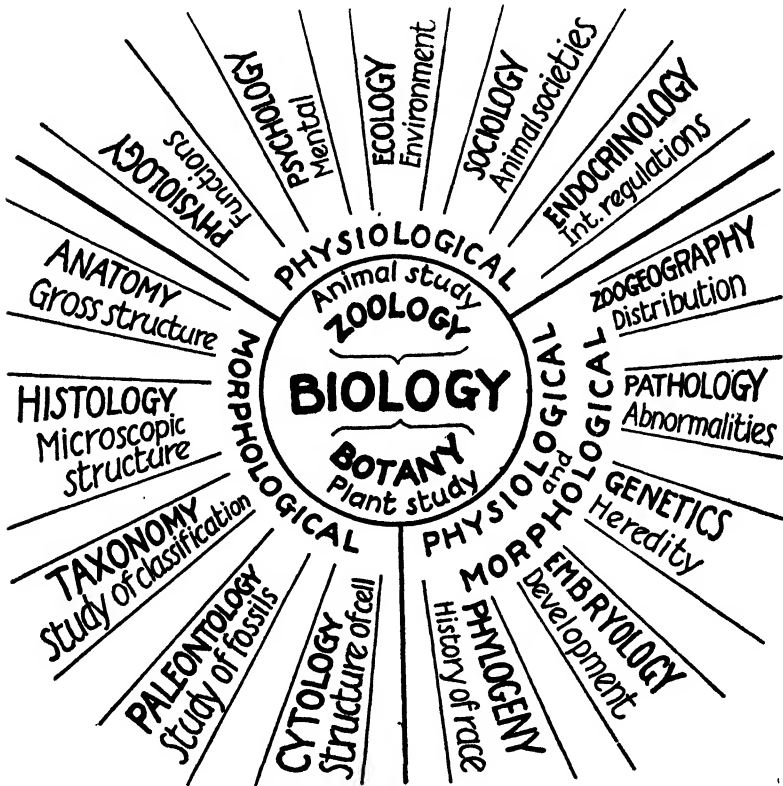
Fig. 1.—Divisions of study in the field of biology.

Science lays its foundation on accurate observations and depends on the ability of the senses to reveal the truth. Established facts represent truth, and the scientist respects truth while to him tradition or mere opinion counts for little as such. Science is, therefore, a changing, increasing body of knowledge which is ever becoming more thoroughly established.

Zoology, a Biological Science

The name, zoology, which is derived from the Greek words *zoos,* animal, and *logos,* discourse on, refers to the study or science of animals. The *natural sciences,* as distinguished from the social sciences, are conveniently divided into two groups: the *physical sciences,* such as chemistry, physics, and astronomy, which deal with nonliving bodies; and the *biological sciences,* such as botany and zoology, which are concerned with living organisms. Zoology and botany together constitute the science of biology. The expression *animal biology* is often used as a synonym for zoology. A person who specializes in the study of zoology is known as a zoologist. There was at one time an erroneous popular impression that zoologists were simply ''bug-hunters.'' This conception of the field has been greatly expanded until now it is considered one of the valuable and serious fields of science.

The Subdivisions of Zoology

Zoology as one of the divisions of the general field of biological science is such a broad field that it is necessary to subdivide it into several subdivisions for convenience in study. It has been a relatively short time since all of the known biology, geology, and related subjects were studied under the head of natural history. But now the subject matter of zoology alone has grown to such magnitude that it has become necessary to divide it into numerous special fields. These subdivisions may be summarized as follows:

1. **Morphology** is the study of the form and structure of the bodies of animals. It is one of the older fields, and is further divided into several branches.

A. *Gross anatomy,* which literally means cutting up, includes all that may be studied of form and structure of bodies by dissecting them. Human anatomy, which is one of the fundamental subjects of study in the preparation of the medical student, is usually separated from comparative anatomy. The dissection, observation, and study of the parts, form, and relationship of parts of the digestive system of the cat would be a good example of anatomical study.

B. *Histology* or *Microscopic Anatomy,* is a study of the microscopic structure of the various parts of the animal body. The histologist studies the relationship and arrangement of the cells as they cooperate to comprise the substance of the organism.

C. *Cytology* is the study of the minute structure of the cells which, we will learn, are the units of structure of all living matter. This field of study has yielded many fundamental concepts of the factors involved in the living process.

2. **Taxonomy** is the subdivision which deals with the classification or orderly arrangement of organisms according to their natural relationships. This field is often spoken of as systematic zoology. The number of described species of animals as given by different authorities ranges from 840,000 to well over a million. One well-known writer says there are probably no less than 2,000,000 species of living animals. Besides these, there are large numbers of extinct forms. It can readily be seen that a system for putting these large numbers of different kinds of animals into a known order is one of the first prerequisites for dealing with them. On a much smaller scale, the department store is systematized for some of the same reasons. One can see that it would be next to impossible to do business if a company were to provide a large floor space, go out and buy the thousands of different kinds of articles that are handled by a department store, and just throw all of them on its floors at random.

The relationships of animals are discovered from similarity of structure, from facts of distribution, from embryological similarities, and many other comparisons. A group in which the members are very closely related is likely to be comparatively small. These groups are ranked together according to evident relationships. Zoologists recognize a number of large divisions of the animal kingdom based on certain general characteristics. Each of these divisions is known as a phylum and is divided into classes, each class is divided into orders, each order into families, each family into genera, and each genus into species. Taking the classification of man as an example we have:

> Phylum: Chordata
> > Subphylum: Vertebrata
> > > Class: Mammalia
> > > > Order: Primates
> > > > > Family: Hominidae
> > > > > > Genus: Homo
> > > > > > > Species: sapiens

The scientific name of man is written, *Homo sapiens* Linnaeus. Such a name is composed of the genus name and species name, and followed by the name of the person who wrote the first authoritative description of the particular species. This always gives a double name to a kind of animal, and for that reason it is the *binomial* system of nomenclature. This system was originated by Linnaeus. The names are in Latin instead of common vernacular because Latin is a constant and almost universal language. The common names would be almost certain to vary with each different language, but the Latinized form *Homo sapiens* Linn. is the same in Dutch as it is in English.

3. **Physiology** is the study of the functions of the various parts of the organism as well as its living process as a whole. It involves a consideration of metabolism, growth, reproduction, sensitivity, and adaptation. In this field is included the study of many special functions, such as digestion, circulation, respiration, excretion, glandular secretion, nervous activity, muscular contraction, and others. Many of the processes which occur in the developing embryo are also included here. Much of the present study referred to as cytology is physiological. Physiology, like morphology, is an old branch of zoology. Physiology depends upon an understanding of physics and chemistry on one hand, and anatomy on the other.

4. **Pathology** is the study of the abnormal structures and abnormal functioning of life processes. It is really the science of disease in all of its manifestations.

5. **Embryology** is a study of the origin and development of the individual and may be spoken of as *ontogeny*. It usually involves the changes occurring in the organism from the time of fertilization by the union of two cells, one derived from each parent, through the numerous cell divisions, growth, organization, and differentiation leading to the adult condition.

6. **Genetics** is the division which deals with the study of variations, resemblances, and their inheritance from parent to offspring. Fairly definite laws governing this inheritance of qualities have been established by the geneticists.

7. **Phylogeny** is a study of the origin and relationships of the different groups and races of organisms. It is based on the results of studies of morphology, embryology, genetics, zoogeography, and paleontology.

8. **Ecology** is a study of the relation of the organism to its environment. Many adjustments in structure and function have been made by animals to bring them into harmony with the conditions of the environment. Such conditions as the relation of the organism to the medium in which it lives to temperature, to light, to food, to competition, to enemies, to mating, and many other factors, all become a part of an ecological study.

9. **Zoogeography** or geographical distribution of animals is concerned with the extent of the regions over which species are distributed and the association of species in individual regions. It is concerned with the regions in which species exist and with the factors affecting their distribution. The regional distribution of an animal group is limited in part by the extent and relations of favorable environmental conditions, but no species occupies all of the regions where environment would permit. The point of origin of the group may be cut off from other favorable regions by unsurmountable obstacles. Conditions which prevent dispersal of animals from one area to another are known as *barriers*. Oceans, mountains, forests, deserts and land are all barriers to different types of animals. The Starling, which originated in Europe, was not found in America until after it was introduced by man, and in recent years it is becoming a dominant bird.

10. **Paleozoology** is a study of the animals of the past as they are presented by their fossil remains. Parts of many of the ancient animals are embedded and preserved in the sedimentary rocks. The relative age of the fossils is determined from the depth of the rock strata in which they are found. Many of the probable lines of descent of animals have been discovered by studies of the fossils. Much concerning the facts and the fate of extinct species has been learned through this field of study.

Classification of the Animal Kingdom

Few people realize the number of different kinds of existing animals and their variation in size, structure, and habits of life. The estimated number of kinds is all the way from 1,000,000 to 10,000,-000. To date, approximately 840,000 species have been named and described.

The entire kingdom is divided into two subkingdoms: Protozoa, or all single-celled animals, and Metazoa, the many-celled animals,

The secondary groups are phyla, and they in turn are divided into classes. The principal groups subordinate to the class are order, family, genus, and species. Later in the book there is a chapter devoted to the classification of animals but the principal phyla are listed and briefly described here:

Phylum Protozoa.—Individuals consist either of a single cell or of aggregates of cells, by each of which are performed all the essential functions of life. They are mostly microscopic in size and largely aquatic in habit. Some live in the ocean, some in fresh water, and still others as parasites in man and other animals. About 15,000 are known.

Phylum Porifera (Sponges).—Mostly marine aquatic metazoans which live attached. The body is supported by fibrous, calcareous, or siliceous spicules, and the body wall is perforated by many pores. There are approximately 3,000 known species.

Phylum Coelenterata (Jellyfish).—All are aquatic and most of them are marine. They possess radial symmetry, a single gastro-vascular cavity, and tentacles provided with stinging bodies, *nemato-cysts.* The described species number at least 4,500.

Phylum Ctenophora (Sea Walnuts or Comb Jellies).—Free swimming, delicate, marine animals that possess biradial symmetry. They are triploblastic and hermaphroditic. Less than one hundred species are known, and twenty-one of these are American.

Phylum Platyhelminthes (Flatworms).—These are flat, unsegmented, bilaterally symmetrical, triploblastic worms. "Flame cells" are characteristic excretory structures. These animals may be free-living or parasitic. Tapeworms, liver flukes, and the free-living, aquatic Planaria are commonly known. Approximately 6,500 species have been described.

Phylum Nemathelminthes (Threadworms or Roundworms).—Unsegmented, bilaterally symmetrical, enlongated worms which possess both a mouth and an anus. Some are free-living, others are parasitic. The hookworm, ascaris, and the "horsehair worm" are common representatives. About 3,500 species are known.

Phylum Echinodermata.—Marine animals which have a spiny skin and the body wall usually supported with calcareous plates. They are radially symmetrical and have tube feet as organs of locomotion. The common representatives are starfishes, sea urchins, sea cucumbers, and sea lilies. There are about 4,500 known living species.

Phylum Annelida (Jointed worms).—This group is characterized by segmented body, well-developed body cavity, and nephridia as tubular excretory structures. They live in marine waters, fresh water, and in the soil. The earthworm and leech are well-known examples of the phylum. There are at least 4,500 known species.

Phylum Arthropoda.—The group includes crayfishes, lobsters, crabs, centipedes, scorpions, and all insects. Their bodies are segmented, and they have segmented appendages. This is by far the largest single phylum. Some authors believe as many as 675,000 species belong to it.

Phylum Mollusca.—Unsegmented animals that are usually enclosed in a calcareous shell. The single muscular "foot" is a characteristic structure. Common forms include clams, snails, slugs, and octopuses. About 78,000 species have been recognized.

Phylum Chordata.—Segmentally constructed animals with bilateral symmetry and an endoskeletal axis or notochord at some stage. Many of our best known animals belong here; the phylum includes lampreys, sharks, bony fish, frogs, salamanders, alligators, snakes, turtles, rats, birds, horses, sheep, cows, monkeys, and men. Approximately 40,000 species have been described in the group.

In addition to the above generally recognized phyla, there are several other more or less independent smaller but distinct groups. Most of these groups have certain of the wormlike characteristics. Many authors have dignified each of these as a phylum. They are: **Nemertinea**—nearly unsegmented, contractile, wormlike forms; **Trochelminthes**—unsegmented and frequently similar to certain larval stages of annelids and molluscs, rotifers being typical; **Bryozoa**—colonial, marine, or fresh-water forms, of which there are about 1,750 known species; **Brachiopoda**—marine animals enclosed in a bivalve shell, the majority of which are fossil; **Phoronidea**—sessile marine worms living in chitinous tubes in shallow water; **Chaetognatha**—marine, transparent, carnivorous worms of which *Sagitta* is an example; **Sipunculoidea**—unsegmented, elongated marine worms, living either free, in tubes, or in snail shells. A number of these are sometimes described under the phylum name **Molluscoida.**

Balance in Nature

The influence exerted by one animal or one group of animals on another can hardly be estimated until one of them leaves the picture. In an established animal community which might be said to
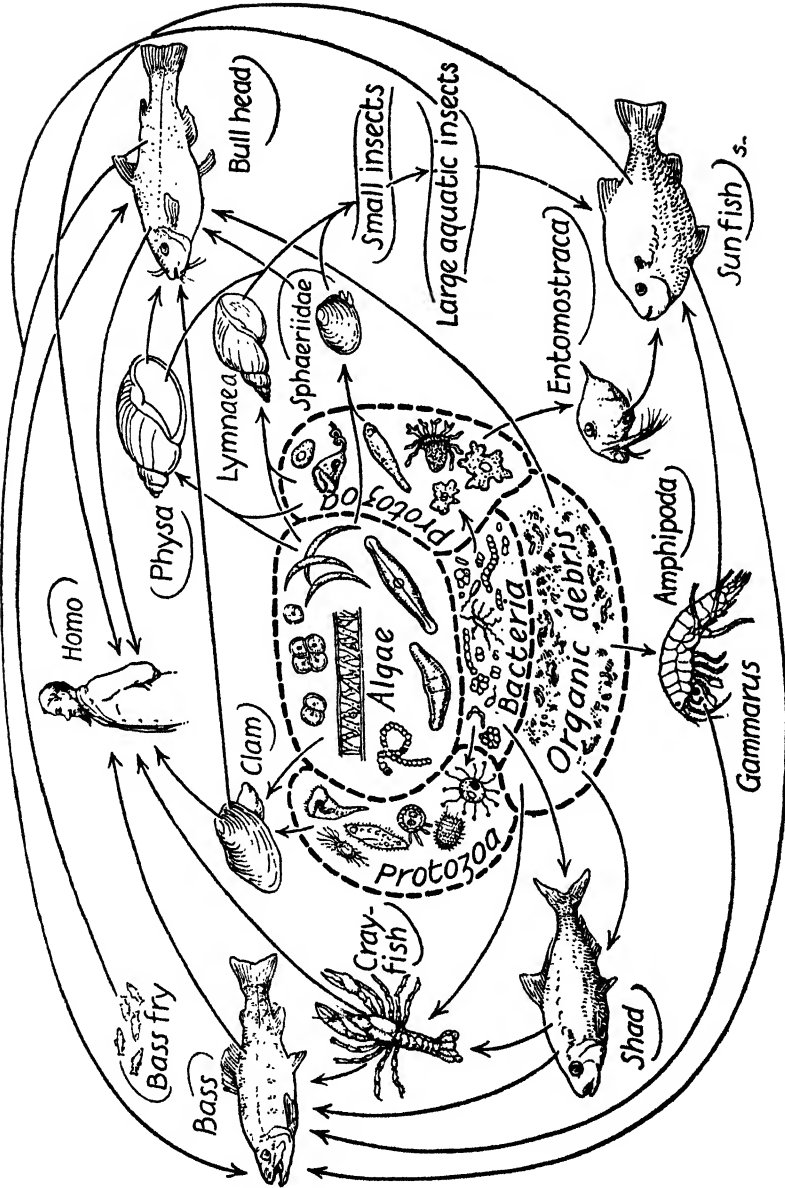
Fig. 2.—Balance in life. A food chain as illustrated by relationships among fresh-water animals.

be balanced, all groups are held in bounds by their enemies. Balanced animal communities can be found the world over, and we are only beginning to get a notion of the extensive ramifications of the forces concerned in maintaining that balance. Quite clearly most animals live in a state of repression because relatively few of them become pests and overrun the country. About eighty-five years ago someone who had admired the remarkable spirit of the English sparrow in its native European home thought this hardy little bird would be a cheerful addition on this side of the Atlantic. Consequently, a few pairs were landed in Brooklyn. In the short years that have elapsed, this sparrow has proved so hardy and free of enemies here that it is now our dominant bird.

The story of the rabbit in Australia is likewise an interesting example of the effect of balance or lack of it. Not many years ago Australia had no rabbits. It was hoped and intended by English immigrants there, that a few imported pairs of rabbits would increase sufficiently so that the old English sport of riding to the hounds might be developed in Australia. To the surprise and dismay of these people, the rabbits flourished until now they are jeopardizing the enterprises of man.

Again, we have an example of the effect of the natural agents of repression. The Japanese beetle which was recently introduced in the United States by accident has ravaged the vegetation in several eastern states and threatens other areas. When our investigators went to Japan to study the enemies of the beetle in an effort to find a means of control, they had to search for weeks to find a seriously infested area. So impressed are some biologists becoming with the potential danger of interfering with the natural balance, that even when some irritating pest is under discussion, whose extermination is easily possible, they will advise against it until all phases of the animal's existence are thoroughly investigated. To wipe out this form might remove the check on others that are still more obnoxious.

Vital Relations of Animals and Plants

There are certain single-celled organisms that are claimed as animals by zoologists and as plants by botanists. It is difficult to draw an absolutely clear-cut line of distinction. Of course, it is easy to recognize the extremes. Anyone holding a sunflower in one hand and a frog in the other has no difficulty in determining which is animal and which is plant. The distinctly typical animal forms
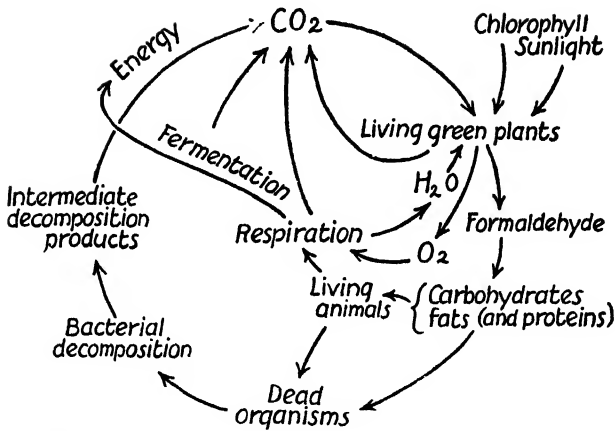
Fig. 3.—The carbon cycle as it occurs in living organisms.
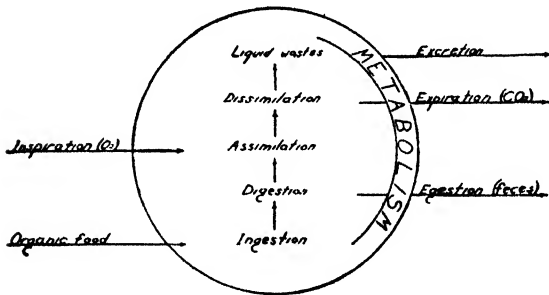
a Animal
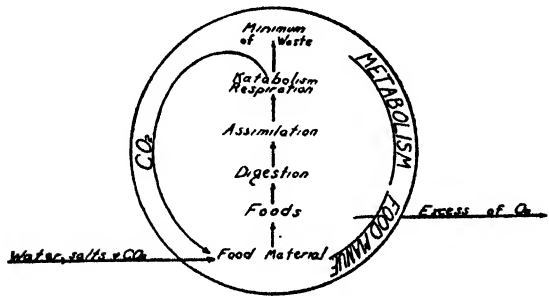
b Plant

Fig. 4.—The metabolic processes of plants and animals as well as the food manufacturing process (photosynthesis). (Redrawn by permission from Wolcott. *Animal Biology*, published by McGraw-Hill Book Company, Inc.)

depend on green plants for their organic food. It is derived either directly or indirectly from the process of *photosynthesis* carried on by green plants to manufacture starch which is stored in plant tissue. Green plants by effect of their chlorophyll (green pigment)
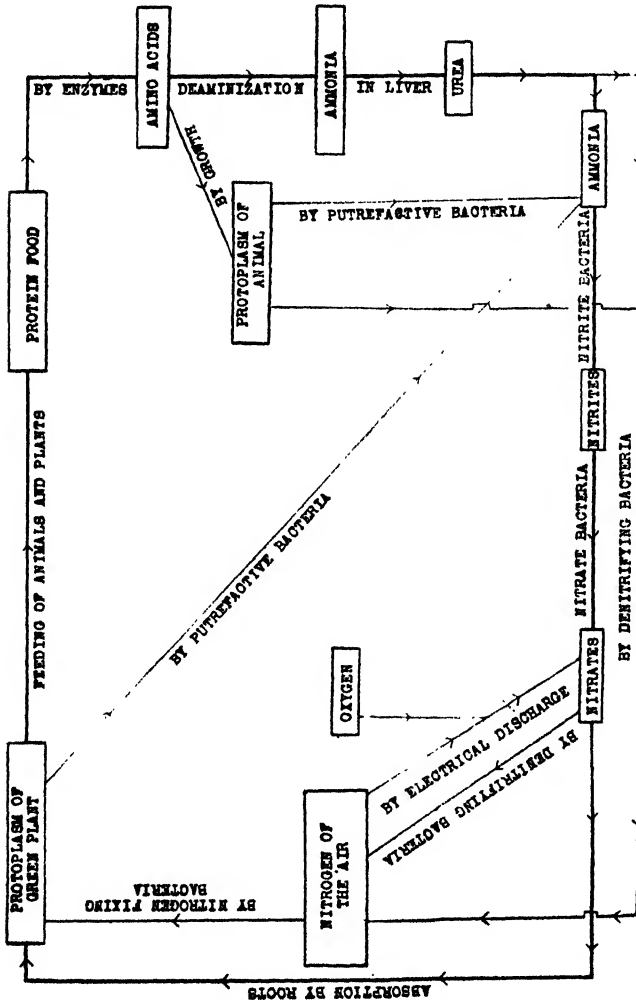
Fig. 5.—The nitrogen cycle. (From White, *General Biology*, The C. V. Mosby Company.)

in sunlight cause carbon dioxide, a gas of the air, and water to unite in the formation of a simple carbohydrate. *This is the basic food material of plants as well as of animals.* During daylight hours while photosynthesis is in progress, oxygen is discharged into the

air as a product of the process. This oxygen adds to the atmospheric supply and is used by animals in respiration. The carbon dioxide discharged by respiration of plants and animals is made use of by plants in this synthesis of material. The excretory products of animals contain nitrogen which is easily transformed into a soluble form and absorbed by plants to be combined with the simple carbohydrate, already described, to produce protein for themselves and indirectly for animals.

Zoology as Related to Man

The values of the study of zoology may be placed in two classes: cultural and practical. There is hardly a field of endeavor in the realm of human activities which is not greatly influenced by zoology and biology generally. The study of philosophy, the formulation of our conception of religion, the comprehension of social welfare problems, and many other similar intellectual and social accomplishments are greatly facilitated by a knowledge and recognition of biological principles. From the purely practical or economic side, of course, agriculture, medicine, and their related sciences have profited enormously. In fact, these fields are in themselves applied biology. Most of the great discoveries as to the nature and control of disease, the manner of inheritance of human characteristics, and the knowledge of fundamental physiological processes occurring in our own bodies have been attained by studies on other animals. What is found to be true in a dog, frog, rabbit, rat, monkey, or guinea pig, usually has its application to man. The loss of their lives is constantly saving millions of human lives. One of the most obvious uses of other animals is as a source of food supply. We have only to think of such forms as mammals, birds, turtles, frogs, fish, crabs, lobsters, clams, oysters, and even snails.

Many animals are important because of their destructive tendencies in regard to articles valued by man, or to the health and life of man. It is likely that the parasites which live on and in the bodies of men, and on domesticated plants and animals have been much more costly than the depredations of the more conspicuous predators.

Agriculture and Zoology

A recent instance of the economic importance of zoological knowledge is found in the saving of the entire citrus industry in Florida

from the Mediterranean fruit fly. Injurious insects alone cause an annual loss in the United States of more than one and one-half billion dollars' worth of products if they could be sold at the price the remaining portion brings. With proper knowledge of animal life and application of this knowledge it is likely that at least half of this loss could be prevented. Losses almost as important are caused each year by the parasitism of our domestic animals by bacteria, protozoans, worms, and arthropods.

Agriculture has benefited greatly from the application of the principles of heredity to plant and animal breeding. Much fundamental knowledge has come from the extensive studies on the genetics and breeding of the common fruit fly, Drosophila. It produces a new generation about once every nine days. More improvement of strains of animals and plants, too, can be made in one man's lifetime than was previously possible through ages. The United States Department of Agriculture, the Division of Entomology and the United States Fish and Wildlife Service have taken the lead in much of this type of zoology.

Fisheries and the Application of Zoology

A very practical and profitable application of zoology has been made in the fishing industry. The annual salmon catch alone on the Pacific coast has been known to be worth $25,000,000. The fishing industry cultures, collects, and markets not only fish of many kinds but also oysters, clams, lobsters, crabs, shrimp, and even sponges. The United States Fish and Wildlife Service does an extensive and remarkable work in the study, propagation, and care of this natural zoological resource. Even with this work and that of all the State Fisheries Departments, the natural fish life does not flourish as it might, had our public more appreciation of conditions necessary for a fish to live. A fish needs suitable water conditions including proper gas content, salt balance, nesting places, vegetation, and freedom from chemical, soil, or oil pollution.

The strictly intellectual and cultural endowments which zoology has given man are no less valuable than the tangible gifts. To understand something of the orderly conduct of Nature and to see that her operations are in accord with definite principles, gives one insight to the solution of many of the problems of life. Many of the superstitious dreads of unseen monsters have been eliminated by the knowledge of the fundamental principles of life processes.

CHAPTER II

HISTORY OF ZOOLOGY

This brief chapter is organized to afford a slight preview of the works and lives of a selected few of the historic pioneers of zoology. This is not an attempt to give a complete history of the subject. The works of numerous pioneers in special fields are being considered throughout the text rather than in a given chapter.

There were individual persons interested in and studying natural history long before there was any organized field of study recognized under the name of natural history or the more limited divisions of it, including zoology. Some of the translations from the early Egyptians and later from the Greeks indicate that there had been some concern for the problems of life as well as medicine a number of centuries before Christ. Some of the early Greek scholars believed that the ocean supported all of the original life. **Hippocrates,** a Greek living from 460 to 370 B.C., was the first to think of medicine on a scientific basis. **Aristotle** (384-322 B.C.) was an outstanding Greek philosopher and scholar. To him goes the credit for establishing the scientific method of study which is based on gathering facts from direct observations and drawing conclusions from a study of these facts. His observations on the structure and development of embryo sharks, chicks, and many other animals, as well as his introduction of animal classification, are contributions which caused him to be called a biologist. He had the assistance of the armies of Alexander the Great in collecting materials. Alexander had been one of Aristotle's pupils and had become interested in the development of scientific endeavor. He made a grant of 800 talents ($200,000 or more) for use by Aristotle in his investigations. Thus even in those times endowments were being set up for the support of research. The other Greeks who followed Aristotle added very little of importance.

Early Roman Scholars.—From shortly before the time of Christ and extending for about sixteen centuries was a period of "dark ages" in scholarly endeavor. However, a few contributions of note were made. **Pliny** (A.D. 23-79), a Roman general, compiled a 37-volume work in which much of the scientific knowledge of the time

and traditional superstitions are woven together. His work was limited to compilations, and because of the indiscriminate mixing of fact and fancy it is not scientifically valuable. It does reflect the tendency of the time in that scientific observation had given way to speculation.

Galen (A.D. 131-201), coming in the midst of the "dark ages" as he does, should be particularly credited for the contributions he made. He was of Greek ancestry but moved to Rome early and became a successful physician. His anatomical studies were made principally from direct observations on elephants, Barbary apes, and swine. During his time it was strictly against the law to make dissections of the human body so he was not allowed this privilege. Unfortunately, Galen did not take advantage of the work of certain of his predecessors who had been privileged to study human bodies. His conviction in the matter of direct observation as a basis of study handicapped him in this respect. His textbook on anatomy became the authority for the next eleven or twelve centuries.

Andreas Vesalius (1514-1564).—The return of interest in zoology came about through the medical schools. Vesalius was an active young student and was not satisfied to accept the authority of Galen's textbook. Therefore, after beginning his medical education at Brussels, he transferred to Padua where human dissection was then allowed. He later became professor of surgery there. He was the first, since the time of Aristotle and Galen, to prove that direct observation is the only true criterion of knowledge. Vesalius is thought of as the "father of modern anatomy," and his teaching is really responsible for the rapid development of biology and medicine following his time.

William Harvey (1578-1657).—Following closely upon the epoch-making work of Vesalius and inspired by several of his pertinent observations on the anatomy of the circulatory system, William Harvey, an Englishman, began experiments on the movement of blood in the vessels. Galen, Vesalius, and three or four others had suspected a circuit of the blood from the heart to the lungs and return, but Harvey was the first to demonstrate circulation, and the first to arrive at an idea of a complete circulation of all of the blood through a closed system of vessels. This new idea was presented in 1628. He also did notable work in embryology.

Marcello Malpighi (1628-1694) was a famous Spanish anatomist, histologist, and embryologist. His observation of blood corpuscles

in capillaries, studies on glands, and his work on the structure and metamorphosis of the silkworm take rank with outstanding contributions to zoological knowledge. Numerous organs of the human

Fig. 6.—Vesalius (1514-1564), pioneer anatomist. (From Locy, *Growth of Biology,* published by Henry Holt and Company, Inc.)

body are named for this renowned scientist of his time. Like other early microscopists, he had to build his own microscope.

Antonj van Leeuwenhoek (1632-1723) lived almost contemporaneously with Malpighi and like him made many contributions to the development of the microscope. He is said to have possessed a total of 419 lenses, most of which he had ground. Further study on capillary blood circulation, first descriptions of spermatozoa, extended observations on bacteria and microscopic animals, and his valuable contributions to the development of the microscope are the enviable accomplishments of this man.

Fig. 7.—Linnaeus (1707-1778), first great student of taxonomy. (Reprinted by permission from Locy, *Growth of Biology,* Henry Holt and Company, Inc.)

Carolus Linnaeus (1707-1778) was a very eminent Swedish biologist, who, like many early students of this subject, was educated as a physician. He followed somewhat in the footsteps of Ray (1628-1705), who had paved the way by fixing a definite conception of a species and introduced the use of anatomical features in dis-

tinguishing the larger groups. Linnaeus believed in a rigidly fixed species and had divided the animals into six classes, 32 sub-classes, and numerous genera and species. In spite of his idea of the invariability of species his classification system was so simple, clear, and flexible that it has persisted to the present time. His was the first natural system of classification, and it is known as the *Binomial System of Nomenclature*. Each individual not only fits into larger general groups by this system, but it is specifically known by the genus name and species used together, hence the two names. Linnaeus is said to have classified and listed 4,378 species of plants and animals.

Almost immediately following Linnaeus came the Frenchman, **Lamarck** (1744-1829), who among other important things is credited with being first to realize that there are different lines of descent and that no living species is absolutely fixed. Much later, in 1866, **Ernst Haeckel** organized the modification of this system as used in modern times.

Georges Cuvier (1769-1832) is credited with establishing the field of comparative anatomy. He was of French ancestry and largely self-educated by his studies at the seashore. A number of anatomical structures bear his name.

Karl Ernst von Baer (1792-1876), a Russian biologist, is one who really established embryology as a field of study. His notable paper on the development of the chick was published in 1832. He established the "germ layer theory," thus explaining the unfolding and differentiation of the various organs of the developing animal. The recapitulation theory, which is explained elsewhere, came as a result of his work and thought.

Johannes Müller (1801-1858), a German scientist, is referred to as the founder of comparative physiology and the first to apply the facts of physics and chemistry to living protoplasm. His work was a great impetus to modern physiology.

Matthias Schleiden (1804-1881) and **Theodor Schwann** (1810-1882) are the two Germans who in 1838-1839 arrived at one of the most important generalizations of biology, the cell theory (principle). This is to be discussed further in the following chapter.

Louis Agassiz (1807-1873) is commonly regarded as the father of American zoology and a renowned student of comparative anatomy. His great inspiration has permeated through his students to nearly

every institution in the land. He was a recognized paleontologist as well as zoologist. He is responsible for one of our first and oldest Marine Biological Laboratories.

Charles Darwin (1809-1882), an Englishman, made extensive studies on the problem of the manner and means by which new species of organisms arise. He very effectively developed the thesis that they originate by a process of natural selection. This was based on the idea that no two individuals are exactly alike, that new variations are constantly appearing, and finally that those individuals or groups best suited to their environment would be the ones to

Fig. 8.—Charles Darwin (1809-1882), the author of *Origin of Species.* (From **Garrison,** *History of Medicine,* W. B. Saunders Company.)

persist and produce progeny. His conception of the factors and limitations determining the development of new species, pictures a constant struggle for existence among organisms, with those whose natural variations happen to fit them best to the changing features of the environment persisting as dominant species and others being crowded out. Those least fitted to the environment would naturally become extinct.

Darwin did not claim originality in his idea. Lamarck, Buffon, and Erasmus Darwin, grandfather of Charles, had presented similar ideas before him. It was the vast accumulation of facts covering

a period of twenty years which commanded the attention of scientists as well as of the public generally. In 1858 he read a joint paper with Alfred Russel Wallace, a contemporary who had reached the same conclusion, on the theory of natural selection. That same year Darwin published his book *Origin of Species* which is a classic in its field and familiar to all scholars.

Gregor Mendel (1822-1884) was an Austrian monk who carried on experiments with the breeding of garden peas in the cloister garden. From his work there, he derived the original laws of heredity. His results were first published in an obscure Swiss paper
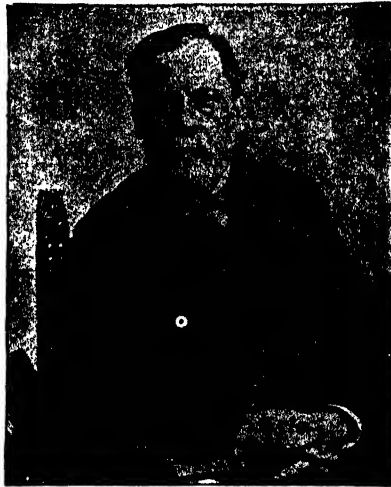
Fig. 9.—Louis Pasteur (1822-1895) contributed much to the knowledge of bacteria and disease. (From Garrison, *History of Medicine,* W. B. Saunders Company.)

in 1866 and were not really discovered and appreciated until 1900. He was the founder of genetics. He crossed different kinds of peas and found that the offspring in the first generation all resembled one parent. When these offspring were interbred he found that three-fourths of their progeny resembled one grandparent, and the remainder resembled the other. From these facts he referred to characteristics of the former group as *dominant* and those of the latter as *recessive*. The facts which he established are now known as Mendel's Laws of Heredity.

Louis Pasteur (1822-1895) was a French scientist who had been trained in chemistry but became one of the outstanding pioneers

in applied biology and medicine. In 1861 he put an end to the controversy regarding spontaneous generation of living organisms and established the idea that all life in present times comes from preexisting life. He showed that living organisms cause fermentation and demonstrated that these organisms and others could be killed by heating them to a certain temperature. He showed that materials thus heated and then sealed would not ferment until after they were exposed to the organisms in the air. The pasteurization process grew out of these experiments. He rescued the silk industry of southern Europe by discovering the organism which killed the insects, and he also discovered an immunization process and treatment for hydrophobia.

The works and lives of such prominent pioneer zoologists of the Southwest as **Jacob Boll, Gustaf W. Belfrage, Lincecum, Vliet, Walker, Webb,** and others have been described in the recent book by *Dr. S. W. Geiser* of Southern Methodist University, entitled *Naturalists of the Frontier.* This book is extremely interesting to read.

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CHAPTER III

PROTOPLASM AND THE CELL

Living Matter, or Protoplasm

Little is known concerning the origin of living matter, or protoplasm, as it is called, but more and more is being learned about its nature, characteristics, structure, and activities. Living matter is always active in some degree, and this activity attracted the attention of scholars at a rather early date, but serious study of the material was not begun until approximately one hundred years ago. A Frenchman by the name of Dujardin, in 1835, realized that some of the simple microscopic animals he was studying were composed of a soft, gummy substance and called it *sarcode,* which means "flesh." He was able to test its solubility and its behavior with alcohol and acids sufficiently to satisfy himself that it differed from ordinary gelatin or albumin, with which it might be confused. In 1840, Purkinje, a Bohemian biologist, gave living matter the name *protoplasm,* which comes from the Greek *protos,* first, and *plasma,* anything formed or molded. In 1846 von Mohl, a German botanist, saw in plants a granular, viscous substance similar to that already seen in animals, and called it *protoplasm.* He was instrumental in bringing this name into common use. During these years it had gradually dawned on biologists that this matter is found in all living things.

The Cell Principle

Cells had been seen and even superficially described during the latter part of the seventeenth century and numerous times during the eighteenth century, but their significance was not realized. Hooke, an Englishman, in 1665 in observing cork with the microscope he made made, saw the spaces in it and called them cells because they reminded him of prison cells. This name later came to be applied to the real cells. It was an unfortunate term, for cells do not have a hollow structure but are typically semisolid bodies. Leeuwenhoek saw spermatozoa and bacteria and included them with single-celled animals as "little beasties"; Malpighi had described the nature and appearance microscopically of several organs of the

body; Grew had made rather extensive microscopic studies of plants, and in 1831 Robert Brown had discovered the nucleus of the cell, but not until the work of Schleiden in 1838 and Schwann in 1839 was the *cell theory* formally enunciated. The former a botanist and the latter a zoologist, each working independently, came to the same conclusion and in 1839 collaborated their ideas. This theory, as they gave it, was in substance, *All living things (plants and animals) are composed of cells.*

It is no discredit to this theory or these men that they and many other biologists of the time had erroneous ideas concerning the essential features of the cell. Although Brown had recently discovered the nucleus, the cell wall was thought to be the essential part, though now we know it is not a universal structure of all cells since practically no animal cells have a cell wall. The notions of the origin of cells and the functional significance were almost wholly fantastic, yet the cell theory proved to be such a unifying generalization and inspiring stimulus to investigation that it became the turning point in the development of biological study.

The bare statement that living beings are composed of cells soon became inadequate as studies of cells progressed. It was soon found that some tissues are made up not only of cellular structures but included also certain noncellular materials produced by the cells. The matrix, so abundant between the cells of cartilage, was soon found to be noncellular and to be produced by the cartilage cells which became embedded in it. This matrix is not strictly living matter since it is inactive and passive as far as life processes are concerned. Connective tissue fibers fall in the same category. Since living bodies are composed of such an abundance of this noncellular material produced by the cells, the cell principle soon came to be stated thus: *All living things are composed of cells and cell products.* With the years, the conceptions of the nature of the nucleus, the cell membranes, and the composition of protoplasm itself have all added their contributions to the present understanding of the meaning and application of the cell principle. The cell is now regarded as a physiological unit as well as a structural one, and as almost a corollary to the original statement of the principle, namely, that the activities of the organism equal the sum of the activities of its cells.

With the embracing of the functional activity of the cell as a part of the principle underlying living processes, comes also the inclusion

of heredity and development. Cell division, growth, tissue formation, migration of cells, formation of cell products, chromosome relationships and modifications have come to be recognized as being brought about in or by the cells. Through the rather rigid and constant set of developmental changes for which the cells are responsible, there is developed a new individual which usually resembles its parents quite closely.

The influence of the cell theory on biological thinking and progress as well as its effect on fundamental thinking generally, can hardly be over-estimated. The conception of this idea was one of the great landmarks in development of biological and scientific thinking. It was the first great generalization in biology. It is comparable in the field of biology to Newton's law of gravitation in the field of physics. Up until this time there had been no single fundamental idea applied to living material that was recognized as being universally true. This conception focused the thinking of all biologists in the same direction and therefore it had a great unifying influence. Deliberation and meditation on this fundamental idea seemed to prepare biologists for other great generalizations which followed quite rapidly. Many new problems arose with this new knowledge of plants and animals. Comparative morphology was extensively investigated, and physiology now has become physiology of cells as a result of this impetus. An understanding of the permeability of cellular membranes, the transformation of energy by chemical reaction within cells, the roles of electrolytes in living substance, and the principles of heredity are some of the results of this new conception of life embraced in the cell theory.

General Characteristics of Protoplasm and the Material of the Cell

To begin with, it may be said that this substance has a variable degree of fluidity under different conditions. The range of this variation may be from semisolid to semiliquid. It is viscid and gelatinous in consistency. It is more or less granular, nearly colorless, and more or less translucent; however, it is never perfectly transparent. The translucency causes a mass of it to have a lustrous gray appearance. As a constituent of protoplasm there is always a considerable percentage of water, which conditions the degree of viscosity.

It is in a *colloidal* state of the emulsoid type. In the *emulsoid,* or colloidal emulsion, the substances are distributed through the more watery or *dispersion* medium. A colloid is identified by the presence of particles which are groups of molecules dispersed through a more fluid or watery phase. These particles, of course, are larger than molecules, but they are too small to be seen with the ordinary microscope. It is possible for water and substances in solution to enter protoplasm from without, and this is reversible. With loss of water from the dispersion medium the dispersed particles of the colloid become congested by loss of general fluidity. This condition is known as the *gel* state. When there is increased water in the dispersion medium and the particles move with greater ease in the more fluid medium, the colloidal state tends to become *sol*. This transfer of water may be due to chemical changes in the dispersed particles or in the dispersion medium of the colloid. The ability
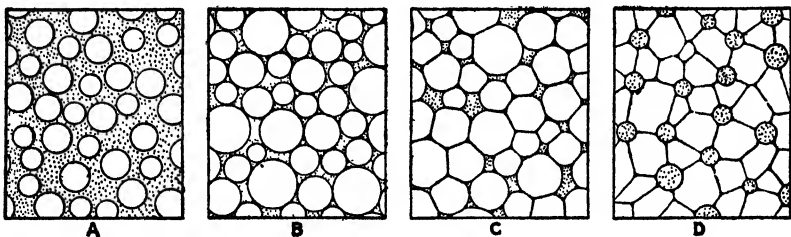
Fig. 10.—The change of a colloidal emulsion from sol to gel state. In *A* the droplets of the disperse phase (not stippled) are shown scattered through the dispersion medium (stippled), and the emulsion is a sol; in *B* the droplets are shown taking up liquid and swelling; in *C* this is continued until they press upon one another; in *D* the droplets are so crowded as to become continuous and to have become in fact the dispersion medium, while that which was the dispersion medium is now in droplets and has become the disperse phase. The emulsion has become a gel. (From Wolcott, *Animal Biology,* McGraw-Hill Book Company, Inc.)

of protoplasm, because of its colloidal nature, to change from sol to gel state and back to sol repeatedly is the basis of many of the vital activities, such as utilization of food, disposal of waste, and movement.

Fundamental Properties or Activities of Protoplasm

In addition to the general characteristics, there may be mentioned and described briefly a number of important activities common to all protoplasm. These properties are:

1. *Irritability,* which refers to the capacity present in all protoplasm for responding to changes in environmental conditions, or external stimuli.

2. *Conductivity* refers to the fact that the impulses produced by stimuli or irritations at one point in protoplasm are conducted to other parts of not only a single cell but also to adjoining cells.

3. *Contractility,* which is the power of contraction and relaxation that is common to the substance of every cell.

4. *Metabolism,* the process of continual exchange of food and fuel materials being built into the protoplasm, while, at the same time, materials there are being oxidized to liberate kinetic energy, such as heat and movement, and produce waste by-products.

5. *Growth* is recognized as any increase in volume. When the rate of the building side of metabolism exceeds the oxidation rate in the protoplasm, there is storage of materials in the mass of the protoplasm and hence growth. All protoplasm has this capacity.

6. *Reproduction* is the capacity for producing new individuals of the same kind. All living organisms are capable of this by some means. Simple cell division is the most primitive process of reproduction among animals.

Consciousness, which refers to the awareness of one's own existence, is frequently given as a property of protoplasm. It is certain that some protoplasm possesses consciousness, but evidence of this quality is rather intangible. *Spontaneity* is also considered a property of protoplasm by some. To be certain that the activity and source of all reaction comes from within is likewise rather difficult of definite proof, so this is simply mentioned here as another property which is often listed.

Physical Nature of Protoplasm

Protoplasm is a semifluid material which is heavier than water and somewhat more refractive to light. Its physical constitution is similar to glue or gelatin, rather than to crystalloids, such as sugar or ordinary table salt (sodium chloride). Instead of being in the form of a true solution like salt in water, it consists of suspensions of relatively large molecular aggregations varying roughly between 0.0001 and 0.000001 millimeter in diameter. These particles keep up an expression of energy in that they move against each other as though they were dancing in a limited space. This activity can be seen only with a special optical arrangement known as the ultramicroscope and the phenomenon is known as *Brownian movement* (characteristic of colloidal substances). Protoplasm dif-

fuses slowly or not at all through animal membranes. It changes from a fluid or sol state to a more solid or gel state and may return in the other direction. Ordinarily the viscosity of the continuous phase or supporting liquid is only three or four times that of water, while with the dispersed particles included it is only eight or ten times that of water. The viscosity of the nuclear fluid is only twice that of water. Since glycerin has a viscosity about a thousand times as great as water, it will be realized that most protoplasm is quite fluid in its active state. Changes in viscosity accompany and are essential to the activity and functioning of it.

Protoplasm is not a single compound; it is a *colloidal system* of a number of chemical compounds existing together. Colloidal systems are known as *disperse* systems of the *emulsoid* type. The more watery or continuous part of the system is known as the dispersion medium, while the particles or molecular aggregations constitute the dispersed phase. An important consequence of the colloidal systems in protoplasm is the enormous surface of particles exposed to the continuous phase. If a sphere of material has a radius of one centimeter its total surface will be 12.6 square centimeters. Now, if the same volume of material is in colloidal particles of the average size given above, the total surface of these will be approximately 7,000 square meters. This increase in surface is one of the significant effects of colloidal organization of substances, because many important reactions occur at these surfaces. By the presence of salt ions in the continuous phase and these becoming adsorbed upon the surfaces of the colloidal particles, they acquire an *electric* charge. Protoplasm exhibits these several phenomena because of its colloidal nature.

Chemical Nature of Protoplasm

Up to the present time, protoplasm has eluded complete and exact chemical analysis. Nevertheless the compounds of living matter are composed of several elements, many of them the most ordinary and abundant in the world. The list of elements necessary to make human protoplasm could be gathered in almost any locality on the face of the earth. As a rule the elements found in protoplasm are oxygen, carbon, hydrogen, nitrogen, sulphur, phosphorus, calcium, sodium, chlorine, magnesium, iron, potassium, iodine, and frequently others like silicon, aluminum, copper, manganese, bromine, and fluorine. The most abundant of these are found named in the

first part of the list. A few of them are usually given as constituting approximately the following percentages of protoplasm: oxygen 65 per cent, carbon 18 per cent, hydrogen 10 per cent, nitrogen 3 per cent, calcium 2 per cent, phosphorus 1 per cent, and all others making up the remaining 1 per cent. These elements are found combined to form compounds. The organic compounds include *carbohydrates, fats, proteins,* and also *enzymes.* The inorganic compounds consist of several *inorganic salts* and *water.*

The carbohydrates, which include starches and sugars, are compounds of carbon, oxygen, and hydrogen. The proportion of the hydrogen to oxygen in the molecule is the same as found in water, two to one. The principal carbohydrate found in protoplasm is the monosaccharid, or simple sugar, *glucose,* whose formula is $C_6H_{12}O_6$. This is actually built into some parts of the cell, but its chief function is to furnish the most available source of energy by its ready oxidation. When a molecule of glucose is burned, the potential energy is released as kinetic or mechanical energy, and there are formed six molecules of water (H_2O) and six molecules of carbon dioxide (CO_2). Glucose is converted to a starchlike substance, *glycogen,* for storage in the various animal tissues. This substance must be reconverted to glucose before it is available for production of energy.

Fats, like carbohydrates, are composed of carbon, hydrogen, and oxygen but in more complex molecular arrangement. There is much more carbon and hydrogen with less oxygen, which allows the fats to combine with more oxygen in oxidation and therefore release more energy. Fat is extremely well adapted as a form of material for storage, since weight by weight it contains more potential energy than any of the organic group. Such common substances as lard, butter, tallow, whale blubber, and cottonseed oil are good examples. Fats serve a double function in protoplasm: constitution of a part of the structure of the cell and the storage of food.

Proteins constitute the bulk of the foundation or framework of the cellular structure and are the most abundant organic constituents. They are composed of carbon, hydrogen, oxygen, and nitrogen, with the frequent addition of traces of sulphur, phosphorus, magnesium, and iron. All of the proteins have large molecules, each being composed of thousands of atoms; as an illustration, take hemoglobin of the red blood corpuscles with its formula $C_{712}H_{1130}N_{214}O_{245}FeS_2$. Pro-

teins have a slow rate of diffusion, high resistance to electric current, and usually coagulate upon heating or upon addition of acids, alcohol, or salts to form a clot. Egg albumen, gelatin, and lean meat are common examples of proteins. They are split into numerous *amino acids* which serve as the building stones of the stable portions of protoplasm.

Enzymes are substances whose exact chemical nature is not yet known, but whose importance to protoplasm is probably unequaled. Chemically and physically they seem to be more like proteins than anything else. These substances are not only found in the cells, but they are also secreted by cells into the digestive tract and into the blood stream, where they act as *organic catalysts*. The general function of the catalyzer or catalytic agent is that of facilitating and speeding up certain chemical exchanges without the agent itself entering into the reaction. The well-known example of catalysis is the effect of a small amount of platinum in increasing the rate at which hydrogen and oxygen combine to form water. A particular enzyme is usually specific for one kind of reaction, but not for the species of animal in which it will function. Enzymes taken from one species will usually facilitate the same kind of specific reaction in other species. The digestive enzymes may be thought of as an example. Of these, pepsin will bring about the same general reaction, whether it is in the stomach of a frog or of a man, under favorable conditions. Since many enzymes influence only one specific type of chemical reaction and since there are numerous types of reactions going forward in active protoplasm, it is seen that there must be numerous enzymes present in the cells of every organism.

Water constitutes 60 to 90 per cent of protoplasm and maintains many substances in solution. Water is not only a very efficient solvent; but it is important to protoplasm because of its comparatively high surface tension, because its presence gives the protoplasm a consistency compatible with the range of variation necessary for metabolism, and because of its high specific heat. This latter point is important in maintaining protection against sudden and extreme temperature changes in the living organism. Young cells contain more water than old ones, young organisms likewise contain more than old ones. The relative amounts of water in relation to other materials of the protoplasm vary in different cells and in different species.

The *inorganic salts* are present in considerable numbers but in relatively small amount. They are electrolytes, and therefore split up in aqueous solution into ions, which are able to combine with all the other substances in protoplasm. The chlorides, phosphates, carbonates, and sulphates of sodium, potassium, calcium, magnesium, and iron are important salts of living cells. The relative proportion of these salts is kept at a fairly constant level, and slight changes in this balance have regulatory effects on metabolism.

From the chemical standpoint, living protoplasm is considered the most complex of all systems of compounds. Even the proteins, as a part of protoplasm, are more complex than any other substances. In a sense, protoplasm is quite unstable in that it changes its composition in response to every change in the environment, and when active it is not the same for any two consecutive moments. The exceeding variability of protoplasm chemically, makes possible all of the necessary adjustments of living matter to its environment. On account of the extreme complexity of protoplasm it is not surprising that the chemistry of all of its activities is not yet completely understood.

Structure of a Typical Animal Cell

The quantity of protoplasm comprising a single cell varies within wide limits; therefore cells vary greatly in size. The majority of cells, but not all of them, require considerable magnification. Certain of the single-celled blood parasites are about as small as any cells known. They are barely seen with our highest magnifications. At the other extreme of size we may refer to another parasitic single-celled animal, *Porospora gigantea,* which lives in the intestine of the lobster, and may reach from one-half to two-thirds of an inch in length. Egg cells, including the yolk, may exceed this size. Some of the nerve cells, though of less mass, may be several feet in length. Muscle cells are relatively long also.

The *shape* of the typical cell is spherical; but due to the effects of mechanical pressure, specialized functions, and unequal growth almost all cells are far from this shape. They vary greatly in shape and include platelike, cubical, columnar, polygonal, and spindle-shaped forms. The particular form of any cell is not a haphazard matter but strictly controlled by morphological and functional necessities.

A cell consists of a mass of jellylike cytoplasm surrounding a nucleus. The outer surface of the cytoplasm is modified, the protoplasm having more density here to form the *plasma membrane,* or cell membrane, which is the outer covering of the animal cell. It is living and semipermeable.

The *cytoplasm* usually includes the larger part of the substance of the cell. It may be subdivided into the more nearly clear, structureless fluid, *hyaloplasm,* and the interspersed fibrillar substance known as *spongioplasm.* Within the cytoplasm, lying near the nucleus, in most animal cells is the *centrosome.* Its substance is known as *kinoplasm* and is made up of two parts, the larger *centrosphere,* enclosing

CELL MEMBRANE
PLASMA MEMBRANE
CENTROSOME
CENTRIOLE
NUCLEAR MEMBRANE
NUCLEOLUS   NUCLEUS
CHROMATIN RETICULUM
NUCLEAR SAP
PLASTID
VACUOLE
ENDOPLASM
ECTOPLASM
CHONDRIOSOME
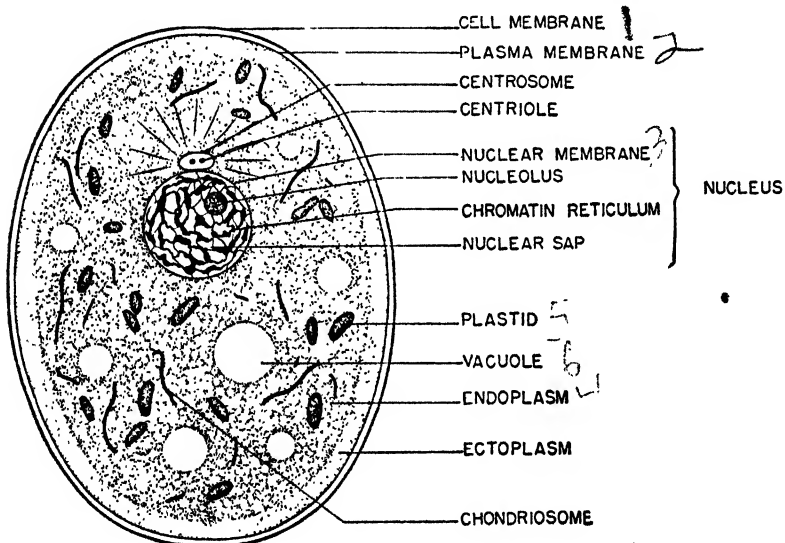
Fig. 11.—Diagram, showing a typical cell. (From Parker and Clarke, *Introduction to Animal Biology,* The C. V. Mosby Company.)

a (two if divided) *centriole.* Vacuoles are often present as small cavities filled with water, gases, or oils. Scattered through the cytoplasm also are numerous rod-shaped bodies known as *mitochondria.* Threadlike *golgi elements* or apparatus may be observed in the cytoplasm, particularly near the nucleus. Secretions produced in the cell may be stored as granules in the cytoplasm, also certain inclusions may be seen here.

The *nucleus,* which is usually round and centrally located, is surrounded by the cytoplasm and separated from it by the *nuclear*

membrane. This membrane, like the plasma membrane, consists of a part of the protoplasm whose density is somewhat greater than the adjacent portions. The protoplasm which constitutes the nucleus is usually known as *karyoplasm.* The more nearly fluid, transparent portion of this is *karyolymph,* or nuclear sap, while the meshwork of fine fibers extending through it is called *linin net.* Supported on this net is a dark-staining granular or fibrillar substance known as *chromatin,* which is thought to be the center of functional activities of the nucleus. In instances where the chromatin is fibrillar, the threads of it are called *chromonemata.* During division of the cell this granular material becomes arranged into definite bodies, the *chromosomes.* It is generally thought that in these bodies are located the units of material (genes) which function in the transmission of hereditary characteristics from one generation to the
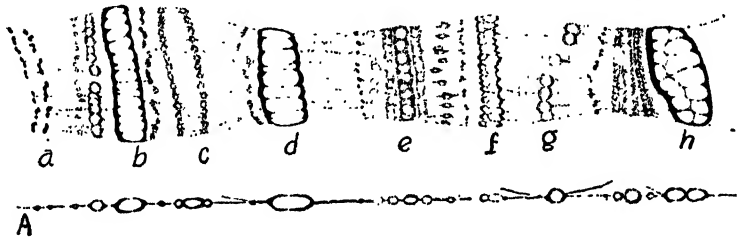
Fig. 12.—The upper surface of a fully developed salivary gland *chromosome* (large vesicle type) from Simulium fly larva. The longitudinal, threadlike bands are called *chromonemata,* and these consist of a linear series of granules, the *chromomeres,* which have a specific arrangement of grouping. *A* is a semidiagrammatic representation of the types of chromomeres and the ways in which they are connected. At *a* in the main figure there are two rows of dotlike chromomeres which tend to associate in pairs. The band labeled *b* is composed of 15 or 16 vesiculated chromomeres closely pressed together. *c* to *h* are other groupings of chromomeres along the chromonemata of the chromosome. (From Painter and Griffen: *Chromosomes of Simulium,* Genetics 22: 616, 1937.)

next. There are usually one or two knots of more dense chromatin in the nucleus which are called *karyosomes.* Then besides these, most nuclei have another body composed of material thought to be temporary storage products of nuclear metabolism, the nucleolus, or *plasmosome.* Mitochondria, similar to those of the cytoplasm, are also found in the nucleus. The cell is often spoken of as the unit of structure and function in living material. Both nucleus and cytoplasm are necessary for its normal activities. It is not entirely possible to define the part each plays in the metabolism of the whole. Since the development of the microdissector by Dr. Chambers, it

is possible to dissect the nucleus of a cell. Cells that are deprived of their nuclei are unable to carry on assimilation, although catabolism goes on until the cytoplasm is depleted.

Cell Division

The cell is limited in its size, as is the complete organism. This limit of size is fixed primarily by the physiological necessities which are transmitted through the surface of the cell. There is a definite relation between volume and surface in any mass of material, and this may be expressed in a ratio. With variation of the size of the mass, the volume varies according to the cube of the diameter while the surface area varies according to the square of the diameter. When the limit of growth is reached the cell divides, and this restores the proportion of the surface area to volume that will again permit growth. Remak, in 1855, was the first to describe cell division. His idea was that the nucleolus split first, then the entire nucleus, and finally the cytoplasm divided, placing each portion with its share of the nucleus. This direct method of division was called *amitosis*. Its actual occurrence is quite rare. The usual method of cell division is far more complex and less direct. There are several preliminary changes or phases which must occur before the actual cleavage of the cell into two new ones. This is mitotic cell division, more briefly *mitosis*, or indirect cell division. This method of division was first described by Fleming in 1878, though Schneider in 1873 described much of the complicated process.

Although the process of mitosis is a continuous series of changes, for convenience in study, these changes will be set out as six phases. Following the *resting cell* condition come the first changes, and the *early prophase* condition is seen. In this stage the centriole has divided, and the two pieces have moved considerably apart. The surrounding protoplasm has produced some rays radiating from each centriole. These two bodies are now known as asters because of their starlike appearance. The two asters taken together are called the *amphiaster*. The nucleolus disappears and the chromatin becomes organized into a long, tangled fiber, which is called the *spireme thread*.

In the *middle prophase* stage the centrioles have migrated still farther from each other, and the spindle fibers between the centrioles as well as the astral rays around them have become well established. The spireme thread has thickened and divided into segments in the

formation of *chromosomes*. During these changes the nuclear membrane begins to degenerate. In the *late prophase* stage the centrioles have reached the polar positions on opposite sides of the nucleus. The spindle extends between the two asters, and the chromosomes become
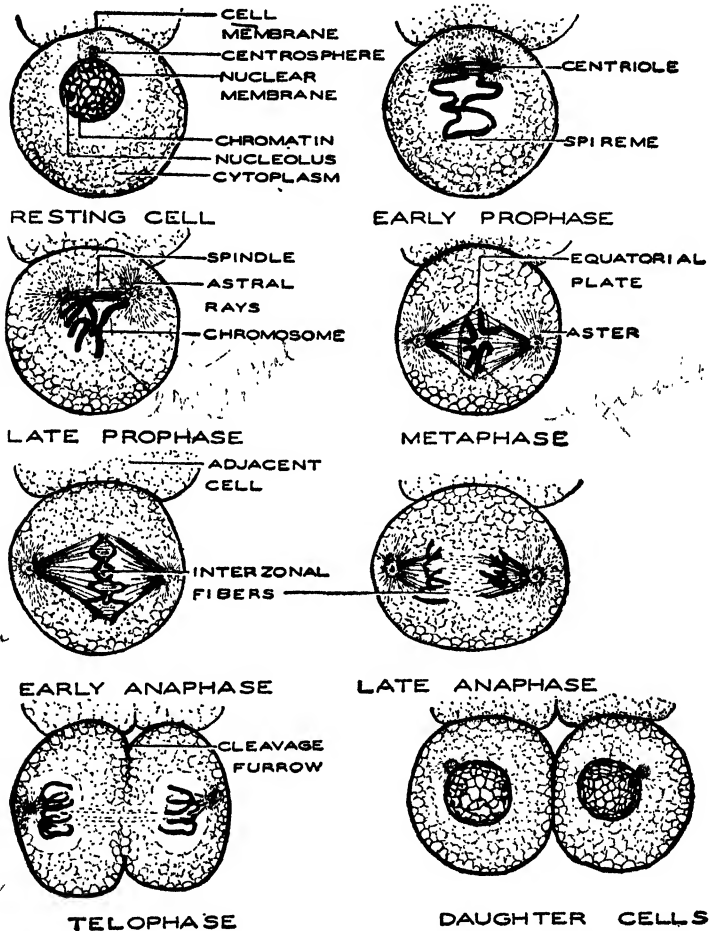
Fig. 13.—Stages of typical mitosis (indirect cell division) as shown in fertilized *ascaris* eggs. The sequence of the stages is in the following order: resting phase, early prophase, late prophase, metaphase, early anaphase, late anaphase, telophase, and daughter cells. (Drawn by Titus C. Evans.)

arranged on the spindle fibers, end to end in a row at the equatorial position. This plate of chromosomes constitutes what is called the *equatorial plate*. The nuclear membrane has almost completely de-

generated. The chromosomes lying in the equatorial plane of the spindle now undergo an equatorial division, each being divided into two corresponding halves. The actual division of the chromosomes here constitutes the *metaphase* stage. Following this stage each of the chromosomes resulting from the division migrates along the spindle fibers toward its respective centriole, or pole. The stage during which occurs the migration of the chromosomes from the equatorial position to the poles is called the *anaphase*.

As the chromosomes near the poles of the spindle they crowd very close to each other. At this time a constriction of the cytoplasm begins in the plane of the equatorial plate. This is the beginning of the *telophase* stage. The cytoplasm perfects its constriction and divides into two parts. A nuclear membrane forms to enclose each chromosome group, and immediately the chromosomes begin to separate from the group, although certain ones still clump together. The chromosomes progressively lose their identity and their staining qualities. The nucleus resumes its granular appearance of the resting cell. One or more nucleoli soon become evident. The formation of the new nuclear membrane excludes the centrosome, so it takes its normal position just outside the nuclear membrane in the cytoplasm. At about this time the centriole divides into two. These two new cells resulting from the division are spoken of as *daughter cells*. These cells have each received the same quantity and quality of chromatin material.

Following the organization of these daughter cells, which are in the resting stage as far as division is concerned, growth is rapid until they reach their typical limit of size. For most average cells under optimum conditions, it is stated that this requires less than two hours. Then after a further period of from one to twelve hours, another mitotic division may take place. The universality of this process in all types of organisms, both plant and animal, and the regularity of the occurrence of the phases of the process suggest that it is of vital significance. The great precision with which the chromatin is divided between the two cells seems to indicate that this is a most significant step. Chromatin is recognized as the material which makes possible the inheritance of qualities from cell to cell and, in case of sex cells, from generation to generation. The purpose of the splitting of the chromosomes in the metaphase stage seems to be to provide each daughter cell with

identical hereditary qualities. This equal division of chromatin, both qualitatively and quantitatively, has given rise to the thought expressed in the phrase, "continuity of protoplasm," and that present chromatin comes from pre-existing chromatin. In 1855 Virchow, a German pathologist, declared the doctrine that all cells must be derived from previously existing cells, in his statement, "omnis cellula e cellula." This supposes that in the first living material created were inherent all of the possibilities which have been realized in all living things that have existed since.

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CHAPTER IV

METAZOAN ORGANIZATION

All animals whose bodies consist of few or many cells functioning as a unit are called *metazoans*.

The cells of their bodies are definitely organized and classified morphologically as well as physiologically. There is a well-regulated division of labor. Among the single-celled animals each cell is largely independent of its fellows, doing for itself all that is necessary to carry on living processes. In the many-celled animal, as in a highly developed society of men, certain individual cells become more proficient in doing certain kinds of work, and as a result, a special group is able to care for a particular function necessary to the life of the entire organism. In return, other special groups care for other functions. In this way each exchanges the products of its labor for the products of the labors of the other groups. In human society this becomes more and more complicated as civilization advances; so it is with development of complexity in metazoans. Another characteristic of Metazoa is the presence of a definite center of control localized in a particular group of cells which becomes the nervous system in higher forms.

Cellular Differentiation

In Protozoa (single-celled animals) there is seen fair development of *intracellular* differentiation, making it possible for one part of a cell to perform a particular function, and for other parts to perform other functions. The complexity of Metazoa is not the result of great complexity of the individual cells, but it is due to the special differences between them. The presence of a variety of cells within one body is spoken of as *intercellular* differentiation. The modification of metabolic activity is the basic factor in the development of all differentiation. Certain groups of cells become specialists in a particular phase of the metabolic activity. Some become protective surface cells, others secrete special enzymes, still others specialize in excretion, and so on.

The entire metazoan body is usually divided into *germ cells*, which are specialized for reproduction, and *somatic cells* or body cells, which compose the remainder of the body and are grouped in layers.

The germ cells are set aside early in the life of the individual for reproductive purposes. They develop in the reproductive glands or *gonads* of the two sexes. The protoplasm of these cells is known as *germ plasm.* The female germ cells are eggs or *ova,* and those of the male are *spermatozoa.* When the germ cells reach maturity, they become separated from the body and may give rise to a new generation. About forty years ago Weismann presented the idea of the continuity of heredity from generation to generation by way of the germ plasm. The germ plasm, according to this idea, gives rise not only to the protoplasm of the germ cells of the new individual but to the somatic cells as well. In Protozoa the entire material of the individual is passed on to the two offspring and, for this reason, this protoplasm is spoken of as being immortal. Potentially, germ plasm is likewise immortal.

The protoplasm of the somatic cells is known as *somatoplasm.* This is rebuilt with each generation, and when the individual dies, all of the somatoplasm perishes. In final analysis, the somatoplasm serves as a means of conveyance for the germ plasm through the current generation.

Cellular Organization

The simpler Metazoa are composed of only two kinds of somatic cells. These cells are grouped according to kind in two layers. With advanced differentiation, a rather wide variety of cells has been produced.

A *tissue* is an organization of similar cells into a group or layer for the performance of a specific function. A certain amount of intercellular substance is characteristic of most tissues and enhances their usefulness. The entire living mass of the metazoan animal body may be classified under five fundamental (four by some authors) kinds of tissues, and when it is so distributed, there is nothing left. These classes of tissues are: *epithelial,* protective or covering; *sustentative,* connective or supporting; *muscular,* contractile; *nervous,* irritable or conductive; *vascular,* circulatory.

Epithelial Tissue.—A sheet of cells that covers external or internal surfaces of the body is known as an epithelium. The epidermis or outer layer of the skin and the layer of column-shaped cells lining the inside of the intestine are good examples. According to function, this type of tissue can be classified as protective epithelium, glandular epithelium, and sensory epithelium. The epithelium which covers external surface of an organism usually de-

velops various protective structures in the different groups of animals: the hard, horny chitin of insects; scales of fish; horny plates and scales of reptiles; feathers of birds; hair and nails of mammals. The glands of the body are developed from epithelium. Secretions from these various glands lubricate the surfaces, contain enzymes for digestion of food, supply regulatory substances directly to the blood, serve as poison to other animals, and some are repellent to enemies.

Sustentative Tissue.—This type comprises all tissues whose function is to bind together or support the various parts of the body. Connective tissue is, in most cases, composed of slender cells with an abundance of intercellular material. This tissue is almost universally present in the various organs throughout the body. *Tendons*, the tough cords that connect muscles to bones, of which the
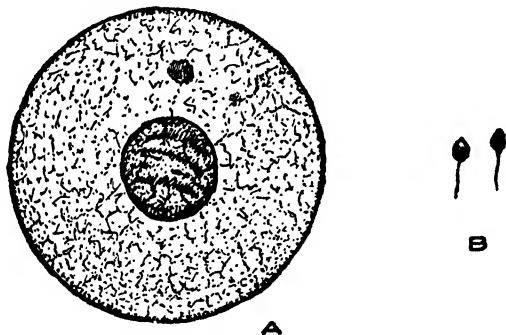
Fig. 14.—Germ cells. *A*, Ovum of female; *B*, spermatozoa of the male.

"hamstring" is a good example, and much of the dermis of the skin are composed of connective tissue. Bone and cartilage, which make up the framework of the body and support the other tissues, are called *supporting tissues*. In crayfishes and grasshoppers the supporting tissue is *chitin* instead of bone or cartilage. Cartilage is composed of scattered cells interspersed with abundant, homogeneous, granular, semisolid matrix or intercellular substances. Bone is somewhat similar, except that the matrix has been replaced by a heavy deposit of calcium phosphate and calcium carbonate, two solid salts. The scattered cells are present as bone cells.

Muscular or Contractile Tissue.—This is distinctive because of its ability to contract and in that way produce movements. Cells adapted to this function are more or less elongated and fiberlike.

There are three types of muscular tissue: smooth, involuntary, and nonstriated, as found in the wall of the intestine; striated, voluntary, skeletal, as found in the muscle of the arm; and striated, involuntary, cardiac, as found in the wall of the heart. Skeletal, voluntary muscle is made up of large multinucleate (many nuclei) fibers, each composed of many fibrils (myofibrils) along which are evenly distributed dense and light areas, giving the general appearance of stripes across the cell, because the dense areas on the adjacent fibrils come at the same level. The smooth involuntary muscle is composed of individual, spindle-shaped (fusiform) cells, the cytoplasm of which is largely myofibrils but without striations and therefore smooth. There is a single oval nucleus, centrally located. The outer membrane of a muscle cell is the sarcolemma. The cardiac involuntary muscle is said to be made up of individual cells, highly modified in arrangement. The definition of cells in this tissue is rather difficult, but the fibers are faintly segmented by thin *intercalary disks* which define areas each with a single nucleus. The cells branch laterally to join each other quite frequently, producing a condition of netlike branching known as *anastomosis*.

Nervous Tissue.—This is specialized to receive stimuli and transmit impulses which have been set up by some stimulating agent in some part of the body. The structural features consist of *nerve cell bodies* and their processes. Two kinds of processes are recognizable: (a) the *axone*, usually a single unbranched fiber except for infrequent *collateral* branches; and (b) dendrites, frequently much branched and arborlike. An axone may be several feet long, e.g., one extending from the spinal cord to the hand or foot. Dendrites may be lacking. The impulses are conducted toward the cell body over the dendrites and away over the axone. A nerve cell body together with its processes is called a *neuron*. The neurons approach each other and pass impulses from one to the other at the *synapses*, where the brushlike ending of the axone of one comes into close proximity with a dendrite of another. In this way an impulse can be transmitted from one part of the body to other parts. The chief function of the nervous tissue is to relate the organism to its environment.

Vascular Tissue.—This is fluid tissue consisting of cells known as corpuscles in a fluid medium called *plasma*. The cells are the red corpuscles (erythrocytes) and white corpuscles (leucocytes), while the plasma or fluid is the intercellular substance. Blood and lymph

are the two common vascular tissues. Lymph has no red corpuscles. In the blood of mammals the red corpuscles are without nuclei; while in fish, frogs, turtles, and birds these cells are nucleated. The chief function of this tissue is the transportation of digested food and oxygen to the cells of the body and the removal of waste by-products of metabolism from them.

An **organ** is an arrangement of two or more tissues as a part of the body which performs some specific function or functions. Some organs are made up of all of the different types of tissues just described. For example the stomach is an organ with an internal
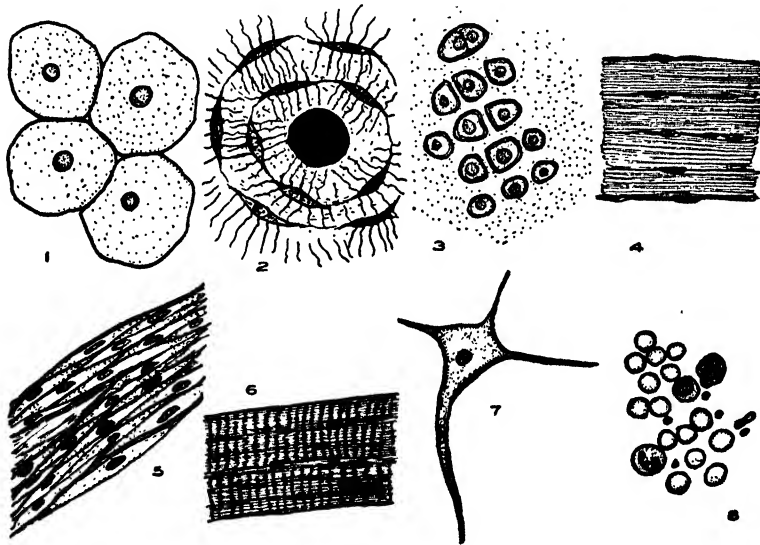
Fig. 15.—Typical somatic cells from vertebrate animals. *1,* Squamous epithelial cells; *2,* section through a portion of bone showing Haversian canal (in center), bone cells, lacunae, canaliculi, and matrix; *3,* section of hyaline cartilage showing cartilage cells in lacunae, and matrix between lacunae; *4,* section of tendon which is composed of white fibrous connective tissue; *5,* longitudinal view of smooth (involuntary) muscle cells; *6,* striated (voluntary) muscle; *7,* motor nerve cell, showing processes; *8,* human red blood corpuscles (nonnucleated) and human white corpuscles (nucleated). (Drawn by Titus C. Evans.)

cavity. It is covered and lined with epithelium; the wall contains two strong layers of muscular tissue; blood vessels carrying blood, and lymph spaces bearing lymph, branch through the wall; nervous tissue reaches all parts of the organ to receive stimuli and distribute impulses; and connective tissue serves to bind all the others in proper relation.

A **system** is an aggregation of organs properly associated and related to perform some general function of life. There are ten different systems usually recognized:

a. The *Integumentary System* is composed of the skin and its outgrowths, such as hair, nails, scales, horns, hoofs, and similar structures. Its principal purposes are protection, primarily, with some degree of excretion and respiration, some absorption, and regulation of body temperature.

b. The *Skeletal System* composes the supporting framework of the body. The bony and cartilaginous tissues make up the material of this system. The vertebral column, skull, ribs, sternum, and bones of the limbs are the general parts of the vertebrate skeleton, and they serve for the support of the body as a whole and for the protection of the internal, vital organs.

c. The *Muscular System* consists of muscles, the voluntary, striated group moves skeletal parts and accomplishes locomotion; the nonstriated, involuntary group is concerned with the movements of the internal organs (viscera), and the cardiac muscle produces the heart action.

d. The *Digestive System* of the higher animals includes the mouth, pharynx, esophagus, stomach, small intestine, large intestine, and accessory glands. The general form of the system is that of a tube, and it is frequently called the *alimentary canal*. The functions of ingestion, digestion, egestion, absorption, secretion, and very little excretion are performed by this system. In general, it puts the food in solution so that it may be absorbed by the blood.

e. The *Respiratory System* consists of structures capable of delivering oxygen to the body and eliminating carbon dioxide. In some forms the general surface of the body serves the purpose, but in all higher forms there are special structures for this function. Tracheae are found in insects, gills of various modifications in many aquatic Metazoa, and lungs in the terrestrial vertebrate forms; accessory to the lungs are the nasal passages, pharynx, larynx, trachea, and bronchi.

f. The *Circulatory* or *Vascular System* is a very extensive one consisting of the heart, arteries, veins, capillaries, lymph spaces, lymph nodes, and lymphoid glands. The general functions are: (1) to distribute blood carrying food, oxygen, and hormones from glands of internal secretion to the tissues; (2) to collect and transport to the point of exit carbon dioxide, liquid wastes, bacteria, and other foreign matter.

g. The *Excretory* or *Urinary System* is made up of tubular struc-
tures and accessory parts, such as flame cells, nephridia, Malpighian
tubules, green glands, and kidneys.   In the mammals, the ureters,
urinary bladder, and urethra are accessory to the kidneys.   The kid-
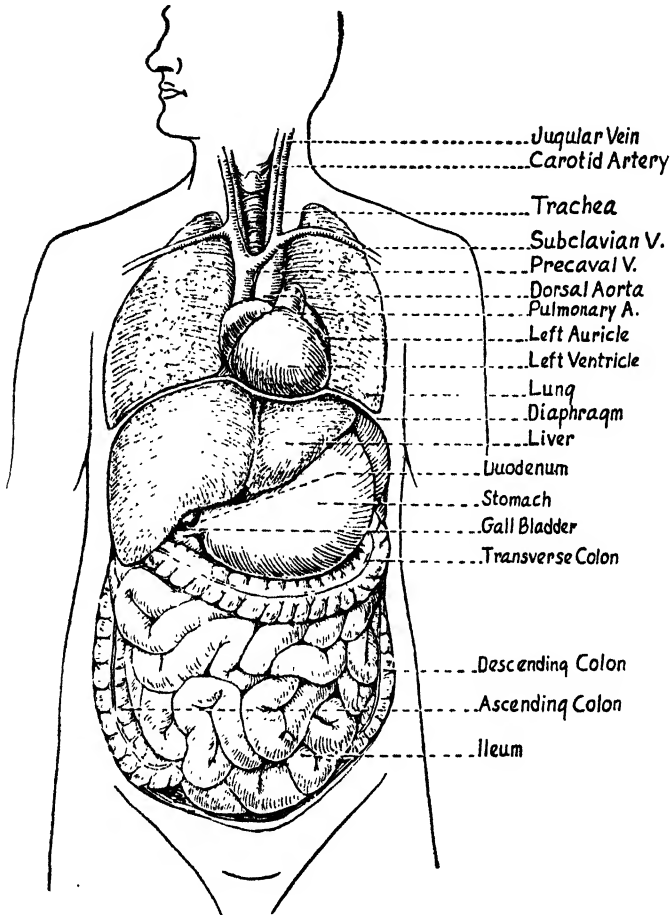
Fig. 16.—Human manikin showing parts of the principal systems from ventral
view.   (Drawn by Edward O'Malley.)

neys withdraw liquid waste products of metabolism from the blood
and deliver them to the outside of the body.   The nitrogenous sub-
stances, urea and uric acid dissolved in water, are the principal prod-
ucts discharged.

h. The *Reproductive System* is a closely related arrangement of glands, ducts, and accessory structures which function to produce new individuals of the species. Additional features of sexual reproduction are given in a separate section on that topic below.

i. The *Endocrine System* includes a number of different glands located in various parts of the body. These glands discharge chemical substances, known as hormones, directly into the blood. The hormones cooperate to regulate the metabolic activity of the entire body. The thyroid gland of the neck region, adrenals located near the kidneys, and the islands of Langerhans of the pancreas are typical examples of these organs. They go under the names of ductless glands and organs of internal secretion also.

j. The *Nervous System* is an organization of the nerve cell bodies and their processes in such a way as to receive stimuli, carry sensations, correlate them, and coordinate the activities of the parts of the body. By the function of the sensory portion of the system, the animal becomes aware of the environment and relates itself to it. In vertebrates the principal parts of the system include the brain, spinal cord, peripheral nerves, autonomic nerves, sense organs, and ganglia.

The body might be thought of as being constructed by relating cells to cells to form tissues, tissues to tissues to form organs, organs to organs to form systems, and systems to systems to form the *metazoan organism*. These will all be studied in more detail in connection with the study of specific animals.

Development of Sexual Reproduction

Reproduction makes great advances among the metazoans. The simple fundamental process of reproduction by cell division or binary fission has been studied already. This is not possible for most metazoan animals, but, in general, this type of animal begins life as a single cell resulting from the fusion of two sex cells, one produced by each parent. In some of the colonial Protozoa and also in Sporozoa, as well as possibly in *Paramecium,* there seems to be the beginning of sexual reproduction. The individuals in a colony, by peculiarities in cell division, become differentiated into two types: (a) the ordinary, *nutritive* individuals, whose means of reproduction is fission and (b) *reproductive individuals* or *gametes* of two forms: the large, egglike, inactive macrogametes and the smaller, motile microgametes. In reproduction these two types of cells unite to form a single *zygote,* from which a new colony arises by

repeated divisions. In a number of the Sporozoa, both sexual and asexual generations occur. The zygotes, which are formed in the sexual phase or generation, produce a number of spores which develop sporozoites (already studied under *Plasmodium*). These become nutritive trophozoites and are capable of production of another generation of gametes. Conjugation of *Paramecium* is also looked upon as a forerunner of sexual reproduction.

In simple Metazoa there are likewise two forms of reproduction: *asexual* (without sex), including budding and fission, and *sexual,* which involves the union of two germ (sex) cells, one male and one female. In simple forms like sponges and jellyfish the germ cells arise from general formative interstitial cells between the two primitive germ layers to form temporary gonads. When the germ cells are mature, they break through the wall to the outside of the body. Again, among the simpler metazoans a single individual produces both male and female germ cells. Such an organism is said to be *hermaphroditic* or *monoecious*. Most of the types of animals in the phylogenetic scale, up to and including the worms, are normally hermaphroditic.

Infrequent examples of hermaphrodites occur either normally or occasionally abnormally here and there among the higher groups of metazoans, even in man.

In higher forms the usual method of reproduction involves germ cells produced by two individuals. Each cell is either male or female, the gonads of the other sex having degenerated in that individual. The sexes are separate under such conditions and are said to be *dioecious*.

There are some forms, particularly insects, in which it is possible for the unfertilized egg cell to develop without union with another germ cell. This is known as *parthenogenesis*. The case of the ordinary aphids or plant lice, known to every gardener, is a good example. In the spring an egg which was *fertilized* and laid the previous fall hatches to produce an individual known as a *stem-mother*. This individual feeds on the sap of the particular plant on which she lives and grows to maturity. Instead of mating (there are no males in her generation) she produces a series of eggs (macrogametes) which continue to develop without union with a sperm (male germ cell). Another generation of female aphids arises from these eggs which in turn reproduce in a similar manner. A series of female generations appears in succession during the summer. No males are

produced until the last generation of the season, and this time there are both males and females. These mate, the females lay fertilized eggs which pass through the winter and hatch as the first generation next spring. These individuals are the stem-mothers for the new season. Some authors speak of this process as "virgin birth." The honey bee queen can control her offspring to some degree. If her eggs are not fertilized, the offspring are all males (drones). If the eggs are fertilized, as most of them are, only females are produced, these becoming queens if fed abundantly on proper food or workers if fed otherwise. In regard to this state of affairs Lane puts it this way, "So it comes about, that though a drone bee may become the father of thousands of daughters, he never has a son, nor did he himself have a father."

The eggs of a number of animals, such as frogs, molluscs, worms, sea urchins, and others have been artificially stimulated to continue development by application of chemical, electrical, or mechanical agents. This goes under the name of *artificial parthenogenesis.*

Metagenesis is a phenomenon occurring in the life history of a number of scattered species of Metazoa, including the coelenterate, *Obelia;* two or three marine worms; and *Salpa*, the tunicate (a chordate animal). This process is an alternation of production of sexual individuals in one generation and asexual in the next. The offspring in each case differs from its parents. This is spoken of as *alternation of generation.* In *Obelia*, a coelenterate related to Hydra (to be studied shortly), there is a plantlike, *asexual, colonial* form, which gives rise to sexual, free-swimming *medusae.* The medusae produce eggs and sperms which unite in the water and develop into asexual colonies. Metagenesis really involves two methods of reproduction in successive generations of the same species. The significance is somewhat uncertain, but possibly it insures better and more complete distribution of individuals than could be secured by only the budding colony. Many of the sexually reproducing plants have a similar alternation of sexual and asexual generations.

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CHAPTER V

THE BULLFROG AS A TYPICAL VERTEBRATE ANIMAL

(CLASS AMPHIBIA)

(BY OTTYS SANDERS, SOUTHWESTERN BIOLOGICAL SUPPLY COMPANY)

As there are many vertebrate animals which lead an amphibious life, it was natural for Linnaeus to group these together under the class Amphibia. This, of course, was classification based on habits rather than on structure, and as soon as such animals as the seal and crocodile were studied structurally they were removed from the class. Today the name is restricted to a group of vertebrates which we know as frogs, toads, salamanders, and caecilians. They are intermediate between fishes and reptiles. They have paired limbs, usually with fingers and toes, and never have paired fins like fishes. They have a moist, naked skin lacking the protective hair of mammals or the feathers of birds. With the exception of caecilians, they do not have scales as do the reptiles. The caecilians, none of which has been reported from the United States, are worm-like burrowing creatures of the tropics. They have small scales between their transverse body rings, although these are not usually seen unless a dissection is made. The amphibians are cold-blooded vertebrates, in contrast to the warm-blooded mammals and birds.

The frogs, toads, and salamanders usually lay their eggs in water. These develop into tadpoles or larvae breathing with gills before metamorphosing to become adults which breathe with lungs. A few species of frogs and salamanders lay their eggs on land and pass their entire development in the egg.

There are other exceptions to the general characteristics of this diverse class. A large group of salamanders, the plethodontids, do not have lungs even as adults, and their respiration takes place through their skin, which is richly supplied with blood vessels.

Habitat of the Bullfrog

The bullfrog is a solitary animal except during the breeding season. It is strictly aquatic and does not leave the pools as does the leopard

frog. It prefers bodies of quiet water where there are both shallows and deeper water, such as lagoons, small lakes, and the cypress ponds of swampy regions. Crayfish, insect larvae, water beetles, snails, and other aquatic organisms make up the bullfrog's diet. This diet is quite varied and may even include younger frogs.

Bullfrogs are found in North America east of the Rockies from Canada to Mexico. They have also been introduced into the western portion of the United States and into various foreign countries.

Fig. 17.—The bullfrog, *Rana catesbeiana*. (Courtesy of Southern Biological Supply Company.)

External Structure

Bullfrogs obtained in the South and Southwest are usually of two species, *Rana catesbeiana* Shaw, the common bullfrog, or *Rana grylio* Stejneger, the southern bullfrog. Individuals of the former species attain larger sizes, and the giant bullfrogs of the southern swamps usually are *Rana catesbeiana*. The two species differ not only in size but also in external appearance, particularly when alive. However, they are essentially the same anatomically, and this chapter is based on a study of *Rana catesbeiana*.

The common bullfrog is ordinarily greenish or olive brown. Underparts are mottled with dark spots on a white background, and the upper surfaces may be plain or marked with large dark splotches.

The legs are marked with crossbars and other splotches of dark color. Preserved specimens appear brownish gray with the dark mottling lighter in color than on the living specimen.

The body of the bullfrog includes the *head* and *trunk*. Attached to the trunk on either side anteriorly are the *forelegs* and posteriorly the *hindlegs*.

The head has two prominent eyes which protrude above its surface. These can be drawn back into their orbits and forced somewhat into the mouth cavity. The *lower lid* of the frog's eye with its attached *nictitating membrane* is drawn up over the eye, not by independent movement of the eyelid, but as a result of the retraction of the eye into the orbit. The *upper eyelid* is immovable. Back

A   B
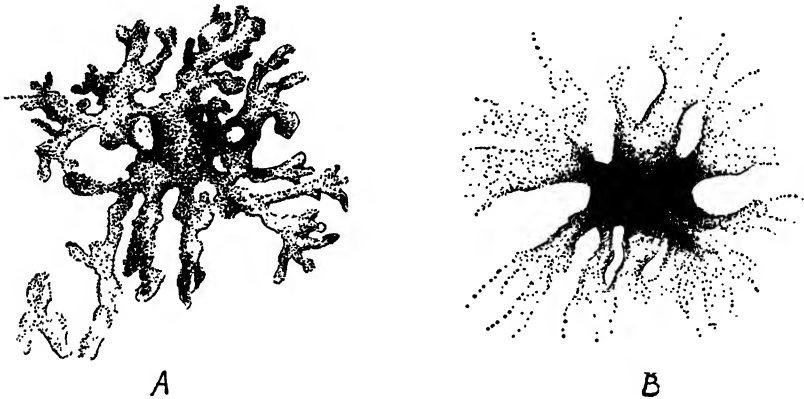
Fig. 18.—Melanophore from *Rana temporia. A,* Pigment distributed in response to light; *B,* pigment contracted. (Redrawn and modified from Noble, *Amphibia of North America,* McGraw-Hill Book Company, Inc.)

of each eye is a circular oval area, the *tympanum* or eardrum. In the females this is about the size of the eye, while in the males it is larger than the eye. A small fold of skin, the *tympanic fold,* runs from the eye around the posterior margin of the tympanum. The two nostrils or *nares* are near the anterior part of the head, and each is guarded by a valve. The mouth reaches from one side of the head to the other and has an upper and lower jaw. The *anus* or vent is at the extreme posterior end of the trunk.

The forelimbs are composed of the upper arm, which joins the trunk, the *forearm,* wrist or *carpus,* and the *hand* with its four *digits.* In the male, particularly during the breeding season, the innermost

digit, or *thumb*, is enlarged, whereas the thumbs of females remain apparently the same size. The digits may have tubercles on them, and their positions in relation to various bones of the hand give rise to specific names for these tubercles. The forelimbs are used not only to help support the body but also as an aid in pushing food into the mouth.

The hindlimbs are long and have powerful muscles. Bullfrogs ordinarily leap about three feet but can easily cover a distance of five or six feet. The hindlegs are composed of the *femur,* which joins the trunk; the tibio-fibula; and the ankle, or tarsus. Following the tarsus is the foot with five digits (toes), which are connected by a web, producing a very efficient swimming organ. The point at which the tarsus joins the tibio-fibula is known as the heel.

Digestive System and Digestion

The mouth cavity, or *buccal cavity,* is large. It narrows toward the *esophagus,* which is a short gullet leading directly from the mouth to the stomach. The lining of the esophagus has a number of longitudinal folds and is ciliated. The stomach normally lies on the left side of the body. It is curved, with the convex side toward the bullfrog's left. Its anterior or *cardiac* end is wide, and the *pyloric* or posterior end is narrowed and constricted where it joins the small intestine. The *duodenum,* or anterior part of the small intestine, runs forward almost parallel with the stomach. At the point where the intestine turns back posteriorly the duodenum becomes the *ileum,* which composes the remainder of the small intestine and is considerably coiled. The large intestine or *rectum* is sharply marked off from the small intestine and is wide and short. It passes directly into a muscular part, the *cloaca,* which terminates in the anus or vent.

The *buccal cavity* has in its roof near the end of the snout two patches of small conical teeth which are cemented to two bones in the roof of the mouth, known as vomers. These teeth consequently are called *vomerine teeth.* In addition, the upper jaw has a single series of small conical teeth on its edge known as *maxillary teeth.* These teeth serve primarily to help hold the crayfish, insect, or other animal captured for food, and they may help at times in crushing it. The *tongue* is somewhat leaflike in shape and is deeply notched behind, making it bicornate. Its anterior half is attached

to the floor of the mouth just back of the tip of the lower jaw, and
its posterior end is free. Taste buds are present on the tongue and
palate.

Esophagus, stomach, and intestine have an outer longitudinal and
an inner circular layer of smooth muscle. The peristaltic contrac-
tions of these muscles pass the food through the digestive tract and
aid in mixing it with the gastric juice in the stomach. They may
also be used to regurgitate a disagreeable substance swallowed by
the frog, in which case the stomach turns inside out and protrudes
into the mouth cavity.

The liver lies on each side of and behind the heart. It is three-
lobed, two lobes being on the left and one on the right, connected
by narrow bridges of liver tissue. Between the right and left lobes
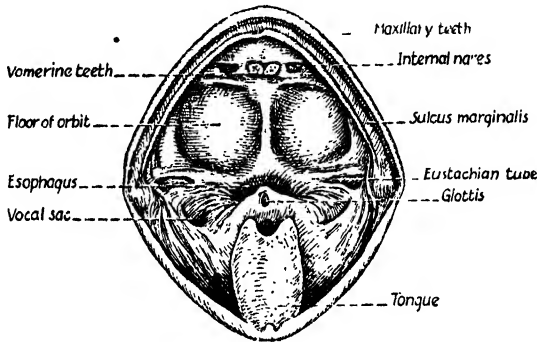
Fig. 19.—Mouth, or buccal cavity, of the bullfrog.

is the *gall bladder,* which receives an alkaline secretion known as bile
from the liver and stores it until needed in the process of digestion.
Bile is carried from the gall bladder to the duodenum by the *bile
duct,* which passes through the pancreas on its way. The liver is
not primarily a digestive gland, for, while the bile it secretes per-
mits the fats to be more easily digested by a lipase from the pan-
creas, the bile itself probably contains no digestive enzymes. Al-
though its function in altering fatty substances is important, of
prime importance is its ability to store glycogen and the fat upon
which a hibernating frog lives. It is also concerned in the formation
of urea and in the destruction of red blood corpuscles.

The *pancreas* lies in the loop between the stomach and duodenum.
It is a long, whitish, irregularly-lobed gland whose alkaline secre-
tion is of considerable importance in digestion, for it contains three

digestive enzymes. This secretion is taken from the pancreas by pancreatic ducts which empty into the bile duct that runs through the pancreas before entering the duodenum near its beginning.

Intestines, liver, and pancreas are covered with *peritoneum*. The mesenteries which hold the body organs in position and the internal surface of the body wall likewise are made up of this peritoneal membrane.

Digestion.—Since frogs live primarily on insects, crayfish, and other small invertebrate animals, their food is very rich in proteins. Their vomerine and maxillary teeth are too feeble to do more than slightly crush their prey, so digestion begins in the stomach. Here the gastric glands secrete *hydrochloric acid* and an enzyme, *pepsin,* which convert the proteins to peptones. The muscles of the stomach cause a thorough mixing of the gastric juice with the food and then pass the partly digested food *(chyme)* posteriorly into the small intestine. Here, activated by the acid nature of the food, the intestinal glands release into the blood stream a substance, *secretin,* which on reaching the pancreas causes it to pour forth into the duodenum its highly alkaline secretion. In addition, this pancreatic juice contains three digestive enzymes: a *protease, trypsin,* which continues the digestion begun by pepsin in the stomach, converting proteins to amino acids; an *amylase, amylopsin,* which changes starches into sugars; and a *lipase, steapsin,* which, aided by the bile, causes a splitting of the fats into glycerol and fatty acids.

The process of digestion is completed in the intestine and the food products are taken up by absorption in its mucosa layer. These foods in solution are taken by the blood stream and lymph vessels to various parts of the body where they are utilized for building tissue or for supplying energy, leaving as by-products *urea* and carbon dioxide. Sugars that are not used are stored as *glycogen* in the liver and in voluntary muscles. The liver also serves to store fats and to secrete urea and sugar directly into the blood stream.

Food that is not digested passes to the large intestine where it is retained for a time and then passed to the outside through the anus as feces.

Other Glands.—Attached by a mesentery to the wall of the intestine near the anterior end of the rectum is the spleen. It is a small, reddish, spherical, lymphoid organ, the functions of which are but incompletely known. The destroying of red blood corpuscles is an

important duty, as possibly also is the formation in its tissues of lymphocytes, one type of white blood corpuscle. In mammals the spleen is also believed to accumulate iron freed by the metabolism of other tissues. This iron is subsequently used in the formation of hemoglobin.

The two *thyroid* glands are small and lie in front of the glottis under the floor of the mouth. There is one on each side of the hyoid apparatus. The secretion and functions are discussed in the chapter on *Endocrine Glands and Their Functions*.

A *thymus* gland lies under the skin behind the tympanic membrane on each side. It is partly covered with muscle and is small. Further discussion of it will be taken up in the chapter on *Endocrine Glands and Their Functions*.

Circulatory System

The circulatory system comprises the *blood vascular system* and the *lymphatic system*. The two systems are closely interrelated in that they both carry to the tissues of the body nutritive material necessary for metabolism and remove from them to the excretory organs, waste products of body activity. They differ in several respects; the lymph neither contains red blood corpuscles for transporting oxygen nor moves in a continuous closed vascular circuit as does the blood. Other differences will be noted in the discussion.

The Blood Vascular System.—The blood moves through a closed system of tubelike vessels of various sizes which distribute it to all parts of the body. The pump is the *heart,* which, by its contractions, forces the blood to flow to the tissues.

The blood vessels leading away from the heart are the *arteries.* When these reach the tissues, they break up into very small vessels, the *capillaries.* The vessels leading back to the heart are the *veins.* The arteries and veins are connected by the capillaries.

Blood is comprised of a clear liquid called the *plasma,* suspended in which are blood corpuscles of three kinds, the red blood corpuscles or *erythrocytes,* the white blood corpuscles or *leucocytes,* and the spindle cells or *thrombocytes.* In addition, the blood may contain dissolved nutritive substances from the digestive system, waste products from tissue repair and destruction, hormones being transported from organs of one part of the body to another, or foreign substances accidentally introduced.

The capillaries are very small vessels, the walls of which are made up of endothelium continued from the linings of arteries and veins. They connect the distal ends of the arteries with the proximal ends of the veins, but in so doing they branch extensively and anastomose to form fine networks in the tissues invaded. Through their thin walls, acting as semipermeable membranes, food products brought by the arterial blood pass into the tissues, oxygen is unloaded from the red blood corpuscles, and carbon dioxide and waste products are taken up to be conducted into the veins. Leucocytes are able to get out of the capillaries, squeezing their way between the cell walls, and thus become free to engulf bacteria or other harmful objects.

The arteries are large vessels with elastic walls and carry blood from the heart to the capillary networks in the various organs and tissues of the body. The arteries arise from the conus arteriosus which divides just above the auricles into a right and left truncus arteriosus. Each of these trunks splits into three arches going to each side of the body, the anterior *carotid* arch, the middle *systemic* arch, and the posterior *pulmocutaneous* arch.

The Carotid Arch.—Each carotid arch divides into two branches. The more ventral, *lingual artery,* or external carotid, passes forward, giving branches to the thyroid, pseudothyroid, muscles of the hyoid and tongue, and then extends along the edges of the lower jaw. The internal branch is larger and is called the *internal carotid.* It has at its base a spongy enlargement known as the *carotid gland* which by its structure serves to steady the pressure of blood passing into the artery. This artery goes to the base of the skull, giving off the *palatine artery* to the roof of the mouth, the *cerebral carotid* which enters the skull and supplies the brain, and the *ophthalmic artery* to the eye.

The Systemic Arch.—The systemic arch soon after it leaves the truncus supplies a small laryngeal artery to the larynx and muscles of the hyoid. It then curves downward and around the esophagus on each side. It gives off an *occipitovertebral artery* which sends a small artery to the dorsal side of the esophagus, then branches at the spinal cord into the *occipital artery,* running anteriorly on the dorsal side of the skull to the orbit and tympanum, and the *vertebral artery,* turning posteriorly along the spinal column. Immediately posterior to the occipitovertebral artery the large *subclavian*

artery rises from the systemic arch. It branches to the shoulder and adjacent body wall and enters the arm as the *brachial artery.*

The systemic arches from each side, after curving under the alimentary canal, meet near the anterior end of the kidneys and fuse into a single large artery, the *dorsal aorta,* which extends posteriorly. At or just posterior to this meeting point, there arises from the aorta
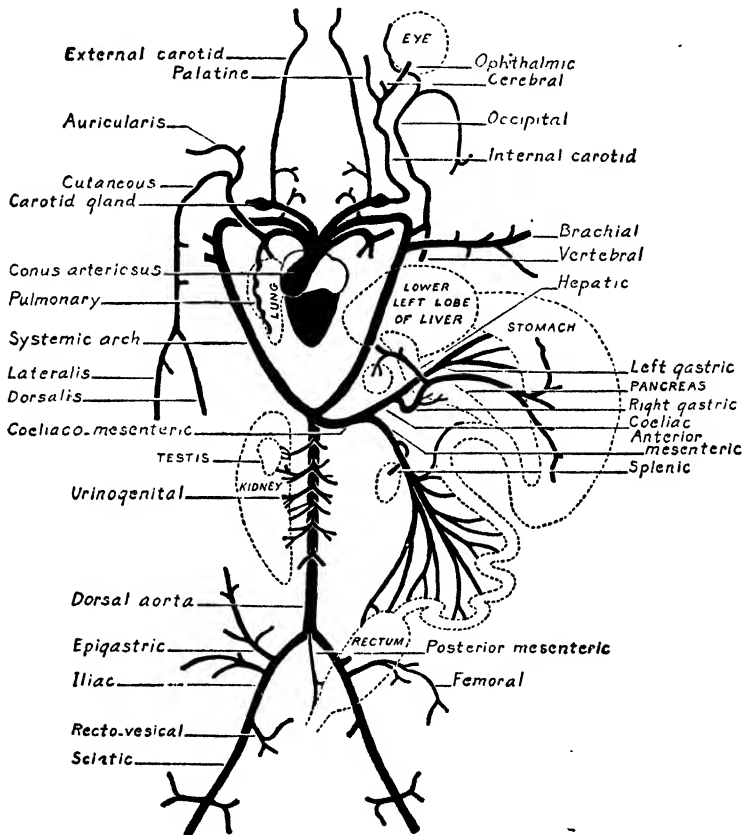
Fig. 20.—Arteries of the bullfrog from ventral view. (Drawn by Ruth M. Sanders.)

the large *coeliaco-mesenteric* artery which divides into an anterior branch, the *coeliac artery,* and a posterior branch, the *anterior mesenteric artery.* The coeliac artery divides into *right* and *left gastric arteries.* The latter runs directly to the dorsal or left side of the stomach, while the former sends off small *pancreatic arteries* to the pancreas; a larger *hepatic artery* to the pancreas, gall bladder, and

liver; and continues to the ventral side of the stomach, where it is distributed. The anterior mesenteric artery gives off the *splenic (lienal) artery* to the spleen and then divides into two parallel vessels which send numerous smaller arteries to the small and large intestines.

The *urinogenital arteries* consist of about four to six small much-divided arteries which are given off from the ventral side of the dorsal aorta to right and left, supplying the kidneys, reproductive organs, and fat bodies. A few small lumbar arteries arise either as branches of these or directly from the aorta and go to the body wall on each side. The small *posterior mesenteric artery* is given off near the posterior end of the aorta, passing to a portion of the rectum and, in the female, to the ovisac.

Near the posterior end of the body cavity the dorsal aorta divides into two *iliac arteries* going to the hind legs. Each of these gives off (1) an *epigastric artery* supplying the bladder and dorsal and ventral body walls of the region, and (2) just below it, a *femoral artery* passing to the body wall, skin, and proximal muscles of the thigh. As the iliac artery enters the leg, a *rectovesical artery* is sent off to the rectum, bladder, and skin on the dorsal surface of the thigh. In the upper leg the continuation of the iliac, now called the *sciatic,* gives off a branch to the right and to the left, supplying the muscles, and then continues down the leg, sending off several branches at the knee.

The **pulmocutaneous arch** takes blood to the respiratory organs: the lungs, skin, and buccopharyngeal cavity. The pulmocutaneous arch on each side divides into a *pulmonary artery* to the lungs and a large *cutaneous artery,* which passes outward to the skin.

The Veins

The veins usually parallel the arteries that brought blood to the tissues from which the veins are returning it. The walls of the veins are thinner and not as elastic as those of the arteries. Many veins, particularly those of the limbs, have *semilunar valves* on the internal surface of the wall which open in the direction of flow and prevent the backflow of blood.

In returning blood to the heart, the venous system carries some of the blood through the kidneys or through the liver, providing *renal*

or *hepatic* filters to eliminate urea and other waste products from the blood or chemically to alter it. Pulmonary veins from the lungs carry oxygenated blood.

The venous circulation, therefore, may be divided into four main systems: the *systemic, hepatic portal, renal portal,* and *pulmonary* systems.
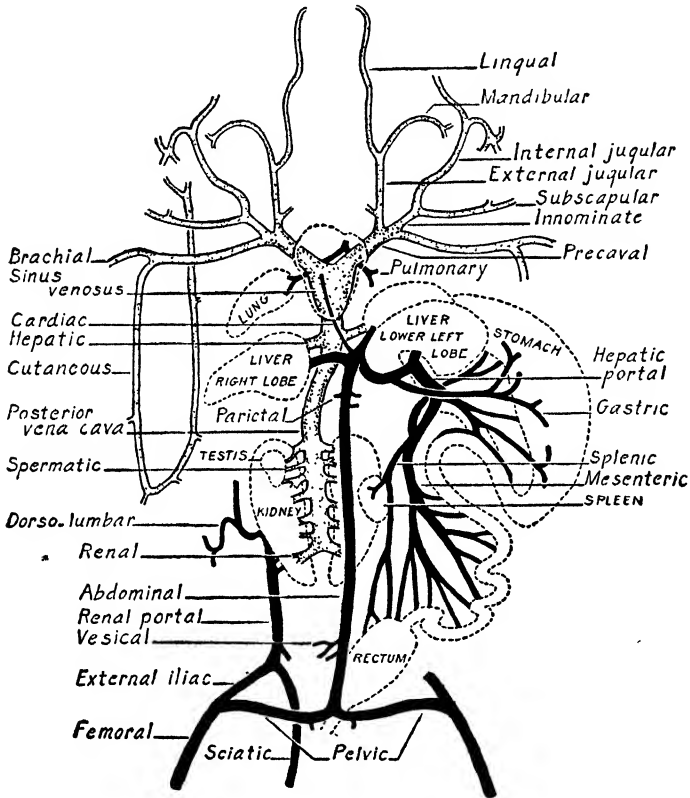
Fig. 21.—Veins of the bullfrog from ventral view. (Drawn by Ruth M. Sanders.)

The systemic veins carry the greatest load of blood to the heart. The larger collecting veins of the system consist of two *precavals* receiving blood from the anterior parts of the body, except the lungs, and a single *postcaval* or *posterior vena cava* receiving blood from the posterior parts of the body. The two precavals empty into the anterior end of the *sinus venosus* of the heart, and the posterior vena cava empties into its posterior end.

Each of the two anterior precavals receives blood from three branches: (1) the *external jugular* bringing blood from the tongue, hyoid, thyroid, pseudothyroid, and floor of the mouth; (2) the *innominate vein,* made up of a fusion of the *internal jugular* returning blood from the brain and other parts of the head, and the *subscapular vein* bringing blood from the back of the arm and shoulder; and (3) the *subclavian vein,* a fusion of the *brachial vein,* returning blood from the forelimb, and the large *musculocutaneous vein,* which forms an ellipse down the side of the body and extends up into the head region, returning blood from the skin and outer muscles in these regions.

The large *posterior vena cava* originates between the kidneys and receives blood from each kidney by five or six *renal veins,* from the gonads by small *spermatic* or *ovarian veins,* and from the fat bodies by other small branches. Near the heart the vena cava receives two large *hepatic veins* from each side of the liver.

The hepatic portal system is comprised of two chief veins, the *hepatic portal vein* and the *ventral abdominal vein.* These veins, instead of carrying blood directly to the heart, bring it to the liver to pass through a network of sinusoids (modified capillaries). It is returned to the systemic system through *hepatic veins* that join the postcaval.

Veins from the large and small intestines unite to form the *mesenteric vein* which is joined as it progresses forward by the *splenic vein* from the spleen, *pancreatic veins* from the pancreas, and *gastric veins* from both sides of the stomach. The vessel resulting from these unions is the *hepatic portal vein.* It passes through the anterior portion of the pancreas and sends a large branch into the lower left lobe of the liver. At about this point it often receives a final gastric branch which has passed over the pancreas to join it. It then continues a short distance to join the *abdominal vein* just below the heart.

The abdominal vein arises as follows. Two large veins, the *sciatic* and *femoral,* bring blood from the hindlimbs. The femoral, as it enters the body cavity, gives off the *pelvic vein.* The pelvic veins from each side of the body join in the middle to form the large *ventral abdominal vein.* As the abdominal vein proceeds toward the heart along the median portion of the ventral body wall, it receives *vesical veins* from the bladder, *parietal veins* from the body wall and, at its anterior end, a *cardiac vein* from the heart. In the region of the liver

it leaves the body wall, is joined by the *hepatic portal vein,* and enters the right and upper left lobes of the liver by short branches, discharging its blood into sinusoids.

The renal portal system, like the hepatic portal system, diverts blood to a purifying organ instead of carrying it directly to the heart. In this case, the blood is taken to the kidneys.

The outer *femoral vein* and the medial *sciatic vein* collect blood from the hindlegs. The femoral vein, after giving off the pelvic vein, passes anteriorly and joins the sciatic, to make the *renal portal vein.* Near the kidney this vein receives the *dorsolumbar veins* from the body wall and, in the female, several vessels from the ovisacs. The renal portal vein follows the dorsolateral margin of the kidney, sending numerous transverse branches into the organ, where they break up into capillaries. Blood which passes through these capillaries is purified of some of its waste products and then leaves the kidney through the renal veins which empty into and form the posterior vena cava of the systemic system.

Pulmonary veins run along the inner walls of each lung, returning the oxygenated blood to the heart. The right and left pulmonary veins unite to form a single vessel which empties into the left auricle on its dorsal side. Other veins which take on oxygen are those coming from the skin and bucco-pharyngeal cavity.

The Heart.—The heart is enclosed in the pericardial cavity, which is lined by a transparent tissue, the *pericardium,* and is separated from the remainder of the body by the *transverse septum.* It is the rhythmically contracting organ that circulates the blood. It is conical in shape and in the frog consists of a right and left thin-walled auricle above a single thick-walled ventricle. On the ventral side is a muscular tube, the *conus arteriosus,* described with the arteries. It conducts blood away from the heart. On the dorsal side of the heart is a thin-walled sac, triangular in shape, the *sinus venosus,* which receives venous blood from the systemic veins.

The sinus venosus empties into the right auricle through the *sinu-auricular aperture.* This aperture has liplike valves on each side to prevent the blood from flowing back into the sinus when the auricle contracts. The smaller left auricle receives oxygenated blood from the pulmonary vein. Valves are not necessary at this opening, for pressure on the auricular walls tends to close the small oblique aperture when the auricle contracts.

Both auricles pass blood into the ventricle through a common opening, the *auriculo-ventricular aperture,* which is divided by the *inter-auricular septum* separating the two auricles. This aperture has two large valves on each side and two small valves at each end which regulate the discharge of blood into the ventricle and prevent its backflow.

Blood leaves the ventricle and enters the arterial system through the conus arteriosus. The opening into the conus is protected by three pocketlike *semilunar valves* which open inwardly into the conus
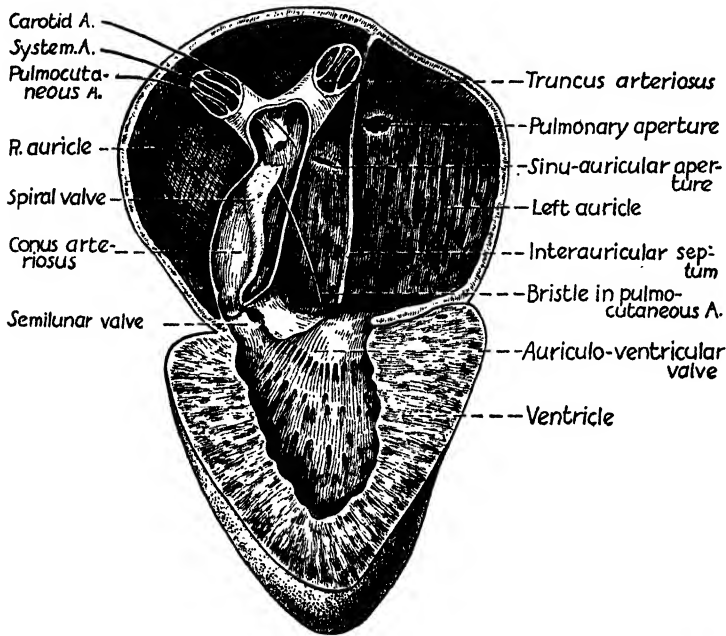
Fig. 22.—Heart of the frog with the ventral wall removed and bristles shown in the arteries branching from the truncus arteriosus.

when blood is passing out but are tightly closed at other times. The proximal portion of the conus is known as the *pylangium,* and the distal portion as the *synangium.* Running through the length of the pylangium is a longitudinal *spiral valve,* one edge attached to the dorsal wall of the pylangium and the other edge lying free in the vessel. Upon contraction of the conus this structure is brought into contact with the ventral wall and helps direct the flow of blood into the arches.

Near the anterior free end of the spiral valve where it is the widest, there is a pair of small synangial valves which, together with the end of the spiral valve, separate the pylangium from the synangium. Just below these valves is an aperture which leads into the trunk formed by the union of the two pulmocutaneous arteries.

The synangial chamber is very short and gives off almost immediately two large branches, one to the right and the other to the left. In each of these branches originate the three main trunks or arches of the arterial system. They are formed by two longitudinal septa dividing the vessel into three compartments. All three trunks are therefore enclosed in one large vessel for a short distance before breaking up into three separate vessels. The carotid arch originates from the anterior compartment, the systemic arch from the middle compartment, and the pulmocutaneous arch from the posterior compartment. Blood enters the anterior and middle compartments from the synangium, but enters the posterior compartment, or pulmocutaneous arch, from the pylangium.

The heart beats in a wavelike peristaltic manner. The sinus venosus contracts first, then the auricles (the right auricle preceding the left by a moment), then the ventricle, and finally the conus.

Venous blood from the right auricle enters the right side of the ventricle, and oxygenated blood from the left auricle enters the left side. Muscular ridges of the ventricular wall tend to hold the blood and reduce mixing. Since the heart's contractions are wavelike, the ventricle immediately forces the blood into the conus through the semilunar valve. Venous blood from the right auricle is closest to the conus, and it passes out first, flowing into the closest opening offering the least resistance. This is the opening in the pylangium to the pulmonary arch, leading to the lungs. As the contraction of the ventricle comes to an end, forcing out the remaining oxygenated blood, the pylangial part of the conus contracts, bringing the spiral valve against its ventral wall. This action, together with that of the synangial valves which are anterior to the common opening of the pulmonary arches, completely shuts off the flow of blood into these arches. The blood therefore passes into the synangium and enters the chambers leading to the systemic arteries or the carotid arteries. Since the carotid arteries offer some resistance to blood flow, the blood tends to enter the larger systemic arteries first. As the systemic arteries fill, they offer more resistance

to the blood, while resistance in the carotid arteries decreases due to their emptying into capillaries; so the last oxygenated blood from the ventricle passes into the carotids and is conveyed to the head region.

Blood corpuscles, which are of three kinds, float in the plasma. The erythrocytes are flattened and elliptical, with an oval nucleus in the center. They contain a pigment, *hemoglobin,* which has the property of absorbing oxygen. The colorless thrombocytes or spindle cells are not as large as the erythrocytes but resemble them except for their tapering ends. When these cells contact certain foreign bodies, they break up, releasing a substance that causes, upon contact with air, the coagulation of certain proteins in the blood plasma in which blood corpuscles become entangled, forming a clot. The insoluble protein strands thus formed are called *fibrin* (see chapter on *Physiology*). After the frog has been injured, the formation of a clot prevents indefinite bleeding and makes it possible for the tissues to begin repair.

The white blood corpuscles or leucocytes are of three kinds: *lymphocytes, monocytes,* and *granulocytes.* Their outlines are irregular, due to their amoeboid movement, and the shape of their nucleus varies greatly. They are much less numerous in the blood stream than are the red blood corpuscles and spindle cells. Leucocytes may escape from blood capillaries and engulf bacteria and other harmful substances in the tissues. They are finally returned to the venous system by lymphatic vessels. Worn-out corpuscles are removed from the blood stream chiefly by the spleen. The spleen seems to be the primary organ concerned in supplying new leucocytes, while the bone marrow furnishes most of the new erythrocytes. Leucocytes may also increase by fission.

Lymphatic System.—The lymphatic system of the bullfrog is an open system comprised of a series of large irregular sinuses in various parts of the body. It collects lymph from the tissues and eventually returns it to the veins. The lymph is a colorless fluid containing leucocytes but no erythrocytes. It is derived from seepage of plasma from the capillaries. It bathes all of the cells, collects wastes, and distributes food products. In the region of the intestinal tract, lymphatics absorb a considerable amount of fat and are called *lacteals.* Lymph removes cellular debris and transports leucocytes which engulf harmful material and cleanse the tissues of the body.

Between the skin and muscle are a series of *subcutaneous lymph sacs;* other sinuses are in the mesenteries, around the vertebral column, and elsewhere. The peritoneal and pericardial cavities are connected with the lymphatic system. *Nephrostomes* on the ventral surface of the kidney convey lymph from the peritoneal cavity into the renal veins.

Respiratory Organs and Respiration

Air enters through the nostrils, passes into a small olfactory chamber and then into the mouth cavity through the *internal nares,* which open in the roof of the mouth. The mouth is kept tightly closed in breathing. Air is sucked in by lowering the floor of the mouth and is then forced into the lungs by raising the floor, the external nares being closed by valves. This pushes the air through the slitlike *glottis* immediately behind the tongue in the floor of the mouth, thence into a short larynx which connects with the lungs.

The wall of the larynx is reinforced by a framework of cartilage, and the laryngeal chamber supports two horizontal fleshy folds, the *vocal cords,* which extend across the passageway. When a frog croaks, its mouth and nostrils are kept tightly closed, and the air is forced back and forth between lungs and mouth cavity, causing the *vocal cords* to vibrate.

The two lungs lie dorsal to the heart on each side and dorsal to the liver. They are very elastic sacs with their inner walls raised into a number of ridges, forming chambers which are called *alveoli.* These chambers are richly supplied with a network of blood vessels for facilitating the oxygenation of the blood. In the bullfrog the lungs are also important as a hydrostatic organ.

While the lungs play the major role in respiration, other factors are of considerable importance. The lining of the mouth of the bullfrog contains a large number of blood vessels and serves for a type of respiration known as *bucco-pharyngeal respiration.* With the glottis closed, air is drawn into the mouth cavity and forced out by rhythmical movements of the throat. Oxygen is taken up by blood vessels in the lining of the mouth by diffusion.

The skin of the bullfrog plays a large part in its respiration, and frogs that are not protected from drying out soon die. Gaseous exchange of carbon dioxide and oxygen can take place through the moist vascular skin, and is known as *cutaneous respiration.* During

hibernation, practically all respiration of the bullfrog is of this nature. Even at other times, the skin releases more carbon dioxide than do the lungs. The functions of respiration are discussed in the chapter on *Physiology.*

Excretory System and Excretion

The two kidneys lie between the parietal peritoneum and dorsal body wall in the posterior region of the body cavity. The space in which they are enclosed is called the *cisterna magna.* They are dark red in color, flattened and elongated. They are made up of a very great number of *uriniferous tubules.* A *mesonephric duct* runs from the posterior lateral border of each kidney and empties into the dorsal side of the cloaca. The *urinary bladder* also opens into the cloaca but does so on its ventral surface, and the ducts do not join the bladder. The bladder is a two-lobed sac with very thin walls which stores the urine collected from the cloaca. When filled, the bladder contracts and forces the urine back through the cloaca and outside through the anus. Embedded in the ventral surface of each kidney is a yellowish red patch, the *adrenal gland,* which will be discussed in the chapter on *Endocrine Glands and Their Functions.*

The waste products resulting from the vital processes of destruction, repair, and growth in the body must be removed if the organism lives. These are taken from the tissues by the blood and more especially by the lymph. We have already mentioned the expulsion of carbon dioxide and water through the skin and lungs. Another product of protein metabolism is *urea.* This soluble crystalline substance, formed to a large extent in the liver from the nitrogen of protein metabolism, enters the blood stream and is removed by the kidneys, The kidneys also remove foreign substances from the blood and pass these to the outside through their mesonephric ducts and the cloaca.

Frogs and toads excrete considerably more urine .per day proportionally than does man. It has been estimated that, while man excretes about one-fiftieth of his weight per day, the frog excretes about one-third of its weight. During the winter, however, in common with the slowing down of its other body functions, the kidney function of the frog is practically stopped.

The kidney is not only concerned with the elimination of waste products but also has other functions. One of these is the reabsorption by its tubules of useful substances, such as some of the salts

and glucose which have filtered out, and their reintroduction to the blood stream. In their food frogs obtain less sodium chloride than do mammals, and this is compensated for in part by a retention of salts from the water taken in, while in mammals water is retained and the salts are eliminated.
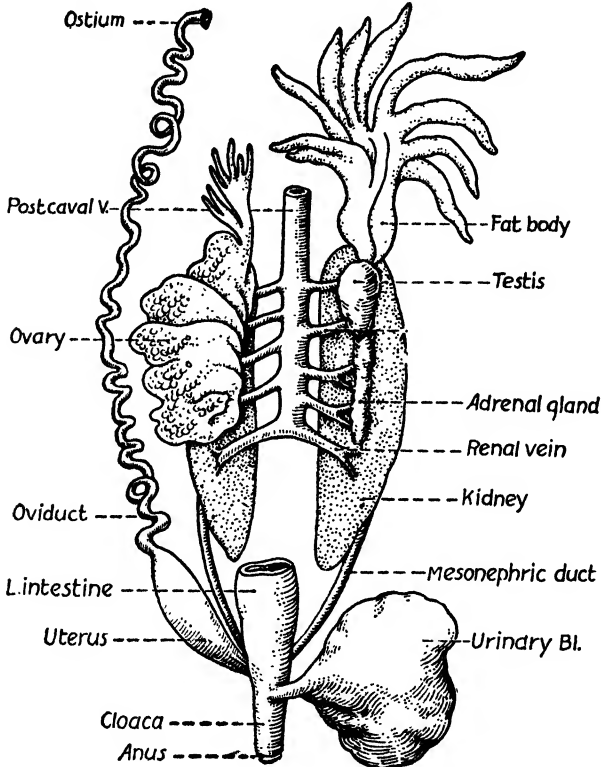
Fig. 23.—Urogenital system of the frog from ventral view. Male organs shown on right side of figure and female on the left. The single urinary bladder is present in both sexes.

Another function is in maintaining the concentration of body fluids. Frogs absorb water through their skin at a rather constant rate, varying with the temperature. The kidney in turn expels water at the same rate and thus maintains the proper balance. In addition to its usual function the urinary bladder may be used as a storage reservoir for water during temporary drought. The water may be absorbed from it by other tissues until the proper osmotic equilibrium of the tissues with the blood is produced.

Skeletal System

The bullfrog has no exoskeleton, its body being covered by smooth skin. The *endoskeleton* may be considered in two main divisions, the *axial* and *appendicular* portions. The axial part includes the skull and vertebral column; the appendicular portion consists of the bones of the limbs and their supports, the pectoral and pelvic girdles.

Bones are joined to one another by structures made up of connective tissue which allow varying degrees of movement between them. These structures are called *joints* or articulations. In some cases, as in the skull, the joints are immovable and the bones are separated only by a thin sutural ligament of connective tissue. In other cases, the joints are slightly movable, as in the vertebral column where a plate of dense tissue and cartilage connect the vertebrae. In still other cases the bones are freely movable, as in the limbs, and here the bones are entirely separated, but are held in place by ligaments.

The Axial Skeleton.—The *skull,* which is composed of cartilage, cartilage bones, and membrane bones, forms a case for the brain and capsules for the sense organs. Cartilage bones are the *sphenethmoids, pro-otics, exoccipitals, pterygoids, palatines,* and *cartilaginous quadrates.* The membrane bones develop from ossifications of membranes which cover the cartilage and cartilage bones. They are thin and may be separated from the others. The membrane bones are the *premaxillaries, maxillaries, nasals, frontoparietals, quadratojugals, squamosals, parasphenoids,* and *vomers.* The bones enclosing the brain constitute the *cranium.*

On the dorsal surface of the cranium, the two frontoparietals form most of the roof, the pro-otics form the roof of the auditory capsule (inner ear capsule), the sphenethmoids form the posterior wall of the olfactory capsule (nasal chamber), and the two triangular nasal bones lie above. On the ventral surface of the cranium are the slender palatines extending laterally on each side from the anterior end of the sphenethmoid to the upper jaw. The vomers form the floor of the olfactory capsules, and their ventral surfaces bear the vomerine teeth. The parasphenoid forms the floor of the brain case.

At the posterior end of the cranium is a large opening, the *foramen magnum,* through which the spinal cord passes. On each side of this

opening are the exoccipital bones. Each bone has a rounded projection at its base, an *occipital condyle,* which articulates with the vertebral column.
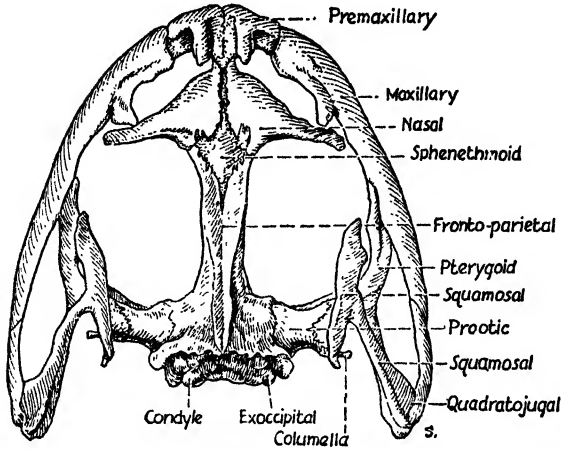
Fig. 24.—Dorsal view of the skull and upper jaw of the bullfrog.
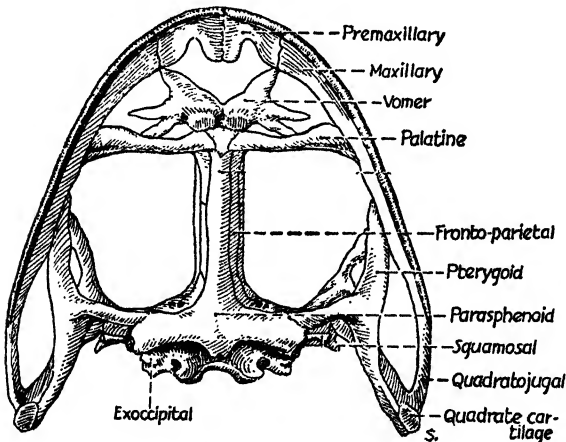
Fig. 25.—Ventral view of the skull and upper jaw of the bullfrog.

The *visceral skeleton* is that part of the axial skeleton which is composed of the jaws and hyoid arch in the adult. The gill arches of tadpoles are included in this portion.

The hyoid apparatus is primarily cartilaginous and serves as a support for the base of the tongue and the larynx. According to some authors, the jaws and the hyoid were originally the branched

arches supporting the gills, and evidence of this is seen when the frog tadpole breathing with gills transforms to the frog breathing without gills.

The upper jaw consists of a pair of short premaxillary bones in front, a pair of long maxillae forming the sides, and a pair of short quadratojugals as the posterior portions. The premaxillae and maxillae each bear a row of small conical teeth. The lower jaw is formed primarily of a cartilaginous rod known as *Meckel's cartilage*.

At the extreme anterior tip of the jaw the rod is ossified to form two small bones, the *mentomeckelian* bones. It is subsequently covered anteriorly by a *dentary* bone and posteriorly by an *angulosplenial* bone. The jaws are attached to the cranium by a combination of three bones on each side, the squamosal, pterygoid, and palatine, to form a suspensory mechanism.
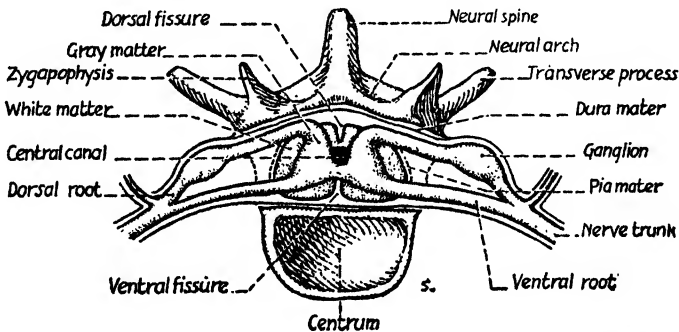
Fig. 26.—Structure of a single vertebra and cross section of the spinal cord of frog. (Redrawn and modified from Holmes, *Biology of the Frog*, by permission of The Macmillan Company, after Howe, *Atlas of Zootomy*.)

The *vertebral column* is made up of a series of nine typical vertebrae and a long bone, the urostyle, which includes a fusion of the vertebrae from the tadpole tail with the tenth.

In the neck region, there is one *cervical* vertebra, the *atlas*, which articulates with the skull. This is followed by seven *trunk* vertebrae, then one *sacral* vertebra whose processes support the pelvic girdle, and finally the urostyle, which contains all of the caudal vertebrae fused into one piece.

The basal portion of the typical vertebra is known as the *centrum*. The centrum is concave in front and convex posteriorly, and therefore is *procoelous*. Attached to the centrum is a bony ring, the neural arch, which extends dorsally from the centrum around a portion of the spinal cord. The neural arch has extending from its sides

a pair of riblike *transverse processes* to which muscles are attached, and a dorsal projection is the *neural spine*. In addition, the neural arch has at each end a pair of processes known as *zygapophyses* by which the vertebrae are coupled together, the posterior zygapophyses of one vertebra overlapping the anterior zygapophyses of the succeeding one. This arrangement furnishes a protected canal for the spinal cord and a firm axial support which also allows bending of the body. The spinal nerves emerge between vertebrae through an *intervertebral foramina* protected by the cartilaginous pads between the vertebrae.
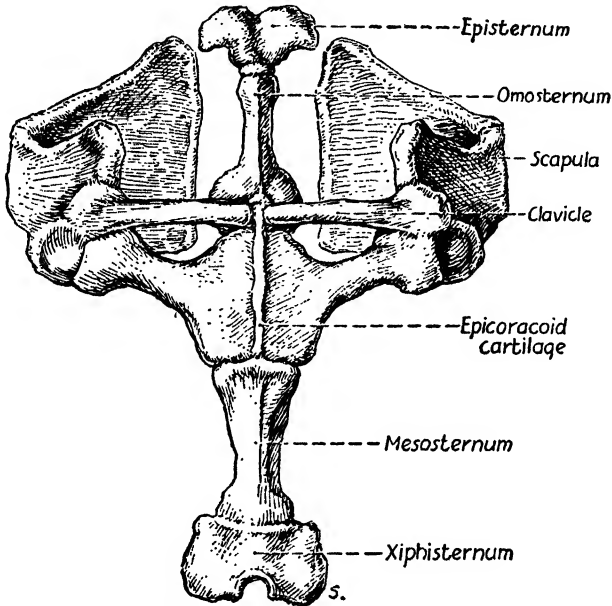
Fig. 27.—Ventral view of the pectoral girdle of bullfrog in natural position.

Appendicular Skeleton.—The anterior portion of the appendicular skeleton is composed of the pectoral girdle, sternum, and bones of the forelimbs. The posterior portion has the pelvic girdle and bones of the hindlimbs.

The *pectoral girdle* and *sternum* furnish a support and place of attachment for the forelimbs and their muscles. They also provide a case to protect the heart, lungs, and other organs in the anterior part of the body. This girdle is not connected to the vertebral column. Each side of the dorsal part of the girdle is composed of a large flat bone, the *suprascapula,* which curves ventrally and joins the *scapula.*

From the ventro-anterior end of the scapula two bones extend to the mid-ventral line of the body and would meet their fellows from the opposite side except that the narrow *epicoracoid cartilage* intervenes. The anterior of these two bars is the *clavicle* and the posterior one the *coracoid*. At the junction of coracoid and scapula a depression is formed, known as the *glenoid fossa,* into which the forelimb articulates. The ventral sternum is separated into two portions by the pectoral girdle. The anterior portion is composed of a bone, the *omosternum,* to which is attached anteriorly a rounded plate of cartilage, the *episternum*. The posterior portion is composed of a bone, the *sternum* proper, and a rounded cartilage, the *xiphisternum,* which has a notch at its posterior margin through which the abdominal vein runs as it leaves the body wall.
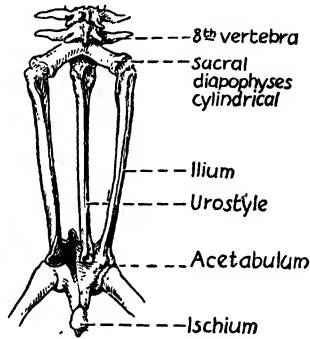
Fig. 28.—Pelvic girdle of bullfrog, dorsal view.

The *pelvic girdle* furnishes a place of attachment and support for the hindlimbs. Each half of the pelvic girdle is composed of three bones, the *ilium, ischium,* and *pubis*. The more slender ilium is attached anteriorly to the transverse process of the ninth vertebra, and posteriorly it fuses with the pubis and ischium, forming a dishlike concavity, the *acetabulum,* which receives the hindlimb. The pubis is ventral to this point of fusion, and the ischium is posterior.

The *forelimbs* join the body by a ball and socket joint at the glenoid cavity in the pectoral girdle. The large bone which makes this articulation is the *humerus*. The succeeding bone of the forearm is the *radio-ulna,* a fusion of two originally distinct bones. The wrist, which follows, contains six *carpal* bones arranged in two rows. Each hand, or *manus,* contains four *metacarpals* following the *carpals,* and distal to these are four complete digits and an exceedingly small

rudimentary fifth near the thumb, the *prepollex*, consisting of only a single bone. Each of the four digits, or fingers, extends from a *metacarpal* bone. This is followed in digits II and III by two phalanges and in digits IV and V by three phalanges.

The *hindlimbs* have essentially the same structure as the forelimbs. The large bone which joins the girdle at the socketlike acetabulum is known as the *femur*. This bone articulates with the *tibio-fibula*, which, like the bone of the forearm, is a fusion of two bones. The tarsus or ankle differs from the wrist, being composed of two long bones, the *tibiale (astragulus)* and *fibulare (calcaneum)*, and two small *tarsals*. There are also two extremely small bones forming the *prehallux*, or rudimentary sixth toe. Distal to the tarsals are five long *metatarsals*. Each foot contains five complete digits, each following a metatarsal bone. In digits I and II are two phalanges, in digits III and V three phalanges, and in digit IV four phalanges.

Muscular System

Muscular tissue controls the movements and positions of various parts of the body of the bullfrog. This it does by contracting, that is, by shortening and thickening its elements.

Movements may be under voluntary control, as the skeletal muscles, involved in moving the limbs, in which case the muscle fibers are striated and are known as *voluntary muscle*. Other movements, such as the heartbeat and the peristaltic movements in the intestines, are not under control of the will. Muscles concerned in these actions are known as *involuntary* and are usually made up of *smooth muscle* fibers except in the heart, which contains *striated cardiac muscle*.

Most voluntary muscles are attached to bones at one end or at both by specialized connective tissue bands known as *tendons*. The end of the muscle which is attached to a relatively fixed and immovable part is called the *origin;* the end which is attached to the part which moves when the muscle contracts is known as the *insertion*. A typical voluntary muscle is made up of three parts: the tendons attached at its ends; the membrane surrounding the muscle, known as the *fascia;* and the belly, or fleshy part, of the muscle.

The different actions performed by the various skeletal muscles give rise to descriptive names applied to them. Some of these are as follows:

Extensor—one that straightens a part, such as extending the foot.
Flexor—one that bends a part, such as a joint.

Adductor—one that draws the limb toward the median ventral line.

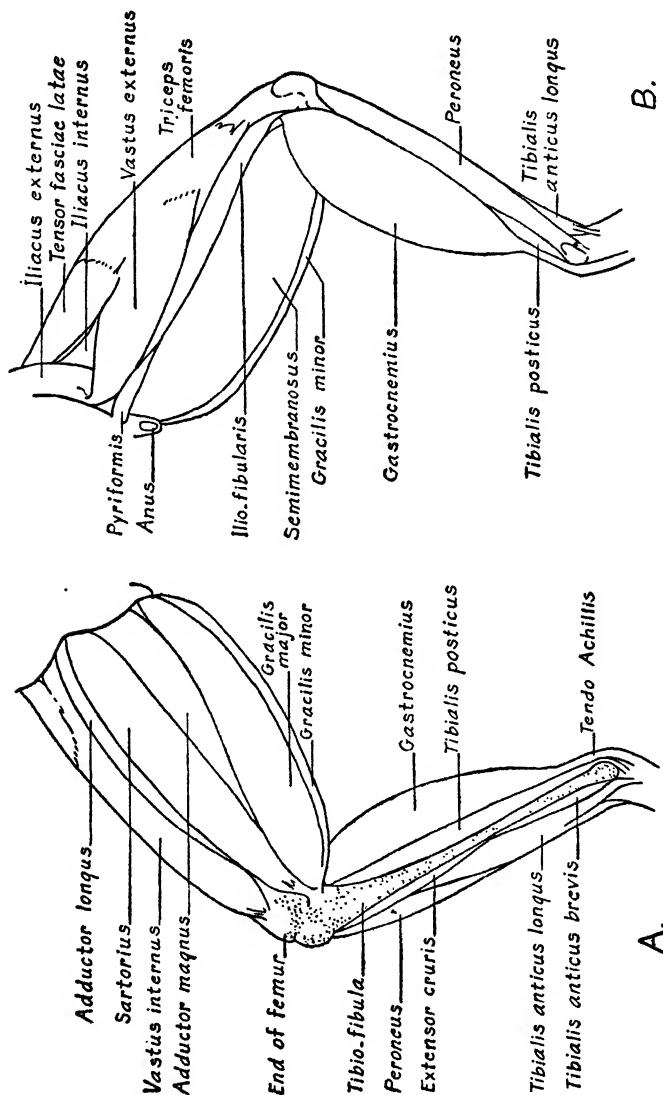Abductor—one that draws the limb away from the median ventral line.

Fig. 29.—Muscles of the hind leg of frog. A, ventral view; B, dorsal view. (Drawn by Ruth M. Sanders.)

Levator—one that raises a part, such as the lower jaw.

Depressor—one that lowers a part, such as the lower jaw.

Rotator—one that rotates one part on another.

The *pectoral muscles* cover the chest and ventral portion of the upper body region; the *rectus abdominis* extends along the median ventral region; the *paired obliquus externus* and *internus* cover most of the sides of the trunk. The muscles of the limbs are numerous. There are some eighteen separate muscles which control various movements of the legs. A detailed description of these and other muscles of the frog would be confusing to the elementary student and therefore is not included.

Nervous System

The three divisions in which the nervous system of the bullfrog may be considered are: (1) central nervous system, (2) peripheral nervous system, and (3) autonomic or sympathetic nervous system.

The central nervous system, so called because it comprises the larger number of nerve centers, consists of the brain and spinal cord. The peripheral nervous system consists of (1) the paired cranial and spinal nerves which connect the brain and spinal cord with other organs of the body and (2) a large number of small nerve centers, *ganglia,* distributed throughout the body. The sympathetic nervous system is a part of the peripheral nervous system. It is made up of a large number of small ganglia, two rows of which form the *sympathetic trunks* on each side of the vertebral column and connect with the spinal nerves. The branches of these sympathetic trunks connect with numerous small ganglia throughout the tissues of the body. This system controls and regulates primarily the involuntary movements of such organs as the heart, digestive tract, glands, and organs of respiration.

Central Nervous System.—The brain is covered with a pigmented membrane known as the *pia mater.* The brain has three main divisions, the *forebrain, midbrain,* and *hindbrain.* The forebrain consists of a pair of elongated cerebral hemispheres, separated from each other by a fissure, and two enlargements at the anterior end of the hemispheres known as the *olfactory lobes.* These lobes are fused on the dorsal side but separated by a groove on the ventral side. Immediately behind the forebrain is the *diencephalon.* On its dorsal surface is a vestige of the *pineal organ* which was more developed in the tadpole. On its ventral surface is the *optic chiasma,* a crossing of the optic nerves formed by fibers from the right and left sides, each crossing to supply the eye of the opposite side. Just behind the optic

chiasma is the infundibulum, and somewhat behind this is the *pituitary body,* or *hypophysis.* The pituitary is of dual origin, developing in part from the diencephalon and in part from the roof of the mouth cavity. The *midbrain* contains two large rounded *optic lobes.* The ventral part of the brain below these lobes is the *crura cerebri.*
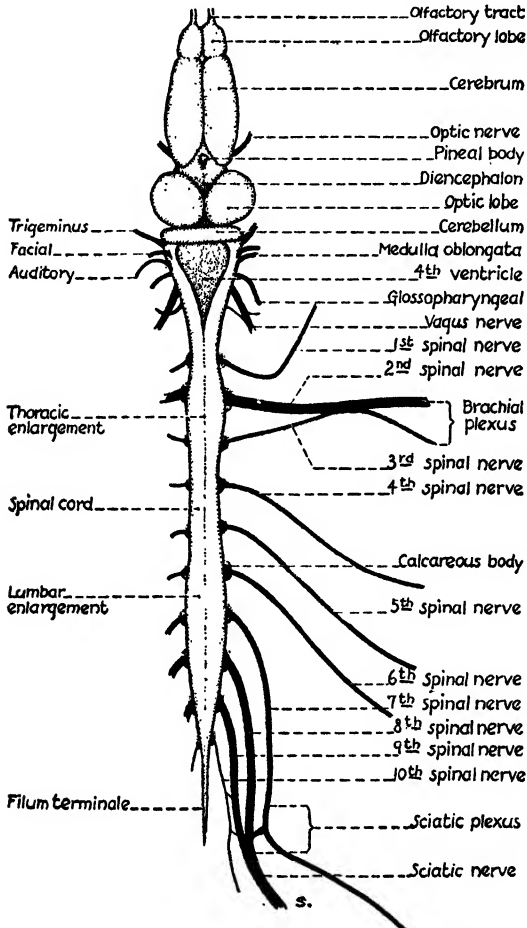

Fig. 30.—Dorsal view of nervous system of a frog.

The *hindbrain* consists of the *cerebellum* and the *medulla oblongata.* The cerebellum in the frog is almost rudimentary and consists of a transverse fold of tissue immediately posterior to the optic lobes. The cerebellum is in close connection with the large triangular

medulla oblongata which constitutes the most posterior part of the brain and is continuous with the spinal cord.

Internal Organization.—The central nervous system is hollow. In the brain the cavities, known as *ventricles,* form a continuous channel for the flow of cerebrospinal fluid. The ventricles are connected one with another by openings known as *foramina.* The cavities are large in four regions: (1) the paired lateral ventricles in the cerebral hemispheres, (2) the single third ventricle in the diencephalon, (3) the paired optic ventricles in the optic lobes, (4) the single large triangular fourth ventricle in the medulla oblongata. Vascular nets of blood vessels called *chorioid plexuses* are found in each of these four regions, and most of the cerebrospinal fluid is derived from the blood vessels of these plexuses.

The *spinal cord* is continuous with the medulla oblongata anteriorly, runs posteriorly through the canal formed by the vertebrae, and finally tapers to a narrow filament which ends within the urostyle. It is covered by two membranes, an outer *dura mater* and an inner *pia mater.* It is somewhat flattened, and a median fissure occurs on both its dorsal and ventral sides. The central part of the cord comprising its bulk is made up of gray matter consisting primarily of nerve cells. In the center of this gray matter is a small hollow canal, the *neurocoele,* which communicates with the ventricles of the brain. Surrounding the gray matter is white matter consisting chiefly of nerve fibers.

Peripheral Nervous System.—The peripheral nervous system is composed of the cranial, spinal, and sympathetic or autonomic nerves, the last of which will be considered separately.

The *cranial nerves* arise from the brain, and there are ten pairs of them in the bullfrog. Counting from the olfactory lobes backward, they are as follows: *olfactory, optic, oculomotor, trochlearis, trigeminus, abducens, facial, auditory, glossopharyngeal,* and the *vagus.* All of these, with the exception of the tenth or vagus nerve, run to parts of the head. The vagus nerves branch to the heart, lungs, and digestive system.

The bullfrog has ten pairs of *spinal nerves.* Each spinal nerve originates in the gray matter in the spinal cord by a *dorsal* and a *ventral* root. These roots pass out of the vertebral column between vertebrae through an opening or *intervertebral foramen* and unite into a nerve trunk, branches of which extend to the muscles and skin

of the body and limbs. The dorsal root is known as the *sensory* or afferent root and has a *ganglion;* the ventral root is known as the efferent or *motor root* and has no ganglion. Where these roots meet after leaving the spinal cord, they are covered on the ventral side by a large calcareous body, the *periganglionic gland,* or "gland of Swammerdam."

The first spinal nerve arises between the first and second vertebrae, the second between the second and third vertebrae, and so on until the tenth, which is small and emerges from the urostyle near its anterior end. These nerves frequently send branches to preceding or succeeding nerves to form plexuses. Two large plexuses in particular are present. Branches from the first and third nerves join with the large second nerve to form the *brachial plexus,* which supplies nerves to the muscles of the forelimbs and shoulder. Nerves number seven, eight, and nine fuse to form the large *sciatic plexus* which supplies the sciatic nerve to the hind leg.

Sympathetic or Autonomic Nervous System.—From the first sympathetic ganglion, nerves are given off which form a *cardiac plexus* on the heart. Another plexus, formed primarily from nerves of the third, fourth, and fifth sympathetic ganglia, is the *solar plexus* on the dorsal surface of the stomach. In addition, numerous ganglia are scattered throughout the tissues of the body, all being connected by sympathetic nerve fibers and finally communicating with the sympathetic trunks.

The Sense Organs

The *olfactory sacs,* or nasal chambers, are located internal to the external nares. The median portion of the nasal chamber is lined with *olfactory epithelium* which contains sense cells possessing protoplasmic processes known as *olfactory hairs* on their free ends. These olfactory hairs are stimulated by chemical substances present in the air and pass the stimuli received through the olfactory cells to the olfactory nerves.

The degree to which the sense of smell is used by amphibians is not known. It is likely, however, that it may cause the frog at times to approach objects and may serve to test the food substances it takes into its mouth.

The *eyes* lie in cavities, or orbits, on the dorsolateral sides of the head. The exposed portion of the eyeball is covered by a transparent membrane, the *cornea,* which is continuous with the opaque connec-

tive tissue sheath covering the remainder of the eyeball and known as the *sclera*. Attached to the sclera are several muscles which move the eye in various directions. The *iris* of the bullfrog is colorful, being either golden or reddish bronze, and is clearly visible through the transparent cornea. In its center is an oval opening, the *pupil*, which can be contracted or expanded by the action of muscle fibers in the iris and, like the shutter of a camera, regulates the amount of light which enters the inner chambers of the eye. The *lens* lies behind the iris and is flattened on its outer surface. It is enclosed in a membrane and held in place by delicate fibers to the *ciliary body*. The space between the cornea and lens is filled with a watery transparent substance, the *aqueous humor*.

The main cavity of the eye back of the lens is filled with a gelatinous tissue, the *vitreous humor*. The walls of this cavity are made up of three layers, the outer sclerotic coat, previously mentioned, then a *vascular pigmented chorioid* and the innermost layer, the *retina*. The anterior portion of the chorioid forms the ciliary body, which subsequently is continuous with the iris.

The retina contains the photosensitive cells of the eye which pass the stimuli received on to the optic nerve. These sensitive cells, known as the rods and cones, lie embedded in the tissue so that light has to pass through several layers of nerve fibers, as well as much supporting tissue, before reaching them. The rods and cones communicate with fine branches of the optic nerve, which enters the eye posteriorly.

The *ear* of the bullfrog is covered externally by a membrane, the *tympanum*. A *Eustachian tube* runs between the middle ear and mouth cavity. The tympanum has attached to it a bony rod, the *columella,* the other end of which is joined to a portion of the inner ear.

The inner ear lies in a cavity of the skull known as the *auditory capsule*. The structures of the inner ear compose a *membranous labyrinth* which is surrounded by a lymphlike fluid, the *perilymph*. The labyrinth is formed of a dorsal utriculus concerned with equilibrium and a ventral *sacculus* functioning as an auditory organ. The utriculus is connected with three semicircular canals which are placed in planes almost at right angles to one another. Two are vertical canals, and the third, on the outer side of the utriculus, is horizontal. The sacculus is irregular, pouchlike, and filled with a fluid, the *endolymph*. It also contains the nerve endings which receive the stimuli and convey them to the auditory nerve.

Sound progresses in the following fashion. The tympanic membrane vibrates to sound waves, and these are transported by the columella to the inner ear. These vibrations are taken up by the endolymph of the sacculus and are received by the nerve endings which lead to the auditory nerves. These nerves convey the impulse to the brain, subsequently giving rise to auditory sensations.

In a similar manner, movements of the endolymph in the utriculus affect sensory cells and cause a reaction associated with a sense of position or equilibration.
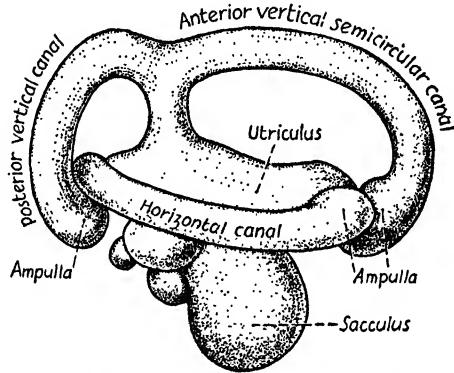
Fig. 31.—The right internal ear of the frog, lateral view.

Reproductive Organs

The ovoid *testes* of the male bullfrog are attached to each kidney by a fold of peritoneum, the *mesorchium*. In this fold, running between the testes and kidneys, are several small ducts, the *vasa efferentia*. These ducts connect with the mesonephric duct through Bidder's canal and the collecting tubules of the kidney. Spermatic fluid containing the spermatozoa passes from the testes through the vasa efferentia into the kidney, then into the mesonephric duct, which opens into the cloaca, and thence to the outside through the anus. In some species, this duct is slightly expanded prior to its opening into the cloaca to form the *seminal vesicle,* a reservoir for spermatozoa. This is poorly developed in the bullfrog.

The two *ovaries* of the female bullfrog, when filled with eggs, occupy a large part of the body cavity and consist of folded sacs covered with peritoneum. They originate in about the same position as do the testes and lie in a fold of the peritoneum, mesovarium, ventral to the kidneys.

The two *oviducts* are greatly convoluted white tubes, one on each side of the body cavity, running from near the base of the lungs to the dorsal wall of the cloaca. Their anterior ends are funnel-shaped *ostia,* and open into the body cavity. Their posterior ends are dilated to form thin-walled *ovisacs* or uteri which open into the cloaca near the entrance of the mesonephric duct. They are not connected at any point with the ovaries.

When the eggs are mature at the breeding season, they break through the walls of the ovary and its peritoneal covering and are free in the body cavity. They make their way to the *ostium* of the oviduct and, probably by ciliary action or movements of the female, are squeezed into it. The oviducts contain a large number of glands which secrete a clear, jellylike material. As the eggs are forced down the oviduct by ciliary action, they become coated with the gelatinous material, which swells enormously when it contacts water.

Fertilization in the bullfrog is external, and the spermatozoa of the male enter the eggs after they have been laid in the water.

Attached to the anterior end of the testes of the male frog and to the ovaries of the female are fingerlike projections known as *fat bodies.* These serve to store a reserve fat supply which the bullfrog may draw on during hibernation or at other times. They are largest before hibernation and smallest after egg laying. Recent experiments have also shown that these fat bodies are essential for allowing the normal development of the sex organs and for maintaining their health. When they are removed, there is a deterioration of eggs and sperm.

Embryology

The bullfrog lays its eggs in a large floating mass, forming a surface film on the water, usually among brush or plants near the pool's edge. This mass may be from 1 to 2½ feet in diameter and may contain ten to twenty thousand eggs. In Texas, bullfrogs may lay their eggs as early as February, though it is more common for them to be laid later in the season.

The eggs of the bullfrog are smaller than those of the leopard frog. They hatch in about four or five days, depending on the temperature. After hatching, the tadpole normally spends about two years in the water before transforming as a young bullfrog. The tadpole may grow to be four to six inches long, but the average body length of the young bullfrog as it metamorphoses is about

1¾ to 2 inches. It usually takes about three to four years for this young frog to attain maturity and begin egg laying.

The embryology of the bullfrog does not differ materially from that of the leopard frog, and the following account is based, except where otherwise noted, upon the development of the latter.

The egg when laid is a single cell. The upper portion of the egg has considerable pigmentation, making it black. This part of the egg is known as the animal hemisphere, and it is thought that
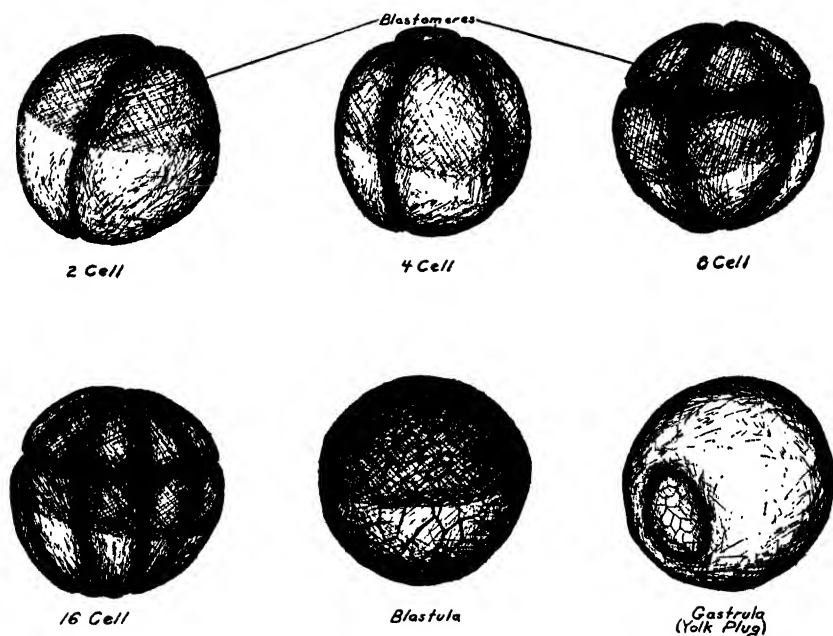
Fig. 32.—Diagrams of early cleavage stages, blastula and gastrula of the frog. This is holoblastic, unequal type of cleavage. The upper, shaded portion of each of the first five diagrams represents the *animal hemisphere*, and the lower portion of each, the *vegetal* hemisphere. The circular plug seen in the gastrula stage is the yolk plug.

the pigmentation serves to absorb and retain heat necessary for development. The lower portion is white and is known as the vegetal hemisphere. The bullfrog egg is surrounded by a layer of transparent jelly, but does not have an inner envelope of jelly, as does the leopard frog egg. This jelly protects the egg and helps it to retain heat. The nucleus of the egg, or germinal vesicle, lies near the animal pole. The boundary of the egg is known as the *vitelline membrane*.

The eggs are fertilized externally by the male, who is clasping the female as the eggs are laid and discharges *spermatozoa* into the water. The first spermatozoon to swim to the egg and enter it by piercing the vitelline membrane initiates fertilization. After the sperm has entered, a *fertilization membrane* is formed which prevents the entrance of additional spermatozoa. Only the head of the spermatozoon enters, the remainder being discarded. This head, which is composed primarily of the male spermatozoan nucleus, fuses with the nucleus of the egg to complete fertilization and start development.
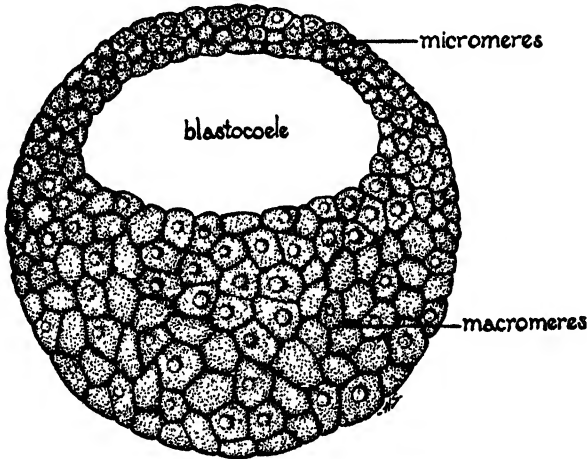
FROG EGG, CROSS SECTION OF BLASTULA

Fig. 33.—Section through blastula stage of developing frog. (Courtesy of General Biological Supply House.)

Development begins with cleavage, which is a series of mitotic divisions. Cleavage results in the rearrangement of nuclear material in relation to the cytoplasm. The furrow made by cleavage cuts through the entire egg, and such cleavage is known as total, or holoblastic.

Cleavage and Blastula Formation.—The first and second divisions run from pole to pole at right angles to each other and divide the egg into four equal *blastomeres*. The third cleavage is parallel to the equator of the egg and somewhat above it. This produces four cells at the animal pole that are smaller than the four cells at the vegetal pole. Subsequently the cells at the animal pole *(micromeres)* divide more rapidly than the cells at the vegetal pole, for they contain less yolk. Such cleavage is known as unequal, and as divisions

proceed the cells at the animal pole become smaller and more numerous than those at the other pole. The final result of the following divisions is to form a hollow sphere, the *blastula,* whose cavity is known as the *blastocoele.* The blastula is essentially one cell layer thick, although in reality some cells have been crowded from the surface, giving the appearance of additional layers.*
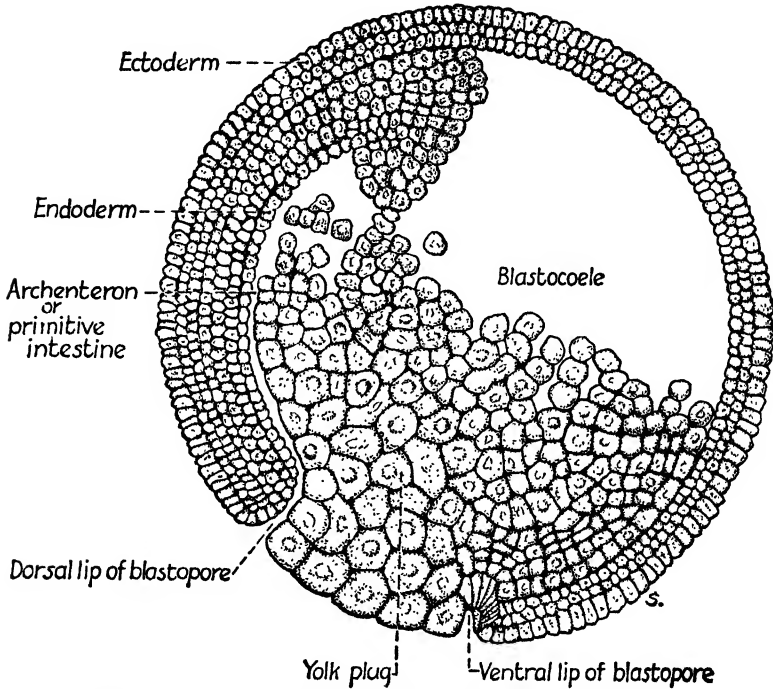
Fig. 34.—Section through gastrula stage of developing frog.

Gastrulation.—Gastrulation begins with the appearance of a small groove slightly below the equator of the egg. The upper edge of this groove is known as the *dorsal lip of the blastopore.* Coincident with the appearance of this groove, the pigmented animal cells begin to grow down over the white vegetal, or yolk, cells; and the dorsal lip moves downward as the line advances. It also extends its edges in a *crescent shape* laterally around the egg until they finally meet to form a circle. The area enclosed by this circle shrinks as the cells grow down from all sides and its rim moves downward. Cells on the side where the groove began advance more rapidly than the others;

and the rim on this side, or the dorsal lip, is forced down to the vegetal pole and a little beyond on the other side before gastrulation is complete. The area enclosed by the circle or blastopore is finally very small, and the white vegetal cells which fill it are called the *yolk plug.*

While the animal cells have been advancing and covering the vegetal cells, changes have been going on within the egg. The appearance of the groove or dorsal lip of the blastopore was caused by an infolding or *invagination* of outside cells. This invagination progresses around the egg as the crescent groove extends itself. The cells which consequently come to lie inside are known as *endodermal cells,* those on the outside as *ectodermal cells.*

Section through otic pit

otic pit

ectoderm
neural tube
mesoderm
notochord
hypochord
somatic mesoderm
splanchnic mesoderm
midgut
foregut
yolk

Section through mid-gut

FROG EMBRYO, SHOWING MESODERM FOLDS
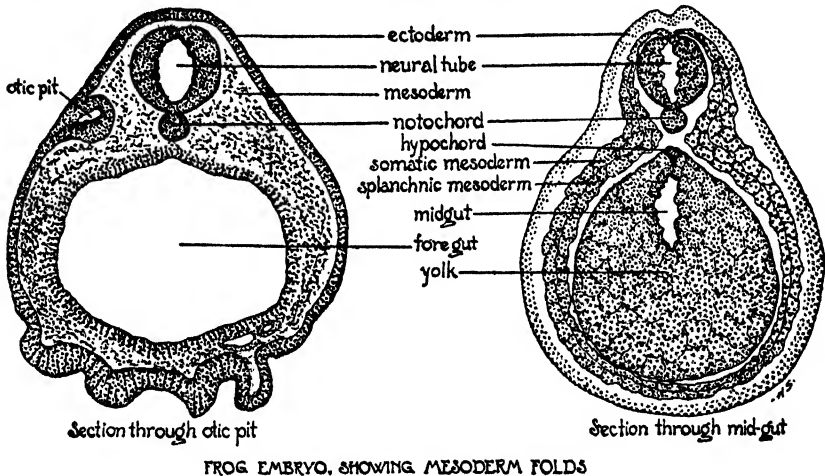
Fig. 35.—Sections through two levels of the neural tube stage of the developing frog. (Courtesy of General Biological Supply House.)

By this invagination a cavity known as the *archenteron* is formed, the walls of which are made up of the invaginated endoderm cells. At first it is quite flat, but it expands as invagination and the other processes of gastrulation proceed, and soon it takes up the space formerly occupied by the cleavage cavity or blastocoele. Its posterior end is the blastopore, and this, as previously mentioned, is plugged with yolk or vegetal cells known as the yolk plug. As a final result, the gastrula forms a two-layered embryo of ectoderm and endoderm cells, each layer of which may be several cells thick.

Mesoderm Formation.—Before the process of gastrulation is completed, a sheet of cells forms between the ectoderm and endoderm

cells. This sheet of cells is known as mesoderm. As the mesoderm grows it splits into two sheets, an outer, or *somatic layer,* which lies next to the ectoderm of the embryo wall, and an inner, or *splanchnic layer,* which lies next to the endoderm cells of the archenteron. The cavity formed between these two layers is the beginning of the *coelom,* or body cavity. From these three layers, ectoderm, endoderm, and mesoderm, all the body structures are formed.

Formation of Nervous System.—With the reduction of the blastopore to a very small area, there appears on the dorsal side of the embryo a thickened plate of ectoderm known as the *neural plate.* This plate soon is flanked on each side and in front by ridges known as *neural folds.* As these folds arise, the remainder of the plate forms a groove known as the *neural groove.* The neural folds or lateral edges of the plate curl in and meet in the dorsal midline, where they fuse to form the *neural tube.* The neural plate is wider at its anterior end than it is nearer the blastopore, and at this expanded anterior end the brain arises, while the remainder becomes the spinal cord.

During these changes, the egg, which previously was spherical, has elongated in the axis of the neural tube. The blastopore has been covered by the folding of edges of the neural groove extending to its borders. Subsequently the embryo takes on form so that definite body regions can be identified.

Later Development.—In the head region appears an elevated side plate, the *gill plate,* where later the gills develop. Anterior to this, a swelling on each side of the head denotes the beginning of certain sense organs. A depression on the anterior ventral surface is a forerunner of the mouth, and posterior to this a crescent-shaped area indicates the beginning of a *ventral sucker* by which the newly hatched larva may attach itself to objects. At the posterior end of the body a *tail bud* appears, and the region of the blastopore becomes the anus. The embryo soon hatches, branched *external gills* which serve as respiratory organs make their appearance, and definite sense organs can be found on the head. This is the *external gill stage.* The intestine becomes coiled; the tail elongates; and muscle segments, or *myotomes,* can be seen along the sides of the body. Shortly after hatching, the external gills are absorbed and internal gills take their place. A fold of skin, the *operculum,* develops over this region. There remains on the left side, however, a small opening, the *spiracle,* through which water may pass out after coming into the mouth over

the internal gills. The skeleton is cartilaginous; lateral line sense organs are present on the sides; the pineal organ is evident; and the animal is similar to a fish.

The tadpoles feed primarily on plant substances. In the mouth of the bullfrog tadpole is one row of teeth above and three rows below, plus a border of projections, known as *papillae,* for testing food substances. Between the lips is a *horny beak* somewhat like that of a bird's with which the tadpole can scrape thin pieces from leaves of aquatic plants, or algae and other plant material from sticks and stones.

Near the end of the larval period (about two years in the bullfrog), which varies considerably with species and environment, the tadpole prepares to metamorphose into a frog. First the hind legs push through the skin at the base of the tail; then the forelegs appear, forcing their way through the operculum on the right and the spiracle on the left side. As the lungs develop, the tadpole has to come to the surface of the water frequently to give out a bubble of impure air and take in a purer one. The tail is gradually absorbed, the intestines shorten, the horny beak disappears, the mouth widens, the gills are resorbed, the legs develop, and the tadpole becomes a frog.

In general, it may be stated that the ectoderm gives rise to the nervous structures, the epidermis and its outgrowths. The endoderm forms the epithelial lining of the intestine, and outgrowths of the intestine, such as the epithelial lining of gills, lungs, liver, pancreas, gall bladder, urinary bladder, etc. From the mesoderm are formed the muscular, vascular, and skeletal systems. Most of the organs are formed not from a single germ layer but from a combination of these tissues. The elementary tissues have been discussed in the chapter on *Metazoan Organization.*

Economic Importance of Amphibia

The entire group of Amphibia is of considerable economic value because they feed to such a large extent on insects, thus becoming valuable aids to the farmer in controlling noxious insects. In the flooded rice fields of Louisiana, bullfrogs grow fat eating insects, crayfish, and other small animals.

Frogs are used throughout the world as an article of food by man as well as by other animals. In the eastern United States, large quantities of the leopard frog and wood frog are consumed.

In the southern states, bullfrog legs have been a favorite food for years. Within recent years businesses have developed which are devoted to supplying bullfrog legs, and the demands for these from all parts of the country have been so great that it may become necessary to afford some protection to prevent the rapid depletion of these animals. Attempts have been made to operate frog farms and raise a supply. Most of these attempts have been failures because of the high overhead cost. The axolotl is used in Mexico as food; and water dogs, such as our Necturus, are reputed to have a good flavor.

Dried frogs and toads have been used in China both as a source of food and for medicinal purposes. It is reported that toad skins have been used in Japan and elsewhere for making a fine type of leather. Dried salamanders have been used as a vermifuge. Adult frogs and salamanders, as well as larval stages, are widely used as laboratory animals.

Classification of Amphibia

There are estimated to be about 1,900 known species of living frogs, toads, and salamanders in the world, and about 60 species of caecilians. None of the caecilians have been reported from the United States. In the United States there occur about 70 species
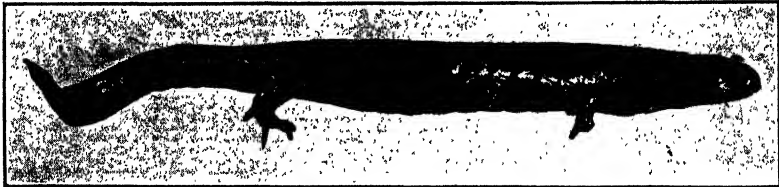

Fig. 36.—*Ambystoma texanum*, a very common salamander in Texas. (Photograph by Ottys Sanders.)

of salamanders and about 67 species of frogs and toads. Many of these species are subdivided into several subspecies. The Southwest contains a large proportion of all of these, and Texas has within its boundaries more species of toads than does any other state in the Union.

Some characters used in classifying salamanders are: the presence or absence of gills, either external or internal; color markings; shape and appearance of body; length; number of costal grooves;

number of digits; position of teeth; presence or absence of a naso-labial groove; plantar tubercles; shape of vertebrae; form of cranial bones and cartilages; presence or absence of lungs; presence or absence of ypsiloid cartilage; and other factors.

Some characters used in classifying adult frogs and toads are: color markings; length of body and of hind limb; shape of head; nature of skin; presence or absence of parotoid glands and their shape; presence or absence of tympanum; presence or absence of cranial crests and their shape; presence or absence of teeth and their situation; the shape of the vertebrae; shape of the sacrum and pectoral girdle; shape of pupil of the eye; presence or absence of adhesive discs at the ends of digits; and other characters.

The student interested in classification and identification of species should consult appropriate keys for the various groups of Amphibia.

A List of Families of the Amphibia in the United States

The ranges cited below are not exact but give an idea of the distribution of the genera.

Order Caudata (Tailed Amphibians)

Suborder Cryptobranchoidea

Family Cryptobranchidae
> *Cryptobranchus alleganiensis* (1 species). This so-called "hellbender" ranges from the eastern states west to Iowa, south to Louisiana.

Suborder Ambystomoidea

Family Ambystomidae
> *Ambystoma* (about 12 species). Common species in the Southwest are: the Tiger salamander *(A. tigrinum)*; the Texan salamander *(A. texanum)*; and the Marbled salamander *(A. opacum)*.
> *Dicamptodon ensatus* (1 species). Washington to Southern California.
> *Rhyacotriton olympicus* (1 species). Olympic Mountains, Wash.

Suborder Salamandroidea

Family Salamandridae
> *Triturus* (about 3 species in the United States). The common newt of the Southwest is *Triturus viridescens louisianensis*. The other species represented is *T. meridionalis*.

Family Amphiumidae
> *Amphiuma* (2 species). *A. tridactylum,* the three-toed congo eel, ranges from northern Florida to eastern Texas.

Family Plethodontidae
> *Gyrinophilus porphyriticus* (1 species). Eastern states west to Kentucky, south to Georgia.

Pseudotriton (2 species). Pennsylvania to Louisiana.

Eurycea (7 species). Range from New England to Texas. *E. quadridigitata,* the dwarf salamander, has only four toes.

Stereochilus marginatus (1 species). Dismal Swamp, Virginia to Georgia.

Typhlotriton spelaeus (1 species). The blind salamander of the caves of Missouri and Arkansas.

Typhlomolge rathbuni (1 species). The blind cave salamander of Texas.

Leurognathus marmorata (1 species). North Carolina mountains.

Desmognathus (5 species). Southern Canada to the Gulf of Mexico, eastern states westward to Illinois. Most common species in Southwest is *D. brimleyorum,* Brimley's triton.

Plethodon (11 species). Distributed over almost the entire United States. Common in the Southwest is *P. glutinosus,* the slimy salamander.

Hemidactylium scutatum (1 species). Canada to Louisiana. Another four-toed salamander.

Batrachoseps (2 species). The worm salamander. Both species on the Pacific.

Ensatina (3 species). All on the Pacific Coast.

Aneides (4 species). On Pacific Coast and in southeastern states.

Hydromantes platycephala (1 species). Yosemite salamander.

Suborder *Proteida*

Family Proteidae (with external gills and 2 pairs of limbs)

Necturus. According to a recent revision of the genus by Mr. Percy Viosca, of New Orleans, describing two new species from Alabama and one new species from Louisiana, the number of species in the U. S. is increased from three to six. The common large Necturus from the Great Lakes region is *N. maculosus;* the species which seems to be the most common in southern states is *N. beyeri* Viosca.

Suborder *Meantes*

Family Sirenidae (with external gills, without hind limbs)

Siren (2 species). Eastern Virginia to Texas. Both *S. lacertina* and *S. intermedia* are found in the Southwest.

Pseudobranchus striatus (1 species). South Carolina to Florida.

Order Salientia (Tailless Amphibians)

Suborder *Amphicoela*

Family Liopelmidae

Ascaphus truei (1 species). Washington and a few other points on the Pacific Coast.

Suborder *Anomocoela*

Family Pelobatidae (Spadefoots)

Scaphiopus (3 species). One species in the East; all three species in the Southwest. These are the spadefoot toads, the pupils of whose eyes are vertical when in daylight.

Suborder Procoela

   Family Bufonidae (Toads)

      Bufo (16 species). Species of Bufo are distributed over the entire United States. Among common species in the Southwest are *B. cognatus, B. compactilis, B. debilis, B. fowleri, B. punctatus, B. valliceps,* and *B. woodhousii.*

   Family Leptodactylidae (Robber Frogs)

      Leptodactylus albilabris (1 species). Found only in Texas.

      Eleutherodactylus (3 species). One species in Texas (Texas cliff frog), one species in Arizona, one species in Florida.

      Syrrhophus (2 species). Both species limited to Texas.

   Family Hylidae (Tree Frogs)

      Acris gryllus (1 species). The cricket frog, widespread throughout eastern and central United States, including the Southwest.

      Pseudacris (5 species). Throughout the same regions as *Acris.* Various subspecies of the swamp cricket frog *(P. nigrita)* are common in the Southwest. The recently described *P. streckeri* Wright, ranging through Texas and Oklahoma to Mississippi, is a very colorful species, and its high-pitched staccato chirp is one of the earliest to be heard at breeding pools in Texas.

      Hyla (14 species). Various species in all of the United States. They are the most colorful of all the frogs. Common species in the Southwest include: *H. arenicolor, H. cinerea, H. crucifer, H. squirella, H. versicolor.*

Suborder Diplasiocoela

   Family Ranidae (True Frogs)

      Rana (18 species). Various species occur in all parts of the United States. Common species in the Southwest are: *R. sphenocephala, R. pipiens, R. catesbeiana, R. clamitans.*

   Family Brevicipitidae (Narrow-mouthed Toads)

      Hypopachus cuneus (1 species). In southern Texas.

      Microhyla (2 species). Ranges from Virginia to Texas, northward to Missouri and Indiana.

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CHAPTER VI

THE RAT, A REPRESENTATIVE MAMMAL

This animal is regarded with disdain usually because of the damage and destruction it does, but it is a very valuable mammal for study because of its availability and convenient size. Its structures and metabolic activities are similar to those of the larger mammals including the human being. The most common example in this country is the brown or Norway rat, of which the white or albino is ordinarily a variety.

The classification of the brown rat in the animal kingdom may well be summarized at this point. It of course belongs to the phylum *Chordata,* subphylum *Vertebrata,* class *Mammalia,* subclass *Eutheria,* order *Rodentia,* family *Muridae,* genus *Rattus,* and species *norvegicus.* The scientific name therefore is *Rattus norvegicus.* Its albino variety is *Rattus norvegicus albinus.* The black rat, which is less abundant, is named *Rattus rattus.* Another rat which is very common in some localities of the southern United States is the long-tailed *Rattus alexandrinus.* The home of the brown rat is thought to have been in Northern Asia originally. In the wild form the color is brown above and gray beneath, but many color varieties have developed to include gray, yellow, and albino. The most conspicuous characteristic distinguishing the brown (Norway) rat from the black rat or the roof rat is the shorter tail of the former. Its tail is shorter than the body while in the other two the tail is as long as the body or longer.

Habitat and Habits

The rat is secretive in its abode, living most commonly in woodpiles, trash, stacks of hay or straw, under the floors, and in the walls of buildings, attics, and basements. Nests are built of available material such as cloth, paper, shavings, twine, grass, and fibers. A warm temperate climate where there is an abundance of available food and nest-building material furnishes the ideal habitat. Rats are largely nocturnal in their habits and quite shy in their activities. They are capable of gnawing their way through wooden partitions and even lead sewer pipes. Rats are capable of an independent life, but they flourish when associated with the haunts of man because

of the abundance of available food and shelter. Natural enemies of the rat are dogs, cats, coyotes, foxes, minks, weasels, skunks, owls, hawks, king snakes, black snakes, and bull snakes.

External Structure of the Rat

The rat is a quadruped and is quite well adapted for climbing as well as for walking. The body, with the exception of the tail, is covered with thick fine fur mixed with stiff hairs. The heavy hairs or "feelers" about the face are called *vibrissae*. Those around the mouth are known as buccal vibrissae and. are divided into two groups: the *mystacial* in several rows above the upper lip in front of the eye, and the *submental* group on the chin. Above the eye is the *superciliary* group and the single bristle on each side of the face below the outer corner of the eye is a *genal* vibrissa. The *interramal* group is a tuft in the ventral midline between the angles of the jaws. All of these bristles are very sensitive to touch and are of great use to an animal whose habits are primarily nocturnal.

The body of the rat may be divided into four regions: head, neck, trunk, and tail. In addition, there are the two pairs of appendages.

The head is rather pointed at the anterior end, and located terminally are the two nostrils, each shaped like an inverted comma and capable of being closed in case the animal goes under water.

The naked skin around the nostrils is very sensitive to touch. The *mouth* is located in a subterminal position. There is a cleft in the upper lip which exposes the incisor teeth, even when the mouth is closed. The two sides of the cleft extend inward toward the midline behind the upper incisors almost to meet each other and practically exclude these teeth from the buccal cavity proper. In the hare this cleft in the upper lip is very prominent, and it is from this that the abnormally cleft lip in man has come to be known as "harelip." The *eyes* of the rat are small with relatively large pupils. They are well set in the lateral orbits and protected by upper and lower eyelids. There is a nictitating membrane, supported by a semilunar cartilage, in the medial corner of the eye. The eyelashes are fine and short. The eyeballs are kept moist by secretions from Harderian and lacrimal glands, spread over their surfaces by winking. The *ears* are located well posterior on the head. The *pinna* which is the conspicuous part of the external ear is large, erect, and supported

in part by cartilage. It is nearly devoid of hair. At the base of this is an ear opening, the *external auditory meatus,* which leads to the interior of the skull and to the *tympanic membrane.* The head region is well supplied with the endings of all the five principal senses: sight, hearing, smell, touch, and taste.

The trunk is the large portion of the body posterior to the head. The relatively short *cervical region,* or neck, joins the head and trunk. Behind the cervical region is found the chest or *thoracic* region and following this is the *abdominal* region. The latter may be divided into the *lumbar* region (small of the back) and *sacral* or hip region. Continuing posteriorly from the trunk is the tail or *caudal* region. Attached to the sides of the trunk are the two pairs of limbs or *appendages.* The fore limbs or arms are composed of the following parts in order: upper arm or *brachium,* forearm or *antebrachium,* wrist or *carpus,* and hand or *manus* with its fingers or *digits.* There are four well-developed digits and a vestigial thumb. Beginning at the body each hind limb consists of *thigh, shank, ankle* (tarsus), and *foot* (pes) with its plantar region (sole) and five digits (toes). There are claws on the digits of both fore and hind limbs. Since the rat walks with the soles and palms of the feet in contact with the ground, it is said to be *plantigrade* in its gait. Animals like cats and dogs which walk with only the lower sides of the digits on the ground are digitigrade while animals like horses and cattle which walk on the tips of the digits are unguligrade.

Along the ventral side of the abdomen are five pairs of *nipples* or *teats* in the albino and six pairs in the Norway rat. In the *perineal* region, just beneath the base of the tail is located the *anus* or opening through which the fecal matter is discharged from the digestive tract. Situated also in the perineal region are the external genital organs. In the male the *scrotum* is the conspicuous swelling ventral to the anus. The two *testes* (sex glands) are usually held inside the scrotum, but sometimes they lie up in the body cavity instead, in which case they are poorly developed and much reduced. The external opening of the male urogenital system is in the midventral line near the anterior end of the scrotum. The *prepuce* (foreskin), which is hairy externally, forms the aperture and surrounds the distal end or *glans* of the *penis.* The latter is withdrawn. In the perineal region of the female there are three openings: the *anus,* ventral to the base of the tail; the *vaginal orifice* (exit from female

reproductive organs) just ventral to the anus, and below this is the smaller opening from the excretory system at the distal end of a prominent elevation or papilla.

Skeleton

Characteristic of verebrates the skeleton of the rat is principally an *endoskeleton* which is completely enclosed by the soft parts. It is composed of 223 bones (exclusive of the teeth, chevron bones and sesamoid bones) and a number of cartilages. There are present both *cartilage bones,* which are preformed in cartilage and then replaced by bone, and *membrane bones,* which are formations of bone in the dermis in certain portions of the skin. *Chevron bones* are paired and extend ventrally from the anterior ends of several of the caudal or tail vertebrae. The sesamoid bones are pieces of bone formed in the tendons. The kneecap is a good example of these.

The principal functions of the skeleton are to support the body, give it form, furnish a sturdy attachment for voluntary muscles, and to protect internal organs. The bones performing the latter function are usually flattened while those which serve for attachment primarily are long, somewhat cylindrical, and are joined by movable joints.

It is customary to divide the skeleton of higher vertebrates into *axial* skeleton and *appendicular* skeleton for convenience in study. The axial portion extends in the main axis of the body and consists of the skull, vertebral column, ribs, and sternum. The appendicular portion includes the bones of the fore and hind limbs as well as the pectoral and pelvic girdles which support them.

The skull is rather conical in shape and somewhat elongated. It is composed of the cranium, which encases the brain, the jaw structures, and the hyoid. For the most part these bones are joined to each other by immovable joints or *sutures* which are usually marked by a line of fusion. There are forty-two bones included in the skull. The dorsal portion or roof of the cranium includes the paired *frontal* bones, paired *parietals,* and the *interparietal.* The lateral walls are composed of the *tympanic* and *squamosal* portions of the *temporal, alisphenoid, orbitosphenoid,* and the lateral portions of the frontals and parietals. The floor is formed by the *basioccipital, basisphenoid,* and *presphenoid* in order from posterior to anterior. The posterior
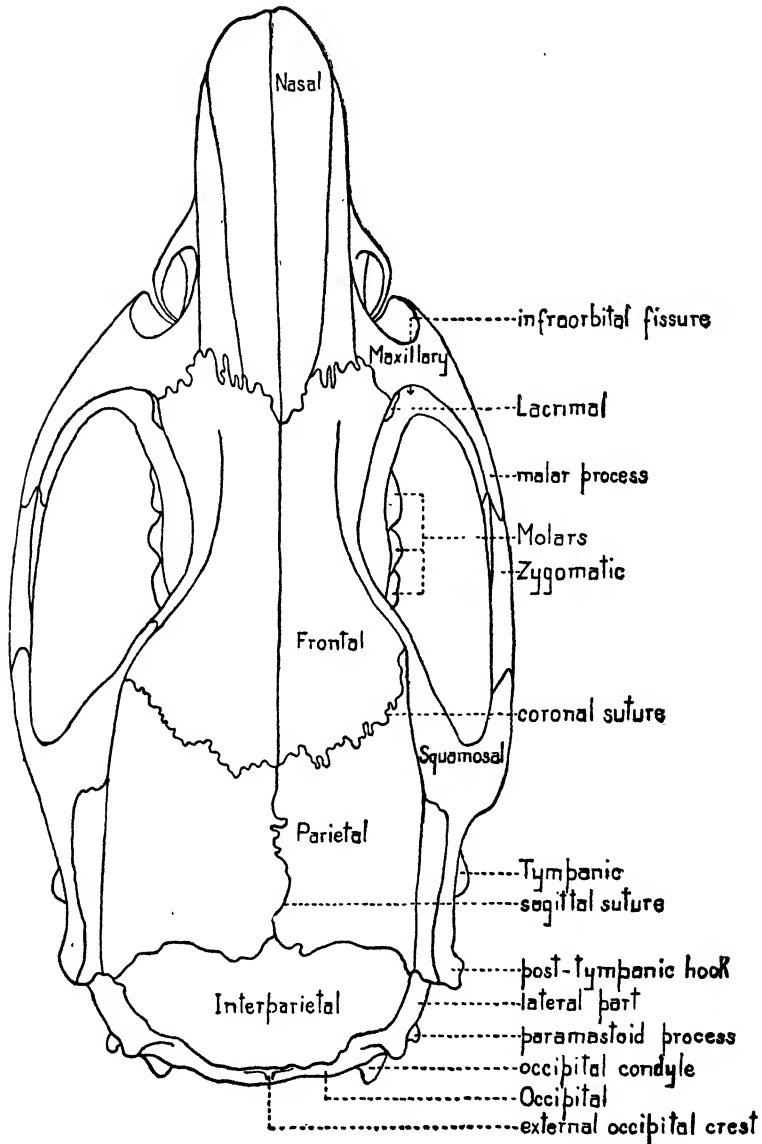
Fig. 37.—Skull of the rat, dorsal aspect. (From Greene, *Anatomy of the Rat*, Transactions of the American Philosophical Society, New Series, Vol. XXVII, 1935.)

end of the skull is composed of the *exoccipitals* lateral to the foramen magnum (opening), *supraoccipital* dorsal to it, and the basioccipital ventrally.

The face is composed of the *nasals,* located just anterior to the frontals, the bones of the jaws, and the zygomatic arches or cheek-bones. The upper jaw is formed by the two anterior *premaxillae,* and the two longer *maxillae.* The palatine processes of the maxillae and premaxillae fuse with the *palatine* bone to form the hard palate or roof of the mouth. The skeleton of the nasal chamber is formed by the *vomers* and palatines as a floor, *ethmoids* as walls, and nasals as the roof. The zygomatic arches are composed of the zygomatic processes of the maxillae anteriorly, the *malar* or *jugal* bone, and the zygomatic processes of the *temporal* (squamosal) bones. The lower jaw is composed of the two *dentary* bones which meet at the anterior midline in the mandibular symphysis. The hyoid bone is U-shaped and lies at the base of the tongue just anterior to the larynx or voice box.

In addition to the nasal capsule (chamber) mentioned above, there are the optic capsule or orbit and the auditory capsule. The orbit is formed by the frontal bone, the *lacrimal,* orbitosphenoid, alisphenoid, and the zygomatic arch. The auditory capsule is enclosed in the tympanic bulla, a part of the temporal bone.

The rat has only the *permanent* set of teeth, and does not have these preceded by the milk or deciduous teeth found in many other mammals. There are sixteen teeth in all, including a pair of *incisors* and three pairs of *molars* in the upper jaw and the same number in the lower. The incisors, located at the front, are long and chisel-like. The lower pair protrudes farther into the mouth cavity than the upper pair. The upper incisors incline slightly posteriorly. On the jaws just behind the incisors is a toothless space, which is known as the *diastema.* The molars are broad and cusped for grinding the food gnawed free by the incisors. The number and location of teeth in an animal's mouth are often given in a *dental formula* which shows the teeth of either the right or left half of the mouth. The formula for the adult rat would be: incisors 1/1, molars 3/3 (1/1, 0/0, 0/0, 3/3). This is a marked modification for the mammals. The dental formula for the cat is: incisors 3/3, canines 1/1, premolars 3/2, molars 1/1. For the hog it is: incisors 3/3, canines 1/1, premolars 4/4, molars 3/3 which is the

typical complete dentition for mammals. This formula for the sheep is 0/3, 0/1, 3/3, 3/3; for the horse: 3/3, 1/1, 3 or 4/3, 3/3; for rabbit: 2/1, 0/0, 3/2, 3/3, and for man 2/2, 1/1, 2/2, 3/3. The teeth of mammals are set in sockets or *alveoli* in the jaws, a condition known as *thecodont,* and since there are different kinds in the same mouth they are also *heterodont.*

The skull serves primarily as a protection for the brain and the special sense organs of the head and furnishes a means of securing and masticating food material. Numerous muscles are attached to the external surfaces of its bones.

The *vertebral column* or backbone is a series of bones, the *vertebrae,* extending from the skull through the axis of the trunk and tail. This column is divided into five regions or groups of vertebrae: seven *cervical* in the neck, thirteen *thoracic* in the chest; six *lumbar* in the small of the back or loin region; four in the *sacral* or pelvic region; and twenty-seven to thirty in the *caudal* or tail region. Each vertebra articulates with the adjacent one but is separated from it by intervertebral discs of cartilage. *Intervertebral ligaments* serve to connect the adjacent vertebrae. The vertebral column supports the ribs and pelvic girdle as well as serves for attachment of numerous muscles.

The typical parts of the typical vertebra are the solid, rather cylindrical, ventral body or *centrum;* the *neural arch* at the dorsum over the *central canal;* the *neural spine* or *spinous process* projecting dorsally from the arch; the *transverse processes,* one extending laterally on each side; *zygapophyses* or *articular processes,* a pair projecting anteriorly and a pair posteriorly from the arch to articulate with adjacent vertebrae. The two most anterior cervical vertebrae, the atlas and axis, are highly modified. The *atlas* is a heavy ring of bone with a distinct ventral process; broad, flat transverse processes; a large spinous process; and anterior articular processes, articulating with the occipital condyles of the skull, and posterior zygapophyses articulating with the axis just behind. The *axis* has a broad, flat centrum, reduced transverse and ventral processes, and a large neural spine. The caudal vertebrae are modified by presence of ventral *chevron* bones on the anterior ones and almost complete loss of processes as well as reduction of size in the posterior ones.

There are thirteen pairs of ribs which articulate with the thirteen thoracic vertebrae. The anterior seven pairs are the *true ribs,* for

they are attached to the sternum by costal cartilages. The other six pairs are *false ribs* because their costal cartilages do not join the sternum. The eighth, ninth, and tenth pairs attach to the posterior border of the seventh rib and by cartilage to the sternum. The three posterior are free at the ventral ends and are known as *floating ribs*. The *sternum* or breastbone consists of seven segments called *sternebrae*, which join each other end to end. The most anterior one is known as the *manubrium* and the seventh one, which terminates in a rounded plate of cartilage, is the *xiphoid process*.

The *appendicular skeleton*, consisting of the two girdles and pairs of limbs, is quite well developed. The pectoral girdle is composed of the shoulder blade or *scapula* which is a dorsally located, broad, flat, more or less triangular bone, and the collar bone or *clavicle*, which is a slender, double-curved rod of bone extending from the acromion process on the apex of the scapula to the manubrium of the sternum. At the level of the junction of the clavicle and scapula a socket is formed for articulation with the bone of the upper arm. This is the *glenoid fossa*. The bone of the upper arm is the *humerus*. On its proximal head portion are the *greater* and *lesser tuberosities* which are muscle attachments. The *shaft* is nearly cylindrical except in the proximal portion where it is flattened to form the prominent *deltoid* ridge on its anterior surface. The distal end is formed by a medial head, the *trochlea*, and a lateral head, the *capitulum*. The two bones of the forearm are the *radius* on the thumb side and the *ulna*, parallel to it, on the opposite side. The radius articulates with the capitulum of the humerus, and the ulna articulates with the trochlea. The ulna is the larger and longer of the two bones. Its projection beyond the articulation with the humerus forms the elbow or *olecranon* process, and its projection at the articulation with the wrist forms the *styloid* process. The radius is slender and shorter. Its articulation with the capitulum forms a pivot and allows some rotation of the forearm at the elbow. The hand is composed of the nine *carpals* of the wrist, arranged in two series; the five *metacarpals* of the palm (the first is small); and the *phalanges* with three in each digit except the thumb which has only two. The claw or nail is borne on the terminal phalanx.

The *pelvic girdle* supports the hind limbs. This girdle is composed of three pairs of bones. The three bones of each side are very

closely fused together to form the *innominate* bone. The three bones here are the long, anterior *ilium*, the ventral *pubis*, and the posterior *ischium*. The socket into which the bone of the thigh fits is located on the side of the innominate at the position where the three bones unite. This socket is the *acetabulum*. Ventrally the two pubic bones meet and fuse in the pubic symphysis. The bone of the thigh is the *femur*, and it extends from the acetabulum, into which its head articulates, to the knee. Besides the head at the proximal end there are the greater and lesser *trochanters*. At the distal end the femur is divided into medial and lateral *condyles* which articulate with the bones of the shank. The small *patella* is the kneecap. The *tibia*, the large bone of the shank, extends to the ankle. The slender arched bone is the *fibula*, which articulates proximally with the lateral tuberosity of the tibia and returns distally to fuse into the side of the tibia. The ankle is composed of eight *tarsals* arranged in two rows. The large bone of the proximal row is the *calcaneum* or heel. The arch of the foot is supported by the five metatarsals, and the bones of the digits (toes) are also phalanges. There are three in each except the first toe, which has only two.

The Muscular System

Myology is the term applied to the study of muscles. The fundamental property of contractility in protoplasm is highly specialized in muscular tissue. The function of muscular tissue, to produce movement, is accomplished by shortening the muscle cells and later relaxing them. Those muscles which are contracted under control of the will are *voluntary*, and the others are involuntary. Most of the skeletal (attached to the skeleton) muscles are voluntary, and the *visceral* muscles of the internal organs are involuntary in their action. The voluntary, skeletal muscles are the ones considered in this chapter. This group functions primarily in locomotion. For the most part each skeletal muscle is attached by one or both ends to the periosteum (membranous covering) of bone, usually by *tendons*. The *origin* of a skeletal muscle is the point of attachment on a fixed bone or other part, which does not move as a result of the contraction of the muscle. The end of the muscle attached to the bone that moves when the muscle contracts is the *insertion*. According to function, muscles are classified as flexors, extensors, protractors,

supinators, levators, depressors, sphincters, dilators. A *flexor* muscle is one which bends the part on itself. An *extensor* is one which by its action tends to extend or straighten the part. An *adductor* muscle is one attached to a long bone in such a way as to move it toward the ventral midline of the body. An *abductor* opposes the action of the adductor. *Pronator* muscles rotate the part forward toward the ventral side while supinators rotate the part back toward the dorsal side. A *levator* (elevator) raises or elevates, and a *depressor* lowers the part concerned. A *sphincter* muscle is one encircling an aperture which it closes by contraction. The *orbicularis oris* in the lips around the mouth is an example. A *dilator* is antagonistic
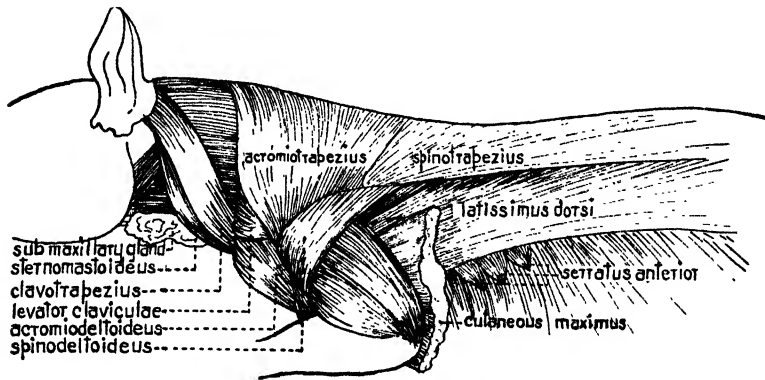
Fig. 38.—Superficial muscles of the shoulder and neck of the rat, lateral view. (From Greene, *Anatomy of the Rat*, Transactions of the American Philosophical Society, New Series, Vol. XXVII, 1935.)

to a sphincter muscle. *Protractor* muscles cause the part concerned to be thrust out as in the case of the tongue while the action of *retractors* is to withdraw the part.

Muscles are usually attached to bones in such a way that the bones serve as levers with the articulations serving as fulcra. Advantage of power is usually gained in machines by causing a small force to act through a great distance by use of a long lever thereby moving a heavy load a short distance. It has been observed by students of myology that most skeletal muscles operate in an almost opposite manner, in that usually a powerful muscle acts on a shorter lever to produce a rapid movement of a small load at the end of a longer lever. This arrangement produces more speed but it is less

efficient. The two common classes of levers used in the body are (1) those in which the fulcrum lies between the load and the muscular attachment, and (2) those where the fulcrum is at one end of the lever, with the muscle attached in the middle, and the load at the other end.

Fig. 39.—Superficial muscles of the lateral surface of the right thigh: *b.f.*, biceps femoris; *c.f.*, caudofemoralis; *g.x.*, gluteus maximus; *s.t.*, semitendinosus; *t.f.l.*, tensor fasciae latae; *v.l.*, vastus lateralis. (From Greene, *Anatomy of the Rat*, Transactions of the American Philosophical Society, New Series, Vol. XXVII, 1935.)

The following table has been prepared to give a summary of pertinent information concerning the conspicuous superficial muscles of the rat:

SUPERFICIAL MUSCLES OF THE RAT

LOCATION	NAME	ORIGIN	INSERTION	ACTION
Head	Platysma	Fascia of deeper muscles	Inner surface of the skin	Moves skin of face and neck
	Masseter	Zygomatic arch and process of maxilla	Side of mandible and mandibular ramus	Elevate lower jaw
	Temporal	Parietal and squamosal bones	Coronoid and other parts of mandible	Elevates the lower jaw
Face	Levator labii superioris	Premaxilla	Mystacial (whisker) pad	Lifts upper lip
	Dilator naris	Premaxilla	Margin of naris	Dilates nares
	Orbicularis oris	Margin of mouth	Margin of mouth	Close mouth (sphincter)
	Levator auris longus	Cervical vertebrae	Base of auricle	Moves ear
Neck	Clavotrapezius	Nuchal line	Clavicle	Raises clavicle
	Sternomastoid	Manubrium	Mastoid process	Turns head
	Digastric	Occipital region	Mandible	Lowers the mandible
	Mylohyoid	Mandible	Hyoid	Raises floor of mouth
	Sternohyoid	Manubrium	Hyoid	Moves hyoid posteriorly
Chest	Scalenes	Cervical vertebrae	1st to 6th ribs	Move ribs or flex head
	External intercostals	Anterior of adjacent ribs	Posterior of adjacent ribs	Elevate ribs
	Serratus posterior	Vertebrae and dorsolumbar fascia	Sides of ribs	Raises ribs
	Pectoralis major	Manubrium	Deltoid ridge of humerus	Adductor of arm
	Pectoralis minor	Sternebrae and xiphoid process	Deltoid ridge of humerus	Adductor of arm
Shoulder	Acromiotrapezius	Cervical and 1st thoracic vertebrae	Acromion process and spine of scapula	Moves scapula dorsally and medially
	Spinotrapezius	Thoracic and 1st lumbar vertebrae	Spine of scapula	Moves scapula dorsocaudad
	Latissimus dorsi	Lumbosacral fascia	Medial surface of humerus	Moves arm dorsocaudad

Region	Muscle	Origin	Insertion	Action
Shoulder	Acromiodeltoid	Acromion process of scapula and clavicle	Deltoid ridge of humerus	Raises and rotates humerus
	Spinodeltoid	Spine of scapula and adjacent fascia	Deltoid ridge of humerus	Raises and rotates humerus
	Rhomboideus	Cervical vertebrae	Vertebral border of scapula	Moves scapula craniad
	Serratus anterior (magnus)	1st seven ribs	Vertebral border of scapula	Rotates scapula and holds it to body
	Levator scapulae	Last cervical vertebrae	Near vertebral border of scapula	Moves scapula craniad
Abdomen	External oblique	Slips from ribs and lumbo-dorsal fascia	Linea alba and pubic symphysis	Constrictor of abdomen
	Rectus abdominis	Pubic symphysis	1st rib, manubrium, and clavicle	Retracts sternum, and compresses abdomen
Forelimb, upper arm	Triceps brachii— long head	Axillary margin of scapula	Olecranon (elbow)	Extends forearm
	lateral head	Tubercle of humerus	Olecranon	Extends forearm
	medial head	Length of humerus	Olecranon	Extends forearm
	Biceps brachii	Coracoid process and glenoid fossa	Radius	Flexes forearm
	Brachialis	Neck of humerus	Ulna	Flexes forearm
Forearm	Pronator teres	Medial epicondyle of humerus	Middle of radius	Rotates forearm
	Extensor carpi radialis	Lateral epicondyle of humerus	2nd and 3rd metacarpals	Extends hand at wrist
	Extensor carpi ulnaris	Lateral epicondyle of humerus	5th metacarpal	Extends hand at wrist
	Extensor digitorum	Lateral epicondyle of humerus	Phalanges	Extends digits
	Flexor carpi radialis	Medial epicondyle of humerus	3rd metacarpal	Flexes hand at wrist
	Flexor carpi ulnaris	Medial epicondyle of humerus and olecranon (elbow)	Pisiform bone (carpal)	Flexes hand at wrist
	Flexor digitorum	Medial epicondyle humerus, radius, and ulna	Phalanges	Flexes digits
	Palmaris longus	Medial epicondyle of humerus	Palm of hand	Flexor of first phalanx

SUPERFICIAL MUSCLES OF THE RAT—CONT'D

LOCATION	NAME	ORIGIN	INSERTION	ACTION
Hip and Thigh	Gluteus maximus	Ilium, sacral and caudal vertebrae	Trochanter of femur	Abducts thigh
	Biceps femoris	Ischium, sacral and caudal vertebrae	Distal femur and proximal tibia	Abducts thigh and flexes shank
	Tensor fasciae latae	Crest of ilium	Fascia lata of thigh	Tightens fascia lata
	Semitendinosus	Ischium	Tibia	Flexes shank
	Semimembranosus	Ischium	Tibia	Flexes shank
	Quadriceps femoris (vastus)	Ilium and proximal femur	Tibia	Extends shank
	Gracilis	Pubic and ischial symphyses	Proximal tibia	Adductor of leg
	Adductor longus	Ramus of the pubis	Distal femur	Adductor of thigh
	Adductor magnus	Pubic ramus and symphysis	Proximal tibia	Adductor of leg
Shank	Tibialis anterior	Lateral epicondyle, tuberosity and crest of tibia	Cuneiform tarsal and 1st metatarsal	Flexor of foot
	Peroneus	Proximal fibula and epicondyle of tibia	Cuneiform tarsal and metatarsals	Flexor and rotator of foot
	Gastrocnemius	Two epicondyles of the femur	Calcaneum	Extensor of foot
	Soleus	Head of fibula	Calcaneum	Extensor of foot
	Plantaris	Lateral epicondyle of femur and head of fibula	Phalanges	Flexor of digits
	Tibialis posterior	Proximal tibia and fibula	Navicular and 1st cuneiform tarsals	Extensor of foot
	Flexor digitorum longus	Side of tibia and head of fibula	Phalanges	Flexor of digits
	Extensor digitorum longus	Lateral epicondyle of the femur	Phalanges	Extensor of digits

The structure of muscle is discussed in more detail elsewhere in the book but a brief statement concerning it may be appropriate here. Each skeletal muscle is composed of a large number of fibers or cells as they are called. These are bound together by connective tissue *(fascia)*. An individual fiber is slender and enclosed in an elastic membrane called the *sarcolemma*. Within, is the general mass of protoplasm, which is composed quite largely of the longitudinally disposed *myofibrils*. These are surrounded by the more fluid portion of the *sarcoplasm*. Each fibril in certain states of contraction shows alternate dense and light areas along its length. Adjacent fibrils across the entire fiber have these areas at approximately the same level, thus giving the appearance of cross-striation through the entire fiber. This is the basis for speaking of this tissue as striated muscle. Each fiber possesses numerous nuclei, making it *multinucleate*. Smooth muscle of the visceral organs does not possess the dense and light areas on the fibrils of the cells.

In detailed study of the muscles they are usually taken by regions or groups according to location. It is assumed that the student will have more detailed descriptions of the muscles in laboratory directions if they are studied there. Reference should be made to Greene, "Anatomy of the Rat," Tr. Am. Philosophical Soc., Vol. XXVII, 1935, for more detailed descriptions and illustrations.

Digestive System

This system is in the form of a tube with various outgrowths and extends from the mouth to the anus of the animal. It serves primarily in digestion of complex food material, converting it into a soluble form which may be absorbed by the blood and lymph. The entire system may be divided into a number of parts as follows: buccal cavity (mouth), pharynx, esophagus, stomach, small intestine, large intestine, salivary glands, liver, and pancreas.

The most anterior portion, the *buccal cavity,* is bounded dorsally and ventrally by the upper and lower lips. The space between the teeth and the inner surface of the lips and cheeks is called the *vestibule.* The teeth have been described previously with the skull. The *tongue* is a well-developed organ lying in the floor of the mouth, but it does not have the usual *frenulum,* or band of connective tissue, extending from its ventral side to the floor of the mouth. There are papillae (horny processes) over the anterior and lateral portions of the dorsal surface. There are taste buds in the walls of some of

these papillae. The roof of the mouth is composed of the hard palate at the posterior margin of which is the soft *palate*, a muscular flap hanging down to separate the buccal cavity from the pharynx just behind. The space between the base of the tongue and the palate, which provides the opening between mouth and pharynx, is known as the *fauces*.

The *pharynx* also receives the *nares* just dorsal to the palate and this portion of it is called the *nasopharynx*. It contributes then to both digestive and respiratory systems. The two Eustachian tubes from the middle ears enter the pharynx. There are two passages continuing posteriorly from the pharynx. The aperture leading to the esophagus which is usually constricted except when food is passing through it, and the *glottis,* which is located just posterior to the tongue, leads to the larynx. The glottis is guarded by the flaplike *epiglottis* to prevent food material and water entering it. The epiglottis is quite important in swallowing.

The *esophagus* is a distensible tube extending from the pharynx to the *stomach.* It passes through the dorsal portion of the thoracic cavity, and immediately posterior to the diaphragm it enlarges to become the stomach. The esophageal end of the stomach is known as the *cardiac* portion, and the more inflated, left-hand portion which follows the cardiac portion is the *fundus.* The tapering posterior portion which comprises the right-hand side of the organ is the *pyloric* portion. In the epithelial lining of the internal wall are many fine foldings in which are imbedded the gastric glands. They secrete gastric juice into the cavity. This is an acid solution containing the *enzymes* (ferments), *pepsin* and *rennin.* The former converts complex proteins to *peptones,* an intermediate stage of digestion of this class of food, and the latter coagulates (clots) the protein portion of milk to concentrate the *casein.* The pyloric portion of the stomach leads directly into the small intestine through a sphincter valve located at the junction of these two. This is the *pyloric valve,* and it is usually closed. When the *chyme* (food in process of digestion) reaches a certain level of acidity (0.4 to 0.5 per cent), the nerve endings controlling the valve are stimulated and cause it to open, allowing the chyme to rush into the intestine.

The *small intestine* is the longest division of the alimentary canal, being approximately six times the length of the body from snout to anus. Coiled in a manner which almost defies description, it occupies a large portion of the abdominal cavity between the liver and
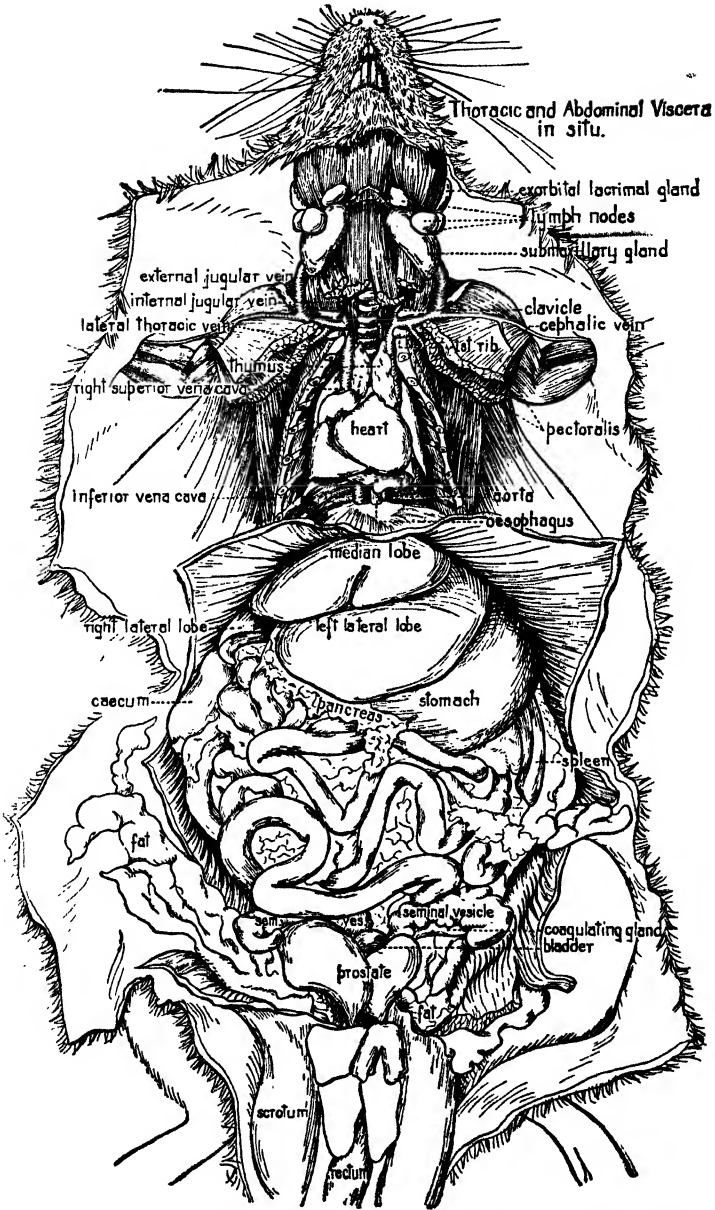
Fig. 40.—Thoracic and abdominal viscera of a male rat, ventral view. (From Greene, *Anatomy of the Rat*, Transactions of the American Philosophical Society, New Series, Vol. XXVII, 1935.)

pelvis and ends by joining the colon of the large intestine near the right hip bone. Its first turn behind the stomach is the *duodenum* and takes the shape of an inverted J turned backwards, to give a short ascending limb from the stomach and a long descending limb proceeding posteriorly. The *pancreas,* which is a branched (often divided), thin gland, is held in the gastroduodenal mesentery. It follows the curve of the duodenum extending posteriorly and to the left into the gastrosplenic mesentery. The pancreatic juice, which it produces, is collected by numerous, small, paired pancreatic ducts. The ducts join the distal portion of the bile duct which enters the duodenum. Posteriorly the duodenum continues into the *jejunum* whose boundaries are not very clearly defined anatomically but more readily distinguished in histological studies. The *ileum* is the rather tightly coiled portion which extends to the large intestine. The contents of the ileum at this point pass through the *ileocolic valve* which communicates with both the *colon* (large intestine) and *cecum.* The latter is a broad, curved sac on the right side of the abdominal cavity and is about an inch to an inch and one-half in length. It occupies the position of the vermiform appendix of man. This blind sac serves as a cavity for the storage of partially digested food and fecal matter in the rat. The cecum and ileum join the *colon* or large intestine in its ascending portion. This part extends anteriorly to the region . of the stomach where it crosses to the middle of the cavity or beyond as the *transverse colon,* turns posteriorly, and continues as the *descending colon.* The *rectum* is the continuation of this portion of the colon through the pelvis, and it terminates externally at the *anus.* The fecal matter forms pellets and the masses of these pellets in the colon influence the shape of certain portions of it.

GLANDS ASSOCIATED WITH THE DIGESTIVE SYSTEM

Salivary Glands.—The *parotid* gland is a rather loosely organized but conspicuous structure extending from the ventrolateral surface of the neck to a position around the base and behind the ear. Its posterior extremity reaches the shoulder, covering the outer half of the clavicle. The parotid duct (Stenson's duct) is formed by the union of three branches and proceeds across the masseter muscle to enter the mouth through the cheek just opposite the upper molar teeth. The *submaxillary* glands are large, elongated, and located on the ventral surface of the neck. They are in contact with each other along

the midventral line from the hyoid almost to the manubrium. A submaxillary duct (Wharton's) leaves the anterior end of each gland and leads anteriorly along the medial border of each mandible, entering the floor of the mouth just posterior to the incisor teeth. Joining the anterior ends of the submaxillary glands and covering their ducts, the *sublingual* glands are found, the ducts of which enter the floor of the mouth also. The salivary glands secrete saliva, which contains mucus and the starch-digesting enzyme *ptyalin*. This enzyme converts starches in the food to the intermediate sugar, maltose.

The Liver.—This large gland is located ventrally in the cavity, just posterior to the diaphragm at about the level of the junction of esophagus and stomach. It is divided into four parts: the two *lateral lobes;* the *median* (cystic) *lobe;* and the *caudate lobe,* which is smaller and partially encircles the esophagus. No gall bladder is present. The *bile duct* (ductus choledochus) is formed by tributaries (hepatic ducts) from various lobes of the liver. This duct in the rat seems not to substitute for a gall bladder as it does in some other animals where the bladder is absent. The bile duct enters the duodenum a little more than an inch from the pylorus. The liver not only secretes the bile which is important in alkalizing the chyme and emulsifying the fats in the intestine as well as possibly producing some fat and carbohydrate digesting enzymes, but it is also an organ for the storage of digested carbohydrates and fats. Furthermore, it is an important organ in the formation of urea which is then carried by the blood to the kidneys for excretion.

The gastric glands located in the fine folds (crypts) of the mucosa of the stomach have been mentioned already. The mucosa or inner lining of the small intestine also has numerous simple glands which secrete intestinal juice. This juice protects the walls of the intestine, lubricates them to assist in the movement of food, contains the protease enzyme (protein-splitting) *erepsin* for digestion of peptones, and probably produces *maltase* for the conversion of maltose to glucose. It may be that there are even other enzymes produced here.

Of course, the digestive action of the three pancreatic enzymes occurs in the small intestine. These are as follows: *trypsin,* a protease, converting complex proteins and peptones to amino acids; *amylopsin,* a diastase, converting starches into maltose; and *steapsin,* a lipase, converting complex fats into fatty acids (oleic. stearic, butyric, palmitic) and glycerin.

In general, the primary function of the digestive system is to convert the complex food material into an absorbable solution which may readily be taken up by the blood and in turn by the protoplasm of the tissues. The digestive enzymes are indispensable agents in this function.

Circulatory System

This system includes the blood vascular and lymphatic vascular portions. The former consists of the heart, arteries, capillaries, and veins. This system transports dissolved food materials, oxygen, carbon dioxide, excretions, hormones, and antibodies to and from the cells over the body. In addition, the distribution of the blood helps in equalizing the temperature throughout the body. Blood and lymph are the two vascular fluids.

The Heart.—This muscular organ is located in a division of the thoracic cavity, the pericardial cavity, which is separated from the remainder of the chest by the transparent *pericardium.* The heart of the rat is quite representative of the mammalian heart with its two auricles (atria) and two ventricles. The right and left sides of the adult heart are quite distinct. The right atrium (auricle) receives systemic blood from the precaval (superior vena cava) and postcaval (inferior vena cava) veins which collect the venous blood from the various organs of the body. Contraction of the right atrium forces the blood through the right auriculoventricular orifice which is guarded by the *tricuspid valve* and into the *right ventricle.* At the same time the contraction of the left atrium, which has received aerated blood from the lungs, forces that blood through the left atrioventricular orifice which is guarded by the *bicuspid* or *mitral valve* and into the left ventricle. Immediately following the simultaneous contraction (systole) of the two atria, the ventricles contract. The blood from the right ventricle is forced into the *pulmonary* arteries and carried to the lungs while the blood from the left ventricle is entering the aortic arch to be distributed to all parts of the body. There is no direct connection between the cavities of the two sides of the heart. The principal valves of the heart are the tricuspid and bicuspid mentioned above, and the two *semilunar* valves. There is one of the latter in the proximal portion of the pulmonary artery and the other in the aorta. The function of these valves is to prevent backflow of blood, in order that the blood may be kept in circulation

in a given direction. The heart is a muscular pump which forces the blood through the body. Its complete failure causes almost immediate death.
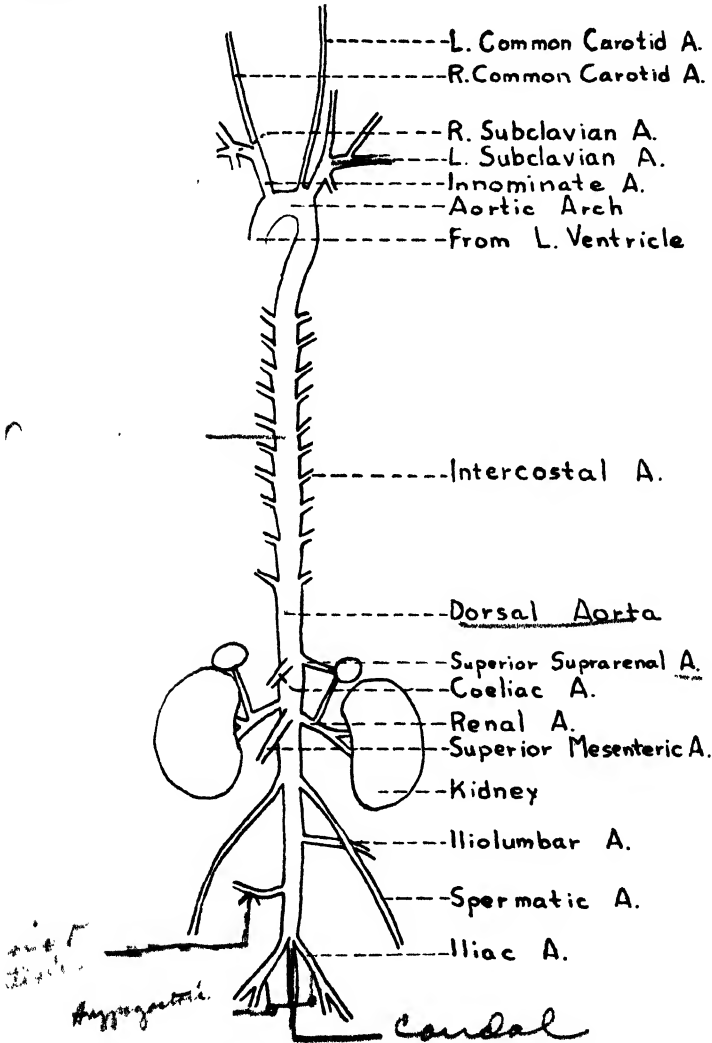
Fig. 41.—Diagram of the arteries of the rat from ventral view.

Blood Vessels.—The large artery leaving the left ventricle is the aorta, and it soon branches to supply the principal organs of the body. From its arch arise the *innominate, left common carotid,* and then

the *left subclavian* arteries. The innominate artery then divides quite shortly into the *right common carotid* and the right *subclavian* arteries. The carotids supply the head and neck; the subclavians supply
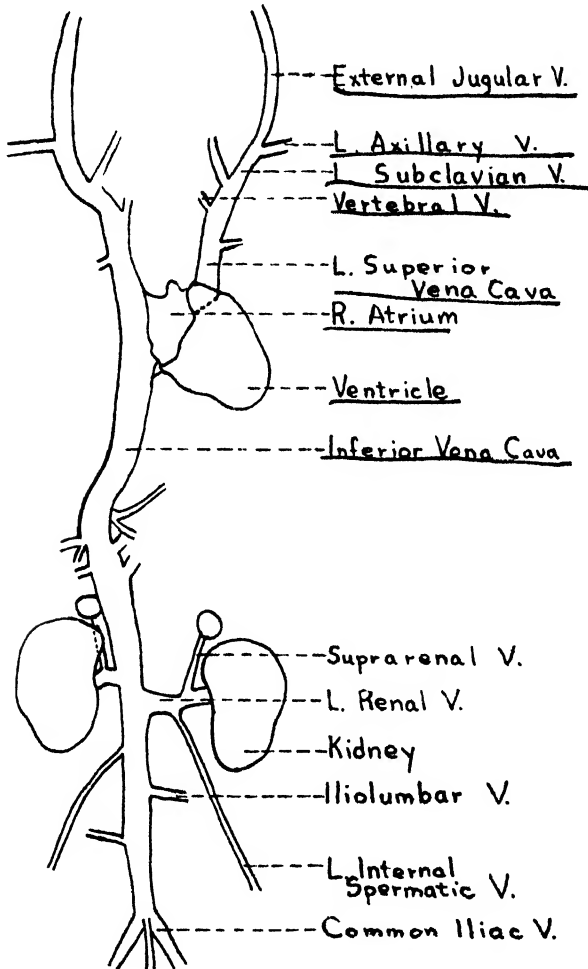
Fig. 42.—Diagram of the veins of the rat from ventral view.

the shoulders and arms; the aorta takes a mid-dorsal position and extends the length of the trunk and tail. It is known as the *dorsal aorta* and from anterior to posterior it gives rise to the *intercostal* arteries to the ribs; *phrenic* artery to the diaphragm; *celiac* artery to the

esophagus, stomach, duodenum, liver, pancreas and spleen; *superior mesenteric* artery to the pancreas, small intestine, cecum, and colon; *inferior mesenteric* artery to the colon and rectum; *lumbar* arteries, paired to the back; *renal* arteries, paired to the kidneys; and finally at the posterior, the division into the two *common iliac* arteries in the pelvic region. These each branch into *external* and *internal iliac* arteries and supply the pelvis and hind limbs. The aorta proceeds posteriorly as the *caudal* (coccygeal) *artery* to supply the tail.

In the tissues of the organs over the body the arteries continue to branch and rebranch until their diameter becomes small enough to allow them to pass between individual cells. These minute vessels are called *capillaries* and while in them the blood exchanges oxygen and food material for carbon dioxide and excretory wastes from the cells of the tissues. After passing among the cells of an organ the capillaries converge to form small veins (venules), which join each other in forming the larger ones.

The large veins joining the heart have already been mentioned. They are the *postcava* from the posterior and *precavae* from the anterior. The single postcava is formed by the union of the caudal and the paired common iliacs in the pelvis. This vessel lies in the mid-dorsal line, receiving paired renal veins from the kidneys, genital veins from the gonads, and the suprarenal veins from suprarenal glands. At the level of the liver, hepatic veins join the postcava. Anterior to this it enters the right atrium. The blood in the stomach, intestines, pancreas, spleen is collected by the branches of the *hepatic portal* vein, which delivers the blood to the liver where it distributes through the special capillaries (sinusoids) and is collected by the hepatic veins. The precaval veins are formed one on each side by the *subclavian* veins from the forelimbs, the internal and external *jugular* veins from the head and neck, and the *vertebral* from the brain. The precavae, like the postcava, enter the right atrium of the heart bringing in the venous blood.

Blood.—Generally speaking, thirty rats are approximately equal to one human metabolically. If this holds true in regard to the quantity of blood in the body of a rat, it has approximately 170 c.c. of blood since it is held that the human body carries between 5 and 6 liters. Blood is a scarlet substance composed of a fluid in which cells float. Its specific gravity is about 1.055. The liquid basis is called *plasma,* and the cells are known as corpuscles. Plasma con-

stitutes approximately 60 per cent of the volume of blood. It is itself about 90 per cent water and 10 per cent dissolved solids, chiefly proteins and salts. Sodium chloride is the most abundant salt here. Calcium and phosphorus salts are present in small proportions but, nevertheless, are very important. An interesting suggestion has even been made: that salts of the plasma are the same in kind and proportion as those which were present in the prehistoric sea. The primitive marine animals are thought to have had body fluids based on sea water. Their descendants seem to have carried this composition down through time. However, modern sea water has become about 3 times as concentrated. The plasma carries also carbon dioxide collected from tissues, hormones, and antibodies. The hormone materials serve to regulate the metabolism of different tissues over the body, and the antibodies bring about immunity to certain diseases.

The *corpuscles,* or formed elements, as they are often called, are of two classes, the red corpuscles, or *erythrocytes,* and the white corpuscles, or *leucocytes.* The red corpuscles are small, nonnucleated cells measuring about $\frac{1}{3200}$ inch across the face of each in man, and approximately the same in the rat. These cells contain *hemoglobin,* a red pigment, which is apparent in the mass but not evident in a single corpuscle. Single corpuscles have a greenish amber cast, and are in the shape of biconcave discs. There are about 5,000,000 red corpuscles in each cubic millimeter of blood in the male human (4,500,000 in female). This furnishes an idea of the number which may be present in the rat. Hemoglobin is capable of combining readily with oxygen in such a way that the oxygen may be given up easily to cells with lower oxygen content. Red cells, then, are the oxygen carriers of the blood. In adult animals these corpuscles are formed primarily in the red bone marrow. In earlier life the liver and spleen supplement this. The total surface area of all the red corpuscles in the body of a rat has been estimated as the equivalent of about 3 square rods.

The leucocytes are nearly colorless in their natural condition. They are quite variable in size and shape. The majority of the white cells are of the amoeboid type and many have different types of granules in the cytoplasm. These cells are classified according to nuclear condition or shape, size of cell, and staining reaction of these cytoplasmic granules. These serve the body in devouring foreign material, including bacteria. In this way they protect the animal's body against toxins and disease.

Because of the presence of the substances *fibrinogen* (a protein), *thrombin,* and calcium salts, in the blood, it clots upon exposure to air. The solid fibrous material formed in clotting is *fibrin.* The thin, watery straw-colored liquid which separates from the clot is *serum.*

Lymphatic System.—As the blood passes through the tissues of the various organs, it loses a portion of its fluid base. This liquid which seeps from the capillaries is *lymph* and is collected in the lymph spaces surrounding the cells in most tissues. It is quite similar to plasma, and it distributes food and other necessities to the individual cells and collects carbon dioxide and other waste products to be returned to the blood when it finally returns to it by way of the *thoracic lymphatic duct* and the subclavian veins. The thoracic duct, the largest in the body, lies in the dorsal part of the trunk between the dorsal aorta and the vertebral column. It receives the various lymphatic vessels. These vessels have ultimately been formed by the union of the lymph spaces between the cells in the tissues. Along the lymphatic vessels at certain points are glandular masses, the lymph glands or nodes. These bodies produce lymphocytes, a type of white cell carried in the lymph and blood. In certain portions of the body these glands are abundant, as the inguinal (groin), axillary (armpit), popliteal (knee), cubital (elbow), tracheal, and submaxillary regions.

Respiratory System

In mammals the special organs of respiration are the lungs, wherein the carbon dioxide is taken from the blood and oxygen is taken from the air by the blood. The nasal passages lead through the nasopharynx to the pharynx and from here through the glottis to the larynx (voice box), thence by trachea (windpipe) to the bronchi, and into the lungs. The air is warmed as it is passed through the nasal chambers and pharynx. The turbinated bones form extensive convolutions in the lining of the inner surface of the nasal chamber. The tear ducts lead from the eyes into the nasal chamber while the Eustachian (auditory) tubes lead from the middle ear into the naso-pharynx. Air passes from the pharynx, around the fingerlike *epiglottis* which guards the slitlike *glottis* leading into the *larynx* or voice box. The epiglottis closes the entrance of the glottis only during swallowing in order that food or other material may not enter. The *vocal cords* are located on the inner wall

of the larynx. They appear as folds of the epithelial lining. The larynx which is similar to a small box continues into the tubular *trachea* or windpipe posteriorly. The presence of a number of C-shaped cartilages embedded in its wall prevents it from collapsing as air is drawn through. The trachea extends parallel to, and is in contact with, the ventral side of the esophagus. At the posterior end, it bifurcates to form two primary *bronchi,* each of which leads to a lung in which it is partially embedded. The left lung has but one lobe while the right has four, three of which may be seen from the ventral surface.

Each lung is completely invested externally by a delicate, though tough, transparent *serous membrane* called the *pleura.* This membrane is continuous with the lining of the wall of the *pleural cavity.* The portion adherent to the surface of the lung is the visceral pleura, and the portion lining the inner surface of the body wall is the parietal pleura. Within the lungs the primary bronchi branch and continue to branch as secondary and tertiary bronchi, finally becoming small *bronchioles* which lead into the *alveoli,* or tiny terminal air sacs.

Breathing is affected by increasing and decreasing the volume of the thoracic cavity. To do this the ribs are moved forward and spread by intercostal and other muscles, while the diaphragm which usually arches anteriorly is contracted to a flat position. As the chest cavity is thus enlarged, the internal pressure is reduced, and to balance the pressure, air naturally rushes into the lungs from the outside. When relaxed, the walls of the thorax and the diaphragm both return to their original positions and expel the air. Drawing air into the lungs is called *inspiration,* and discharging it is *expiration.* While the air is in the alveoli of the lungs, oxygen is absorbed from it by hemoglobin in the blood distributed in the capillaries of the pulmonary veins embedded just beneath the epithelium here. At the same time carbon dioxide is given up by the blood to the air. The pulmonary veins return the oxygenated blood to the heart for redistribution to all parts of the body.

The Nervous System

In the simple forms of life and in individual cells of the higher forms, the cell membrane is the area where vital reaction takes place. The two fundamental properties, *irritability* and *conductivity,* operate to receive the stimuli and conduct the impulses in the

protoplasm. As nervous tissue develops, these. properties are specialized, and the efficiency of the organism increases as the awareness of the environment increases. The development of sense organs increases and enhances this awareness. Although animals without nervous systems exhibit *excitation, conduction,* and to some extent *correlation,* these functions expand in range and power when the sense organs and nerve pathways become available. As complexity and range in the mechanism of the nervous system increase, centers of correlation arise for a more precise analysis of the excitation in order that an appropriate reaction will result. Thus, means is provided for the organism to relate itself better to the environment.

The fundamental units of the nervous system consist of a sensory neuron and a motor neuron. The *neuron* (nerve cell with all of its processes) is the unit of structure in nervous systems, from the simplest to the most complex, even to include those of rats and men. Two or more neurons may be associated to function as a *reflex arc,* and this *arc* rather than the single neuron becomes the functional unit. In higher forms of vertebrate animals there is more and more organization and concentration of neurons which brings about increasing prominence of the brain portion of the system. In man, cerebral activity takes a dominant part in the functions of the entire system; however, there has been no loss of significance or extent of development and activities of the other parts. The entire system controls and coordinates the activities of the other parts of the body.

The entire system of the rat and other higher vertebrates is usually divided into four general divisions: (1) *central,* including the brain and spinal cord; (2) *peripheral* nerves, including cranial and spinal nerves; (3) *sense organs,* as eyes, ears, tactile corpuscles, taste buds, and olfactory structures; and (4) *autonomic* (sympathetic), including the two trunks of ganglia.

Central Nervous System.—The central portion of the system is tubular, having developed as a simple neural tube. This portion of the system is covered by three membranes called *meninges.* The outer tough membrane is the *dura mater;* beneath this is the delicate *arachnoid* layer; and adhering to the surface of the nervous tissue is the vascular *pia mater.* The anterior region of this central portion is the brain. It is considerably broadened and thickened, presenting five divisions. From anterior to posterior these divisions are: telencephalon, diencephalon, mesencephalon, metencephalon and myelencephalon.

The anterior division is the *telencephalon,* which includes the *olfactory lobes* and *cerebrum.* The former are paired lobes at the most anterior end. They are well developed and serve as centers of the sense of smell which is quite specialized in the rat. The cerebrum is divided longitudinally into two hemispheres one on each side of the dorsal median fissure. There are no deep furrows or convolutions in the surface of the cerebrum as is the case in the cat, man, or a number of other mammals. The cerebrum is relatively large and has spread until the two middle divisions of the brain have been covered by it. Between the two hemispheres is a broad band of fibers, the *corpus callosum,* which connects them. The fornix, anterior commissure, and posterior commissure are other bundles of nerve fibers connecting the two hemispheres. Thus there is coordination of function in the two halves of the cerebrum. This division of the brain serves as the center of voluntary control, correlations, and many associations.

The *diencephalon* or *thalamus* which is in the anterior portion of the brain stem and is covered by the cerebrum forms the principal connections between the cerebrum and other parts of the brain. In particular there is a relationship between the olfactory lobes and this part. The diencephalon is another important center of the sense of smell.

The *mesencephalon,* or *midbrain,* is located just posterior to the preceding division and is also covered by the posterior portion of the cerebral hemispheres. On its dorsal side are located the *corpora quadrigemina.* There are four of these prominences, and they are homologous to the paired optic lobes of the frog and other simpler vertebrates. The ventral portion of the midbrain consists primarily of two large bundles of nerve fibers called the *cerebral peduncles.* The fibers of these make the numerous connections between the cerebrum and medulla, which in turn leads to the spinal cord. There are visual and auditory centers located in the midbrain.

The *cerebellum* is the convoluted portion of the brain which appears externally, just posterior to the posterior margins of the cerebral hemispheres. Its position is just posterior to the midbrain also. Its median lobe is the *vermis,* and at the sides of this are the right and left *hemispheres.* The large bundles of fibers extending to the ventral side of the brain at this level constitute the *pons* and represent the only portion of the cerebellum to appear on the ventral side. This division of the brain serves as a center of coordinated movement and is particularly associated with balance.
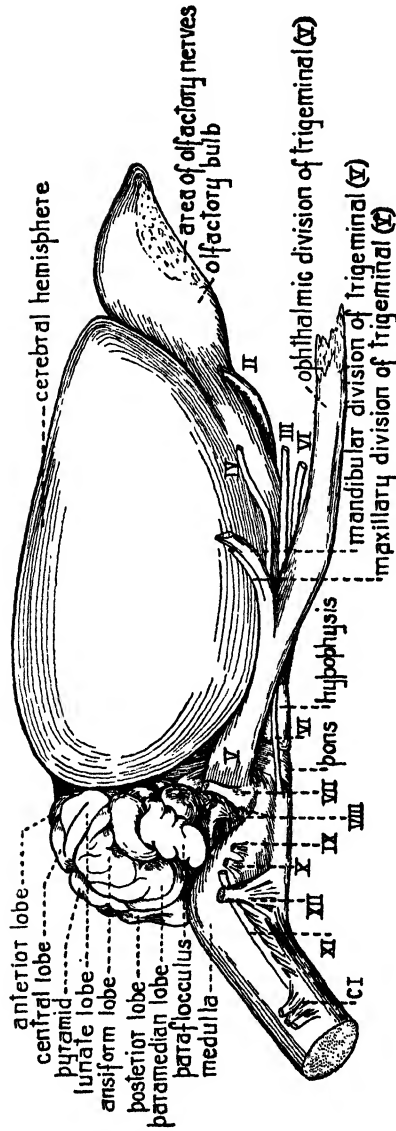
Fig. 43.—Lateral aspect of brain and roots of cranial nerves of the rat. (From Greene, *Anatomy of the Rat,* Transactions of the American Philosophical Society, New Series, Vol. XXVII, 1935.)

The *medulla oblongata* is the most posterior division of the brain. Its anterior portion is somewhat covered by the cerebellum, and ventrally it has only the pons between it and the midbrain. The cavity of the medulla (fourth ventricle) is ventral to the posterior portion of the cerebellum and is covered by a vascular membrane which is a part of the *chorioid plexus*. The respiratory center and certain of the other reflex centers are located in this division. It serves also as the important pathway for the bundles of nerve fibers extending from other parts of the brain to the spinal cord.

The brain developed as a specialized anterior portion of the embryonic neural tube and has retained the hollow form. This original cavity is modified into spaces within the principal divisions and lobes in the form of *ventricles*. The first two, the *lateral ventricles,* are located one in each of the cerebral hemispheres, and extend anteriorly into the olfactory lobes. Posteriorly they join the *third ventricle* of the diencephalon by way of the *foramen of Monro*. This third ventricle extends ventrally into the infundibulum, which is a downpushing in the floor of the diencephalon. A narrow channel, the *cerebral aqueduct* (aqueduct of Sylvius), leads posteriorly from the third ventricle through the midbrain and ventrally to the cerebellum to join the broad fourth ventricle of the medulla oblongata. The fourth ventricle continues posteriorly into the narrow cavity (neurocoele) of the spinal cord.

Spinal Cord.—This is the division of the central portion of the nervous system which extends through the length of the trunk and into the tail. This elongated cord is in the shape of a somewhat flattened cylinder which tapers to a fine-pointed *filum terminale* at the posterior end within the anterior portion of the tail. There are two enlargements along the length of the cord. They are the *cervical enlargement* in the neck-shoulder region, and the *sciatic enlargement* in the lumbar region. The large nerves supplying the front and hind limbs arise at these levels, respectively. Spinal nerves are distributed in pairs and leave the cord segmentally. The neurocoele is the small continuous cavity through the length of the cord, joining the fourth ventricle at the anterior. The *gray matter* containing nerve cell bodies surrounds the neurocoele in the shape of the letter H or, perhaps more accurately, in the shape of a butterfly with wings spread. The *white matter,* which is largely nerve fibers, surrounds the gray matter. These fibers extend lengthwise through the cord and connect

different levels of the cord with each other and the brain. Each of the spinal nerves, which were mentioned above, joins the gray matter of the cord by two roots, a ventral root which enters the ventral column and a dorsal root which enters the dorsal column of gray matter. The dorsal root carries the afferent nerve fibers to the cord, while the ventral root carries the efferent fibers. A spinal ganglion containing cell bodies of afferent fibers is associated with each dorsal root.

The trunk and limbs receive many impulses produced by environmental stimuli, as well as entertaining most of the activities of locomotion, digestion, circulation, excretion, respiration, reproduction, etc. All of these must be kept properly related and coordinated in order that the organism be kept alive and carrying on normal activities. This is done largely by the spinal cord and associated autonomic portion of the system. Certain impulses are transmitted by the cord to the brain for association and reaction there. In general, it may be said that the cord functions as a center with some power of integration, particularly for reflexes of the trunk and limbs, as well as a pathway to the brain.

Peripheral Nerves.—Twelve pairs of *cranial* nerves leave the brain of the rat and thirty-four pairs of *spinal* nerves are given off by the spinal cord. These make connections with the sense organs (receptors), motor end plates in muscles (effectors), as well as the autonomic portion of the system. The nerves are composed of bundles of nerve fibers, and each fiber is the extended process of a neuron. These processes are axons (neurites) and dendrites. All portions of the head, trunk, and limbs are supplied with nerve fibers, which are in communication with the central nervous system.

The paired cranial nerves all pass from the skull through foramina, and all except one are distributed to the head and neck. They are divided according to function into *motor, sensory,* or *mixed* (having both motor and sensory fibers). The *olfactory* (I), *optic* (II), and *auditory* (VIII) are the only cranial nerves which are wholly *sensory*. The *oculomotor* (III), *trochlear* (IV), *abducent* (VI), *spinal accessory* (XI), and *hypoglossal* (XII) are motor. The *trigeminal* (V), *facial* (VII), *glossopharyngeal* (IX), *vagus* (X) are mixed. The last two named are mainly motor, having only a small number of sensory fibers. Some of the sensory roots of these nerves bear ganglia (aggregations of nerve cell bodies). The more important of these is the *Gasserian* (semilunar) ganglion of the trigeminus.

CRANIAL NERVES

NAME	ORIGIN ON BRAIN	DISTRIBUTION	FUNCTION
I. Olfactory	Telencephalon, olfactory bulbs	Olfactory membrane	Sensory—smell
II. Optic	Diencephalon, optic chiasma	Retina of eye	Sensory—sight
III. Oculomotor	Midbrain, cerebral peduncle	Inferior oblique; inferior, superior, and internal rectus muscles of the eye	Motor—movement of eyes upward and medially
IV. Trochlear	Midbrain, dorsal surface	Superior oblique eye muscle	Motor—moves eye laterally and downward
V. Trigeminal	Medulla oblongata, dorsal to pons varolii	Ophthalmic division to eyeball and integument of nose and orbit. Maxillary div. to maxillary teeth, nose, lachrymal gland and palate. Mandibular div. to integument and muscles of mandibular region, mandibular teeth and tongue	Mixed—ophthalmic and maxillary wholly sensory while mandibular carries both motor and sensory fibers
VI. Abducent	Medulla oblongata, ventral	External rectus muscle of eyeball	Motor—moves eye laterally
VII. Facial	Medulla, anterolateral	Salivary glands, epithelium of tongue, and muscles of face	Mixed—secretion of saliva, taste, and movement of face
VIII. Auditory	Medulla, anterolateral	Internal ear	Sensory—hearing, and equilibrium
IX. Glossopharyngeal	Medulla oblongata, lateral	Tongue, pharynx, palate, and parotid gland	Mixed—pharyngeal movements, taste, secretion of saliva
X. Vagus or Pneumogastric	Medulla, lateral, just posterior to preceding	Pharynx, larynx, heart, lungs, stomach, intestines	Mixed—movements of larynx and viscera. Regulates heartbeat and respiration
XI. Accessory	Medulla, posterior to preceding and from spinal cord	Palate, muscles of neck and trapezius	Motor—movement of neck and shoulders
XII. Hypoglossal	Medulla oblongata	Muscles of hyoid and tongue	Motor—movements of tongue and throat

A summary of pertinent information concerning this group of nerves is organized into the accompanying table.

The paired spinal nerves are connected to the spinal cord by a *dorsal* (sensory) root and a *ventral* (motor) root. The former transmits impulses to the cord, and the latter consists of fibers carrying motor impulses away from the cord. A small ganglion is located in each dorsal root. The two roots forming each nerve join each other while still within the neural canal of the vertebral column, and the nerve then emerges through the intervertebral foramen of that level. Immediately outside the intervertebral foramen each nerve gives off a dorsal branch (ramus) to the muscles of the back, the main ventral branch, and a small connecting bundle (ramus communicans) to the autonomic system. In general, a pair of spinal nerves leaves the spinal cord at each meeting of adjacent vertebrae for most of the length of the vertebral column. In certain regions these nerves anastomose (join in a network), forming *plexuses*. In the neck region is the *cervical* plexus; in the region of the shoulder and forelimb, the *brachial* plexus; in the region of the loins, the *lumbar* plexus; and in the region of the sacrum, the *sacral* plexus.

Sense Organs.—The organs of sense, or receptors, and specialized peripheral endings of the sensory nerves, are constructed to be particularly efficient in receiving a certain type of stimuli. The eyes, ears, olfactory membrane of the nose, taste buds, pressure and tactile corpuscles are all endings of this kind. The stimuli for the eye are in the form of light waves; those of the ear are ether vibrations; those of taste and smell are chemical; and those of touch are pressure and contact. These organs and their function will be discussed in the chapter on Physiology.

Autonomic Nervous System.—The mere sight of food to a hungry person causes the flow of both saliva and gastric juice. This activity occurs without conscious control and is one of the multitude of examples of the functioning of the autonomic portion of the nervous system. The principal parts composing this system include two trunks or chains of ganglia, one at each side of the vertebral column on the dorsal wall of the coelome. The anterior extremity of each trunk is the *superior cervical ganglion* near the angle of the jaw and covered by the submaxillary gland. In each trunk there are *cervical* (or cranial) ganglia with fibers extending to the ciliary body in the eye, salivary glands, heart, bronchi, stomach, intestines,

liver, pancreas, kidneys, and spleen; *thoracicolumbar* ganglia with fibers to muscles of hairs, skin arterioles, eye, viscera, blood vessels, and certain urogenital structures; *sacral* ganglia with fibers to external genital organs, urinary bladder and large intestine. Autonomic impulses either stimulate or inhibit action in the organs supplied. Each autonomic ganglion is connected to the nerve of its level by a band of fibers called the *ramus communicans.*

Excretory System

The principal organs constituting this system are a pair of kidneys, a pair of ureters, a single bladder and a single urethra. These organs relieve the blood of urea, various salts, excess water, etc., and discharge these substances from the body as urine.

The *kidneys* are bean-shaped structures located dorsal to the peritoneum in the lumbar region of the trunk. The two kidneys are not exactly opposite each other on the two sides of the midline, the left one being about a half a length more posterior. At the medial side of each kidney is a depression called the *hilum* where the renal blood vessels and ureter join it. The *ureters* are tubules leading, one from each kidney, to the urinary bladder. The internal structure of the kidney consists of a more peripheral or outer layer, the *cortex,* which lies just internal to the capsule, and the inner *medullary* portion. The cortex contains the *Malpighian corpuscles* which are essential structures in receiving urine from the blood. The medullary portion is composed largely of tubules. These tubules converge in the papillae which lead to the sinus in the hilum. Here the papillae empty into the widened end of the ureter, which fills the renal sinus and is called the *renal pelvis.* The Malpighian (renal) corpuscle is composed of the inverted, swollen end of a uriniferous tubule and a mass of blood capillaries enclosed by it. The former is known as *Bowman's capsule* and the knot of capillaries enfolded by it is the *glomerulus.*

The *urinary bladder* is a thin-walled oblong sac in the posterior portion of the abdominal cavity. It receives the urine from the ureters. The narrowed neck which continues from it to the exterior is named the *urethra.* The urethra becomes tubular, and in the male extends through the penis to its tip, serving both excretory and reproductive functions through most of its length. In the

female it is strictly excretory and its aperture is near the clitoris. In passing from the blood to the exterior, urine would follow about the following course: glomerulus, Bowman's capsule, uriniferous tubule, collecting tubule, papilla, renal pelvis, ureter, urinary bladder, urethra to the external orifice. The urine which is excreted
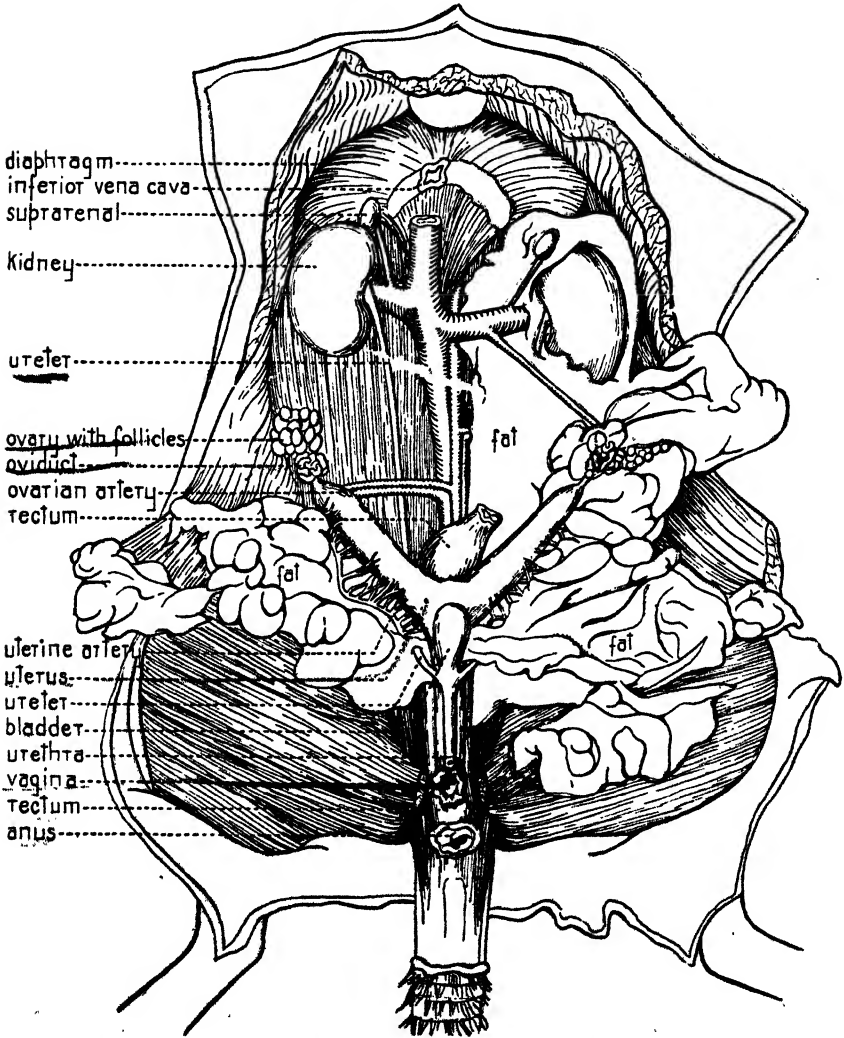
Fig. 44.—Female urinogenital system of the rat, ventral view. (From Greene, *Anatomy of the Rat*, Transactions of the American Philosophical Society, New Series, Vol. XXVII, 1935.)

carries excess nitrogenous materials and must be eliminated. These wastes are principally in the form of urea, uric acid, and creatinin in water solution. The passage of urine from the blood to the uriniferous tubules is a complex process combining secretory activity and osmosis.

The kidneys of the rat, all other mammals, birds, and reptiles belong to the type known as *metanephros* or true kidney. Fishes and amphibians in adult form have a different kidney structure, called *mesonephros*. The higher vertebrates possess this as an embryonic structure also.

Reproductive System

In the early stages of the development of the individual the organs of sex show no indication as to its future sex. The gonads and external genitalia of both sexes are similar up to a certain point, and both sets of accessory tubules develop in each individual. At a certain stage in the development of the individual the sex becomes established. The gonads take on characteristics of either ovaries or testes, one set of accessory ducts is accelerated in development while the other is inhibited, and there is a modification in the developing external genitalia in keeping with the sex to be. The manner in which this differentiation occurs is shown in the following table:

INDIFFERENT EMBRYONIC CONDITION	MATURE MALE	MATURE FEMALE
Primitive genital gland	Testis	Ovary
Mesonephros	Epididymis Paradidymis	Epoöphoron Paroöphoron
Mesonephric duct	Vas Deferens	Disappears
Müllerian duct	Vestigial appendix of testis	Oviduct, uterus, and vagina

The principal function of this system is the production of germ cells (sex cells or gametes). Female germ cells are produced in the ovaries and are called *ova*. The male germ cells are produced in the testes and are called *spermatozoa*.

The Female Reproductive Organs.—Included under this title are external genitalia, two ovaries, pair of oviducts (Fallopian tubes), uterus, and vagina. The external structures are in the perineal region just ventral to the anus. The diminutive *clitoris* is a fold of tissue here which is terminated by the *glans clitoris*. The clitoris

is homologous to the penis of the male and is similarly erectile tissue which becomes engorged with blood during sexual excitement. The *vaginal orifice* is immediately ventral to the anus and the *urinary aperture* just ventral to this, being at the base of the clitoris.

Internally, the *ovaries* are located in the pelvic portion of the abdomen. They are small and flattened. The mesentery which supports each ovary is the *mesovarium*. The *oviducts* are rather slender and less than an inch in length. The mouth of each oviduct is near the ovary of that side and is called the *ostium*. It is funnel-shaped and has a row of fingerlike *fimbria* around its margin. From this, the tube extends to the horn of the uterus. There is no direct connection between the ovary and oviduct, but the ostium usually covers the side of the ovary through which a mature ovum is to rupture in order that the germ cell will be received by the oviduct. In this animal there are two horns to the *uterus*, each receiving an oviduct. These horns converge and almost immediately join the *vagina* which leads to the exterior. Embryos develop in the horns of the uterus.

In summary, the germ cells are produced in the ovary, are freed by rupture through its wall, are received by the ostium of the oviduct, are moved through the oviduct (fertilized here, if fertilized) to the horn of the uterus where the fertilized ovum (zygote) becomes implanted and a placenta is formed. If not fertilized, the ovum passes from the uterus to the vagina and out by way of vaginal orifice. The vagina receives the penis during copulation (sexual act), and the spermatozoa are discharged from the penis here.

Male Reproductive Organs.—Included here are the penis, scrotum, testes, epididymis, vasa deferentia, seminal vesicle, urethra, prostate glands, and Cowper's glands. The penis is composed of erectile tissue and covered by the integument. The erectile tissue is engorged with blood during sexual excitement and causes the organ to become enlarged and rigid. The parts of the penis are the *base* or bulb at the proximal end, the body, and the *glans* or head at the distal end. The *prepuce* is the loose skin which covers the glans.

The *scrotum* is a prominent sac in the perineal region of the male. Internally it is divided into two pouches which are strictly outpushings of the coelomic cavity in that the peritoneum continues through each inguinal canal to line each of these pouches. The testes descend from the abdomen to the scrotum during breeding

season and are again withdrawn following it. The *testes* are oval
in shape, being about twice as long as broad. In large fully matured
rats the testis may be two centimeters in length. Associated with
the testes, in the composition of what is often called the *testicle*,
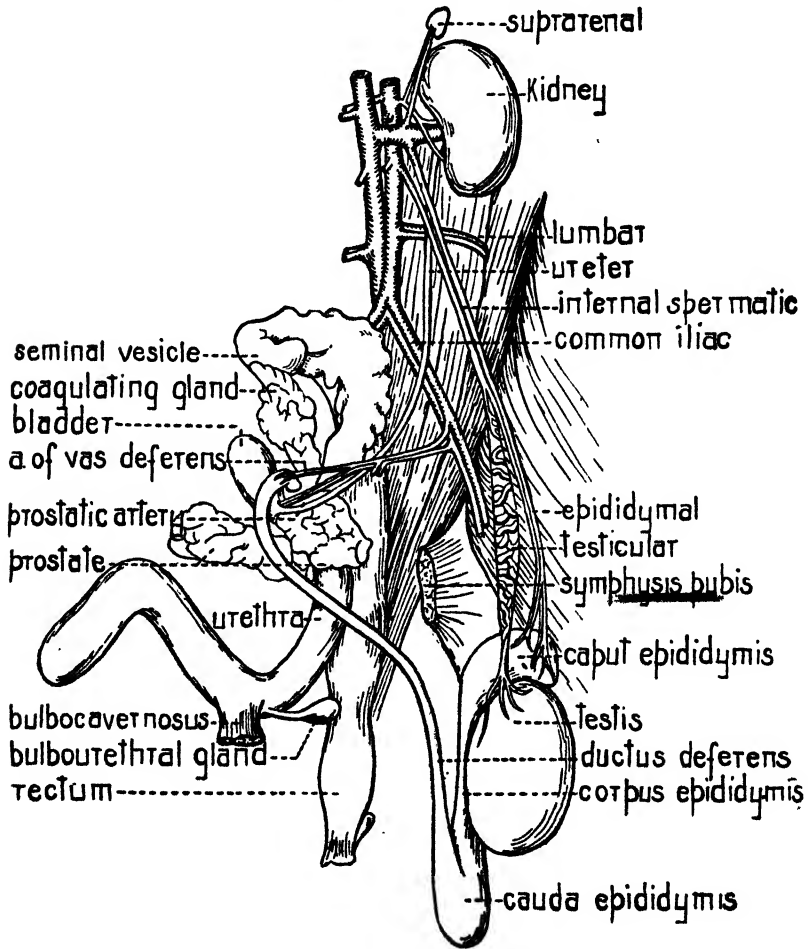
Fig. 45.—Lateral view of a dissection showing male urinogenital system of the
rat. (From Greene, *Anatomy of the Rat,* Transactions of the American Philosoph-
ical Society, New Series, Vol. XXVII, 1935.)

is the tubular *epididymis*. The testis is the reproductive gland. It is
composed of *seminiferous tubules* and interstitial tissue. Sperma-
tozoa are shed from the inner surface of these tubules where they

mature.   With a microscope it is possible to study the different stages of spermatogenesis in the epithelial walls of these tubules. The spermatozoa of the rat are somewhat the shape of diminutive harpoons with a head, middle piece, and tail.

The *vas deferens* leaves the scrotum along with the nerve, artery, and vein as the *spermatic cord.* It passes through the *inguinal canal,* then looping anteriorly and dorsally, to pass dorsal to the ureter and return posteriorly to join the urethra (tube from bladder to exterior).   The *seminal vesicle* (vesicular gland) is a conspicuous sac which joins the vas deferens near its point of entrance into the urethra.   The seminal vesicle probably does not store spermatozoa in the rat but is thought to produce an alkaline solution which is mixed with the sperm.   Partially surrounding the urethra at this point and also on the ventral side of the urinary bladder is the *prostate gland.*   Both parts of this gland empty into the urethra. It has been suggested that their secretion assists in the locomotion of spermatozoa as well as their nourishment in rodents.   The urethra leads on through the length of the penis as a common excretory and reproductive canal and ends in a slit in the end of the glans.

Rats are sexually mature at two or three months of age.   Ovulation (discharge of mature ova from the ovary) occurs at intervals of about three weeks after maturity in the female, except during pregnancy.   This continues until the age of 15-18 months, when ovulation ceases.   The stoppage of sexual activity at this time is known as *menopause.*

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CHAPTER VII

CHORDATES IN GENERAL

Phylum Chordata (kôr dā′ tȧ, cord) is made up of the group of animals which includes man himself and in general the more conspicuous, better known animals. There is a rather wide range of variation as to form and size in the group. It includes minute sessile forms, small colonial forms, mud-burrowing forms, and on up to the largest and most complex of living animals.

Characteristics

All individuals classified in the phylum possess three distinctive characteristics that are most conspicuous in certain primitive forms. The three features clearly distinguish the phylum from all others and bind together individuals which are widely separated in appearance but characterized by certain traits peculiar to this group alone. These three characteristics are: (1) *notochord,* a flexible rod extending from anterior to posterior in the longitudinal axis of the body, lying dorsal to the digestive tube and ventral to the nerve cord; (2) *pharyngeal clefts* or gills, a series of paired slits in the wall of the pharynx and in the body wall of some; (3) *dorsally located tubular nerve cord,* extending the length of the body dorsal to the notochord and other organs.

The notochord serves as a stiffening rod and is the foundation axis for the endoskeleton. It is present as such at some time during the life of every chordate animal. In the adult vertebrate it is replaced by the centra of the vertebrae. The gill clefts are present at some time in the life of all individuals placed in this phylum. Although the gills become modified to form other structures in the adult terrestrial chordates including man, they have had rather typical ones as embryos. The pharyngeal clefts or gills provide a more effective mode of respiration for aquatic animals than that used by most nonchordates because the gills are thus interposed directly in the course of the circulation, and the entire blood supply of the body passes through them. The central nervous system is derived from the ectoderm along the middorsal line of the embryo, first as a plate, then as a groove, and finally a tube which results in the spinal cord and brain. In higher forms the anterior end of the tube be-

comes expanded and modified to form the brain. The continuous tubular nerve cord is at the apex of the development of centralization in the nervous system, and allows for an increase in number of nerve cells, increased accessibility, and more intimate association of ganglionic masses to furnish better coordination. These are all advances in both structure and function when compared with other groups. The chordates possess segmentation (metamerism), but it is progressively obscure as one proceeds from simpler to more complex forms. There is a tendency toward fusion of *metameres* and shifting of superficial muscles. The internal skeleton of this group compared with the external one of others to be studied does not give as great a leverage for the muscles, but it greatly increases the mechanical freedom allowed and this is a distinct advantage as well as an advance in structure.

Classification

There are approximately 40,000 different species in this phylum which is divided into four established subphyla as follows:

Hemichorda (hĕm ĭ kôr′ dȧ, half cord) or sometimes known as Enteropneusta (ĕn tēr ŏp nūs′ tȧ) includes order *Balanoglossida* with its four families, ten genera and twenty-eight species, and order *Cephalodiscida* with its two genera *Cephalodiscus* and *Rhabdopleura*. These are all small wormlike animals.

Urochorda (ū rō kôr′ dȧ, tail cord), or Tunicata (tū nĭ kā′ tȧ) includes the tunicates, all of which are marine and mostly small. Adults show a high degree of degeneration so it is the larvae only that exhibit distinctive characteristics of the phylum. *Molgula, Cynthia, Appendicularia,* and *Salpa* are examples.

Cephalochorda (sĕf ȧ lō kôr′ dȧ, head cord) includes approximately twenty-eight different species of marine, shore-loving, fishlike forms of which *Amphioxus (Branchiostoma lanceolatus)* is the most common representative.

Vertebrata (vēr tē brā′ tȧ, jointed) animals with backbone—frog, man. These are the larger, more conspicuous animals. In most recent classifications this subphylum is divided into seven classes; however, the second is sometimes found as a subclass under the third. These classes are as follows:

Cyclostomata (sī klō stō′ mȧ tȧ, circle and mouth). Round-mouthed fish with only median fins, unsegmented notochord, and jawless. Lampreys and Hagfish.

Elasmobranchii (ē lăs mō brăn' kǐ ī, metal plate and gills). Fish with jaws, cartilaginous skeleton, persistent notochord, and placoid scales. Sharks, Rays, and Chimaeras.

Pisces (Pǐs' ēs, fishes). True fish with bony skeleton, gill respiration, with jaws and paired lateral fins. Catfish, Perch, Bass.

Amphibia (ăm fǐb' ǐ à, both lives). Cold-blooded, nonscaled aquatic and terrestrial vertebrates with five-fingered, paired appendages. Most of them breathe by gills in the larval stage and by lungs in the adult. Toads, Frogs, and Salamanders.

Reptilia (rĕp tǐl' ǐ à), crawling). Cold-blooded forms which are fundamentally terrestrial, usually possessing a scaly skin and breathing by lungs. Turtles, Lizards, Snakes, and Crocodiles.

Aves (ā'vēz, birds). Warm-blooded, erect forms possessing feathers. The forelimbs have become wings. All birds.

Mammalia (mă mā' lǐ à, mammary or breast). Warm-blooded vertebrates with hair and with mammary glands for suckling the young. Cats, Men, Monkeys, Whales, Seals, Bats, etc.

Phylogenetic Advances of Chordata

(1) Notochord and endoskeleton, (2) pectoral and pelvic girdles with limbs, (3) development of dorsally located nerve cord with anterior brain, (4) development of five senses, (5) pharyngeal gills and lungs for respiration, (6) voice production, (7) specialization and coordination of muscles.

Protochordata (lower chordates). Until relatively recent years the two subphyla, Hemichorda and Urochorda, were not classified as Chordata; the former was with Annelida and the latter was independent. With the exception of the value as biological specimens and the use of amphioxus as food by Chinese, this group is of no economic importance.

Subphylum Hemichorda

Dolichoglossus, kowalevskii is the common example studied. It is a wormlike animal which burrows into the mud and sand along the seashore. They range from 6 to 10 inches in length. Others of the genus may be as short as one inch or still others as long as four feet. The three portions of the body are proboscis, a ringlike collar, and a segmented trunk. The proboscis, as well as the collar, is hollow and serves as a water chamber. The cavity of the proboscis is filled

with water which is drawn in and expelled through a *proboscis pore* or vent located on its dorsal side and just anterior to the collar. Supporting the base of the proboscis is a short skeletal process which is stiff and extends anteriorly from the roof of the mouth region and assists in burrowing. This process, called the *diverticulum,* is usually referred to as the *rudimentary notochord.* However, it is very poorly developed and in a peculiar position. Nevertheless, it has the relationship to the digestive tube which is characteristic in the embryonic development of the notochord for certain higher chordates.
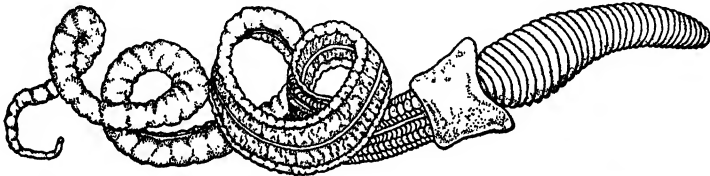
Fig. 46.—External features of *Dolichoglossus kowalevskii.* (Courtesy of Denoyer-Geppert Company.)
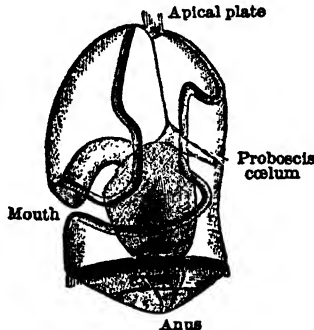
Fig. 47.—Tornaria larva of *Hemichorda.* (From Hegner, *College Zoology.* The Macmillan Company, after Metchnikoff.)

The mouth opens on the ventral side just anterior to the collar and leads into the straight alimentary canal which extends to the posterior end of the body and ends in the *anus.* Like the earthworm, this animal utilizes the mud in which it lives for food, absorbing the organic matter from it as nutriment. Balanoglossus has numerous paired gill slits, located in the lateral walls of the anterior (supposedly pharyngeal) position of the digestive tube. In some of the other representatives the gills are much reduced in numbers or are lacking. Where gills are present, water is passed through them for

respiratory purposes, oxygen being absorbed and carbon dioxide being discharged from the blood here. There is no differentiation of a distinct pharynx.

The **nervous system** is composed of a dorsal cord which is tubular in the region of the collar and extends the length of the trunk, a more or less concentrated center of nerve cells in the collar, and a ventral cord running longitudinally on the floor of the trunk. The ventral cord certainly is not a chordate characteristic, but the dominance and hollow structure of the anterior portion of the dorsal one represent features which are homologous to the central nervous system of higher chordates.

These animals are dioecious, with *gonads* in the form of a genital ridge extending lengthwise along each side of the anterior portion of the trunk. The mature germ cells escape through the body wall, are fertilized in the water, hatch out and become *tornaria* larvae, which are globular in shape and form a pattern of ciliated bands over the body. In this respect and in habit of life these larvae resemble the larvae of the echinoderms. On this basis a theoretical relationship has been proposed. Until relatively recent times this larva was mistaken for a form of adult nonchordate animal and went under the genus name of Tornaria.

Balanoglossus and other representatives of its subphylum, though lacking in complete conformity to chordate characteristics, are classified here because of the diverticulum supposedly representing a rudimentary notochord, the gill clefts in the alimentary canal, and the dominance and grooved structure of the dorsal nerve cord.

Subphylum Urochorda, Molgula

Subphylum Urochorda includes a number of common representative marine forms, such as *Salpa, Cynthia, Ciona, Clavelina, Ascidia,* and *Molgula*. The latter genus represented by *M. manhattensis* will be given particular consideration here. This animal is commonly known as sea lemon, sea peach, or sea squirt. The body of the adult is saclike and averages about one inch in diameter. In this condition it would be an outcast among chordates because as an adult it has no notochord, and no dorsally located, tubular nerve cord. However, it does present pharyngeal gill slits.

It is saved to the chordates by the presence of all three of the characteristic features in the larval stage. The larva is free-swimming and shaped like a tadpole, while the adult is globular and sessile

in most of the common forms. Some are brilliantly tinted with color. The adult is covered externally by a cellulose coat or *tunic* (test), which is secreted by the cells of the underlying *mantle*. Inside the mantle is the extensive *atrial cavity*. On the dorsal (unattached) side of the body are two funnellike siphons. The anterior one is the *branchial siphon* (oral funnel or incurrent siphon or mouth) and the other is the *atrial siphon* (atrial funnel, excurrent siphon, or atriopore). When the tunic of *Molgula* is removed, one may see most of the internal organs through the transparent mantle.

These animals are hermaphroditic or monoecious. Each has two compound sets of gonads, one on the left side in the loop of the intestine and the other on the right side of the body. Some of the
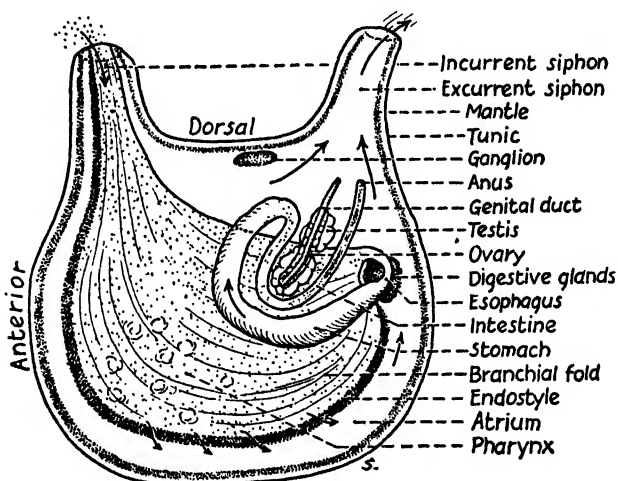
Fig. 48.—Diagram of *Molgula manhattensis* from the left side to show the structure with the courses of water and food indicated by arrows.

sessile tunicates, as *Molgula,* reproduce by budding. The life history of the tunicate is one of interest. Cross-fertilization is the rule; that is, spermatozoa from one individual usually fertilize ova from another; however, there may be exceptions to this. The fertilization occurs in the water outside the body. The eggs hatch to produce larvae somewhat similar to amphibian tadpoles which are free-swimming. The larva possesses the typical notochord, gills, and nerve cord of Chordata. For some reason it then settles on the bottom and attaches itself by adhesive papillae located in the anteroventral position. Some authors express it by saying this larva settles on its

"chin." It now undergoes regressive changes involving loss of tail, notochord, and posterior portion of nerve cord. The anterior portion of the cord becomes a simple ganglion. The paired eyes and otocysts (ear structures) also disappear. This process of metamorphosis has caused an active respectable chordate to become a lazy, stationary form which is not much more than a water-bag whose level of development has degenerated almost to that of a sponge. In a few instances tunicates reproduce one generation sexually, and the next is produced by budding (asexually). This alternation of generation is another retrogressive feature.

Subphylum Cephalochorda, Amphioxus

There are usually listed twenty-eight species in this group which are rather locally distributed over the world. There are four species on American shores: *Branchiostoma virginiae, B. floridae, B. bermudae,* and *B. californiense.* Amphioxus or the lancelet, *Branchiostoma lanceolatus,* the European form, is an admirable representative of the subphylum and has become classical in its use. However, it is likely that *B. virginiae* or *B. floridae* is more commonly studied in the United States. It is a small, fishlike, marine animal whose average adult length is about two or three inches. In its adult form it represents clearly the distinctive characteristics of the phylum in a simple condition. It is usually referred to as.a close ancestral relative of the Vertebrata.

Habitat.—It is found in shore water and on the sandy beaches of the subtropical and tropical portions of the world. These animals are found along our Atlantic Coast as far north as Chesapeake Bay, at certain points in the Gulf of Mexico, and on the southern Pacific Coast. They may be found along the shores of the Mediterranean Sea, the Indian Ocean, and along the southern coasts of China.

Habits and Behavior.—It burrows rapidly, head first, in the sand by means of a vibratory action of the entire body, but comes to rest with the anterior end exposed to the water. At times, particularly at night and during breeding season, the animal leaves the burrow and swims about like a fish by means of lateral strokes of the posterior portion of the body.

External Structure.—The body of this animal is shaped like a small lance, the tail being the point. In general, it is similar to a small fish, but it does not have a distinct head. The *mouth* opens
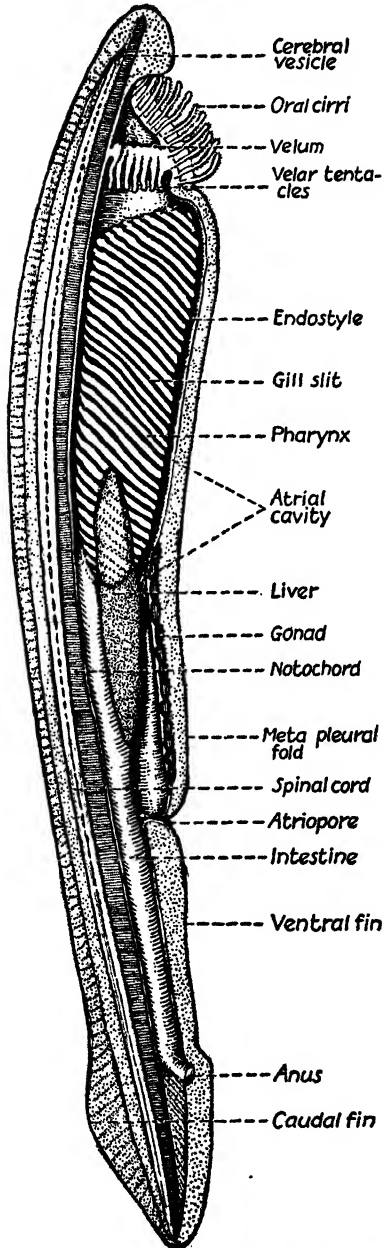
Fig. 49.—Diagram of Amphioxus (*Branchiostoma lanceolatum*) from the right side, showing the structure.

on the ventral surface of the anterior portion of the body.   There are
no clearly defined lateral fins, but a pair of skin structures, the
metapleural folds, extending along the anterior two-thirds of the ven-
tral surface of the body are thought to be their forerunners.   The
ventral and dorsal fins are supported by small vertical rodlike *fin
rays.*   On the ventral side, just posterior to the metapleural folds, is
an opening, the *atriopore,* and beside the ventral margin of the caudal
fin is the *anus.*   The segmental divisions of the muscles are apparent
on the body wall, and they are known as *myotomes.*   The myotomes
on the two sides are not paired, but alternate with each other. Adja-
cent ones are separated by a myocomma or myoseptum.
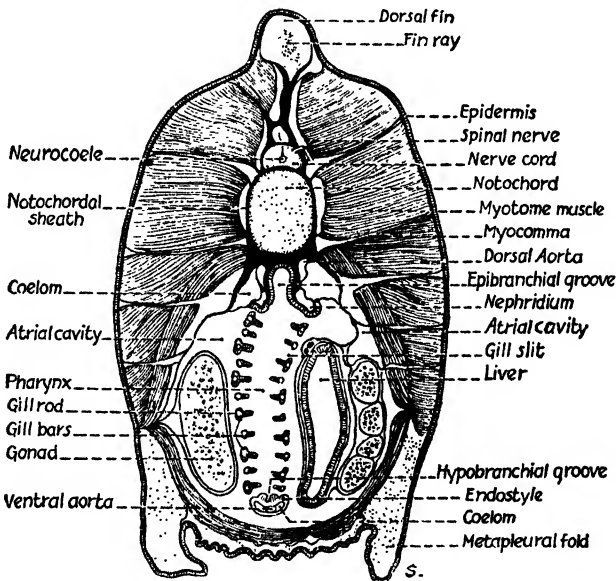
Fig. 50.—Cross section of Amphioxus through the level of the posterior portion of
the pharynx.

Internal Structure and Metabolic Activities.—The *notochord* ex-
tends the length of the body as a slender rod of vacuolated cells
which are filled with fluid to give it turgor or stiffness.   Immediately
dorsal to this rod is the *nerve cord,* which also runs the length of the
body.   It has a small central canal or *neurocoele* extending length-
wise through it and is dilated at the anterior end to form the *cerebral
vesicle* or rudimentary brain.   A mass of dark pigment is located at
the anterior end which is known as the eyespot.   There are smaller
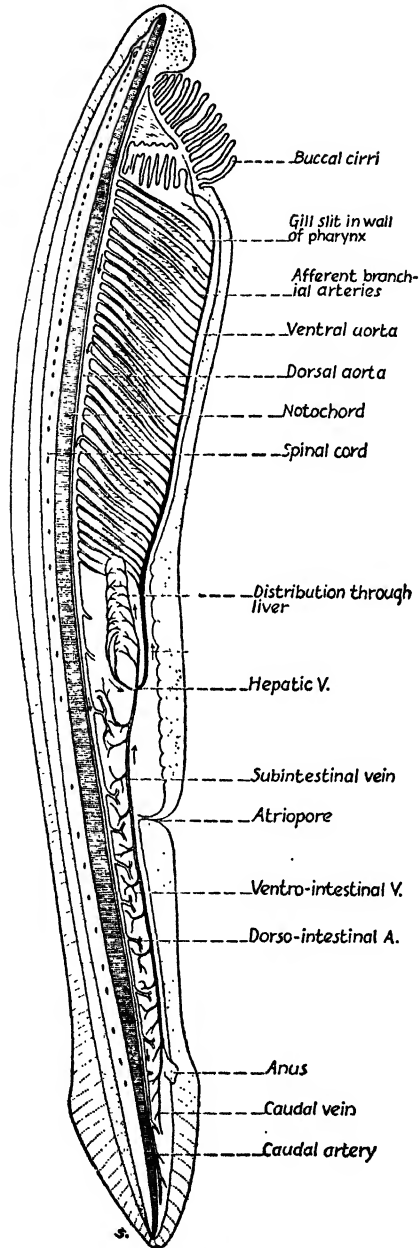
Fig. 51.—Circulatory system of Amphioxus.

pigment bodies distributed along the length of the cord. These are thought to be sensitive to light. The nerve cord gives off nerves to the organs of the body.

The **circulatory system** does not include a heart, but the blood is moved by the contractions of a *ventral aorta,* which branches to form the *afferent branchial arteries* to the gills. Here these vessels branch into capillaries, providing aeration for the blood. These capillaries converge to form the *efferent branchial arteries* which lead dorsally to join those from the opposite side in forming the *dorsal aorta.* The dorsal aorta extends posteriorly to the tip of the body giving off numerous branches to myotomes and internal organs along the way. The posterior direction of the flow of the blood is just opposite to that in the dorsal vessel of the earthworm. The *subintestinal vein* receives the blood from the intestine and continues anteriorly to the liver as the *hepatic portal vein.* The *hepatic vein* collects from the liver and leads forward as the ventral aorta. The blood in the subintestinal and hepatic portal veins is laden with dissolved nutriment. The blood in these ventral veins flows from posterior toward the anterior.

Digestive System.—A current of water is carried into the mouth by the ciliated bands on the inner surface of the oral hood. Surrounding the mouth is a membranous *velum* to which are attached twelve *velar* tentacles, which fold across the mouth and serve as a strainer to hold back the coarser particles, as well as being sensory. The mouth leads to the large, barrel-shaped pharynx. The gill slits are clefts in the lateral walls of the pharynx. These open into the atrial cavity which surrounds the pharynx and other visceral organs. In the midline of the roof of the pharynx is an inverted trough, the *hyperbranchial groove,* which is ciliated. In the floor of the pharynx is the *hypobranchial groove* in whose walls is located the glandular *endostyle,* capable of secreting mucus. The endostyle functions on the same plan here as in tunicates. The strings of mucus entangle the food particles and are moved anteriorly, and then by *two peribranchial grooves* are carried dorsally to the hyperbranchial groove. The cilia here move the mass back to the intestine. A blind, fingerlike diverticulum of the intestine, the *liver* or *hepatic caecum,* extends anteriorly from its connection on the anterior part of the intestine to lie on one side of the pharynx. This organ is a digestive gland and empties a digestive juice containing enzymes into the

intestine. The intestine extends posteriorly to the *anus* as a relatively straight tube. The food is digested in, and absorbed from, the intestine.

Respiratory System and Respiration.—As stated above, the water in passing through the gill slits delivers oxygen to the blood in the capillaries there and absorbs carbon dioxide from it. The water then passes back through the atrial cavity and out through the atriopore. The blood then distributes the oxygen to all tissues of the body. The *gill-bars,* which separate the slits and support the gills, contain the blood vessels, and are supported by chitinous rods.

Excretory System and Excretion.—Ciliated *nephridia* similar to those of the earthworm lead from the dorsal portion of the coelom to the atrial cavity. The coelomic cavity is reduced in the pharyngeal region to a narrow space surrounding the dorsal aorta above the pharynx and a narrower one around the ventral aorta below. Between the posterior end of the pharynx and the atriopore, the coelom consists of a narrow space surrounding the intestine. Behind the atriopore it is relatively larger.

Reproductive System and Life Cycle.—This animal is dioecious with each mature individual possessing 26 pairs of (31 to 33 pairs in *B. californiense*) nodular *gonads* embedded in the body wall near the base of the metapleural folds. When the germ cells mature, they break through the wall of the gonad into the atrial cavity and pass out through the atriopore with the water. *Fertilization* occurs in the water. Following fertilization comes a series of *cleavage divisions* which are total and equal. This is followed by the infolding of one side of the spherical body to form the *gastrula* and this in turn becomes a free-swimming *larva* which reaches adult condition without metamorphosis.

The Vertebrate Animal: Subphylum Vertebrata

In this group to which man himself belongs are found the distinctive chordate characteristics at some time in the life of the individual. Metamerism and bilateral symmetry are universal characteristics among vertebrates. The *segmented vertebral column* and other supporting structures form an endoskeleton (internal skeleton) which is the basic support of the body. *Paired appendages* are usually present at some time in the life of the individual. The majority have two pairs of fins or limbs in adult condition. There is a ven-

trally located *heart* which is divided into chambers. The *blood* contains *hemoglobin-bearing red corpuscles* and amoeboid *white* corpuscles. In the vertebrate body is a well-developed *coelom,* which encloses advanced systems of organs for digestion, excretion, circulation, reproduction, and, in terrestrial forms, respiration. *Cephalization* is developed in all vertebrates and along with this they possess a hollow, five-lobed brain located in the more or less distinct *head.* The *sense organs* are in an advanced state of development. The body is divided into head, trunk, and tail. The *tail* is a posterior prolongation of the body behind the anal opening and is found in some degree in all vertebrates. The *neck* which is a constricted region between trunk and head is conspicuous in terrestrial forms. The appendages are usually arranged with one pair attached to the anterior, pectoral portion of the trunk and one situated at the posterior, pelvic region. This arrangement is less consistent in the aquatic types where the weight of the body is buoyed up by the water and the limbs are used less for support and locomotion. In different types of vertebrates there are various modifications of pectoral appendages as arms, wings, pectoral fins, forelegs, and flippers. The same is generally true for the pelvic limbs.

The vertebrate animal is covered by an *integument* or *skin* which serves as a protective and sensory organ. It also helps in excretion through the *sweat glands, mucus glands,* and *oil glands* as well as facilitating temperature regulation in some. Such exoskeletal structures as scales, nails, hoofs, claws, feathers, hairs and enamel of teeth are produced by the skin.

The skeleton is quite well developed in the vertebrates and serves them quite efficiently for support, stature, protection, and muscle attachment. It is composed of *cartilage* entirely in some of the simpler forms and of bone and cartilage in higher types. The exoskeleton is a rather minor part in vertebrates and consists of nails, claws, scales, hair, feathers, and other outgrowths. The endoskeleton includes the *axial* and *appendicular* portions. The first is composed of the skull, vertebral column, ribs, and in some a sternum. The appendicular portion is composed of the anterior and posterior girdles and two pairs of limbs. The vertebral column is composed of segmental divisions, the *vertebrae,* and is divided into five regions as follows: *cervical vertebrae* of the neck, *thoracic vertebrae* of the chest, *lumbar vertebrae* of the small of the back, *sacral vertebrae* of the hip region, and the *caudal vertebrae* of the tail region.

DIVISIONS OF SKELETON OF TERRESTRIAL VERTEBRATE

I. Axial Skeleton
   (a) Skull
      1. Cranium
      2. Sense capsules
      3. Jaw apparatus
         (Visceral arches)
   (b) Vertebral column
      1. Cervical vertebrae (neck)
      2. Thoracic vertebrae (chest)
      3. Lumbar vertebrae (small of back)
      4. Sacral vertebrae (hip)
      5. Caudal vertebrae (tail)
   (c) Thoracic basket
      1. Ribs (paired)
      2. Sternum (breastbone)

II. Appendicular Skeleton (girdles and limbs)
   (a) Pectoral (anterior)
      1. Girdle: scapula, clavicle, procoracoid and coracoid
      2. Limb: Humerus (upper arm), radius and ulna (forearm), carpals
         (wrist), metacarpals (palm), phalanges (bones of digits)
   (b) Pelvic (posterior) .
      1. Girdle: ilium, pubis, and ischium
      2. Limb: Femur (thigh), patella (knee cap), tibia and fibula (shank),
         tarsals (ankle), metatarsals (sole), phalanges (bones of toes)

The **muscular system** represents a system of cells highly specialized in contractility. *Voluntary* muscles are usually connected with the skeleton; those of the visceral organs, e.g., intestine, are involuntary. *Cardiac* muscle is the highly specialized involuntary muscle which makes up the wall of the heart.

The **digestive system** is typically a straight tube extending through the length of the trunk of primitive vertebrates. In the higher forms there are many outgrowths, such as digestive glands and respiratory organs. The anterior region of the digestive tube is the *mouth cavity* which contains teeth on the jaws, a tongue, and receives saliva from salivary glands. Following the mouth is the pharynx or throat region. Next comes the *esophagus* which is usually tubular and propels the "swallows" of food posteriorly by consecutive waves of contraction, a process known as *peristalsis*. It leads to the saclike *stomach,* whose walls possess gastric glands for secretion of a digestive fluid containing enzymes (ferments) and weak hydrochloric acid. The peristaltic contractions continue along the

wall of the stomach to help digestion by churning and mixing the food with digestive juices. At the posterior end a *pyloric* valve in the form of a sphincter muscle guards the entrance to the small intestine which follows. This is the convoluted intestine which is divided into the anterior *duodenum*, middle *jejunum*, and posterior *ileum*. Its walls produce digestive enzymes from glands and it receives digestive juices from two other glands: the liver and the pancreas.
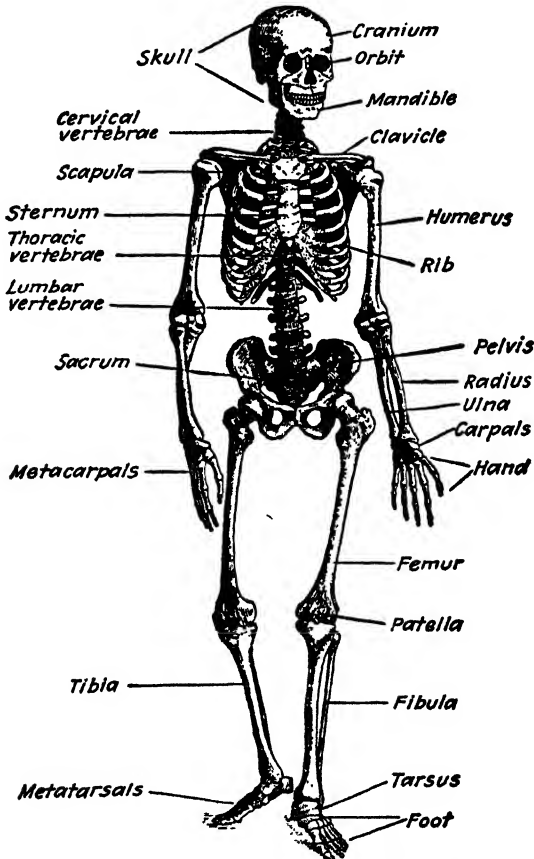
Fig. 52.—Human skeleton. (From Wolcott, *Animal Biology*, McGraw-Hill Book Company, Inc.)

The digested food is taken up by the lymphatic spaces and by blood vessels which are embedded in the wall just outside of the lining epithelium. The liver is the largest organ in the body of

most vertebrates. It secretes the bile and also serves to convert carbohydrates to *glycogen* (animal starch) to be stored for future energy production. It is also in the liver that protein wastes are converted into urea and uric acid in order that they may be excreted from the blood in the kidneys. The *large intestine* which is shorter than the small intestine possesses no villi or digestive glands. It receives the fecal matter and delivers it to the anus. The chief function of this entire system is that of dissolving and converting complex food materials into a form which may be absorbed and assimilated by the protoplasm of cells throughout the body.

The **respiratory system** is at least in part an outgrowth of the digestive canal. In most aquatic vertebrates respiration is accomplished by drawing water through gill slits in the wall of the pharynx. Air-breathing, terrestrial forms have developed the trachea (windpipe) and lungs as another outgrowth of the pharynx. A certain amount of respiration takes place through the skin. The respiratory process is composed of two phases: *external respiration* which includes the exchange of the gases, oxygen and carbon dioxide, between the external medium and the blood; and *internal respiration* which is the exchange of the gases between the blood and the protoplasm of the cells over the body. Hemoglobin in the red corpuscles of the blood has a loose affinity for oxygen, is capable of carrying it, and then gives it up at points where there is demand for it. Much of the carbon dioxide given up by the cells becomes carbonic acid and carbonates which may be transported by the plasma (fluid) of the blood.

The **circulatory system** is a closed system of vessels supplying all parts of the body with blood and a system of spaces, sinuses, and vessels collecting lymph from the various organs to return it to the blood vessels. The blood circulatory system centers in a contractile heart from which tubular *arteries* lead out to various organs of the body where they branch into minute vessels or *capillaries*. The capillaries converge as they carry the blood away from the organs to form the veins which carry the blood back to the heart. This is a closed system of vessels. The blood is composed of the clear fluid, *plasma,* and the *blood corpuscles.* The red corpuscles contain the red pigment matter, hemoglobin with oxygen-carrying power. The white corpuscles or *leucocytes* are of several varieties and they are amoeboid in character. These cells may make their way among cells of other

tissues where they engulf bacteria and foreign matter. Upon exposure to air the dissolved *fibrinogen* in the blood becomes fibrin and forms a *clot* which is semisolid and blocks flow of blood from most wounds. The remaining fluid after the blood clots is called *serum*. Lymph is a fluid similar to plasma which has seeped through the walls of the capillaries in the various organs, and it carries amoeboid white corpuscles.
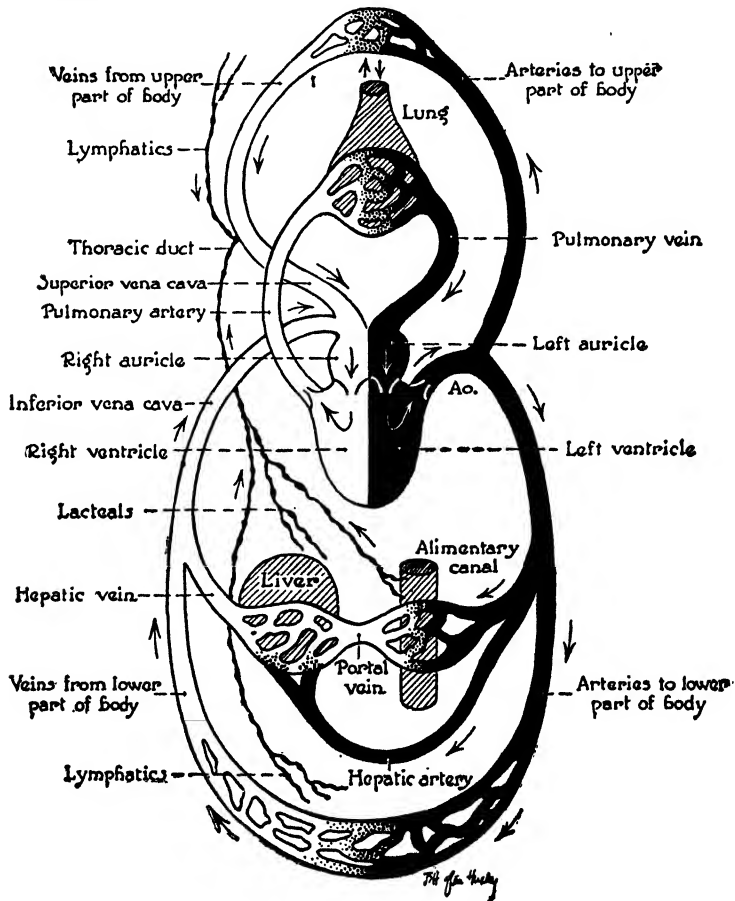
Fig. 53.—Diagram of circulation of a mammal. The oxygenated blood is shown in black; the venous blood in white. The lymphatics are black irregular lines. (From Pettibone, *Physiological Chemistry*, The C. V. Mosby Company.)

The excretory system of vertebrates consists of kidneys, excretory ducts, and often a urinary bladder. The kidneys serve to remove

from the blood, waste nitrogen products and excess salts in solution as well as to dispose of excess water. The life history of higher vertebrate individuals includes successive stages as follows: the pronephros, the sole kidney for a time; followed by the mesonephros which is the dominant functional excretory organ; and, finally, the development of the metanephros with retrogression of the others. This is an illustration of the *Theory of Recapitulation* which says that each individual in its development lives through abbreviated stages of the history of the development of the race, since these transitional stages represent adult kidneys for more primitive vertebrates.
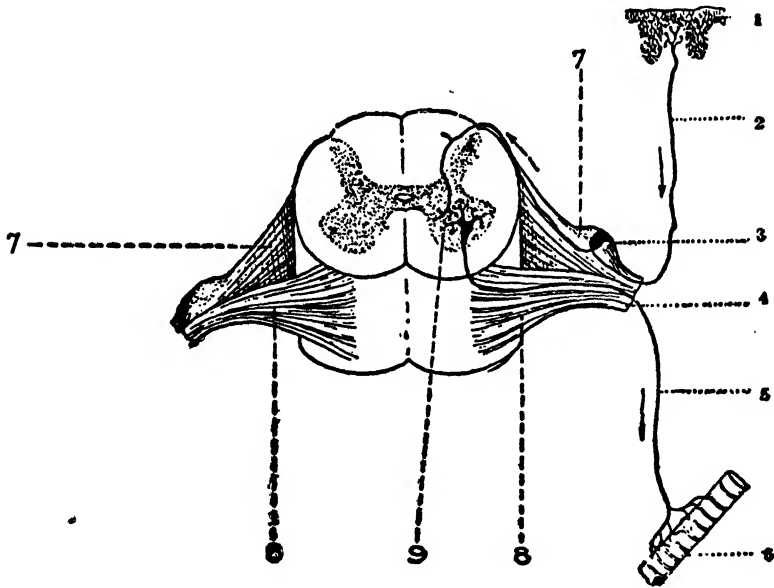
Fig. 54.—Cross section of spinal cord and roots of the spinal nerves, showing a simple reflex circuit. *1*, Sensory surface of skin; *2*, afferent nerve fiber with *3*, its cell of origin, located in the spinal ganglion; *4*, cut end of spinal nerve; *5*, efferent nerve fiber; *6*, voluntary muscle; *7*, dorsal root of spinal nerve; *8*, ventral root of spinal nerve; *9*, dendrites of motor nerve cell body in gray matter of the cord. (From Zoethout, *Textbook of Physiology*, The C. V. Mosby Company, after Morat.)

The **nervous system** in this type of animal is composed of a *brain* and *spinal cord* forming the *central nervous system; nerves* extending to all parts of the body, *ganglia* which are groups of nerve cell bodies outside the central nervous system, and the sense organs which serve for receiving stimuli are usually grouped together under the name *peripheral nervous system*. A portion of this latter division, consisting of two longitudinal trunks with ganglia distributed along

them, lies parallel to the spinal cord, and constitutes the *autonomic system*. The peripheral system includes ten to twelve pairs of *cranial nerves* from the brain, and ten to thirty-one pairs of *spinal nerves* in different forms of vertebrates. Each spinal nerve has two roots where it joins the spinal cord.

A high development of sense organs for the senses of *sight, hearing, smell, taste,* and *touch* is characteristic of vertebrates. The organs are *receptors* and they are stimulated by changes in external environmental conditions, such as light, sound waves, chemical changes, and contact. The eye, which is the organ of sight, is a highly developed organ. It is constructed on the plan of a camera with the eyeball forming the light-tight box.

The *ear* structures provide most classes of vertebrates with facilities for two functions: hearing and equilibrium. This organ consists of an *external ear*, which serves in catching and directing sound waves within, a *middle ear* or *tympanum*, containing ossicles, and the *inner ear*, which contains the sensory *cochlea* with its *organ of Corti* for hearing, and the *semicircular canals*, which are concerned with equilibrium rather than hearing. The latter are common to all vertebrates while the cochlea is limited to Amphibia and higher classes.

The sense of *smell* is centralized in the epithelial lining of the nasal chamber. Special olfactory cells are stimulated by particles of material from the air dissolving on this membrane and making contact with the sensory cells. The sense of *taste* is similar except that it is located in sensory cells in *taste buds* on the tongue, epiglottis, and lips (and barbels of some vertebrates). The particles come in by way of food and drink and as the material dissolves, it reaches the taste cells.

Most of the tactile and pressure sense organs are located just beneath the skin over different parts of the body. A few of the pressure sense organs are found in certain of the internal structures of the body. The lateral line system in fishes is sensory to vibrations carried in the water and is quite important to aquatic animals of this type.

The vertebrate **reproductive system** shows a fairly high degree of development. The sexes are almost universally separate, with the exception of some cyclostomes. The distinct gonads develop to produce special germ cells. The male gonads are *testes*, and they produce *spermatozoa* which are carried from the gonads by the *vasa*

deferentia. The female gonads are *ovaries,* and they produce *ova* or *eggs*. They are carried from the body by *oviducts*. The males of some classes possess for use in copulation certain accessory organs, which tend to insure fertilization.

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CHAPTER VIII

PHYSIOLOGY

The maintenance of any living body requires the cooperation of several functions which will attain similar fundamental results wherever they occur in living material. The principal functions performed by the structures in the animal body are: (1) support and protection, (2) movement and locomotion, (3) digestion, (4) respiration, (5) circulation, (6) excretion, (7) reproduction, (8) reception and conduction of stimuli, and (9) internal regulation. These functions merge into one living process which involves the building up of protoplasm, transformation of energy, and reproduction. During the execution of these activities energy is constantly being changed from the potential to the kinetic form.

The collective term *metabolism* is employed when referring to all of the interactions involved in the living process of protoplasm. It includes the processes concerned with conversion of food into protoplasm, release of energy through oxidation, production of heat, movement, elimination of wastes, or in other words these processes are chiefly: *ingestion, digestion, egestion, absorption, transportation, assimilation, respiration, oxidation,* and *elimination.* The processes concerned with the conversion of food material into protoplasm (building up) constitute the phase of metabolism known as *anabolism.* Included here are ingestion, digestion, absorption, transportation, and assimilation. The oxidation of materials of the protoplasm to liberate energy, and the elimination of wastes incidental to it, is known as *catabolism* or the "breaking down" phase.

Metabolism is one of the fundamental features of all protoplasm; therefore all physiology, since it is a study of the functions of living organisms, must be concerned with metabolism. It includes all of the chemical changes and transformations by which energy is supplied for the activities of the protoplasm. For convenience, the several functions will be discussed separately with the thought of bringing out their expression in different types of animal life.

Support and Protection

In Protozoa there is no very elaborate adaptation in this direction. The presence of a cuticle in some and the secretion of a hard

shell in others seem to be the particular developments related to these special functions in this group.

The skeleton and integumentary structures serve the Metazoa primarily for a support and protection. The corals of the phylum Coelenterata secrete a calcareous or horny skeleton around the external surface of the body proper. The sponges, as a rule, each have a calcareous, siliceous (glassy), or horny skeleton extending throughout the body. Such forms as snails, crayfishes, beetles and representatives of their respective phyla secrete a well-developed exoskeleton as an external cover over most of the other tissues of the body. The muscles and other tissues are attached within. There are special cells of the epidermis which function primarily in production of this skeletal material. The echinoderms, including animals like the starfish, possess calcareous skeletal plates which are essentially similar to exoskeleton except that they are principally beneath the skin.

There is no well-developed *endoskeletal* structure known in non-chordate animals but the endophragmal structures extending into the thorax of some Crustacea are thought to be the forerunner of the endoskeleton. A number of exoskeletal modifications are used for protection and temperature regulation in most of the groups of vertebrates. Such structures as scales, shells, feathers, hair, nails, horns, and even enamel of teeth are of this type.

Primitively the *notochord* is the original *endoskeletal* structure of the chordate group. Around it are developed the basic structures of the vertebral column which functions as the principal axial support of all vertebrates. The sternum, girdles, and paired limbs have developed with the terrestrial life of vertebrates and the necessity for locomotion on land.

Bone is a firm, hard tissue consisting of abundant *matrix* composed of inorganic salts, and the bone cells which are held in pocketlike *lacunae* in the matrix. The outer membranous covering of bone is called *periosteum*. The mineral part of the bone consists chiefly of calcium phosphate and calcium carbonate. They give it firmness and rigidity. The animal matter is composed of the bone cells and cartilage which serve to give the bone life and resilience. A weak acid, such as the acetic acid in vinegar, will dissolve the mineral matter of the bone if allowed sufficient time, in which case the bone will lose its rigidity. Caustic solutions will destroy the animal matter and make the bone brittle.

Movement and Locomotion

Independent power of movement is almost a characteristic of animal life. *Contractility* as a property of all protoplasm is the fundamental basis for all animal movement. The adult forms of certain animals, such as sponges, corals, oysters, barnacles, and others, are sessile; however, they all pass through a free, active larval stage. Most of them retain the power to move separate parts in adult condition. Simpler forms of *locomotion* are seen in Protozoa which move from place to place by means of *pseudopodia, cilia,* or *flagella.* In ciliary movement the numerous small strands of protoplasm beat rhythmically with a stroke in one direction, so timed that the beat passes in a wavelike progression from one end of the ciliated area to the other.

The development of a high degree of contractility in muscle cells makes possible *muscular movement.* A muscular locomotor system consists of sets of opposing muscles. In muscular contraction there is a cycle of rapid chemicophysical rearrangement in the cells. Oxidation and heat production are involved in the process. Carbohydrates in the form of glucose are oxidized (burned) in the reaction. During the shortening of the muscle there is a hydrolysis or absorption of water by the protein product, creatine-phosphoric acid. By-products of the process include carbon dioxide, lactic acid, urea, creatinine, and phosphoric acid.

In animals without a skeleton, muscle bands are arranged in both circular and longitudinal directions. The contraction of the circular group tends to lengthen the body, and the shortening of the longitudinal strands draws the body along. The pressure exerted on the coelomic fluid is thought to be a factor in bringing about an even extension of the body by this means. In echinoderms with the water vascular system the pressure is exerted on water in a system of tubes which extend to make contact with the surface over which the animal is moving.

Digestion

The general function of digestion, which is to convert complex raw food material into a soluble, absorbable form, has already been pointed out. The materials commonly used for foods have large molecules, and are usually colloidal in nature. Digestion then must serve to break up these large molecules into smaller ones, thus forming solutions of substances which will readily diffuse through membranes. Digestive enzymes are responsible for placing the food

materials in solution. By enzyme action, proteins are converted to soluble amino acids, starches and sugars to maltose and finally glucose, and fats to fatty acids and glycerin.

In general, an *enzyme* is an organic substance which by its presence under certain conditions will cause or hasten chemical reaction between other substances without itself being consumed. The enzymes are formed in the protoplasm of cells, and their action is similar to that of a catalyst, since they accelerate chemical action. There are different types of enzymes each capable of producing specific kinds of reactions. There are oxidizing enzymes (oxidases) capable of bringing about oxidation; reducing enzymes (reductases), which produce reduction in tissues; coagulating enzymes (coagulases), which cause clotting or coagulation; and hydrolyzing enzymes (hydrolases), which act by causing a reaction between a substance and water. Most of the digestive enzymes fall in this latter class. Most enzymes consist of a parent substance or precursor, *zymogen,* which becomes active only in the presence of a certain other substance, termed activating agent or *co-enzyme.* As an example, the precursor of pepsin is pepsinogen which becomes activated in the presence of dilute acid.

CLASSES OF DIGESTIVE ENZYMES

1. *Diastases or diastatic enzymes*--split carbohydrates
   (a) Ptyalin in saliva
   (b) Amylase in pancreatic juice
   (c) Glycogenases—liver and muscles
       Converts glycogen to glucose
2. *Lipase or lipolytic enzyme*—splits fats
   (a) Steapsin in pancreatic juice
3. *Inverting enzymes*—convert disaccharids to the less complex monosaccharids
   (simple sugars)—intestinal juice
   (a) Maltase
   (b) Lactase
   (c) Sucrase (invertase)
4. *Proteases or proteolytic enzymes*—split complex proteins
   (a) Pepsin in gastric juice
   (b) Trypsin in pancreatic juice—functions in small intestine
   (c) Erepsin in intestinal juice
5. *Clotting or coagulating enzyme*
   (a) Rennin in gastric juice

In higher Metazoa digestion is accomplished principally extra-cellularly through secretion of enzymes by certain groups of cells. Such systems consist of: (1) an alimentary canal proper; and (2)

associated glands which discharge digestive juices into it. The relative length of this canal varies considerably depending on the habitual diet of the organism. In carnivores (flesh-eaters), such as cats and dogs, it is from three to five times as long as the body; while in herbivorous forms (plant-eaters), such as horses and cows, it is over twenty times as long as the body. The length of the human digestive tract is approximately ten times the length of the body. The relative proportion of the internal absorptive surface of the alimentary canal to the external surface of the body is significant. In carnivorous animals it is about one-half the area of the skin while in herbivorous animals it is about twice the area of the skin.

The process of digestion in man is quite well understood, and it is fairly typical and general because of the omnivorous food habits. The action of the several *enzymes* produced by different glands is a very essential part of the process. The digestion of all organic food materials is brought about by *hydrolysis* in the same kind of chemical change. In hydrolysis the large molecules of protein, carbohydrate, or fat first combine with water and then split into simpler products. Some foods may require more than one such splitting. The splitting of the *disaccharide,* maltose, will serve as an example of this process:

$$C_{12} H_{22} O_{11} \quad + \quad H_2 O \quad = \quad 2 C_6 H_{12} O_6$$
$$\text{(Malt sugar)} \qquad \text{(Water)} \qquad \text{(Glucose)}$$
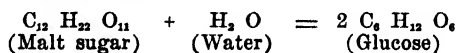
The two molecules of glucose formed are in a form for ready absorption.

Gastric Digestion.—The tubular *gastric glands* located in the mucous layer of the stomach secrete the acid *gastric juice* which is a solution of 0.2 to 0.5 per cent hydrochloric acid and two important enzymes, *pepsin* and *rennin.* The pepsin when present in the acid medium brings about the splitting of complex proteins into intermediate proteoses and *peptones. Rennin* causes the casein in milk to coagulate. This is the first step in its digestion. It is claimed by some that emulsified fats, such as cream, are partially digested by a gastric *lipase.* The digesting mass or chyme in the stomach is continually churned and mixed by muscular activity of the walls. When it becomes saturated (0.4 per cent) with acid and has been reduced to the consistency of soup, it is discharged through the pylorus.

Intestinal Digestion.—When the chyme is ejected through the pylorus into the duodenum, the hydrochloric acid stimulates cer-

tain cells of the intestinal lining, causing them to secrete into the blood a substance of hormone nature, known as *secretin*. Upon reaching the pancreas this secretin stimulates it to secrete the digestive fluid, *pancreatic juice*, into the small intestine by way of the pancreatic ducts. There is some evidence that secretin also stimulates secretion in the liver.

Pancreatic juice is a clear, watery, alkaline solution containing inorganic salts (carbonates, etc.) and three enzymes; the protease, *trypsin*, the diastase *amylopsin*, and the lipase, *steapsin*. These act respectively on proteins and peptones, starches and sugars, and fats. This protease is in the form of *trypsinogen* until it reaches the intestine and is activated by an intestinal enzyme, *enterokinase*. Trypsin completes the work begun by the pepsin in that it converts proteoses and peptones into *amino acids,* but it also digests complex proteins which have escaped the action of pepsin. It acts more rapidly and efficiently than does pepsin. There are nineteen amino acids that are regarded as *building stones* of the protein molecule. In a complex protein like casein, as many as sixteen of these amino acids will be found. The tissues of the animal body must not only have available a wide range of amino acids but must also select in the proper proportion the ones needed to reconstruct their specific protein constituency.

Amylopsin is the pancreatic diastase, and it is able to bring about hydrolysis of carbohydrates in the alkaline medium of the intestine without activation. It produces dextrin and maltose (malt sugar). The pancreatic lipase, steapsin, brings about the splitting of fats into glycerin (glycerol) and one or more fatty acids, such as stearic acid, oleic acid, butyric acid, etc. The alkaline salts, which are introduced by the bile, combine with these fatty acids to form soaps which help in emulsifying the remaining fats, thus making them more readily split.

Intestinal secretions or *succus entericus* which are produced by glands in the mucous membrane of the small intestine include five enzymes. *Enterokinase,* which activates trypsinogen to form trypsin, has been mentioned already. *Erepsin,* the intestinal protease, supplements the activity of trypsin by converting proteoses and peptones into amino acids. *Maltase* converts maltose and dextrin into dextrose (glucose). *Invertase* changes sucrose (cane sugar) into dextrose and levulose. *Lactase* converts milk sugar (lactose) into galactose and dextrose, both simple sugars.

THE DIGESTIVE ENZYMES AND THEIR FUNCTIONS

ENZYME	REGION OF DIGESTIVE TRACT*	DIGESTIVE JUICES	FOODS AFFECTED	SUBSTANCES PRODUCED
Ptyalin	Mouth	Saliva	Starch (carbohydrates)	Maltose
Pepsin	Stomach	Gastric juice from gastric glands	Proteins in acid medium	Proteoses and peptones
Rennin in mammal	Stomach		Protein of milk	Coagulated to form paracasein
Gastric lipase	Stomach		Emulsifies fats	Glycerol and fatty acids
None	Liver	Bile	Emulsifies fats	None
Amylase or *amylopsin*	Produced in pancreas	Pancreatic juice produced in pancreas but acting in small intestine	Carbohydrates	Maltose
Steapsin	Produced in pancreas		Lipins (fats)	Glycerol and fatty acids
Trypsin	Produced in pancreas		Proteoses and peptones in alkaline medium with enterokinases	Polypeptids
Erepsin	Small intestine	Intestinal	Polypeptids	Amino acids
Maltase	Small intestine		Maltose	Glucose (dextrose)
Lactase in mammals	Small intestine		Lactose	Glucose and galactose
Invertase or *sucrase*	Small intestine		Sucrose	Glucose and levulose

*The esophagus and colon do not secrete any enzymes.

The undigested residue passes into the large intestine where probably no enzyme digestion occurs. Certain bacteria (*Escherichia coli* and others) attack any undigested foods (especially protein) and bring about putrefactive fermentation. Products of this action may be absorbed; some of them are frequently toxic and must be eliminated in either the urine or the feces. Certain other bacteria here feed upon cellulose and may produce some sugar from it. When the chyme reaches the large intestine, it is about the consistency of thick cream, but it becomes more and more solid by absorption of water here until finally only concentrated fecal matter remains.

Functions of the Liver

The secretion of the liver is *bile* and is discharged into the duodenum of the small intestine by way of the *common bile duct*. This is an alkaline solution which serves to help neutralize the acidity of the chyme as it comes from the stomach. This with the pancreatic juice brings about the emulsification of fats mentioned above. *Cholesterin* and two pigment materials are excreted in the bile. Bile is secreted continuously, but between meals it is stored in the *gall bladder* and supplied in quantity at meal time.

Besides these digestive and excretory functions the liver serves in another capacity. It is a storehouse for carbohydrates which it converts to *glycogen* (animal starch) by enzyme action. This substance is also stored in the voluntary muscles. It is easily reconverted to dextrose for ready oxidation. Most of the protein by-product *urea* (and *uric acid* in some forms) is formed in the liver and carried by the blood to the kidneys for excretion. The removal of toxic protein substances and toxic heavy metals is another function of the liver.

Absorption and Utilization of Food Materials

The soluble products of digestion are absorbed through the semipermeable epithelial lining of the intestine into the blood of the adjacent capillaries, or in the case of fats into the *lacteal* lymphatics and from here into the subclavian vein through the thoracic lymph duct. The blood supplying the intestine is collected by the *hepatic portal* vein and delivered to the liver.

The two functions of proteins in the body are: to rebuild debilitated protoplasm; and help supply heat and energy to the body by oxidation. Carbohydrates and then fats are more economical and efficient as sources of fuel for production of heat and energy. Oxidation of protein requires the disposal of much more waste products. The comparative heat production values of the three are as follows:

One gram of protein	= 4100 small calories*
One gram of carbohydrate	= 4100 small calories
One gram of fat	= 9305 small calories

Some portion of the dextrose is distributed and oxidized directly for immediate energy, but much of it is transformed into glycogen by the enzyme *glycogenase* in the liver. This may be stored here or

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*A small calorie equals the amount of heat necessary to raise one gram of water one degree centigrade under standard conditions, while a large calorie equals the amount of heat necessary to raise one liter of water one degree centigrade under standard conditions.

in the muscles to be reconverted into dextrose for oxidation by the
tissues as needed. Normally there is a constant supply of dextrose
(0.1 to 0.15 per cent) in the blood and this level must be maintained.
The final oxidation products of carbohydrates in the body are heat,
kinetic energy, water, and carbon dioxide. The last two are dis-
charged from the body as waste products. Fat is converted to dex-
trose and oxidized to produce heat and kinetic energy. It is usually
stored as a reserve fuel supply in adipose tissue over the body. Car-
bohydrates in excess may be converted to fat, and stored.

Vitamins and Their Functions

Besides proteins, carbohydrates, fats, inorganic salts, and water
there is another indispensable class of food material, the *vitamins.*
They are natural substances found in relatively small quantities in a
number of different foods. In general, their function is related to the
regulation of certain phases of metabolism. They are recognized usu-
ally through the abnormal condition brought on by their deficiency.
There is little danger of vitamin deficiency for adults living on a bal-
anced and mixed diet. Much of our knowledge concerning the symp-
toms brought on by lack of different substances has been gained by
feeding experiments on different kinds of laboratory animals. This
information is then applied to human beings. The following outline
summarizes the essential points concerning vitamins.

THE VITAMINS AND THEIR CHARACTERISTICS

I. *Vitamin A* ($C_{20}H_{30}O$)—antixerophthalmic—fat soluble.

    (a) Sources: carotene ($C_{40}H_{56}$) a yellow pigment in green plant leaves,
    carrots, and such plant tissues. Transformation of this pigment into
    the vitamin which is especially stored in shark, cod, halibut or other
    fish liver oil, egg yolk, and milk.

    (b) Functions: Influences efficiency and acuity of vision, important fac-
    tor in regeneration of visual purple of retina, strengthens and pro-
    motes hardiness in epithelial tissue.

    (c) Effects of Deficiency: Xerophthalmia (lack of tear secretion and dry
    cornea), and ''night blindness'' in human. ''Nutritional'' roup in
    birds.

II. *Vitamin B** ''Complex.''

    1. B_1 or Thiamin ($C_{12}H_{17}ON_4S$)—Antineuritic.

        (a) Sources: Germ of wheat and other cereal grains, peanuts, liver, and
        egg yolk.

*There are still other recently discovered fractions of Vitamin B, whose func-
tions are specific.

    (b) Functions: Promotes tone in alimentary tract, stimulates appetite, essential for normal growth, essential for carbohydrate metabolism.

    (c) Effects of deficiency: Beri-beri (neurodigestive disturbance following diet of polished rice), loss of tonus and muscular activity of digestive tract. Cessation of growth. Polyneuritis develops in birds.

2. Riboflavin ($C_{17}H_{20}O_6N_4$).

    (a) Sources: Eggs, liver, milk, green leaves, yeast.

    (b) Functions: Necessary for growth, active relation to several enzymes with intermediate metabolism of food.

    (c) Effects of deficiency: Irritation and inflammation at corners of mouth in human (cheilosis). ''Yellow liver'' of dogs. ''Curl-toe'' paralysis of chickens. Dermatitis of turkeys.

3. Nicotinic Acid ($C_6H_5NO_2$)—antipellagric.

    (a) Sources: Meat, liver, egg yolk, green leaves, wheat germ, yeast.

    (b) Functions: Produces active ''coenzymes'' (I and II), balances cellular function.

    (c) Effects of deficiency: Pellagra in primates (man and monkeys). Black-tongue in dogs. Swine pellagra.

4. B_6 or pyridoxine ($C_8H_{12}O_2N$).

    (a) Sources: Milk, liver, cereals, yeast.

    (b) Functions: Necessary for growth. May influence oxidation of food.

    (c) Effects of deficiency: Paralysis in chickens.

5. Pantothenic acid ($C_9H_{17}O_5N$).

    (a) Sources: Liver, milk, egg yolk, yeast, molasses, peanuts.

    (b) Functions: Essential for growth.

    (c) Effects of deficiency: Graying in black rats. Dermatitis in rats and chickens.

6. Biotin ($C_{10}H_{16}O_3N_2S$).

    (a) Sources: Egg yolk, yeast, cereal grains, molasses.

    (b) Functions: Essential for growth.

    (c) Effects of deficiency: Thickening of skin and dermatitis in chicks and rats.

III. *Vitamin C or Ascorbic Acid* ($C_6H_8O_6$)—antiscorbutic-water-soluble.

    (a) Sources: Citrus fruits, tomatoes, turnips (most mammals except primates and guinea pig can synthesize this vitamin).

    (b) Functions: Maintains structure of capillary walls.

    (c) Effects of deficiency: Scurvy in human and guinea pig (bleeding in mucous membranes, beneath skin and into joints).

IV. *Vitamin D* ($C_{28}H_{44}O$)—antirachitic.

    (a) Sources: Tuna and cod-fish liver oils. Exposure of skin to ultraviolet radiation.

    (b) Functions: Regulation of calcium and phosphorus metabolism. Required for normal growth and mineralization of bone.

    (c) Effects of deficiency: Soft, deformed bones in young (rickets). Soft bones (osteomalacia) especially in women of the orient.

V. *Vitamin E or Tocopherol* ($C_{20}H_{20}O_2$)—antisterility.

    (a) Sources: Wheat germ oil, green leaves, other vegetable fats.

    (b) Functions: Promotes rapid cell proliferation and differentiation.

    (c) Effects of deficiency: Sterility in male fowls and rats. Failure of spermatogenesis. Death of rat embryos in uterus.

VI. *Vitamin K* ($C_{31}H_{46}O_2$)—antihemorrhagic.

    (a) Sources: Green leaves, alfalfa, also certain bacteria of the "intestinal flora."

    (b) Functions: Influences the production of prothrombin by the liver (prothrombin is necessary for blood clotting).

    (c) Effects of deficiency: Blood fails to clot.

Respiration

Respiration has been defined as the process involving the exchange of gases between the protoplasm of an organism and its environment. All living protoplasm must be provided with a means of receiving oxygen and giving up carbon dioxide. In Protozoa and simple Metazoa, such as sponges, coelenterates, flatworms, roundworms, and even some annelids, this gaseous exchange is made by almost direct diffusion through the cell membranes to the surrounding medium. This movement of gas through the cell membranes depends on the partial pressure of the particular gas on the two sides of the membrane. Gas will flow in the direction toward the least pressure.

In the larger and more complex animals where the volume of tissue is such that a more active interchange of gases is required than the general body surface will permit, special organs or modifications of the surface must be provided. Also the possibilities of oxygen absorption are greatly increased by the development of respiratory pigments, like hemoglobin and hemocyanin, which are carried in a blood vascular system all over the body. These pigments readily unite with oxygen to form oxyhemoglobin in the case of the former. Thus the blood is enabled to absorb far more oxygen than an equal quantity of ordinary liquid. When the oxygen pressure of the surrounding tissue is sufficiently low, the oxyhemoglobin releases its oxygen rapidly. Carbon dioxide accumulates in excess in the tissues and diffuses from the cells to the lymph, thence to the plasma where much of it combines with sodium as sodium carbonate. Small amounts of CO_2 combine with the hemoglobin.

In these larger organisms, the respiration process is divided into *external respiration,* the gas exchange occurring between the circulatory medium and the environmental medium (air, water, etc.), and *internal respiration,* the exchange of gases occurring between the circulatory medium (blood, etc.) and the protoplasm of the organism.

The gills of most aquatic forms are richly supplied with a capillary supply of blood and then membranous surfaces are directly exposed to surrounding water from which the dissolved oxygen is absorbed. In many aquatic worms the gill filaments are outgrowths of the sides of the body wall. Likewise, the more or less plumelike gills of crayfish are pocketlike outpushings of the body wall. In a number of aquatic insects, worms, fishes, and turtles, the rectum serves as an accessory respiratory organ.

Aerial respiration is accomplished in terrestrial animals through special internal surfaces which must be kept moist. In insects a system of branched tubes called trachea, which open through spiracles along the sides of the body, distribute oxygen to and receive carbon dioxide from all of the cells of the body. In pulmonate snails the "lung" is simply an invagination of the skin, as are also the tracheae of insects. The real lung is a development found in the terrestrial vertebrate, and it is a specialized surface derived from the anterior or pharyngeal portion of the digestive tube. In higher vertebrates, such as birds and mammals, they are extensively lobed, and made spongy by the innumerable small air sacs which provide the enormous respiratory surface necessary. It has been estimated that if all of these pitlike alveoli of the internal lining of the lungs of the average human being were spread out in an even surface, the area of it would be more than 100 square yards.

The muscles which control the breathing actions in vertebrates are automatically stimulated through the nervous system to contract when the carbon dioxide level of the blood reaches a certain point. A respiratory center, located in the medulla oblongata, is affected by the carbon dioxide and determines the rate of respiratory movements. There are also nerves from the lungs themselves which extend to this center and contribute to the maintenance of the proper rhythm. Abundance of venous blood stimulates an increase of the respiratory action. In addition to exchanging gases the lungs also discharge moisture and give off a certain amount of heat.

Circulation

Transportation of materials through the protoplasm of a single cell or a single-celled organism and from cell to cell of the metazoan is a fundamental function among living things. In most Protozoa there is no special arrangement for this function, but the necessary exchange and movement of food materials, waste substances, and gases is accomplished by simple diffusion of materials. In a few forms, however, of which *Paramecium* is an example, there is a definite course of movement by the endoplasm. This is known as *cyclosis,* and it serves to circulate the food vacuoles.

In double-walled, simple, saccular forms like *Hydra* there is no provision necessary except an exchange of the water in the gastrovascular cavity. In flatworms, such as *Planaria,* the necessity of increased food distribution is cared for by branching of the gastrovascular cavity into diverticula. In sponges the wandering cells assist in transporting materials. A distinct system of tubelike vessels with contractile parts is developed in the annelid worms, as will be studied in the earthworm. Here a closed system of vessels forms a complete circuit to carry a circulating medium to all parts of the body. In this group the fluid is known as *hemolymph* because it bears no red corpuscles. The hemoglobin is borne in the fluid. The vertebrate system is *closed,* i.e., the vessels carry the blood through its entire circulation without being interrupted by extensive sinuses, and the blood is circulated by the action of a single heart. The hemoglobin, an iron compound, is carried in the red blood corpuscles. In mollusks and crustaceans there is a similar respiratory pigment carried in the plasma, which is called *hemocyanin.* Instead of iron, copper is the principal constituent of this pigment. Vertebrate blood is largely water carrying dissolved materials and suspended corpuscles. The fluid part is known as *plasma.* The amount of blood in a mammal is approximately one-twentieth of the body weight, or in the average man a little more than a gallon. The plasma contains enough inorganic salts to taste slightly salty. Its salt content is about equal to that of sea water. When the body is active, the blood is very unequally distributed. One-fourth is always in the heart, large arteries, veins, and lungs. Another fourth is held in the hepatic portal system, the liver and its sinuses; the skeletal muscles require another fourth; and the remaining fourth is distributed through all of the other organs. Human blood contains normally about 5,000,000 *red cor-*

puscles (erythrocytes) per cubic millimeter of volume in the male and about 4,500,000 in the female. The average person, weighing 150 pounds, then, would possess approximately 20,000,000,000,000 (20 trillion) of them. Each erythrocyte is essentially a little capsule filled with hemoglobin which is a compound peculiarly fitted to unite with atmospheric oxygen. When united with oxygen it is known as *oxyhemoglobin,* which is readily reduced to give up the oxygen to the cells when the blood reaches the tissues. The carbon dioxide given off by the cells is collected principally in the plasma and returned to the lungs.

AVERAGE CHARACTERISTICS OF HUMAN BLOOD CELLS

KINDS OF CELLS AND AVERAGE NUMBER PER CUBIC MILLIMETER OF BLOOD	STRUCTURE COLOR WITH WRIGHT'S STAIN	SOURCE	FUNCTION
Erythrocytes (red blood cells) 5,000,000 (males) 4,500,000 (females)	Nonnucleated, circular, biconcave; orange buff; 7.5 to 7.7 microns in diameter	Endothelium of capillaries of bone marrow	Transport oxygen; remain in blood vessels
Leucocytes (white cells) 1. Granulocytes 6,000 to 10,000	Colorless in life Nucleus of lobes joined by thread; stains dark lilac, cytoplasm pale; blue with granules; 9 to 12 microns in diameter	Reticulo-endothelial cells outside capillaries of bone marrow	Amoeboid; can leave blood vessels and enter tissues Defend against infection
a. Neutrophile 60 to 70%	Granules stain weakly		
b. Eosinophile 2 to 4%	Granules few, eosin (red)		
c. Basophile 0.5 to 1.5%	Granules deep blue		
2. Lymphocytes 20 to 30%	Nucleus single, large, round, deep blue; scant cytoplasm, clear blue 4 to 10	Lymphoid tissue, spleen and lymph glands	Nonmotile; related to immunity
3. Monocytes 5 to 10%	Nucleus single, large, round, deep blue; much cytoplasm, muddy blue; 12 to 20	Spleen and bone marrow	Very motile; phagocytic
Platelets 200,000 to 400,000	Small, refractile, no nucleus; dark blue to lilac; 2 to 3	Bone marrow	Provide substance needed in clotting

The *leucocytes* or white corpuscles are quite variable in form and number from 6,000 to 10,000 per cubic millimeter. They are amoeboid and therefore not confined to the blood vessels. One of their chief functions is the destruction of bacteria and other foreign material in the tissues. This process is known as *phagocytosis*.

The plasma of the blood contains a group of substances called *antibodies* (immune bodies). These have been produced by various tissues of the body upon contact with certain foreign proteins. Since bacteria and pathogenic Protozoa react as foreign protein, they stimulate the body tissues to the production of specific protective antibodies and physicians have come to make use of these antibodies in sterile serum for prevention and treatment of several diseases. Some of these *antigen* substances bring about the clumping or agglutination of foreign bacteria, others dissolve the bacteria, and still others cause them to be precipitated. The chemical nature of these bodies is not yet known.

There are individuals, known as *hemophiliacs* or bleeders, whose blood will not clot, and any wound is likely to be fatal. The plasma normally contains a soluble protein, called *fibrinogen,* and calcium in solution. Howell's theory of coagulation of blood holds that there is also an inert substance, *antithrombin,* which prevents the activation of the *prothrombin* of the plasma to become *thrombin.* When blood is shed and exposed to air, the blood cells and platelets produce a substance, *cephalin,* which, in the presence of calcium, neutralizes the antithrombin, allowing the formation of thrombin. Thrombin reacts with fibrinogen to produce *fibrin,* the solid fibers of the clot. The rate of the heartbeat for an average adult man at rest is about 72 times per minute. The contraction phase of the heartbeat is called the *systole* and the relaxation phase is the *diastole.* It has been estimated that an average circuit of the circulation of blood in man can be completed in twenty-three seconds, with about two seconds of this time being spent in capillaries.

Nervous Function—Reception and Conduction

Irritability and conductivity are fundamental functions of all protoplasm, whether it be in the body of *Amoeba* or man. The responsiveness of organisms to change of conditions both externally and internally determines their behavior. Living protoplasm is not only excitable, but it possesses the power to record or store up the

effects of previous stimuli. In the final analysis, the perceptions and reactions of man are but expressions of these primitive functions in a more specialized organism.

The protozoan organism has no special nervous system but depends on the primitive properties of irritability and conductivity to guide its activities. In the simpler Metazoa, such as the coelenterates, there are scattered nerve cells connected with each other by fibers to form a nerve net. The *neuroepithelial* or *neuromuscular* cells which make up this continuous net through the body are the forerunners of the typical neurone and are called *protoneurones* by Parker. A protoneurone transmits in every direction while a true neurone transmits in only one. In the net system there is no central exchange and no specific path of conduction. Every part of the receptor surface of such an organism is in physiological continuity with every other part of the body.

Next comes the linear type of nervous system in the form of a ladder. It is composed of an organization of neurones into a double chain of ganglia, each cord lying lateral to the digestive tract with transverse connectives and predominant ganglia at the anterior end. Such a system will be studied in *Planaria*. In Annelida and Arthropoda the nervous system is a modified ladder type in which the two longitudinal cords of ganglia have fused along most of the midventral line. Toward the anterior end, the cords separate at a paired ganglionic enlargement, the *subesophageal ganglion,* and encircle the alimentary canal to join on the dorsal side as the pair of *supraesophageal ganglia* or "brain." In Arthropoda the ganglia of the thorax have undergone considerable fusion. In Echinodermata, the starfish for example, the central group of ganglia makes up the circumoral nerve ring around the mouth, and radial branches extend into each arm. Branches from these communicate with the sensory structures of the skin and tube feet.

Concentration of the tissue of the nervous system into definite organs is carried farther in vertebrates than in the less highly organized forms. The fact that the central nervous system of vertebrates is dorsally located and hollow has been brought out previously. Even within the group of vertebrates, the nervous system shows a progressive increase in complexity. The highly developed brain of the mammal is the climax of this tendency.

The *neurones* have been referred to before as the units of structure and function of the higher types of nervous system, from worms to

man. Each neurone is a nerve cell with processes extending from it, and each of these units must conduct *nerve impulses* in its normal function. The exact nature of the nerve impulse is still somewhat of a question. It is thought to be transmitted as a metabolic change passing along the nerve fiber (axone or dendrite). This is at least partially a chemical change in which oxygen is necessary and a certain amount of carbon dioxide is produced, but since there is only slight increase in temperature during the change, it seems not to be a typical metabolic oxidation process; furthermore, the activity seems not to fatigue the nerve fiber. An electrical charge follows the wave of activity along the nerve fiber, but it apparently accompanies the impulse or is a result of it rather than the impulse itself. The speed of electrical transmission has been measured in a number of different animals and nervous transmission is much slower than electrical. At room temperature the sciatic nerve of a frog will transmit a nerve impulse at the rate of about 100 feet per second. Conduction over nonmedullated fibers of invertebrates is much slower than this. On the other hand, measurements of the rate of conduction in man show a velocity of about 400 feet per second.

The *reflex arc* and *reflex actions* illustrate the simple form of nervous conduction circuit. In its simplest form the reflex arc is composed of one motor and one sensory neurone; however, it is usually more complex. The classical example involves the spinal cord and a spinal nerve. This is known as a reflex of the first level, because it returns the motor impulse over the motor fibers of the same nerve which brought in the sensory impulse. The motor axone carrying the impulse from the motor nerve cell in the gray matter usually ends in a muscle cell or a gland. There is no protoplasmic union between the axone of the sensory neurone and the dendrite of the motor, for these come in contact only by a *synapse* which brings them in close proximity. It has been found experimentally that nervous impulses may be conducted in either direction by the fiber but can cross a synapse only from axone to dendrite, thus serving like a valve in a pipeline. Reflex actions may be in the form of motion, as withdrawal from unexpected pain, or shivering or formation of goose flesh, or the contraction of the pupil of the eye with increased light intensity. Still other reflex actions include secretion by glands, breathing, movements of speech, individual actions included in walking, and others.

Functions of the Spinal Cord

This organ serves as a system of reflex centers which control the actions of glands of the trunk, visceral organs, and skeletal muscles. The spinal cord is also a nervous pathway between the brain and numerous organs of the body. It is said that more than half a million neurones join the cord through the dorsal roots of the spinal nerves.

Functions of the Divisions of the Brain

Conscious sensations and intelligence are centered in the gray matter or cortex of the *cerebrum*. This section controls voluntary actions and provides memory associations. The diencephalon serves as a center for *spontaneous actions*. The *midbrain* is one of the centers of *coordinated movement* which has to do with posture and eye muscles. The *cerebellum* is another center of *coordinated movement*, particularly with reference to equilibrium. The impulses from the muscles, tendons, joints, and semicircular canals of the ear are co-ordinated so that in a movement or posture the proper muscles may be contracted to the proper extent at the proper time. Below and behind the cerebellum is the medulla oblongata which controls breathing and may be an inhibitor on heart action. It also regulates digestive secretions, movements of digestive organs, and vasomotor activity of the blood vessels. As a whole, the brain serves as the organ of communication between the sense organs and the body and is the coordinator of the bodily activities.

Sense Organs and Their Function

There are five special senses which have rather particularly defined function, and, in at least four of them, quite specialized organs for perception. These five are sight, hearing, smell, taste, and touch. They are all in contact with, and referred to, the external world. The organs in which these senses are stimulated are, respectively, the retina of the eye, the organ of Corti of the ear, the olfactory membrane of the nose, taste buds in the epithelium of the tongue and related parts, and the tactile corpuscles, as well as free nerve endings in the epithelium.

In addition to the senses centered in these specialized sense organs, there are several general senses, such as hunger, nausea, respiratory sensations, and sexual sensations.

Cutaneous Sense Organs (Touch, Pressure, Temperature).—There are endings of sensory nerves in all parts of the skin and the mucous

membranes lining the mouth, nose, vagina, and urethra. The senses of pain and temperature are probably accommodated by unmodified free nerve endings. Sensations of pain may be produced in almost every organ of the animal's body. *Meissner's tactile corpuscles* are located in the dermis generally over the body, but more particularly on the soles of the feet, at the bases of the vibrissae, at the tip of the snout, and tip of the tongue. In human beings the sense of touch is twice as discriminating on the tongue as it is on the finger tip; almost thirty times as great as that of the back of the hand; and sixty-five times as great as that of the middle of the back. Pacinian corpuscles are organs of pressure sense located in the deeper dermis, mesenteries, certain visceral organs, and at the joints.

Sense of Smell.—The organ of the sense of smell lies in that part of the mucous membrane lining the posterior part of the nasal cavity. The portion of the mucous membrane containing the sensory olfactory cells is known as the *Schneiderian membrane* and is grayish in color in a fresh specimen. The remainder, the respiratory membrane, is red in color. The olfactory nerves conduct the olfactory impulses to the brain. This sense is a chemical sense, and stimulation is produced by volatile substances which go into solution in mucus on the membrane.

Sense of Taste (Gustatory Sense).—The mucous membrane of the tongue contains most of the taste buds of the mammal. Fewer taste buds are found on the soft palate and epiglottis. Some animals have taste buds on the lips and snout, and in the catfish the feelerlike barbels around the mouth, and even on the tail, possess taste buds. This sense too is a chemical sense and materials must be in solution before they stimulate the gustatory cells. Many taste sensations are dependent on olfactory cooperation. Taste sensations are grouped into four classes: *bitter, sweet, salty,* and *sour.* In the human being taste buds receiving sweet sensations are located in the tip of the tongue, bitter at the base, salty along the sides, and sour (acid) rather generally in all of these areas. The mid-dorsal portion of the tongue is not very sensitive.

Sense of Sight.—The eye is the special organ of sight, and within it the *retina* contains the sensory cells. Each eye is held in an orbit which is located in the skull. The *conjunctiva* is a thin membrane which lines the eyelids and passes over the front of the eye between the lids. This latter portion of it is transparent. Tear (lacrimal) glands, which are located in the orbit under the base of the upper

lid, secrete tears. This is a salty liquid which lubricates and washes the surface of the eyeball and inner surface of the lids. Seven muscles control the movements of the eyeball. These muscles take their origins on the inner surface of the orbit and have their insertions on the surface of the eyeball. These seven include four straight ones (recti), two oblique ones, and one retractor: *superior rectus, mesial* (internal) *rectus, inferior rectus, lateral* (external) *rectus, superior oblique, inferior oblique,* and *retractor oculi.* The four recti muscles each pull the eyeball in the direction indicated by the name; for example, the superior rectus moves the eyeball upward, and the inferior one moves it downward. The action of the superior oblique muscle is modified by the fact that it pulls through a pulley which results in a twisting or rotating movement for the eyeball. The inferior oblique opposes it by direct attachment at the opposite position. The retractor oculi originates on the boundary of optic foramen and divides into four heads which are inserted in the sclerotic coat (sclera) near the entrance of the optic nerve. This muscle is almost covered by the recti muscles.

The eyeball is composed of three tissue layers, a lens, and two humors. The outer, firm *sclera* is almost white in color and continues forward into the transparent *cornea* which covers this surface. Inside the sclera is the *choroid* coat which is generally black in color. On the inside surface is an irregular area which has a metallic luster and is called the *tapetum.* The choroid extends forward as the *iris* or colored portion in human beings, but in albino rats the pigment is lacking and it is pink, due to the color of the blood in its tissues. The iris is incomplete at its forward side, and the aperture in its center is the *pupil.* Light is admitted through this circular opening. Its size may be adjusted by contraction or expansion of the iris, and in this way the amount of light and divergence of rays are regulated. The inner layer, lining the inner surface of the posterior three-fourths of the eye, is the *retina.* It is a thin gray membrane and contains the sensory cells (rods and cones), which are connected to nerve fibers coming in by way of the optic nerve which enters the back side of the eye. The convex *lens,* which is held in position just behind the iris by the ciliary ligament, is crystalline and focuses the light rays on the retina. The area of the retina directly behind the lens is called the *fovea.* This is the most sensitive part of the retina. Slightly medial and below this is the entrance of the optic nerve, at which point the retina is devoid of rods and cones. The very descriptive

name, *blind spot,* has been applied to this area. The eyeball is divided
into two compartments, the *aqueous chamber* in front of the lens and
the *vitreous chamber* behind it. The *aqueous humor* filling the outer
chamber is of a watery consistency while the clear *vitreous humor*
filling the inner chamber is jellylike. The light, in reaching the retina
of the rat (or human being), would enter the eye through the cornea
and pass through the aqueous humor, pupil, lens, and vitreous humor
in that order.

The eye is capable of perceiving several features of light such as
intensity, distance, color, etc. There are several theories of visual
perception, but those most commonly accepted are based upon chemi-
cal changes in the rods and cones of the retina. Such an explanation
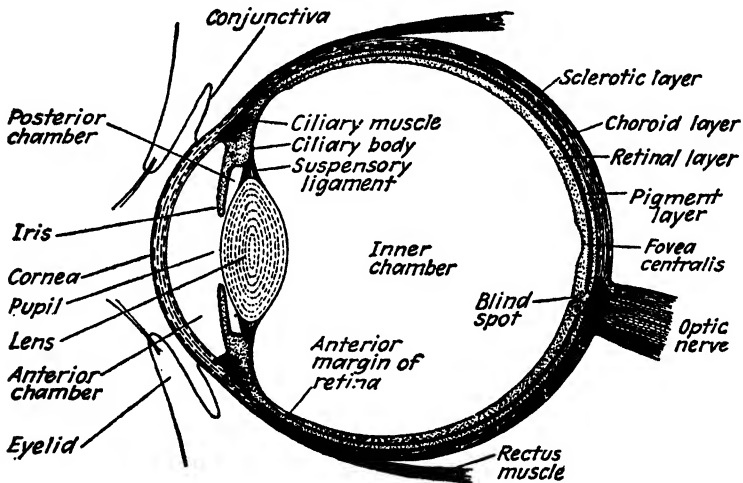
Fig. 55.—Diagram of a section through the eyeball. (From Wolcott, *Animal
Biology,* McGraw-Hill Book Company, Inc.)

considers the presence of a phototropic substance which is called
visual purple, as an essential factor. The rods and cones seem to take
different roles in dim light and white light, but these differences are
interpreted as varying amounts of visual purple in them. The
theories of color vision utilize the presence of this chemical also.
According to this idea, color blindness would be due to deficiency
of visual purple or a peculiar distribution of it.

Sense of Hearing.—The ear, which is the organ of hearing, is com-
posed of external ear, middle ear, and internal ear. The first is com-
posed of the *pinna,* which is funnellike, and the *auditory meatus,* or

canal, leading into the middle ear within the skull. The pinna serves to direct the sound waves to the meatus. The internal end of this canal is covered by a thin, taut membrane which is called the *tympanic membrane or eardrum*. This membrane is set into vibration by the sound waves which reach it. The middle ear ·or tympanic cavity is just internal to the eardrum and within temporal bone. It houses three small bones or *ossicles*, the *malleus* (hammer), the *incus* (anvil), and the *stapes* (stirrup). The malleus is attached to the eardrum and the three bones are in contact with each other in such a way that they conduct the sound vibrations through this cavity to a membrane at the entrance to the inner ear, or *fenestra ovalis.* A tube, called the *Eustachian tube,* leads from the cavity of the middle ear to the
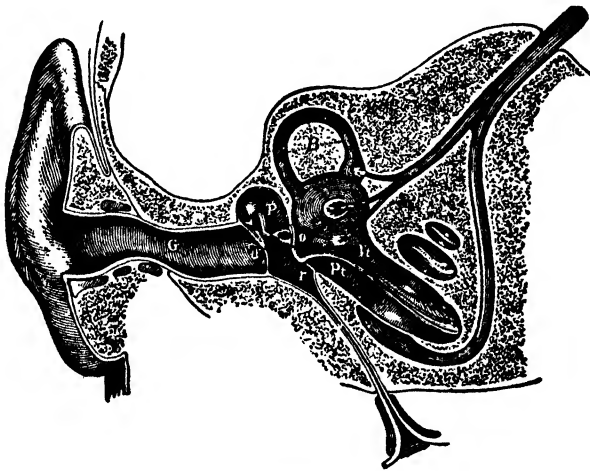
Fig. 56.—Diagram of a section through the right human ear. *B*, semicircular canal; *G*, external auditory meatus; *o*, oval window (fenestra ovale); *P*, tympanic cavity containing the three auditory ossicles; *Pt.*, scala tympani; *r*, round window (fenestra rotunda); below *r* is seen the Eustachian tube; *S*, cochlea; *T*, membrana tympani; *Vt.*, scala vestibuli. (From Zoethout, *Textbook of Physiology*, The C. V. Mosby Company, after Czermak.)

pharynx, and it serves in the transmission of air between the cavity and the exterior in order that the pressure may be kept at a balance on the two sides of the tympanic membrane. This avoids interference which might be caused by undue stretching of the membrane with changes in barometric pressure.

The internal ear contains the sensory apparatus, both for reception of sound waves and for equilibrium. The *organ of Corti* in the *cochlea* performs the first function and the semicircular canals, the latter. The cochlea is a coiled tube filled with *perilymph,* a fluid,

which conducts the vibrations finally to the organ of Corti. The latter is supported by a membrane dividing the cochlea throughout its length. Endings of fibers from the eighth (auditory) cranial nerve reach the cells in this organ and are stimulated by the vibrations of the fluid. The average human ear is said to receive wave lengths of frequencies ranging between 30 and 40,000 per second, but other animals including the rat likely perceive wave lengths of a different range.

Sense of Equilibrium.—The three semicircular canals which were mentioned above stand in three different planes and all join the *vestibule* or general cavity at their bases. One is anterior-vertical in position, another posterior-vertical or at right angles to the first, and the third is in the lateral horizontal position. There are sensory endings of branches of the auditory nerve in the ampullae of these canals, and the canals are filled with a lymphlike fluid. Any change of level or position of the head causes this fluid to move in the canals and stimulate certain of the endings. The individual is able to sense the position and orientation of the body from the impulses produced by these stimulations.

Excretion

A certain result of the oxidation necessary for metabolism is the production of end-products (principally nitrogenous) which are not only of no further use to the protoplasm but may be a distinct menace to the welfare of the organism because of their toxic effects. The substances are usually dissolved and removed as a waste liquid or occasionally as crystals by special parts of the body.

In Protozoa this function is performed by general diffusion through the plasma membrane and in many forms by the contractile vacuoles. The quantity of water which passes through the protozoan in twenty-four hours is several times the volume of the animal itself. Among sponges and coelenterates diffusion of liquid wastes through the general surfaces of the body to the surrounding water serves for excretion.

In an animal like the flatworm, *Planaria,* excretion is accomplished by a system of canals which begins in numerous capillary-sized tubules whose blind ends are composed of individual cells called *flame cells.* These flame cells are irregular in shape and each bears a tuft of *cilia* extending into the end of the tubule. The flickering movement of the cilia in the cell gives the appearance of a flame and moves the accumu-

lated excretion down the tubule. The waste liquid of the surrounding tissues diffuses into this cell. The main excretory ducts open to the surface of the body by excretory pores. This arrangement is sometimes called a *protonephridial* system.

The nephridial system is found in Annelida and has been studied in connection with the earthworm. Here a coelomic cavity is present, and a series of segmentally arranged pairs of coiled tubes or *nephridia* extend through the wall to the exterior. The excreted wastes accumulate in the coelomic cavity and are moved into the nephridia through the ciliated funnellike internal end, known as the *nephrostome.* This coelomic fluid is drawn into the canal of the nephridium by the beating of the cilia and is delivered to the outside of the body at the nephridiopore of the next segment.

The green glands of crayfish are much more concentrated, although they are modified nephridia. They function as a pair of unit organs, each opening by a duct on the basal segments of the antennae. In mollusks there are both nephridia, known as pericardial glands, and the special cells formed from the coelomic epithelium. The echinoderms make use of direct diffusion as well as *intracellular excretion* by which excreted materials are taken up from the coelomic cavity by the numerous phagocytic, amoeboid cells of the coelomic fluid. These cells wander out into the cavities of the respiratory organs where they coalesce into large masses, and finally with their enclosed granules are cast out through the membranes of the respiratory papillae. Soluble materials in solution also diffuse through the membranous walls of these structures. In the insects excretion is taken care of by the *Malpighian tubules,* which are considered modified nephridia. They are bunched in the posterior part of the body cavity and discharge excretions into the intestine at its junction with the rectum.

Kidneys

The chief excretory organs of vertebrates are called kidneys, and they are thought by some authors to have developed by modification and condensation from segmentally arranged nephridial tubules. The fact that in vertebrate embryos as well as in lower chordates, even the frog, these tubules open into the coelom as nephrostomes, makes it seem possible that in vertebrates as well as in annelids the coelom was once important in excretion. The essential structures of the kidney for taking waste substances from the blood and delivering it

to the exterior of the body are the *Malpighian corpuscles,* each made up of a *glomerulus* and a Bowman's capsule, and the coiled *uriniferous tubules* which discharge the excretion through collecting tubules into the *ureter* at the pelvis of the kidney. This canal leads to the cloaca in most vertebrates below mammals (excepting some fish), or to a urinary bladder in the mammals.

The wall of each Bowman's capsule is very thin and readily permits diffusion of water and dissolved materials from the blood into the cavity of the uriniferous tubule on the opposite side of the membrane. The glomerulus carries arterial blood from the afferent arterial branch and discharges it into the efferent arterial branch. The latter soon spreads into a capillary network which surrounds the convoluted portions of the uriniferous tubule. Water constitutes
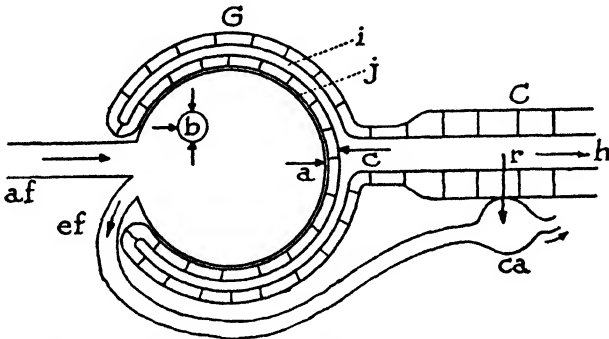
Fig. 57.—Diagram of Malpighian corpuscle and renal secretion. *G,* Malpighian corpuscle with two layers of Bowman's capsule enclosing the space *i; af,* vas afferens vessels supplying the glomerular capillaries which fill the capsule to line *j,* to which the inner wall of the capsule is closely applied; *ef,* vas efferens which drains the glomerular capillaries and supplies the capillaries; *ca,* surrounding the convoluted tubule, *C; a,* blood pressure in glomerular capillaries; *c,* the urine filtrate pressure in the tubule; *r,* the reabsorption from the uriniferous tubule into the capillaries, *ca; h,* the urine on its way to the collecting tubule; *b,* the restraining osmotic pressure of the protein molecule. (From Zoethout, *Textbook of Physiology,* The C. V. Mosby Company.)

the largest volume of materials to be excreted in most animals, except in some desert forms where water is conserved and the excretion is in crystalline form. Water is eliminated by lungs, skin, alimentary canal, and kidneys. In man the quantity of sweat discharged may amount to two or three liters a day. In the dog, which has no sweat glands, the water eliminated by the lungs, through panting, is proportionately greater than in man. The kidneys are the most important organs in the excretion of water, and the amount they eliminate is inversely proportional to the amount

excreted by the skin. Most of the water to be excreted is taken from the blood in Malpighian corpuscles.

Some of the nitrogenous wastes are excreted in the form of ammonium salts and some free or combined amino acids. However, most of the ammonia which results from protein metabolism is converted into urea in the liver and is carried in that form to the kidneys where it is removed from the set of capillaries ramifying over the convoluted tubules by a process of true secretion. According to this idea, the *urine* which consists of urea, various salts, other soluble materials, and water is excreted by different parts of the uriniferous tubule. The substances which are excreted by the kidney are not formed there, but are merely removed from the blood by this organ.

Reproduction

A living organism is in numerous ways similar to a machine, but reproduction of new units of living material by existing organisms is hardly comparable to any mechanical processes known in our industries. New organisms all arise from preexisting organisms of the same kind. The process of cell division is the fundamental basis for all reproduction. For centuries before the invention of the microscope it was commonly believed that living things arose spontaneously from nonliving material, or from the dead bodies of plants and animals. Certain old books carry directions for the artificial generation of mice or bees. Louis Pasteur did as much as anyone to discredit this idea of spontaneous generation. Our present conception is that the protoplasmic substance of the new individual is but a continuation of the specific protoplasm peculiar to an earlier individual or in sexual reproduction to two individuals. Therefore, under ordinary circumstances the structural and physiological complexities which arise through embryonic development must be generally similar to those of the predecessors.

In most of the single-celled organisms reproduction may occur by such equal division of the protoplasm (binary fission) that the new individuals cannot be distinguished as parent and offspring. Protozoa may reproduce also by sporulation, by which process the cell forms a protective *cyst* and by a series of simple divisions (fragmentation) the internal protoplasm breaks into a number of smaller units. Following this the cyst ruptures and releases these new units as independent individuals. For the most part, reproduction among

protozoans is taken to be asexual, but according to a recently published work by Sonneborn, a distinct sexuality exists in *Paramecium.* Examples of asexual reproduction by budding and fission may be found in the studies of reproduction of sponges, *Hydra, Planaria,* and even in tunicates.

Sexual Reproduction.—In certain of the colonial Protozoa, *Volvox* for example, the colony may reproduce for several generations by asexual division of the individual cells but sooner or later the cells of the colony become specialized into conjugating individuals. In some forms this goes to the extent of certain cells becoming distinct gametes with male and female characteristics. In such forms it is possible to see foreshadowed sexual reproduction as it is known in Metazoa.

In the simplest of Metazoa, as in sponges, there are no specially organized *gonads* for the production of germ cells, but as a rule the germ cells are produced in such organs set apart for this purpose. The *ovary* produces mature or nearly mature ova and the *testis* produces mature spermatozoa.

Hermaphroditism is the condition in which the same individual produces both ova and spermatozoa. It occurs principally in the simpler Metazoa, a few higher ones, and rarely among normal vertebrates. Studies made on the reproduction of *Hydra* have shown that the gonads are temporary, both being formed by aggregations of formative or interstitial cells between the ectoderm and endoderm. After the seasonal production of germ cells is completed, the gonads disappear. In flatworms and annelid worms the gonads are permanent structures of the mesoderm. Both ovaries and testes are present. Even in these true hermaphrodites cross-fertilization is insured by copulation or union in such a way that the spermatozoa of one individual fertilize the ova of another. In certain other hermaphroditic forms (as some cyclostomes) the spermatozoa and ova of a particular individual are usually not mature at the same time.

Bisexual reproduction is the form of reproduction common to many groups of the higher invertebrates and nearly all vertebrates. Here the sexes are distinct, each with functional gonads and accessory structures capable of producing only one kind of germ cells. In some of the types of animals, individuals of the two sexes simply deposit the mature germ cells in the same vicinity and at about

the same time. Under the section on reproduction in starfish such
a procedure is described. In animals like the toads and frogs,
a special provision is made to bring the individuals of the op-
posite sexes together in that the male clasps the female and
sheds sperm over the eggs as they are expelled from the cloaca.
This act is known as *amphiplexus*. The first and second pairs
of abdominal appendages of the male crayfish are modified for trans-
ferring spermatozoa into the *seminal receptacle* of the female, where
they remain until the eggs are laid. This represents a beginning in
the development of a copulatory organ. The majority of bisexual
or dioecious animals make a still greater provision to insure fertili-
zation of the ova by *copulation* or *coitus*. At the time of breeding
the mature spermatozoa are delivered to the cloaca or vagina of the
female, and the ova are fertilized within the urinogenital tract of the
female.

In birds and reptiles after the addition of nutritive and protective
coats the egg passes to the outside to develop and hatch *(oviparous
animals)* but in all mammals, except monotremes, it is retained
within the uterus during the period of embryonic development, and
the young are born as more or less developed individuals *(vivipa-
rous)*. In the females of viviparous mammals the posterior portions
of the two oviducts are modified into a uterus within which the young
are retained and nourished until ready for birth. The internal wall
of the uterus and the external embryonic membranes (serosa and
allantois-chorion) cooperate to form a placenta through which food,
metabolic wastes, and respiratory gases diffuse between parental and
embryonic blood. The blood does not pass from parent to embryo or
vice versa but the necessary materials are allowed to diffuse through
the tissue of the placenta in which both systems are distributed.

Parthenogenesis.—In some species of invertebrates, sexual repro-
duction may lapse for considerable periods of time, during which
period no males are developed. The female produces ova which
develop into new individuals like herself without fertilization for
a whole season. This is known as *parthenogenesis*. Usually in the
fall of the year males are developed, and fertile eggs, provided with
protective hard shells, are produced by the females of this generation
to live through the winter. After winter is over such fertile eggs
hatch into parthenogenetic females for the next season. This process
is common in many smaller Crustacea, aphids, scale insects, some ants,
bees, wasps, thrips, a few moths, and rotifers. Artificial partheno-

genesis may be induced in many mature eggs by change of osmotic pressure due to change of salt content in the surrounding medium. Fatty acids, saponin, solanin, bile salts, benzol, toluol, chloroform, ether, and alcohol are other substances which will induce it. Electric stimulus, mechanical prickling, and change of temperature are also used. Such methods have produced artificial parthenogenesis in eggs of sea urchins, starfish, molluscs, annelids, moths, and frogs. The immediate cause of the development by an egg thus stimulated is not known.

In normal fertilization of an egg by only one spermatozoön, it has been found that the rate of oxidation then increases from 400 to 600 per cent. There are indications that this is also the case in artificial parthenogenesis. This oxidation may be the cause of the development in the ovum. Fertilization, where it occurs, has a dual function: (1) that of stimulating the egg to develop, and (2) that of introducing the genetic characteristics of the male parent.

Other features of reproduction are given in the chapter on Sexual Reproduction and the Development of the Individual.

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CHAPTER IX

THE ENDOCRINE GLANDS AND THEIR FUNCTIONS

The great complexity of the structure of organisms, particularly of those animals in the higher ranks of the animal kingdom, makes necessary a means of regulation and coordination of the functions of the organ systems individually and a means of intercommunication between them. This work is cared for in part by the nervous system; but another agency of regulation is present in all higher organisms and many of the lower forms of life, which is of first importance in this respect, one so complex and interwoven with other organs in carrying out its functions that it is not thoroughly understood at the present time. The group of organs doing this work we designate as the *endocrine glands.* They manufacture and furnish the body with chemical compounds called *hormones,* a term which refers to compounds formed in the body and capable of encouraging or exciting activity in another part of the body; they are *chemical messengers.* The endocrine glands pour their hormones directly into the blood stream without the assistance of ducts, and the blood carries them to other parts of the body; but they are never carried to the outside of the body directly, as in the case of secretions from the *glands of external secretion,* and for this reason the endocrine glands are often referred to as *organs of internal secretion,* or *ductless glands.*

The functions of the hormones are numerous, and current research and investigation in the new field of endocrinology are constantly presenting new activities and interrelationships of these secretions. The manner in which the endocrine organs produce their secretions, the hormones, the manner in which they choose the raw materials, combine them, and give forth products which are vital to the welfare and happiness and often to the very existence of an organism, is of most intense interest and of the greatest importance.

The hormones may be classified, arbitrarily, according to function in three main groups. The *first* of these groups includes those hormones which arouse specific responses in particular organs or in localized parts of the body. A *second* group is composed of those hormones which affect the general metabolism of the body. The

third group is that of the hormones which affect, in particular, the growth and development of the organism. Another general method of classifying substances of this nature terms those substances which serve as *excitors* or accelerators "hormones" and those which *inhibit* or depress activities as "chalones." Illustrations of each of these will be found in the discussion of the individual organs and their functions.

Hormones are found in plants as growth hormones, in the invertebrate animals, and are best known in vertebrate animals. The following examples will serve to demonstrate the nature of endocrine function in invertebrates: Earthworms whose testes are completely destroyed, do not develop the clitellum, the band-like organ which functions during and following copulation. In *Bonellia,* another annelid worm, there seems to be a relation between sex determination and certain hormones, in that the week-old larvae are indifferent sexually, but those that attach to the proboscis of the female parent become males due to some agent received there. All others develop to become normal females. Among the crabs there is a parasite which attacks and destroys the gonads, and it is found that the parasitized male crab will take on distinctly female characters due to the lack of some humoral agent lost with the destruction of these glands. Too, using radium to destroy the gonads of *Asellus,* another crustacean, seems to indicate that the development of the brood pouch is controlled by a substance produced in the normal ovaries. Molting and metamorphosis both are regulated by hormones in insects. The supraesophageal ganglion seems to produce a substance which initiates pupation activities in moths. The endocrine glands of vertebrates which are best known and most clearly understood at the present time are the thyroid gland, the parathyroid glands, the suprarenal bodies, the pituitary body or hypophysis, the thymus, the gonads, and the pancreas.

The Thyroid Gland

The thyroid gland is the most familiar of the endocrine organs to the layman. It is a body of two lobes of about the size of walnuts, slightly flattened, placed one on each side of the upper part of the trachea just below the larynx, or voice box, the two lobes being connected by a saddle-shaped isthmus. The thyroid is well supplied with blood, receiving in proportion to weight, three and one-half times as much blood as the brain; this permits an easy access of the hormone to all parts of the body. The thyroid is

normally not visible externally, but the pathogenic condition of the organ caused by overgrowth, and known as *goiter,* is familiar to everyone.

The functions of the thyroid gland, as recognized today, are two: that of control, in conjunction with other endocrine organs, of the growth and development of the body; and, second, a most important role in the regulation of metabolism. Any upset of the normal functioning of the gland or the removal of the gland results in serious physical and mental disorders, if not in death itself. The hormone produced by this organ, designated *thyroxine,* has been prepared from the fresh thyroid glands removed from various animals and has also been manufactured synthetically. Chemical diagnosis of the hormone reveals the presence of iodine in its composition, and the amount of iodine available in the body seems to be the determining factor in the degree of control which this hormone exerts on bodily functions. In regions of the world in which iodine is scarce in water and food, goiter is a prevalent disorder, and only in recent years has the understanding of the cause been complete enough to suggest as a remedy and a preventive the introduction of additional iodine into the diet by use of iodized salt. Since the amount of iodine required for normal purposes is almost infinitesimal, a sufficient quantity is supplied by this means. The correction of disorders due to a deficient functioning of the thyroid gland by use of natural thyroxine or by use of the synthetic product is quite common today among human beings.

The removal of the thyroid gland in animals which have not obtained their complete growth results in delayed or arrested development. An interesting example of this is found among certain amphibians. The proper functioning of the thyroid gland is essential for the accomplishment of metamorphosis of the frog tadpole into the adult frog. The tadpole lacking sufficient thyroid extract may grow to an unusually large size, but metamorphosis never occurs without the encouragement of this hormone. In the development of human beings, a deficient supply of thyroxine in early years results in a condition known as *cretinism.* The growth of the bones does not take place, the entire body is stunted and deformed, mental development ceases, the facial features are misshapen, growth of hair is scant, and the development of the sexual organs is incomplete. Before work on the thyroid gland was undertaken, cretins were often seen in certain parts of Europe and occasionally in

America; but the present understanding of the hormone and its use has made possible the prevention and cure of most cases of this nature.

Improper functioning of the gland in adult years results often in a condition known as *myxedema,* in which there is a thickening and drying of the skin, a puffiness of the eyelids and lips, loss of hair due to the condition of the skin, a slowing down of metabolism and heartbeat, a depression of body temperature, the deposition of large quantities of fat, and a final result, in many cases, of imbecility. The administration of thyroxine, especially in the early stages, accomplishes a complete, or at least a temporary, remedy.

An overfunctional thyroid gland, in which the condition is known as *hyperthyroidism,* results in an increased metabolic rate, a loss of body fat, and a condition of hyperirritability of the nervous system. It seems, therefore, that the difference between an overly energetic and a sluggish person, and a lean and an obese person, may often be traced directly to the degree of functioning of the thyroid gland. Hyperthyroidism is accompanied by increased excretion of calcium. It differs from the calcium upset due to parathyroid disturbance in that in hyperthyroidism its concentration in the blood remains normal.

Work on the lower vertebrate groups suggests the probability of an important function of the thyroid gland in determining the hibernation periods of certain animals. The thyroid performs additional functions in conjunction with other of the endocrine glands; e.g., the control of sexual activity; but these interrelationships will not be discussed here. Peculiarly, thyroxin, although an accelerator of oxidation in vertebrates, has a depressor effect on cell division and differentiation in such invertebrates as *Paramecium,* sea urchin, and the hydroid *Pennaria.* This has not been completely explained.

The Parathyroid Glands

Connected with the thyroid body are four little glands about the size of small peas, so insignificant in appearance that they were overlooked for many years. The removal of these small bodies along with the thyroid gland in certain operations provoked such startling results, however, as to attract attention to their presence and to evoke considerable interest in their investigation. A complete removal of the parathyroids results in unbalancing the blood calcium and in a type of convulsion known as *tetany;* death is the usual result. A deficient supply of *parathormone* or *parathyrin,* the hormone of the parathyroid glands, may be responsible for defective growth of the

bones and for deficient formation of enamel and dentine of the teeth. Calcium is needed for both the teeth and the bones and the introduction of either calcium or parathormone into the body is made to supplement a deficient supply of calcium due to malfunctioning of the parathyroids.   Removal of the parathyroids also brings about a fall in the renal excretion of phosphorus, and the injection of parathormone causes an immediate rise in the level of renal phosphorus. Parathyroid activity is particularly useful to laying hens where so much calcium is needed in shell formation.   There is evidence of a close functional relationship between the pituitary gland and the parathyroid.   In dogs the removal of the pituitary causes atrophy of the parathyroids, particularly if the pancreas has been removed also. Conversely it has been noticed that injections of extract from anterior pituitary raises blood calcium in some species because of increased activity of the parathyroids.

Too great an activity on the part of the parathyroid glands results in a decalcification of the bones, and an increased content of calcium in the blood and in the excretion of the kidneys.   The final result of this softening of the bones may cause serious disfiguration and stunting of the body.   Accompanying these results are flabbiness of the muscles, decreased irritability of the nervous system, and other unfavorable conditions.   These may be remedied by the removal of a portion of the parathyroids.

The Suprarenal Bodies

Lying close to and slightly anterior to the kidneys are two small yellow or reddish masses of tissue, which play a prominent role in the regulation of the body and one of such complexity that much is yet to be learned concerning its method of functioning.   These *adrenal glands,* or *suprarenal bodies,* are made up of an inner and an outer portion, the medulla and cortex respectively.   The former secretes a substance designated as *adrenalin* (epinephrine or adrenin), which acts upon various organs and raises the level of their functioning. Adrenalin, at times of excitement or emergency, may cause constriction of blood vessels, increased rate of heartbeat, a greater discharge of glucose from the liver to provide additional energy, erection of hairs, stimulation or inhibition of the various visceral muscles, etc., to provide greater efficiency.   The range of control of the medullary portion of the adrenals is thus wide and complex, definitely interrelated with the functions of the sympathetic nervous

system, with other endocrine glands, and numerous processes of the body, so that its true importance is difficult to estimate. Adrenalin has been obtained from various animals for use in the treatment of certain disorders, as an anesthesia in minor operations, and to stop small hemorrhages. It has also been successfully employed in the relief of asthma and similar troubles.

A hormone known as *cortin* has been isolated from the suprarenal cortex, and, while the removal of this portion of the adrenals results in death, the exact functions of the hormone produced therein are not entirely understood. It does relieve the condition known as Addison's disease. There is, without doubt, a close relationship between the cortex and sexual development; and some workers believe that the cortex regulates the normal flow of blood, which
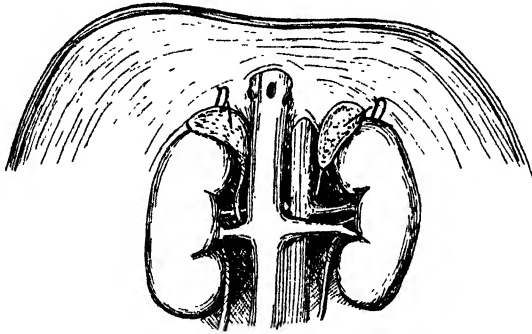
Fig. 58.—The suprarenal glands, *N*, against the anterior portion of the kidneys and close to the diaphragm. (From Stiles, *Human Physiology*, W. B. Saunders Company.)

would account for the fatal results of its removal. An extract has been secured from the adrenal cortex of cattle in particular and is used for the treatment of conditions resulting from malfunctioning of the cortical portion of the adrenals in other organisms. Some have shown cortin to have capacity for delaying the onset of scurvy in vitamin C deficiency.

After complete bilateral removal of the adrenal cortex, the following were the average survival periods for these several animals: opossums, six days; guinea pigs, seven days; dogs, ten days; cats, twelve days; while rabbits and rats may live on quite normally, because of the presence of accessory inter-renal tissue. Symptoms of insufficient cortin are loss of appetite with particular distaste for fats, vomiting, diarrhea, muscular twitching, tetanic convulsions,

lowering of blood pressure and body temperature, and decline in urine secretion and heart rate. Lack of cortin is said to disturb the salt relation in the blood (particularly sodium chloride and potassium), the water metabolism and redistribution in the body, the metabolism (especially absorption) of intermediate carbohydrates and fats, and milk production in females (at least in cats).

The Pituitary Gland

The pituitary gland in the human being is a body weighing about 0.5 Gm., lodged in a depression at the base of the brain. It consists of two principal parts: the anterior lobe and the posterior lobe. These two portions have distinct functions. The vital importance of this body was not realized for many years, but a series of observations has placed it in a position of such importance that it has been referred to as the *regulator of the glandular system*. The pituitary gland is now known to be the source of a number of hormones, and their functions are so closely connected with those of other endocrine secretions that they apparently have a part in all hormonal processes of the body.

The secretions of the anterior lobe of the pituitary affect the growth and development of the organism in general, the general metabolism of the body, the development of the sex organs, and work with other hormones in controlling additional processes. Inefficiency in the anterior lobe, furnishing the body with either too much or too little of the growth-promoting hormone (phyrone) results in the production of giants or dwarfs. A decreased supply of the hormone in an immature individual, if the condition is not remedied by administration of the hormonal extract, retards the growth of the body and may cause a complete cessation of growth. The dwarfs of the circus furnish examples of this unfortunate condition, although not all dwarfism must be thought due to this cause. For example, the cretin described previously is the result of thyroid disorder and is usually a mental dwarf as well as a dwarf in body, while dwarfism resulting from deficient phyrone is accompanied in most cases by a normal mental development.

An overfunctional anterior pituitary results in a marked increase in the growth of bones, although the general development of the individual thus affected may be symmetrical and the physiological processes may be normal in every respect. Cases of this type are commonly seen. One such instance may be cited in which a nine-

year-old boy measured six feet and one inch and weighed 178 pounds. His mental condition was normal.

Another condition, known as *acromegaly*, may result from an overfunctional anterior lobe of the pituitary during adult years. The facial bones enlarge, particularly in the ridges above the eyes, the nose, and the lower jaw, and the soft tissues of the face undergo an overgrowth resulting in a coarsening of the features. The hands and feet may enlarge, also. The disease may prove fatal if it continues sufficiently long.
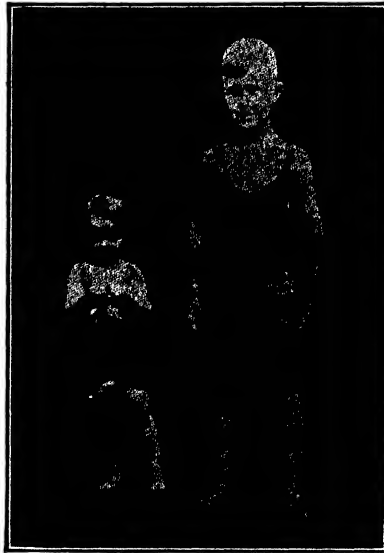
Fig. 59.—A pituitary dwarf at the age of nine and one-half years, compared with a normal child of the same age. (From Zoethout, *Textbook of Physiology*, The C. V. Mosby Company, after Engelbach.)

A second hormone secreted by the anterior lobe has a direct influence on the sex organs. This gonadotropic hormone (prolan) stimulates growth and activity of the gonads, the testes and ovaries, and therefore controls the production of the gonadal hormones, which will be discussed later. The absence of gonadotropic hormone results in an atrophy of the testes and ovaries, and the cessation of the production of the spermatozoa and the ova; its injection increases the activity of the sex organs.

The posterior lobe of the pituitary also produces more than one hormone, although *pituitrin* is the one concerning which we have

the most definite knowledge and which is commonly associated with this portion of the organ. Pituitrin is known to stimulate the muscles of the arterial system, increasing or decreasing the blood pressure according to the amount of the hormone released in the blood. It is also a stimulant for the musculature of the uterus and the intestinal muscles.

It is concerned also with the regulation and disposal of carbohydrates in the body. The body is able to use an increased quantity of sugar when the secretion of pituitrin is reduced; and, on the other hand, when the quantity of the hormone is more than normal, the body needs less sugar; carbohydrates not actually needed are stored as fat, resulting often in abnormally fat people, extreme cases of which are seen in the circus. The posterior lobe of the pituitary probably does not affect the development of the bones, but the function just discussed is quite definite.

The posterior lobe of the pituitary is concerned also with the regulation of the secretion by the kidneys. A diseased condition, known as *diabetes insipidus,* in which the patient voids large quantities of urine, is treated by injection of the postpituitary hormone. It appears that the hormone probably enables tissues to utilize and store larger amounts of water than is possible in its absence.

Still another effect of the secretion is found in the case of certain amphibians and reptiles; that is, its effect on the pigmentation of the skin of these animals. The removal of the pituitary gland of a frog results, among other things, in the bleaching of the animal and the inability of the frog to alter the color scheme of its skin to agree with the surroundings. When in a strong light or on a light background the retinas of the frog's eyes are stimulated by light rays, and some of the impulses reach the pituitary's posterior lobe, resulting in a suppression of its secretion, and consequently a lightening of the frog's skin. When the light is decreased the pituitary increases its secretion and the frog has a darker pigmentation. These reactions probably do not occur so directly in the higher groups of vertebrates. Removal of the pituitary gland tends to cause atrophy of the other endocrine glands.

The Thymus Gland

The thymus, a small glandular structure located in the chest between the upper part of the sternum and the pericardium, is a temporary organ, which normally atrophies in human beings by the time

of the onset of puberty. When the gland is too active, a condition is found in children in which an enlargement of the organ results, and breathing is rendered difficult. No distinct hormone has been obtained from this gland.

It has been claimed recently that accruing acceleration in the rate of growth and development occurs when successive generations of rats are given daily injections of thymus extract. In third and fourth generations, the rats at twelve days of age compared favorably with controls of twenty days. Introduction of thymus extract in young tadpoles causes them to grow rapidly to the size of the adult frog but still retain their tadpole form and appearance. The disappearance of the thymus at the time of puberty permits the differentiation of mature animals and particularly the onset of activity of the sex glands. Some workers claim that the thymus contributes to the orderly and proper development of the bones of the skeleton.

The Gonads and Sex Hormones

In addition to the usual function of producing germ cells for reproduction, the gonads produce hormones which influence the development of secondary sexual characters and which have a regulatory effect on the reproductive processes and activities. Sex differences are caused in part by various hormones which have a selective action on the male or on the female secondary and accessory sex characteristics. The earlier concept that the male sex produces "male" hormones exclusively and the female produces only "female" hormones is no longer held. For example, extracts have been prepared from the urine of women as well as from men which on injection into capons caused growth of the comb which ordinarily fails to develop as it would in the cock. The sex hormone substances affecting the male are spoken of as *androgenic* and those affecting the female as *estrogenic*. The important sex hormones are *androsterone, testosterone, theelin,* and *progesterone* (progestin). The first two are male hormones, and the others are female.

Androsterone is found in male urine and can be crystallized from it. It has a stimulating effect on development of secondary sex characteristics and a definite regenerative effect on accessory organs (seminal vesicles, prostate glands, and penis) of castrated male animals. Testosterone is produced in the interstitial tissue of the testis but is absent from the urine. This hormone is several times as

effective as androsterone in bringing about regeneration of accessory sex organs in castrated males. Recently androgenic hormones, which are potent enough to affect the growth of comb in the capon, have been found in the urine and ovaries of female animals.

Theelin (oestrin, estrogen, folliculin, menoform, progynon) has been isolated from liquor folliculi, pregnancy urine, the placenta, and amniotic fluid. This substance causes (1) increased growth of the accessory female organs (uterus, oviducts, etc.), including changes in the glands of their linings and in vascularization; (2) contraction of the smooth muscle of the uterus; (3) initial growth of mammary glands and nipples; and (4) sudden lowering of theelin concentration in blood (suggested as cause for bleeding during menses). The secretion of theelin is influenced by the gonadrotropic principle of the anterior pituitary.

Progesterone (lutein hormone, corporin, luteosterone progestin) is a female hormone produced by the corpus luteum, the yellow body of material which forms in the ruptured Graafian follicle after the escape of the ovum. It produces the following effects: (1) sensitization of the lining of the uterus so that implantation or attachment of the zygote may take place in case of fertilization; (2) development of placenta; (3) arrest of rhythmic contractions of the smooth muscle of the uterus; (4) inhibition of ovum production and uterine bleeding.

The influence of other hormones of the body is noted in the reproductive and sexual processes. The effect of the pituitary has already been mentioned. The thyroid secretion probably plays a role, not clearly understood, in the female reproductive processes, since the thyroid always enlarges at puberty and during pregnancy. Another hormone is thought by some investigators to be formed in the placenta during the development of an embryo. The interrelationships of these hormones are involved, and doubt exists in some cases as to their exact functions.

The Pancreas

This is one of the organs serving a dual purpose in the body; it secretes from a group of its cells, called *the islands of Langerhans*, a hormone designated as *insulin*. Experiments have shown the action of insulin to be concerned with the metabolism of carbohydrates and fats. Its presence facilitates the combustion of carbohydrates,

ENDOCRINE GLANDS AND THEIR FUNCTION—SUMMARY

NAME OF HORMONE	WHERE PRODUCED	NORMAL FUNCTIONS	OTHER RELATIONS AND REMARKS
Growth hormone (phyone)	Anterior pituitary (ventral side of brain)	Controls size of individual	Hypersecretion during growth period produces giants; hypersecretion after maturity produces acromegaly; hyposecretion during infancy causes normal dwarfs
Follicle stimulating (F. S. H. or prolan or gonadotropic)	Anterior pituitary	Growth and maturation of gonads; and production of female sex hormone	Stimulates formation of estrogen, the female hormone, by wall of follicle
Interstitial cell stimulating hormone of male	Anterior pituitary	Stimulates interstitial cells of testis to produce testosterone	
Thyrotropic	Anterior pituitary	Growth and function of the thyroid gland	
Adrenotropic	Anterior pituitary	Adrenal development and function	
Mammogenic	Anterior pituitary	Development of mammary glands	In cooperation with sex hormone
Lactogenic	Anterior pituitary	Milk production	Important to childbirth
Pitocin	Posterior pituitary	Contraction of uterine muscles	
Pitressin	Posterior pituitary	Contraction of blood vessels	Hypofunction results in diabetes insipidus
Intermedin	Intermediate pituitary	Intensify skin color in lower vertebrates	Opposite or blanching effect produced by adrenalin
Thyroxin	Thyroid (in neck on either side of larynx and trachea)	Regulate body metabolism by increasing sugar oxidation	Hypofunction during infancy produces cretins; excessive growth of the gland due to iodine deficiency causes goiter

Parathormone (parathyrin)	Parathyroid gland (joining thyroid gland in neck)	Regulates calcium metabolism	Hypofunction causes calcium deficiency, nervousness, tetanus, and even death; hyperfunction causes brittleness of bones.
Adrenalin	Medulla of adrenal gland (near the kidneys)	Raises blood sugar, speeds metabolism and raises blood pressure; stimulates contraction of visceral smooth muscle (Super strength Elixir)	Blanches pigmentation of skin of lower vertebrates
Cortin	Cortex (outer layer) of adrenal gland	Regulates sodium chloride level in blood	Prevents emaciation and Addison's disease
Insulin	Islands of Langerhans in pancreas	Helps regulate sugar metabolism and sugar content in blood	Hypofunction produces a condition known as diabetes
Testosterone (male hormone or androgen)	Interstitial tissue of testes	Development of male genitalia and appearance of male secondary sexual characteristics	Size of penis and descent of testes into scrotum; deepening of voice, stature, and beard
Estrogen (female sex hormone or theelin)	Walls of the follicles of the ovary	Development of uterus and vagina	Produces and helps regulate menstrual cycle
Progesterone (corporin)	Corpus luteum which forms in spent follicle of ovary	Maintains pregnancy	Helps regulate menstrual cycle
Secretin	Wall of duodenum	Stimulates pancreas to secrete pancreatic juice	

regulates the rate of sugar production by the liver, and promotes the storage of sugar as glycogen in the muscles. It therefore decreases the amount of sugar in the blood.

Extracts of insulin are obtained from the pancreas of animals and are used commercially for the treatment of the condition known as *diabetes*. This disorder is due to a disturbance of the metabolism of sugars, provoked by a deficiency of insulin. The blood contains too great a percentage of sugar, but this is not turned into needed energy, and much water is excreted by the kidneys in order to eliminate the excess sugar. The patient suffers, therefore, from fatigue, excessive hunger, and thirst. The injection of insulin subcutaneously assists in regulating the condition by restoring the power to transform glucose into glycogen in the muscles. The patient regains strength and weight as a result, but the treatment does not perfect a complete cure and additional insulin must be injected at intervals to maintain normal health. Overdoses of insulin result in very serious disturbances, which may be relieved by ingestion of glucose.

Among the functions of the hormone, *adrenalin*, is the acceleration of the production of glucose in the blood; it is apparent, therefore, that the hormones, insulin and adrenalin, are antagonistic in their effect on sugar metabolism, and an upset of the normal production of these secretions results in metabolic disturbances.

Thus we see the complexity of the performance of these secretions in the body. When they are present in correct proportions, the organism enjoys a smooth functioning of its physiological processes, regulated by the hormones. The malfunctioning of any one endocrine organ results, however, in a disturbance of those processes which it specifically regulates and usually of others which it influences in conjunction with its sister glands of internal secretions or with other regulatory organs of the body. Each gland is called upon, therefore, to function in full cooperation with the other glands as well as to perform duties peculiar to itself.

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CHAPTER X

SEXUAL REPRODUCTION AND DEVELOPMENT OF THE INDIVIDUAL*

Reproduction is one of the fundamental capacities of all living things. New individuals of the same kind can be produced sexually by the activity of special germ cells (gametes) provided for that purpose in metazoan animals. The germ cells of the two sexes are quite different. The processes involved in sexual reproduction and embryology are generally similar in different groups of animals but different in matters of detail.

The male *germ cells* or *spermatozoa* are produced in the male gonads or *testes*. The internal structure of more highly developed testes consists largely of extensive *seminiferous tubules* imbedded in *interstitial* tissue. The cells composing the inner lining layers of these tubules produce the spermatozoa by a process of maturation. The female *germ cells* or *ova* are produced in the *female gonad* or *ovary*. Certain cells of the inner surface of the epithelial covering of the ovary become differentiated as germ cells. They become imbedded in the stroma of the ovary in the process of development. The original epithelial cells from which germ cells arise are known as *primordial germ cells* in either sex.

The maturation (gametogenesis) or development of germ cells consists of a series of cell divisions which is modified at one point to bring about a fusion of chromosomes and subsequently a reduction in their number. In the case of development of spermatozoa the maturation process is completed within the gonad, but in development of ova the last division or in some cases last two divisions are completed after leaving the gonad and uniting with a spermatozoön. The maturation process prepares the germ cells for fertilization. Development of the male germ cell is known as spermatogenesis, and the development of the female germ cells is oögenesis.

Oögenesis begins with the primordial germ cell within the ovary. These cells are typically spherical or oval with a prominent nucleus, having the normal number of chromosomes for the somatic cells of the species. This number of chromosomes is known as the *diploid* number. For purposes of illustration the process will be described

for a form whose diploid number of chromosomes is eight. The primordial cell divides by mitosis to form two *oögonia*. Each of these divides similarly. As is typical of mitotic division, each chromosome divides with the division of the cell. This series of divisions constitutes the *multiplication* period of the maturation process. In some instances each of these cells divides once more. Next, each of these oögonia passes through a *growth* period without division. During this time the chromosomes in each unite in pairs and fuse together. This fusion is spoken of as *synapsis* of chromosomes. At the close of this growth each of these cells is called a primary oöcyte. Each of
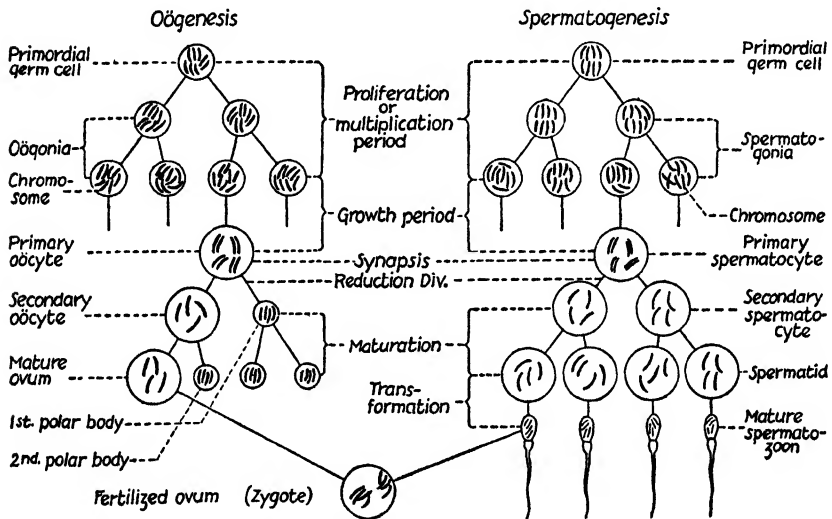
Fig. 60.—Maturation of germ cells. *Oögenesis* includes the maturation divisions in development of the female germ cells or ova, and *spermatogenesis* is a similar process of division in the development of mature male germ cells or spermatozoa.

these oöcytes divides by meiotic division, the fused chromosomes dividing as though they were single ones in normal division. This division, therefore, results in cells with half the somatic (diploid) number of chromosomes and is spoken of as the *reduction division*. The cytoplasm does not divide equally; nearly all of it goes to one of the cells in each case. This large cell is called the *secondary oöcyte* and the small one is the *first polar body*. Each of these cells has four chromosomes. Following this the secondary oöcyte divides to form the *mature ovum* and another polar body. Occasionally the first polar body divides, but none of them have any further signifi-

cance after carrying away half of the chromosomes. They now degenerate, and their protoplasm is reabsorbed by the surrounding tissue. The series of divisions and changes following the primary oöcyte stage constitute the *maturation period* of the process. The ovum containing the *haploid* number of chromosomes is now prepared to unite with a mature spermatozoön in fertilization.

Spermatogenesis is completed within the tubules of the testis, and, like oögenesis, is a series of cell divisions. The primordial germ cells divide by mitosis to form spermatogonia, and this process continues just as it does in oögenesis, until the division of the primary spermatocytes which have developed during the growth period. When the primary spermatocytes divide, the division is an equal meiotic one and all of the resulting cells are typical *secondary spermatocytes* with the haploid number of chromosomes. These cells divide to form *spermatids*. Each spermatid then undergoes a change of shape or *transformation* to form the *mature spermatozoön* with its half number or, in this case, four chromosomes. The change from spermatid to spermatozoön does not involve a cell division but simply rearrangement. The spermatozoön is a slender, motile cell composed of head, middle piece, and tail. It is now able to swim in fluid and prepared to unite with a mature ovum.

The maturation process is very significant for at least two important reasons. First, during the fusion and subsequent divisions of the cells, there is given opportunity for variation of the genetic composition. Secondly, the number of chromosomes is reduced to half in each mature germ cell, thereby making it possible for the germ cells to unite without doubling the typical number of chromosomes in each new generation. These modified divisions of the oöcytes in oögenesis and spermatocytes in spermatogenesis, which bring about the reduction of chromosomes, are termed *meiosis*. Each species has a definite and constant number of chromosomes.

Fertilization involves the union of a mature ovum and mature spermatozoön to produce a fertilized ovum or *zygote*. The spermatozoön swims to the egg and enters it by penetrating the outer membrane which is called the *vitelline membrane*. For most animals, as soon as one sperm enters an egg, the chemical nature of the vitelline membrane changes and prevents entrance of others. The head of the sperm carries the nucleus and soon takes the form of a rounded *male pronucleus* inside the cytoplasm of the egg. The egg nucleus is known as the *female pronucleus*. The male and female pronuclei finally fuse

to form the *fusion* nucleus, and the fertilization is complete. The significance of fertilization is largely centered around two important functions. First, it is the impetus for the development of an embryo from the egg under most normal circumstances; however, parthenogenesis replaces this function in some cases. Secondly, it brings
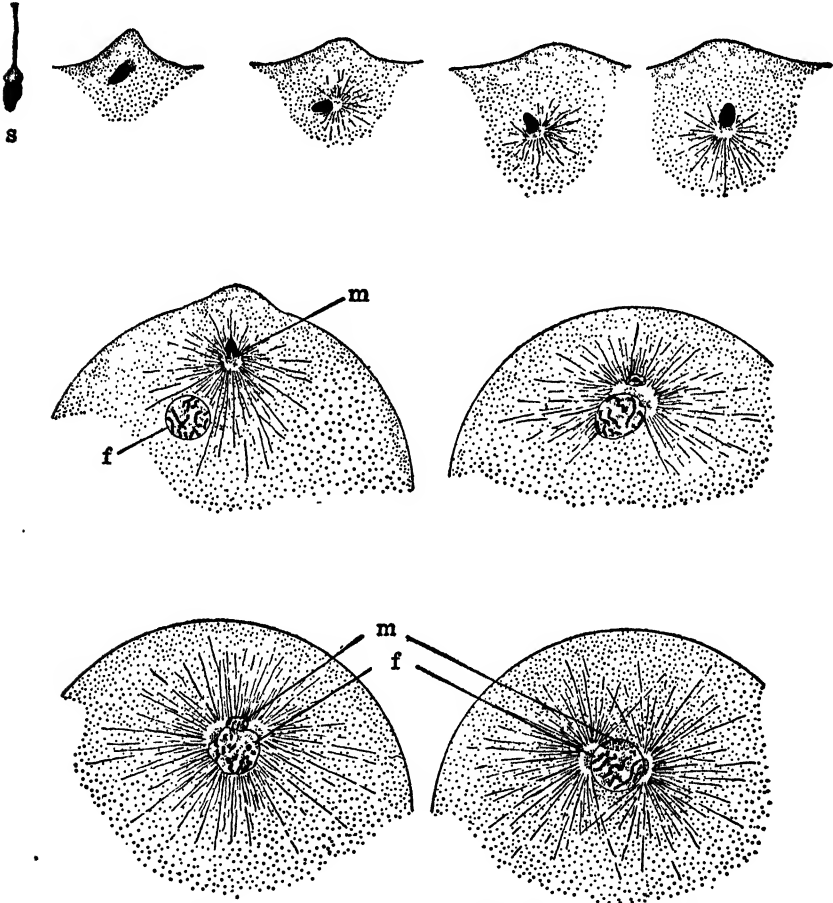
Fig. 61.—Fertilization in the sea urchin, *Toxopneustes*. *S*, mature spermatozoon; *m*, transformation of spermatozoon in male pronucleus; *f*, female pronucleus. Union of pronuclei in lower figures. (Reprinted by permission from *Outline of Comparative Embryology* by Richards, John Wiley and Sons, Inc., after Wilson.)

about the means for inheritance of characteristics from two different lines of ancestry. This union also restores the diploid number of chromosomes.

Cleavage is a series of mitotic cell divisions beginning in the zygote immediately following its formation. These divisions occur in rapid order with but very little intervening growth, and the resulting cells adhere to each other in a body. In eggs where the yolk material is scant and evenly distributed, the ensuing cleavage divisions extend completely through the zygote, forming nearly equal cells. If the yolk is concentrated in one end of the egg, the divisions of the developing embryo are unequal. During the early divisions all of the cells of the body divide at so nearly the same rate that it appears as if the zygote were being cut with a knife or cleaver into
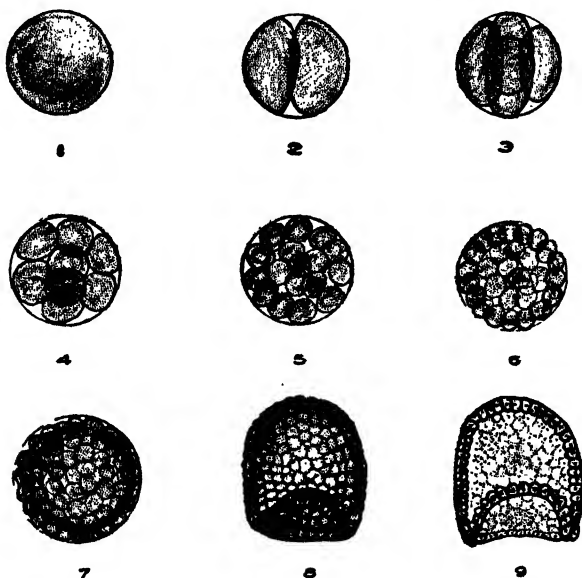
Fig. 62.—Cleavage in the embryo of *Asterias* (starfish). *1,* fertilized ovum (zygote) ; *2,* two-celled embryo following first cleavage division ; *3,* the four-cell stage ; *4,* the eight-cell stage ; *5,* the sixteen-cell stage ; *6,* morula stage (solid) ; *7,* blastula stage (hollow) ; *8,* early gastrula stage (infolding of cell layer at one side) ; *9,* later stage of gastrulation. The infolded layer is the endoderm. (Drawn by Titus C. Evans.)

smaller parts. This process provides for the rapid increase in the number of cells and growth of the embryo which is necessary before any special parts can be formed. Cleavage has been described briefly in an earlier chapter under the discussion of the development of the frog.

As divisions proceed, a *blastula* is formed by the development of a cavity (blastocoele) within the spherical mass of cells, the wall of

which is now a single layer. The formation of the blastula, which usually comes at the sixty-four-cell stage or later, marks the end of cleavage. The blastula stage of an animal like a starfish or a frog resembles somewhat a hollow rubber ball whose wall is made up of a large number of pieces cemented together.
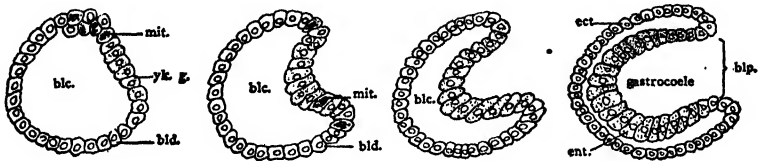
GASTRULATION IN FORM WITH ISOLECITHAL EGG HAVING ALMOST NO YOLK—AMPHIOXUS.
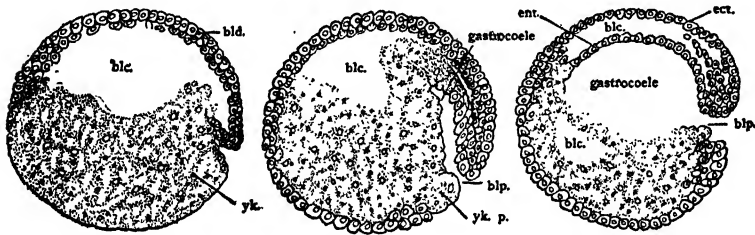
GASTRULATION IN FORM WITH TELOLECITHAL EGG CONTAINING MODERATE
AMOUNT OF YOLK—AMPHIBIA.
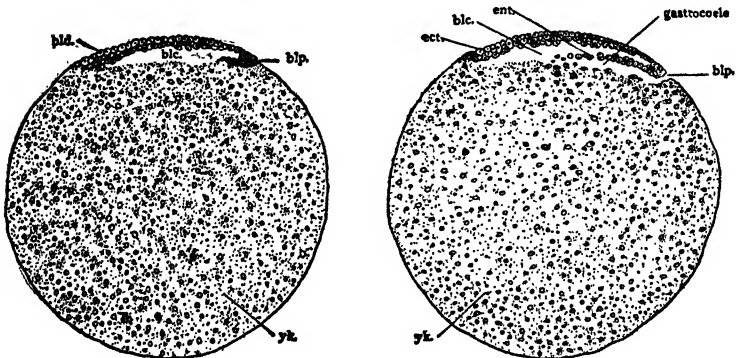
GASTRULATION IN FORM WITH TELOLECITHAL EGG CONTAINING LARGE
AMOUNT OF YOLK—BIRDS.

Fig. 63.—Gastrulation in three types of embryos. Each type begins with the late blastula at the left. *blc.*, blastocoele; *bld.*, blastoderm; *blp.*, blastopore; *ect.*, ectoderm; *ent.*, endoderm; *mit.*, cells undergoing mitosis. (From Patten, *Embryology of the Chick*, by permission of P. Blakiston's Son and Company.)

As cell divisions continue in the blastula, a *gastrula* is finally formed. The blastula does not simply increase in circumference, but there comes a time when the wall on one side pushes in (invaginates), finally meeting the wall of cells from the other side. This gradually crowds out the cavity and forms a wall of two layers of cells. The outer layer is known as the *ectoderm* (outer skin) and represents the portion of the wall of the blastula which has not folded in. The inner layer, or that resulting from the infolding of the wall of the blastula, is called *endoderm* (inner skin). As division of cells in this wall proceeds and the infolding continues, the two margins of the infolded part come nearer and nearer each other. This gradually encloses an outside space which is lined by the endoderm and represents the primitive digestive tract or *archenteron*. This is the beginning of the two primitive *germ layers,* ectoderm and endoderm. In sponges and coelenterates development stops here.

In higher forms, immediately following gastrulation, a third germ layer, the *mesoderm* (middle layer), is organized from cells usually contributed by one or the other or both of the other germ layers. In some cases it arises as two saclike outgrowths from the endoderm, one on each side in the gastrula. These pouches push into the remains of the blastocoele. In other cases separate cells are shed from ectoderm or endoderm or both, or from an undifferentiated portion to organize as a distinct layer between the other two. The position of the mesoderm is external to the endoderm and internal to the ectoderm. It nearly encircles the endoderm. Sooner or later a space forms within the mesoderm, causing the outer limb of it to join the ectoderm and the inner to join the endoderm. This cavity is the coelom or future body cavity. From each of the germ layers, particular parts of the body are derived.

The *fate* of the *germ layers* is determined as cell division and development continue. Cell division proceeds at different rates in different regions and at different times, resulting in various infoldings, outpushings, and extensions which finally bring about the formation of all parts of the mature individual. The ectoderm gives rise to the external surface cells or epidermis of the skin and to the nervous system; the mesoderm furnishes the muscles, skeleton, circulatory system, blood, excretory, and reproductive systems besides nearly all connective tissue; and the endoderm produces the internal linings of the digestive tract, respiratory tract, and such outgrowths as the liver and pancreas

Body Form

Since the development of the frog has been discussed briefly in the chapter dealing with the bullfrog, it will not be included here. In a developing chicken, which is easily studied, the head fold appears in a fertile egg that has been incubated about twenty hours. The *neural groove* (primitive spinal cord) begins its formation at about this time. At about twenty-one or twenty-two hours of incubation, there appear on each side of midline and lateral to the neural
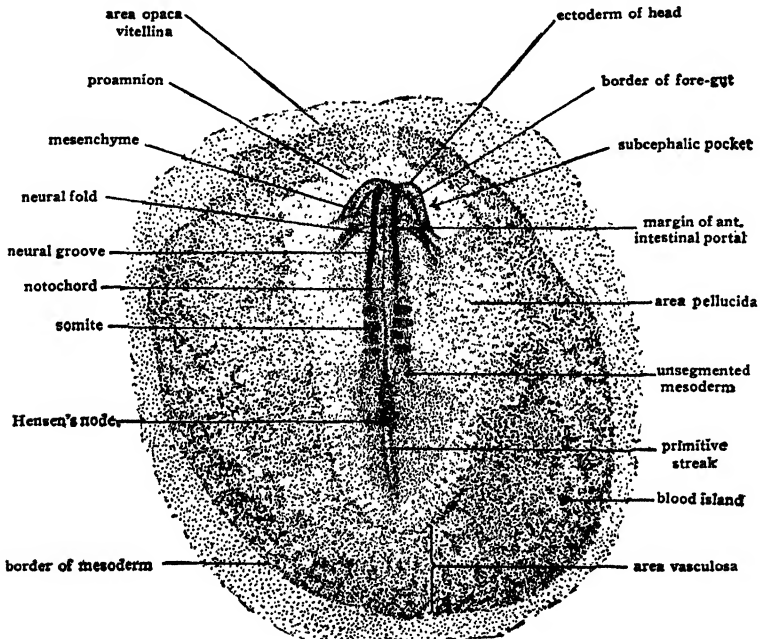
Fig. 64.—Dorsal view of entire chick embryo of about 24 hours of incubation. Notice that the fourth pair of somites is almost developed. (From Patten, *Embryology of the Chick*, P. Blakiston's Son and Company.)

groove blocklike thickenings in the mesoderm. These are *somites*, and they are paired opposite each other, marking segmentation in the body. At twenty-four hours of incubation there are four pairs of these somites, and they increase with growth until at thirty-six hours there are fourteen, at sixty hours thirty-two, and approximately forty at four days. Similar somites develop in a somewhat similar way in other vertebrates including mammals. Rabbit, cat, rat, calf, or man is no exception. In a pig embryo 6 millimeters long there

are thirty-two somites and the body form is becoming defined. The human body can barely be discerned in embryos of one month, and the embryo must be nearly two months of age before it can be identified definitely as human on the basis of morphological features.

The younger embryos of different groups of vertebrate animals are so similar that it is impossible to distinguish them from each other. The illustrations in Fig. 203 in a later chapter will bear this out. At a stage early enough, the embryos of the human being, the pig, the rat, the rabbit, the alligator, the salamander, and the fish all appear very similar. The gill slits and segments are conspicuous on all of them. Much later, the limbs develop from lateral limb buds in the mesoderm. The hind limb buds develop first, and the front ones follow.

Organs and Systems

After the three germ layers, ectoderm, endoderm, and mesoderm, have been established in the embryo, the next step is the differentiation of these layers each in various ways for the formation of particular organs and systems of organs. The development of the typical vertebrate systems is generally similar in all of the different classes of this group. The development of the different organs in the body is often referred to as *organogenesis.*

Digestive System.—This system takes its beginning in the *archenteron* which is formed as a new cavity at the time the endoderm becomes differentiated from the germ plate of cells. The endoderm becomes the lining of the alimentary canal and its outgrowths, with exception of the mouth and anal cavity. And the splanchnic portion (medial sheet) of the mesoderm comes in to cover it. The muscles, connective tissue, and blood vessels in the wall of the canal are provided by this mesoderm sheet. Immediately posterior to the mouth is the pharynx, which has lateral *gill pouches* or pharyngeal pouches. In the higher vertebrates there are typically five pairs of these pouches. In fishes and amphibians these pouches break through to the exterior, forming gill clefts. In higher forms these pouches are transient structures which remain to call attention to existence of functional gills in their phylogenetic ancestors. Certain adult structures do arise from these pouches even in mammals. Such structures as the middle ear, Eustachian tube, hyoid, thyroid, thymus, tonsil, and others are products of these pouches.

The tubular canal is inflated and curved in the formation of the stomach some distance posterior to the pharynx. The small and the

large intestines develop from the posterior portion of this originally straight tube with relatively slight modification. The liver appears as a tubular outgrowth from the duodenum as likewise does the pancreas.

The Respiratory System.—The trachea develops as a posterior extension of the pharynx, which is separate from the esophagus. It begins as a groove, extends posteriorly, and soon bifurcates, forming the bronchii from which the two lungs develop. This original structure, therefore, is endoderm, and the internal lining of the adult trachea and lungs is the portion derived from this. Again, the splanchnic mesoderm has contributed the muscle and connective tissue outside of the lining.

Nervous System and Sense Organs

At the end of gastrulation the ectoderm has become a distinct layer. The portion of it which will become the mid-dorsal area of the body thickens to become the *neural plate*. This plate sinks, forming a *neural groove* with a *neural fold* as each lateral boundary of it. The groove deepens, and the folds grow to meet each other over the cavity thus forming the *neural tube*. This tube is the forerunner of the spinal cord and brain.

The Brain.—The anterior end becomes swollen and thickened for the development of the brain. This brain structure divides by constrictions into the anterior *forebrain* (prosencephalon), *midbrain* (mesencephalon), and the posterior *hind brain* (rhombencephalon). Later, the forebrain divides into two regions, the anterior *cerebral hemispheres* (telencephalon) and the posterior *diencephalon*. The midbrain, or mesencephalon, remains undivided to become optic lobes and related structures. The hind brain divides to furnish the *cerebellum* (metacephalon) from its anterior portion and the *medulla oblongata* (myelencephalon). During the time of this development the brain becomes bent or *flexed* ventrally on itself so it becomes shortened and compact.

Sense Organs.—These organs all develop from the ectoderm. The organs of four of the principal senses develop from the peripheral ectoderm, but those of the fifth, the sensory portions of the eyes, are essentially processes of the ectoderm wall of the brain.

The sensory portions of the *eyes* form as hollow evaginations (outgrowths) from the sides of the forebrain (diencephalon portion) growing laterally toward the peripheral ectoderm of the head.

These expanded outgrowths are known as *optic vesicles* and the narrowed connection of each to the brain is an optic *stalk*. The lateral wall of the vesicle inverts into its cavity. The indented portion thus forms the *optic cup*, the internal lining of which becomes the retina. Slightly later, the *crystalline lens* is formed by a thickening of the peripheral ectoderm which covers the optic cup. Along the ventral side of the optic stalk is a furrow, the *choroid fissure* in which blood
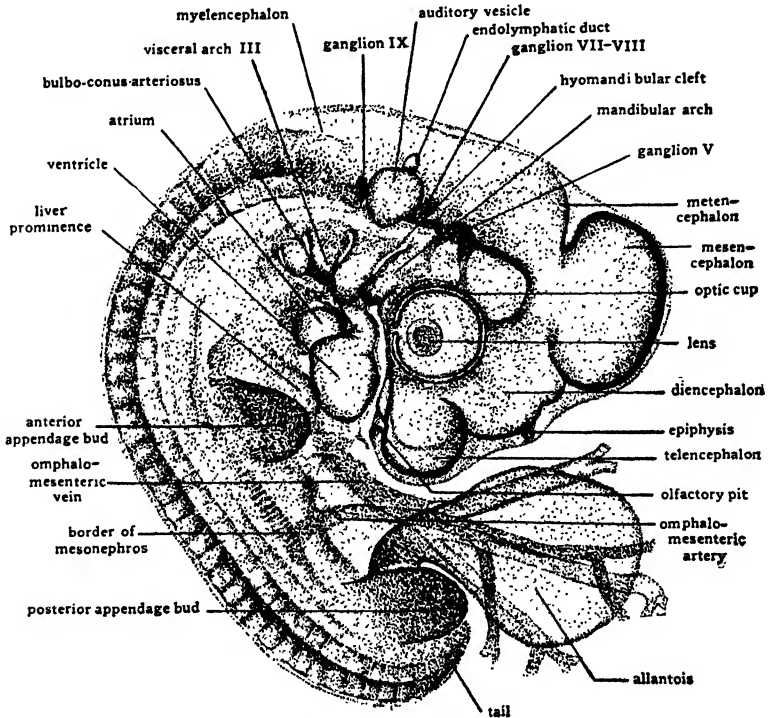
Fig. 65.—View of right side of entire chick embryo of about four days of incubation. Heart, brain, sensory organs, gill slits, and appendages are in the process of development. (From Patten, *Embryology of the Chick*, P. Blakiston's Son and Company.)

vessels and the optic nerve will later lie. The choroid, sclera, ciliary process, and muscles all develop from surrounding mesoderm, just a little later.

Olfactory organs begin as two areas of thickened ectoderm on the head, anterior to the oral aperture. The plates of ectoderm sink to form olfactory sacs which later open through to the mouth cavity, or pharynx in higher vertebrates. The walls of the chamber thus

formed become deeply folded, and sensory cells are distributed in the epithelial lining.

The *ear* originates in the individual as a thickened plate of peripheral ectoderm on each side of the hind brain region of the head. These plates invaginate (fold in), forming an *auditory vesicle* or sac on each side and are later freed from the external ectoderm. Each becomes a *membranous labyrinth* of the inner ear, which includes the sensory cochlea and the semicircular canals. The middle ear develops later from the first gill pouch forming a *tympanic cavity.* The *ossicles* or ear bones follow later from the mesoderm. The connection of this pouch to the pharynx is retained and becomes the Eustachian tube on each side. The *tympanic membrane* develops as the mesodermic sheet between the outer extremity of the gill pouch and the depression of the external cleft, which becomes external *meatus.* The external ear arises as a mesodermal outgrowth beneath the skin.

The taste-buds develop in the epidermis of the tongue and elsewhere in some forms. Thus they are ectodermal.

Circulatory System.—This system develops in the mesoderm. The formation of the earliest blood vessels has not been studied in man because they have already formed in the earliest embryos critically studied. But in cats and other vertebrates they are formed from small spaces which develop among the mesenchymal cells. These spaces extend and fuse, usually developing along the longitudinal axis. The *heart* develops as a pair of *amnio-cardiac* vesicles in the mesoderm, one on each side of the wall of the foregut, which at that time has not closed ventrally. As the digestive tube closes ventrally, the vesicle from each side moves ventrally until it meets its fellow. By this time each vesicle has extended lengthwise to become a tube which is the *omphalomesenteric* vein. The anterior portions of these two cavities join to form the tube which is the primitive heart. This tube then bends on itself with one limb of the fold becoming the *atrium,* which receives blood from the veins, and the other limb of the fold becoming the *ventricle* and *bulbus,* which deliver blood to the arteries. This represents the primitive condition as found in the two-chambered heart. As development progresses a septum forms in the atrium dividing it into right and left chambers and similarly an *interventricular* septum forms to produce right and left ventricles. These septa are completed at about the time of birth.

In the embryo, the gill arches are supplied with branches of the ventral aorta, which leads anteriorly from the heart. These branches

extending through the gill arches are called *aortic arches* (Fig. 204). The typical number of these arches in the vertebrate is six, but in the embryos of most higher vertebrates the fifth one is quite transitory. The first and second pairs degenerate, except for remnants which unite with the third in forming the carotid arteries. The fourth pair of arches becomes the systemic arteries in amphibia and reptiles, but in birds only the right side of the arch persists while in mammals only the left. The sixth pair of arches give rise to the pulmonary arteries.
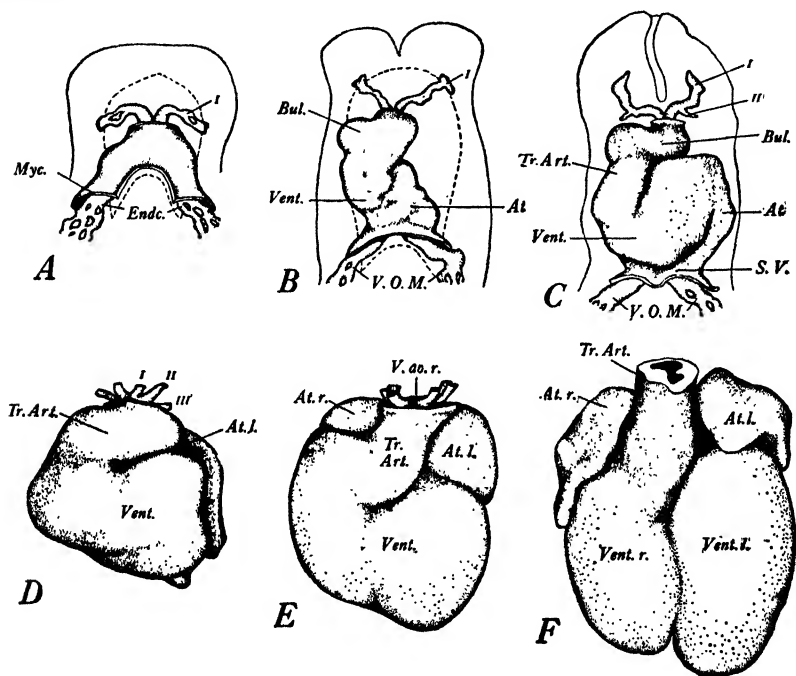
Fig. 66.—Ventral view of the development of the heart of the pig. The stages shown bring out the changes involved in converting the primitive tubular vessel into a four-chambered heart.

A, from 7 somite embryo; *B,* 13 somite embryo; *C,* 17 somite embryo; *D,* 25 somite embryo; *E,* from embryo 3.7 mm. in length; *F,* from 6 mm. embryo. *At.,* atrium (*r,* right; *l,* left); *Bul.,* bulbus arteriosus; *Endc.,* endocardial tubes; *Myc.,* cut edge of epimyocardium; *S. V.,* sinus venosus; *Tr. Art.,* truncus arteriosus; *V. ao. r.,* ventral aortic roots; *Vent.,* ventricle (*r,* right; *l,* left); *V. O. M.,* omphalo-mesenteric veins. (From Patten, *Embryology of the Pig,* P. Blakiston's Son and Company.)

Urogenital System.—It is convenient to present the excretory and genital systems under one head because certain parts are developed in common and others in close relation to each other. The principal

structures of this system arise from the middle portion (mesomere) of the mesoderm germ layer. This portion of the mesoderm develops as a fold of tissue just lateral to the midline on each side, extending from the thorax to the pelvis and projecting down into the body cavity slightly. The earliest and most anterior part of this fold is the *pronephros.* In higher vertebrates this is strictly an embryonic structure, though it does develop some Malpighian corpuscles which exist for a time. The pronephric duct which develops and leads from the pronephros to the cloaca persists, later becoming the *Wolffian duct.* Next follows the *mesonephros,* which is more elaborate and really functions as a kidney for a time in the embryo of reptiles, birds, and mammals, and throughout the life of fishes and amphibia. It partially overlaps the posterior portion of the pronephros and extends several segments farther posteriorly. The collecting tubules, which receive urine from the Malpighian corpuscles, reach the surface of the mesonephros and join the pronephric duct leading to the cloaca.

In the reptiles, birds, and mammals, the permanent kidney arises from still a third development, the *metanephros.* This is formed at the free end of the metanephric duct which is an outgrowth of the pronephric duct near the cloaca. The metanephros overlaps the posterior portion of the mesonephros. There are numerous Malpighian corpuscles in the tissue of this body, and the metanephric duct becomes the *ureter.* The Wolffian duct becomes the vas deferens of the male but degenerates in the female except for a vestige. The urinary bladder develops as a ventral downpushing from the cloaca.

A genital ridge develops along the ventral margin of each mesonephros before it degenerates, and from this fold a gonad arises. Regardless of future sex, there develops also in each individual, a Müllerian duct from the ventrolateral portion of the mesonephric body. This duct becomes the functional oviduct of the female, but it degenerates in the male except in animals like the leopard frog.

The ovaries develop in their permanent location, but the testes of most male mammals are derived from the mesonephros in the dorsal part of the body cavity and at a certain age descend through an inguinal canal to the scrotum which is outside the body wall.

The external genital organs develop as general structures with no distinction as to sex until about the end of the second month in the human being. At that time the *penis* takes form from the phallus or genital tubercle, if the individual is to be male. In the female

the *clitoris,* a relatively small body of erectile tissue, which develops ventral to both the genital and urinary apertures, is homologous to the glans portion of the penis.   The labia, which are folds of tissue at each side, are homologous to the scrotum of the male.

Intrauterine Development

There are several groups of animals, particularly among chordates in which the zygotes are retained within the uterus for a considerable portion of the embryonic and fetal development.   In such chordates as some of the common sharks; a few of the bony fishes, as *Gambusia* the mosquito minnow; certain snakes and lizards; and in all mammals except the lowest group, the Prototheria, there is some form of intrauterine development.   In the groups mentioned, other than the mammals, the egg bears an abundant supply of yolk, and the developing embryo, although retained in the uterus for protection, depends on the yolk supplied by the egg for nourishment.   In mammals, including the human being, the egg has a very meager supply of yolk.   It becomes attached (implanted) in the epithelium lining the internal surface of the wall of the uterus, which is highly vascularized.   In all forms where intrauterine development occurs, as well as in many others, the ovum is fertilized within the genital tract of the female by introduction of spermatozoa in the act of *copulation* or *coitus.*   Among the mammals the penis of the male is well developed as an intromittent organ which is received in the vagina of the female where the semen, carrying spermatozoa, is discharged.   The motile spermatozoa swim up the oviduct and meet the ovum shortly after it enters.   Fertilization occurs here, and the zygote moves down the oviduct, developing as it goes.   By the time it reaches the uterus the embryo is in the gastrula stage of development.   The embryo is attracted to the wall of the uterus, where it is partially embedded and attached.   This procedure is known as *implantation.*   Due to the influence of a sex hormone, the uterus becomes highly vascularized and increases in size.   The extra-embryonic membranes develop rapidly to cover the embryo.   These embryonic membranes unite with the epithelial lining of the uterus at the point of contact to form the *placenta.*   The uterine portion of this membrane receives an abundant supply of maternal blood, while the embryonic portion receives a rich supply from the embryo by way of the umbilical vessels which pass through the umbilical cord.   In some mammals the layers of the placenta contributed by parent and embryo become inseparably fused, but in

others, as for example the pig, they separate and only the embryonic portion is shed at time of birth. In the other forms, some of the uterine portion is shed along with the embryonic, and together they are known as "afterbirth."

The circulation of blood in the placenta is by distinct maternal and embryonic vessels which do not join each other. The materials in solution in the blood of either can reach the other by diffusion only, as the vessels and sinuses come in intimate contact in the membrane. The embryo then does not receive the mother's blood as such, because there is not a direct connection between the two systems. The embryo, or later the *fetus,* receives its nourishment and oxygen through diffusion in the placenta and disposes of carbon dioxide and nitrogenous wastes by similar diffusion in the opposite direction.

The time elapsing from time of *conception,* or fertilization, to time of birth is called the *gestation* period. In the human being this period is of nine months' duration.

In the female mammal there is a definite cycle of changes which occur in the uterus, in other sexual organs, and in physiologic relations of the body. This cycle is called the *oestrus cycle.* In the human being the period required for this complete cycle averages twenty-eight days. At one point in this cycle there occurs rather severe degeneration of the uterine lining and some bleeding. This period in the cycle is known as *menstruation period.* It was thought earlier that the ovum was discharged from the ovary at this time and entered the oviduct, but at present it seems to be more commonly accepted that *ovulation* occurs during the 13th to 15th day following the onset of menstruation. The length of the oestrus cycle varies widely in different mammals. In most of them the female will mate only at a certain period in the cycle. This is designated in common terms as the "heat" period.

Biogenetic Law, or Theory of Recapitulation

It is almost impossible to study the embryology of vertebrate animals of the different classes without observing some features of the apparent progressive development in regard to particular organs and systems. In a number of respects the more highly developed forms seem to recapitulate or pass through the stages which existed through the long history of their ancestors. The appearance of gill arches and even part of the slits in certain stages in the embryonic development of mammals indicates that these animals pass

through a stage comparable in this respect to adult fish. There are many examples of such comparisons among animal groups. It is not likely that any animal in its development repeats every stage in its racial development or phylogeny, because many are fused and new ones are introduced. In general, however, the statement, *"Ontogeny recapitulates phylogeny,"* is recognized as having some application. Ontogeny refers to the embryonic development of the individual.

Homology.—The principle of homology is another concept which is employed in studies of development as well as in taxonomy and anatomy. Structures are said to be homologous when *they have similar morphological nature and similar embryonic origin.* For example, a pectoral fin of a fish, the wing of a bird, and the arm of the human are homologous. The eye of the fish and that of man are homologous, but the eye of a crayfish is analogous rather than homologous to these. Its function is similar but its structure and embryonic origin are different.

Theory of Metabolic Gradients (Axial Gradients).—In connection with the orientation and polarity of developing embryos, there is definite and normal order in the physiological phenomena involved. Dr. C. M. Child has related this to regions along the principal axis in forms which possess one. He holds that there is a relative metabolic dominance of certain regions of such a body over succeeding regions with a center or centers of high rate of metabolism and a gradation to lower rates as progressing away from the center. The animal pole of the embryo is such a center; this area sets the pace in the development. In vertebrates the head structures develop most rapidly and tend to dominate the developmental activity posteriorly along the axis of the body. The posterior portions are slower to develop. According to this theory, the organization and orientation of developing parts are determined by the interaction of chemical substances of cellular origin, with the rate of metabolism as the most important factor in influencing the sequence of appearance of parts.

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CHAPTER XI

ANIMAL ANOMALIES

It is rather generally understood among students of biology that no two animals, even of the same species, are exactly counterparts of each other. There is a certain normal range of variation in size and structure as well as in functional efficiency. Any variations beyond these rather fixed limits are classified as *malformations* or *anomalies*. A study of such abnormalities is known as *teratology*. Abnormalities may occur at almost any stage in the life of the individual, but a large majority result from abnormalities in the process of development. Many are due to failure of development and some to over-development. In turn, much of this is due to malregulation resulting from failure of balance in the functioning of the endocrine system. The occurrence of striking malformations in newborn human babies is in approximately the ratio of one to 165. Fortunately, many of the most grotesque anomalies do not reach full development and the monsters are born dead.

Causes of Anomalies.—There are both internal and external agencies which bring about malformations in the individual. Both embryology and pathology contribute to the explanation of the causes of these abnormal conditions. The development may be perfectly normal and a subsequent disease may be the cause of striking abnormality. On the other hand, certain diseases of the parent will influence the normal development of the fetus. Even twinning by itself is an abnormal process in most animals. It, however, is not usually thought of under the title of anomaly, except when they are physically connected or the individuals are otherwise malformed. The causes of anomalies may be summarized as follows:

1. *Internal Causes.*

a. The germ plasm carries hereditary causes for some, and these characteristics are transmitted as are normal traits. Color blindness and hemophilia (bleeder condition) are examples.

b. Diseases which cause abnormal growths and conditions, as elephantiasis.

c. Unbalancing the chemical regulators (hormones) which are produced by the *endocrine glands.* (Overactivity of the hypophysis causes *gigantism; cretinism,* a dwarf condition, results from deficiency in thyroid activity.)

d. Fortuitous abnormalities whose causes are not apparent or are influenced by certain variations in other organs. Such anomalies show up most frequently in the circulatory and nervous systems. Venous or nervous connections to organs are often modified. Another example is the rearrangement brought about by diaphragmatic hernia.

2. *External Causes.*

a. *Environmental agencies* may affect almost any individual whose development occurs outside the body of its parent. Exposure to radium or x-ray radiation, sharp variations in temperature, excessive salt content, or contact with toxic substances may all be responsible for various degrees of abnormality. The same factors are also effective, if present, in the uterine environment of the placental type of animal.

Fig. 67.—Grasshoppers at time of diapause, showing some of the abnormalities which very infrequently occur in their natural development. *1*, Normal embryo; *2*, embryo with two extra heads and mouth parts; *3*, embryo with lateral twin joined at the abdomen; *4*, almost complete twins back to back; *5*, embryo with a double abdomen. (From Evans, *Effects of Roentgen Radiation*, Physiol. Zool., Vol. X.)

b. *Mechanical factors,* such as abnormal pressure, blows, and falls, may cause some abnormalities.

c. *Abnormal implantation* in the wall of the uterus resulting in deficiencies in nourishment and support of the fetus.

d. Such *diseases* as syphilis, which may be transmitted from mother to offspring, are responsible for some types of defects, as impaired vision.

e. *Developmental inhibition or arrest* brought about by deficiencies in metabolism at a time when the rate or efficiency should be high.

The work of several embryologists seems to indicate that the production of twins either as normal individuals or otherwise is related to this condition.

Harelip and Cleft Palate

These two defects are related and are sometimes found together. The lateral palatine processes may fail to complete growth and unite properly, thus leaving a gap in the roof of the mouth which opens directly into the nasopharynx above.
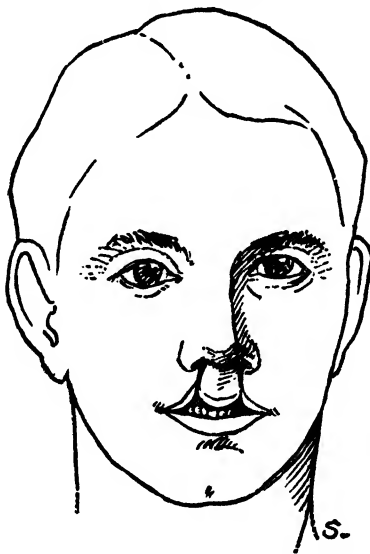
Fig. 68.—A case of harelip due to arrested development.

Harelip (cheiloschisis) is a very common defect and is due to the failure of union of the nasal and maxillary processes. There may be double harelip or single harelip. In connection with double harelip it sometimes happens that the premaxilla projects beyond the outline of the face to form what is called *wolf-snout*. Harelips are frequently remedied by a surgical operation early in life.

Diaphragmatic Hernia (Open Diaphragm)

An extreme case of this was found in a cat which was being used for dissection purposes in Baylor University. The animal had lived an apparently normal life and had been killed for laboratory study without showing evidence of its abnormality until dissected. From

all appearances the diaphragm had not completed its development, but had formed a fringelike projection which reached inward about half an inch from the thoracic wall and extended the entire circumference of the inside of the thorax. The aperture in its center measured one and three-fourths inches in diameter.

Due to this condition the arrangement of several visceral organs was greatly affected. The thorax was somewhat elongated, and the right side of the cavity comprised about two-thirds of the space of the chest. The mediastinum (supporting median mesentery of heart and lungs) had its attachment more than half an inch to the left of the midline.

Almost the entire liver was turned forward to occupy the right two-thirds of the chest cavity, and this placed the gall bladder at the level of the junction of the auricle and ventricle of the heart. Approximately half of the spleen, the pyloric portion of the stomach, and a large portion of the omentum had been drawn through the aperture in the diaphragm. The right lung was extremely crowded and small.

Polydactyly (Extra Digits)

There are numerous abnormal variations in the number and arrangement of digits, ranging from a stumplike structure of no digits through the ''lobster claw'' condition of two or three, to as many as two more than normal. The polydactylous condition is rather
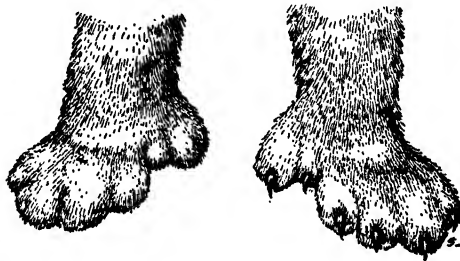
Fig. 69.—Front feet of a half-grown kitten with six digits. The claws are protracted on the left foot and retracted on the right. There were five toes on the hind feet of this cat.

frequently found in cats. In fact, Wilder once reported that possibly 25 per cent of the cats of the vicinity of Ithaca, N. Y., possessed an extra digit on each foot. The forefeet shown in Fig. 69 are from a living cat in Waco, Texas, which came from a litter of four,

two of which showed these complete characteristics on all feet, one of the litter had only an extra toe on one foot, and the fourth was normal. Both hind feet of this animal had five well-developed digits instead of the usual four. This condition is a hereditary one and is brought about by partial duplication of elementary structures.

Conjoined Twins

Instances occur in which individuals of about equal size or of unequal size are fused together. If this occurs at the hips with dorsal sides together, the condition is usually known as *Siamese*
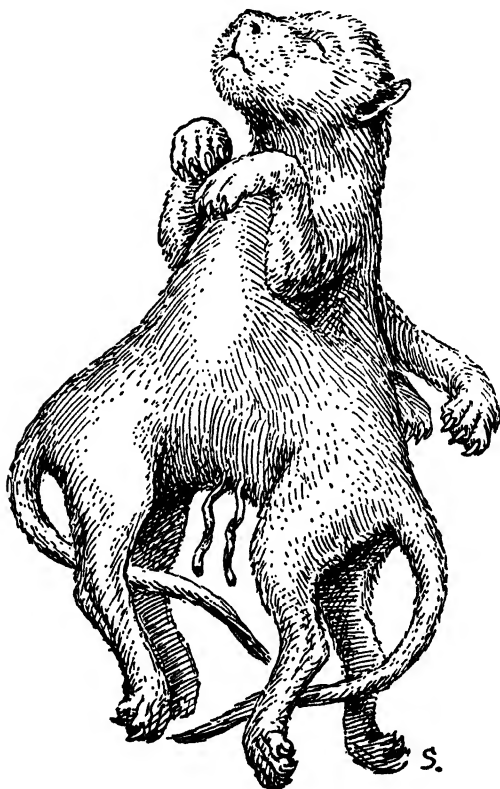
Fig. 70.—Conjoined twins of cat showing single head, but double trunk and appendages.

twins. There are a number of different varieties of fusion, including the head region, chest region, or complete fusion of trunk into a single body with two heads and vice versa. A chicken with two

pairs of legs and wings, two backs, and a single head has been dissected and described by Dr. F. L. Fitzpatrick. The feather tracts were double on the neck and trunk. Internal dissection showed the single digestive system to extend between the two necks, follow through the combined body cavity with some modifications, and
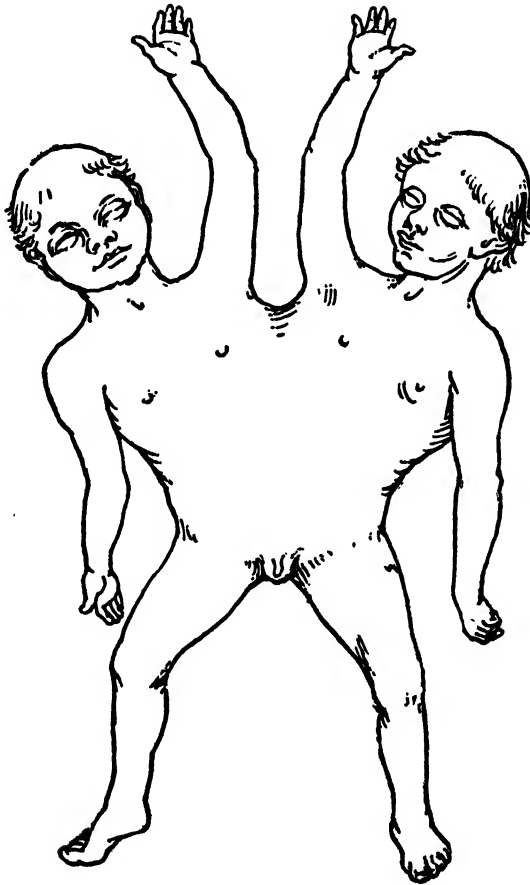
Fig. 71.—Conjoined human twins showing single hips but double trunk and head. (Redrawn and modified from Arey, *Development Anatomy,* W. B. Saunders Company.)

empty into the cloaca of the right back region. No cloaca was present in connection with the left back. There was a single heart, two very unequal lungs, two pulmonary arteries and veins to the larger lung, while there was only one common carotid artery, that being

the right. Two trachea were present, the right being rather normally developed while the left was rudimentary. The brain was normal, but joining the medulla were two separate and complete spinal cords, one passing to each back region. Most of the internal organs "favored" the right side, except the lungs, of which the left was much more developed.

Dr. F. L. Fitzpatrick reports upon the anatomy of a double pig also. This freak had two tracheae leading to two sets of lungs. The brain consisted of a three-lobed cerebrum, two cerebellums,
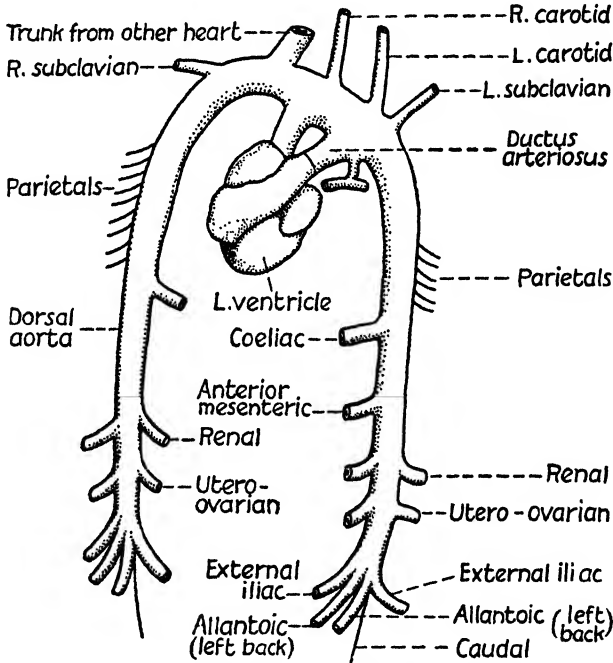
Fig. 72.—Dorsal aortae and branches in embryo pig which had a single head and two bodies. (After Fitzpatrick.)

and two medullas. There was a spinal cord in each of the two backs. A third or median eye was present on a ventral stalk beneath the third or transverse lobe of the cerebrum. Two pairs of kidneys, two bladders, four ovaries, double sets of oviducts and uteri, as well as a double cloaca, were present. There was a single but modified heart and two aortas leaving it. Externally the animal had two sets of limbs, two tails, two sets of mammae, two anal apertures, and two urinogenital openings.

It is suggested that such individuals have developed from a single zygote which underwent an abnormal cleavage. Examples of these conditions are shown as they occur in cats. Similar fusions occur in human beings as is illustrated in the accompanying diagrams.

Hermaphroditism

There are abnormal cases of sexual development in vertebrates, including man, in which the organs of both sexes are combined in one individual. In true cases there are present both ovaries and testes in the one individual, but no cases are known in which both have functional capacity. The external organs are partly male and partly female, and the secondary sexual characteristics, such as voice, mammae, stature, and beard, may be of a mixed nature. Hermaphroditism is the normal condition in the coelenterates, flatworms, annelid worms, and mollusks. Here both sets of organs are capable of function. Birds and mammals are rarely subject to this condition.

A condition spoken of as *false hermaphroditism* involves the presence of gonads of one sex but the secondary sexual characteristics and external genitalia of the other. In masculine hermaphroditism testes are present but not usually descended into the scrotum, while the external genitalia and secondary characteristics are those of the female. In feminine hermaphroditism ovaries are present, even descended into a scrotum in rare cases, but the clitoris is enlarged and labiae are fused to resemble the penis of the male. In some instances the lips of the slitlike urinogenital aperture on the under side of the penis fail to fuse.

There is a very close homology in the organs of the two sexes. The external genitalia are indifferent or sexless until the end of the seventh week of embryonic development in human beings. Then the determination comes, causing normally the modifications of development to form the organs of one sex or the other. The development of the external organs of the two sexes is strictly parallel. It is likely that this development is controlled by hormone relationships, and it is in cases in which this balance is disturbed that hermaphrodites occur. There is still much to be learned concerning the causes of this condition.

Cardiac Anomalies

Transposition of the heart to the right side of the midline of the body is known as *dextrocardia* and occurs rarely. It is usually associated with displacement of other visceral organs.

Due to faulty development, an incomplete interventricular septum is occasionally found in the four-chambered hearts. The failure of complete development of the septum between the auricles to close the *foramen ovale* is a more common anomaly. It has been reported that this occurs in some degree in one case in four for the human being. Actual mixing of auricular blood sufficient to interfere with normal function is much less common, however, because of the overlapping of the membranous walls which are pressed together by the pressure of contraction. In a small number of human cases the aerated blood and unaerated blood from the two auricles do mix and produce a purplish colored blood which in turn affects the color of the skin. Such a case is known as a *"blue baby"* and often leads to early death.

Abnormalities of Brain and Sense Organs

Encephalocoele is due to the protrusion of a sac of the meninges and part of the brain through a defect in the roof of the cranium. An abnormally large brain, which is usually associated with the distention of the cranium by superabundance of cerebral fluid, is known as *hydrocephalus,* or the size may be *macrocephalus.* The opposite extreme in which the head and brain are abnormally small due to failure of development is known as *microcephalus.*

There are cases of cleft nose in which the nostrils are in independent projections. This condition is usually associated with harelip and cleft palate. With regard to the eyes there are several possible abnormalities. *Cyclopia* is a condition in which there is a single median eye like that of the Cyclops instead of the usual paired arrangement. In such cases the nose is usually at the base of the forehead, above the eye, and cylindrical in shape. Failure of complete development of the iris or chorioid, thus leaving a gap or open sector in the margin of the pupil, is known as *coloboma.*

CHAPTER XII

GENETICS AND EUGENICS

(By Frank G. Brooks, Cornell College, Iowa)

The History of a Great Discovery

"Like father like son" is a very ancient adage. Since man has been able to think, he has pondered the problem of heredity. Although very early he had observed evidence of the inheriting of parental characters by the offspring of the various forms of life with which he was familiar and was convinced by these observations that heredity *did* take place, he has not known the "how" or "why" of it until recently. The science of heredity, therefore, is very new. The fundamental law on which it is based was announced by Gregor Johann Mendel in 1866. However, Mendel, an Austrian monk, published his discovery in an obscure journal and it did not receive general recognition until its rediscovery in 1900.

Mendel's success in finding the underlying principle of heredity was due, in part, to his choice of an experimental unit. Instead of following the usual trend by considering how a parent conveys his various traits to his offspring, thus making the individual the unit of observation, he chose a definite inheritable character and considered how it was transferred from many parents to all their offspring. In addition to this wise choice of an investigational unit the patience, mathematical ability, skill as a gardener, and analytical insight of the investigator contributed also to the success of the research.

Mendel chose the garden pea as the material for his work. This was a fortunate choice for, although the law that he was to discover underlies practically all inheritance, it is not always as free from complications as it is in the case of those traits of the pea which he investigated.

Mendel's Law

For one of his projects he planted seeds from stock that had been known to produce nothing but tall plants for many generations. He planted also seeds from stock that had produced nothing but dwarf plants. When the two types of plants were in blossom, he transferred the pollen from the stamens of the one to the stigmas of the other. The seeds that resulted from the cross were collected and planted.

To the amazement of the investigator they produced nothing but tall peas; peas as tall as the original tall parents. Dwarfness seemed to be lost and tallness was certainly dominant. A less thorough investigator might have called his experiment finished and have proclaimed as a rule, the fact that a trait can disappear when it is crossed with its opposite. But not so with the patient monk. He pollinated these plants with their own pollen and planted another generation. This time three-fourths of the plants were tall and one-fourth of them were as short as the original dwarf parents. Not being ready even yet to formulate a law, he self-pollinated his plants for several more generations and got results that required his best mathematical skill to interpret. The dwarf peas produced only dwarf peas. Of the tall
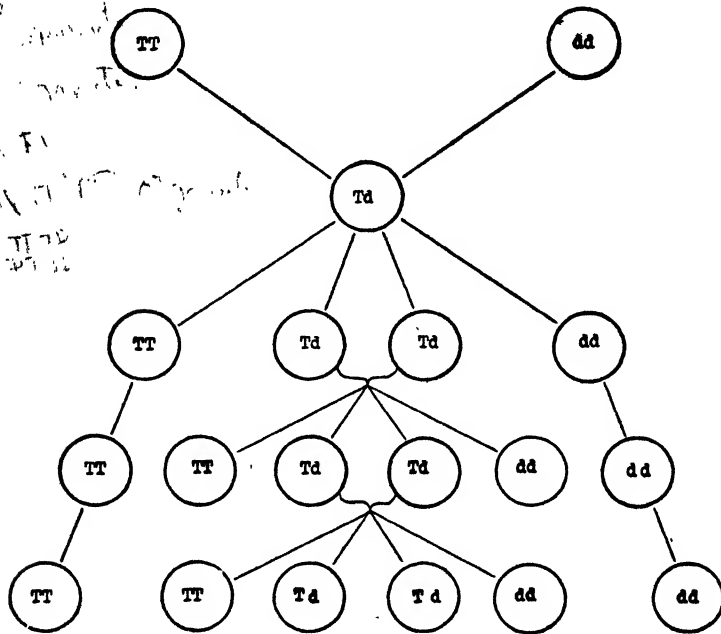
Fig. 73.—Diagram to show the result of crossing tall and dwarf peas. *TT*, at upper left, is an individual which is pure dominant for tallness. At upper right, *dd* is pure recessive for dwarfness. When two such individuals are bred together, or crossed, all of their offspring will carry both characters, but appear tall, since tallness is dominant. The *Td* individual in the upper middle is representative of this generation, which is the F_1 (1st filial). When two of these mixed, *Td* individuals are crossed, the offspring (F_2 or 2nd filial generation) present what is known as the 1:2:1 ratio, i.e., one pure tall (*TT*) individual (at left), two mixed (*Td*) individuals (in center), and one pure dwarf individual (*dd*) at right. The bottom and next to bottom rows show (at left) continued generations of crossing pure tall *TT* with *TT* to consistently produce pure tall offspring. The middle of the rows shows the consistent production of the 1:2:1 ratio when the mixed *Td* individuals are crossed. The pure dwarf individuals *dd* at the right in these lower rows show succeeding generations of breeding together to produce all pure recessive dwarf (*dd*) offspring.

peas, one-third of them (constituting one-fourth of the whole number) produced tall peas without deviation, but the other two-thirds (half of the whole number) produced stock that repeated the production of tall and dwarf peas in the same proportion as did the preceding generation. Here, then, was a definite ratio of 1:2:1. Mendel tested his findings with six other traits of the pea and with more than a dozen other kinds of plants, and after verifying his results he was able to announce the following law: *When members of a species having contrasting characters are crossed, all the immediate offspring will show the trait that is* **dominant,** *but if the members of this generation are bred to themselves, one-fourth of the offspring will show the dominant trait and breed true for it; one-fourth will show the* **recessive** *trait and breed true for it; the remaining two-fourths of the offspring will show the dominant trait, but will reproduce the contrasting characters in the same proportion as did their immediate parents.*

Derivatives of Mendel's Law

From the fundamental law which Mendel discovered, several corollaries can be drawn, based on factors responsible for the distributional behavior of inheritable characters. These corollaries are:

Principle of Dominance.—The determiner for one member of a pair of contrasting characters (which we shall call an *allelomorph*) may take precedence over the other member when the two have been brought together in a cross between unlike parents. Which trait is dominant and which is recessive can be determined only after a cross has been made, and the determination holds only for the species observed. Thus, tallness may be dominant over dwarfness in one species of plant and recessive in another. In many cases, dominance is not complete, and in a few classic instances it is lacking altogether. These cases will be discussed later in this chapter.

Independence of Unit Characters.—The determiner for any given character acts as an independent hereditary unit as it is passed along from generation to generation. In each generation it may have a different set of associates, but its associations in one generation do not affect the company it may keep in the next. Thus tallness in peas may be associated with yellow pod and with wrinkled seed coat in one generation, but it may form a combination with green pod and smooth seed coat in the next. This important principle is responsible for the great variation we find in plants and animals and makes it possible

for a breeder to bring about any desired combinations of the traits possessed by the species of plant or animal with which he is working. Thus the modern Shasta daisy has a combination of the three important characters, size of flower, gloss of petal, and prolific growth, each of which was procured from an original variety having one, but not the other two, of these traits.

Principle of Segregation.—Since unit characters are independent, it follows that they can go into various combinations and are free to segregate out again. This was illustrated by dwarfness in Mendel's peas which went into a cross with tallness, but segregated out again to form peas that were as consistent for dwarfness as was the original dwarf stock. To illustrate both the principles of unit characters and the related phenomenon of segregation we might use an analogy. If a gallon of white marbles were mixed with a gallon of black marbles, they would make a mass of marbles that, at a distance at least, would look gray. But the mixture is not irrevocably gray as would be the case if a gallon each of black and white paint had been mixed. The white marbles and the black marbles can be segregated out again if it is so desired and either variety can then be put into combination with marbles of any other kind. Inheritable traits, like marbles, can make various combinations which last for one generation only, after which they can make new combinations with other traits.

The Physical Basis

With the simple facts in mind of how heredity works, it is desirable to consider the germinal background of the laws governing it.

The tiny sperm cells of both plants and animals and the egg cells which, deprived of their food-containing yolk, are almost equally small, contain within them something that determines all the traits which the individual resulting from their combination will develop. In fact, the body of the sperm cell and the nucleus of the egg contain little else than a material that carries the combined inheritable traits of one generation over to the next. This important material is called chromatin and during mitosis it becomes arranged in series of hereditary units called genes. Each gene has a definite causal relationship to an inheritable trait. Both the sperm cell and the egg cell contain a complete gene complex, and each, under favorable conditions, could produce a complete individual.

When the two totipotential gametes are brought together at fertilization, the resulting zygote contains two genes for each allelomorph.

When the two genes are for the same trait, the resulting individual is said to be *homozygous* for that trait and, of course, shows it. When each of the two genes is for a different member of the allelomorph, in which case we use the term *heterozygous,* one gene takes precedence over the other, but the recessive gene is in no way destroyed; it simply lies dormant and bides its time. How these genes are arranged into a limited number of packages called *chromosomes* and how chromosomes are distributed in the process of sperm and egg formation have been explained in a previous chapter.

Plotting Crosses

The Monohybrid Cross.—When the genetic constitution of parental stocks is known, it is possible to plot out the results of various kinds of crosses. The checkerboard is the simplest device for such

	T	d
T	**TT**	**Td**
d	**Td**	**dd**

Fig. 74.—The outcome of a monohybrid cross between two heterozygous (*Td*) individuals is according to the ratio 1:2:1, i.e., (*TT*), (*Td*), (*Td*), (*dd*).

	T	d
Y	**TY**	**dY**
g	**Tg**	**dg**

Fig. 75.—The checkerboard may be used to determine the possible gene combinations in the ova and sperm of a possible dihybrid cross. A tall green-podded pea (*Tg*) is crossed with a dwarf yellow-podded pea (*dy*).

computations. The genetic constitution of the various kinds of male gametes is set down along the ordinate and that of the various kinds of female gametes along the abscissa. These values are then copied into the squares horizontally and vertically and their sums give the values of the various kinds of gametes that will result from the cross. In the F_2 (second filial generation) cross of Mendel's experiment

with tall and dwarf peas, half of the male gametes and half of the female gametes contained a gene for tallness (T) and half in each case contained a gene for dwarfness (d). The outcome, therefore, is shown in Fig. 74.

The Polyhybrid Cross.—It is often desirable to know the outcome of a cross in which two or more characters are considered together as in the case of crossing a tall, green-podded pea (Tg) with a dwarf, yellow-podded pea (dY) (Fig. 75). The determination of the possible kinds of gametes may be simplified by first making a small checkerboard for them. Thus we find that there are four kinds of male gametes and four kinds of female gametes which may be listed as TY, Tg, dY, dg. Now we make a checkerboard of sixteen squares and proceed as we did before.

	TY	Tg	dY	dg
TY	TY TY	Tg TY	dY TY	dg TY
Tg	TY Tg	Tg Tg	dY Tg	dg Tg
dY	TY dY	Tg dY	dY dY	dg dY
dg	TY dg	Tg dg	dY dg	dg dg

Fig. 76.—The outcome of a dihybrid cross between two heterozygous individuals is according to the ratio of 9:3:3:1. The four kinds of male and female gametes, tall yellow (*Ty*), tall green (*Tg*), dwarf yellow (*dy*) and the recessive dwarf green (*dg*) are employed as they would combine in this ratio.

The computation of the dihybrid cross (Fig. 76) indicates that nine-sixteenths of the progeny will *show* the two dominant traits. Three-sixteenths will *show* the dominant trait of the first allelomorph and the recessive trait of the other. Another three-sixteenths will show the recessive trait of the first allelomorph and the dominant trait of the second. One-sixteenth of the offspring will show both recessive traits. It will be noticed, however, that the nine squares showing individuals that will be tall and yellow vary with each other in regard to their entire content. Further examination of the squares will indicate

that there are nine different combinations of letters and that in only one case as many as four are exactly similar. Individuals whose genes cause them to look alike are called *phenotypes;* those whose genes are exactly alike are called *genotypes.*

A trihybrid cross, such as one between a tall yellow-podded pea with a wrinkled seed-coat (TYw) and a dwarf green-podded pea with a smooth seed-coat (dgS), can be plotted by using a checkerboard of sixty-four squares. There are eight different kinds of male and female gametes found in this arrangement. The ratio of phenotypes of a trihybrid cross is 27:9:9:9:3:3:3:1.

	T	T
T	TT	TT
d	Td	Td

Fig. 77A.

	d	d
T	Td	Td
d	dd	dd

Fig. 77B.

Fig. 77A.—A cross between heterozygous (*Td*) and homozygous tall peas (*TT*) produces a 2:2 ratio. The resulting individuals are two pure tall (*TT*) and two phenotypically tall or mixed (*Td*).

Fig. 77B.—A cross between heterozygous tall (*Td*) and homozygous dwarf peas (*dd*) also produces a 2:2 ratio. The resulting individuals here are two pure dwarf (*dd*) and two phenotypically tall or mixed (*Td*).

The Back Cross.—The checkerboard is also useful in computing the results of a cross between a heterozygous and a homozygous individual as would be the case in which the offspring of a cross between a homozygous dominant and a homozygous recessive individual is bred back to either of the parental stocks, a procedure often followed in practical animal and plant breeding. When such a cross is made to the homozygous dominant stock the results, in terms of pea traits, are TT, TT, Td, Td.

When the heterozygous stock is bred back to the homozygous recessive parental stock a 2:2 ratio is also produced, but between heterozygous and homozygous recessive individuals as: Td, Td, dd, dd.

Complications of Mendelian Inheritance

If all inheritable characters followed Mendel's law in as simple a fashion as do the pea traits that Mendel first investigated, the science of genetics would be much more elementary. Unfortunately this is not the case. Although Mendel's law is found so consistently as the

underlying principle of heredity that it can be said to be practically universal in its application, it is often modified and complicated in various ways.

Multiple Allelomorphs.—Instead of the allelomorph consisting of the usual two factors, a larger number of alternatives sometimes appear. Dominance in these cases occurs in a graded series, each member, between the extremes, being dominant to the lower members and recessive to the higher members of the series. A simple case of multiple allelomorphs is found in the inheritance of color in rats where there are three factors; namely, ordinary pigmentation, ruby-eyed dilution, and albinism. In a cross between heterozygous parents any two of the three factors may be brought together in the offspring. If ordinary pigmentation is present with either of the other two, it will determine the color, since it is first in the series of dominance. If the other two are the ones present, the color will be ruby-eyed dilution, the second member of the series.

A large series is presented by eye color in the common fruit fly, *Drosophila melanogaster,* in which case there are eleven members which are, in the order of their dominance: red, apricot, coral, ivory, ecru, buff, tinged, blood, cherry, eosin, and white. Each parent may have any two of these in its germ plasm and transmit either of them to the offspring.

Plural Genes.*—Several cases formerly interpreted to be simple blending inheritance not conforming to Mendel's law have been explained by the discovery that there can be more than one allelomorphic pair concerned with the inheritance of the trait. Thus, instead of there being one gene located at some definite place on a chromosome, there are two or more genes variously located. Cases of plural genes fall into two categories. In the one, each gene inherited as a dominant, produces part of the result, and the effects are cumulative. In the other type of case, the inheritance of one dominant gene produces the entire effect.

A common example of the cumulative type is the inheritance of skin color in man. It has long been known that a cross between a white man and a negro produces offspring of a medium shade called *mulatto,* and that a cross between two mulattoes will produce offspring with a range of color varying from intense black to a shade that may allow

*Other names used for this are multiple factors and duplicate genes. I avoid the first term because it is likely to be confused by the beginning student with the term *multiple allelomorph* and I object to the second because of the connotation of only one repetition.

the person to pass for white. This is explained by the fact that there are two allelomorphic pairs concerned with the inheritance of color, the dominant of either of which will produce a certain amount of pigment per square millimeter of skin surface. The negro of pure skin inheritance is homozygous for both pairs. Using P and P′ to represent the dominant factors of these two allelomorphs and p and p′ the recessives, the homozygous negro would have PPP′P′ while the homozygous white person would have ppp′p′ and the mulatto resulting from the first cross would have PpP′p′. The cross between two mulattoes would be a dihybrid cross which could be plotted by a checkerboard similar to that of Fig. 78. The accompanying summary shows that there can be four, three, two, one, or no dominant factors present, thus accounting for the series: "negro," "chocolate," "mulatto," "quadroon" and "pass for white."

	PP′	Pp′	pP′	pp′
PP′	PP′ PP′ negro	Pp′ PP′ choc.	pP′ PP′ choc.	pp′ PP′ mulat
Pp′	PP′ Pp′ choc.	Pp′ Pp′ mulat	pP′ Pp′ mulat	pp′ Pp′ quadr
pP′	PP′ pP′ choc.	Pp′ pP′ mulat	pP′ pP′ mulat	pp′ pP′ quadr
pp′	PP′ pp′ mulat	Pp′ pp′ quadr	pP′ pp′ quadr	pp′ pp′ white

Fig. 78.—The inheritance of color by children of mulatto parents can be shown by the checkerboard for a dihybrid cross.

The other type of case in which plural genes occur is exemplified by a certain brown-seeded variety of oats in which there are two pairs of genes concerned with the determination of color. Here the presence of the dominant gene of either pair produces the entire effect. This case, too, can be plotted on the dihybrid checkerboard, but the result is a 15:1 ratio, for fifteen of the sixteen squares would show at least one dominant gene. Crosses between a red and a white variety of wheat in which there are three pairs of genes for color, produce a 63:1 ratio. This is a trihybrid cross in which each dominant gene can produce the entire effect.

Complementary Genes.—In a number of cases color is produced by two genes, the dominants of which must react on each other to produce the color effect. In the sweet pea, if the dominant factor of the red allelomorph (Rr) is acted on by the dominant factor of the color allelomorph (Cc), then red is produced. If either of these dominant genes is present without the other, white flowers are produced, and if two white-flowered plants of the genetic constitution Rc and rC are crossed, a part of the progeny will be red. A student familiar with elementary chemistry may understand this better if he thinks of the red factor as being represented by a colorless solution of phenolphthalein and the color factor as a colorless alkaline solution. When both solutions come together, red is produced, but neither can produce the color without the other.

Supplementary Genes.—But sometimes purple sweet peas appear when two white varieties are crossed or when a red variety is crossed with a white variety. Purple is produced by a third gene for blue which intensifies red if it is already present, but has no effect unless the RC genes are likewise inherited. Thus we find that its effect is to supplement that of the two genes R and C which are complements to each other in the production of red. The accompanying list shows some of the surprising crosses that may be made with sweet peas. Of course the combination of genes shown in the last column is not the only one that will come about in each of the various cases, but it is the one that emphasizes the point desired.

White + White = Purple	RcB + rCb = RCB
Red + White = Purple	RCb + RcB = RCB
Purple + Red = Red	RCB + RCb = RCb
Purple + White = Purple	RCB + rcb = RCB
Purple + White = White	RCB + rcb = rcB
Purple + White = Red	RCB + rcb = RCb

Lack of Dominance.—In several classic cases, some of which are among plants and others among animals, neither factor of an allelomorph is dominant over the other. In the F_1 generation, these cases seem to produce perfect examples of blending inheritance, but the F_2 generation exemplifies the 1:2:1 ratio so beautifully that these exceptional cases are often used to explain Mendel's law to beginning students.

The Andalusian breed of chickens includes both black and white individuals. When black fowl are crossed with white fowl, all the off-

spring are of a slate color technically known as "blue." When a blue chicken is crossed with another blue chicken, one-fourth of the progeny is black, one-fourth is white and the remaining two-fourths are blue. The blacks and the whites are homozygous for their respective colors while the blues are heterozygous. The inheritance of color in short-horn cattle, and of the color in the four-o'clock flower are also examples of this. In still other cases in which there is not neutrality of dominance, the dominant effect may not be complete. Very often the heterozygous individuals can be picked out from the homozygous dominant ones by casual inspection.

Inheritance of Sex

In certain lower animals and in the early embryos of mammals, both male and female reproductive systems are present in each individual.
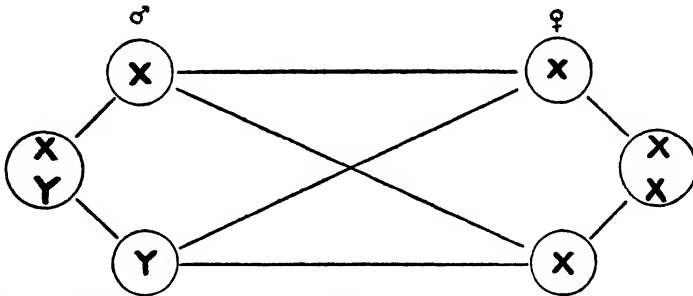
Fig. 79.—Diagram to show the combinations in an *XY* sex chromosome pattern. Half of all possible fertilization combinations of sex chromosomes will be male (*XY*, at left) and half will be female (*XX*, at right).

Typically in higher forms, one of these systems is repressed, and we speak of the individual as being either male or female. The determination of whether the male or the female system will develop is an inherited trait. The chromosome that carries the gene of sex determination has come to be designated as the X-chromosome. In typical cases, the female has in each of her germ cells, two of these X-chromosomes and the male has only one. Therefore, when, in the process of spermatogenesis, the chromosomes match with their homologous chromosomes and separate again to give each of the resultant cells one complete set of chromosomes, the X-chromosome cannot pair with another like itself, and when the chromosomes are distributed in sets, half the sets will lack an X-chromosome. The sperm cells that do not have an X-chromosome will produce males while those that have such a chromosome will produce females.

In other cases that include man and Drosophila, the X-chromosome will pair with a Y-chromosome which has been described as "an empty case" or a "ghost chromosome." In cases in which a Y-chromosome is present, we cannot say that the male has one less chromosome than the female, but it practically amounts to that since the Y-chromosome seems to contain not more than a few genes (Fig. 79).

Linkage

Since the number of inherited traits of an animal or plant is very great while the number of chromosomes is quite small, it is apparent that a single chromosome must contain many genes. This being so, there is not absolutely free assortment of traits as they are passed from parent to offspring, but rather the offspring must inherit his traits in groups that are not, ordinarily, broken up. Therefore, when two genes, A and B, are on the same chromosome of one of the parents, if the offspring inherits gene A, he must inherit gene B. In Drosophila we know that the gene which determines whether or not the wing will be fringed occurs on the same chromosome as the one that is responsible for the body being or not being black. Now if one of the parents is fringed-winged and black-bodied, the offspring will have to inherit both these traits from that parent if he receives either one of them. This phenomenon is called linkage.

Sex Linkage

Since there are other genes than those concerned with sex on the X-chromosome, it is to be expected that their inheritance will differ somewhat in the two sexes. This is strikingly illustrated by certain abnormalities of man in whom the abnormal condition is inherited as a recessive; for example, color blindness, blindness resulting from atrophy of the optic nerves (Leber's atrophy), and hemophilia or bleeder's disease, in which great loss of blood occurs even from slight wounds because clotting will not take place. Since the abnormality is a recessive trait produced by a gene on the X-chromosome, its effect can be offset by a dominant for normal in the female, but not in the male, because in the latter case there is not another X-chromosome present. Therefore, the daughter of a color-blind father will not show the defective trait but may pass it to her son.

Fig. 80 shows a cross between a color-blind father and a normal mother. Two kinds of male gametes are produced, half of which carry the father's gene for color blindness on the X-chromosome, and half of

which have no X-chromosome and therefore, have no such gene. All female gametes have one X-chromosome bearing a gene for normality. The various possible combinations of the two kinds of sperm with the single type of egg will produce two types of offspring; namely, sons who will be strictly normal in regard to the trait in question and daughters who will inherit the gene, but who will not show the trait because its effect will be overcome by the presence of a gene for normal. Therefore, the daughters will be heterozygous for the trait and might be spoken of as *carriers*. Fig. 81 shows a cross between such a daughter and a normal male.
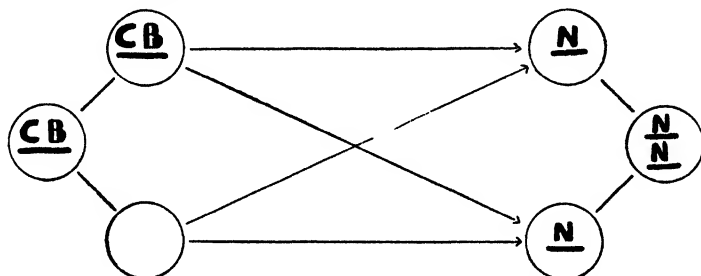
Fig. 80.—In the cross between a color-blind male (at left) and a normal female (at right) the results (*N, cb*), (*N, cb*), (*N*), (*N*) indicate that all daughters, being heterozygous, will not show the defect though they might transmit it to their offspring, while the sons are entirely free from it. *NN*=normal female individual; *cb*=Color-blind individual; and *N, cb*=normal function but carrier of the color-blind gene.
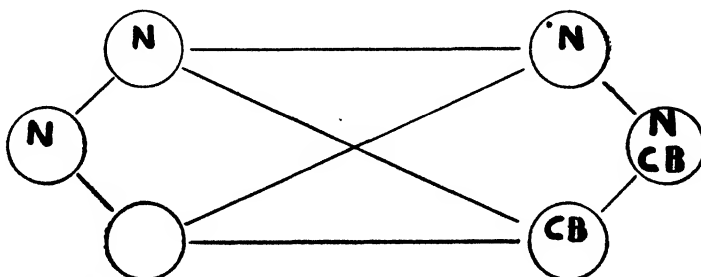
Fig. 81.—Results (*N, N*), (*N, cb*), (*N*), (*cb*). In a cross between a normal male (at left) and a female who is heterozygous for color blindness (at right), half of the sons will be normal and half will be color-blind. Half the daughters will be homozygous for normal and half will be heterozygous.

Inspection of this figure will show that such a cross will produce four types of offspring; namely, normal daughters, "carrier" daughters, normal sons, and color-blind sons. Thus, we see that half the grandsons of a color-blind man will receive the trait through their mothers, and that all daughters and half the granddaughters of the color-blind male will be carriers of the trait, but will have normal

color vision. Of course, from the mating of such a person with a color-blind man, all the sons and half the daughters will be color blind, but a young woman who is used to having her father buy orange-colored neckties, thinking they are blue, is not likely to marry a man similarly defective.

Crossing Over

Genetics might be defined as an exact science which has exceptions to many of its rules. A previous paragraph describes the principle of linkage which provided for the inheriting as groups of those traits whose genes occur together on a chromosome. Certain gametogenetic accidents bring about occasional exceptions to this principle. It will
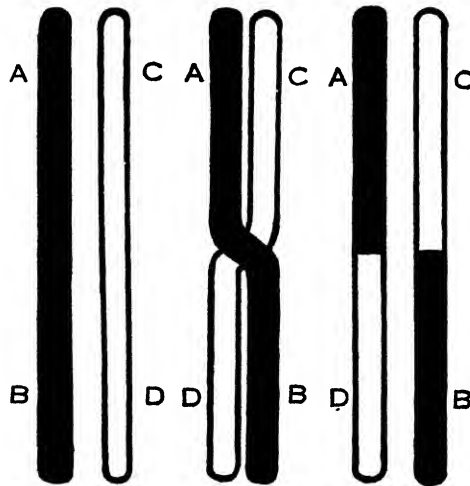
Fig. 82.—Crossing over occurs when chromosomes break apart after synapsis. *AB* and *CD* are the original chromosomes while *AD* and *CB* are the chromosomes resulting from the cross-over.

be remembered (Fig. 60) that at synapsis the chromosomes pair and the homologous chromosomes become loosely attached to each other. At times, the pairing chromosomes will even twist around each other. When they come to separate in the maturation division, instead of making a complete separation they sometimes break off at some point so that a part of each will be joined to a reciprocal part of the other, as is shown in Fig. 82. Thus, as a result of *crossing over,* instead of traits A and B, and C and D being associated in the offspring as they were in the respective parents, A will be associated with D, and C with B.

Crossing Over, a Useful Tool.—The process of crossing over has proved to be a valuable means of determining something of the nature

of genes and chromosomes and, especially in Drosophila, it has enabled us to locate the positions of many of the genes on their respective chromosomes. If two linked traits are separated every time crossing over occurs, it is obvious that their genes lie at opposite ends of the chromosome, but if they are separated only half the times, it is apparent that half the length of the chromosome lies between them. Therefore, by computing the percentages of such separations and noting which traits are affected, it has been possible to make chromosome maps showing the positions of the various genes and the distances separating them. The chromosome maps for Drosophila are quite complete.

Mutations

When chromosomes separate from each other at synapsis, aside from breaking so that a piece of one will adhere to the correlative piece of the other, various additional "chromosomal accidents" will occur which change the organization of the chromosome. A piece of chromosome, for example, might break off from the end of one chromosome and adhere to the end of its homologue. Any disarrangement of the genes of a chromosome results in structural or physiological changes in the organism into which it goes. Such changes are inheritable and are called *mutations*. Since there are places on the chromosomes where these accidents occur more frequently than at other places, there is a tendency for certain mutations to occur with fairly determinable regularity, say once in every hundred thousand cases. Some mutations are useful and are preserved to the species to such an extent that De Vries believed they were the principal factor in bringing about evolution. Other mutations are a disadvantage to the species, and the organisms possessing them are eliminated in Nature's fierce struggle for existence unless they are saved from that cruel fate by man's interference.

Human Heredity

Man, very naturally, is interested most in the heredity of man. In spite of this supreme interest, his knowledge of his own heredity is much more limited than his knowledge of inheritance in any of a number of other organisms. There are two reasons for this: namely, he is not free to experiment with his own kind; and, as would be expected, the application of Mendel's law to inheritable traits in this, the most complex of all living forms, is correspondingly complicated. Although there are cases in which the 1:2:1 ratio occurs in as simple a form as

in Mendel's peas, there are many more cases in which the Mendelian principle is manifested as multiple allelomorphs, plural genes, modifying factors, complementary factors, incomplete dominance, changeable dominance, etc. There is a tendency among some to depreciate our knowledge of human heredity on the ground that there is so much that we do not know. It is scientific to admit the extent of our lack of knowledge, but it is wise to give proper credit to our present store of information and to take cognizance of the rapidity with which the gaps in our knowledge are being filled in. One by one the complicated problems of human heredity are being solved by patient investigators, and by putting what we already know to use, we stimulate the accession of more data.

Some Cases of Human Heredity.—To give a complete summary of our knowledge of human heredity would be beyond the scope of this chapter. The accompanying table gives some of the data that have been accumulated:

DATA ON HUMAN HEREDITY

TRAIT	HOW INHERITED	DOMINANCE
General Physique and Skeleton		
Stature	A composite character	Many genes for shortness are dominant
Body build	Plural genes, two or more pairs of factors	Factors for stoutness are dominant
Polydactyly (extra digits)	Simple	Abnormality dominant
Brachydactyly (short digits and limbs)	Simple	Abnormality dominant
Symphalangism (fused fingers and toes)	Simple	Abnormality dominant
Zygodactyly (webbed fingers and toes)	Simple	Abnormality dominant
Lobster claw (split hands and feet)	Simple	Abnormality dominant
Exostoses (outgrowths of long bones)	Simple	Abnormality dominant
Abnormal fragility of bones	Simple	Abnormality dominant
Amputation (entire absence of hands and feet)	Simple	Abnormality dominant
Skin and Hair	Simple. Lethal when homozygous	
Ichthyosis (scaly skin)		Abnormality dominant
Keratosis (thickened skin on palms and soles, suggestive of hoofs)	Sex-linked	Abnormality dominant
Normal pigmentation	Plural genes	Cumulative
Piebald (spotted skin)	Simple	Piebald dominant
Premature grayness	Simple	Abnormality dominant
Blaze (a white forelock)	Simple	Blaze dominant
Epidermolysis (excessive formation of blisters)	Simple	Abnormality dominant

DATA ON HUMAN HEREDITY—CONT'D

TRAIT	HOW INHERITED	DOMINANCE
Skin and Hair—Cont'd		
Albinism (lack of pigment in skin, eyes, and hair)	Simple	Recessive to all types of pigmentation
Beaded hair	Simple	Abnormality dominant
Ovoid hair form (kinky or wavy)	Probably simple	Partial dominance
Alopecia (baldness)	Sex-linked	Dominant in men Recessive in women
Hair color (brunette or blonde)	Plural genes, probably two pair	Dark shades dominant
Red hair	Probably simple	Red pigment dominant
Eyes		
Eye color	Modifying factors and variation in dominance	Dark shades tend to be dominant over blue
Hereditary cataract	Simple	Abnormality dominant
Color blindness	Sex-linked	Abnormality usually recessive
Night blindness	Sex-linked	Abnormality usually recessive
Atrophy of optic nerve	Sex-linked	Abnormality recessive
Large, irregular pupils	Simple	Abnormality, an irregular dominant
Ear Structure and Hearing		
Complete absence of external ears	Simple	Abnormality dominant
Cup ears (small, deformed, inverted pinnae)	Simple	Abnormality dominant
Otosclerosis (progressive hardening of ear drums)	Simple	Abnormality dominant
Nervous System		
Feeblemindedness	Can be simple	Abnormality recessive
Amaurotic family idiocy	Simple	Abnormality recessive
Huntington's chorea	Simple	Abnormality dominant
Manic depressive insanity	Plural genes	Abnormality chiefly dominant
Dementia praecox (schizophrenia)	Plural genes, 32 pair	Abnormality seems to occur as an incomplete recessive
Dipsomania	Probably simple	Abnormality recessive
Diseases and Diatheses		
Hemophilia	Sex-linked	Abnormality recessive
Allergy (predisposition to hay fever, asthma, eczema, migraine, etc.)	Simple	**Abnormality dominant**
Gower's muscular atrophy	Simple	Abnormality recessive
Diabetes insipidus (excessive production of urine)	Simple	Abnormality dominant

Matings Among Defectives

It is obvious that persons who have inherited scaly skin, lobster claws, amputated hands and feet, exostotic bones, or who might have any of many other inheritable defects that incite pity or repulsion will find difficulty in securing mates. When these abnormalities occur as mutations, the afflicted persons are not likely to marry on their own social level, but will probably mate with others who are of lower
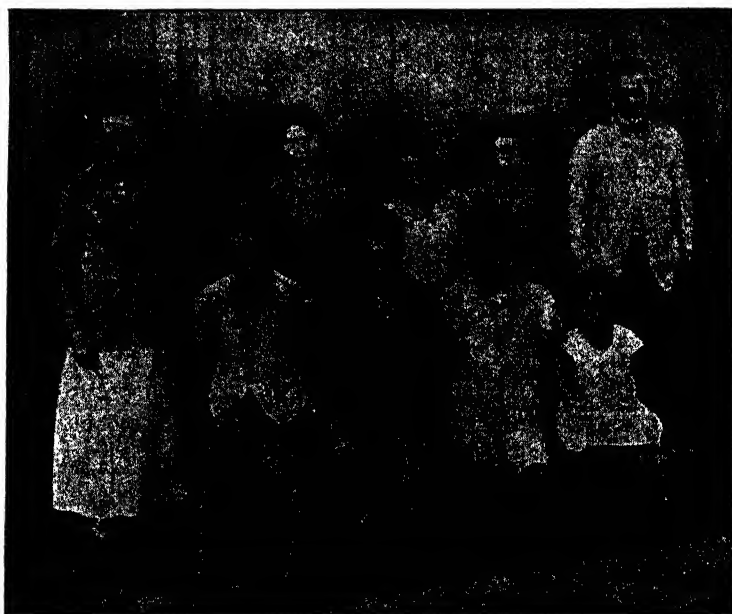
Fig. 83.—Family from Brazil showing hereditary absence of hands and feet. The man at the right rear is the uncle of the children shown. The father, who is dead, had the same deformity. Of the twelve children born, six were normal and six were deformed. (From Holmes, *Human Genetics and Its Social Import*, McGraw-Hill Book Company, Inc.)

grade mentally or who have other abnormalities that make them objectionable to normal people. Thus there is a tendency for defectiveness to be precipitated to a social group that can clearly be called *dysgenic*. By her process of eliminating the unfit who could not survive the fierce struggle for existence, Nature formerly kept this group at minimum size. Today its numbers are being added to, not only by recruits from higher groups who have a poor heredity either by unfortunate segregation of undesirable genes or by the occurrence of

such mutations as have been mentioned, but also by increased reproduction by the members of the dysgenic group itself.

The Differential Birth Rate

Nature keeps her creatures fit by giving reproductive advantage to the best members of each species. Various dioecious animal forms produce from dozens to millions of young per pair from which, on an average, two individuals are selected to replace the parents. As a rule, the two selected are the ones that are strongest and the most free of defects—these are usually the ones that are best adapted to their environment. Man has, in the case of his own kind, preserved the weak and defective individuals that Nature would have eliminated had it not been for the application of medical science, together with public health and other measures that have come with the development of a humanitarian consciousness. Nothing but praise should be given to an altruism that saves lives and relieves suffering, but the effect on our race of man's present practice of preserving individuals that Nature would have destroyed, without safeguarding the reproductive advantage of the fitter group, is worthy of consideration.

It has been shown by Lorimer and Osborn* that certain large groups are increasing so rapidly while others are so diminishing, that the surviving children of a million women of reproductive age of the first category will be twice as numerous as the surviving children of a similar group of women of the second classification. Carried on at the same rate for three generations (which is only a long lifetime) the descendants of the first groups will be sixteen times as numerous as those of the second groups.

Casual observation will make evident that such grouping is likely to be on a basis of eugenicity and dysgenicity. A number of studies have been made of the reproductive rate of groups classified by vocation. These studies reveal that passing from the professional and successful business classes through the various occupations to that of the unskilled, transient, agricultural laborer, the number of children per family rises steadily.

Family Size in Eugenic Groups

The vocational group made up of college teachers might be taken as an example of a profession whose members have a low reproductive

*Lorimer, F., and Osborn, F.: Dynamics of Population, Macmillan.

rate. A recent study made by Kunkel* shows that 4,567 college teach-
ers have 5,932 living children, an average of 1.3 children per teacher.
Dividing the teachers surveyed into three groups according to age, he
found that in the oldest group there is an average of 1.6 children, the
middle group averages 1.42, and in the youngest group, which consists
of those less than forty-three years of age, there are 0.86 children
per teacher. Since the families of this last group are not complete, the
average of the other two groups, or about 1.5 children per family,
might be taken to indicate the reproductive rate of college professors.

A correspondingly low birthrate is found among other groups whose
members would be expected to possess traits that should be preserved
for our race. Cattell reports that the average number of children in
the families of the persons listed in *American Men of Science* is 1.88.
But small families are not limited to college professors and scientists,
for those distinguished people whose names are recorded in *Who's
Who in America* have families averaging only slightly more than two.

Since the families from which college students come can reasonably
be taken as a eugenic group, several studies have been made of the
sizes of the families represented on the campuses of various American
colleges and universities. The author kept a record for a ten-year
period of the sizes of the families represented by the students of a city
university of the Southwest. The average number of children in those
families was found to vary from year to year from slightly under to
slightly over three. Since there were no childless families represented,
these figures are high for the social stratum concerned. What effect
college education may have on family size may be inferred from other
studies. Harvard graduates whose year of graduation would give us
reason to suppose that their families are complete, have produced 1.9
children per married alumnus; allowing for the members of the group
who did not marry, the average falls to 1.6 children. Corresponding
averages for Yale are 1.9 and 1.5, for Swarthmore 2.15 and 1.9, and
for Vassar 2.15 and 1.25.

A false sense of eugenic security might be prompted by the belief
that the figures exceeding two in the foregoing citations indicate that
the parents are being replaced and that any residual value represents
a gain. But in the cases of two-child families, what assurance have we
that those children will live to reproductive age, that they will marry,
and if they marry that they in turn will have children? Considering

these possibilities, it is evident that fertile families must provide for more than replacement if the group to which they belong is to be perpetuated. Various computations have been made of the average number of children per fertile family necessary to maintain the numerical strength of a group. These estimates range from 3.1 to 4. Considering that the current incidence of childless families in America is 20 per cent, probably the higher number is more nearly correct, and it is not safe to place the figure at less than 3.5.

Family Size in Dysgenic Groups

Various studies have shown that larger families occur among people who have but a poor store of those qualities of intelligence, stability, and physical traits that go to make up racial excellence.
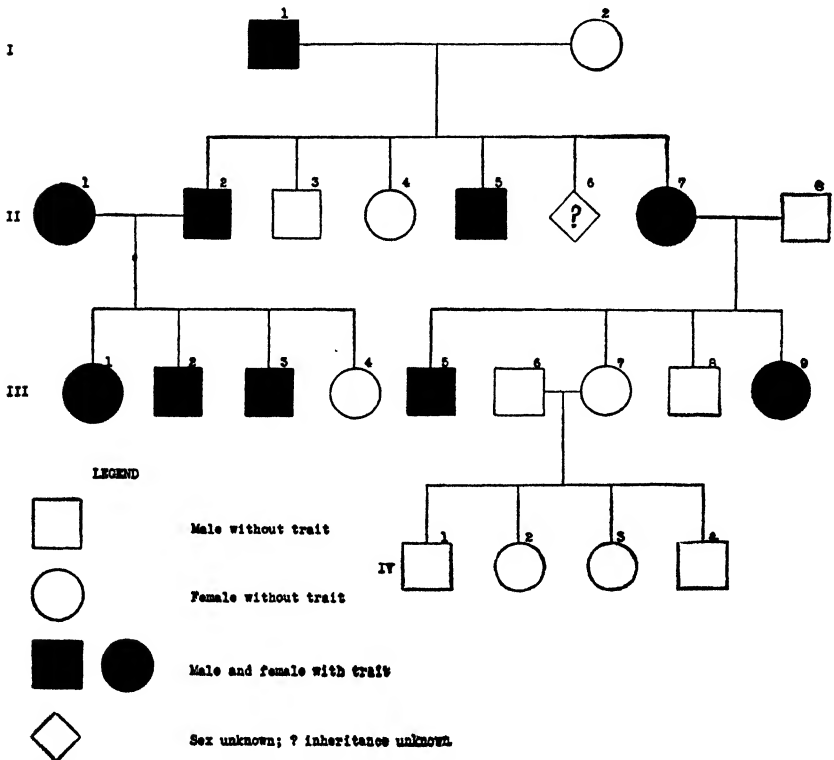
Fig. 84.—Standard pedigree chart. Charts such as this can be used in tracing a trait through several generations of a family. This particular chart shows the inheritance of a dominant trait starting with a cross between a male who was heterozygous for the trait and a female in whom it was homozygously recessive.

Lorimer and Osborn found in their study of the school children of selected eastern cities that children with the lowest intelligence scores (I.Q. below 60) came from families that averaged nearly six children; that those with medium scores (I.Q.'s 90 to 110) came from families averaging less than four; and that the children of superior intelligence (I.Q.'s 140 and over) came from families that averaged less than two and a half children.

The author's study of nearly a thousand improvident families of a type well known to the social workers of southwestern cities revealed that in this group the number of births occurring in completed families averaged 7.9 and the average number of children born to mothers of all ages was 5.7. The average number of surviving children of the two groups was 6.1 and 4.6 respectively. The significance of these data in comparison with those concerned with the size of the families from which college students come can be realized from the fact that if the reproductive rates in these two groups continue for ten generations, the descendants of one hundred families of the dysgenic group will number more than twenty-eight thousand, while in the same generation, one hundred families of the present-day college-student group will be represented by eleven persons.

What Can Be Done?

It must be admitted that the present racial situation has been brought about through the advance of humanitarianism and science. The cure for the situation must come through the application of greater humanitarian and scientific measures. The many corrective panaceas that have been suggested must be tested carefully and applied cautiously. Some reforms can be applied at once and are being applied today to some degree; others must wait until the time for their application is more opportune.

Some Eugenic Measures

The step that would be most fruitful of racial betterment is general education along eugenic lines. If a sufficient number of thoughtful citizens were informed about racial trends, a eugenic consciousness would be developed that would cause every proposed social or economic change to be considered from the standpoint of its genetic significance.

The marriage and divorce laws of the various states should be unified and rewritten along eugenic lines. They should provide for ad-

vance notification of applications for marriage licenses as is provided for by the California laws, and should contain provision for health examinations as already enforced in Illinois. The latter practice should be extended to include the examination of family histories.

Many positive measures have been proposed for granting aid of various kinds to large families. At the present time most of these proposals are impractical, but we might look forward to wage adjustment to family size starting with government employees, and rental rates of government-owned houses based on a fixed percentage of the family income regardless of the size of the house required.

It has been proposed that those who are clearly unworthy of parenthood should be segregated in colonies of their own sex. The expense of this as well as the probability of many social and other problems that would arise in such a situation challenges the wisdom of such a measure beyond the degree it is now being practiced in our eleemosynary and punitive institutions.

Twenty-nine of our states have adopted laws providing for the eugenic sterilization of such persons as those who have been committed to sanitaria for mental cases because of an inheritable type of insanity and who are to be returned to their families. A few states provide also for such sterilization of habitual criminals and those who are clearly feebleminded. Eugenic sterilization consists of vasectomy and salpingectomy—operations that bring about sterility without interfering with endocrine function or normal sexual reactions. Over twenty-five thousand such sterilizations have been performed under the present laws.

It is evident from the data previously discussed that family limitation is being practiced by the eugenic group. It is suggested by many who are facing squarely the problems of racial welfare that those who are mentally and in other ways far below the majority of our people should have made available to them the means of similarly limiting the sizes of their families. The number of clinics where such measures are made available to persons who will make proper use of them already number in the hundreds.

Some of these eugenic measures are questioned on the grounds that they violate human rights. We should also be considerate of the rights of the unborn. It is reasonable to say that every child that is to be born into this world has:

The right to be born with a sound mind.

The right to be born with a strong and normal body.

The right to be born into an environment in which his inherited potentialities will have a fair chance to develop.

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CHAPTER XIII

CLASSIFICATION OF ANIMALS

For practical reasons it is necessary to classify the animals of the animal kingdom, listing and arranging them in a definite, orderly, systematic fashion in order that they may be recognized and named. Since there are at least 840,000 different species of animals already described and more being added continually, this becomes significant. In addition to the matter of convenience in cataloguing animals, our present system of classification, which is based primarily on structures, brings to light many of the phylogenetic relations between groups. The study of classification is called *taxonomy*, of which some mention has already been made in the introductory chapter.

The usual method of classification of animals originated with Linnaeus who lived from 1707-1778. He recognized groups of four different values: class, order, genus, and species. Since his time several other divisions of the classification have been added, as the phylum, subphylum, subclass, suborder, family, subfamily, subgenus, and subspecies. The Linnaean system designates the species by two Latin or Latinized names; the first is the *generic* name and the second is the *specific* name. For example, we have *Rana catesbeiana,* the bullfrog, and *Rana pipiens,* the leopard frog, as two species of frogs belonging to the same genus. Because of the necessity for two names for the designation of each species this is known as the *binomial system of nomenclature.* In cases where subspecies or varieties have been recognized, the genus, species, and subspecies names all are used, making the arrangement trinomial instead of only binomial.

The basis for our present classification is largely relationship of structure with groups formed because of genetic relation and descent from common ancestry. Animals whose characteristics are similar and whose relationship is evidently very close are placed in the same species. Species which are quite similar are placed in the same genus. Families are each composed of genera which resemble each other in certain respects much more than they resemble other genera. Orders are composed of related families, classes of related

orders, and phyla of related classes. These groups are regarded as having arisen from successively more remote ancestors. To the extent that evolution has proceeded in the different groups, this system of classification carries a fairly accurate outline of the phylogenetic background of any modern animal. Forms possessing homologous structures (structures of similar form and similar embryonic development) are described as of close relationship. Since similarity in embryonic development is regarded as most important evidence of homology, the theory of recapitulation (individual in its life lives over the history of its race) enters strongly in determining relationships of animals and animal groups.
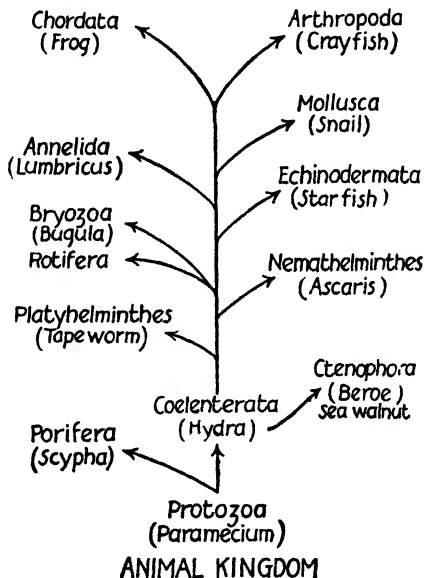
Fig. 85.—Phylum relations in the animal kingdom.

Rules of Nomenclature

In order that each kind of animal may have a valid and recognized scientific name, and not several different names, and also that two different animals will not have the same name, some definite rules of nomenclature have been organized into a code. The code which is most generally used is the *International Code of Zoological Nomenclature*. It was adopted by the International Zoological Congress and is administered through a Commission on Nomenclature.

they serve the animal as its means of locomotion. In some species they serve the organism in feeding. The flagellum is a contractile structure. There are some species in which exist both flagellate and amoeboid stages. This seems to show a rather close relation of this class to the next. The class also has a close relationship with plants in that many of its representatives possess chlorophyll. These forms are frequently classified as plants by botanists. The class Mastigophora is divided into two groups: (a) the animal-like forms which may be holozoic, saprophytic, or entozoic, and (b) those more plantlike forms which may be holophytic, saprophytic,
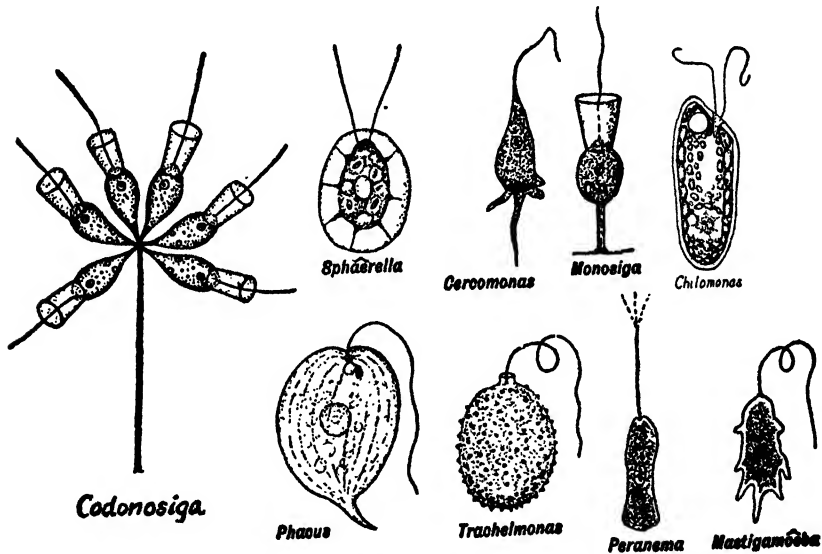
Fig. 86.—Group of representative Mastigophora. (Reprinted by permission from Curtis and Guthrie, *Textbook of General Zoology*, John Wiley and Sons, Inc.) (Figure of *Chilomonas* modified.)

or entozoic. *Holozoic* refers to forms which ingest and digest food material. *Saprophytic* refers to the habit of absorbing nonliving organic matter in solution directly through the surface of the body. *Entozoic* is a name applied to forms which live within the body of other animals, as in the intestine or the blood stream.

A large number of Mastigophora live in quiet streams, ponds, lakes, and in the ocean. Euglena is a very commonly studied fresh-water form. *Noctiluca* is an interesting marine form which is pelagic (lives at the surface) in its habits and appears as a thick, creamy scum.

This soupy mass of organisms may cover an area of hundreds of square rods. When stimulated, these animals are luminescent and at night frequently give out an attractive greenish or bluish white light; Uroglena is a fresh-water form which is often found in water supply basins and causes a pungent, oily odor and unpleasant taste in the water. *Giardia, Trichomonas, Chilomastix, Retortamonas* and *Enteronomas* are all genera with representatives occurring in the digestive tract of man.

2. **Class Sarcodina** (sär kó dĭ′ nȧ, fleshy) or **Rhizopoda** (rī zŏp′ ô dȧ, root foot).—A distinctive feature of nearly all species of this class is the capacity to form protoplasmic processes called pseudopodia (false feet) which are temporary structures and can be withdrawn. The animal is able to accomplish locomotion by extending the protoplasm into these pseudopodia. The representatives of this class
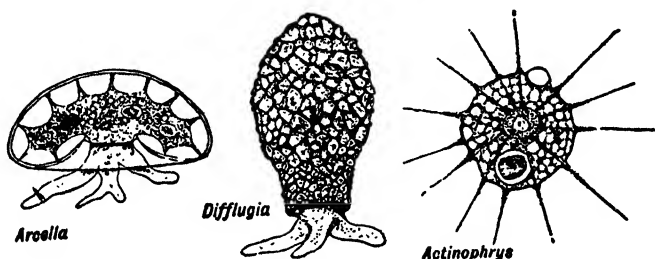
Fig. 87.—Group of typical Sarcodina. (From Curtis and Guthrie, *Textbook of General Zoology*, John Wiley and Sons, Inc.)

include many free-living forms as well as numerous parasitic ones. A number of the representatives of class Sarcodina secrete an external shell of lime, silicon, chitin, cellulose, or some bind in sand or other solid substances with one of the secretions. The class is commonly divided into five orders. (a) *Amoebina* are irregularly-shaped forms with lobelike pseudopodia. Some of the species are naked, and others are covered by a shell. *Amoeba proteus* is the free-living naked form which is commonly studied. *Endamoeba histolytica* is the most common parasitic form. *Arcella*, which secretes its shell, and *Difflugia*, which constructs its shell of sand cemented together by a secretion, are two of the most commonly observed shell-bearing forms. (b) *Foraminifera* is an order of shelled forms whose pseudopodia are very slender and reticular. The pseudopodia are extended through small pores in the shell. Only a very few of this group live in fresh water. The vast majority are marine, and *Globigerina*

is a typical example.   The disintegrating calcareous shells of this organism constitute a great mass of material on the bottom of the ocean which is known as globigerina ooze and from which chalk is formed. (c) *Mycetozoa* are characterized as being able to produce enormous plasmodia containing hundreds of nuclei and contractile vacuoles, as well as having ability to reproduce by spore formation.   They live quite commonly in masses of decaying vegetable material upon which
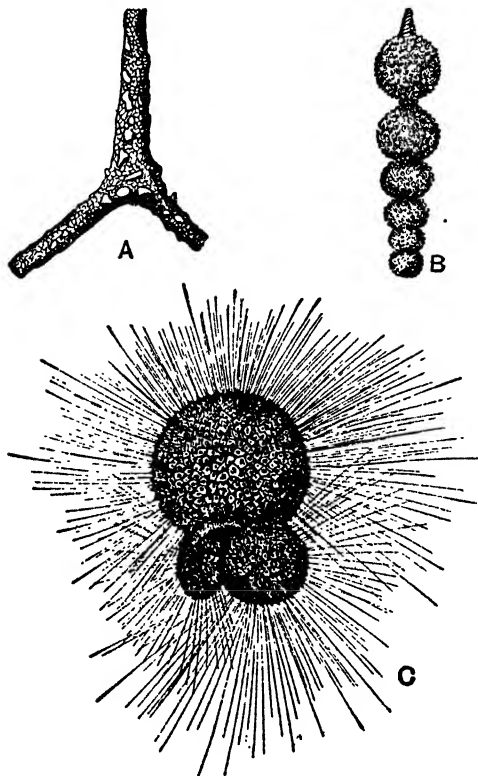
Fig. 88.—Shells of different Foraminifera.   *A*, *Rhabdamina abyssorum* (×4.5) ; *B*, *Nodosaria hispida* (×18) ; *C*, *Globigerina bulloides* (×55).   (From Borradaille and Potts, *The Invertebrata*, The Macmillan Company.)

they feed.   (d)   *Heliozoa* is a group with thin, radially arranged, threadlike, unbranched pseudopodia.   *Actinophrys sol* is a common one found in fresh-water streams and ponds.   (e) *Radiolaria* is a marine group with fine, raylike pseudopodia and a shell composed largely of silica.   The pseudopodia extend through the relatively large apertures in the shell.

3. Class Infusoria (ĭn fŭ sō′ rĭ á, crowded).—This group includes those single-celled animals covered with small hairlike, cytoplasmic processes known as cilia. They occur in both fresh and marine waters as free-swimming organisms. There are a few parasitic forms, notably *Balantidium coli. Paramecium, Stentor,* and *Vorticella* are the commonly studied Infusorians. The class may be divided into two subclasses, *Ciliata* and *Suctoria.* The first, Ciliata, is composed of

Coleps

Didinium

STENTOR

VORTICELLA
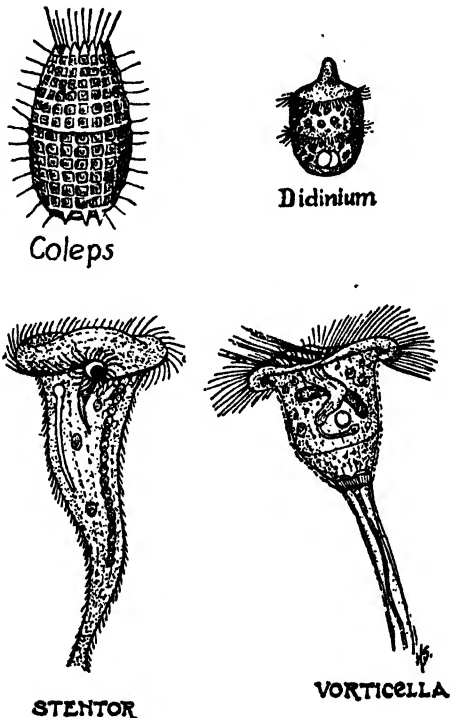
Fig. 89.—Group of typical Infusoria. (Courtesy of General Biological Supply House.)

four orders (or five by some). (a) *Holotrichida* possess cilia of equal length over the body, or they are restricted to particular regions in specialized forms; a cell-mouth is present in most forms. *Paramecium* is our most common genus living in fresh water. *Didinium, Frontonia, Chilodon,* and *Coleps* are other common forms. *Opalina* is a well-known parasitic genus which inhabits the large intestine of the frog. (b) *Heterotrichida* possess a well-developed undulating membrane in the cytopharynx. The body cilia are small or partially absent,

but the cilia of the oral region are well developed. In some forms this oral region possesses membranelles. *Stentor, Halteria,* and *Bursaria* are common fresh-water genera while *Balantidium* is a parasite in the intestine of man and some other mammals. This order is often divided into two orders, forming a second by the name of *Oligo-trichida,* of which *Halteria* is typical. (c) *Hypotrichida* possess cirri or structures formed by fusion of cilia; these are found principally on the ventral side. The cell is flattened dorsoventrally and most of the genera use creeping as their means of locomotion. *Stylonychia,*

Prorodon Frontonia

Euplotes Stylonychia Lacrymaria

Lionotus
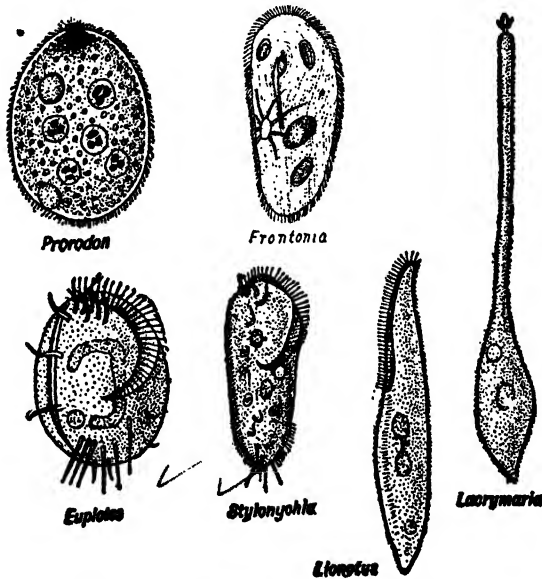
Fig. 90.—Representatives from class Infusoria. (Reprinted by permission from Curtis and Guthrie, *Textbook of General Zoology,* John Wiley and Sons, Inc.) (Figure of *Frontonia* modified.)

Oxytricha and *Euplotes* are common fresh-water genera. *Kerona* is parasitic and is often found creeping over the external surface of fresh-water Hydra. (d) *Peritrichida* is an order composed of seden- tary ciliates with a whorl of oral cilia continued into a depression in which are located the oral spot and aperture of the contractile vacuole. At the base of this depression is located the mouth. There are no body cilia in certain phases of the life history. These forms are typically attached by stalks. *Vorticella* is probably the most common living genus. *Epistylis* and *Carchesium* are well-known

colonial genera. *Vorticella* and *Carchesium* have contractile stalks while *Epistylis* is attached by noncontractile branching stalks.

The second subclass, *Suctoria* or *Tentaculifera*, as it is sometimes called, includes animals that are not ciliated, except during a free-swimming stage which may occur following division or encystment. These are attached forms with protoplasmic projections which are used in the capture of food. Most of them are marine, but *Podophrya* is an example of a fresh-water genus. This subclass is frequently given the standing of a class, giving the phylum five classes.

4. Class Sporozoa (spō rō zō′ ȧ, seed animal).—These protozoans in their early stages are often amoeboid, but in the completed life history locomotor structures are wanting. During the life cycle there is a spore stage. The animals of this class are entirely parasitic and they are usually transmitted to other animals in the spore stage. They often pass from one host in its feces and enter another in contaminated food or drink; or they are drawn from one host by a blood-sucking animal and transmitted to the blood of another. All Sporozoa reproduce by sporulation in which asexual, multiple fission is followed by gamete formation, and the gametes fuse to form a zygote. The spores are produced by the parent animal dividing into fragments while it is encysted. These little cysts, which are secreted by the protoplasm of the animal, are protective and enable them to withstand adverse conditions. The cyst is dissolved upon entrance to a host and liberates the organisms.

This class of Protozoa is among the most widely distributed of the animal parasites, and their life cycles are often quite complicated. There are three subclasses of the class, and each of these is divided into some orders. The first subclass is *Telosporidia* in which the spores produced have neither a polar capsule nor polar filament. In this group are three orders. (a) *Gregarinida*, commonly called gregarines, inhabit the cells (cystozoic) of earthworms, cockroaches, other insects, and occasionally vertebrates in their early stages, but later they may become free in the cavities of the host. They may attain considerable size. (b) *Coccidia* are minute monocysted forms which are permanent intracellular parasites of molluscs, arthropods, and vertebrates, including man. The life history involves a period of asexual reproduction (schizogony) and a period of so-called sexual reproduction which ends in spore formation (sporogony). (c) *Haemosporidia*. The representatives of this order live chiefly in the

red blood corpuscles of vertebrates. Again the life cycle involves both schizogony and sporogony. The former occurs in the blood of the vertebrate and the latter takes place in such hosts as insects, leeches, and ticks. The malaria parasite and the causal agent of Texas fever in cattle are the most important forms.

Cnidosporidia is the name of a second subclass, the spores of which contain from one to four polar capsules each with a coiled polar filament. There are two orders: (a) *Myxosporidia* are found chiefly as fish parasites, but occur occasionally in reptiles and amphibia. The gall-bladder, uriniferous tubes, and urinary bladder are usual seats of infection for the free forms, while the gills and muscles of the fishes are choice tissues for the cysts. *Myxidium* and *Myxobolus* are characteristic genera. (b) *Microsporidia* have in each spore a single polar capsule. This group is parasitic chiefly in arthropods, and occasionally in other invertebrates, fish and amphibia.
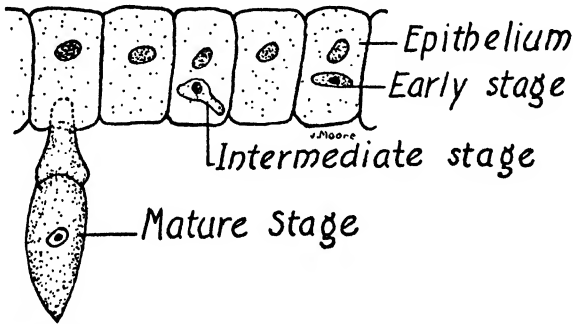
Fig. 91.—Gregarina attached to an epithelial cell of a host's intestine. Other stages of its development are shown within adjacent cells.

The third subclass *Acnidosporidia* includes forms which produce simple spores. Again there are two orders: (a) *Sarcosporidia*. As the name infers, these occur in muscles of several mammals. The encysted forms attain a length of several millimeters, and ultimately each becomes a mass of sickle-shaped spores. The complete life cycle is not known, but the saclike, encysted form in muscles of mammals is known as Miescher's corpuscle. (b) *Haplosporidia* are single cells, each with a single nucleus, and they have a relatively simple structure. Individuals of this order parasitize fishes and certain insects, notably the cockroach.

Plasmodium, the malaria parasite, is one of the *Haemosporidia,* and its life cycle will be given to illustrate the intricate life history

of certain of these forms. Life cycles in which there are primary and intermediate hosts are quite common among parasites. This example will illustrate also the relationship of insects to disease-producing organisms. There are three species of human malaria-causing organisms: (a) *Plasmodium vivax,* which causes tertian fever, is characterized by an attack each forty-eight hours. (b) *Plasmodium malariae,* which causes quartan fever, is characterized by an attack every seventy-two hours. (c) *Plasmodium falciparum,* causing estivo-autumnal or subtertian fever, the attacks of which recur each day, or there may be a somewhat constant fever. The parasite (see Fig. 176) may live in the blood of man by a series of asexual generations which may continue throughout the life of the person. The parasite, while in the spore stage, invades the red corpuscles, where it reproduces by a sort of multiple division called *sporulation,* in which there are numerous nuclear divisions before the mass of cytoplasm divides. The new individuals (merozoites) are freed by destruction of the corpuscle and almost immediately enter new corpuscles where repetition of events occurs. Some of these merozoites become sexual cells (gametocytes). Part of the gametocytes develop into *macrogametes,* spoken of as female, and others become *microgametes* which develop from the male gametocyte. If a female *Anopheles* mosquito bites and sucks blood from this person, the mosquito becomes infected with gametocytes of the *Plasmodium.* A union of the flagellate microgametes with the egglike macrogametes takes place in the stomach of the mosquito. The union is commonly called fertilization, and a fused cell or zygote thus formed soon becomes a motile, wormlike form, known as an *oökinete.* This oökinete enters the wall of the mosquito's stomach where it encysts in the form of a ball with a shell, and is now called an *oöcyst* which grows at the expense of the adjacent tissue. This cyst protrudes like a little wart on the outside of the wall of the stomach. Inside of the oöcyst the nucleus divides repeatedly, forming *sporoblasts.* These enlarge and coalesce, while slender, spindle-shaped *sporozoites* develop within, each with a chromatin dot as a nucleus. The capsule of this oöcyst is crowded full of these sporozoites which may number 10,000 or more, and there may be 500 capsules in one mosquito. Depending somewhat on the temperature, it requires twelve days or more for this development to go on in the mosquito. These little parasitic sporozoites make their way to the salivary gland of the mosquito

Behavior

Euglena usually lives near the surface of the water if the light there is not too intense, and when in the active phase swims about. This animal displays positive phototropism and is easily stimulated by changes in intensity of light. .If the light is too intense, there will be a negative response. A medium light is optimum for it. There is naturally an attraction to light in those forms which utilize it in the manufacture of food by photosynthesis. Direct, intense sunlight, however, is injurious to them. When *Euglena* swims through the water, its anterior end with the flagellum goes foremost and is first to reach any injurious or distasteful environment. When it encounters such a condition in the medium, it stops and turns sharply in another direction and attempts to move out of danger. This is known as the *avoiding reaction*. In these and other reactions this cell exhibits the irritability that is characteristic of all protoplasm.

Locomotion and Flagellar Movement

Contractions and expansions take place in Euglenae when they are not actively moving about. These movements resemble waves of contraction (peristaltic contraction) passing over the cell. Some of the larger species move about in a crawling fashion by taking advantage of this movement. This activity is known as *Euglenoid movement*. The chief method of locomotion is swimming by means of the whiplike movements of the flagellum through the water. A spiral path is followed due to the continuous turning of the body. The flagellum is made up of an elastic outer sheath which encloses an axial filament composed of one or more contractile fibrils.

AMOEBA, OF CLASS SARCODINA

It is likely that no microscopic organism has attracted so much attention and popular interest as Amoeba. Amoeba is recognized by the public generally as a simple and low form of life. Even the writers of fiction speak of the range of the span of complexity of animal life as extending "from Amoeba to Man." The pedigree of Amoeba is probably as long as that as of any of the animals we know and involves hundreds of times as many generations as many of the common animals; yet Amoeba remains in a relatively primitive and simple state. Little or nothing is known about the real ancestry of Amoeba. There are many kinds or species of Amoeba,

some simpler and some more complex than *Amoeba proteus*. *Chaos diffluens* is a very desirable species for study. Recently *Chaos chaos* Schaeffer has been rediscovered. It is enormous in size and can be seen with the unaided eye.

Characteristics and Habitat

The many kinds of Amoeba live in fresh water, marine water, soil, or as parasites in the fluids of the visceral organs of higher types of animals. *Amoeba proteus* may be collected in a variety of places where conditions of water, temperature, and organic food are favorable, such as debris from watering troughs, bottoms of ponds, spring pools, drain ditches, abandoned tanning pits, in streams where the water runs over rocky ledges, and wherever there is abundant aquatic vegetation. It is often found on the surface of submerged lily pads. A mass of pond weed may be brought into the
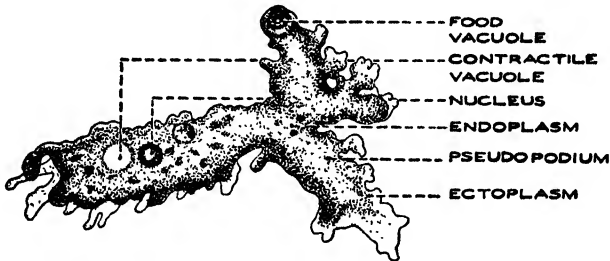
Fig. 94.—The structure and appearance of living *Amoeba proteus*.

laboratory in some of the pond water and allowed to stand in the container a few days. If amoebae are present, they will likely be in the brown scum which forms, or in the sediment at the bottom.

The general appearance of this animal is that of a slate-colored, lustrous, irregular mass of gelatinlike substance with slowly-moving, fine particles within. When it is active, the outline is constantly changing.

Structure

Amoeba proteus is one of the largest of the fresh-water forms. Its average diameter is about $\frac{1}{100}$ inch (0.25 mm.), while its extreme diameter is $\frac{1}{50}$ inch or barely visible as little specks to the unaided human eye. The animal owes its irregular shape to the fact that protrusions of its own substance are formed at its surface.

These are known as *pseudopodia,* and they are constantly changing in shape in the active animal by the flowing of the protoplasm.

Under favorable conditions the protoplasm can be differentiated into two portions. The firmer, somewhat tougher outer portion, the *ectosarc* (ectoplasm), is nearly homogeneous and includes the *plasma membrane* (or plasmalemma) : the more fluid inner portion, *endosarc* (endoplasm), is much more granular and contains the *cytosome,* cell inclusions as well as the *nucleus.* The larger bodies in the cytosome are *food vacuoles,* single, shiny, contractile vacuoles containing watery fluid and varying in size; water vacuoles; various granules; mitochondria; fat globules; and crystals. Some authors distinguish two types of protoplasm in the endosarc; the inner more fluid, *plasmasol,* in which the streaming movements take place and, surrounding this a more viscous, passive portion, the *plasmogel.* The nucleus usually appears somewhat dense and granular, and is located in the portion away from the end which is advancing in a moving specimen.

Metabolism

This refers to the constant building up (anabolism) of living protoplasm and its concurrent oxidation (catabolism). It includes all activities necessary for maintenance of itself and its race. These phenomena are the same as those found in the highest forms of life but reduced to very simple terms. Here we may study the entire metabolic cycle in progress within the confines of a single cell. Its phases are as follows:

Food.—Its prey consists chiefly of smaller Protozoa, small single-celled plants, such as diatoms and desmids, and portions of filamentous algae. Bacteria may be used to some extent and rotifers (small Metazoa) are sometimes devoured.

Ingestion.—Amoeba has no definite mouth but the food is taken into the body by engulfing it at any point that comes in contact with it. A pseudopodium is formed at this point, and the end of it flows around the food particle until the particle is entirely enclosed. A droplet of water is included with the food to form what is called a *food vacuole.* These vacuoles move about in the endoplasm.

Digestion.—The food gradually disintegrates and much of it goes into solution in the fluid of the vacuole. The function of digestion is to convert complex materials into a soluble, absorbable form. It is assumed that the surrounding cytoplasm secretes *enzymes* into the

food vacuoles of Amoeba to perform this function, since enzymes serve this purpose in larger animals where exact study can be made on the process. A circulatory system is not necessary since the vacuoles with the food in the process of digestion circulate so widely in the endoplasm that all parts of the cell may receive nourishment by direct absorption.

Egestion.—Indigestible material or debris that has been ingested with the food is carried to the surface of the cell and cast out or egested by simply being left behind as the animal moves away.

Assimilation.—This is the process of transforming the digested food material into protoplasm. In Amoeba the digested food material is absorbed directly from the food vacuoles by the surrounding
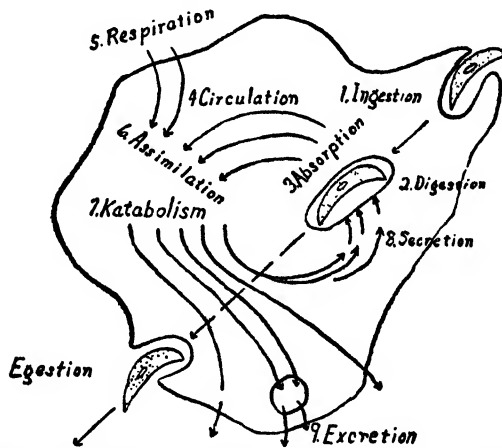
Fig. 95.—Diagram showing the phases of the metabolic process as it occurs in amoeba. (Redrawn by permission from Wolcott, *Animal Biology*, McGraw-Hill Book Company, Inc.)

cytoplasm. Since the vacuoles move rather generally through the endosarc, most of the protoplasm of the cell is in rather close contact with the dissolved food.

Respiration.—This is a process whereby the gas, carbon dioxide (CO_2), leaving the protoplasm, is exchanged for oxygen (O_2) entering it. Such a process is essential to all living protoplasm. In Amoeba this exchange is carried on primarily through the general body surface. The water in which the animal lives must contain dissolved oxygen in order that this diffusion may go on. Amoebae, however, are able to and do live in rather foul water where the oxygen content is rather low and the carbon dioxide high because

of the decaying vegetation present. Amoebae may live several hours in water from which the oxygen is removed before asphyxiation occurs. The contractile vacuole likely assists in discharging CO_2.

Catabolism or **Dissimilation.**—The chemical union of the oxygen with the organic substance of the protoplasm liberates kinetic *energy* and heat. This is known as oxidation and is a burning process which goes on within the protoplasm. Water, some mineral matter, urea, and carbon dioxide are residual products of this process.

Excretion.—These by-products of metabolism in the form of waste liquids must be disposed of. They cannot be allowed to accumulate beyond certain limits in the living organism if life is to continue. Urea and uric acid, which are protein by-products, excess water, and salts, are discharged from the body of Amoeba by way of the *contractile vacuole* along with some carbon dioxide. The contractile vacuole is formed by the union of small droplets of liquid under the plasma membrane. It fills out with liquid which is forced out through the membrane as the vacuole disappears. Its location apparently is not fixed in the cell but is often near the nucleus. The contractile vacuole is absent in some forms, and in such cases, excretion occurs only by diffusion through the cell surface. There is likely some excretion by this means in all Amoebae.

Growth.—If there is increase in the volume of a body, this is spoken of as growth. In all living organisms growth is accomplished by addition to the protoplasm. If food is plentiful, more material is added to the protoplasm than is used up in the oxidation which produces active energy. In other words, growth occurs when the rate of anabolism exceeds the rate of catabolism in the organism.

Reproduction and Life Cycle

The life history of the many-celled animals to be studied later includes a series of changes from egg, through embryo state, to adult. In Amoeba the cycle is likely only partly known, because it is difficult to maintain cultures in perfectly normal conditions for sufficiently long periods to get this complete story. Ordinarily, the animal grows when conditions are favorable until it attains a certain size; when this limit of size has been reached growth ceases. Why does the cell cease to grow? Why should it not attain the size of a man? Or why should a tree not continue to grow until it reaches the sky, or a man take on the proportions of an elephant?

We have not been able to put our fingers on any one factor that completely controls growth. We do know of certain relationships that influence it. It will be recalled that all materials used by a cell must pass through the cell membrane, and likewise all waste substances must be discharged in a similar manner. Mathematics states that the volume of a cell increases according to the cube of its diameter; while its surface increases only according to the square of its diameter. In other words, the amount of material in
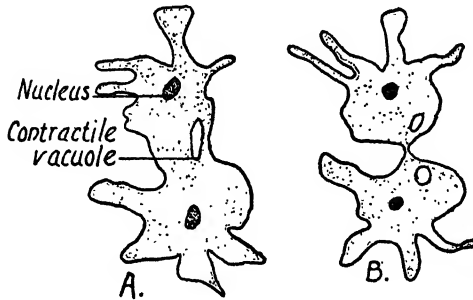
Fig. 96.—Binary fission in amoeba. *A,* Beginning of the process; *B,* nearing the completion of two new cells. (Drawn by Joanne Moore.)
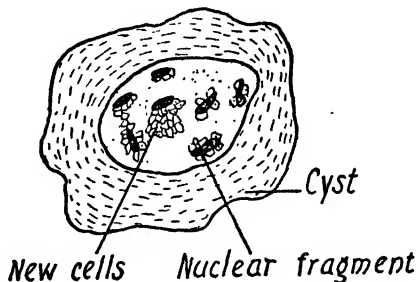
Fig. 97.—An amoeba encysted and undergoing the process of sporulation. (Drawn by Joanne Moore.)

a growing cell increases approximately twice as fast as the plane surface needed to surround it. It is logical, then, to assume that a point may be reached when the surface area will not be sufficient for the passage of necessary materials into and out of a cell. There is, however, considerable variation in the size of cells; hence it seems there must be other factors besides volume and surface relation in operation. Modified surface and difference in the rate of metabolism certainly would be factors affecting the size of the

organism. When Amoeba reaches the limit of size, a division oc-
curs. *Binary fission,* by which two new individuals are produced,
has been definitely established, and some other methods of reproduc-
tion have been presented. Calkins, an authority on the Protozoa,
states that Amoeba starts out as a tiny *pseudopodiospore* which has
only one pseudopodium. It then passes through a growth period and
increases in complexity until it reaches the full-grown condition. It
then divides by binary fission into two daughters. When each daugh-
ter has grown to nearly twice its original size, fission is repeated.
Environmental conditions and the variety of Amoebae determine the
number of times this phase is repeated. Occasionally the fission seems
to be an amitotic one. At the close of the fission phase, there is a
period of encystment and subsequent *sporulation.* During the en-
cystment the protoplasm undergoes several divisions to produce the
several pseudopodiospores which later break from the cyst as infant
Amoebae. It is felt that the complete details of the life cycle of many
common Sarcodina are not yet available.

Behavior

All of the activities of an animal which come in response to in-
ternal or external stimuli make up the "behavior." The activities
of the animal under discussion include the formation of pseudo-
podia, ingestion of food, locomotion, and others. *Amoeba proteus*
exhibits either positive or negative reactions to various stimuli. An
environmental change to which an animal reacts is known as a
stimulus, while the reaction of the animal is called the *response.* The
movements made by an animal in response to stimuli are called
tropisms. Amoeba exhibits all of the tropisms discussed in Chapter
XIV. To physical contact, it responds positively if the impact is
gentle; otherwise the response is negative. It responds negatively to
strong light and finds its optimum in a moderately reduced light.
When some part of the body surface of this animal comes quietly
into contact with food, there is a characteristic response. This part
of the protoplasm stops flowing while other parts continue, thus form-
ing a pocket around the particle of food. The edges of the pocket
fold in, meet, and join so as to enclose the object. This attraction to
food is likely a positive chemotropism. Amoeba reacts negatively
to concentrated salt, cane sugar, acetic acid, and many other chemi-
cals which have been tried. Amoebae have an optimum tempera-
ture range between 15° and 25° C. Temperatures approaching the

freezing point inactivate the animal, while temperatures above 30°
C. (86° F.) also retard their activities and may soon become fatal.
A weak electric current has an effect on the physical condition of
the protoplasm on the side nearest the cathode. The tendency is
toward the sol state here, hence the animal turns toward the cathode.
According to Jennings, who has done extensive research on be-
havior of Protozoa, these activities are "comparable to the habits,
reflexes, and automatic activities of higher animals." He also feels
that Amoeba probably experiences pain, pleasure, hunger, desire,
and the other simple sensations.

Amoeboid Movement and Locomotion

The flowing or streaming of the protoplasm and extending the cell
in some direction by the formation of pseudopodia is usually called
amoeboid movement. It is so named from the perfect exemplification
of such activity by Amoeba. Locomotion is accomplished by the
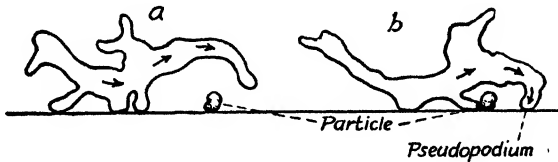
Fig. 98.—Successive positions in the movements of an amoeba viewed from the
side. Notice the formation of new pseudopodia and the engulfing of the particle on
the surface. (Modified from photographs by Dellinger, 1906, Journal of Experi-
mental Zoology.)

pseudopodia, and the process of their formation in most Amoebae.
Successive pseudopodia are formed in the moving *Amoeba proteus* as
it goes in a given direction. The pseudopodia are temporary loco-
motor structures. Most zoologists explain this movement as being
due to the contraction of the more viscous ectoplasm, particularly in
the "posterior" region. This brings about a forward movement in
the more fluid endoplasm (plasmasol) which causes an outflow at
points where the ectoplasm is thinnest, or where surface tension is
lessened. As this plasmasol approaches the advancing tip of the
pseudopodium, it turns to the sides and changes to more solid endo-
plasm (plasmagel). This process continues, pushing the advancing
tip farther and farther forward. At the opposite side, the plasma-
gel continues to become plasmasol to provide for fluent material.
At the side of the animal away from the advancing pseudopodium,
the cell membrane (plasmalemma) moves upward and over the up-

per side of the body; it continues to move forward to the tip of the pseudopodium where it dips down and is laid on the substratum over which the animal is moving and becomes a part of the stationary portion. If the specimen has several pseudopodia, one or more may be developing while others are receding. In the latter, the flow of plasmasol is back through the centers of the pseudopodia toward the main mass. Temperature and other environmental factors affect the rate of locomotion.

Dillinger mounted some of the animals on the edge of a slide in a groove formed by the projecting edges of two cover glasses and observed their movement from side view by tilting the microscope to a horizontal position. He describes their movement as a sort of walking on the progressively forming pseudopodia. The new pseudopodia are formed at the advancing margin of the cell.

PARAMECIUM, OF CLASS INFUSORIA

This animal has been the subject of much study and the victim of considerable experimentation. *Paramecium caudatum* is probably the species most commonly studied. It is easily available and is large in size, ranging between 0.2 and 0.3 mm. in length.

Characteristics and Habitat

Paramecium is an active cigar-shaped animal, just about large enough to appear as small white specks in the water. It has a definite axis and permanent anterior and posterior ends, but it is asymmetrical in shape. Paramecia are easily cultured by collecting some submerged pond weeds and allowing them to stand in a jar of the pond water for several days. Or some natural creek or pond water may be placed in a jar with some old dry grass or cabbage leaves and allowed to stand about ten days. These animals occur abundantly in any water which contains considerable decaying organic matter. They thrive in all streams, creeks, or ponds polluted by sewage. They tend to congregate at the surface and particularly in contact with floating objects, where they frequently form a white scum. This animal is a great favorite in zoology laboratories.

Structure

Paramecium is sometimes described as being slipper-shaped. The anterior portion, which is blunt but generally narrower, represents

the heel part; while the posterior portion, which is generally broader but pointed, represents the sole portion.

At one side is a depression, the *oral groove,* which passes diagonally from the anterior end to about the middle of the body. It is broad and shallow anteriorly but it becomes narrow and deeper as it ends in a mouth, which leads to the *gullet.* The groove usually extends

CILIA

CONTRACTILE VACUOLE

ORAL GROOVE

MACRO-NUCLEUS

MICRO-NUCLEUS

MOUTH

GULLET

FOOD VACUOLE

ANAL PORE

CONTRACTILE VACUOLE

TRICHOCYSTS

PELLICLE
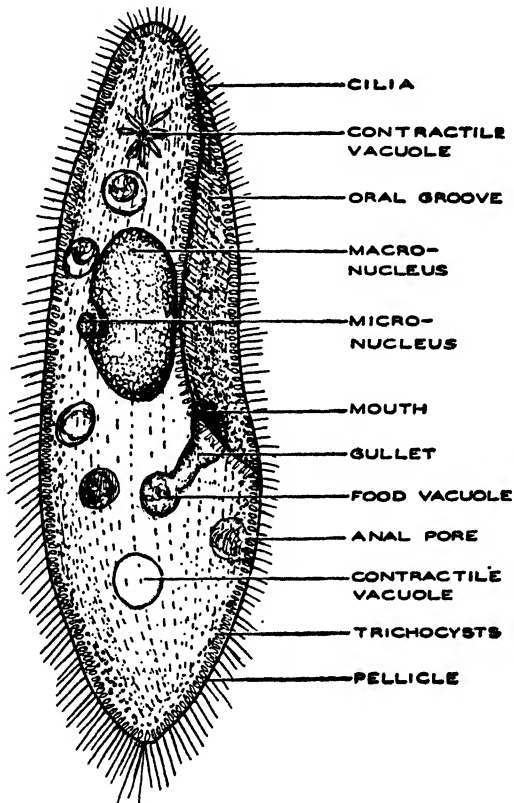
Fig. 99.—Paramecium, much enlarged to show structure. (Drawn by Titus C. Evans.)

obliquely from right to left in *P. caudatum* as the animal is viewed from the oral side. Occasionally cultures are found in which the majority of the individuals show the groove extending from left to right from this view. The body is covered with fine hairlike cilia which are of even length except in the oral groove and at the posterior extremity, where they are noticeably longer. The cilia within

the gullet are fused together into a sheet, forming the *undulating membrane*.

The cell is divided into the outer, tough, nongranular ectosarc which is composed of ectoplasm. The outer surface of it is a thin, elastic *cuticle* or *pellicle* which is marked in hexagonal areas by the distribution of the cilia. The cilia are direct outgrowths of the ectosarc. There are a great many spindle-shaped cavities located in the ectosarc with their long axes perpendicular to the surface. These structures, *trichocysts,* are filled with a semifluid substance and each opens to the outside through the pellicle. The endosarc, composed of endoplasm, is within. It contains food vacuoles, two contractile vacuoles, macronucleus, and other granular masses. The numerous food vacuoles are formed, one at a time, at the inner end of the gullet by a mass of food material coming in with a droplet of water, a process similar to that described in Amoeba. The vacuoles circulate through the endoplasm in a rather definite course. This activity is called *cyclosis.* The contractile vacuoles are located near each end of the animal. Each vacuole has several radiating canals entering it. These vacuoles expand and contract alternately. The macronucleus is located slightly posterior to the center and somewhat beside the mouth. It is relatively large and rather bean-shaped. The micronucleus is located in the curved surface of the macronucleus and is much smaller. *P. aurelia,* another species, ordinarily has two micronuclei instead of one.

Metabolism

The same general outline of activities as described in Amoeba and others occur, differing only in certain details. These same vital functions must take place in all living things (organisms).

Food.—Smaller protozoans, bacteria, and particles of debris constitute the principal items on the menu for Paramecia.

Ingestion.—This animal hunts its food, and when it locates a region where food is abundant, it settles down and becomes relatively quiet. The food is swept through the oral groove by the beating action of the cilia, and carried back through the mouth into the gullet. Finally it passes by means of the action of the undulating membrane into the endoplasm in the form of one *food vacuole* after another. These food vacuoles move in a definite course through the endoplasm. Since this course is in the form of a cycle, the circulation is known as *cyclosis.*

Digestion, Assimilation, Respiration, and Catabolism or Dissimilation all occur in a manner very similar to that described for Amoeba. *Egestion* occurs at a definite *anus*.

Excretion of the waste products of metabolism in solution is by means of the alternate filling and expelling of fluid by the two contractile vacuoles, or it may occur to some extent by diffusion through the entire cell membrane.

Growth occurs as it does in Amoeba and in all other organisms. Under favorable conditions the storage of nutrient materials, like starch and fats, occurs in the cytosome. Nutrition in this animal is holozoic, and its living process is essentially like that of all higher forms of animal life.

Reproduction and Life History

The actual reproduction is by transverse binary fission which in itself is asexual. The cell divides transversely into individuals, and this is repeated for long series of generations, one after another. During this division process in *P. caudatum,* both the macronucleus and the micronucleus divide, the old gullet divides into two, and two new contractile vacuoles are formed by division of the old ones. The micronucleus divides by mitosis, but the division of the macronucleus is not distinctly so. The time required for the completion of a division ranges between thirty minutes and two hours, depending on environmental conditions. Division is repeated at least once each twenty-four hours and under especially favorable conditions, twice a day. It has been estimated that if all survived and reproduced at a normal rate, the descendants of one individual over a month's time would number 265,000,000 individual Paramecia.

P. caudatum is a conjugating form of paramecium, while *P. aurelia* and others seem not to conjugate. *Conjugation* is a temporary union of two individuals with exchange of nuclear material. Calkins carried some cultures of *P. caudatum* through a long series of generations and observed that conjugation occurs at intervals of approximately every two hundred generations. When two Paramecia are ready to conjugate, they come in contact, with their oral surfaces together, and adhere in this position (as A and B in Fig. 100). A protoplasmic bridge is formed between the two individuals. This union resembles a sexual act and has recently been described as such. The conjugants are usually small, rather unhealthy appearing individuals. Shortly after the adherence of the conjugants the
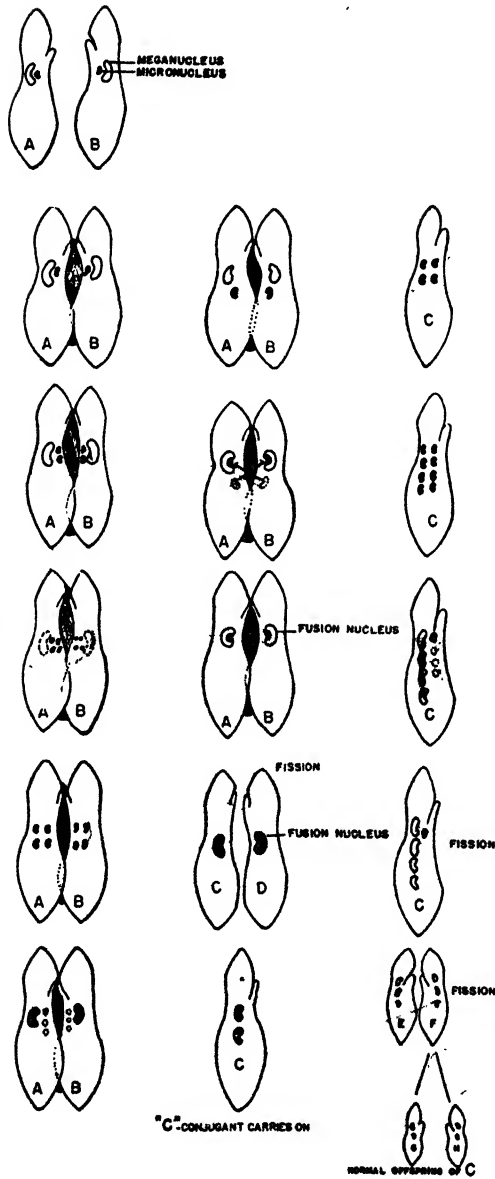
Fig. 100.—A series of diagrams to show the progressive changes involved in conjugation in *Paramecium caudatum*. The process begins as shown in the upper left of the illustration and follows down the column and then to the top of the next column. (From Parker and Clarke, *Introduction to Animal Biology*, The C. V. Mosby Company.)

nuclei of each undergo changes. The micronucleus enlarges and divides, forming two micronuclei, while the macronucleus undergoes disintegration and final disappearance. Each of these two new micronuclei again divides to form four, three of which disintegrate, but the fourth divides again, forming one large and one small micronucleus (as in those at the top of the 2nd column in Fig. 100). Sometimes the smaller of these nuclei is spoken of as the "male" nucleus and the larger, as the "female." In each animal the smaller nucleus moves across the protoplasmic connection to the other animal and fuses with the larger nucleus there. Each individual now has a fusion nucleus. The two conjugants now separate, and very shortly the fusion nucleus of each divides by mitotic division (C of the illustration); these divide, forming four nuclei in each animal, and these four divide to form eight. The descriptions of the subsequent events vary somewhat. At least it is known that four of the eight nuclei enlarge and become macronuclei; three of the others degenerate, and one remains as a micronucleus. This micronucleus divides, and almost immediately the entire animal divides by binary fission with two macronuclei and one micronucleus going to each cell. These daughter cells then divide to produce a total of four Paramecia which have the typical number of one micronucleus and one macronucleus of the active phase. Following this comes the long series of generations formed, one after the other, by transverse binary fission.

The whole series of changes involved in conjugation has been compared to maturation of germ cells and fertilization in sexually reproducing metazoans. The degeneration of the three micronuclei is compared with reduction division in maturation, and the fusion of the small "male" micronucleus with the larger "female" micronucleus of the other conjugant is compared to fertilization.

A phenomenon, known as *endomixis*, has been found occurring in *P. aurelia* by Woodruff. It occurs in a single individual. This species has two micronuclei and one macronucleus. At regular intervals of about every forty or fifty generations, the macronucleus disintegrates, and the micronuclei undergo two divisions which produce a total of eight. Six of these disappear, and then the cell divides; one of the remaining micronuclei goes to each. This nucleus then undergoes two divisions. Two of these four become macronuclei, and two remain as micronuclei. The micronuclei then divide again as the entire cell divides to form daughters, each with

two micronuclei and one macronucleus, the typical condition for this species.   Endomixis may occur in *P. caudatum* also.   Endomixis seems to have about the same effect as conjugation.

There is still difference of opinion as to the exact function of conjugation and endomixis, but the chief result of the processes seems to be the reorganization of the nuclear substance.   This may allow for variations in the fundamental constitution of the race.   According to some authors these processes rejuvenate or renew the vitality of the individuals.   Very recently, not only sexual reproduction but also distinct sexes have been described for Paramecium.*   These results are all possibilities.

Behavior

This animal is an active swimmer and necessarily shows ready response to environmental factors.   Its behavior consists of its spiral course in locomotion, avoiding reactions, responses to food
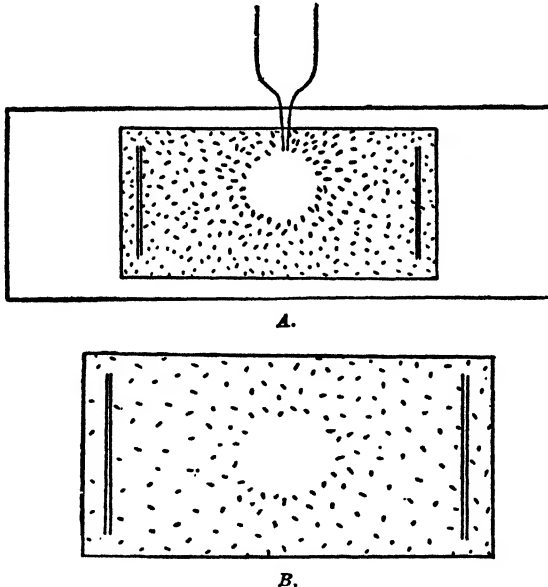
Fig. 101.—Reaction of paramecia to a drop of 0.5 per cent NaCl. *A*, Introduction of the drop beneath the cover glass; *B*, four minutes later.   (From Jennings, *Behavior of the Lower Organisms*, The Columbia University Press.)

material, contact and other minor reactions.   Its reactions to stimuli are somewhat similar to those described for Amoeba; however, it

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*Sonneborn, Science News Letter, Aug. 21, 1937.

seems not to be affected by ordinary light. It reacts either positively or negatively to contact, change of chemical constitution, change in temperature, to gravity, and to electric current. The response to contact is positive, negative to ultraviolet light, negative to sodium chloride, positive to weak acetic acid, and positive to the negative pole of a weak, galvanic electric current. The optimum temperature for Paramecium ranges between 24° and 28° C. (71° F.). Gravity causes the anterior end to point upward, and when placed in moving water, the animals will swim upstream. If Paramecium comes in contact with a solid object when it is moving, it will back away, swing on its posterior end to a slightly different
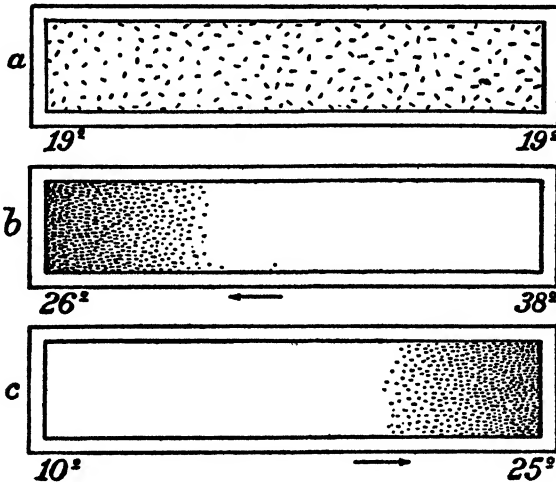
Fig. 102.—Reactions of paramecia to temperature. *a*, Paramecia in a trough with a uniform temperature of 19° C. The animals are evenly scattered through the water. In *b*, the temperature is held at 26° C. at the left end and 38° C. at the right. The animals are congregated at the end of the lower temperature. In *c* the temperature is 25° C. at one end and 10° C. at the other and the animals have all collected in the region of the higher. An optimum temperature for these animals is evident. (From Jennings, *Behavior of the Lower Organisms*, The Columbia University Press.)

direction and try again. This may be repeated, and is known as the "avoiding reaction." Such a reaction really involves simply one or more negative responses. These animals are constantly sampling the water and avoiding the conditions which are least favorable. This may be repeated in all directions. The same type of persistence is practiced in attempting to surmount a solid barrier. Such successive attempts to gain the result desired constitute what is known as the "*trial* and *error*" mode of behavior.

Fig. 108.—Diagram of the course and movement of paramecium through the water. Notice the spiral path. (From Jennings, *Behavior of the Lower Organisms*, The Columbia University Press.)

In an effort to defend itself when severely irritated, Paramecium will discharge the contents of the trichocysts, which harden on contact with the water and form a mass of fine threads. These threads will entangle many of the aquatic enemies of these animals.

Locomotion

The beating action of the cilia against the water serves as the principal means of locomotion. The stroke of the cilia is rather oblique and this coupled with the increased length of the cilia along the oral groove causes the body to turn on its long axis while swimming. The total effect of these activities causes the course followed through the water to be that of a spiral. Paramecium may reverse the direction of the stroke of the cilia and thus move backward just as a car can be thrown in reverse.

The cilia are contractile outgrowths of the ectosarc. Each has an elastic sheath and a fibrillar core. Contraction of the protoplasmic substance on one side, bends the cilium in that direction. The reverse stroke is much more passive. The movement of one tier of cilia seems to stimulate the adjacent ones to bring about coordinated, rhythmic ciliary activity and movement.

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CHAPTER XVI

HYDRA, OF PHYLUM COELENTERATA

The phylum name, coelenterata (sēl ĕn tēr ā′tà), means "hollow intestine," and all of the representatives bear this out by possessing a single large cavity in the body. There is a single opening to this cavity, and it functions as both mouth and anus. There are two general types of coelenterates; the *polyp* form and the *jellyfish* form. They are all modified gastrulas, have *radial* symmetry, and possess tentacles with "sting bodies" or nematocysts. Most of the species are marine, but there are a few fresh-water forms. The body wall is composed of two layers of cells, and for that reason they are said to be *diploblastic*. These two layers are the outer *ectoderm* and inner *endoderm*. Most of the representatives do not develop skeletal structures, but coral polyps produce hard, calcareous cases around themselves. In several species there is the typical alternation of generations of attached and free-living forms. Most coelenterates are attached or very sedentary for at least a part of the life span.

The radial symmetry is correlated with an attached habit of life. A good many of the attached forms look much like plants and were so described for a long time.

The digestive process is principally extracellular, being accomplished by *enzymes* which are secreted by special cells of the endoderm into the internal or *gastrovascular cavity*. A limited amount of the digestion, however, takes place within the endoderm cells after particles of partially digested food have been engulfed by these cells. This is called *intracellular* digestion. *Excretion* and *respiration* are carried on by the general surfaces of the body. Asexual reproduction is accomplished by budding and fission. Sexual reproduction, involving production of ova and spermatozoa and their union in fertilization, occurs here too.

The group is considered among the simplest of metazoans and shows, in a simple way, typical features of this great division of the animal kingdom. Hydra will be studied in detail, because it is readily available, easily collected and handled, and is representative

of multicellular animals of simple formation. The study of **Hydra** as a simple metazoan will go far in giving insight into the much more complex make-up of the body and life of man.

Classification of the Phylum

The phylum is divided into three classes, each with three or four orders.

Class Hydrozoa.—These are typical polyp forms, many of which produce medusae forms by budding. The group includes marine, colonial polyps, or hydroids, floating colonial hydroids, such as Portuguese man-of-war, one special group of corals, some smaller jellyfishes, and the fresh-water polyps.
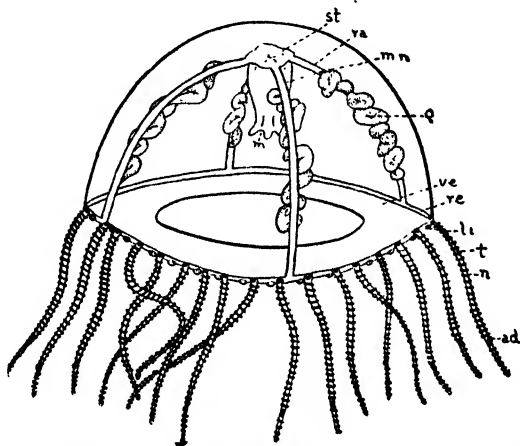
Fig. 104.—*Gonionemus. ad*, Adhesive pad; *g*, gonads; *li*, lithocyst; *m*, mouth; *mn*, manubrium; *n*, nematocyst; *ra*, radial canal; *rc*, ring canal; *st*, stomach; *t*, tentacle; *ve*, velum. (From White, *General Biology*, The C. V. Mosby Company.)

Order Leptolina (may be divided into Anthomedusae and Leptomedusae)—a group which has a sedentary or sessile polyp stage. Such examples as *Hydra, Obelia, Gonionemus, Campanularia, Tubularia,* and *Craspedacusta* are well-known forms.

Gonionemus is a small jellyfish form, measuring about a centimeter across, and is found in the pelagic waters along our eastern shores. Its shape reminds one somewhat of an umbrella with a fancy fringe but with practically no handle and made of clear cellophane. The *exumbrella* is the convex upper, or aboral side while the *subumbrella* is the concave, lower, oral side. A short stalklike part, the *manubrium*, hangs down from the center of the subumbrella. At

Obelia habit
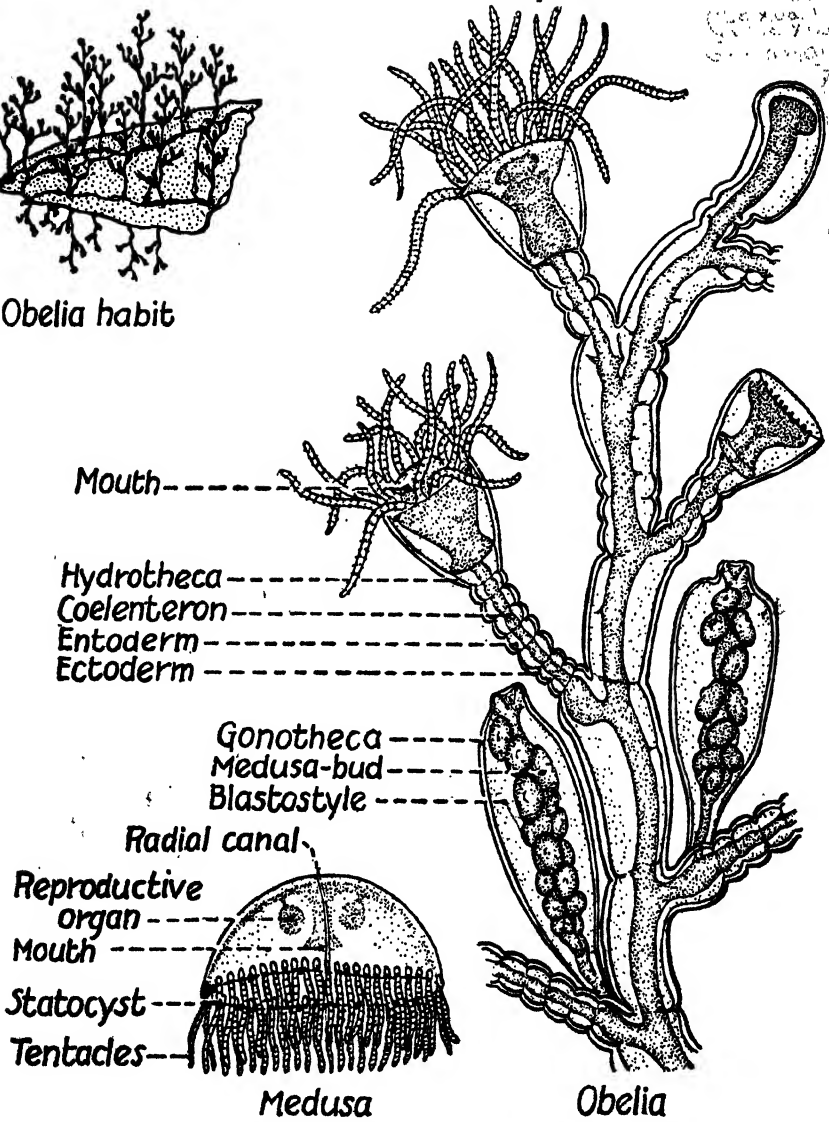
Mouth - - - - - -

Hydrotheca - - - - - - -
Coelenteron - - - - - - - -
Entoderm - - - - - - - - - -
Ectoderm - - - - - - - - - -

Gonotheca - - - -
Medusa-bud - - - -
Blastostyle - - - - -

Radial canal

Reproductive organ - - - -
Mouth - - - - -

Statocyst - - -

Tentacles - -

Medusa   Obelia

Fig. 105.—*Obelia*, hydrozoan colonial coelenterate, showing asexual generation, sexual generation (medusa), structure, and habit of life. (Courtesy of General Biological Supply House.)

its distal end is the *mouth,* bordered by four *oral lobes.* The mouth is the aperture leading into the internal or *gastrovascular* cavity which has four radial branches or canals.

Obelia is a marine, colonial type resembling a branched plant in appearance. The individuals are attached to each other in the colony, and it is fastened to a rock or other substratum by a root-like *hydrorhiza.* They are distributed in the Atlantic Ocean and Gulf of Mexico out to forty fathoms in depth. The colony begins
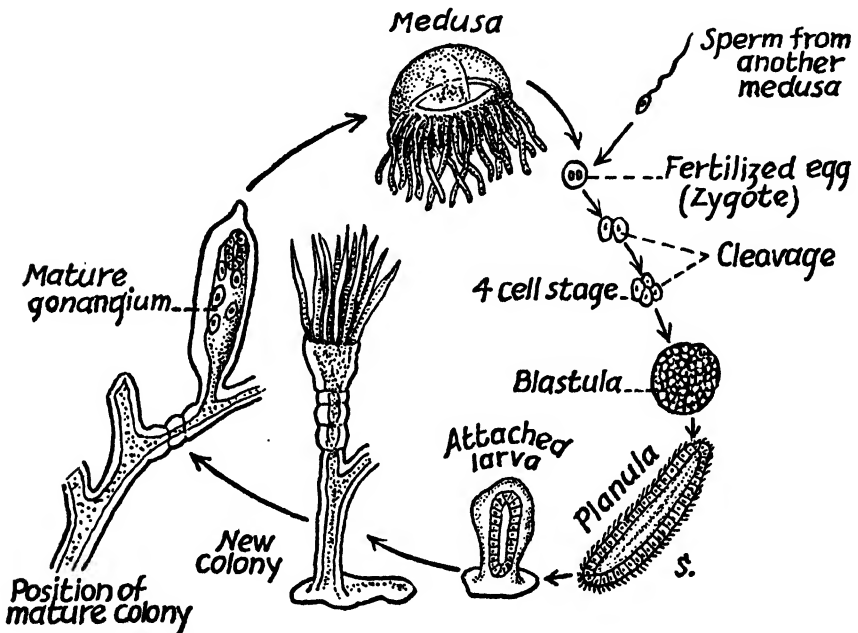
Fig. 106.—Life cycle of *Obelia,* illustrating polymorphism and metagenesis. Adult hydroid colony with mature gonangium gives rise to sexual medusa which is produced in the gonangium and set free in the water. Germ cells produced by the medusae complete the cycle. Blastula and planula stages are free swimming. (Redrawn and modified from Wolcott, *Animal Biology,* McGraw-Hill Book Company, Inc.)

as a single individual which buds, but they do not separate from the preceding or parent generation. This may continue for several generations.

The reproductive cycle is both sexual and asexual, alternating between the sexually produced polyp or hydroid generation and the asexually produced sexual generation, the medusa or jellyfish form. The medusae arise as buds from the special individuals,

blastostyles, escape through the distal pores, and develop to sexual maturity as free-swimming individuals. The sexes of these are separate; some produce eggs, and others, spermatozoa, which are discharged into the water at maturity and unite to form *zygotes*. The zygote develops into the free-swimming, ciliated *planula* stage which soon attaches and develops into a polyp from which a new colony arises. After producing a generation of medusae, this colony

Fig. 107.—*Physalia*, the Portuguese man-of-war, a floating colonial coelenterate. (From Hegner, *College Zoology*, The Macmillan Company.)

disintegrates, and after producing germ cells, the medusae die. This process, involving alternation of generation, is called *metagenesis*.

Order Trachylina.—This order includes two suborders of hydromedusae which come from the egg directly with no polyp stage. *Trachynema, Campanella,* and *Liriope* are generic examples.

Order Hydrocorallina.—This group resembles the corals by producing strong calcareous skeletons. They have extensive, branched hy-

drorhiza and powerful *nematocysts (stinging bodies)*. *Millepora,* the staghorn or stinging coral, as it is called, is a good example.

Order Siphonophora.—This is a pelagic order of colonial coelenterates with extreme polymorphism. A common tube of the coenosarc unites the five kinds of individuals of the colony, and this cavity is continuous from one individual to another. The blind end of the coenosarcal tube is an air-filled, bladderlike float *(pneumatophore)* with a superior crest. The polyps hang down into the water beneath this float. Most of the individuals are specialized to such a degree that they care for only limited functions. This specialization and diversity of forms is such that the entire colony appears as a single individual. *Physalia,* the Portuguese man-of-war, is a typical example. Its sting is quite poisonous; bathers coming in contact with the trailing tentacles, which bear batteries of nematocysts, suffer severe pain.

Class Scyphozoa.—The coelenterates belonging here are large jellyfishes having an alternation of generation in which the medusa form is dominant. There are records of individuals of this group twelve feet in diameter, and possessing tentacles one hundred feet in length.

Order Stauromedusae.—Conical or vase-shaped medusae which usually lack marginal sense bodies (tentaculocysts). *Tessera, Lucernaria,* and *Haliclystus* are usually cited as examples.

Order Peromedusae.—These are cup-shaped, free-swimming forms with four interradial tentaculocysts. They occur in the open sea. *Pericolpa* and *Periphylla.*

Order Cubomedusae.—Forms which have rather cubical shape, four perradial tentaculocysts, interradial tentacles, and are chiefly tropical. *Chiropsalmus* and *Charybdea* are examples.

Order Discomedusae.—Scyphozoa whose medusae are dominant, saucer-shaped and almost transparent. Some of them are more than seven feet in diameter. Tentacles are usually present also on the margin of the bell. This is the most numerous and extensively distributed group of Scyphozoa. *Aurellia* and *Stomolophus* are common examples.

Aurellia* is the typical example, and, like most jellyfishes, is composed largely of water. This is a common one and ranges from

**This spelling is according to Mayer's monograph. The generic name first proposed by Peronas Le Sueur was so spelled.

New England to the Gulf of Mexico. It may reach a foot in diameter and has the appearance of a transparent umbrella. Many of these animals produce a calcareous external skeleton called coral. Both sexual and asexual reproduction are common.

Class Anthozoa.—This class, of the polyp form, has two subclasses. The group includes the corals and sea anemones.

Subclass Zoantharia.—This group has numerous paired septa, typically occurring in multiples of six, and plain tubular tentacles. It includes sea anemones and corals.

Labels (top to bottom, right side):
- Cut surface of body wall
- Stomach
- Gonad
- Sub-genital pit
- Upper portion of manubrium
- Lateral mouth
- Radial canal
- Sub-umbrella space
- Circular muscle
- Central mouth
- Oral tentacles

Labels (left side):
- Manubrium (cut surface)
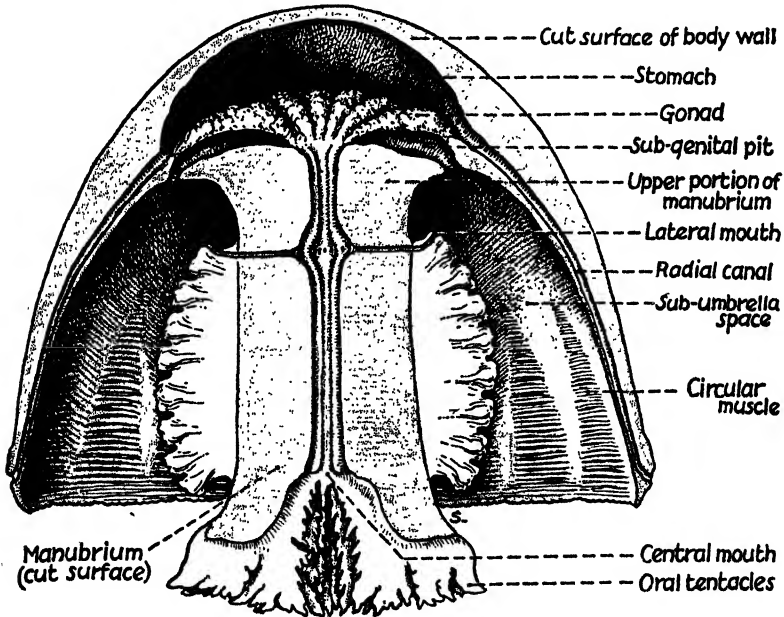
Fig. 108.—Cabbage-head jellyfish, *Stomolophus*, a very common form in the Gulf of Mexico. Bisected to show internal structure.

Order Actinaria.—These anemones are usually solitary polyps; they have many complete septa and numerous tentacles but no skeleton. *Sagartia, Cerianthus,* and *Metridium* are common examples.

Metridium usually lives attached to rocks or to solid bodies in the water near shore, even in tide pools. They average about three or four inches in height and two or two and a half inches in diameter. The free end of the jar-shaped body is covered with tentacles which are provided with nematocysts. The entire body can be

expanded and contracted, and it can change its location by "scooching" on its *basal disc* (attached end). The *mouth* is located in the center of the crown.

Asexual reproduction by *budding* from the margin of the basal disc is practiced by this animal. Occasional *longitudinal fission* may occur. The gonads develop on the edges of the lower part of the septa to provide for sexual reproduction. The sexes are distinct. Mature ova and spermia are discharged into the water of the cavity and escape through the mouth to unite in fertilization outside.
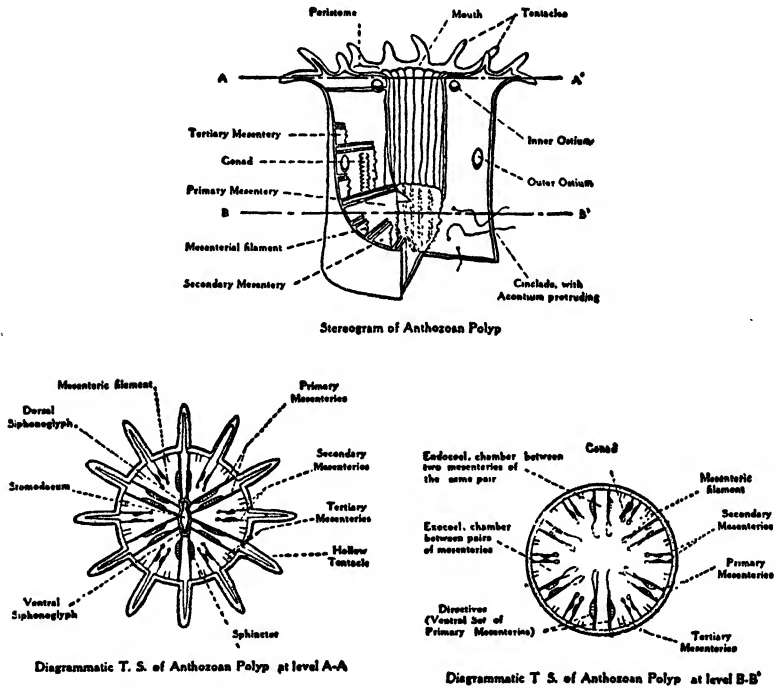
Fig. 109.—Diagrams showing structure of the anthozoan, *Metridium*. (Courtesy of Pacific Biological Laboratories.)

Order Madreporaria.—The representatives of this order secrete an external limestone skeleton; most of them are colonial. *Astrangia, Madrepora,* and *Oculina* are examples.

Astrangia is the common coral polyp, and it is quite similar to a small sea anemone to which calcium carbonate has been added by secretion from the ectoderm cells as well as having budded to form a colony of numerous individuals. In time continually growing colo-

nies of these animals can produce enormous stony barriers (reefs) in the sea. Many corals are of beautiful colors.

Order Antipathidea.—An order composed of branching colonies whose individuals are joined by a branched tubular axis which is covered by an epidermal layer. *Cirripathes* and *Antipathes* are typical examples.

Many authors recognize *Zoanthidea, Cerianthidia,* and *Edwardsiidea* as orders in this subclass also.

Subclass Alcyonaria.—The features of this division include eight hollow, feathered tentacles, eight mesenteries, and one siphonoglyphe. Colonial and polymorphic forms are not uncommon.

Order Alcyonacea.—A colonial group which has calcareous spicules but lacks an axial rod. Body walls of individuals fuse together as one. Organ pipe coral belongs in this order.

Another order, *Stolenifera* with *Cornulariella* as an example, is frequently set apart.

Order Gorgonacea.—This is another colonial coral which is sessile and has a calcareous axial rod. The common sea fan. *Gorgonia,* as well as the precious *Corallium rubrum* are well known examples.

Order Pennatulacea.—Another colonial form whose body is modified so that one portion is submerged in the substratum. The colony takes a bilateral form, and the individuals are born on a disc or axial stem which is supported by a hard skeleton. *Renilla* and *Pennatula,* sea pens and sea feathers, are typical examples.

Habitat and Behavior of Hydra

Hydra (Chlorohydra) viridissima is likely the most common hydra available. It is the small green hydra which is very active and has short tentacles. Most of the hydras are found in cool fresh water, attached to the surface of plant leaves, smooth sticks, debris, or even the surface film of the water. The brown hydras, such as *H. americana, H. carnea,* and *Pelmatohydra oligactis,* are sluggish and have longer tentacles than the green ones.*

Hydra is a sedentary kind of animal and may remain stationary for a considerable period of time if living conditions are uniformly good. When the environmental conditions are changing, and the animal is in need of food, it becomes quite active, moving about

*Recent taxonomic information concerning Hydras of the United States may be found in the papers of Libbie H. Hyman, published in the Transactions of the American Microscopical Society, Vols. 48, 49, and 50.

from place to place. It keeps the tentacles extended, ready to grasp any food which may come into its reach. Nematocysts or sting bodies are discharged when the tentacle comes in contact with potential food, and if it chances to be a small animal, it will likely be paralyzed by the toxin which is injected by the nematocysts. The prey is then carried to the mouth and tucked into it by the tentacles. Frequently hydra is able to stretch its body over articles of food which are actually larger than the hydra usually is in normal condition. Hydra will eat only when it is hungry and will not react to food at other times. It is more sensible than many people in this respect. On the other hand, it has been authentically reported that a hungry hydra will perform the characteristic feeding movements when only beef extract is in solution in the water. Thus it responds to a chemical stimulus alone, but it will not respond to a mechanical stimulus only.

These animals show response to a number of environmental conditions. Any sudden change is likely to bring about a negative response. 'If the stimulus is of a general nature and of considerable intensity, the animal will contract all of the tentacles and the body also. If the stimulus is restricted to one locality and is not too strong, the animal will contract in the affected area, by the withdrawal of one tentacle.

The common *tropisms,* which have been described previously, are present in hydras. They respond to light and will find an optimum intensity which varies with the different species. Green hydras react positively to sunlight and withstand moderate temperature; hence they are adapted to the Southwest. They likewise possess an optimum for temperature and prefer relatively cool water. As pointed out previously above, both chemotropism and thigmotropism are concerned in food-taking. Contact stimuli are of considerable significance in a sedentary animal like this. It remains attached in contact with some solid body most of the time. Sudden mechanical stimulation like stirring the water or jarring the attachment of the animal will cause it to contract vigorously.

Locomotion is accomplished in at least four ways. *Gliding* from one point to another by partially releasing the basal disc and slipping it to a new location is common. Or the animal may bend over and cling to the substratum by the tentacles, release the basal disc, then draw the body toward this point of the tentacles, where the basal disc

is reattached. This process is consecutively repeated and is called "looping." Occasionally the animal bends over, holds by the tentacles, then turns a "handspring" or "somersault" to attach the basal disc beyond the attachment by the tentacles. The fourth means by which locomotion is effected is by dropping to the bottom, then secreting a bubble of gas at the basal disc and floating back to the top on that.
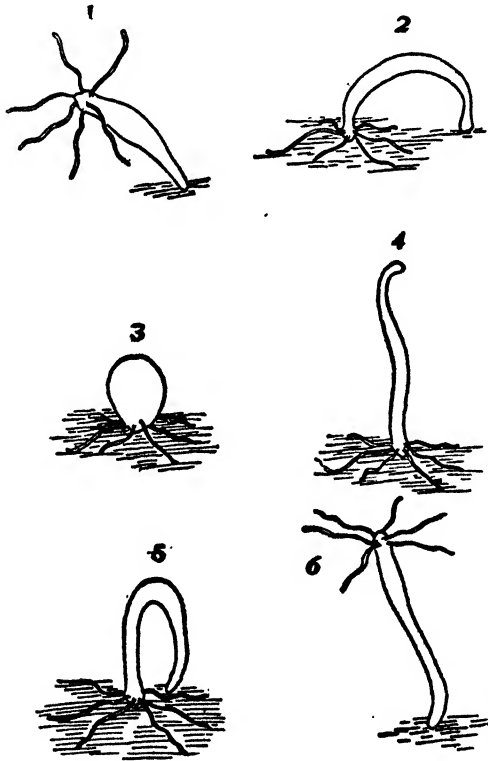
Fig. 110.—Locomotion in hydra. Successive positions taken when progressing by somersaults. (From Jennings, *Behavior of the Lower Organisms*, The Columbia University Press.)

External Anatomy

Hydra is a macroscopic animal, but it is relatively small. Its body is quite contractile, being able to extend from a contracted length of two or three millimeters to a length of eighteen or twenty millimeters. The *column* or body is a tubular, cylindrical trunk which ordinarily stands in a vertical position. In some forms the distal

(free, oral, or anterior) end of the column is much stouter than the proximal (attached, aboral, or posterior) end, but in *H. viridissima* there is only a slight tapering toward the basal end. Attached around the free end of the column is a circlet of from four to seven fingerlike *tentacles,* which extend free in the water. Tentacles may stretch out to be slender threads five to seven centimeters in length. They are very useful either singly or as a group in capturing and delivering food to the mouth. The mouth is located in the center of the distal end of the column and is surrounded by the tentacles. This conical elevation between the bases of the tentacles in which the mouth is located is called the *hypostome.* The mouth when closed and viewed from the top looks something like an asterisk. From the side it appears simply as an indentation or notch in the conical end of the hypostome. The proximal or attached end terminates in a *basal disc* or foot, which secretes an adhesive substance which helps the animal in attaching to objects. From one to several *buds* are often found on the sides of the trunk, and these occasionally bear buds before the first is separated from the original parent. Buds are lateral outgrowths of the column and are found when the animal has favorable living conditions. Budding usually occurs at about the middle of the body in *H. viridissima.* Occasionally there may be observed rounded projections on the side of the column which are seasonal reproductive organs. Both *ovaries* (female gonads) and *testes* (male gonads) may be formed on a single individual, but they are usually seen on separate individuals. If these projections are conical and located nearer the tentacles, they are testes or spermaries; if they are more nearly knoblike and are located nearer the base, they are ovaries. This animal possesses radial symmetry. Sedentary and sessile animals very commonly have radial symmetry, while the motile or free-living organisms tend toward bilateral symmetry.

Internal Anatomy

Another feature of the organization of this animal is the diploblastic structure which consists of two layers of cells or the germ layers surrounding an internal space, the *gastrovascular cavity* or enteron. These are studied on stained sections. The outer one is the *ectoderm,* which is thinner and is composed of four types of cells. The most numerous ones are typically cuboidal in shape and serve both as contractile units and as the general external surface of the

body; they are appropriately called *epitheliomuscular cells*. Each of these cells consists of a polyhedral outer or epithelial portion and a basal portion which is drawn into one or two long, slender *fibrils* extending in a direction parallel to the length of the animal. These cells contract to shorten the length of the animal. Interspersed occasionally among these cells are the larger *cnidoblasts* in which develop the *nematocysts,* stinging cells or nettle cells. These are distributed over all the body except the basal disc, but they are much
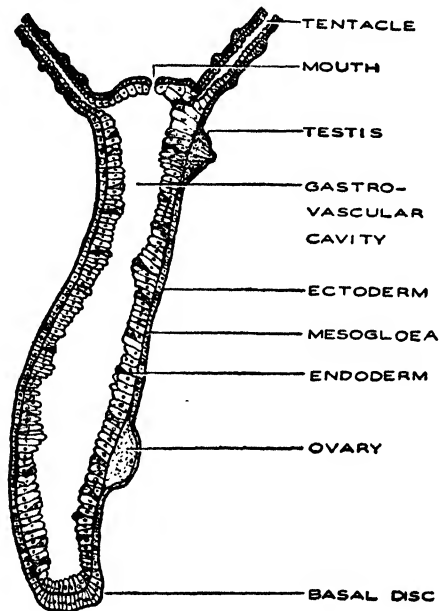
Fig. 111.—Diagrammatic longitudinal section of hydra, showing mature gonads and typical cell layers. (Drawn by Titus C. Evans.)

more numerous near the distal part of the column and on the tentacles. The nematocysts are usually contained in little raised tubercles in the ectoderm. Each tubercle contains a large barbed one and several of a smaller variety. Four different kinds have been described. Since the *large* barbed type is the most conspicuous, it will be described here. Within the cnidoblast it is principally a sac of fluid within which is inverted a stalk with some barbs and a coiled thread attached. Projecting out of the superficial surface of the cnidoblast is a triggerlike process called the cnidocil, which when chemically stimulated causes the cnidoblast to discharge the nemato-

cyst. Chemicals, such as weak iodine, acetic acid, or methyl green, when added to the water, will bring this about. Contact will not. In this reaction the stalk and thread are everted, probably by development of pressure. This type of nematocyst produces a *hypnotoxin* which anesthetizes the animals into which it is discharged. In another form the sac is small, the stalk is barbless, and the thread is elastic; it becomes coiled around the object against which it is discharged, and thus impedes locomotion of the victim.
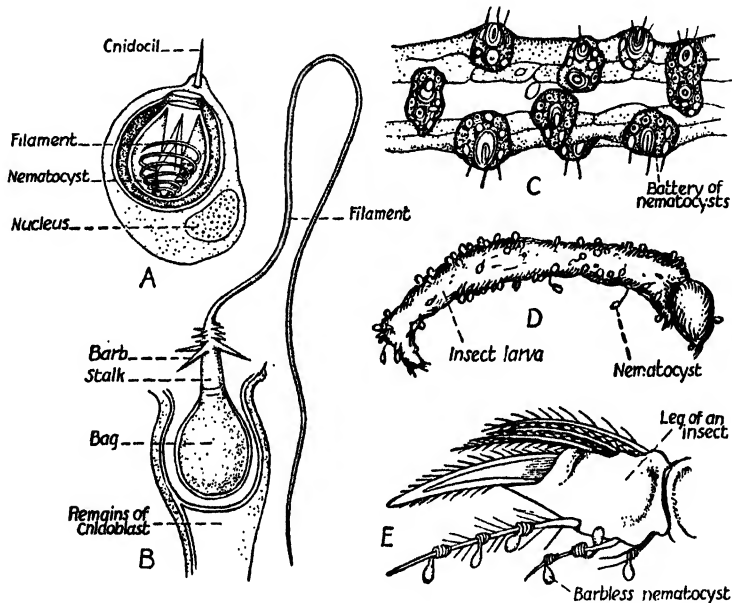
Fig. 112.—Nematocysts and their function. *A,* Cnidoblast containing an undischarged nematocyst, after Schneider; *B,* nematocyst everted and extended but still held in the cnidoblast, after Schneider; *C,* portion of tentacle, after Jennings; *D,* insect larva attacked by hydra, after Jennings; *E,* leg of small aquatic insect with barbless nematocysts on its spines, after Toppe. (Redrawn and modified from Wolcott, *Animal Biology,* McGraw-Hill Book Company, Inc.)

The cnidoblasts are produced by a third type of cell, the *interstitial cell,* which is small and rounded. These are formative cells about the size of the nuclei of the epitheliomuscular cells and quite densely granular in nature. They crowd in between the other cells, especially near their bases. As a nematocyst is discharged, the entire cnidoblast is replaced by an interstitial cell migrating into position. A damaged or spent cell of the body may be replaced from the interstitial cell. Besides these three types, there are the scattered, ir-

regular, slender, neuro-epithelial cells which are joined into a net by intercellular processes. These cells fit between the others and are either sensory or motor in function thus receiving external stimuli and also causing contraction of the contractile cells at proper times.

Beneath the ectoderm and embedding the bases of the cells is a very thin layer of noncellular substance called *mesogloea*. It is produced by the cell layers and serves as attachment for them, particularly for the fibrils of the epitheliomuscular cells. In some of the other coelenterates, this layer is exceedingly thick and heavy.
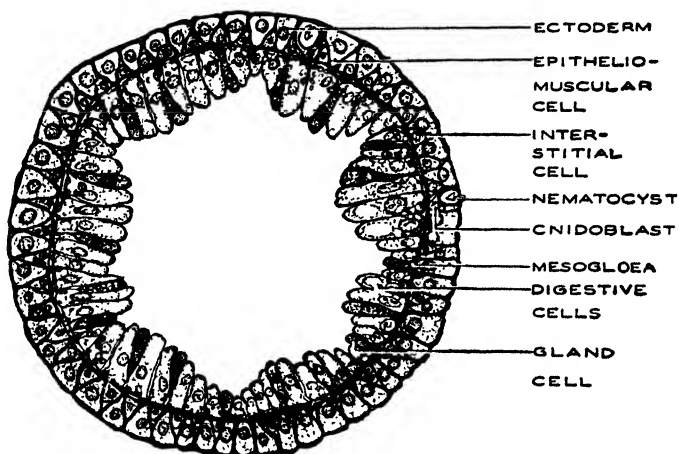
Fig. 113.—Cross section through the column of hydra. The central space is the gastrovascular cavity. (Drawn by Titus C. Evans.)

The inner, thicker cell layer of the wall is the *endoderm* which lines the lumen of the gastrovascular cavity. The most conspicuous cells here are the *nutritive-muscular cells* which are long, vacuolated structures attached to the mesogloea by fibrils which extend in it parallel to the circumference of the animal. By contraction these cells increase the length of the animal by reducing its circumference. These cells often possess flagella at the free margin and at times engulf particles of partially digested food like an amoeba. It is seen then, that they serve both as muscles and as digestive cells. Glandular cells are also present in this layer. Being slender, they wedge themselves between the nutritive-muscular cells and secrete what is probably a digestive fluid into the gastrovascular cavity. Neuroepithelial and interstitial cells are also interspersed among the

other cells of this layer. The general morphology of the adult animal is very similar to the gastrula stage of the developing embryo of more complex metazoans.

Metabolism

The food of hydra consists of small insect larvae, minute worms, small bits of organic matter in the water, water fleas, and other small crustacea. *Ingestion* of the food has been described already. Upon entering the mouth the morsel of food is moved some distance down in the cavity by successive wavelike contractions of the column progressing from distal to proximal. Such serial contractions are usually called *peristaltic contractions*. Here in the upper half of the enteron digestion takes place. The wall possesses many more of the gland cells in the endoderm, and the food material disintegrates into smaller particles here in this region. The digestion which occurs here is spoken of as *intercellular digestion* and is brought about by enzymes produced by the secreting cells of the endoderm. The dissolution of the food by the enzymes is augmented by the churning effect of the contractions of the body. The flagella present on the nutritive-muscular cells create currents of water which also hurry the process. The dissolved material is presumably *adsorbed* by the cells of the endoderm, and by diffusion the nutrient solution reaches the ectoderm cells just outside. Small particles of the partially digested substance are engulfed by the free ends of many of the nutritive-muscular cells by virtue of their *amoeboid activity*. These particles are taken in food vacuoles, and the digestion is completed there just as it is in an amoeba or paramecium. This illustrates something of the primitive organization of Hydra as a metazoan. As will be remembered, this process of converting the digested food into an integral part of the protoplasm is known as *assimilation*. The food is distributed to all parts of the enteron, which extends into the tentacles and buds, by the action of the flagella and by bodily contractions. There is no separate system of transportation or circulation of nutriment. This dissolved material reaches the remote parts of the protoplasm by diffusion through the membranes and protoplasm generally. The gastrovascular cavity has the dual function of digestion and circulation.

Many of the animals used as food have hard skeletal parts that will not digest. These indigestible portions are ejected from the cavity through the mouth by reverse peristalsis, and the process is

known as *egestion*. *Respiration* furnishes the necessary exchange of oxygen and carbon dioxide by diffusion through the plasma membranes. The dissolved oxygen in the water in which the animal lives is the source of this element.

Catabolism or dissimilation takes place in the protoplasm and involves the union of oxygen with the substance of the protoplasm to transform potential energy there to kinetic energy and heat. Accompanying this oxidation there are produced several waste by-products in solution including urea, uric acid, and water which must be expelled from the body. In Hydra this *excretion* is accomplished by diffusion through the general surface of the body. There is some indication that there may be accumulation of waste products in endoderm cells as cytoplasmic granules, which finally escape through the gastrovascular cavity and mouth. It will be noticed that these phases of metabolism are, in general, very similar to the comparable processes in Protozoa and the same similarity will be noticed when they are compared later with the higher forms of animals, because the protoplasmic requirements are the same in all animals.

The Nervous System and Nervous Conduction

The *neuro-epithelial* cells are distributed among the other cells of the germ layers. There is a greater abundance of them on the hypostome, basal disc, and tentacles than along the length of the column. The greatest concentration of these cells is in the hypostome around the mouth, which makes this region in a sense comparable to a primitive brain. These cells all over the body are in contact with each other by means of their processes forming what is called a *nerve net*. When one sensory cell is stimulated, all of the sensory cells seem to be stimulated in some degree. A sufficiently strong stimulus affecting any sensitive point will stimulate the entire body. This is a definite organized type of nervous system but not a very efficient one.

Reproduction and Life Cycle

Reproduction is both *asexual* and *sexual*. **Asexual reproduction** is accomplished very efficiently and quite rapidly. This process is essentially reproduction by somatic cell division. The bud first appears as a slight superficial bulge. The cell division at this point is very rapid, involving considerable activity in interstitial cells. An

extension of the enteron extends into the bud, which is essentially an outgrowth of the body wall. Tentacles appear as outpushings of ectoderm and endoderm, and in the terminal position a mouth is developed. After the bud has attained some size, a constriction occurs between it and the parent, finally separating the two to form a free individual.

Sexual Reproduction.—During the summer and fall particularly, hydra reproduces sexually. This involves the production, maturation, and union of germ cells. Testes may appear first and ovaries later on the same individual or both gonads may be present at the

Hydra – Budding

Hydra – Sexual Reproduction
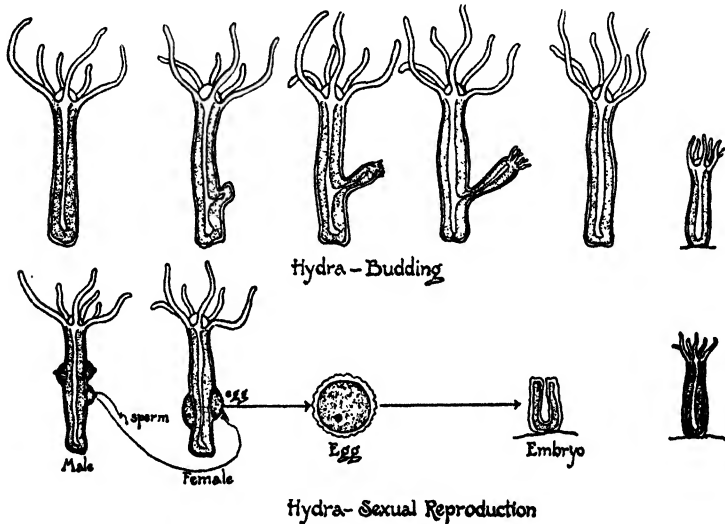
Fig. 114.—Methods of reproduction in hydra. (Courtesy of General Biological Supply House.)

same time in which case self-fertilization is possible. As a rule, these animals are *hermaphroditic* or *monoecious* as suggested before, but it has been reported that individuals of separate sex *(dioecious)* have been found. The germ cells or *gametes* develop from interstitial cells which accumulate at a certain place between the ectoderm and endoderm, where they multiply by division to form oögonia in the female gonad and spermatogonia in the male. All phases of maturation (gametogenesis) may be observed in the testis and ovary. The testis produces large numbers of motile spermatozoa, which when mature emerge periodically from an opening in the tip of the testis and are discharged free in the water. In the ovary a single egg

develops at the expense of the other oögonia, which are engulfed bodily and used for food. This one cell grows rapidly, and when mature it fills the ovary. Fertilization is accomplished by the entrance of spermatozoa through a rupture in the overlying ectoderm and cross-fertilization usually prevails. A single sperm unites with the mature ovum, and this zygote undergoes the total and equal divisions of cleavage here in place. The process continues until a hollow *blastula* of many cells is formed. Then follows the formation of the *gastrula* by a shedding of cells into the cavity (blastocoele)
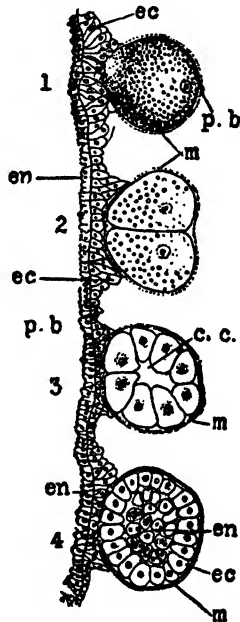
Fig. 115.—Development of hydra. *1*, Fertilized ovum; *2*, two-cell stage; *3*, blastula stage; *4*, gastrula, showing ectoderm (*ec*) and endoderm (*en*); *cc*, cleavage cavity (blastocoele); *m*, cyst; *p.b.*, polar bodies. (After Tanreuther, Biological Bulletin. Vol. 14.)

from the inside of the original layer of cells. These new cells on the inside become organized as an *endoderm* layer, while the original outer layer is now known as *ectoderm*. Further changes involve the secretion of the thin mesogloea which seals the two layers together. In the meanwhile a shell is produced about the outer surface of the embryo, and this encysted body falls from the parent to the bottom. If conditions are favorable for development, it increases in length within the cyst; when it has attained some size it breaks out, after

which tentacles and a mouth appear at one end, while the enteron develops within the endoderm. This individual steadily grows and soon attains adult condition. When the zygote is formed in the fall, the embryo does not emerge from the cyst until spring.

Regeneration

As is the case in many invertebrate and a few vertebrate animals, Hydra is able to replace mutilated parts or an entire animal from a portion of one. Complete animals may be formed from very small pieces (⅛ mm. in diameter) of a hydra. This process is known as *regeneration,* and while it is not normally a method of reproduction or multiplication, it is of great advantage to the animal. This phenomenon was first discovered in animals from studies on Hydra in 1744 by Trembly.

Economic Relations of the Phylum

The entire group is not worth much in dollars and cents to man directly. A number of different ones are made use of as food by some of the useful fish. The corals are of importance both positively and negatively. Many of them are valuable as ornaments, while the large coral reefs are very costly to navigation of marine waters. Many corals are quarried for building stone, and in some instances they protect the shore from being washed by the waves.

Phylogenetic Advances of Coelenterates

(1) Definite organization of diploblastic condition; (2) well-defined gastrovascular cavity with one opening, the mouth; (3) presence of tentacles with (4) nematocysts or sting-bodies; (5) continuance of sexual reproduction; (6) distinct radial symmetry; and (7) a nerve net.

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CHAPTER XVII

THE FLATWORM, PLANARIA, OF PHYLUM PLATYHELMINTHES

The representatives of Phylum Platyhelminthes (plăt ĭ hĕl mĭn' thēz, broad worm) are usually called flatworms and in many ways show considerable advance over the coelenterates. Some of the species are parasitic, and the remainder of them are free-living. The common fresh-water *Planaria* is an example of the free-living type; while the parasitic flatworms are known as *flukes* or *trematodes* and *tapeworms* or *cestodes*. All of these worms are bilaterally symmetrical and triploblastic. The nervous system in the free-living forms is of the "ladder-type," and centralization is developed. They possess a fairly well-differentiated mesoderm, and along with it have developed some systems of organs. The alimentary cavity functions as a gastrovascular cavity and has only one opening (the mouth) to the exterior. The excretory system is composed of a pair of longitudinal tubules, branch tubules, and *"flame cells."* The gonads are within the body and are connected with the exterior by accessory organs. There are definite muscle cells, and excretory and reproductive systems composed of the new mesoderm layer.

The representatives of the two parasitic classes have, for the most part, quite complex life histories and special adaptations. They are very important economically because of their injury to man and the domesticated animals.

Classification

There are four recognized classes in the group.

Class Turbellaria (tẽr bĕ lā' rĭ ȧ—little stirring).—This class consists of a group of soft-bodied, elongate and usually free-living forms. There are both land and water forms. Four orders (may be combined into three) are known: Acoela, Rhabdocoelida, Tricladida, and Polycladida. *Planaria* and *Stenostomum* are examples.

Class Trematoda (trè mȧ tō' dȧ—having pores).—These animals, commonly called flukes, have no epidermis but a thick nonciliated cuticle. This entire class is parasitic, and the immature stages fre-

quently make use of snails and crabs as hosts for a phase of their life history. This group is divided into only three orders: Monogenea, Digenea, and Aspidocotylea. *Cotylapsis, Paragonimus, Clonorchis, Fasciola* are genera representing the class.

Class Cestoda (sĕs tō' dȧ—girdle form).—This group is also characterized by a heavy cuticular cover, and a long, ribbonlike body divided into sections called proglottides.

These tapeworms each have a knoblike "head" or *scolex* on the anterior proglottid. This structure is supplied with suckers for attachment and sometimes has hooks. There is no alimentary tract, and the group is parasitic. A developmental stage of the life history is the bladder worm or cysticercus which lives embedded in the muscular tissue of several different animals. The class includes four orders: Bothriocephaloidea, Cyclophyllidea, Tetraphyllidea, Trypanorhyncha. *Taenia, Diphyllobothrium, Hymenolepsis* are examples.

Class Nemertina.—It seems difficult to know where to classify this group since some systematists give it the rank of phylum while others give it lower ranking. The Nemertinea (nĕm ĕr tĭn' ē ȧ— unerring) as individuals, are unsegmented "band worms." Most of them are free living and marine. A long *proboscis,* the *newly developed blood vascular system,* the alimentary canal, two apertures, and cilia over the body are all characteristic of this type. There are present a mesoderm, nervous system, and excretory system, but there seems to be no coelom. The animals feed on the bodies of other animals and on certain types of general organic matter. They usually live in burrows in sand or mud or beneath solid objects. The larger ones reach a length of ninety feet. The animals are frequently brightly colored. There are numerous mucus glands in the skin which may produce a tubelike dwelling for the worm. The larva is usually called *pilidium. Prostonia, Cerebratulus, Tetrastema* are representatives.

Habitat and Behavior of Planaria

This free-living, fresh-water, flatworm thrives beneath the rocks, logs, leaves, algae, or debris at the bottom of shallow spring-fed brooks and pools. They must have pure, clear, cool water. These animals are rather gregarious and when at rest will group together beneath objects where the light is not intense. They respond negatively to bright light. They usually feed upon minute plants and

animals, dead animal bodies, and living forms, such as small arthropods and molluscs. Planaria partially encompasses the food with the body, while the pharynx is protruded to eat it. If tiny scraps of meat are placed in a dish with hungry planarians, they will form a wad of living protoplasm about it. The mouth is located at the middle of the ventral side of the body, and the pharynx is everted through it as a *proboscis* which is used to draw food within. It is interesting to watch these animals passing the proboscis about over the surface of fresh meat, apparently sucking up the nourishing fluids from the meat. If very minute quantities of meat juice are liberated in the water at specific points, the planarians are attracted to those points.

The locomotion is accomplished in an easy gliding fashion by the action of the beating cilia and muscular contractions of the body. The ability to move along in this way is enhanced by the secretion of slippery mucus which essentially lays a smooth track for the
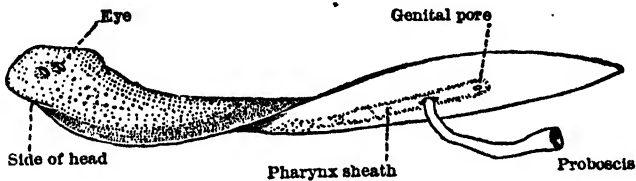
Fig. 116.—Entire planaria with pharynx extended in position for feeding. (From Hegner, *College Zoology,* The Macmillan Company, after Shipley and McBride.)

moving animal. It glides over a surface, even the under side of the surface film of water, and adjusts itself easily to any irregularities because of the soft, flexible nature of the body. The ciliary action and muscular contractions are both rhythmic and progress in waves from anterior to posterior.

The behavior of this animal is of a *reflex* or automatic type. The receiving or *receptor* sensory cell transfers the impulse produced by a stimulus to a ganglion cell or *adjustor* in the central nervous system which in turn transmits an impulse to an *efferent* cell carrying it to a muscle or gland. The planarians respond to several tropisms. They possess negative *phototropism* and *thermotropism* (as regards high temperatures). They react positively to contact *(thigmotropism)* and water currents *(rheotropism)*. The responses to chemicals are positive in case of food juices and the like; while they are negative to alkalies, acids, strong salts, alcohol, etc. The common species are *Planaria maculata, P. agilis,* and *P. dorotocephala.*

External Anatomy

The body is elongated, flat, broadly wedge-shaped at the anterior and tapering to a point at the posterior end. It is *triploblastic* since the ectoderm, endoderm, and mesoderm are all differentiated and present in a clear-cut fashion for the first time in our studies so far. The symmetry is distinctly *bilateral*. In *Planaria maculata* there is considerable pigment in the skin; while in *Dendrocoelum lacteum* there is much less. On the dorsal side of the anterior region are two pigment bodies called *eyespots* which are sensitive to light. At each side of the "head" region is a pointed, sensitive extension of the epidermis in the form of a lappet or "ear," called an *auricle*. These are sensitive to touch and chemical stimulations but not to sound. The mouth is located in the midventral portion of the body. The *pharynx* may be protruded through the mouth in the form of a long, trunklike *proboscis* which is used in feeding. Posterior to the mouth is a small, constricted, scarlike aperture, the *genital pore*. Externally the epidermal cells are soft and the general surface is nearly covered with patches of *cilia* which are cytoplasmic extensions of these cells. These cilia along with muscular contractions accomplish *locomotion*. The average length of fully developed active *P. maculata* is about three-fourths of an inch.

Internal Anatomy

The ectoderm covers the outer surfaces of the body and composes the nervous system; the endoderm lines the intestine and its branches; while the mesoderm constitutes the muscular, excretory, and reproductive systems. The undifferentiated mesoderm lying outside the intestine is composed of a meshwork of large cells and is called *mesenchyme* or *parenchyma*. Many of the structures of the animal, which have been observed in none of the forms previously studied, have come into existence with the development of mesoderm.

The **digestive system** is composed of a *mouth* in the midventral position; a prehensile *pharynx* held in the pharyngeal chamber or buccal cavity which it nearly fills; a three-branched *enteron* or intestine, which branches immediately from the anterior end of the pharynx into an anterior trunk; and two lateral trunks that turn posteriorly, one along each side of the pharynx, and extend nearly to the posterior end. The pharynx is in the form of a cylindrical fold

projecting through the full length of the pharyngeal chamber. It is attached only at its proximal or anterior end and is perfectly free otherwise. When it is extended or protruded through the mouth opening which it fills, it forms a *proboscis* whose length may be as great as, or greater than, that of the entire body. The trunks of the
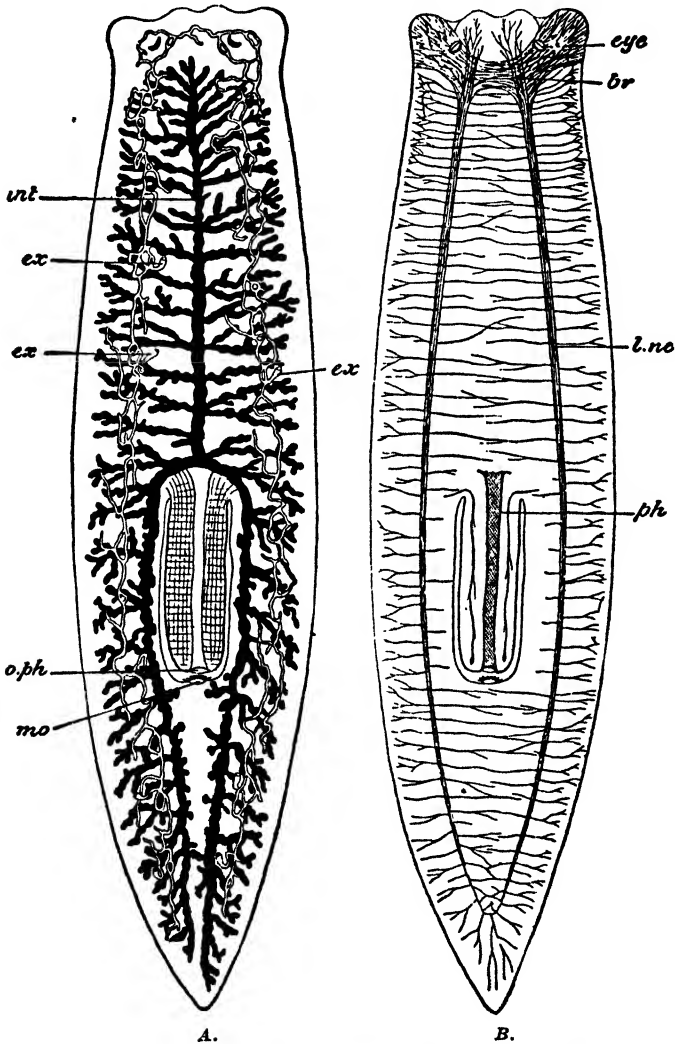
Fig. 117.—Structure of planaria. *A*, Digestive and excretory systems; *B*, nervous system; *br*, cephalic ganglia (brain); *ex*, excretory pore; *int*, intestine; *l.ne*, longitudinal nerve; *mo*, mouth; *o.ph*, opening of pharynx; *ph*, pharynx. (From Parker and Haswell, *Textbook of Zoology*, The Macmillan Company.)

enteron have many lateral, blind extensions or pockets called *diverticula* which greatly increase the surface exposure of the organ and project among most of the other tissues of the body. The whole arrangement represents a complicated *gastrovascular cavity* whose wall is endodermal.

The excretory system is new to our study and is composed of a set of tubules which relate themselves to all parts of the body. There are two principal, longitudinal, coiled tubules, one along each side of the body, which receive many small branches and open by minute pores located just posterior to the eyespots, and by several other pores along the length. All of the smaller branch-tubules have at their blind ends a *flame cell* which is hollow and contains a mass of
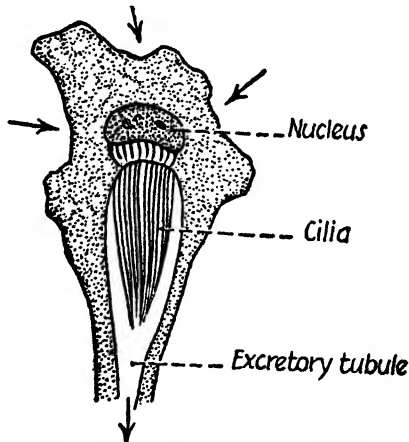
Fig. 118.—Flame cell of planaria.

long cilia that are continually beating in a direction toward the tubule, the movements appearing something like a flickering flame. The cellular walls of the tubules as well as the flame cells arise in the mesoderm. Under strict definition, some authors object to calling this arrangement a system.

Another mesoderm organization is the muscular system. It is composed of an outer *circular* layer just under the epidermis; an outer longitudinal layer just medial to the circular layer; *oblique* bundles of fibers; and at the medial margin of the mesoderm is another irregular, internal, longitudinal layer just medial to a circular layer. By the alternate activity of these layers the animal is capable of great extension and contraction,

Another advanced development is the "ladderlike" **nervous system** which consists of two contiguous lobes of nerve cells just ventral to the eyespots, two ventrolateral *longitudinal nerve cords, transverse commissures, branch nerves,* and *sensory end areas* of the epidermis. The double ganglion at the anterior is the central portion of the system. It is known as the *cephalic ganglion* and gives branches to sensory areas of the head, auricles, etc., besides joining the longitudinal nerve cords. The transverse commissures connect the two longitudinal cords at from 15 to 20 points like the rungs of a ladder. At each point where a transverse commissure meets a longitudinal cord, is a small ganglion composed of a few nerve cell bodies. The branch nerves extend to the surrounding tissue from these points.

The **reproductive system is** fairly well developed in most species except *P. dorotocephala* which rarely develops sexual organs. Its reproduction is entirely by asexual fission. The sexual reproduction of other planarians is hermaphroditic, which is rather characteristic of sedentary animals. The male organs consist of numerous globular *testes* located in the parenchyma through most of the length of the body. Vasa efferentia are slender, thin-walled ducts leading from the testes to two larger, longitudinal ducts, the *vasa deferentia.* These in turn lead posteriorly, enlarge to become seminal vesicles, and converge to form the *penis* or *cirrus,* the copulatory organ. This opens into the common cavity called the *genital atrium* or *genital cloaca,* which opens externally at the genital pore. Some authors describe glands which pour a seminal fluid into the system. The female organs in the same animal consist of two ovaries located well toward the anterior, a tubular oviduct leading posteriorly from each to join the genital atrium at a common point near its posterior end by way of the *vagina.* There are numerous *yolk glands* joining each oviduct along its length; a glandular structure of questionable function, in the form of a blind tube with an inflated end, is connected with the genital atrium. It has been suggested that the fertilized eggs accumulate and are retained here for a time. The system is notably quite elaborate, and it is found generally that the flatworms have a highly specialized reproductive system.

The planarian worms and the representatives of this phylum possess no skeletal system, no respiratory system (it breathes through its skin); no coelom or body cavity; and no circulatory system;

this function, however, is performed by the branched enteron. It is significant that the reproductive system upon which the continuance of the race depends is highly specialized, this succeeded by the digestive system responsible for nourishment of the individual, and this followed by the nervous system which relates the organism to its surroundings.
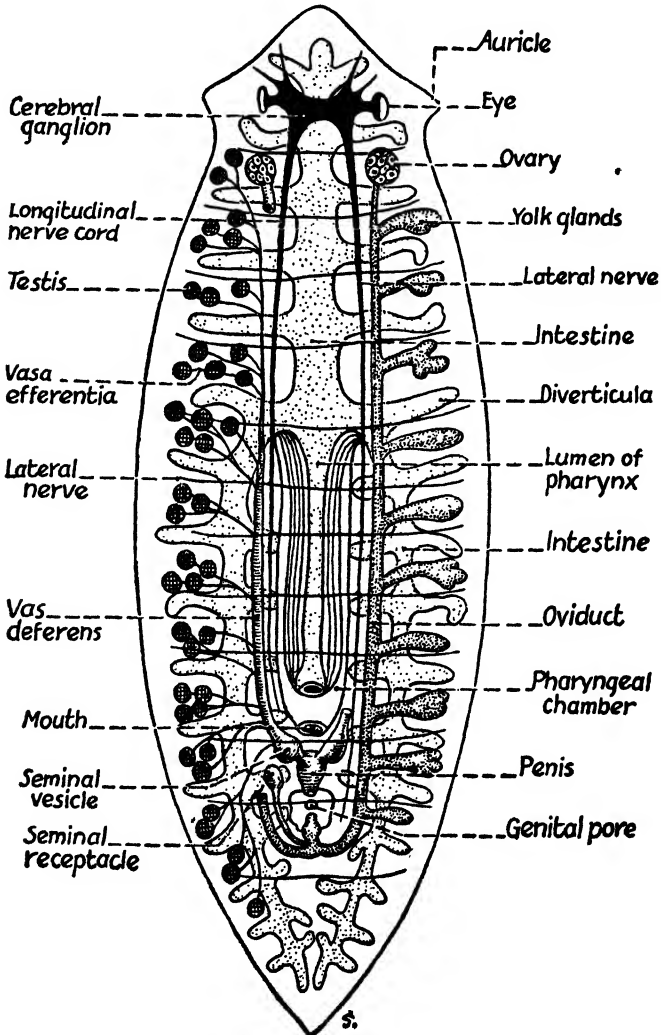
Fig. 119.—Reproductive system of planaria. Male organs are shown on one side only.

Metabolism

The *food* is principally animal tissue with some plant matter, and *ingestion* takes place through the proboscis. The food may be partially digested by a fluid produced in the pharynx. The principal process of *digestion* occurs in the cavity of the enteron. Here the process is similar to that of Porifera and Coelenterata, being both intercellular and intracellular; that is, part of the food in the intestinal cavity is digested by secretions from cells in their walls, while other food particles are engulfed by pseudopodia extended from cells lining the cavity and are digested in food vacuoles inside the cells. *Absorption* and *assimilation* take place through the plasma membranes of adjacent cells. Since the diverticula of this system penetrate all parts of the body, and the diffusion of materials supplies all other cells, no circulatory system is necessary to transport nutriment. There is no anus, so all indigestible material is *egested* by way of the mouth. *Respiration* is accomplished through the general surface epithelium, and oxygen is distributed by diffusion through the protoplasm and fluid-filled spaces of the parenchyma. Catabolism or dissimilation takes place in the cells by union of the oxygen with the organic components of the protoplasm. *Excretion* or elimination of nitrogenous waste liquids is cared for by the flame cells and system of tubules. The flame cells absorb these wastes from the surrounding tissues and force the fluid into the tubules by the action of the cilia.

Reproduction and Life History

Sexually the individuals are hermaphroditic. The spermatozoa or male germ cells mature in the testes, then pass through the vasa efferentia and vasa deferentia, to the seminal vesicles where they are stored in advance of copulation. Here they become organized into pockets known as *spermatophores*. The ova mature in the ovaries, pass down the oviducts where yolk cells or nurse cells are added by the yolk glands, through the vagina to the genital atrium, and probably from here to the uterus or seminal receptacle where they are thought to be stored. *Cross-fertilization* or self-fertilization may occur, due to the fact that both the cirrus and the vagina open by way of the genital atrium. Planarians have been observed to copulate with an apparent exchange of spermatozoa in the form of spermatophores. In copulation the cirrus or penis is protruded through the genital pore and enters the genital pore and on into the

uterus of the other copulant. In this way spermatozoa may be transferred from each animal to the other. Spermatozoa have been found along the oviduct as far as the anterior portion, so fertilization likely occurs somewhere along this tube. At breeding time zygotes are found in the atrium, and each is surrounded by a large number of yolk cells (nurse cells). Each yolk cell contributes its store of nourishment to the egg cell to which it is attached. From one to several *zygotes,* surrounded by many thousands of yolk cells, become enclosed in a capsule-like shell secreted by the genital atrium and known as a *cocoon.* These are expelled from the atrium and each is attached by a stalk to the under sides of submerged stones or vegetation in the water. In the cocoon the embryo passes through cleavage divisions, blastula stage, gastrulation and even later stages before the cocoon ruptures and the small wormlike planarians escape into the water.
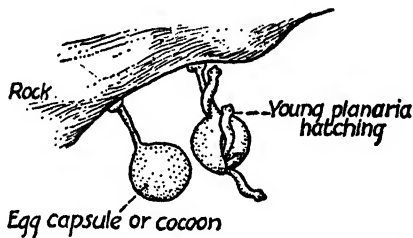
Fig. 120.—Planarian cocoons with young emerging from one.

Asexual reproduction by transverse fission occurs quite frequently when the mature animals become slowed down. The individual constricts and then divides into anterior and posterior portions, each of which forms the missing parts by rapid cell division. The axial orientation of the tissue is retained; i.e., an anterior portion develops in the position of the original anterior portion, and a posterior portion at the original posterior position. This process is not fundamentally different from budding in Hydra or strobilization in the Scyphomedusae.

The retention of the axial orientation during fission has been explained by Dr. Child of Chicago University. The animal possesses a well-defined axial organization in which the "head" portion as usual has the highest metabolic activity of the body. Beginning at the anterior there is a *gradient* of decreasing metabolic activity until a level just posterior to the mouth is reached, and here a sudden increase occurs. Posterior to this the decreasing gradient

again follows to the posterior tip of the body. The level where the metabolic rate suddenly rises represents the point of fission or the anterior end of the second individual. This seems to indicate a kind of zoöid organization in the animal. In larger, older individuals there may be other such points of increased metabolism posterior to this first one. Such zoöids are the result of successive functional isolations of the basal structure accompanying growth in length. This graduation of the rate of metabolism along the principal axis of an axiate animal has been called an *axial gradient (metabolic gradient)* by Dr. Child. When the animal is young, it is

Fig. 121.—Fission in *Planaria dorotocephala.*

relatively short and the entire body, but particularly the "head," carries on a high rate of metabolism. The head at this time holds a dominance over the length of the organism. As the animal grows older, it becomes longer, and the entire metabolic rate decreases. This means that the head loses its dominance over the entire length. A new center of dominance and increased metabolism is established just posterior to the point where this "head" dominance fades out.

Regeneration

This group shows remarkable powers of replacing lost or mutilated parts of the body. It can be cut into several pieces, and each

piece will replace the missing parts about as the process is carried out in fission. A piece from the middle of the animal will regenerate a head portion at the anterior margin and a tail portion at the posterior margin.

Economic Relations of the Phylum

The planarians and other free-living flatworms are of practically no economic importance, but the phylum includes a large number of forms, principally Trematodes and Cestodes, which are parasitic in higher vertebrate animals, including man. Such groups as the intestinal flukes, liver flukes, lung flukes, blood flukes, pork tapeworm, beef tapeworm, margined tapeworm of dog, gid worm, hydatid worm, common tapeworm of dog, chicken tapeworm, dwarf tapeworm, sheep tapeworm, tapeworm of horse, and fish tapeworm are all serious parasites. They cost many thousands of dollars and much debility each year.

Phylogenetic Advances of Platyhelminthes

(1) Anteroposterior principal axis, (2) bilateral symmetry, (3) a distinct third germ layer, the mesoderm, (4) an excretory system of flame cells, (5) central nervous system extending with the axis of the body, (6) specialized gastrovascular cavity, and (7) permanent sexual reproductive organs.

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CHAPTER XVIII

THE ROUNDWORM, ASCARIS, OF PHYLUM NEMATHELMINTHES

This group is known as the unsegmented *roundworms* or thread-worms. Some of the Nemathelminthes (nĕm à thĕl mĭn' thēz, thread-worms) are free-living in soil, fresh water, and salt water; some are found living in plant tissues; and others live in animal tissues as parasites. The majority of them are microscopic, but a few are macroscopic in size. These worms are long, slender animals whose bodies are more or less cylindrical but tapering toward each end. The range of length is from ¼ mm. to four feet. They lack respiratory and circulatory systems, true coelom, and definite locomotor organs. The group is very widely distributed and is deserving of considerable attention. Some of the better known forms are Ascaris (pigworm or eelworm), "horsehair snake," hookworm, pinworm, *Trichinella, Filaria,* Guinea worm, whipworm, and eye worm.

Classification

Three classes are usually recognized in the phylum, although some authors prefer to use only two. The three classes are Nematoda, Gordiacea, and Acanthocephala.

Class Nematoda (nĕm à tō' dà, threadworm) is a group occupying almost every possible habitat capable of supporting life. There are many free-living, fresh water, marine, and soil-inhabiting species, and large numbers of parasitic forms living at the expense of other animals and plants. This is a very important class parasitically. In size they range from ⅒ mm. to more than a meter in length. Locomotor organs are found in a few forms, no segmentation is present, and there is no true coelom.

Order Ascaroidea.—This group includes both parasitic and free-living forms. Ascaris, the common intestinal worm, is the most abundant. *Enterobius vermicularis,* the human pinworm; *Strongyloides stercoralis,* another parasite of man; *Ascaridia lineata,* the chicken worm, and *Toxocara canis* of dogs are other familiar examples. *Ascaris lumbricoides* will be discussed later as a typical example of Nemathelminthes.

Order Strongyloidea.—This is an entirely parasitic group. The males have caudal bursae with rays. The club-shaped esophagus is without a posterior bulb. The hookworms of man, the Strongylus roundworms of horses, and *Syngamus trachea* which causes gapes in birds by obstructing the windpipe, are all common representatives.

Order Filaroidea.—This is a completely parasitic order, modified for living in such tissues as lymph, blood, connective tissue, and
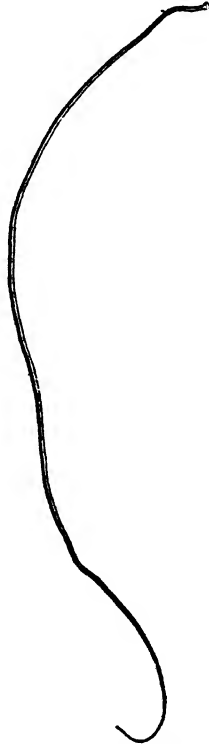
Fig. 122.—Hair "snake," *Gordius,* an aquatic roundworm.

muscle of chordate animals, and transmitted by certain insects. Guinea worm, eye worm, and *Filaria* are the common human parasites. Some species cause elephantiasis through occlusion of blood and lymph vessels. This disease results in enormous swelling of the affected parts. These organisms are transmitted by mosquitoes. Several Filaroidea are parasites of horses and dogs.

Order Dioctophymoidea.—This is another parasitic group living in the kidneys, body cavity, and alimentary canal of mammals and

birds. The genus *Dioctophyme* includes the largest roundworms, some reaching more than three feet in length.

Order Trichinelloidea.—This parasitic group has a peculiar cuticle lining the esophagus, outside of which is a single layer of epithelial cells. The common trichina and the whipworm are well-known examples.

Class Gordiacea (gôr dĭ ā' shē ȧ, a knot).—Superficially these animals resemble the nematodes, but the fundamental structure is quite different, and therefore, it is likely proper to give them the rank of a class. They are free-living as adults, but as larvae they are parasitic on larval May flies and other insects. They leave this host and take up abode in a terrestrial form like that of grasshoppers or beetles. After complete development the adult "hair snakes" escape into the water of some stream, puddle, or watering trough. These females again lay eggs in the water in long strings. In the adult worm the intestine is a straight tube, often without a mouth, but opening at the posterior end by an anus. Some have no intestine at all. The outer surface of the body is covered by a cuticle. The body is cylindrical and without lateral lines, excretory organs, or circulatory system. *Gordius aquaticus* and *Paragordius varius* are the common examples of the group.

Class Acanthocephala (ȧ kăn thŏ sĕf' ȧ lȧ, thorn head) includes a group, known as "spiny-headed worms," which is absolutely parasitic in its habits. The adults are from a few millimeters to fifty millimeters in length and have an elongated, flattened body when found in the intestine of a vertebrate but become distended to a cylindrical shape when removed to some solution outside the body. The protrusible *proboscis* is a peculiar and characteristic structure located at the anterior end of the body. It bears numerous recurved hooks or spines, and in many species it is capable of receding into a *proboscis receptacle* or *sheath*. There is no digestive tract in this parasite, and its food is absorbed through the surface of the body even though it is covered with a cuticle. A single ganglionic mass constitutes the central nervous system

Habitat and Behavior of Ascaris

Ascaris lumbricoides frequents the digestive tract of men and hogs. It is entirely dependent on its host for furnishing suitable food and environment. The only time this organism is at the mercy of the

elements of nature is during the egg stage, when it may remain potent for months or even years if it falls in an environment unsuitable for development.

External Anatomy

This is one of the largest nematodes, females commonly reaching a length of from eight to fourteen inches and males averaging six
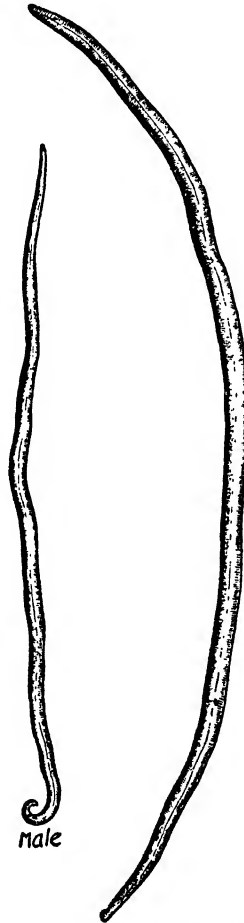
Fig. 123.—External anatomy of *Ascaris lumbricoides*, male and female.

to twelve inches. Males are always more slender and have a curled tail instead of the blunt tail of the female. The mouth is guarded by three lips, two in lateroventral positions and one dorsal. These

lips have small papillae on their surfaces, two on the dorsal and one on each of the ventral. The shape of the body is generally cylindrical with tapering ends. The smooth surface is marked by four longitudinal lines, two lateral, one dorsal, and one ventral. The *genital pore* in the female is located on the ventral midline approximately one-third of the length of the body from the anterior extremity. The *anus* is located near the posterior tip of the body, and in the male the reproductive aperture and two *penial setae* or *spicules* are located just within this opening.

Internal Anatomy

The body wall is composed of the thin, outer, smooth cuticle, the epidermis, whose cells run together, and a thick layer of longitudinal muscle fibers, whose medial margins are rather baggy. There are thickenings of the epidermis in the positions of the longitudinal lines. The *excretory* tubes follow the lateral lines. The body cavity of this animal is a *primitive* or *false coelom* which is lined externally by the mesoderm of the body wall and internally by the endoderm of the intestinal wall. Ordinarily the coelom, when fully developed, is lined both laterally and medially with mesodermic peritoneum. This is the simplest type of animal in which the body cavity or coelom is found. In higher forms the outer coat of the intestine is mesodermic. The *alimentary canal* is quite straight and simple and lies in the dorsal part of the body cavity. There is no need for great specialization of the digestive system since the food is taken from the digested material in the intestine of the host. A contractile pharynx, which acts as a pump, draws fluid into the long epithelial intestine from which it is absorbed by the other tissues. The narrowed posterior portion is the *rectum* and leads to the *anus* at the posterior portion of the body. The two laterally located, longitudinal ducts open externally by a single pore near the anterior end of the body. There is a nerve ring around the pharynx which gives off a large dorsal longitudinal nerve and a large ventral longitudinal nerve. There are usually four other smaller longitudinal nerves and some connectives. In the males the *testis* is a threadlike structure which is much coiled in the cavity. This tube enlarges posteriorly to become the *vas deferens* which in turn enlarges still more before reaching the aperture to become the *ejaculatory duct*.

In the female the threadlike ovaries join the coiled oviducts which lead forward and join the two *uteri*. These tubes join in the *vagina*, which is a short tube leading to the *genital pore*.
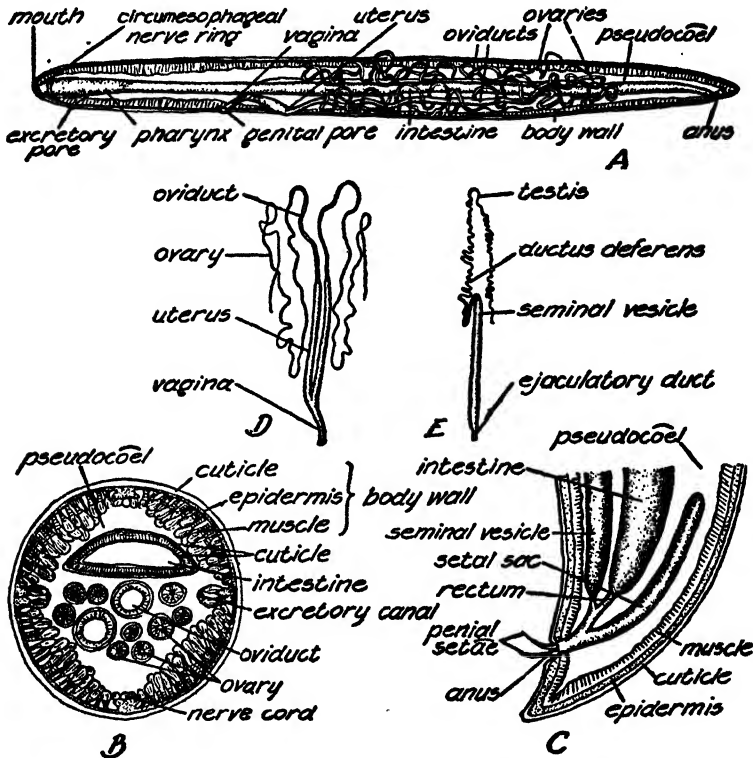
Fig. 124.—Internal anatomy of *Ascaris lumbricoides*. *A*, Diagram showing lateral view of dissection of female; *B*, cross section through the mid-region of the body of the female; *C*, longitudinal section of the posterior portion of the male; *D*, reproductive system of female; *E*, reproductive system of male. (From Curtis and Guthrie, *Textbook of General Zoology*, John Wiley and Sons, Inc., modified from Leuckart.)

Reproduction and the Life Cycle

The animals copulate, and this time the spermatozoa are introduced into the vagina of the female to fertilize the mature ova in the oviducts. A mature female may contain as many as 27,000,000 eggs. These eggs pass from the host with the feces. Some workers have reported that each female worm in an infected host may produce a crop of eggs in excess of two thousand per gram of feces. Based on this figure, the daily production is computed to be some-

thing like 200,000 eggs. These eggs are so resistant that they can be successfully cultured in 1 to 2 per cent formalin, and they may be stored successfully for four years in a refrigerator. The life history is completed only in case the eggs are swallowed by a susceptible host. They hatch in the small intestine of the host and then go on a ten-day journey by way of the blood stream to the liver, thence to the heart, and thence to the lungs. By burrowing out from here, these larvae make their way to the throat, esophagus, and back to the stomach and intestine. After reaching the intestine, the larval worms, 2 to 3 mm. long, grow to maturity in two to two and one-half months. They likely live a little less than a year in the host.

Relations to Man

Heavy infestation in man may cause severe hemorrhages and set up pneumonia that is often fatal. Anemia is often the result of such infection; in certain cases the organisms may even tangle in masses and block the intestine until surgical operation is necessary to remove them. The toxic substances from these parasites may bring on coma, convulsions, delirium, nervousness, and other similar symptoms. Drugs like chenopodium, santonin, and hexylresorcinol have been used successfully under physicians' directions as a cure. Effective sanitary disposal of fecal material is the most successful preventive.

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CHAPTER XIX

EARTHWORM, OF PHYLUM ANNELIDA
(By J. Teague Self, University of Oklahoma)

The Phylum Annelida (ă nĕl' ĭ dȧ, form of a little ring) comprises an extremely large group of worms characterized by (1) the presence of a coelom surrounded by two layers of muscle, (2) metameres or segments, (3) a ventrally located segmental nervous system, (4) segmented, nonjointed, chitinous appendages in most cases, (5) an excretory system composed of nephridia, and (6) a nonchitinous cuticle covering the body. These worms are found in almost every type of free-living habitat where moisture is present. There are many forms which live in the ocean, either swimming freely, burrowing in the sand, or living in especially prepared tubes. Fresh-water streams and ponds are inhabited by numerous forms of annelids, and moist soil is usually alive with terrestrial earthworms. From this it is evident that the phylum as a group has become adapted to many varied living conditions and comprises one of the large groups of the animal kingdom from the standpoint of numbers. In the process of adaptation the annelids have become diversified in their anatomical features until only a very few characters, such as those mentioned in the beginning of this chapter, are common to the entire phylum. Even then, these distinguishing features are sometimes modified until only an expert can recognize them.

The Phylum Annelida may be divided into four classes:

Class   I.   Chaetopoda
             Order 1. Polychaeta
             Order 2. Oligochaeta
Class II. Archiannelida
Class III. Hirudinea
Class IV. Gephyrea
             Order 1. Echiuroidea
             Order 2. Sipunculoidea

Class Chaetopoda (kĕ tŏp' ó dȧ, hair and foot).—This class includes the most commonly known forms of the phylum. There are marine, fresh-water, and terrestrial forms; and they all possess *setae*

(chaetae), or bristlelike appendages on the body segments. The *setae* are chitinous and are embedded in pits of the integument. They bear muscle attachments which make them movable and therefore useful in locomotion. The coelom, which surrounds the straight digestive tract, is divided between the segments by partitions known as *septae*. Typically, each coelomic space possesses a pair of nephridial tubules which communicate with the coelom at one end by means of a ciliated, funnellike opening, the *nephrostome*. The other end opens to the outside by means of a *nephridiopore*. The *nephridia* remove nitrogenous waste materials from the coelomic cavities and from the blood.

The inner body wall of each segment is made up of an inner longitudinal layer and an outer circular layer of muscle. Segmental nerves which are derived from segmental nerve ganglia innervate the metameres and coordinate the movements of the body. The segmental ganglia communicate with each other through connections extending from one segment to the other. At the anterior end is the brain, which is composed of a supra-pharyngeal and a subpharyngeal ganglion joined together by a pair of commissures. The brain, however, has little to do with the coordination of different parts of intersegmental and intrasegmental reflexes, so that the stimulation in one segment automatically stimulates the adjoining ones. Reactions which require immediate coordination of the whole body are controlled by three giant nerve fibers which run through the entire length of the nerve chain. The primary function of the suprapharyngeal and subpharyngeal ganglia is to relay sensory impulses.

The principal vessels of the circulatory system are a dorsal one, through which the blood moves forward, and a ventral one, through which the blood moves posteriorly. These are connected in the anterior region of the body by a varying number of paired, segmental hearts or connectives. The dorsal vessel exhibits wavelike contractile movements (peristaltic contractions) which force the blood anteriorly. The latter passes through the hearts, which also pulsate, then backward through the ventral vessel to the skin, intestine, and other organs. Hemoglobin is suspended in the blood plasma of some Chaetopoda; in others, a green pigment known as chlorocruorin is found; in still others no known blood pigment occurs. The principal vessels and hearts have valves on their inner surfaces which prevent the blood from flowing in the opposite direction.

The class Chaetopoda may be divided into two orders; namely, (1) the Polychaeta and (2) the Oligochaeta.

Order Polychaeta.—The polychaetes (many bristles) are typically marine Chaetopoda. One of the most widely known forms of this group is *Nereis virens* or the clamworm. It possesses many *setae* (chaetae) located in fleshy *parapodia.* In this case the parapodia with their setae constitute the segmented appendages. The parapodia are used principally as locomotor and respiratory organs.

The head of *Nereis* seems to have resulted from the fusion and specialization of the anterior segments. It is composed of a *prostomium,* which bears a pair of *tentacles,* a pair of *palps,* and two pairs of *eyes.* The *peristomium* constitutes the first segment and bears four pair of *cirri* or *tentacles.* The *pharynx* is equipped with muscles by which it can be everted, and a pair of *chitinous jaws* which protrude when the pharynx is extended. The jaws serve in capturing small organisms and crushing anything which is to be swallowed. The succeeding segments are all alike except the posterior one which bears a pair of ventral *cirri* extending posteriorly.

The circulatory system is composed principally of a *dorsal* and a *ventral blood vessel* joined in each segment by a pair of connecting vessels. The blood is forced anteriorly through the dorsal vessel and passes posteriorly through the ventral one. Its movement is effected by wavelike contractions in the walls of the dorsal vessel.

Each segment of the body except the peristomium has two nephridia (excretory tubules) opening directly from the *coelom* to the outside. The nephridia serve to convey the excretory products to the outside. The sexes are separate and there are *gonads* in all the segments except those in the anterior end of the body. The *sex cells* arise from the walls of the coelom and when ripe pass to the outside, fertilization taking place in the water. The fertilized egg develops into a *trochophore larva,* which metamorphoses into the adult animal.

In the central nervous system there are two *suprapharyngeal ganglia* dorsal to the pharynx. These are connected by means of *commissures* to the *subpharyngeal ganglion* ventral to the pharynx. A nerve chain, composed of *segmental ganglia* joined by intersegmental connections, extends posteriorly on the ventral side of the body to the anal segment. *Lateral nerves* from the ventral nerve chain innervate the various organs of the worm.

Order Oligochaeta.—The best known example of the order Oligochaeta is *Lumbricus terrestris,* the common earthworm, which is used

almost universally as a laboratory specimen. Lumbricus is not as common in the Southwest as are other large forms of earthworms, but is used here as an example because it is so well known and because its features represent so well those common to the entire order.

External Anatomy of the Earthworm

The body of *Lumbricus* varies from six to fourteen inches in length and gives the appearance of a series of rings joined in a
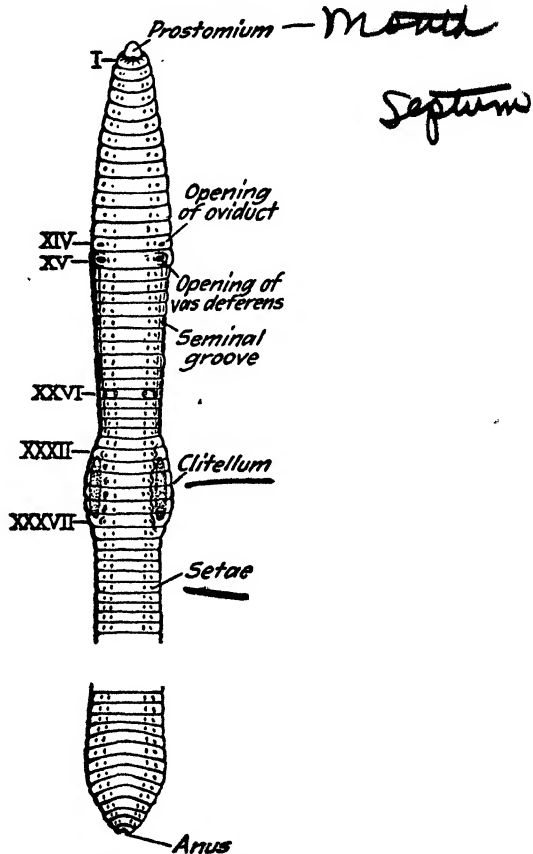
Fig. 125.—External anatomy of earthworm, ventral view, segments numbered in Roman numerals. (From Wolcott, *Animal Biology*, McGraw-Hill Book Company, Inc.)

linear arrangement. The rings are the body segments, or metameres, and vary in number up to 150. In the adult the number of segments from the anterior end to the posterior end of the *clitellum*

remains constant, while the number posterior to this varies. This is because growth is accomplished by the addition of segments posterior to the clitellum.

The peristomium is a sort of knoblike lobe at the anterior end, projecting out over the mouth. It is not considered a true metamere. The first segment is incomplete due to the opening of the mouth through its ventral side. The openings of the oviducts through which the eggs pass to the outside are seen as minute pores, one on each side of segment XIV. The pores of the seminal receptacles occur in pairs, one pair in the groove between segments IX and X, and one between X and XI. The openings of the vasa deferentia (sperm ducts), which convey sperms to the outside, are located, one on each side, in the anterior part of segment XV. In sexually mature worms, segments XXX, XXXI, or XXXII to segment XXXVII are swollen to form the *clitellum*, a sort of saddle-shaped structure, the function of which is to secrete the cocoon in which eggs are deposited during reproduction.

Each segment, except the first and last, bears four pairs of chitinous *setae*, which are fine, stiff bristles. They are moved by protractor and retractor muscles and serve to help the worm move through the soil. A pair of *nephridiopores* (the external openings of nephridia) is situated on the posterior ventral side of each segment except the first two or three.

The body of the earthworm is covered by a thin, transparent *cuticle* which is secreted by the epidermal cells just beneath it. It serves as a protection against physical and chemical injury to the animal's body and as a respiratory membrane.

Internal Anatomy

The body of the earthworm is in the form of a tube within a tube, the digestive tube being the inner one and the body wall the outer one. The space between them is the coelom. The constricted regions dividing the segments on the outside correspond to the positions of the *septae* which divide the coelom into separate segmental compartments. These coelomic divisions communicate with each other by means of pores in the septae so that the clear fluid which fills the coelom can circulate freely. The septae are absent between segments I and II and incomplete between segments III and IV, and XVII and XVIII. The walls of the coelom are lined by a thin layer of cells known as *peritoneum* (mesothelium).

Reproductive Organs

The earthworm is hermaphroditic, the organs of both sexes being present in every animal. The *seminal receptacles, oviducts, and ovaries* are female organs, and the *testes* and *seminal vesicles* are male organs. The seminal vesicles are three pairs of light-colored bodies located in segments IX, XI, and XII. In sexually mature individuals they may extend back through the septae as far as the fifteenth segment. If their contents are examined with a microscope, they
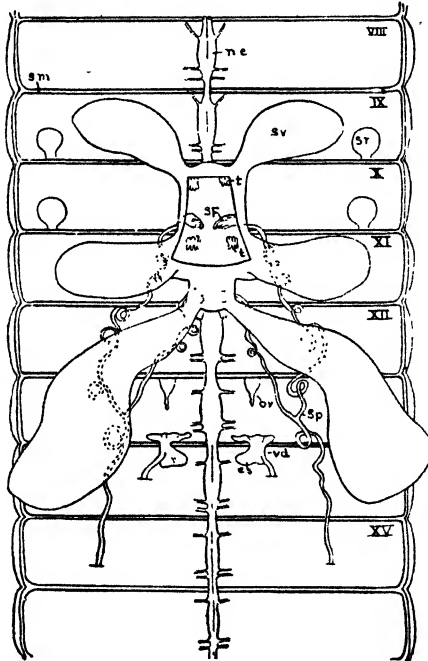
Fig. 126.—Reproductive organs and nervous system in segments VIII to XV of an earthworm. A portion of the seminal vesicles has been removed in segments X and XI to disclose the testes and sperm funnels. *es*, egg sac; *nc*, nerve cord; *ov*, ovary; *SF*, seminal funnel; *sm*, septum between two somites; *Sp*, sperm duct (vas deferens) opening in the fifteenth somite; *sr*, seminal receptacle; *sv*, seminal vesicle; *t*, testis; *vd*, oviduct. (From White, *General Biology*, published by The C. V. Mosby Company.)

are seen to contain the various stages of developing spermatozoa coming from the sperm mother cells. The *testes* are the two pairs of very minute bodies projecting into the seminal vesicles in segments X and XI and cannot be seen without first removing the dorsal part of the seminal vesicles. The union of the vasa efferentia coming from the vesicles on each side forms a single pair of vasa

deferentia in segment XII. The seminal receptacles are pairs of small white bodies located in segments IX and X. The *ovaries* are two minute bodies located one on each side of segment XIII.

Digestive System

The *mouth* cavity extends through segments I to III and leads into the bulbous, muscular *pharynx* which extends through segment V. The pharynx plays the part of a sucker in securing food for
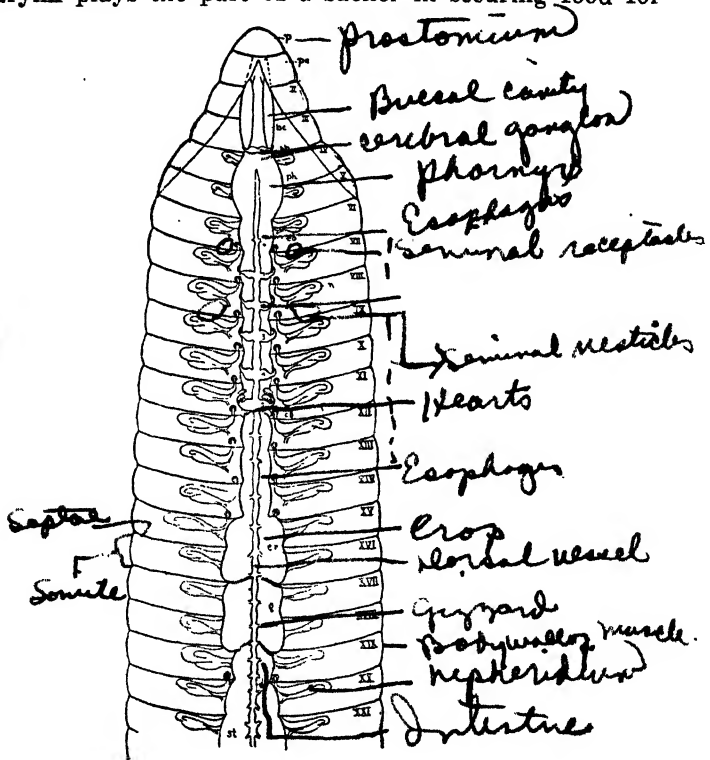
Fig. 127.—Dorsal dissection of an earthworm in the region of segments I to XXI. *bc*, buccal cavity; *cg*, calciferous glands; *cr*, crop; *dv*, dorsal blood vessel; *eo*, esophagus; *g*, gizzard; *n*, nephridium; *sb*, subpharyngeal ganglion; *st*, intestine; *pe*, peristomium; II-XXI, somites; *ph*, pharynx; *p*, prostomium. (From White, *General Biology*, The C. V. Mosby Company.)

the animal. The *esophagus* is a straight narrow tube extending from the pharynx through the fourteenth segment. In segments X to XII three pairs of yellow lateral pouches open into it. These are the *calciferous glands*, the secretions of which help to neutralize the acid organic matter taken as food. The esophagus opens into the crop.

a larger, thin-walled structure, which extends through segment XVI. This is followed by the muscular *gizzard* in segments XVII and XVIII. A thin-walled *intestine* extends to the *anus*, which opens to the outside through the last segment.

The intestine is not a simple tube but has a large fold, the *typhlosole*, protruding into its lumen from the dorsal side giving it more absorptive surface for the assimilation of food. The coelomic side of the intestine is covered with a layer of brown cells, known as *chloragogen cells*, whose function is doubtful. They are generally believed, however, to play a part in the excretion of nitrogenous wastes.
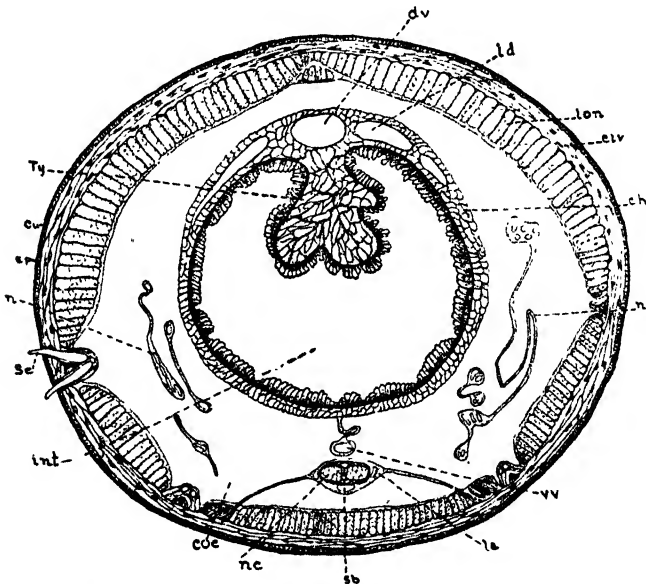
Fig. 128.—Cross section of an earthworm through a posterior segment. *ch*, chloragogue cells; *cir*, circular muscle fibers; *coe*, coelom; *cu*, cuticle; *dv*, dorsal blood vessel; *ep*, epidermis; *int*, intestine; *la*, lateral neural vessel; *ld*, parietal vessel; *lon*, longitudinal muscle fibers; *n*, nephridium; *nc*, nerve cord; *sb*, subneural blood vessel; *se*, seta; *Ty*, typhlosole; *vv*, ventral blood vessel. (From White, *General Biology*, The C. V. Mosby Company.)

The food of the earthworm consists of almost any kind of organic matter which may pass through its digestive tract. The animals remain in the soil during the daytime and work their way through it by passing it continually through the digestive tract. At night they come to the surface of the ground, usually remaining partly within or very near the burrow, and feed on dead organic matter, such as leaves. Food is drawn into the mouth by suction produced

by the muscular pharynx. In the pharynx it receives the secretions from the pharyngeal glands and is then passed on through the esophagus, where it receives the secretions from the calciferous glands. It is then passed into the crop and is stored there long enough for the secretions of the calciferous glands to neutralize the organic acids which may be present in the food. It is then passed into the gizzard, where it is ground by contractions of the muscular walls of that organ. This process is aided by sand grains which are swallowed along with the food. From the gizzard the food is passed into the intestine where digestion is completed and the absorption of digested materials is accomplished.

Circulatory System

The blood of the earthworm consists of a liquid *plasma* in which there are numerous colorless cells. The red color of the blood, as seen in a living specimen, is due to a pigment known as *hemoglobin*
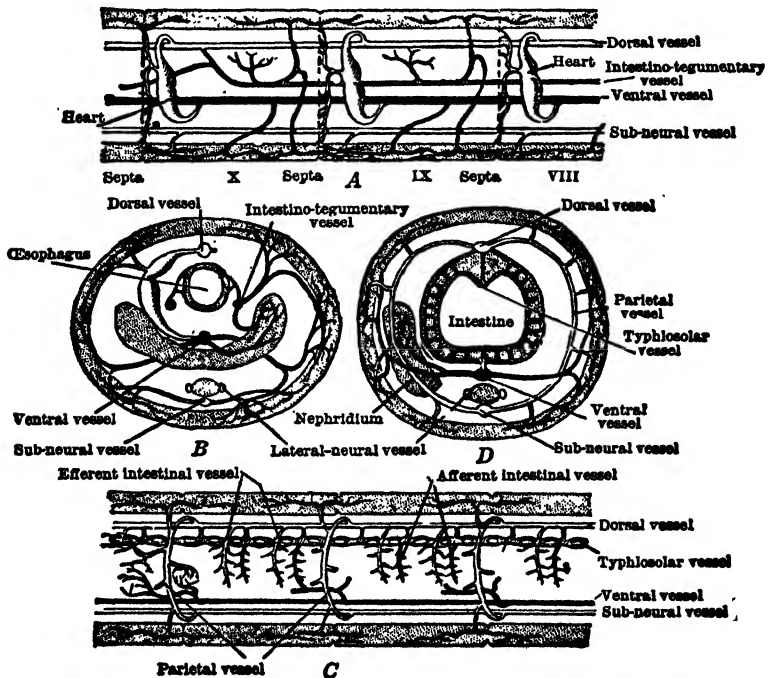
Fig. 129.—Circulatory system of the earthworm. *A*, Longitudinal view of vessels in somites VIII, IX, and X; *B*, transverse section of the same region; *C*, longitudinal view of the intestinal region; *D*, transverse section of the same region. (From Hegner, *College Zoology*, The Macmillan Company, after Bourne, after Benham.)

suspended in the plasma and not in the *corpuscles* as is the case in many animals. A complicated system of blood vessels makes up the circulatory path of the blood. The principal ones are: (1) the dorsal blood vessel, (2) the paired hearts (usually five) in segments VII to XI, (3) the ventral blood vessel, (4) the subneural trunk, (5) the parietal vessels, (6) the typhlosolar vessel, and (7) the intestino-integumentary vessels. The dorsal vessel conveys the blood anteriorly and forces it along by wavelike contractions. The paired hearts receive the blood from the dorsal vessel and by pulsating movements force it into the ventral vessel which distributes it to the body wall, the nephridia, and the intestine. In the intestine food is taken up; in the skin gaseous exchanges are made with the water in the moist soil; and in the nephridia the nitrogenous wastes are removed. The *lateral neural vessels* receive freshly oxygenated blood from the skin; hence the nervous system receives the most highly oxygenated blood. From the lateral vessels it passes into the *subneural,* where it flows posteriorly, and then returns to the *dorsal vessel* by way of the *parietal connectives.* The blood flows from the intestine through the typhlosole into the dorsal vessel by *dorso-intestinal vessels.* Anterior to the hearts the dorsal vessel carries the blood posteriorly and the ventral vessel carries it anteriorly. The circulatory system is equipped with numerous valves which keep the blood from flowing in the wrong direction.

Respiratory System

Respiration in the earthworm is carried on through the skin which is well supplied with blood. Since the animal always lives in a moist environment, this type of respiration is possible.

Excretory System

The function of excretion is cared for principally by the paired *nephridia,* which are found in each segment except the first two and the last one. A single nephridium consists of a ciliated funnel (the *nephrostome*), a thin coiled tube, and a *nephridiopore.* The cilia of the nephrostome create a current which takes the fluid containing nitrogenous wastes from the coelom into the tubule where it can pass to the outside through the nephridiopore. Also the wastes in the blood are excreted by way of the nephridial tubules. The nephro-

stome is located in the posterior part of the segment and leads into
the tubule of the segment just posterior to it. The nephridium coils
two or three times before reaching the nephridiopore.

The Nervous System

The brain of the earthworm consists of the *suprapharyngeal
ganglion*, two *circumpharyngeal connectives*, and the *subpharyngeal
ganglion*. The *ventral nerve cord* extends posteriorly the length of
the body with a ganglion and three pairs of nerves in each segment.
Each ganglion is really the fusion of two, a deviation from the con-
dition found in many annelids and arthropods where there are two
ganglia in each segment and the nerve cord is double. The supra-
pharyngeal ganglion lies dorsal to the pharynx in the third segment
and the subpharyngeal ganglion lies ventral to the pharynx in the
fourth segment. Nerves from these two ganglia innervate the first
three segments and the prostomium.

Stimuli are received by sensory cells and are passed into the
ventral nerve ganglia by the afferent nerves. The stimulus is modi-
fied in the ventral ganglia and sent to the responding organs by
efferent neurons. Nerve impulses then have the nature of a simple
reflex except that the ventral ganglia are connected by association
neurons which conduct stimuli from one to the other. Because of
this arrangement a stimulus applied to any part of the body will
cause responses to occur in a wavelike manner in both directions
from the point of stimulation. Located in the dorsal part of the nerve
cord are three giant fibers which serve as the sole means of conducting
an impulse directly from one end of the body to the other. By this
means the worm can contract its entire body at one time.

Reproduction

As has already been described, the earthworm is hermaphroditic.
Self-fertilization does not occur, however, each egg being fertilized
by a sperm from another individual. In reproduction two animals
come together with their anterior ends pointing in opposite direc-
tions and the ventral surfaces of their bodies in close contact from
the anterior end to the clitellum. With their bodies in close contact a
closed passage is formed between the genital openings of the two in-
dividuals. Sperms pass from the testes out through the seminal

vesicals and vas deferens to the closed passage and move through it to the seminal receptacles of the mate, where they are stored. In the meantime, the clitellum of each individual secretes a band which binds them together at these two points. After each has received sperms from the other, they separate by working themselves through the bands secreted by the clitella. This leaves each animal with a band which is gradually worked off toward the anterior end. As the band passes over the openings of the oviducts, eggs are released into it, and 'as it passes the openings of the seminal receptacles, sperms, which came from the reproductive mate, are released.
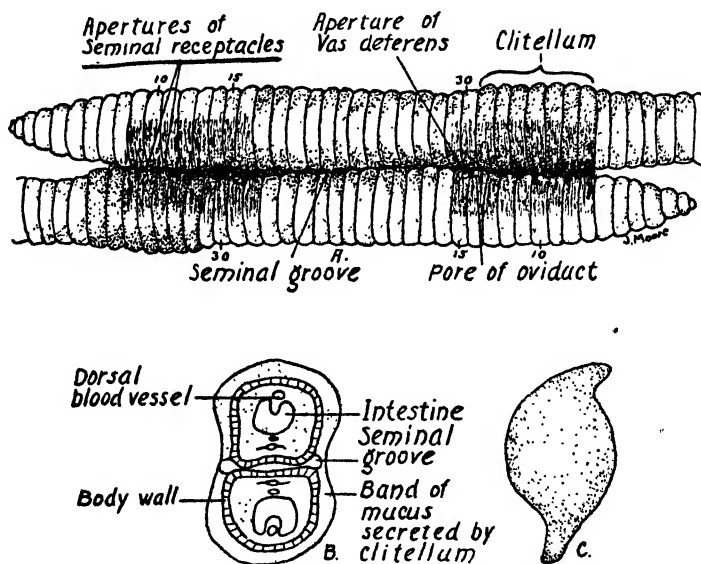
Fig. 130.—Reproduction in earthworm showing copulation and cocoon. *A,* Two worms enclosed in bands of mucus during copulation; *B,* transverse section showing the seminal grooves; *C,* cocoon.

Both ends of the band close, forming a cocoon in which fertilization and development take place.

Cleavage in earthworms is of the unequal holoblastic type. Soon after the segmentation cavity is formed, a certain cell, known as the *mesoblast cell,* is set off, and the cells resulting from its divisions move into the cleavage cavity, and will form the mesoderm. As the mesoblast cells move into the cleavage cavity, *gastrulation* occurs by invagination to form the endoderm and ectoderm. The gastrula elongates and the archenteron opens at both ends to form the mouth

and anus. The mesodermal cells which fill the space between the ectoderm and endoderm develop segmental cavities which are the coeloms of the metameres. This constitutes a tube within the worm from which eventually develop the organs of the adult individual.
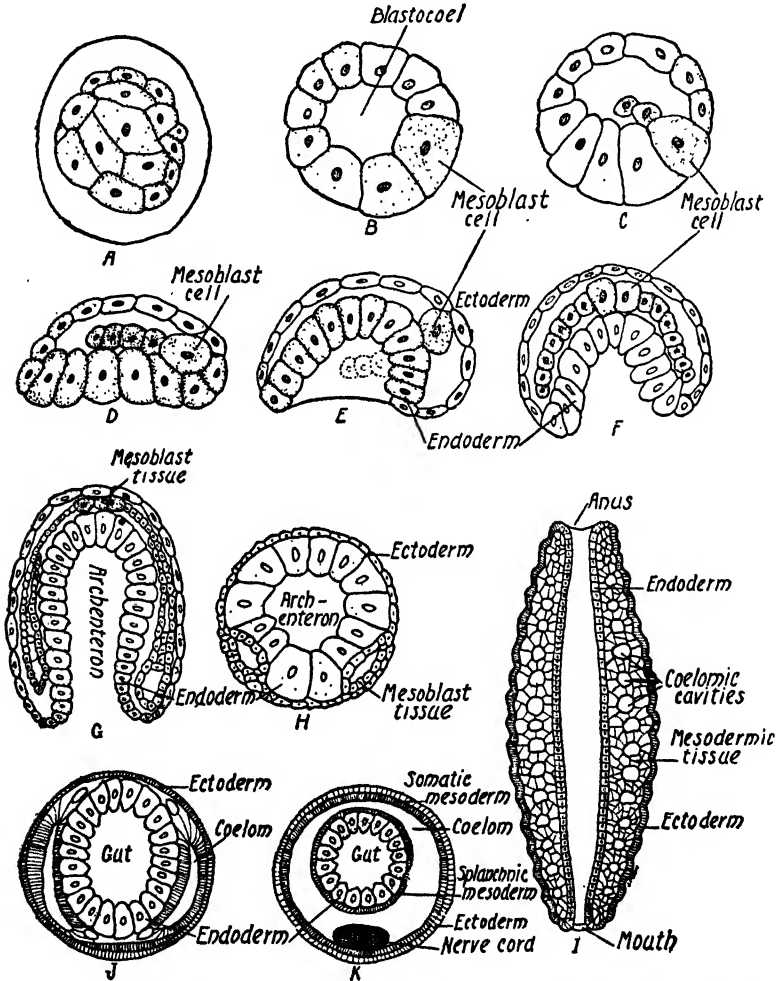
Fig. 131.—Development of the earthworm. *A*, Blastula, surrounded by a membrane; *B*, section of a blastula showing blastocoele and one of the mesoblast cells (primary cell) of mesoderm layer; *C* and *D*, showing stages in the beginning of gastrulation; *E*, side view of gastrula showing invagination; *F*, section of gastrula along a line to show polar cells, mesoderm layers on each side of them and the archenteron; *G*, later stage showing cavities in the mesoderm; *H*, gastrula in cross section; *I*, longitudinal section of a young worm after formation of the mouth and arms; *J*, same as *I* but in cross section; *K*, cross section of later stage. (After Wilson, *Embryology of the Earthworm*, Journal of Morphology, 1889.)

Regeneration

Earthworms have been used extensively in regeneration experiments because they possess the ability to regenerate lost parts. It has been demonstrated that when the anterior end is cut off, in front of the eighteenth segment, the segments from one to five will be regenerated. If the cut is made posterior to segment eighteen a new anterior end will not regenerate on the tail half, but instead another tail will develop from the cut surface. This produces an animal with two tails and no head, and death from starvation results. When any part of the tail region is cut off, the lost parts readily regenerate. Numerous grafting experiments have also been performed on earthworms. Almost any part of an individual grafted to the cut surface (if properly located) of another will fuse to it and grow. In this way numerous unusual forms of earthworms have been produced.

Class Archiannelida (är kĭ ă nĕl′ ĭ då, first Annelida).—This class includes numerous small marine forms which resemble Chaetopoda in a number of ways. It is now believed that they have been derived from that group by changes usually involving the reduction or loss of certain structures. They are very small and lack both setae and paropodia. Internally they are very similar to the earthworm. The best known example of this group is *Polygordius*, which has a long cylindrical, segmented body with a pair of tentacles on the prostomium. Two ciliated pits are present as a retention of juvenile characters. The *trochophore larva* is common to the entire group.

Class Hirudinea (hĭ rŭ dĭn′ ê å, leech).—These animals are commonly known as the leeches. They are usually flattened dorsoventrally, possess both an *anterior sucker* and a *posterior sucker,* have characteristically thirty-two segments and possess no external appendages. The anterior sucker is formed from the *prostomium* and first two segments, and the posterior one comes from the last seven. Each segment shows externally a variable number of *annuli* or rings, making the animal appear to possess more segments than are really present. Leeches are commonly parasitic and live by sucking blood from other animals.

In a typical leech, of which *Hirudo medicinalis* is a good example, there is a muscular pharynx, a short *esophagus,* midgut or *crop, intestine,* and ectodermal *rectum.* Blood which is sucked from an-

other animal receives a ferment from the *salivary glands* of the pharynx, which prevents it from coagulating. It is then stored in the *diverticulae* of the crop. The animal is capable of ingesting three times its own weight in blood, and, since several months may elapse before it is all digested, frequent feedings are not necessary. The coelom is very much reduced due to the excessive development of the mesodermal tissue. Each animal is hermaphroditic. Sperms are placed on the skin of another leech, and they apparently work through it into the *ovaries,* where fertilization occurs. Development takes place in a *cocoon* produced by the *clitellum.* Two *nephridia* are present. The nervous system is typical of the annelids.

Class Gephyrea (jĕ fĭ rĕ′ à, bridge).—This class is a group of marine annelids which are nonsegmented, have no appendages, and possess a trochophore larva. They are usually comparatively large and live in shells, crevices, and such other places as will afford protection. In this class, the representatives of order Echiuroidea have a well-developed prostomium, used in capturing prey and in locomotion. In *Bonellia,* the female is the normal individual, while the male has no proboscis, is ciliated, and lives as a parasite on the proboscis of the female. Representatives of the order Sipunculoidea have no prostomium in the adult.

Importance of Annelids to Man and Other Animals

Even though no casual observer would consider that annelids have any important relationship to other living organisms, they have been found to be of great importance in a number of ways. Darwin concluded from some forty years of observation that the earthworms in an acre of ground could bring to the surface in one year as many as eighteen tons of feces, known as castings. This indicates without doubt that these animals are of great value, because in stirring the soil they cover up objects, causing them to decay. Their continuous burrowing through the soil also makes it porous, a necessary condition for plant growth.

Earthworms have also less desirable qualities. They serve as secondary hosts for parasites of several animals. Most of the parasites having the earthworm as a secondary host live as adults in birds, pigs, and other animals which use the worms as food.

They have created a serious problem in some of the irrigation districts of the Southwest by burrowing through levees until they

are too porous to hold water. Before irrigation was started they did not appear to be at all numerous, but with the presence of water they have become very abundant.

The medicinal leech was once used in the bleeding of individuals as a treatment for various ailments. Various forms of leeches live as parasites on turtles and other forms of animal life in the water. They are not at all averse to attacking human beings when the opportunity presents itself; however, they cause no great injuries and are important only as pests and as secondary hosts for some parasites, thus spreading certain diseases.

Marine annelids are important only as food for larger forms. In many regions the burrowing forms along the tide levels literally form a good grazing ground for fishes. The fish swim along, biting off that part of the worms protruding from the mud or sand. Instead of dying, the injured worms simply regenerate one or more new heads and go about their business.

Phylogenetic Advances of Annelida

(1) Segmentation, (2) coelom, (3) alimentary canal with defined parts, (4) closed circulatory system, (5) excretory system of nephridia, (6) muscular system, (7) concentrated mid-ventral nerve cord connected to a dorsal pair of suprapharyngeal ganglia.

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CHAPTER XX

STARFISH, OF PHYLUM ECHINODERMATA, AND OTHER ECHINODERMS

The Echinodermata (ē kī nŏ dûr′ mȧ tȧ—hedgehog skin) constitute a rather backward phylum of animals which are thought to have undergone a certain amount of retrogression in structural features. That is, they seem to have a lower level of organization than that possessed by some of their ancestors. The modern echinoderms, as the group is commonly called, possess several distinctive characteristics. Some of these characteristics are as follows:[skin covered with spines; lack of segmentation; triploblastic radial symmetry, subduing a primitive bilateral symmetry; water vascular or ambulacral system and tube feet; circumoral nerve ring and radial nerves; a calcareous skeleton composed of plates; pedicellariae; and a coelom. The external opening into the water vascular system is called the *madreporite*. It is located on the dorsal or aboral side, at an interradius between arms in such a position that a line drawn through it and on through the radius of the opposite ray, will divide the body into two similar halves. There will be a half ray and two complete rays in each half of a five-rayed animal divided in this way.

Classification

In earlier classifications as in the case of Cuvier, this entire group was included along with coelenterates in a group called Radiata. The basis for this was the apparent similarity of radial symmetry. It was later discovered that the coelenterates have a typical primitive radial symmetry while the Echinodermata have only a secondary radial symmetry which is derived from a bilateral condition. This is indicated quite definitely by the fact that the larvae of echinoderms have a typical bilateral symmetry. The change which occurs seems to be an adaptation to a sedentary habit. This phylum is usually divided into five classes of modern forms including such common animals as starfishes, brittle stars, sea urchins, sea cucumbers, and sea lilies.

Class Asteroidea.—The general features of the body include a *central disc* usually with five *arms* or *rays* radiating from it. There

are some species which do not adhere to this pentamerous condition and have up to forty rays.   The rays are not usually sharply constricted from the central disc.   *Asterias, Astropecten, Solaster, Oreaster* and *Echinaster* are representative genera.

Class Ophiuroidea.—Brittle stars and serpent stars.   There is a small central disc with five long, slender rays which are clearly marked off from the disc.   The rays are lacking in ambulacral grooves. The tube feet do not serve in locomotor functions but are tactile only.   Both the madreporite and mouth are located ventrally.   The ability of *autotomy* (self-mutilation) is so well developed here that arms will become detached by merely grasping them.   *Ophioderma, Ophiura, Ophiothrix* and *Gorgonocephalus* are common Atlantic and Gulf genera.
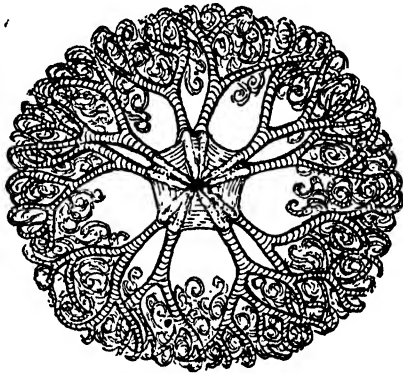
BASKET STAR

Fig. 132.—Oral view of a basket star belonging to class Ophiuroidea.   (By courtesy of General Biological Supply House.)

Class Echinoidea.—Sea urchins and sand dollars are representatives of this group the members of which have lost the rays but still retain the pentamerous (five division) condition of the body. The sea urchins are globular or hemispherical, while the sand dollars are disc-shaped.   The skeleton or *test* is composed of five rows of closely fitting plates which are usually arranged into five pairs of inter-ambulacral rows.   The position and condition of these rows of plates can be compared to a starfish with its arms turned up over its body until the tips all touch each other.   The surface of the skeleton bears processes which support movable spines.   Tube feet may be thrust out through perforations in the plates of the ambu-

lacral rows. These rows correspond in position to the ambulacral grooves of the starfish. The mouth of this type of animal is located ventrally (orally), and it is guarded by five projecting skeletal processes called teeth. These converge over the aperture and are set in a skeletal case which is composed of many hard ossicles and contains the muscles for moving the teeth. The teeth are used in
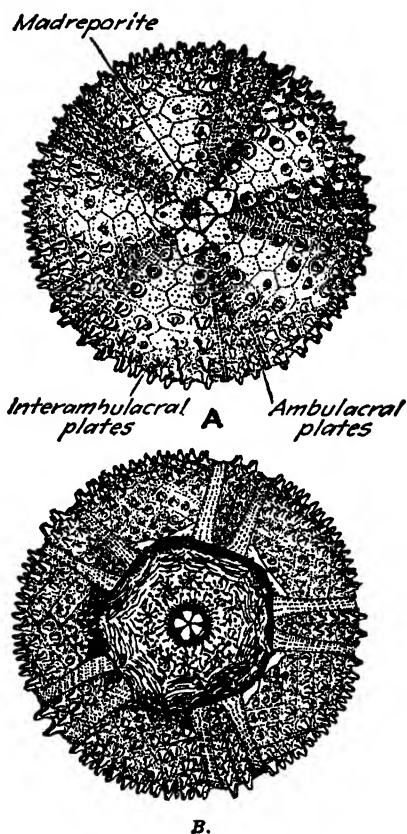
Fig. 133.—Dried test of the sea urchin, *Arbacia*. *A*, Shows arrangement of the plates on the aboral side; *B*, oral view showing mouth and perioral area. (From Wolcott, *Animal Biology*, McGraw-Hill Book Company, Inc.)

removing algae from rocks for food. This arrangement constitutes Aristotle's lantern, and the esophagus leads internally from its aboral part. The principal organs of respiration are the interradial pouches and the tube feet. The nervous system is composed of a circumoral ring with radial cords extending into the ambulacral

areas. *Strongylocentrotus, Arbacia, Tripneustes, Clypeaster,* and
Echinarachinus (sand dollar) are representative genera of the group.

Class Holothurioidea.—The echinoderms of this class have only
an incomplete skeleton, the body is elongated, the mouth surrounded
by tentacles is located at one end and the anus is at the other.
These animals are called sea cucumbers because of their shape and
color. There is some remnant of the pentamerous condition in that
there are five double rows of tube feet extending lengthwise on
five sides of the body of some forms, others have less or none. The
expanded body of a holothurian is soft like a bladder partly filled
with liquid and the body wall is very muscular. Representative
genera of this class include *Thyone, Holothuria, Cucumaria, Lepto-
synapta, Aphelodactyla* and *Caudina.*
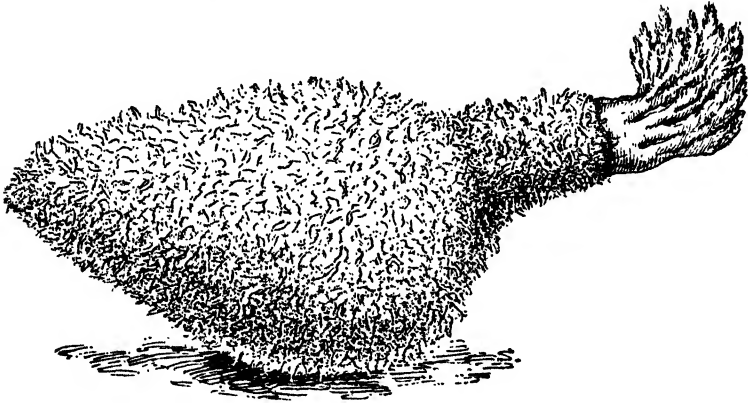
Fig. 134.—Thyone, the common sea cucumber.

Class Crinoidea.—Most of the sea lilies live attached by long
stalks, but a few are free. At the free end of the stalk are located
the five, many-branched *arms.* The mouth is located in the upper-
most center of the calyx and is surrounded by the anus. The anus
is also to be found on the oral side within the enclosure made by the
arms. *Neocomatella, Pentacrinus, Rhizocrinus, Metacrinus* and *Ante-
don* are representative genera.

Habitat and Behavior of Starfish

The starfish lives along the shores and in the shore waters (to a
depth of over 125 feet) of our stony coasts of the Atlantic and
Pacific, with scattered ones occurring in the Gulf of Mexico. A few

scattered individuals may be found on muddy or sandy shores, but they are quite scarce. They are often found clinging to pilings, old boats, and other objects in the water. By action of the tube feet they are able to cling very tenaciously to almost any solid object. At low tide they may be found under the rocks, out of the sun, where they are protected from the heat and drying. Due to a food relationship they are usually found in the same area with marine clams, oysters, and rock barnacles. During the day they
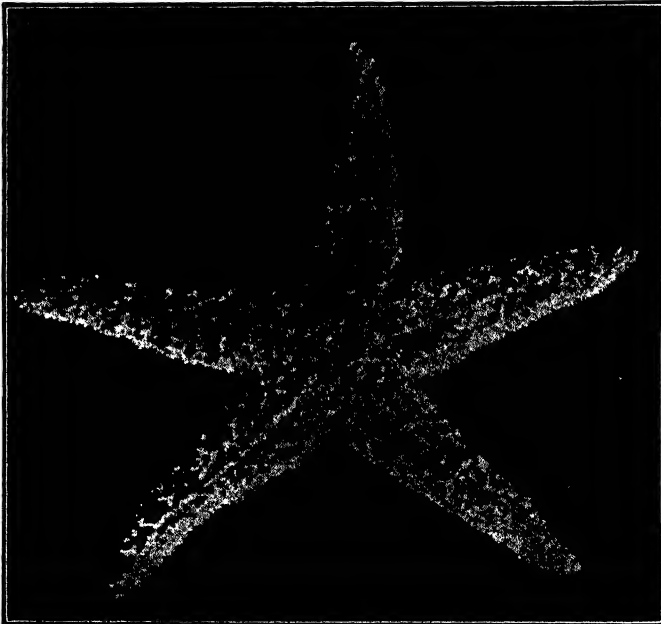
Fig. 135.—The ochre starfish, *Pisaster ochraceus*, an abundant form along the Pacific coast. (Johnson and Snook, *Seashore Animals of the Pacific Coast*, The Macmillan Company.)

are rather inactive, but at night they are much more active and respond to such stimuli as light, temperature, contact, and chemicals. It has been demonstrated experimentally that starfishes may form habits. They ordinarily live and move about with the oral side next to the substratum, and if turned over, will right themselves in the same way time after time. If the arms which are habitually used for this are incapacitated, they will acquire the habit of using another combination of rays in this act.

External Anatomy

The body is composed of a central disc and some (usually five) radiating arms or rays. The mouth is located in the center of the under or *oral* surface while the upper or aboral surface is covered with spines of various lengths. On the arms these spines are arranged somewhat in rows. Between the spines the exposed skin is extended into projections known as *papula* or *dermal branchiae.* There are some small pincherlike structures, called *pedicellariae,* arranged around the bases of the spines, which serve to keep the surface of the exposed papulae clear of debris and foreign material. The pedicellariae are composed of two *jaws* or *blades* and a basal plate with which the jaws articulate. There are large and small pedicellariae. In an eccentric position on the aboral side of the central disc is found the calcareous, sievelike *madreporite.* The portion of the central disc and two rays adjacent to the madreporite constitute the *bivium.* The other three arms and their adjacent portions of the central disc compose the *trivium.* On the oral side surrounding the mouth is a *perioral membrane* or *peristome.* An *ambulacral groove,* containing rows of tube feet, radiates from this along the oral side of each arm. A reddish pigment spot in the end of each arm is called an *eye.* The spines are longer and stronger around the mouth and along the margins of the ambulacral grooves than elsewhere.

Internal Anatomy

The body wall is relatively strong and hard without being perfectly rigid. This condition is due to the presence of the *calcareous skeletal plates* throughout, which are bound together by connective tissue and muscular fibers. These plates are often called *ossicles.* They lie in a flat position in the aboral portions of the body wall. The skeleton of the ambulacral grooves consists of four rows of articulated, oblong ossicles in each arm. These ossicles are arranged with the flat sides together, like cards in a filing case. The two middle rows of ossicles are called *ambulacral plates.* *Ambulacral pores,* through which the tube feet project, are located between these plates. The outer rows of plates, forming the margin of the groove, are shorter and are known as *adambulacral plates.* Five flat *oral ossicles* surround the mouth.

Within the body wall and extending into the arms is a large coelom which is lined by a *peritoneum* and filled with *coelomic fluid.* In

this cavity are located the organs of most of the systems.   The
digestive system is a modified tube extending vertically from the
mouth on the oral side to the minute arms at the aboral surface.
From the mouth a short esophagus leads to the double-pouched
stomach.   The larger cardiac portion (or pouch) receives the esopha-
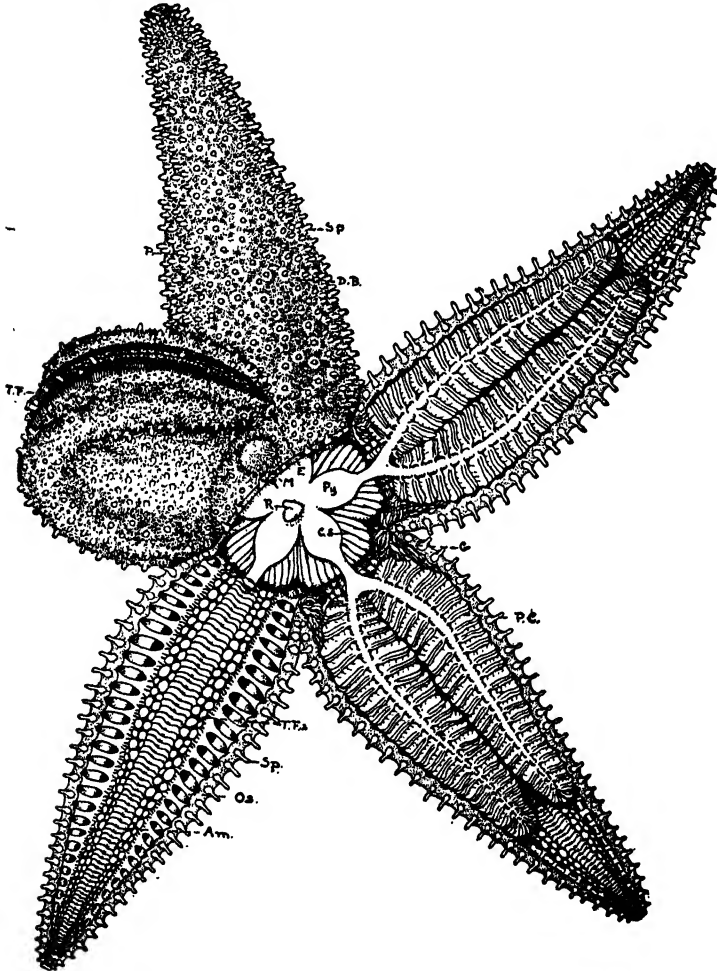
Fig. 136.—Dissection of the starfish, *Asterias*.   The aboral wall has been re-
moved from the trivium and a portion of the central disc.   One ray of the bivium
has been turned to expose the oral surface and tube feet.   The organs have been
removed from one ray of the trivium to expose the skeleton.   *Am*, ambulacral
groove; *os*, cardiac stomach; *D.B.*, dermal branchiae; *E*, eyespot; *G*, gonads; *M*,
madreporite; *Os.*, ossicle; *P*, pedicellariae; *P.C.*, pyloric caeca; *Py*, pyloric sac;
R, rectal gland; *Sp.*, spine; *T.F.*, tube feet; *T.F.₂*, arrangement of tube feet in skeletal
ray.   (From White, *General Biology*, The C. V. Mosby Company.)

gus and is separated aborally from the pyloric portion by a marked constriction. A large pair of branched glandular structures, known as *hepatic* or *pyloric caeca*, is located in each arm, and each pair joins the pyloric pouch by a duct which seems to be a continuation of this pouch. These glands and possibly the pyloric pouch produce digestive enzymes in solution. The fluid secreted by the wall of the cardiac portion probably does not contain enzymes. A short *rectum* or *intestine* leads aborally from the pyloric pouch to the pore-like anus at the exterior surface of the central disc. Two brown, branched pouches arise from the rectum. These are known as *rectal caeca* or glands and probably have excretory function. In feeding, the starfish catches its bivalve prey in the five arms and humps over it. The tube feet are attached to the shells, and, by cooperative activity, an enormous pull is exerted on the valves of the shell. After the shell is open, the stomach of the starfish is everted
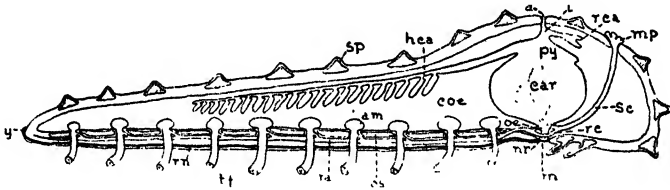
Fig. 137.—Longitudinal section through the central disc and one ray of a starfish. *a,* Anus; *am,* ampulla; *car,* cardiac stomach; *coe,* perivisceral coelome; *ey,* eyespot; *hca,* hepatic caeca; *i,* intestine; *m,* mouth, *mp,* madreporic plate; *nr,* nerve ring; *oe,* esophagus; *os,* ambulacral ossicle; *Py,* pyloric sac; *ra,* radial canal; *rc,* ring canal; *rca,* rectal caeca; *rn,* radial nerve; *Sc,* stone canal; *sp,* spine; *tf,* tube feet. (From White, *General Biology,* The C. V. Mosby Company.)

through its mouth and is spread over the tissues of the prey. An abundance of digestive fluid secreted over the food causes it to be digested in its own shell, and it is then taken into the stomach of the starfish. It is reported that between four and five dozen clams may be eaten by a single starfish in a week. It has also been shown that a starfish may survive after months of fasting. After feeding, the stomach is withdrawn into the body cavity by five pairs of *retractor muscles,* one pair extending from the pyloric portion to the ambulacral skeleton of each arm. The branched, treelike *gonads* fill the remaining space in each arm and the external *pores* from them are located in the crevice between adjacent arms.

The *water-vascular system* is composed of the madreporite, stone canal, circumoral or ring canal, radial canals, Tiedemann's bodies, lateral canals, ampullae, and tube feet. Water is taken in through

the sievelike *madreporite* on the aboral side of the central disc and is conducted by the S-shaped, calcareous *stone canal* (hydrophoric canal) to the *ring canal,* which encircles the mouth. The movement of the water through the madreporite and stone canal is accomplished by the action of cilia, which line them. On the medial surface of the ring canal are nine small *Tiedemann's (racemose) bodies,* the stone canal joining the ring canal where the tenth might be expected. These bodies produce amoeboid cells. The five radial canals extend distally, one in the roof of the ambulacral groove of each ray. Numerous paired lateral canals arise along the length of each radial canal. Each ends shortly by connecting with its *ampulla* and tube foot. The ampulla is bulblike and is located above the roof of the
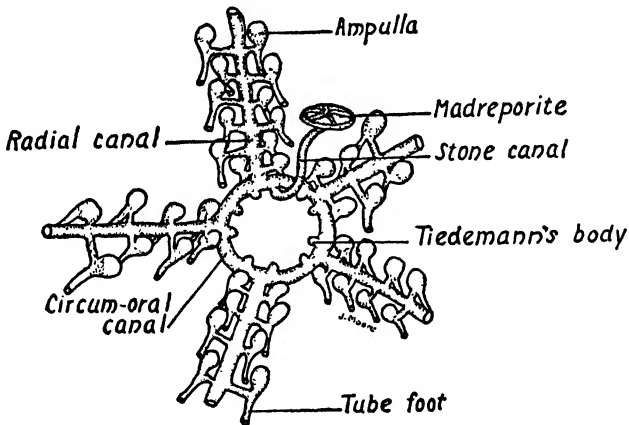
Fig. 138.—Diagram of water-vascular system of the starfish.

ambulacral groove in the coelom. It is connected through its ambulacral pore with the contractile tube foot which hangs down into the ambulacral groove. The distal or free end of the foot has a slightly inverted, suckerlike shape. The proximal pair of ampullae in each arm of some starfish lack the tube feet and are sometimes erroneously called Polian vesicles. Alternate tube feet are farther from the radial canal than the others on each side. The ampullae and tube feet function effectively in locomotion, the ampullae contracting to force water into their respective tube feet to extend them. The walls of both ampullae and tube feet are muscular. In large starfish the tube feet may be extended an inch or two. The sucker ends of these tube feet work like a vacuum cup

and will adhere effectively to surfaces over which the animal is drawing itself. When the pressure is released by the ampulla, the tube foot contracts and draws the animal forward. When water is again forced into the tube, it releases its grip and is again extended. By alternation of the activity of tube feet in different parts of the body the animal is able to move itself from one place to another. The entire water vascular system is a modified part of the coelom.

A thin-walled system of vessels running parallel to the water vascular is the circulatory system. It is enclosed in a perihemal space. In addition to this the coelomic fluid, which occupies the coelom and bathes all of the organs, serves as a circulatory medium
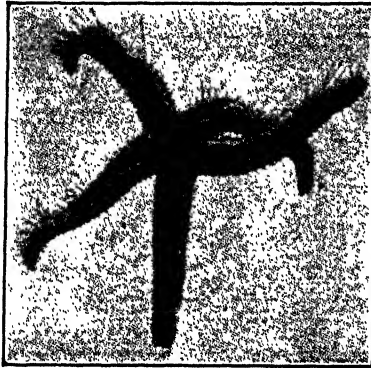
Fig. 139.—Starfish "walking" on glass. Viewed from the oral surface. Notice the extended tube feet. (Courtesy of General Biological Supply House.)

in that it absorbs the digested food and distributes it. This fluid bears *amoebocytes* which are cells capable of picking up particles of waste material and carrying them to the *dermal branchiae,* where they pass through the membrane to the exterior. These dermal branchiae are pouches of the coelomic wall which extend outward between the skeletal plates and have the additional function of respiration. When these pouches are completely extended, they nearly cover the exterior surface of the animal, and thus expose an enormous area to the water for respiration.

Excretion is carried out in part by the amoebocytes which have been produced by the Tiedemann's bodies and have migrated to the coelomic cavity. The rectal caeca serve in respiration to some

extent also. There is a certain amount of diffusion of dissolved wastes through the dermal branchiae and the walls of the tube feet.

The nervous system is radially arranged about the *oral ring* which encircles the mouth just orally to the ring canal. From the oral ring, a *radial nerve* extends the length of each arm and ends in the pigmented *eyespot*. These nerves lie in the roof of the ambulacral grooves. The aboral surface is supplied by a less conspicuous aboral nerve which extends from an *anal nerve ring*. Branches of these nerves extend to the numerous nerve cells distributed in the epidermis above the nerve cords. The pigmented eyespots at the tips of the arms are photosensitive and sensitive to touch. The pedicellariae and tube feet are also sensitive to touch. There is little centralization except in the oral ring and radial cords, still there is sufficient centralization for the necessary coordination exercised by the animal.

Reproduction and Life Cycle

The starfish is dioecious; i.e., the sexes are separate. The reproductive systems of the two are similar and each consists of five paired gonads lying in the cavity of the rays beside the pyloric caeca. They open to the exterior by pores in the angles between arms. Mature eggs produced in *ovaries* of females and mature spermatozoa discharged from *testes* of males are freed in the ocean water where they unite in *fertilization*. Total, equal cleavage is the type of division which follows fertilization, and this finally gives rise to the many-celled, free-swimming, ciliated *blastula*. The wall of this infolds to form a *gastrula*. Following this the rounded body becomes somewhat elongated and lobed. Ciliated bands develop over its surface and it is known as *bipinnaria*. This larval stage has bilateral symmetry, and the larva swims about near the surface for weeks by the aid of its ciliated bands. A later modification of the bipinnaria in which there are several extended symmetrical processes, is known as the *brachiolarian stage*. Following this condition is a metamorphosis during which many processes are formed, and the radial symmetry superimposes the bilateral. The presence of the bilateral symmetry in these larval stages seems to indicate that the ancestors of echinoderms were likely animals with this type of symmetry.
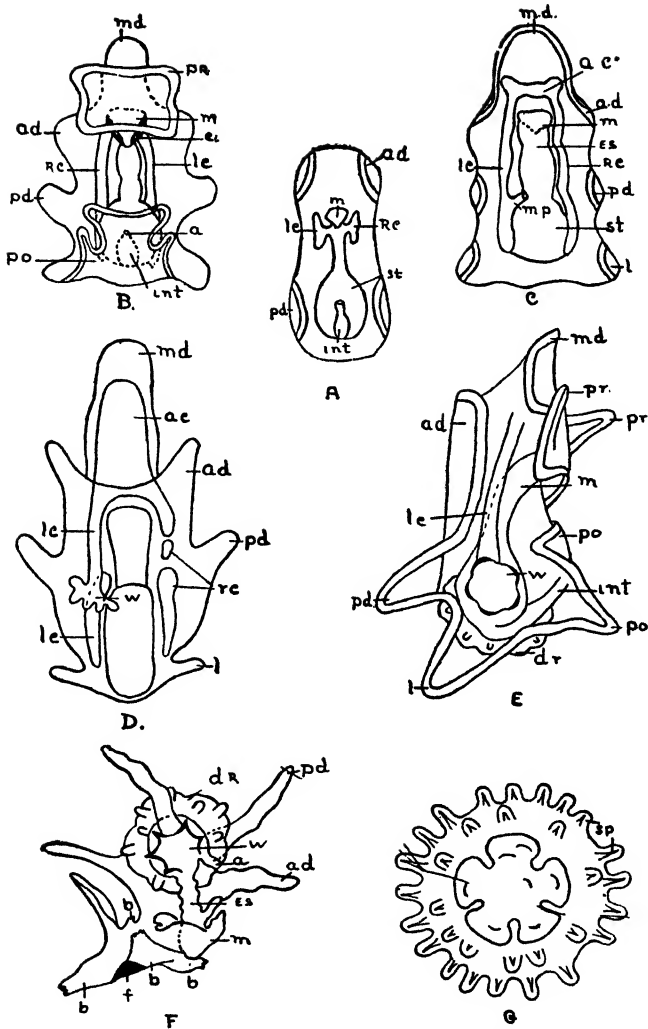
Fig. 140.—Development and metamorphosis of the starfish. *A*, Dorsal view of early ciliated larva, showing ciliated bands and coelomic pouches; *B*, ventral view of bipinnaria larva showing the extension of the left and right coelomic pouches; *C*, dorsal view of the same larva showing the left madreporic pore and water tube, and the fusion of the left and right coelomic pouches to form an anterior coelom; *D*, dorsal view of an older larva showing the budding of the five water tubes from the left coelom; *E*, view of left side of a still older larva showing the water vascular system developing from water tubes, and the rays of the adult starfish developing on the dorsal side; *F*, Brachiolaria larva in the process of metamorphosis. The larva has settled on the preoral region which is greatly shortened; *G*, aboral view of a young starfish showing the developing spines: *a*, anus; *ac*, anterior coelom; *ad*, anterodorsal arm; *b*, brachiolar arms; *ci*, adoral ciliated band; *dr*, dorsal surface developing rays; *es*, esophagus; *f*, point of fixation; *int*, intestine; *l*, lateral arm; *lc*, left coelomic pouch; *m*, mouth; *md*, median dorsal arm; *mp*, madreporic pore and water tube; *pd*, posterodorsal arm; *po*, postoral ciliated band; *pr*, preoral ciliated band; *rc*, right coelomic pouch; *sp*, spines; *st*, stomach; *w*, five water tubes of water vascular system. (Modified from Wilson and McBride. Reproduced by permission of The Macmillan Company.)

Regeneration and Autotomy

Regeneration is the name applied to the power some animals have to replace mutilated or lost parts. The starfish has this phenomenon quite well developed with regard to its arms. Any or all of the

Madreporite

Regenerating ray

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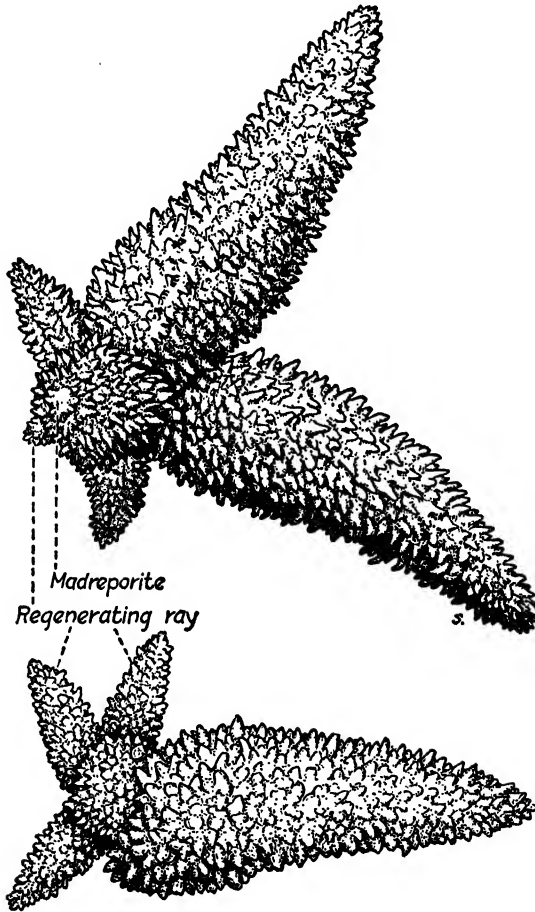
Fig. 141.—Regeneration in the starfish. Above, a starfish regenerating part of the central disc and three arms; below, arm of starfish regenerating the remainder. of the body. ·

arms of the starfish may be lost and the missing parts regenerated. An arm with a small portion of the central disc will regenerate the missing parts under favorable conditions. A mutilated arm or one caught in the grip of some enemy may be cast off by breaking loose

at the constricted point where it joins the central disc. This ability of self-mutilation is known as *autotomy*. Following autotomy there is regeneration of a new part.

Economic Relations

Compared with many other animals the echinoderms are relatively unimportant economically. The sea cucumbers of several different species are used as food by the Chinese and other oriental people. The larger animals, some of them two feet long, are eviscerated, boiled, soaked in fresh water, dried or smoked and sold under the name of *bêche-de-mer* or *trepang*. This dried product is semileathery and gelatinous. It is quite expensive and is usually served as a very palatable soup. The chief fisheries are found along the shores of China, the East Indies, Australia, and the Philippines; some, however, are taken in California, Hawaii, and the West Indies.

Sea urchins of several kinds furnish a sort of caviar known as "sea eggs." The egg masses are taken from the sexually mature females and are eaten either raw or cooked. Each specimen contains a considerable quantity of roe at the season just before spawning. Production of "sea eggs" has become quite an industry in the Orient, Italy, and the West Indies. The Barbados are particularly noted for their production of this commodity.

Perhaps the starfish is the most important of the group, but its relationship is almost entirely of negative importance. It is one of the worst enemies of clams, oysters, and snails. The starfish grows in enormous numbers around the oyster beds of the Atlantic, attacks the oysters, and feeds on them, leaving only the empty shells. A single starfish may eat as many as two dozen oysters in a day. Oyster hunters formerly attempted to protect the oysters and clams by dragging "tangles" made of frayed rope over the beds, catching large numbers of starfish, breaking them in two, and dumping the scraps back into the water. The futility of this was realized when their power of regeneration was learned, so at present they are usually dropped into boiling water or thrown on the bank to dry. Salted or smoked starfish roe (eggs) are considered a delicious food by many people.

The brittle stars and crinoids have little value except as geological indices and biological specimens. Their skeletal parts contribute to the formation of limestone.

CHAPTER XXI

FRESH-WATER MUSSEL AND THE SNAIL, OF PHYLUM MOLLUSCA

(By Elmer P. Cheatum, Southern Methodist University)

GENERAL CHARACTERS

The phylum Mollusca includes such familiar animals as the snails, clams, oysters, and cuttlefish. Even though they appear different externally, all are soft-bodied, unsegmented, usually bilaterally symmetrical, and most of them produce a shell composed principally of calcium carbonate. A muscular foot is present which may be modified for different functions. In the snail it is used for creeping; in the clam for plowing through the substrate, and, in the nautilus or squid for seizing and holding prey. Covering at least a portion of the body is a mantle or dermal fold, the outer surface of which secretes the shell in most species. Between the mantle and main body is a mantle cavity which is usually either provided with gills or modified into a primitive pulmonary sac for use in respiration. Jaws are present in the snails, slugs and cephalopods. Within the mouth cavity of many species is the radula, which is an organ composed of fine chitinous teeth arranged in rows and used in rasping food.

Approximately 78,000 species of mollusks have been described, hence they constitute one of the largest groups of animal life. With very few exceptions they are sluggish animals and occupy a diversity of habitats, occurring abundantly on land, in fresh water, and in the sea. Although most of the species live in moist surroundings, a few inhabit arid regions. Some species, such as the cuttlefish, are strictly carnivorous; many of the snails are herbivorous, and others feed as scavengers. The oyster and other species that are attached during adulthood feed on the floating organisms in the sea.

From the standpoint of their ancestry, the veliger larva of various marine forms bears close resemblances to the trochophore larva of the annelids. Whether or not they are direct descendants of the annelids is a matter for conjecture since some morphologists regard

this similarity in larval forms as an example of adaptive parallelism in a similar type of environment. Certainly, morphological evidence shows a close relationship.

Classification of this phylum is based on the nature of the foot, and respiratory organs; shape and structure of the shell; arrangement and structure of the nervous and reproductive systems.

Class I. **Amphineura**

Includes the Chitons, which are found abundantly on rocks between tide marks along the Atlantic and Pacific Coasts. Bilaterally symmetrical body; tentaculess head, eyes absent; shell, if present, consists of eight overlapping plates. Most species have a flattened foot but other species are slender and wormlike. *(Ischnochiton conspicuus.)*

Class II. **Pelecypoda**

Includes the bivalve mollusks, such as the oysters, clams, scallops, and cockles. More than ten thousand species have been described, of which approximately four-fifths live in the ocean. Division of the class into orders is based on gill characters. (Clams.)

Class III. **Gastropoda**

Includes the snails and slugs. Approximately fifty-five thousand species have been discovered and described. Shell, if present, univalve. (Snails.)

Class IV. **Scaphopoda**

Marine. Mantle edges grown together along ventral side forming tube, with a shell of same shape and open at both ends. Commonly known as tooth shells. Approximately 300 known living species. *(Dentalium.)*

Class V. **Cephalopoda**

Marine. The most highly organized of the mollusks. A definitely formed head is present which bears a pair of eyes that superficially resemble the eyes of vertebrates. The foot is modified into arms or tentacles. They are carnivorous animals and many of them are used as food by man. *(Nautilus, Loligo, Polypus.)*

Habitat and Behavior of the Clam

Mussels or clams are usually found partly buried in the mud, sand or gravel of ponds, lakes, or streams. By means of the muscular foot which is protruded from between the two valves at the anterior end of the shell they plow their way slowly through the stream or pond bed, feeding on the microscopic organisms in the

water. At the posterior end of the shell are two openings: the ventral siphon which pulls in food and water, and the dorsal siphon through which wastes and deoxygenated water are eliminated.

Movement is varied among the pelecypods. Scallops may move rapidly by suddenly contracting the valves, thus ejecting a jet of water. Oysters are motile in their larval stages but in the adult stage are attached to rocks and other objects. Many marine mussels are attached to objects on the bottom or along the shore. Attachment is made possible by the dissolution of a part of the under valve and adherence of a portion of the body thus exposed.

Anodonta
stewartiana

Quadrula
forsheyi

Proptera
purpurata

Amblema
costata

Leptodea
fragilis·

Carunculina
texasensis

Musculium
ferrissi
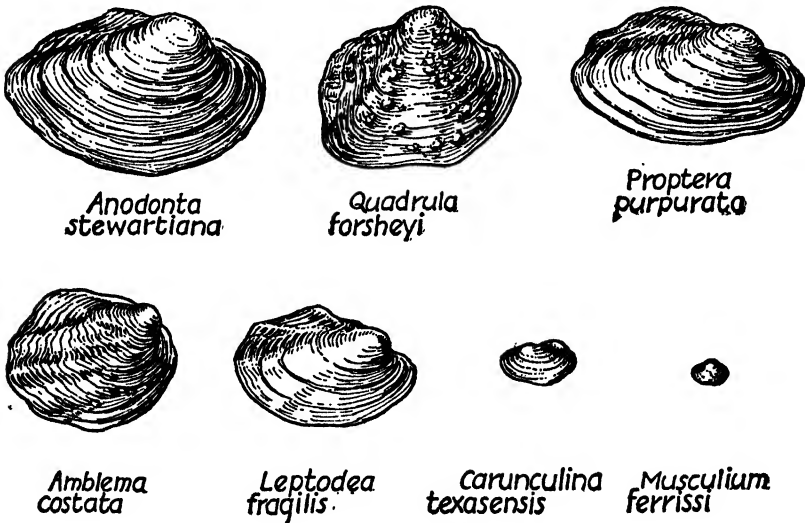
Fig. 142.—Some common fresh-water bivalves.

The life span of clams may be relatively long. It has been estimated that *Anodonta,* one of our common genera of fresh-water clams, attains its maximum growth in twelve to fourteen years.

External Features

Shell.—Unlike the snail whose shell is of one piece, the clam shell is composed of two parts called valves (hence, *bivalves*) which are attached together at the dorsal surface by a hingelike ligament. The oldest part of the shell is the umbo which is usually a rounded protuberance near the top of the valves and is frequently eroded

due to carbonic acid in the water. Extending out from the umbo on each valve in a concentric manner are the growth lines of the shell, evidenced as slight, medium, or heavy ridges.

The shell is covered by a horny, pigmented periostracum. Underlying this is the prismatic layer composed of carbonate of lime. The inner mother-of-pearl or nacreous layer consists of many thin, usually smooth plates, that in reflected light produce an iridescence in many species.
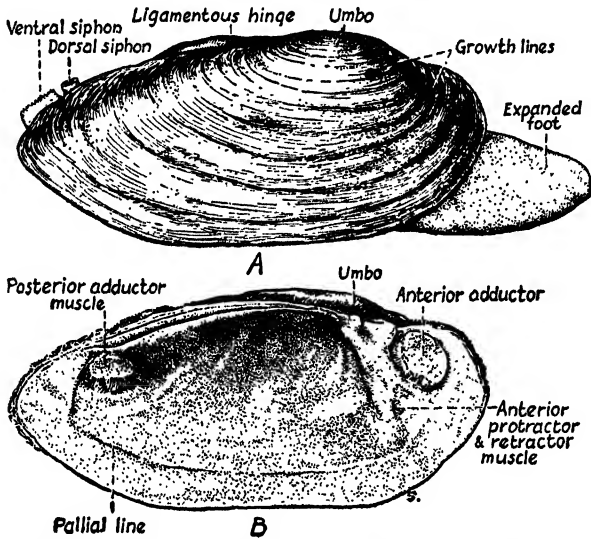
Fig. 143.—External (*A*) and internal (*B*) shell features of *Lampsilis anodontoides*.

Internal Anatomy

(Detailed description based on *Lampsilis*)

The valves are held together by two powerful transverse muscles, the anterior and posterior adductors. Upon cutting these muscles the shells gape open, exposing the underlying organs. The valves are lined with a mantle which secretes the shell. On the inner surface of each shell may be seen the curved pallial line which extends between the two adductor muscles and indicates the partial attachment of the mantle. Teeth which strengthen the closure of the shell may be present where the two valves come together. Between the two walls of the mantle is the mantle cavity which contains the leaflike gills, the foot, and visceral mass.

Digestion

During the activity of the clam a constant current of water is maintained in the mantle cavity. Food material is circulated forward to the mouth which lies between ciliated labial palps. Upon entering the mouth, food is passed through a short esophagus into the saclike stomach. Here it comes in contact with a digestive ferment produced by the digestive gland which is discharged into each side of the stomach through ducts. The crystalline style, a diverticulum of the intestine, and found only in mollusks, produces an enzyme mixed with the stomach content which undoubtedly
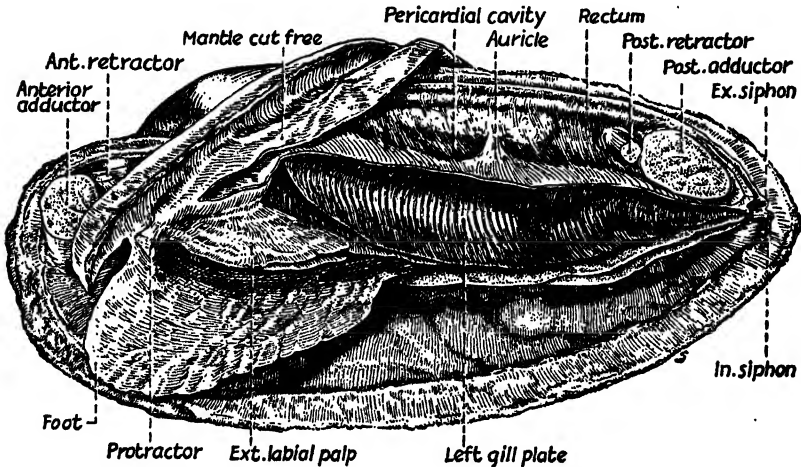
Fig. 144.—*Lampsilis anodontoides* with the left mantle partially removed and turned back to expose the underlying organs.

facilitates the digestion of carbohydrates. The food, having been mostly digested and partly absorbed in the stomach, is passed on into the intestine which makes one or more loops in the foot, passes through the pericardium and terminates in the anus near the dorsal siphon.

Respiration

Respiration is carried on through two pairs of vascularized gills which hang down into the mantle cavity on each side of the foot. Oxygenated water drawn in through the ventral siphon is passed through a rather complicated series of water tubes in the gills.

Oxygen is absorbed by the capillaries and carbon dioxide passed into the water where it is discharged to the outside through the dorsal siphon.

Circulation

The heart which is composed of a ventricle and two auricles lies in the pericardium. The ventricle, a muscular organ, surrounds the rectum and drives blood forward through the anterior aorta and backward through the posterior aorta. Both aortae give off arteries which ramify all parts of the body. Most of the returning blood is carried to the kidneys by means of the vena caval vein. Within the latter, nitrogenous wastes are removed, and the blood then flows to the gills through afferent branchial veins; after purification in the gills it is returned to the auricles by way of the efferent, branchial veins. The blood is colorless and contains several types of white corpuscles.

Nervous System and Sense Organs

Situated on each side of the esophagus is a cerebropleural ganglion, the two ganglia being connected by means of a cerebral commissure which passes above the esophagus. Each ganglion gives
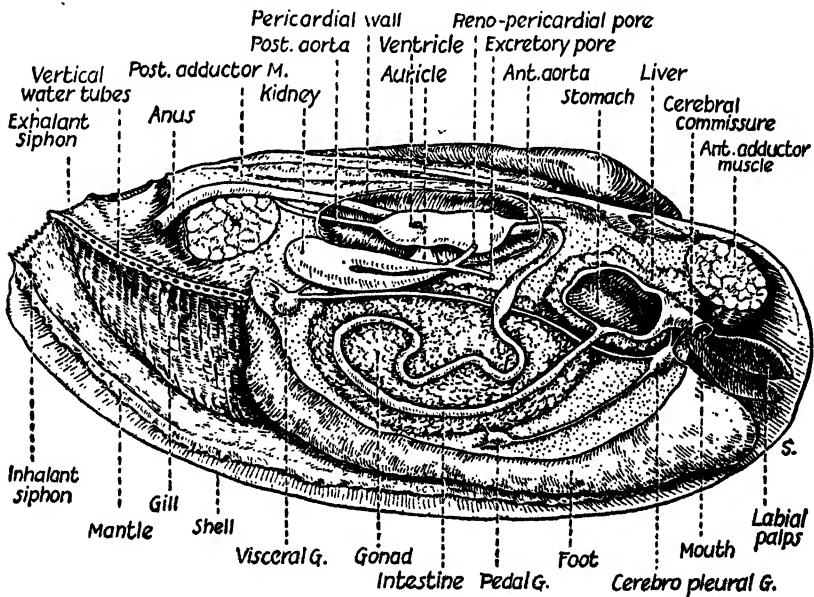
Fig. 145.—Internal anatomy of *Lampsilis anodontoides.*

off two nerve cords, one of which passes ventrally and posteriorly to the pedal ganglion situated at the junction of the visceral mass with the foot. The other nerve cord extends backward, terminating in a visceral ganglion which is usually located just ventral to the posterior adductor muscle. The visceral as well as the pedal ganglia are united.

The sensory organs of the clam are primitive. Covering each visceral ganglion is a patch of sensory epithelium called the osphradium, the function of which may be to test the purity of the water brought in through the respiratory system. A short distance back of each pedal ganglion is a statocyst which functions in equilibrium. It is composed of a small calcareous concretion, the statolith, which is surrounded by sensitive cells. In addition to the sensory organs named there are many sensory cells distributed along the mantle edges and elsewhere which probably react to light and touch.

Excretion

Paired kidneys lie on each side of the body just below the pericardium. Each consists of a glandular portion which excretes waste, and a thin-walled bladder that is connected with an excretory pore through which wastes are discharged to the outside.

Reproduction and Life Cycle

The small bivalves belonging to the family *Sphaeriidae (Sphaerium)* are hermaphrodites, but in the larger ones the sexes are usually separate. The paired gonads are situated in the foot; the testis is usually whitish in color and the ovary reddish. A short duct leads from the gonad and opens just in front of the excretory pore. Sperm are passed to the outside through the dorsal siphon and enter the female clam through the ventral siphon. The ova, having been discharged through the genital apertures, become lodged in various parts of the gills, depending upon the species. Within the gills the eggs are fertilized. Thus, the gills serve as brood pouches or marsupia and may become greatly distended due to the tremendous number (as many as three million) of developing embryos.

The small bivalve larva, which ranges in size from about 0.05 to 0.5 millimeter in diameter, is called a glochidium and has a single adductor muscle for closing the valves which may or may not be hooked. Extending out from the center of the larva is a long secre-

Life history of Lampsilis anodontoides.
(a) ♀ Clam burrowing in gravel floor of
    pool - discharging glochidia
(b) Gar parasitized by glochidia
(c) Section f. highly magnified showing
    glochidia in various positions.
(d) Encysted glochidia in fin of gar
(e) Young clam recently released from
    fish

Attachment of
glochidia

Glochidia stirred up
by fins of fish

Gravel substratum

Cloud of glochidia
discharged from ex-
halant siphon
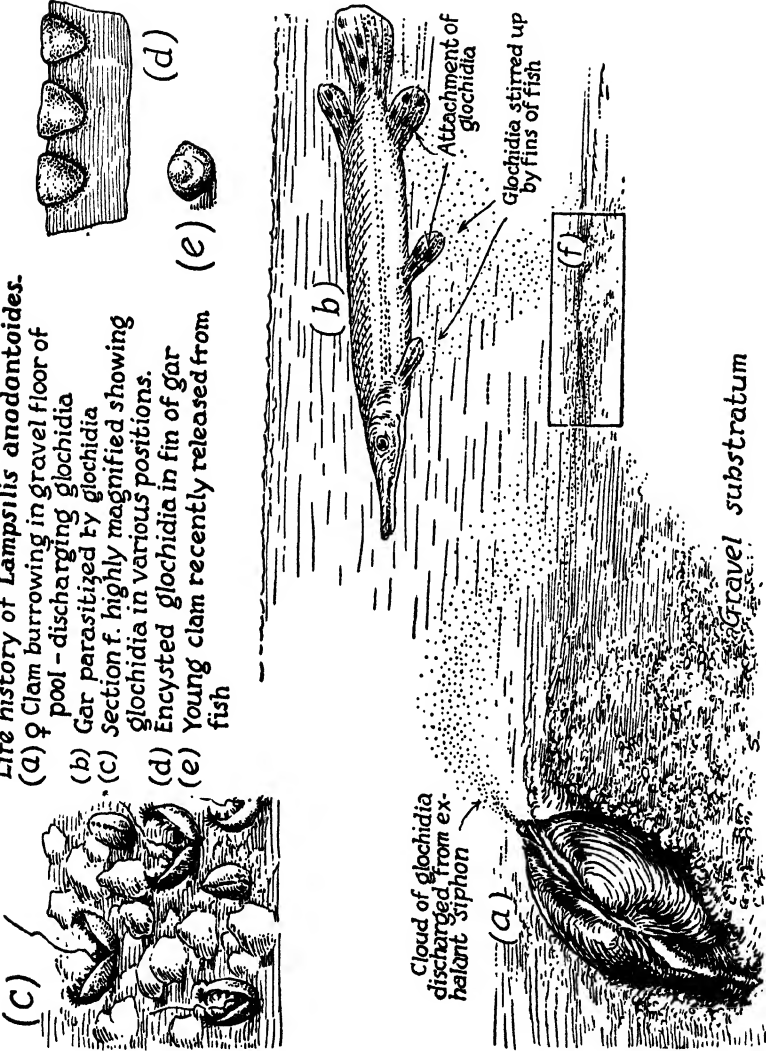
Fig. 146.—Life history of Lampsilis anodontoides.

tory thread, the byssus. In most clams the glochidia are discharged to the outside through the dorsal siphon. They fall to the floor of the river, pond, or lake, and lie with their jaws agape, or snap their jaws on any object. If the soft filament of a fish's gill or a fin of the fish comes in contact with the glochidium, it will close down upon it and remain attached if the fish is the suitable host for the particular species of clam. The tissues injured due to the attachment of glochidia produce by proliferation new cells which group up around and eventually cover the parasites. Thus a cyst is produced about the glochidium and within this structure the larval clam undergoes metamorphosis. It shortly breaks loose from its host, drops to the stream or pond bed, and leads an independent life. The rapid dissemination of mussels in a river system can be accounted for by the movements of their fish-hosts.

THE SNAIL

Habitat and Behavior

Snails occupy a variety of habitats. They occur abundantly in fresh water, salt water, brackish water, and thermal springs; they live in the arid sections of the country and occur abundantly in the tropics where certain arboreal forms are found. Some species belonging to the genera *Caecilianella* and *Helix* live underground, feeding on roots of plants; many other species live deeply embedded in moist humus. Certain species, such as *Helix hortensis* and *Helix aspersa*, excavate holes in rocks and live in them. Although most snails are not tolerant to extremes of cold, *Vitrina glacialis* lives in the Alps above the timberline where the rocks are covered with snow most of the year; even some of our fresh-water snails in this country, such as *Lymnaea palustris*, *Physa gyrina* and *Helisoma trivolvis*, when frozen gradually, can live at least several weeks in solid cakes of ice.

Land snails are most active either during a light rain or immediately following. In heavily shaded woodlands where surface moisture prevails, snails are active during the day as well as at night. The same species of snail that exhibits both diurnal and nocturnal activity in the woodland may show only nocturnal activity in an open, exposed habitat. Movements of most land snails appear to be coincident with moisture rather than darkness. Preceding prolonged periods of cold, land snails may move to protected places, such as beneath dead logs, dense mats of humus, crannies in or under

rocks, and there begin their period of hibernation. During this condition of torpidity the body of the snail may be well protected by one or several thin parchmentlike membranes called epiphragms which are stretched across the shell aperture. When warm weather arrives, the membranes are broken and the snail resumes its activities.

Water snails are active all four seasons, provided open water is available. Naturally their movements are slowed down in the winter due to cold, but when the pond or stream is frozen over, the movements of *Lymnaea, Physa,* or *Helisoma* may be observed through the ice. During periods of dry weather when ponds and creeks dry up, snails embed themselves in moss and mud, and in this manner are able sometimes to survive long periods of drouth. During this condition epiphragms may be formed in certain species (*Lymnaea palustris*), the same as in land snails; these structures probably function in retarding water loss.
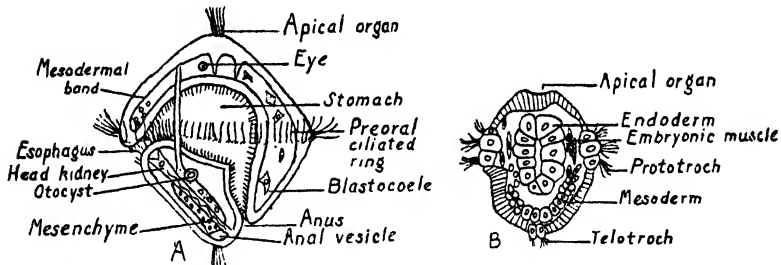
Fig. 147.—*A*, Trochophore larva of *Eupomatus* (a polychaete annelid), side view. (After Shearer.) *B*, Veliger larva of *Patella* (a marine snail) frontal section. (After Patten.) (Drawn by Joanne Moore.)

At least a few species of land snails possess a homing instinct. *Helix aspersa, H. pomatia,* and *Polygyra roemeri* have all been observed to occupy as "home" a definite place and go out from this "home" on nocturnal foraging trips, then return by sunrise the next morning.

The life span seems to vary considerably in snails; some of the aquatic genera, such as *Lymnaea* and *Helisoma* may live two to four years whereas some species of *Helix* may live to be six or eight years old.

Parasitism and commensalism are both exemplified by certain species of snails. A commensalistic relationship exists between the rare mollusk *Lepton squamosum* and the crustacean *Gebia stellata*.

Lymnaea
bulimoides
techella

Lymnaea
stagnalis
(Lymnaeidae)

Lymnaea
palustris

Physa
humerosa

Ferrissia
excentrica
(Ancylidae)

Physa
anatina
(Physidae)

Tropicorbis
liebmanni

Menetus
dilatatus

Helisoma
trivolvis
lentum
(Planorbidae)
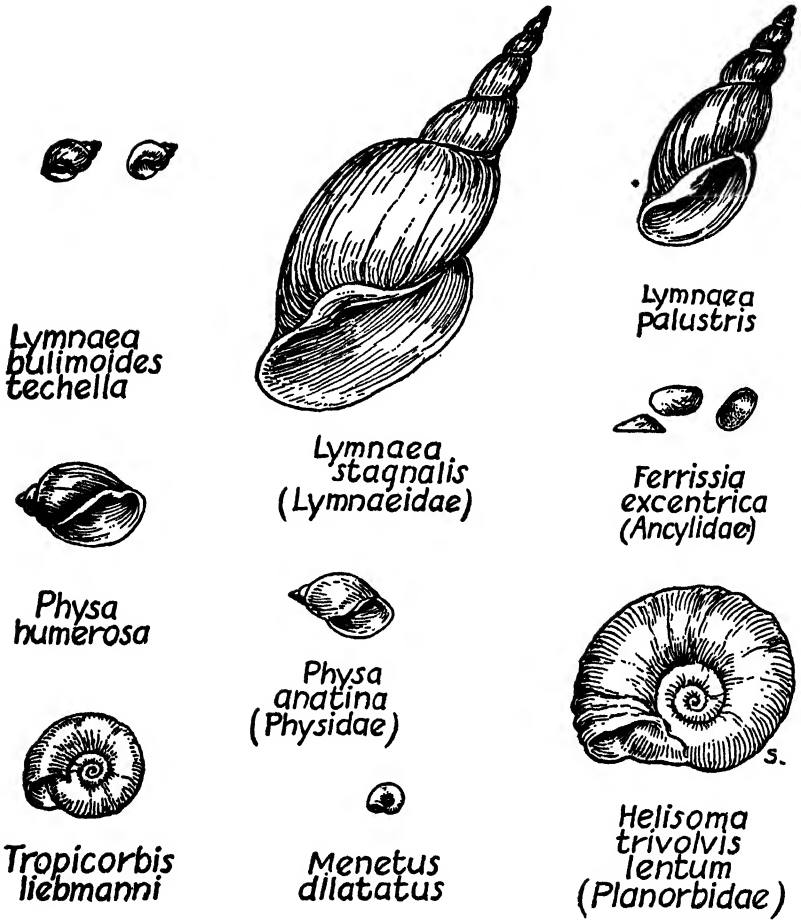
Fig. 148.—Some common fresh water pulmonate snails.

Humboldtiana
chisosensis

Polygyra
roemeri

Bulimulus
dealbatus
liquabilis

Rumina
decollata
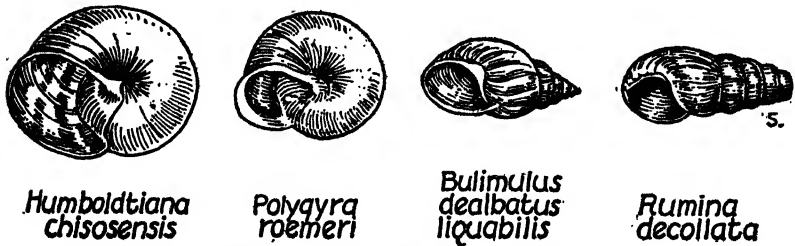
Fig. 149.—Common terrestrial snails.

The former feeds on secretions produced by the latter. A few species of sponges, echinoderms, annelids, and mollusks are parasitized by various species of mollusks. (Detailed Description, based on Helix.)

External Anatomy

Shell.—The *shell* of the snail may be in the form of a low, broad, or flattened spiral (*Humboldtiana chisosensis* and *Polygyra roemeri*), or a long, tapering spire (*Lymnaea stagnalis*); on the other hand, some shells are shaped like house rooms (*Patella* that lives in the sea
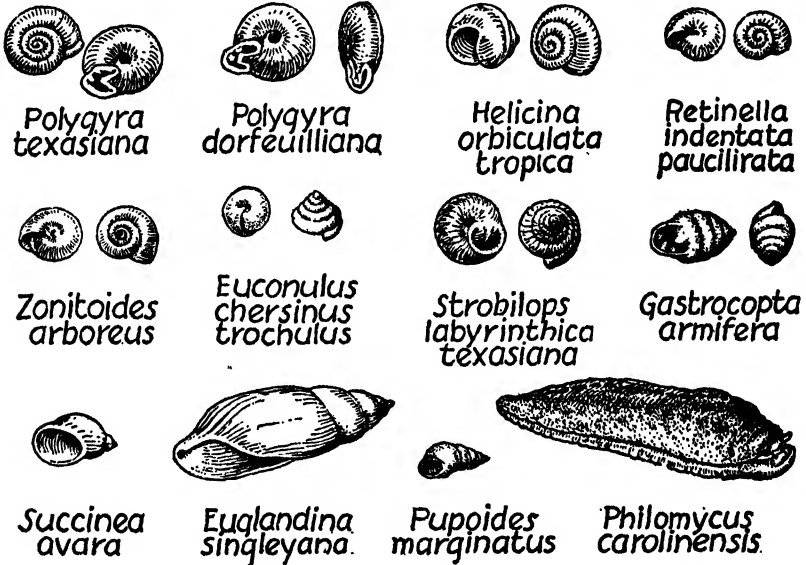
Fig. 150.—Common terrestrial snails.

or *Ferrissia*, a fresh-water form). The worm shell (*Vermetus spiratus*) is so loosely coiled that it superficially resembles a worm. Some shells, such as those belonging to the genus *Murex*, may have long peculiarly curved spines extending out from the main shell body that give to the shell a grotesque appearance. In the sea and land slugs the shell is either rudimentary, internal, or absent.

If the shell is held with the aperture toward the observer and the aperture is on the left, the shell is said to be *sinistral*; if on the right, the shell is *dextral*. Most species are normally dextral, but occasionally a reversal occurs which has been found to be inherited.

The shell which is largely composed of carbonate of lime is secreted by the mantle and usually consists of three layers. Embedded within the latter may be pigments that give the occasional brilliant colors to certain species. The thickness of the layers is dependent on the richness of lime salts in the environment; thus,
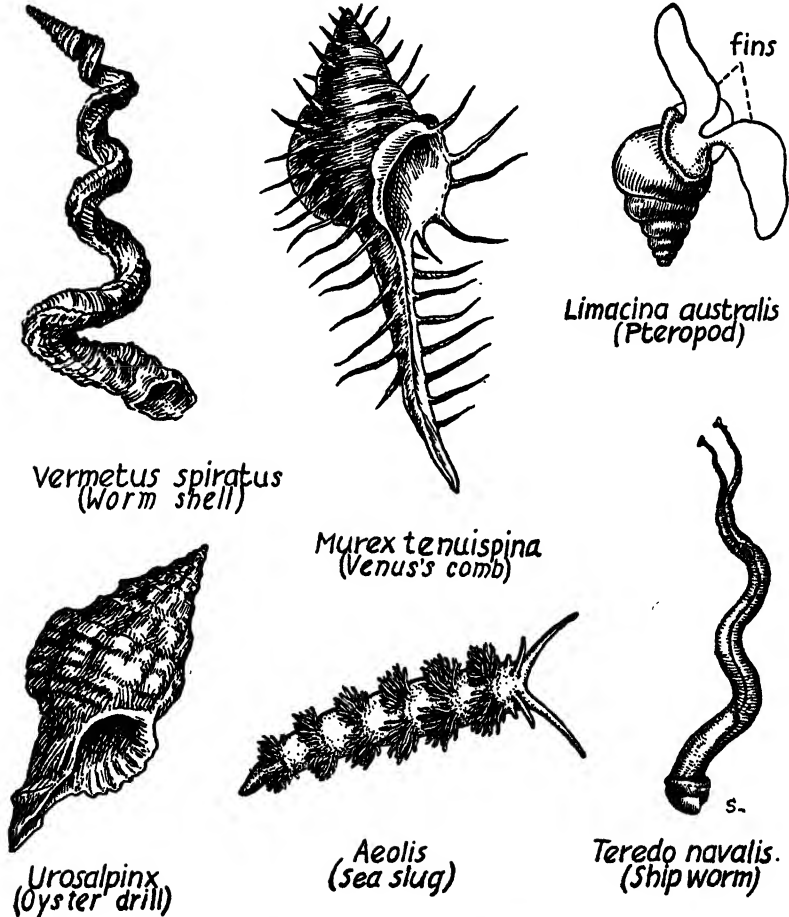
Fig. 151.—Marine mollusks.

snails living in an acid bog have thin transparent shells, whereas the same species inhabiting an area rich in lime salts have thicker, perhaps opaque shells. Certain species, such as *Polygyra roemeri*, *P. albolabris* and *P. texasiana* are capable of repairing broken shells if the damage is not too severe.

Body.—The *body* of the snail consists of a head, neck, foot, and visceral hump. The head of a land snail (*Helix*) has one pair of true tentacles which are probably sensitive to contact and smell, and a pair of stalked "eyes" which can possibly detect different light intensities, but are not sight organs. Our common genera of water
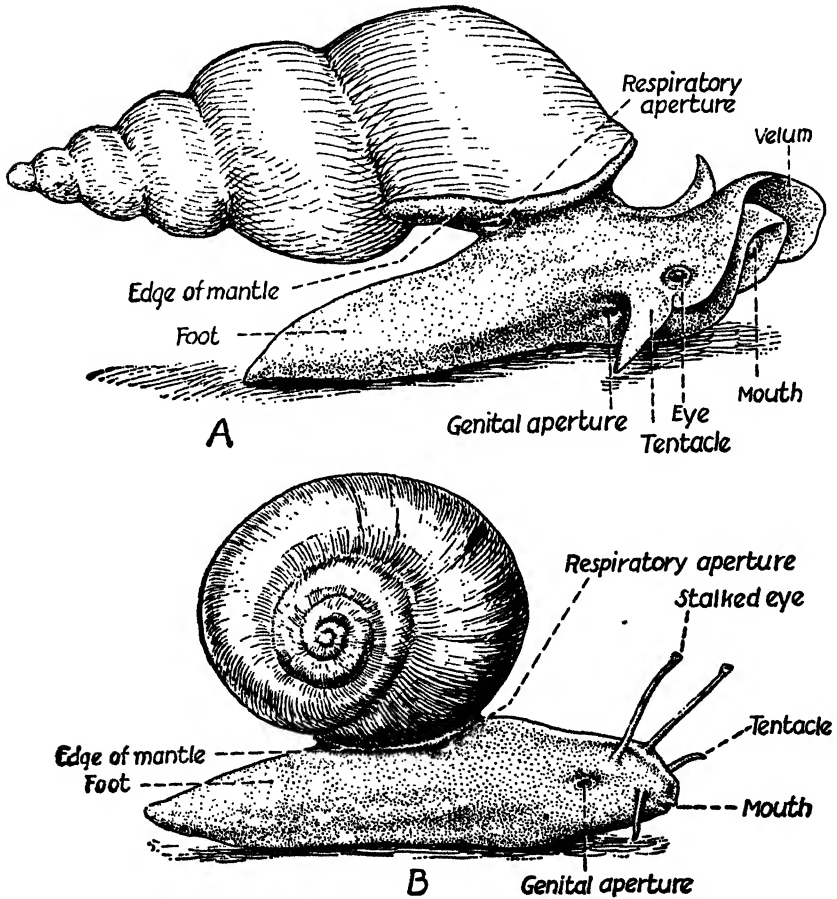
Fig. 152.—Fresh-water and land snails with bodies expanded. *A*, fresh-water snail, *Lymnaea*; *B*, land snail, *humboldtiana*.

snails (*Lymnaea, Physa, Helisoma*) have their eyes situated at the base of the tentacles. Just in front of and below the tentacles is a mouth. Located on the side of the head is the genital pore. The broad muscular foot is covered with a mucus-secreting integument.

Just ventral to the mouth is the opening of the pedal gland which deposits a highway of mucus over which the snail usually glides; the gliding movements are scarcely perceptible. In some marine snails the surface of the foot is covered with cilia, the latter facilitating movement. The visceral hump, which encloses the digestive, circulatory, respiratory, excretory, and reproductive systems, is protected by the shell which is lined with the mantle. A thick collar is produced where the mantle joins the foot, and just beneath this mantle-collar is the respiratory aperture; back of the latter is the anal opening.

Internal Morphology

Digestion.—Just within the mouth of a snail is a rounded organ known as the buccal mass. The latter is composed of a ribbon of minute recurved teeth, the *radula*, supported and moved by connective tissues and muscles. On the roof of the mouth is a horny jaw which pulls food into the mouth cavity. It is then rasped by the radula into fine particles and mixed with saliva which flows into the buccal cavity from salivary glands that lie on each side of the crop. The masticated food is then passed into the esophagus which widens, forming the crop. Here the food may be mixed with a brown liquid produced by the digestive gland which occupies most of the visceral hump. Enzymes produced by this gland convert starches into glucose, and, in the case of *Helix*, the ferment is powerful enough to dissolve the cellulose of plant cells, thus releasing the protoplasm so that it may be utilized. From the crop, food enters the stomach and is passed on into the intestine where absorption takes place. Feces are discharged to the outside through the anus.

Respiration

Land and most fresh-water pulmonate snails breathe by a fold of the richly vascularized mantle which has been modified into a primitive lung, whereas the branchiate snails breathe by true gills.

In all probability pulmonate snails that inhabit the deep water of lakes use the pulmonary sac as a gill and breathe like the branchiates. When the water is cold, it is not necessary for aquatic pulmonate snails to make periodic trips to the surface in order to renew their air supply, but when the water becomes sufficiently warm, cutaneous respiration alone is inadequate and the snail must come to the surface to get additional oxygen. The pulmonary sac

of aquatic pulmonates not only serves in the capacity of a gill or lung but also may serve as a hydrostatic organ, thus enabling snails to ascend to the surface by flotation. Such movements are probably made possible through contraction of the mantle walls, thus decreasing or increasing the volume of air. Most of the marine species are gill breathers, and some, such as the sea slugs, have external feather-like gills.
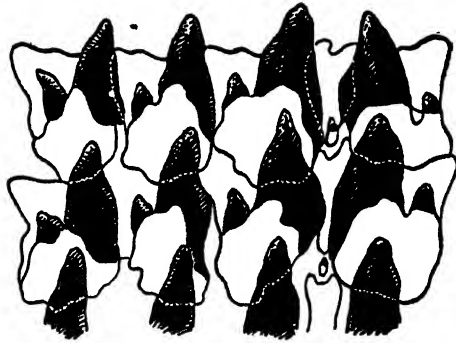
Fig. 153.—Arrangement of teeth in the radula of a snail.
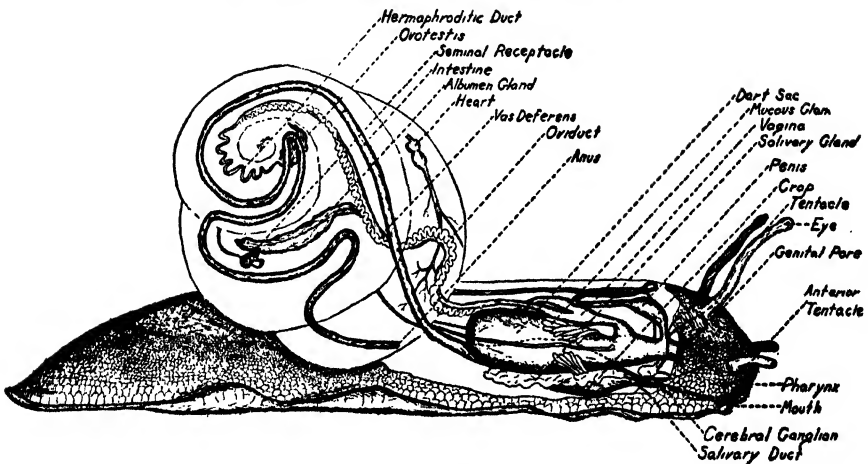
Fig. 154.—Internal anatomy of *Helix*. Shell removed.

Circulation

The blood of the snail consists of a plasma which is usually colorless, but in *Helisoma*, hemoglobin is dissolved in the plasma, thus giving it a red color, and in *Lymnaea* and some species of *Helix* the

blood has a bluish tinge due to the presence of a copper-containing pigment, hemocyanin. In the plasma, float the colorless corpuscles. The blood serves as a transporting medium whereby digested food, excretions, secretions, and gasses may be carried from one part of the body to another. The heart, which consists of an auricle and a ventricle, lies in the pericardial cavity. Blood is pumped from the ventricle through a common aorta which divides into two branches, one of which supplies the head and foot, and the other carries blood to the visceral hump. The terminal branches of these arteries communicate with a hemocoele or series of sinuses. Veins carry the blood from the hemocoele to the mantle walls where it is purified and then passed through the pulmonary vein to the single auricle and on into the ventricle.

Nervous System

Encircling the esophagus is a ring of nerve tissue which includes three pairs of ganglionic swellings: the *cerebral ganglia,* situated above the esophagus, supply nerves to the anterior regions of the body; the *pleural, pedal,* and *visceral ganglia* lie below the esophagus and are connected to the cerebral ganglia by commissures. From them, nerves extend out to the visceral hump and basal parts of the body. The arrangement of ganglia and their connectives is of taxonomic importance.

Excretory

The *kidney* is a yellow gland situated near the heart. Its *ureter,* a thin-walled tube, parallels the rectum and opens near the anus.

Reproduction and Life Cycle

Most fresh-water and terrestrial pulmonate snails, as well as the sea slugs, are hermaphroditic. The majority of the marine shelled gastropods and our fresh-water branchiates, such as *Pleurocera, Goniobasis,* and *Amnicola* are unisexual. The reproductive system of a unisexual snail is relatively simple but is exceedingly complex in the hermaphroditic species.

In bisexual (hermaphroditic) snails cross-fertilization ordinarily occurs. The ova, as well as spermatozoa, are produced by the ovotestis. Some snails are *protogynous,* since the ovotestis functions first as an ovary and later as a testis; others are *protandrous,* since male gametes are first formed, followed by the production of ova.

Spermatozoa pass from the hermaphroditic duct into the sperm duct, and enter the vas deferens which terminates in a muscular penis. By means of the latter organ sperm are transferred into the seminal receptacle of another snail. Ova are passed from the ovo-
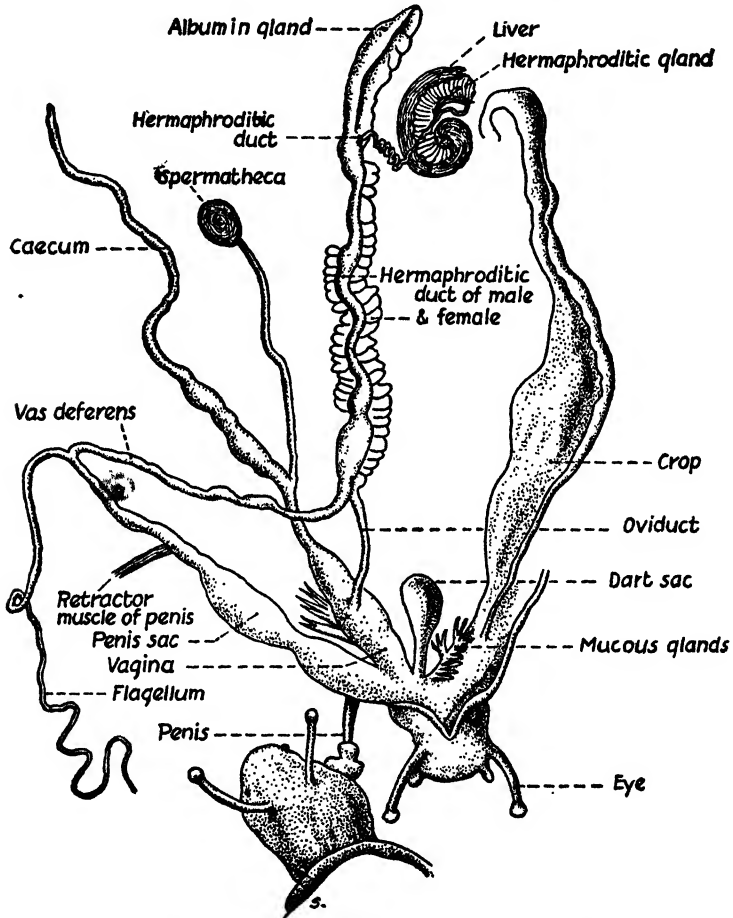
Fig. 155.—Genitalia of *Helix aspersa;* act of union. (Modified, after Cooke, Cambridge Natural History. By permission of The Macmillan Company.)

testis into the hermaphroditic duct, and from there into the oviduct which terminates in a thick-walled muscular vagina. During this journey the ova are fertilized by sperm from the seminal receptacle and coated with albumin from the albumin glands. Both the penis and vagina have a common genital opening to the exterior.
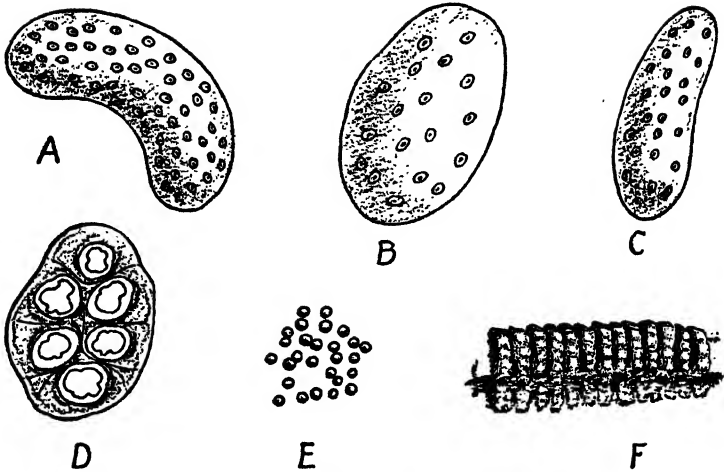
Fig. 156.—Egg masses of common snails. *A, Lymnaea* (fresh-water; gelatinous mass); *B, Heliosoma* (fresh-water; gelatinous mass); *C, Physa* (fresh-water; gelatinous mass); *D, Pleurocera* (fresh-water branchiate; tough gelatinous mass); *E, Polygyra texasiana* (terrestrial; eggs in cluster); *F,* egg capsules of *Busycon.*

Goniobasis comalensis
(Pleuroceridae)

Campeloma decisum
(Viviparidae)

Amnicola comalensis

Cochliopa texana
(Amnicolidae)
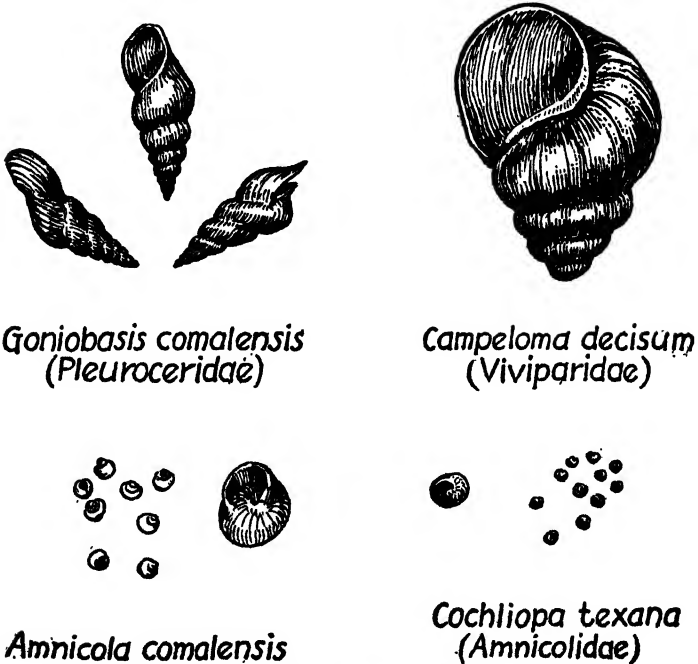
Fig. 157.—Some common fresh-water branchiate snails.

Most of the fresh-water snails deposit eggs in clear gelatinous masses on submerged objects, such as twigs and rocks. The land snails usually deposit their eggs singly or in clusters in well-protected places, such as in rooten wood or beds of humus. The eggs are covered with thin shells which prevent undue water loss. In some marine snails, such as *Busycon,* eggs are deposited in disc-shaped capsules which are spaced equally apart and held together by a tough band. Some snails, such as the fresh-water *Campeloma,* have a brood pouch in which eggs are deposited and the young are born alive. The latter is *ovoviviparous* reproduction in contrast to oviparous reproduction, as described in Helix.

Economic Relations of the Phylum

Mollusks have been used as food by man from the beginning of civilization. Oysters, clams, scallops, snails, and the arms of cuttlefish are found in the menus of peoples all over the world. It has been estimated that the oyster industry along the Atlantic Seaboard approximates 40,000,000 dollars annually. Along the Texas coast alone, Federal statistics show that 51,719 barrels of oysters were sold in 1932. Buttons are made from the shells of the large heavy river clams and along the Ohio, Missouri, and Mississippi rivers the button industry amounted to 5,000,000 dollars in 1931.

Within some of the clams are found pearls which are formed by some irritating particle, such as a parasite or sand grain that becomes lodged between the mantle and the shell. Iridescent protective layers of mother-of-pearl are deposited around the foreign particle, thus producing the pearl. The Japanese have been successful in artificially stimulating pearl production by planting small objects, such as pieces of mother-of-pearl, between the mantle and shell of pearl-oysters.

Pulverized clam shells are also being used as a calcium supplement to chicken feed. Shells have also been used as a medium of exchange. The wampum of the eastern coast of North America consisted of strings of cylindrical beads made from brightly colored clam shells. Shells have always been and still are used for ornamentation. Crushed shells are used in road construction.

Some mollusks are injurious to human interests. Among these might be mentioned the marine snail, *Urosalpinx cinerea,* which drills into and feeds on oysters and other pelecypods; the common

shipworm, *Teredo navalis,* attacks the wood of ships and pilings, making extensive excavations. Certain species of snails serve as the intermediate host of parasitic flatworms or flukes. The liver fluke *(Fasciola hepatica)* whose intermediate host is the small fresh-water snail, *Lymnaea bulimoides,* causes the disease, liver rot in livestock, particularly in the sheep.

Since shells are easily fossilized they serve as excellent guides to the geologists in determining the type of rock formation and relative age of the strata.

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CHAPTER XXII

THE CRAYFISH, A CRUSTACEAN ARTHROPOD

Arthropoda (är thrŏp' ŏ dȧ, joint foot) is the name of the largest known phylum of animals, and the crayfish is a member of this group. As the name implies, all representatives of the phylum have paired, jointed appendages and a definite tendency toward specialization of them. Their bodies are triploblastic, segmented, bilateral, and covered by a chitinous exoskeleton. The coelom is modified by a marked reduction as a result of specialized vascular spaces. The segmentation or metamerism of the body is expressed in a high degree in this phylum and there is a definite relation of appendages to segments. The segments have undergone greater specialization and greater regional differentiation than was the case in annelids. In forms where there is little or no differentiation of segments, the condition is referred to as *homonomous,* while a highly differentiated condition of segments as found in most arthropods is spoken of as *heteronomous.* This group has fairly distinct head, thorax, and abdomen. The appendages on various segments are typically homologous with each other. Some are modified as sense organs, others as mouth parts, others for walking, swimming, and reproduction.

The skeleton is entirely exoskeletal, composed of *chitin,* and fits exactly the shape and contour of the body. Since it is fairly unyielding to growth, it becomes necessary for the arthropod to shed the skeleton periodically during its growing periods. This molting or *ecdysis,* as it is called, is quite characteristic of many of the divisions of this phylum.

The circulatory system is of the open type, since there are large sinuses or spaces surrounding most of the organs instead of a continuous circuit of blood vessels. The nervous system is of a modified ladder type with a ventrally located cord. The digestive system shows specialization in that it is divided into distinct regions as an adaptation to special types of food which require mastication.

Classification

This phylum is divided into two sections and at least five classes; some authors recognize as many as eight. The sections are determined according to the means of respiration.

SECTION I. BRANCHIATA (brăn kĭ ā' tȧ, gill) gill-breathing, aquatic forms for the most part.

Class I. **Crustacea,** crayfish, crab, pill bug, barnacle, water flea, etc.
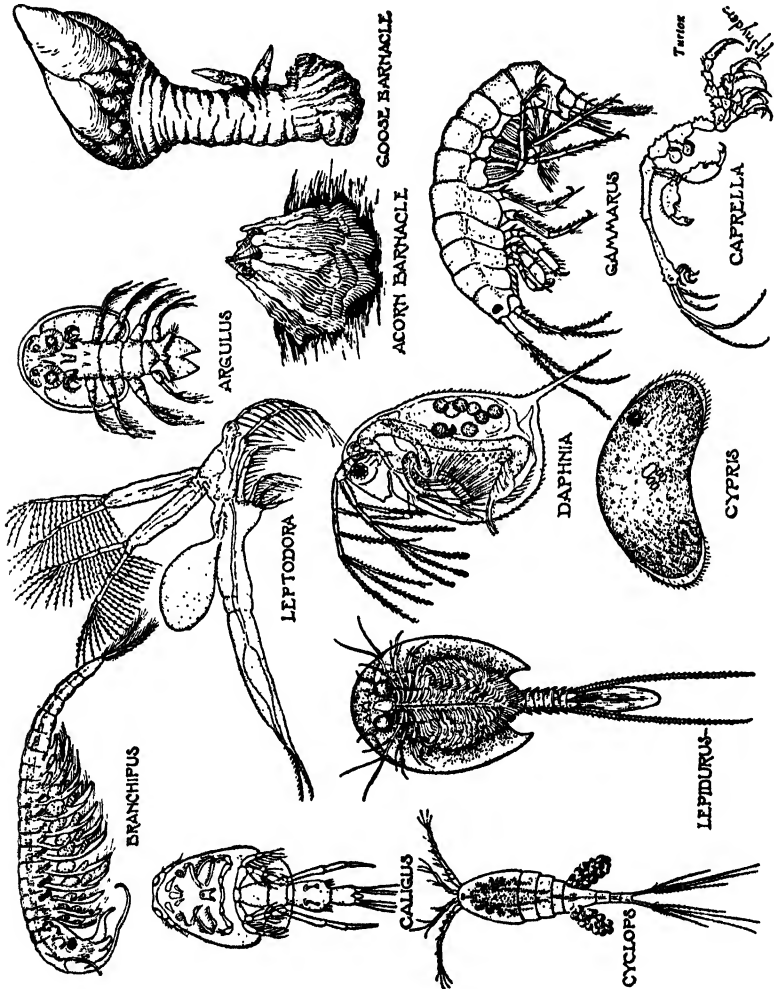
FIG. 158.—Representative Entomostraca. A valuable group because many of them serve as food for fish, young and old. (Courtesy of General Biological Supply House.)

SECTION II. TRACHEATA (trā kĕ ā' tȧ, rough) both terrestrial and aquatic arthropods which breathe by tracheae, book lungs or book gills. This section is divided into three divisions depending on the primitiveness of the characteristics.

Division A. PROTOTRACHEATA. The primitive form with some arthropod characteristics and certain annelid features, such as nephridia.

Class II. **Onychophora,** *Peripatus,* the wormlike arthropod.

Division B. ANTENNATA. More highly specialized forms with one pair of antennae.

Class III. **Myriapoda,** centipedes and millepedes (thousand legs) having one or two pairs of appendages on each segment.

Class IV. **Insecta,** beetles, bees, locusts, etc., all with three pairs of thoracic appendages and most of them with wings.

Division C. ARACHNOIDEA (ă ăk noi' dê â, spiderlike). A group without antennae but with tracheae, book lungs or book gills, and four pairs of thoracic appendages.
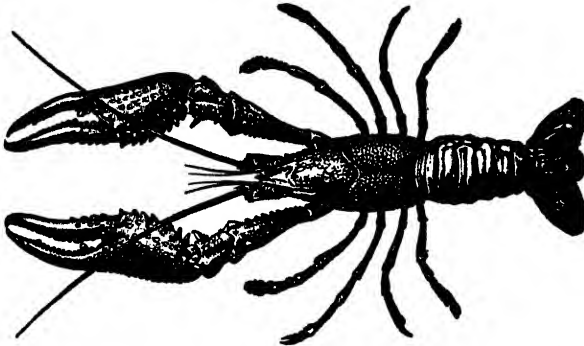
Fig. 159.—*Cambarus clarkii,* the swamp crayfish, common through southern United States.

Class V. **Arachnida,** spider, mite scorpion, king crab, etc.

This summary of the classification of the phylum has been included here in order that the student may realize its magnitude and the great variety of animals included. A more complete outline may be found in the chapter on animal classification. The number of species described under the phylum is approximately one-half million, and there are large numbers still undescribed and unnamed.

Since the **crayfish** represents a relatively simple type of arthropod and is so generally well known, it serves ideally as a representative species for a more detailed study. The two genera *Cambarus* and *Potomobius* are commonly found in the streams of North America. The former is distributed east of the Rocky Mountains and the latter on the Pacific slope.

Habitat and Behavior of Crayfish

For the most part crayfishes (crawfishes, crawdads, fresh-water lobsters) are inhabitants of fresh-water streams and ponds where there is sufficient calcium carbonate in solution for purposes of skeleton formation. These animals may be found moving about on the bottom, or they may be in hiding under some stone or log, or they may be in the mouth of a burrow beneath the water's edge. Some species carry air tunnels vertically from the original horizontal burrow to the surface of the earth and deposit mud around the opening of a tunnel. They are much more active at night than during the day. It is possible for them to walk about on the bottom of the stream or pond, moving the body in almost any direction. Their swimming habits are rather peculiar in that they dart backward through the water, as a result of the strong downward stroke of the tail. One stroke of the tail will carry the animal a yard and this is commonly sufficient to avoid the enemy. The daytime is usually spent in hiding under objects or in the mouth of the burrow. Crayfishes may at times desert their aquatic habitat and go foraging out over swampy land. In some localities certain species build their burrows down to the subterranean water table right out in the fields and become important pests. Sight, touch, and chemoreception are important senses in this animal.

The crayfish captures other animals, such as tadpoles, small fish, and aquatic insects, by waiting in hiding and suddenly seizing them. The crayfish is quite well protected, due to its protective color which matches the background, its chitinous skeletal covering, and its pinchers. In spite of this, they are captured by water snakes, alligators, turtles, fish (such as bass and gars), frogs, salamanders, herons, and raccoons in particular. Many have been exterminated by the drainage of swamps, and by their use as food for man.

External Structure

The chitin-covered body is divided into cephalothorax, abdomen, and appendages. The cephalothorax is a compound division of the body including the thirteen most anterior segments and is divisible into head and thorax. The boundary between these is marked by the oblique *cervical groove* on each side of the region. The shell-like covering, whose lateral edges are free, is known as the *carapace*. The portion anterior to the cervical groove is the head or *cephalic*

portion, while the portion posterior to the groove is the thorax. The anterior end of the cephalothorax is drawn out to almost a point, and this portion is called the *rostrum*. The mouth is located on the ventral side of the head portion and not at the tip of the rostrum where most people look for it. The lateral portions of the carapace are known as *branchial areas* or *branchiostegites,* and they cover the *gills*. Their ventral edges are free. On the ventral side of the thorax between the twelfth and thirteenth segments (about the level of the fourth walking leg) of the female is a cuplike pouch called the *annulus* or *seminal receptacle*. It serves in reproduction for the receipt and storage of spermatozoa.

The portion posterior to the thorax, which is frequently called "tail" by fishermen, is really the *abdomen,* and the tail proper is at the posterior end of this. The abdomen is divided into six typical segments and the terminal *telson,* which has no appendages but is often called the seventh abdominal segment. The *anus* is found on the ventral side of this part. The skeletal part of the abdominal segment consists of: the dorsally arched *sternum;* a thin, overhanging lateral plate, the *pleuron;* and the slender ventral *sternum* in the form of a narrow bar extending from side to side. A thin *arthropodial membrane* extends between successive sterna and allows for movement of the segments upon one another.

The *appendages* are paired, with one pair attached to each typical segment. There are nineteen such pairs. They are all developed on the same plan from the typical biramous (two branched) appendage. The five anterior pairs of abdominal appendages are quite typical of the primitive form except for the modification of the first two in connection with reproduction. This group is known as *swimmerets* or *pleopods* and all have the fundamental parts consisting of a basal *protopodite* composed of *coxopodite,* joining the body and the *basipodite;* the *exopodite* or lateral branch and the *endopodite* or medial branch each have many joints. The first two are much reduced in the female, but in the male the protopodite and endopodite are fused and extended to serve as an organ for transfer of spermatozoa. The posterior pair of swimmerets, attached to the sixth abdominal segment, are broadened into fanlike structures for swimming. They are known as *uropods* and have oval, platelike exopodite and endopodite. The posterior five thoracic appendages are the *walking legs or pereiopods.* These are uniramous due to the complete reduction of the exopodite. Each is composed of the two joints of the protopodite and five of the
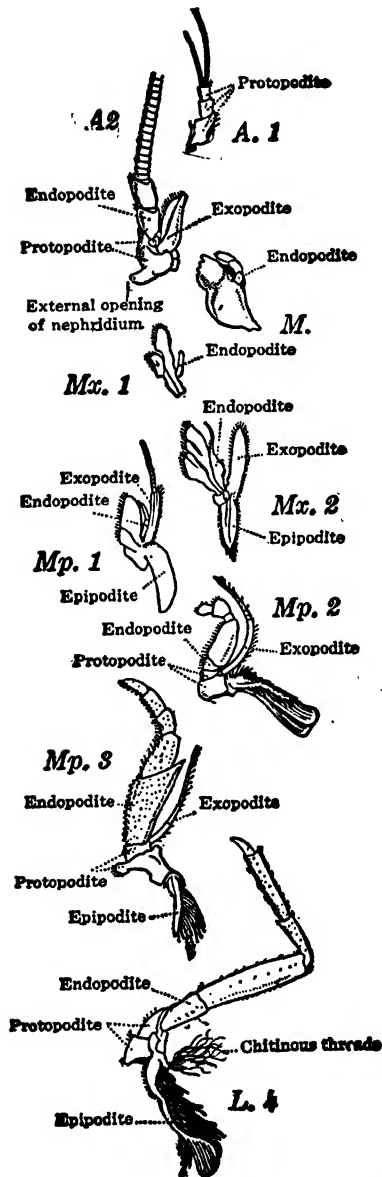
Fig. 160.—Cephalic and thoracic appendages of the crayfish, ventral view. *A.1*, antennule; *A.2*, antenna; *L.4*, fourth walking leg; *M*, mandible; *Mp.1*, first maxilliped; *Mp.2*, second maxilliped; *Mp.3*, third maxilliped; *Mx.1*, first maxilla; *Mx.2*, second maxilla. (From Newman, *Outlines of General Zoology*, The Macmillan Company, after Kerr.)

endopodite. Joining the *coxopodite* (first segment of protopodite) is a sheetlike structure which supports a gill and some *chitinous threads.* The three anterior walking legs possess *pinchers* or *chela* which are formed by the terminal segment being set on the side of the second segment. The walking legs are used in locomotion, offense, and defense. The three anterior segments of the thorax bear three pairs of biramous *maxillipeds.* The parts are quite typical in most respects. Each has an epipodite joining the basipodite and all except the first bear gills. These appendages are used in getting food to the mouth.

To the segments of the head are attached five pairs of appendages. Just posterior to the mouth and immediately in front of the first maxilliped are two pairs of *maxillae,* the second of which overlies the first. They are both leaflike and modified. The epipodite and exopodite of the second are fused to form a bladelike *bailer* or *scaphognathite* which fits over the gills and by its movement helps circulate the water for respiration. The endopodite is slender, but the protopodite is broad and foliate. The first maxilla is reduced to a leaflike protopodite and small endopodite. The jawlike mandible at each side of the mouth is composed of hard protopodite with teeth and a fingerlike endopodite, which is tucked under the anterior edge of the former. This appendage is used for chewing. In front of these are the *antennae* which are biramous and are sometimes called "feelers." They consist of the protopodite of two parts, a long, many-jointed, filamentous endopodite and a relatively short, fan-shaped exopodite. Anterior to these are the *antennules* which are biramous and feelerlike. The exopodite and endopodite are similar in these.

The principle of *homology* is excellently illustrated by the appendages of the crayfish. In general, homologous structures are those which have similar structure and similar origin but may have similar or different functions. By way of contrast, *analogous* structures are those which, when compared, show different structure and origin but similar function. During early development each of the appendages is similar to all others. Some become modified with development. Other illustrations are the human arm and the bird's wing. In organisms like crayfish where the appendages of successive segments are homologous to each other, the condition is spoken of as *serial homology.* Homologous structures are found in many animal groups and are used in establishing relationships. It has been suggested that the parapodia of Nereis represent possible forerun-

ners of crustacean legs. They are both typically biramous and both take about the same position on the body, as well as having a similar segmental distribution. There is also considerable similarity in their structure.

Internal Structure

Beneath the shell-like, chitinous exoskeleton there is a very representative set of systems. As in most higher animals the segmentation is retained in the muscular system, nervous system, and to a degree in the circulatory system. Earlier in the chapter it was pointed out that the coelom is modified as a provision for increased blood sinuses which have occupied much of the space.
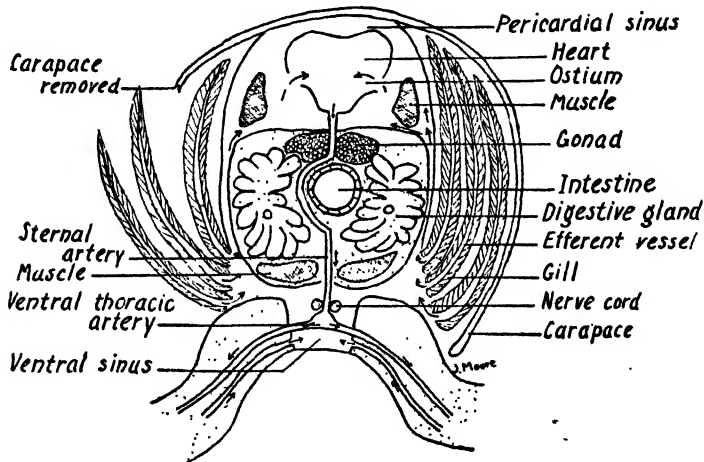
Fig. 161.—Diagram of a cross section through the posterior thoracic region of a crayfish. Arrows indicate the direction of flow of blood in the spaces and vessels.

Respiratory System.—Under the branchial areas of the carapace may be found the paired, feathery gills held in the *gill cavity* or *branchial chamber*. There are three types of gills present here: *pleurobranchiae,* attached to the sides of the thorax; *podobranchiae,* arising from the epipodites of the thoracic appendages; and *arthrobranchiae,* which arise from the coxopodites of the thoracic appendages. Several of the segments have lost the pleurobranchiae. The scaphognathite moves in such a way over the external surface of the gills as to move the water in an anterior direction. The water is brought under the free edge of the branchiostegite or branchial area of the carapace and moved forward to be discharged by an anterior aperture. An almost constant stream of water is pumped
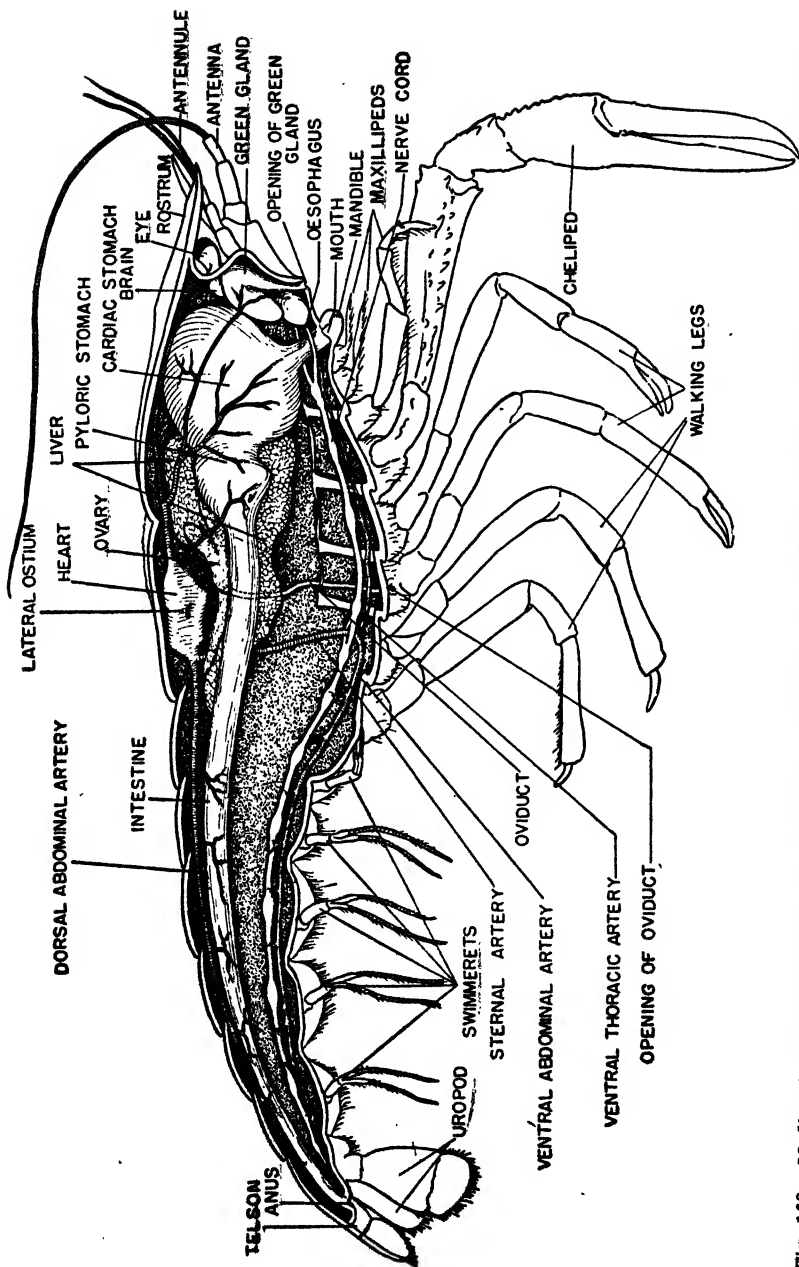
Fig. 162.—Median longitudinal section of crayfish, showing internal organs. (From Parker and Clarke, *Introduction to Animal Biology*, The C. V. Mosby Company.)

over the gills to facilitate the exchange of oxygen and carbon dioxide between the blood in the capillaries of the gills and the surrounding water. The aerated blood is then carried to all of the tissues of the body.

The **digestive system** is in the form of a modified canal and is composed of mouth, esophagus, stomach, and intestine. The *mouth* opens between the mandibles on the ventral side of the third segment. From this the short, tubular *esophagus* leads dorsally and joins the ventral side of the stomach almost directly above the mouth. This larger anterior portion of the stomach is the *cardiac chamber*. Within its wall are a number of hard chitinous bars, known as ossicles, which bear teeth capable of mastication of food when moved over each other by the muscular activity of the wall. This grinding apparatus is known as the *gastric mill*. Between the cardiac chamber and the posterior or *pyloric chamber* is an arrangement of bristles which serve as a strainer that allows only properly masticated food to pass through. The pyloric chamber is considerably smaller and curves downward to continue posteriorly as the tubular intestine which extends almost directly posteriorly through the center of the abdomen to the *anus* in the last segment. Large *digestive glands* (hepato-pancreas) lead into the pyloric chamber through hepatic ducts. The secretion of these glands contains digestive enzymes.

The **vascular system** consists of a heart, the pumping organ; the *arteries,* definite vessels; the *sinuses,* a series of blood spaces; and the *blood* which circulates. It consists of the fluid plasma containing white corpuscles but without red ones. The hemocyanin which absorbs oxygen is dissolved in the plasma. Fresh blood is almost clear and colorless, but it takes a blue color after standing in the air for a short time. The *heart* is somewhat flattened and angular in outline, and has a muscular wall which is perforated with three pairs of slitlike ostia. When the muscular wall of the heart is relaxed, the slits open, and blood is drawn in from the surrounding *pericardial sinus* in which the aerated blood accumulates. When the heart contracts, blood is forced into the anterior region of the body through the single *anterior median artery,* paired *antennary,* and paired hepatic arteries all of which arise from the anterior end of the heart. The large *dorsal abdominal artery* extends from the posterior tip of the heart posteriorly through the abdomen just dorsal to the intestine. It supplies the intestine and muscles of the body wall. The *sternal artery*

is a large branch arising from the dorsal abdominal artery just after it leaves the heart. It passes ventrally through the nerve cord and divides into a posterior, *ventral abdominal artery* and an anterior, *ventral thoracic artery*. These branches carry blood to the ventral portions of the body. Besides the pericardial sinus already mentioned, there are others returning the blood to this one. The *sternal sinus* is the main one, and it is located beneath the thorax. From it
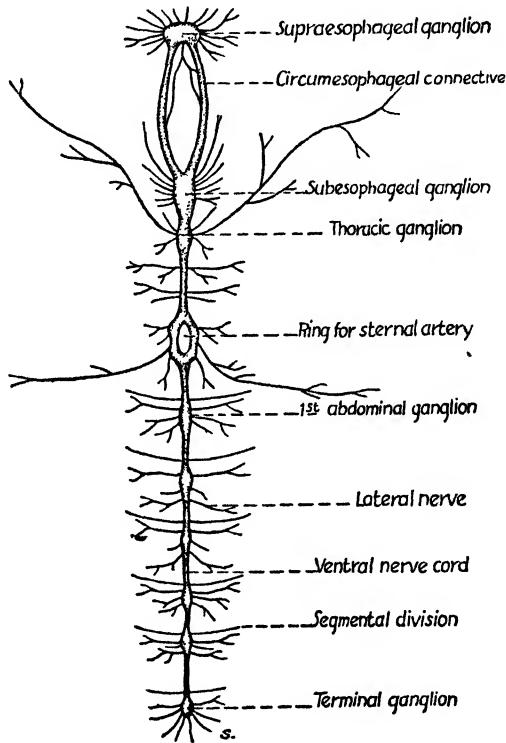
Fig. 163.—Dorsal view of the nervous system of crayfish. The subesophageal ganglion merges with the anterior thoracic ganglia.

several branches lead into the gills. This provides for a course through the gills. From them blood is collected by branchio-cardiac canals and delivered to the pericardial sinus. A *perivisceral sinus* surrounds most of the alimentary canal and collects the venous blood from it. This kind of system is called the *open* type because of the large irregular spaces or sinuses instead of an evenly constructed set of veins which make a complete circuit of the course.

The **excretory system** consists principally of a pair of large bodies (green glands) located in the ventrolateral portion of the head. These are richly supplied with blood and draw the nitrogenous wastes and excess water from the blood to deliver them externally through *excretory pores* located in the coxopodites of the antennae.

The **nervous system** is of the same structural plan as that of the earthworm, which is a modified "ladder type." The two longitudinal cords have come together in the ventral line and run the entire length of the body to form a *ventral nerve cord* with ganglia. This arrangement constitutes the central nervous system. The ganglia of the anterior three segments are fused into the "brain" or *supraesophageal ganglion* which is located anterior to the esophagus and is joined to the cord by two *circumesophageal commissures* or *connectives,* one passing on each side of the esophagus. From this dorsal ganglionic mass, *nerves* pass to the eyes, antennae, and antennules. The most anterior portion of the ventral cord receives these commissures. This portion, which consists of the fused ganglia from segments three to seven, is known as the *subesophageal ganglia.* Nerves go from it to the mouth parts, first and second maxillipeds, green glands, esophagus, and muscles of the thorax. Each segment posterior to the subesophageal ganglia possesses a segmental ganglion with branches to its respective appendages and muscles. The *sense organs* include antennae, antennules, sensory hairs, statocysts, and eyes. The *antennae* are tactile organs (sensitive to touch), the endopodite of which is a relatively long jointed filament. The exopodite is much shorter and fan-shaped. The basipodite and coxopodite are closely fused to the ventral side of the cephalic region. An excretory *pore* opens to the exterior through the coxopodite of each antenna. The hairlike processes along the edge of the carapace, on the legs, and other parts of the body are also sensitive to touch. The *antennules* are tactile and each has two slender filamentous processes, the exopodite and endopodite. In addition to these slender jointed processes each antennule has a saclike *statocyst* in its coxopodite. This structure is an infolding from the outside and is lined with exoskeleton and sensory hairs. Inside of each are small particles of solid material, such as grains of sand, which are called statoliths. As the animal changes its position the statoliths move about inside of the statocyst and stimulate the sensory hairs. From these stimulations the crayfish is able to determine its orientation in space

i.e., it knows whether it is in normal walking position, on its back, or standing on its head. These organs serve for equilibrium. When the crayfish molts, the statocysts are temporarily lost and new ones form as the new skeleton develops. If there are no solid objects in the water in which a crayfish lives during molting, there will be no statoliths in the statocysts and the animal has an impaired sense of equilibrium. Experimenters have placed only iron filings in the water at such a time and the animals present have used them for statoliths. By bringing a magnet near the crayfish in this condition the statoliths are moved and the animal goes through numerous peculiar contortions in attempting to respond to these stimulations of orientation. Besides the above functions the antennules provide the chemical senses of smell and taste.

The *eyes,* which are of the compound type, are mounted on movable stalks, one on each side of the head region. They are described as compound because each one is composed of a large number of individual sight units, each of which is essentially an eye. Each of these units is called an *ommatidium,* and the crayfish has about 2,500 in its eyes. A single one is rather spike-shaped, tapering from the broader superficial end to the rather pointed internal extremity. A single ommatidium has an outer *cornea* which is transparent and supported by some *corneagen cells* on the *vitrella.* Beneath this is the rather long *crystalline cone* beneath which is the rhabdom, another lenslike structure. Surrounding the latter are sensory cells making up the *retinula.* The wall of the ommatidium possesses pigment cells along the sides of the crystalline cone and in the retinula. The distribution of the pigment varies with the intensity of the light. The stronger the light the more these cells are expanded and the more direct must be the ray of light to reach the retinula, because the possibility of reflection within the ommatidium is reduced. In dim light the pigment is concentrated partly toward the outer and partly toward the basal portion of the ommatidia which allows more refraction of rays by the crystalline cones and a combination of images in several adjacent units. In brighter light only the ray from directly in front of the cornea will reach the retinula and stimulate the nerve cells there. These cells are connected internally with the optic nerve. The type of vision produced in the compound eye is "mosaic" in that there is registered only a single image by the eye. Each ommatidium which is in focus on the object registers an image of that part. As the object moves, new ommatidia are

stimulated and movement is indicated by the rate of stimulation of successive ommatidia. The farther the object is from the eye, the fewer ommatidia will be stimulated. The crayfish eye is often termed a modified appendage because an antennalike structure will regenerate in case an eye is mutilated.
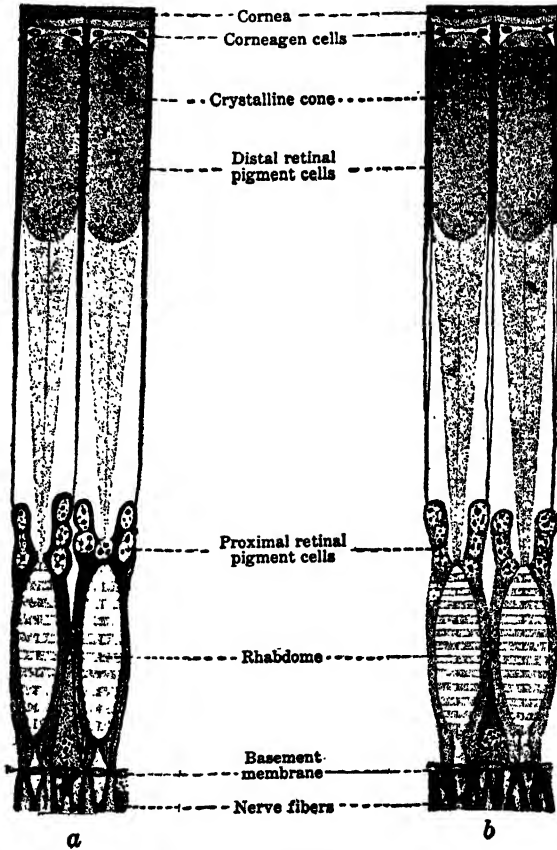
Fig. 164.—Longitudinal section of ommatidia from eye of crayfish. *a*, Position of pigment when light is present; *b*, position of pigment when in the dark. Notice that in the latter the distal pigment is in the outward position and the proximal pigment is concentrated inwardly. (From Hegner, *College Zoology*, The Macmillan Company, after Bernhards.)

Metabolism

The crayfish ingests principally flesh from bodies of fish, snails, tadpoles, insects, and other animals, some caught alive and others found dead. The maxillae and maxillipeds hold the morsels while

they are crushed by the mandibles. Mastication continues in the cardiac chamber of the stomach and chemical digestion begins in the pyloric portion. The digestive juices possess enzymes which convert the food into soluble form, and as it passes along the intestine, it is absorbed by the blood and distributed to the tissues over the body. This conversion of food material into protoplasm is *assimilation*. The external phase of respiration has put oxygen in the blood, and it is distributed throughout the protoplasm of the cells. The energy stored in the food material is released or converted to kinetic form by union with the oxygen (oxidation) in the protoplasm. From this union there is excess heat produced. Mechanical and chemical activity is the result of the harnessing of this energy. As a by-product of this *catabolism,* excretory materials, such as excess water, urea, uric acid, and other substances are formed in solution and are collected by the blood. The green glands relieve the blood of these and deliver them to the exterior. Of course growth results when excess food materials are built into the cells at times when the rate of anabolism exceeds that of catabolism.

Reproduction

These animals are dioecious (sexes separate) and the mating takes place either in the spring or fall or perhaps both. The spring hatch become well developed before winter. The eggs fertilized in the fall may not be laid before spring.

In the case of *Cambarus clarkii* the adults retire to holes or burrows at the water's edge during the summer. It is here that the eggs are laid and carried by the female until after hatching; then the young cling to her swimmerets. In late summer or fall, soon after the young hatch, the adults become very migratory at night, particularly in rainy weather. In this way they help to distribute the young to new water holes.

The *female reproductive organs* are composed of a bi-lobed *ovary* located beside the pyloric chamber of the stomach and beneath the pericardial sinus. During development the eggs appear in the ovary. Two oviducts lead, one from each side of the ovary, to a genital pore in the coxopodite of the third walking leg (pereiopod) of each respective side. The ova develop in follicles in the ovary. The maturation divisions (oögenesis) take place here and, when mature, the eggs break into the central cavity of the ovary, from which at the time of
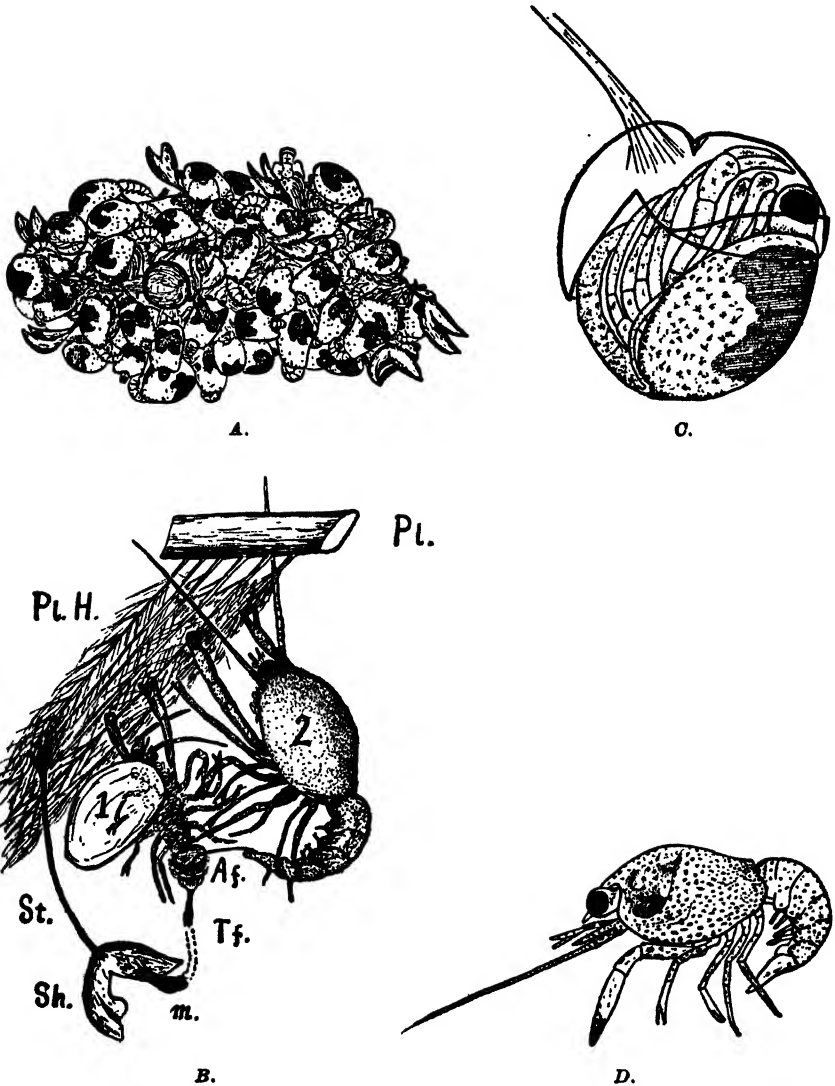
Fig. 165.—Development of the crayfish. *A*, Young crayfish clinging to swimmerets of mother. *B*, Second larval stage (*2*) attached by its chelipeds to hairs (*Pl.H.*) on swimmeret (*Pl.*) of the parent. The molted shell of the first larval stage (*1*) is clinging by chelipeds. A portion of the egg-membrane (*m*) and shell (*Sh.*) are still attached to the swimmeret by a stalk (*St.*). When the first larva hatches it remains attached to the shell by a filament (*Tf*). The second larva is similarly attached to the molted shell of the first by filament *Af*. By means of these filaments the young remain fastened to the mother during development. *C*, first larva hatching through shell. *D*, the second larva. (Reprinted by permission after Andrews, 1916, Smithsonian Contributions, Vol, 35.)

laying, they pass out through the oviducts. The *male reproductive organs* are composed of the bi-lobed *testis* located dorsal to the pyloric stomach and ventral to the heart. Spermatogenesis takes place here and mature spermatozoa are shed. The tubular *vasa deferentia* extend posteriorly and ventrally to open externally on the coxopodite of each fifth walking leg. During copulation (mating) the sperm cells are transferred by the two pairs of anterior swimmerets (pleopods) of the male from the apertures of the vasa deferentia to the annulus (seminal receptacle) on the ventral side of the thorax of the female. When the mature eggs are later laid, they are likely fertilized as they pass posteriorly in the groove between the legs on the two sides of the body. The fertilized eggs are cemented to the swimmerets by a secretion and appear much as small bunches of shot-sized grapes hanging there. The later development continues here, and they are aerated by movements of the swimmerets through the water.

Cleavage divisions follow over the surface of the egg and the embryo develops on one side of the mass. The body form with segments and limb buds appears, and hatching occurs in from five weeks to two months. The larvae grasp the swimmerets with their chela and remain with the mother for about a month. Two or three days after hatching they pass through the first *molt* or *ecdysis;* that is, they shed the outer cuticle. This is repeated seven or eight times during the first season to allow for growth. The average life span of the crayfish that reaches maturity is about four years.

Regeneration and Autotomy

This power is limited to the appendages and eyes in this animal, but it is quite well developed in these parts. The possibilities and rate of regeneration are greater in younger animals. Mutilated or lost legs or mouth parts are readily restored.

The genus Cambarus has the ability to allow a walking leg to break off at a certain line or joint if it is caught or injured. A new leg will develop from this stump. This phenomenon is called *autotomy*. There are special muscles to help in this and a membranous valve stops the passage of blood through the leg, thus preventing excessive bleeding. Bleeding will stop more quickly if the break occurs at such a point than it would otherwise. Autotomy often makes it possible for the animal to sacrifice a leg to save its life.

Economic Relations

Crayfish and the entire class Crustacea are of considerable importance to man. The crayfish, lobster, crab, shrimp, and others are used directly as food to the extent that it is an industry valued at several million dollars annually in the United States. The numerous smaller genera, like *Daphnia, Cyclops, Cypris, Gammarus, Asellus,* and *Eubranchipus,* comprise a large part of the food of many of our food fish either directly or indirectly. The more minute ones also feed many clams and oysters and finally end in human consumption. The shrimp and crab fisheries are the most important ones concerning crustacea on the Texas coast of the Gulf of Mexico. In the Mississippi Valley and on the Pacific Coast the crayfish is used extensively as a food. It becomes a serious pest in the cotton and corn fields of Louisiana, East Texas, Mississippi, and Alabama. They fill the swampy land with their burrows where they come up to the surface and eat the young plants. Frequently their burrows do serious damage to irrigation ditches and earthen dams. Crayfish also capture numerous small fish which are either immature food fish or potential food of such fish.

Characterization of Other Crustacea

Besides crayfish the order Decapoda includes lobster, shrimp, and crab. They all have ten walking legs, for which they are named. The crayfish and lobster are very similar except in size. The shrimps and prawns are marine and resemble the crayfish except that they do not have the great pinchers (chela) and the abdomen is bent sharply downward. The crabs are quite different in shape in that the cephalothorax is broader than it is long, the abdomen is poorly developed, and folded sharply beneath the thorax. Crabs of different kinds vary in diameter from a few millimeters to several inches. There are four species of swimming crabs in the Gulf of Mexico, of which the *blue* or *edible* crab *(Callinectes sapidus)* is the most important and best known. The lady crab and calico crab are also interesting species. When the blue crab is captured at molting time it is called the soft-shelled crab. At other times it is the hard-shelled crab. They may be caught in baited nets or on pieces of meat on a line with which they are brought to the surface and lifted out in a dip-net. The hermit crab (genus *Pagurus*) is smaller and lives in empty gastropod shells by backing into the shell

and carrying it around. Due to the cramping and inactivity the abdomen has become soft and partly degenerate. The fiddler crab (genus *Uca*) is another very abundant form found on the coast of the Gulf of Mexico and elsewhere. These are small semiterrestrial crabs which burrow in tunnels, and may thus honeycomb large areas of salt marshes. They can run quite rapidly, often moving sidewise, and they are peculiar in that one pincher of the male, usually the right, is much enlarged. This gives the appearance of a fiddle and the other, reduced pincher resembles the bow. The large pincher is used in a nuptial dance, and occasionally a large number of these little crabs will be seen raising and lowering these enormous pinchers in concert.

Asellus communio is a common fresh-water form found in streams and pools. A salt-water genus, Idotea, is found in the ocean. The pill

.Asellus

Fig. 166.—Asellus, a common fresh-water crustacean. (Courtesy of General Biological Supply House.)

bug *(Armadillidum)* and the sow bug *(Oniscus asellus* or *Porcellio)* are terrestrial, living in damp places under logs, stones, or heavy vegetation, and in cellars or greenhouses. Their legs are arranged in two groups, which point in opposite directions. Respiration is carried on by gills on the ventral side of the body and for this reason they must live in moist places. They are a garden pest in that they eat leaves of delicate plants. There-are a number of aquatic forms which are parasitic on fish and others, such as the gribble (Limnoria), which tunnel in submerged wood.

The *amphipods* are sand and beach dwellers which may be found burrowing or jumping around on the seashore or walking around on the bottom in fresh water. *Gammarus* is the-best known freshwater form. The legs of representatives of this order are divided

into two groups, with the legs of each group pointing toward each other. These are of particular value as fresh-water fish food.

Entomostraca as a group is composed of many smaller crustaceans occurring in great numbers in both marine and fresh waters. The *fairy shrimps (Eubranchipus)* are delicate, transparent and feathery appearing. They are about three-fourths of an inch in length. They swim with the ventral side up and their long, leaf-life appendages hang from the body. These appendages serve also as respiratory organs. They live in cool streams in the spring and fall, but the summer is passed in the egg, which can withstand complete dryness. Many of them are parthenogenetic, hence, males are rare. The common marine form is *Artemia,* often called brine shrimp.

The *water fleas* including *Daphnia* of order Branchiopoda, *Cyclops* and *Diaptomus* of order Copepoda and other small crustacea constitute an important common group. Daphnia is one that is enclosed in a delicate bivalve shell. The second pair of antennae are very large and are used in swimming. The shell is beautifully marked and terminates in a caudal spine. They are only about one-tenth of an inch in length. Cyclops is another common freshwater form with the antennae shorter than the cephalothorax whose body length is also about one-tenth inch. It has a single median eye, and the females frequently are seen with a pair of egg sacs attached at the base of the abdomen. *Diaptomus,* another Copepod, is a common form of about the same form and size as *Cyclops,* except that the antennae are nearly as long as the body. *Argulus* is a genus of Copepods which is parasitic on fish, and the individuals are called *fish lice* or *carp lice.* They are flat creatures and are found running around over the scales of their hosts. Some of the other forms are parasitic on the gills and fins of fish and their bodies become greatly modified.

The ostracods are small, swimming, bivalve forms that are sometimes called *swimming clams.* This group has beautifully marked valves; in fact, these animals are the most beautiful found in the plankton.

Adult *barnacles* of order Cirripedia bear so little resemblance to other crustacea that they are usually overlooked as such by the layman. They are completely encased in a thick shell of several sections and have the general appearance of an oyster or clam. They are sessile in habit as adults, though free-swimming in the larval stage. Their entire life is spent in marine waters. There

are several characteristic barnacles, *rock barnacles* on rocks, *whale barnacles* from ships and pilings, and *gooseneck* barnacles of the stalked type. After attachment, the legs become modified into feather-like bristles which are used in gathering food. *Sacculina* is a genus related to true barnacles which has gone parasitic on crabs and has lost all resemblance to animal form. It settles on the body of a crab, makes its way to the interior and there becomes a branched mass of tissue which penetrates by roots to all parts of the body of the crab. After a time a baglike portion forms and projects externally on the ventral side of the abdomen of the crab.

Recapitulation Theory or Biogenetic Law

A statement of this idea, which was developed by von Baer, Haeckel, and others, and is so well illustrated by the comparison

Fig. 167.   Fig. 168.   Fig. 169.
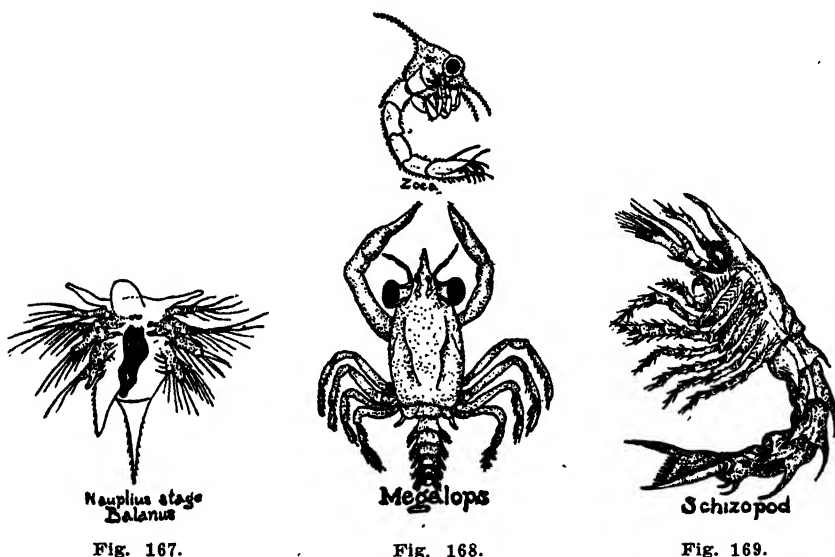
Fig. 167.—Nauplius stage of the barnacle, *Balanus*. (Courtesy of General Biological Supply House.)

Fig. 168.—Zoea and Megalops stages of developing Crustacea. Crabs include these stages in their development. (Courtesy of General Biological Supply House.)

Fig. 169.—Schizopod or mysis stage through which the shrimp and lobster pass in their development. (Courtesy of General Biological Supply House.)

of the phylogenic and embryonic stages of certain crustacea, may well be mentioned again at this point. This theory maintains that certain developmental stages or structures of the individual are re-

lated to ancestral conditions. That is, the individual in its development tends to repeat in an abbreviated fashion the history of the development of the race. Briefly stated *ontogeny recapitulates phylogeny.* There is still some doubt as to the validity of this generalization in direct application.

A classical example which is frequently cited is that of the development of the shrimp, *Penaeus,* which hatches out as a *nauplius larva,* having a single median eye and only three pairs of appendages. Following the molt, this nauplius changes to become the *Prozoea* stage, possessing six pairs of appendages. The next molt brings on segmentation and some change in form. This stage is called the *Zoea* and resembles very closely the adult Cyclops of modern Copepoda. The Zoea transforms during further molts and growth to a stage with thirteen segments and a distinct cephalothorax which resembles the adult *Mysis* and therefore is called the *Mysis* stage. Gammarus is also in about this category of phylogenetical development. Following the next molt the mysis stage becomes a juvenile shrimp with nineteen segments. The life history of the barnacles and Sacculina has illustrated quite forcibly the possibility of such a relationship. There are extinct forms also whose adult condition was that of one of these developmental stages. This idea generally has served as a great stimulus to the study of embryology and the theory of evolution as well as serving to establish natural relationship of animal groups.

Phylogenetic Advances of Arthropoda

(1) Greater specialization of segments, (2) paired, jointed appendages, (3) chitinous exoskeleton, (4) gill and tracheal respiration, (5) dioecious reproduction, (6) development of eyes and other sense organs, (7) green glands and Malpighian tubules (insects) as excretory organs, (8) organization of social life.

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THE LOCUST, A REPRESENTATIVE OF INSECTS

(BY VASCO M. TANNER, BRIGHAM YOUNG UNIVERSITY)

Insects are the most abundant creatures on the earth today. There is said to be over 650,000 living species, many of which have never been seen by the great majority of mankind. This, no doubt, is because insects exist in every type of habitat known. They are found in sea water along the shore; in fresh water that ranges in temperature from 50° C. to ice cold; in the soil; in dry desert conditions; on the vegetation of plain and swamp; from the tundra of the north to the tropical pampas; in trees; on and in animals, as well as man, many of which are carriers of disease. They ravage our crops and damage our stored foods. In short, we may say that insects are omnipresent. One noted entomologist has said that this is an age of insects, and to this we may add that every man's farm is "no man's land" and that the contending forces are insects and man.

This great class Insecta of the Phylum Arthropoda has been upon the earth from the Pennsylvanian times, of the late Paleozoic era, to the present. This means that for probably one hundred million years these arthropods have been adjusting to a changing environmental complex, and the success with which they have met the challenge is quite evident today.

Aside from the chitinous exoskeleton, other distinctive characteristics, such as power of flight, which is possessed by no other invertebrate animal; a tracheal system, which keeps the hemolymph or blood from becoming impure; and finally their great variability and power to reproduce, have made the insects, no doubt, the successful creatures they are today. This leads us to wonder how successful man will be in his evolution during the next fifty million years. Will he be able to meet the demands of a changing environment as the insects have?

Insects are Arthropoda in which the body is divided into three regions, the head, thorax, and abdomen. The head, which consists of six segments, bears a single pair of antennae, the eyes, and the mouth parts; the thorax consists of three segments and is the re-

gion which bears three pairs of legs and two pairs of wings, when they are present in the nymphs and adults; the abdomen bears a variable number of segments in the various groups of insects, also the genital apertures which are situated near the anus at the posterior end of the body.
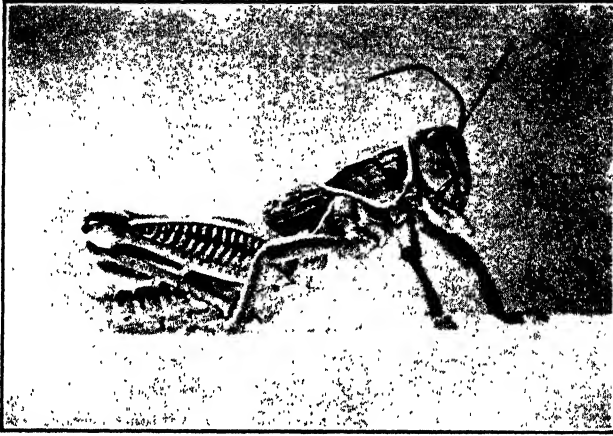
A.

B.

Fig. 170.—Western lubber grasshopper, *Brachypephus magnus*. *A*, male, and *B*, female. This form is found on the plains. (Photographed by Leo T. Murray.)

The **Locust** or grasshopper is one of the most common insects, being known to practically all people, because very few boys and girls grow up without having some experience with a grasshopper. They are widely distributed throughout the world, living on grass

and low-growing plants of the fields and open country. In the United States many destructive species are found. As early as 1743 Mr. Smith reported the damaging activities of *Melanoplus atlanis* in the New England states, and from 1855 to 1877 many outbreaks of grasshoppers were reported in the western United States. Even today the national government is expending large sums annually to keep down the activities of the many destructive species.

The grasshopper is a typical insect, and may serve to illustrate the **general structure** of the class Insecta.
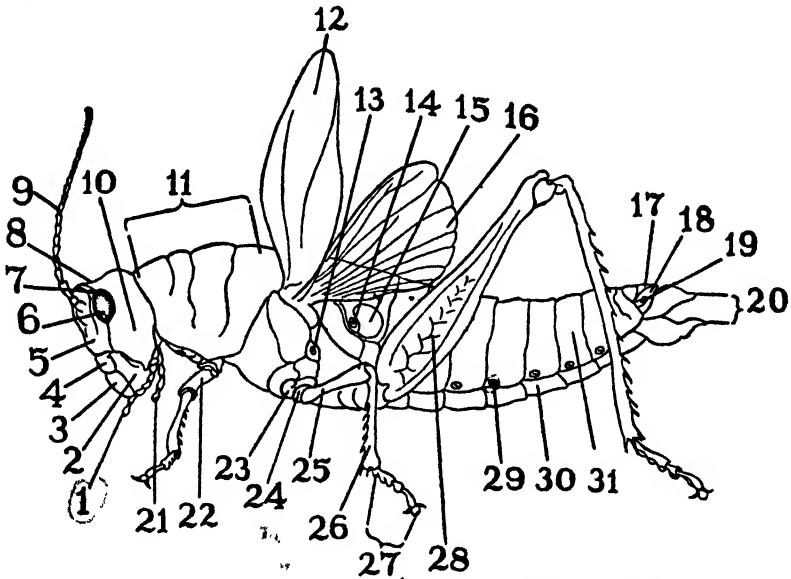
Fig. 171.—External features of a grasshopper. *1*, maxillary palp.; *2*, mandible; *3*, labrum; *4*, clypeus; *5*, frons; *6*, compound eye; *7*, ocellus; *8*, vertex; *9*, antenna; *10*, gena; *11*, pronotum; *12*, wing, mesothoracic; *13*, spiracle, thoracic; *14*, spiracle of first abdominal segment; *15*, auditory apparatus; *16*, wing, metathoracic; *17*, supra-anal plate; *18*, podical plate; *19*, cercus; *20*, ovipositor; *21*, labial palp; *22*, femur of prothoracic leg; *23*, coxa of metathoracic leg; *24*, trochanter; *25*, femur; *26*, tibia; *27*, tarsus; *28*, femur of metathoracic leg; *29*, spiracle; *30*, sternum; *31*, tergum. (Courtesy of General Biological Supply House.)

The insect body is divided into a series of rings, or segments, and the segments are made up of hardened plates. These plates are known as *sclerites,* and the depression between the plates is called a *suture.* The hardness of the plates is due to the deposition of a horny substance called *chitin.* In many places two or more of these rings have grown together, or are fused. Again, in certain regions

of the body, parts of the segments may be lost. Regardless of the amount of variation in this respect, we find that the segments are always grouped into three regions, known as the head, thorax, and abdomen.

The head is made up of a number of segments, which are fused together, forming a boxlike structure known as the *epicranium.* This boxlike piece which surrounds the eyes and forms the basis of attachment for the movable parts of the head extends down the front of the head, between the eyes, to the transverse suture, and down the sides of the head to the base of the mouth parts. The sides of the epicranium below the compound eyes are known as the *genae,* or cheeks, while the front of the head between the eyes is called the *frons.*

The grasshopper has both compound and simple eyes. The compound eyes are situated upon the upper portion of the sides of the head, and are large, oval areas with smooth, highly polished surfaces. If the eye is examined with a dissecting microscope, the surface will be seen to be made up of a number of hexagonal areas, which are known as *facets.* The simple eyes or *ocelli* consist of three small, almost transparent, oval areas. One of the ocelli is situated on the front of the head, just below the margin of the impression which contains the bases of the antennae, and in contact with the upper portion of the compound eye.

The antennae or feelers are two threadlike processes situated median to the compound eyes. Each consists of about twenty-six segments. On the front of the head there is a short rectangular piece, called the *clypeus,* which is attached by its upper edge to the epicranium, and on the lower edge to the labrum.

The mouth parts consist of a number of separate parts attached to the ventral region of the epicranium. The first noticeable part is the *labrum,* or upper lip, a flaplike piece attached to the lower edge of the clypeus. The free edge is deeply notched on the median line. Just beneath the labrum are the mandibles, or first pair of jaws. Each mandible consists of a single piece which is notched on the inner grinding surface to form a number of ridges or teeth. A second pair of jaws, the maxillae, may be exposed by the removal of the mandibles. Each maxilla is composed of a number of parts, consisting of the *cardo* or proximal hinge part of the structure; the *stipes,* the *lacinia,* a sclerite which bears some teeth on its terminal
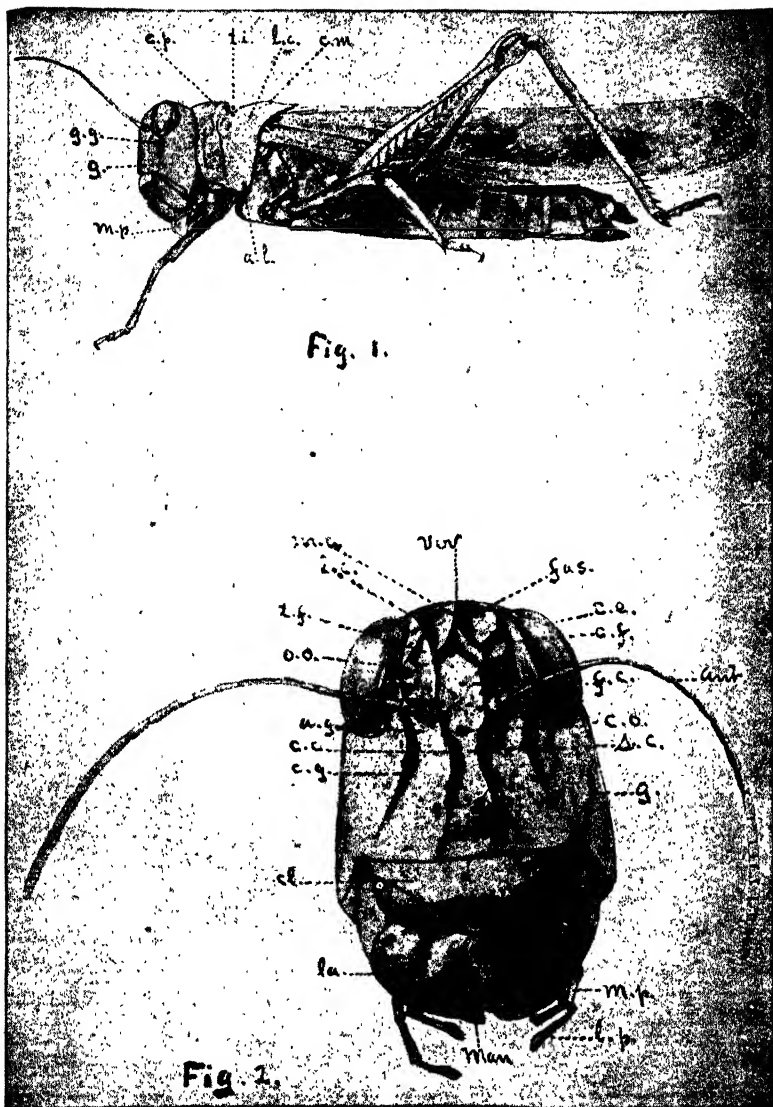
Fig. 172.—1, The external structure of the grasshopper, *Dissosteira spurcata.*
al., Hind angle of lateral lob , *c.m.,* crest of the matazone , *c.p.,* crest of the prozone ;
g., gena ; *g.g.,* genal groove ; *l.c.,* lateral carina of the matazone ; *m.p.,* maxillary
palpus ; *t.i.,* transverse incision. 2, Front view of the head of the grasshopper,
Dissosteira spurcata. a.g., Antennal groove ; *ant.,* antenna ; *c.c.,* lateral carina ;
c.e., compound eye ; *c.f.,* central foveola ; *c.g.,* carina of the antennal groove ; *cl.,*
clypeus ; *c.o.,* central ocellus ; *fas.,* fastigium of the vertex ; *f.c.,* frontal costa ; *g.,*
gena ; *la.,* labrum ; *l.c.,* lateral carina of the fastigium ; *l.p.,* labial palpus ;
man., mandible ; *m.c.,* median carina of the fastigium ; *m.p.,* maxillary palpus ;
o.o., ocellus ; *s.o.,* sulcation of the frontal costa ; *t.f.,* tempora, temporal foveola ;
ver., vertex. (From Henderson, by permission of the Utah Agricultural Experiment
Station.)

end; the outer lobe or *galea;* and the *maxillary palpus.* The caudal part of the mouth parts is the lower lip or *labium,* which is composed of the *submentum* which acts as a hinge on the epicranium above; a *mentum;* labial palpi, and two large outer flaps, the *ligulae.*

The *prothorax* is the segment to which the head it attached. It may be divided into two regions, the dorsal part known as the *pronotum* and the ventral portion known as the *sternum.* The pronotum is a saddle or bonnetlike piece extending over the dorsal and lateral regions of the prothorax. It is made up of a fusion of four plates, which are indicated by the transverse sutures. The sternum or ventral side of the pronotum is also made up of separate plates, or sclerites. The anterior sclerite bears a spine on the median line.

The next two segments, the *mesothorax* and *metathorax,* are made up of sclerites that are intimately associated. Their structure will be discussed together. The mesothorax is joined to the prothorax by a membrane which permits of more or less movement. Posteriorly the metathorax is joined immovably with the first abdominal segment. The mesothorax and metathorax form a strong, boxlike structure for the support of the wing and leg muscles. Like the prothorax these segments are made up of separate plates, held together by a tough, connecting membrane. These plates may, however, be divided into three groups: the *tergum,* or dorsal region; the *sternum,* or ventral region; and the *pleuron,* or lateral region. On the dorsal and ventral regions of the body the sutures separating the mesothorax from the metathorax are not very distinct. On the sides of the body, however, there is a very distinct line, or suture, running from the posterior border of the attachment of the second pair of legs toward the dorsal part of the body. This suture divides the mesothorax from the metathorax. The pleura of each of the posterior thoracic segments are again divided by transverse sutures, so that each pleuron consists of two sclerites.

A pair of legs arises from the lateral and ventral portions of each of the segments of the thorax. Each leg is composed of five parts. The *coxa* is the first segment and is attached to the thorax by a tough elastic membrane. The next segment, the *trochanter,* is a very short piece which is hard to distinguish except in the first pair of legs. The *femur* is the third and largest segment of the leg, and in the case of the metathoracic leg contains the muscles used in jumping. The fourth segment, the *tibia,* is slender, but about the same length

as the femur. The last division of the leg is the *tarsus,* which is made up of three segments, each movable with the other. The segments bear a series of pads, which terminate on the last one in a large suckerlike disc known as the *pulvillus.*

There are two pairs of wings. The first pair, or wing covers, also called *tegmina,* is attached to the dorsal region of the mesothorax. They are leathery in texture and do not fold fanlike over the abdomen. They are strengthened by many veins and cross veins. The second pair of wings is attached to the metathorax. They are membranous, with many veins to strengthen them, and fold fanlike over the abdomen when not in use. The metathoracic wings are used in flight.

The last main division of the insect body is the abdomen. It is composed of eleven segments. The seven anterior segments are similar in both the male and female. In the male the first abdominal segment is made up of a curved dorsal shield, the tergum, which terminates just above the attachment of the third pair of legs. This piece partially surrounds the tympanic membrane, or ear, which is a large, crescent-shaped area covered with a semitransparent membrane. The ventral part of the first segment, the sternum, is not attached to the tergum, owing to the large size of the attachment of the legs. The pleura are entirely absent. The second to the eighth segments are all quite similar, consisting of a dorsal tergum, which extends laterally to near the ventral part of the body, where it joins the sternum. The pleura, or side pieces, noted in connection with the thorax, have been inseparably fused to the tergum. In the ninth and tenth segments the terga are partially fused together, the union of the two being indicated by the presence of a transverse suture. The sterna of these two segments are entirely fused and much modified, forming a broad, platelike piece. The eleventh segment is represented only by the tergum, which forms the terminal, dorsal, shield-shaped piece.   ·

The *cerci* constitute a pair of plates attached to the lateral posterior border of the tenth. segment, and extending back, past the end of the eleventh tergum. The *podical plates* lie directly beneath the cerci and ventral to the eleventh tergum. The *anus* opens between these plates, and the genital chamber lies directly below them. Attached to the ninth sternum is the *subgenital plate* which forms the most posterior ventral plate of the body.
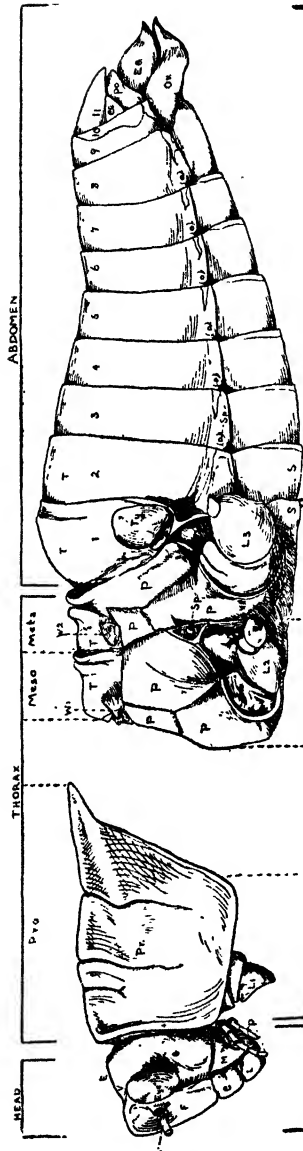
FIG. 173.—External structure of *Rhomaelia*, female. The legs, wings, and antennae have been removed, and the head and prothorax are separated from the mesothorax to show the wing attachment. *A,* antenna; *C,* clypeus; *E,* epicranium; *E.G.,* egg guide; *F,* frons; *G,* gena; *L1, L2, L3,* first, second, and third leg attachments; *L,* labrum; *M,* mandible; *Ov.,* ovipositor; *p,* palps; *P,* pleuron; *po.,* podical plate; *Pr.,* pronotum; *S,* sternite; *Sp,* spiracle; *T,* tergite; *Ty,* tympanic membrane; *V,* vertex; *W1,* attachment of upper wing; *W2,* attachment of under wing; *1–11,* segments of abdomen. (From White, *General Biology,* The C. V. Mosby Company.)

In the female the eighth segment resembles the other segments, except that the sternum is nearly twice as long, and known as the subgenital plate. The ninth, tenth, and eleventh segments are essentially like those of the male, the terga of segments nine and ten being partially fused, and tergum eleven forming the terminal dorsal shield. The plates called cerci and podical plates are similar to those in the male, except that the podical plates are much more prominent.

The *ovipositor* consists of three pairs of movable plates. The dorsal pair lies just ventral to the eleventh tergum and each plate is long, lance-shaped, and with a hard, pointed tip. The ventral pair arises just dorsal to the eighth sternum and resembles the dorsal pair. When these four pieces are brought together, their points are in contact, forming a sharp organ by means of which the female bores the holes in the ground in which to deposit her eggs. The third set of plates are known as the *egg guides.* These are much smaller and are located median to the plates of the true ovipositor.

There are ten pairs of *spiracles,* or openings in the respiratory system, on the body of the grasshopper. Two pairs of these liplike structures are situated on each side of the thorax on the anterior margin of the pleural plates. The mesothoracic spiracle is concealed by the posterior edge of the pronotum. The metathoracic spiracle is located just dorsal to the mesothoracic leg, near the suture separating the two segments. There is another spiracle just dorsal to the attachment of the metathoracic leg, but this belongs to the first abdominal segment. From the second to the eighth abdominal segments there is one pair of spiracles located on the anterior margin of each segment near the union of the sternum and tergum. The spiracles are one of the most useful sets of structures for determining the segmentation of an adult insect body. This is because there are never more than eight pairs of abdominal spiracles present in any fully developed insect. Air passes through the spiracles into the tracheae and is carried to the tissues of the body. This unique system of breathing enables the insect to keep the body tissues well aerated and the carbon dioxide eliminated from the body.

The circulatory system consists of a single dorsal tube, or heart, which extends along the length of the median dorsal part of the body. In the abdomen of the fully developed insect this vessel is

divided into a number of chambers with side valves, which allows the blood to enter but not to escape, except through the vessel toward the head. Due to the pulsating of this portion of the tube, which has been called the heart, the blood is forced to the anterior part of the body where it flows out into the body cavity and slowly returns to the abdominal region. In this process the tissues are supplied with nourishment from the food materials carried in the blood. It will be noted that the circulatory system has practically nothing to do with the carrying of oxygen to the tissues.

The **digestive system** of the grasshopper consists of a practically straight tube extending from the mouth to the anus through the central portion of the body. The food after being ground up by the mouth parts passes into the mouth or pharynx where it is mixed with the salivary mucin, and the action of the enzyme, invertase, begins. From the mouth the food is conveyed through the esophagus to the crop and gizzard which are dilatations of the tract filling a great portion of the thorax. The gizzard is muscular and lined with chitinous ridges which strain the coarse particles of food and prevent their entering the next division of the system, the stomach. The food is acted upon in the stomach by the secretions of the gastric caeca, which are glandular bodies opening into the anterior end of the stomach. They secrete a weak acid which helps in the emulsification of fats and the conversion of albuminoids into peptones. Much of the food is absorbed into the hemolymph from the stomach. Between the stomach and the intestines is a pyloric valve which permits the contents of the system to pass in only one direction. In the intestine, which is divided into the *ileum, colon,* and *rectum,* absorption of food continues, especially in the ileum. Just back of the stomach many threadlike tubes enter the intestine. These tubes are the excretory organs, known as *Malpighian tubules,* and perform a similar function to that of the kidneys of higher animals. The *rectum* has thick muscular walls with six-surface rectal glands. The feces are expelled from the rectum to the outside of the body through the anus.

The **nervous system** consists of a series of ganglia or nerve cells connected by a double set of commissures or connecting nerve fibers lying along the ventral body wall. Five ganglia are located in the abdomen. Since there are at least eleven segments in the abdomen of the adult grasshopper, it is apparent that the ganglia of some of

the segments have fused together. In the larvae of insects there is usually a ganglion to each segment. Three large, well-developed ganglia are found in the thorax; the anterior one is connected with the subesophageal ganglia which in turn are connected with the
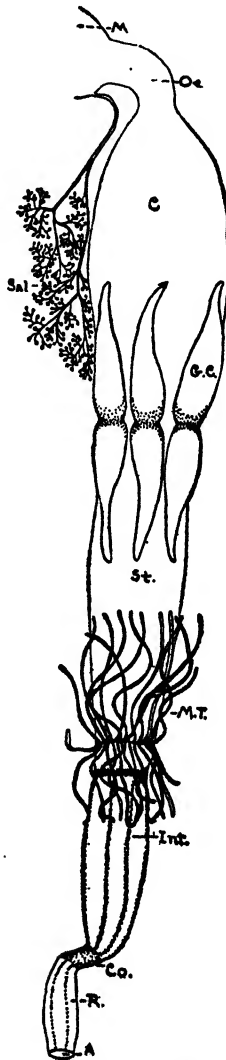
Fig. 174.—Digestive system of *Rhomaelia microptera.* *A*, anus; *C*, crop; *Co.*, colon; *G.C.*, gastric caeca; *Int.*, intestine; *M*, mouth; *M.T.*, Malpighian tubules; *Oe.*, esophagus; *R*, rectum; *Sal.*, salivary glands; *St.*, stomach. (From **White, General Biology,** The C. V. Mosby Company.)

Fig. 176.

Fig. 175.   Fig. 177.

Fig. 175.—Nervous system of *Rhomaelia microptera*. *Ab.*, first abdominal ganglion; *C*, circumesophageal commissure; *Sp.*, supraesophageal ganglion; *Su.*, subesophageal ganglion; *Th.* thoracic ganglion. (From White, *General Biology*, The C. V. Mosby Company.)
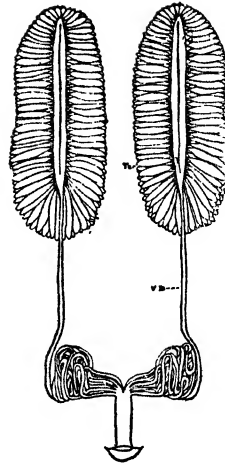
Fig. 176.—Male reproductive organs of *Rhomaelia microptera*. *Te.*, testes; *V.D.*, vas deferens. (From White, *General Biology*, The C. V. Mosby Company.)
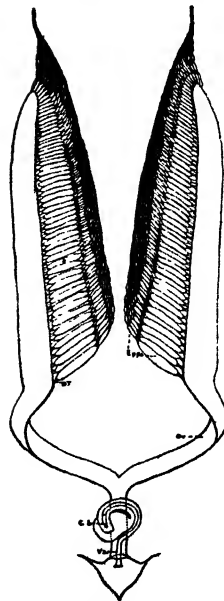
Fig. 177.—Female reproductive organs of *Rhomaelia microptera*. *C.S.*, copulatory sac; *O.T.*, ovarian tube with eggs; *Ov.*, oviduct; *Va.*, vagina. (From White, *General Biology*, The C. V. Mosby Company.)

brain or supraesophageal ganglia by nerve fibers which pass on each side of the esophagus. Nerves pass from the brain to the eyes, antennae, and palpi of the head. The subesophageal ganglia supply the mouth parts with nerves. The legs and wings are coordinated in their movements by the thoracic ganglia. In the vertebrates the nervous system is dorsal to the digestive tract, and the foreshadowing of this evolutionary change is initiated in the insects by the development in the cephalic region.

The grasshopper is dioecious; the abdominal structures separating the two sexes are distinctive. The external genital structures have been discussed above. The male organs consist of testes located dorsal to the intestines. The sperms are borne in ducts which communicate with the penis, which consists of chitinous styles used in copulation with the female. In the female there are two ovaries, which when mature fill the major portion of the abdomen. The oviducts convey the eggs to the vagina, a duct made by the union of the two oviducts, which discharges the eggs through the opening at the base of the egg guide to the outside of the body. The eggs are fertilized by the sperms from the spermatheca, which is dorsal to the vagina and which is connected by means of a sperm duct. The female is able to dig a hole in the ground with the ovipositor and deposit the eggs to the depth of an inch or more. The eggs are covered with a frothy substance which protects them from moisture and, to some extent, from the frost. The eggs are laid in the fall and hatch in the spring of the year. The development of the grasshopper is by gradual metamorphosis.

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CHAPTER XXIV

ANIMAL PARASITISM

(By Sewell H. Hopkins, Texas A. and M. College)

SOCIAL RELATIONS OF ANIMALS

It has been explained in the previous chapter that no animal is ever entirely independent of others, since all plants and animals are influenced, directly or indirectly, by all the other organisms in the community. Most animals, however, can and do catch and eat their own food, and such animals are said to be "free-living." But there are thousands of species which depend either completely or partially on others to provide them with a livelihood. The varying degrees of dependence are called *commensalism, mutualism,* and *parasitism.* The term *symbiosis* is applied to all cases of two different kinds of animals living together, and thus includes *commensalism, mutualism* and *parasitism.*

In *commensalism,* one animal receives all of the benefit from the association while the other is neither benefited nor harmed. The jackal which follows the tiger and cleans up the carcass of the prey when the tiger has eaten his fill, the small fishes which accompany sharks and feed on the scraps wasted by the shark in feeding, and the oyster crab which lives inside the oyster's shell and feeds on the organisms brought in by the oyster's feeding movements, are examples of commensalism.

Mutualism is the kind of symbiosis in which both animals receive benefit from their association. One species of hydra *(Hydra viridis)* is green in color because a certain species of green alga lives within its cells; the alga receives protection and some nourishment from its host, while the hydra benefits from the food manufactured by the green plant. A case of mutualism so far developed that the two animals cannot live separately is the relationship between wood-eating termites and their intestinal protozoa. The termite cannot digest the wood which it eats; the protozoa in the termite's intestine break down the wood into a form in which it can be used by the host; on the other hand, the protozoa are absolutely dependent on the termite for food and the proper environment; neither termite nor protozoan can live without the other partner.

The word *parasitism* in its broad sense applies to all cases in which one animal depends on another to furnish it with food; for instance, ornithologists call cowbirds parasites because they lay their eggs in the nests of other birds and leave the foster-parents to feed and care for the young cowbirds. Most zoologists, however, use the word parasitism only for cases in which the parasite lives in or on the body of its host; for example, lice live on the bodies of many animals, and tapeworms live in them.

Origin of Parasitism

How did it happen that some animals became dependent on others to furnish their food, that is, how did parasitism arise? There is a considerable amount of evidence for the belief that all parasites are descendants of free-living ancestors, and that these descendants, in the course of generations, gradually became more and more dependent on certain hosts, until in some cases they are now absolutely unable to make their own living. For example, certain species of nematodes which are free-living inhabitants of the mud at the bottom of ponds and streams are able to live in the large intestine of a frog if they happen to be swallowed by a frog. Other species, very similar to the mud-dwelling nematodes, have found the intestines of frogs such a good habitat that they live nowhere else; in other words, they have become parasites. Some intestinal parasites, in the course of many generations, have lost their locomotor structures or even their digestive organs and yet continue to thrive because there is little or no need for locomotion or digestion when all food is brought to the parasite already digested by the host's intestine. Since such degenerate parasites are unable to secure food elsewhere, they are condemned by their peculiar structure to live as parasites in the intestine of their host.

Degrees of Parasitism

Free-living animals which sometimes become parasites when they get into another animal (by being swallowed, for instance) are called *accidental* or *occasional parasites,* as in the case of the mud-dwelling nematodes mentioned above. "Vinegar eels," nematodes in vinegar, sometimes establish themselves as harmless parasites in the human urinary bladder. *Facultative parasites* are able to live

almost equally well as free-living animals or as parasites; many leeches are facultative parasites. _Obligate parasites,_ on the other hand, cannot live without the host. Parasites which are free-living during part of the life cycle, as in the case of horsehair worms and some ticks and mites, are called _temporary parasites,_ while animals like Acanthocephala and tapeworms which are parasitic during the entire life cycle are called _permanent parasites._

The Successful Parasite

Like all other ways of living, successful existence as a parasite requires certain modifications or adaptations in structure and function. Parasites which live on the outside of the host's body are called _ectoparasites;_ they must have special organs for attachment in order to maintain their hold on the host; for example, lice have hooklike feet with which they hold on to the skin, hair, or feathers of the host, and ectoparasitic trematodes have either muscular suckers or chitinous hooks for attachment to the outside skin or to the gills of the fishes on which they live. On the other hand, ectoparasitic insects have no need for wings, so fleas and bedbugs continue to thrive without them. Many ectoparasites, such as fleas, lice, bedbugs, mites, and ticks, also have specially constructed mouth parts for piercing their host's skin and sucking blood. _Endoparasites,_ which live inside their hosts, also require special adaptations. For maintaining their positions in the intestine or other organs they must have some sort of attachment organ, such as the muscular suckers of trematodes and tapeworms and the hooks of thorny-headed worms. On the other hand, they live in the dark so eyes may be entirely lacking without inconveniencing the endoparasite; usually all sense organs are either absent or very poorly developed. There is little or no need for rapid locomotion, so most endoparasites have locomotor structures much reduced or even entirely lacking. Many endoparasites also have less of a digestive system than their free-living relatives; parasites in the liver, lungs, blood vessels, etc., usually have some sort of digestive apparatus, but many intestinal parasites, such as tapeworms and thorny-headed worms, have no sign of digestive organs whatever, but depend on the host to furnish them with food already digested and ready for absorption. Most endoparasites have their reproductive organs enormously developed, sometimes so much so that 90 per cent

of the body is taken up by the reproductive system. This is in keeping with the general rule that animals whose offspring have the least chance to survive usually produce the largest number of ova. In the case of a tapeworm, for instance, the chance of any one egg being eaten by the right kind of host, so that it can
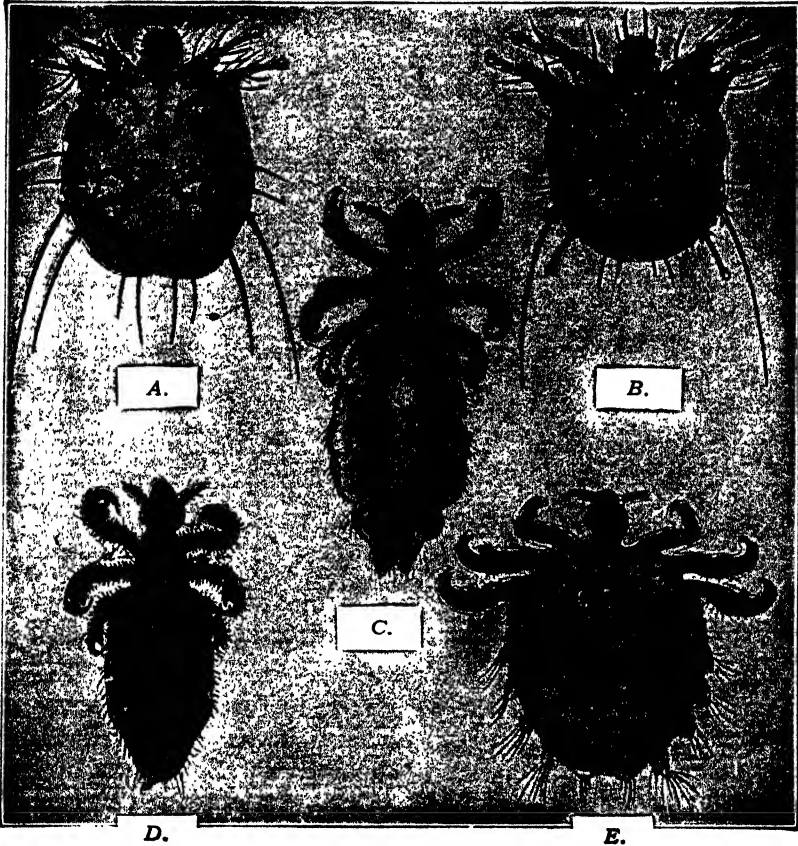
Fig. 178.—Arthropod parasites. *A*, human itch mite, female, *Sarcoptes scabiei*, ventral surface; *B*, ventral surface of male itch mite; *C*, body louse (cootie), *Pediculus humanus corporis*; *D*, head louse, *P. humanus capitis*; *E*, crab louse, *Phthirius pubis*. (From Sutton and Sutton, *Diseases of the Skin*, The C. V. Mosby Company.)

develop into another tapeworm, is only one in a million, and tapeworms would have become extinct long ago except for the fact that each tapeworm produces many millions of eggs. The peculiar habitat and mode of life of endoparasites also make necessary

peculiar adaptations in the functions or physiology of the parasite. A parasite in the intestine, for instance, must be able to carry on respiration in almost complete absence of oxygen, must secrete substances to counteract the digestive juices of the host in order to prevent its being digested, must be adapted to a high concentration of salts, acids, and other substances in solution in the fluid around it, and if in a warm-blooded animal must be able to live at a relatively high constant temperature. The fact that no host is immortal makes it necessary for a parasite to have some special provision for its offspring to escape to another host, in order to maintain the existence of the species; this necessity is met by various peculiar adaptations in the life cycle or development, such as the complex succession of larval stages in the endoparasitic trematodes and cestodes.
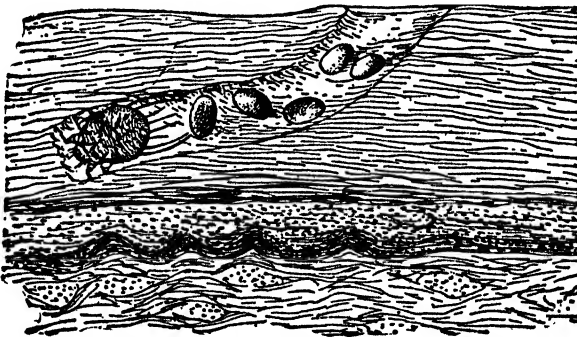
Fig. 179.—Diagram of the tunnel of an itch mite in human skin. The female animal is depositing eggs. (Reprinted by permission from *Introduction to Human Parasitology* by Chandler, John Wiley and Sons, Inc. Adapted from Riley and Johannsen.)

Some parasites are able to carry on parasitic activities without injuring their hosts, while others may weaken or destroy the host. Parasites which injure their hosts are said to be pathogenic (disease-producing), while those which cause no appreciable injury are said to be *nonpathogenic* or commensal. Since most parasites cannot live without their hosts, a parasite which shortens the life of its host destroys its own home and means of livelihood; *nonpathogenic* parasites are more likely to be successful in the long run, and are therefore more abundant. Some parasitologists consider pathogenic parasites to be *imperfect* parasites because they are not quite perfectly adapted for successful parasitic life, while nonpathogenic

species are considered *perfect* parasites. However, no hard and fast line can be drawn between the two. Many parasites which are so perfectly adapted to their customary host that they produce no ill-effects have been found to be strongly pathogenic to other hosts where the adaptation is less perfect; for example, certain trypanosomes which are harmless to the antelopes of Africa, their natural hosts, produce the highly fatal African sleeping sickness when injected into men.

Means of Infection and Transmission

Many different means of transfer from host to host have been developed by the various kinds of parasites. These may be classified as below:

A. Passive transmission.
    1. In food or in water.
    2. By bite of insects.
    3. By sexual intercourse.
    4. By direct contact.
B. Active invasion under own power.

By "passive transmission" is meant the transfer of eggs or larvae from one host to another without any action of their own. For example, the eggs of cestodes and of some nematodes, such as Ascaris, pass out of the host's intestine in the feces; if food of other animals is contaminated by these feces, animals which eat this food will swallow the eggs, which hatch into larval worms within the digestive system of the second host and thus establish a new infection. Sheep may become infected with liver flukes by eating the encysted larvae on grass or swallowing encysted larvae while drinking water. Trichina larvae encysted in hog meat develop into adult worms in the human intestines if infected pork is eaten raw or improperly cooked.

The second means of passive transmission is also widely used. Malaria parasites, the trypanosomes which cause African sleeping sickness, and many parasites of domestic and wild animals are carried from infected individuals to new hosts by biting insects which suck up the parasites with the blood and inject them into the new host with their salivary secretions.

The third means is used by only a few parasites, most of them Protozoa. The spirochete, Treponema, which causes syphilis, a flagellate protozoan called *Trichomonas vaginalis,* and a trypanosome parasitic in the reproductive organs of horses are examples. Some nematode parasites of insects are also transmitted in this way.

The fourth means includes a few cases, such as the acquiring of dog tapeworm by people who kiss dogs and the transmission of pinworm from the hands of infected people who do not have cleanly habits.

Hookworms and the human blood flukes, called schistosomes, are examples of parasites that invade new hosts under their own power. Their larvae are able to penetrate the skin.

Parasitism and Host Specificity

Since the beginning of the scientific study of parasitism, it has been recognized that different animals have different parasites; for instance, the parasites found in and on goats are nearly all different from those of man. Some of the early parasitologists leaped to the conclusion that each species had its own peculiar species of parasites found nowhere else, and carried this idea of *species specificity* so far that they considered presence in different hosts to be sufficient evidence of specific difference of the parasites.

Modern knowledge reveals that while some parasites are actually *species specific* others have a wide range of hosts. Thus the beef tapeworm, *Taenia saginata,* is found in the adult stage in man only, but the fish tapeworm, *Diphyllobothrium latum,* seems to be able to live in nearly all mammals which eat fish.

Three main factors determine whether a parasite will infect any given host: (1) opportunity for infection of host, determined by habits or mode of life of parasite and host (malaria parasites may be injected into any land animal by bite of mosquito, but strictly aquatic animals, such as fish, would not be bitten); (2) the environmental condition of the habitat furnished by the body of the host, involving such factors as body temperature, nature of outside surface, size, chemical content of internal organs, etc (intestinal parasites of birds are seldom found in mammals, which have lower body temperatures, and parasites adapted to the oxygen-rich interior of a frog's lung can find no suitable habitat in a lungless fish); and (3) ability of the parasite to adapt itself to the wide range of environmental conditions found in different hosts; thus *D. latum,* though it

finds its optimum conditions in the human intestine, is adaptable enough to survive under the very different chemical conditions found in the dog, while *Taenia saginata* is usually unable to survive under these conditions.

PARASITES AND THE GROUPS IN THE ANIMAL KINGDOM

What kinds of animals are infested by parasites? Not only all phyla and classes, but all known species and probably all individuals of higher forms serve as hosts for some kind of parasite. Even in
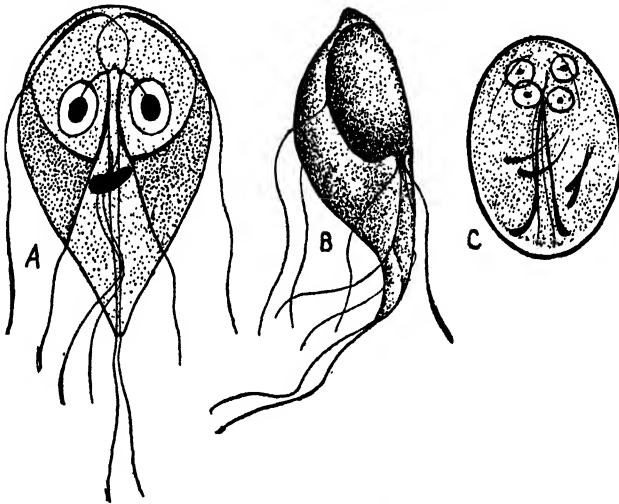
Fig. 180.—*Giardia lamblia,* an intestinal flagellate. *A,* face view; *B,* semiprofile view; *C,* cyst. (Reprinted by permission from *Introduction to Human Parasitology* by Chandler, John Wiley and Sons, Inc.)

the microscopic Protozoa many individuals harbor still smaller protozoans. For example, several species of parasitic Protozoa are found in *Amoeba proteus.*

To which of the main groups of animals do parasites belong? All animal phyla, except Echinodermata, include some species which lives as parasites, but the great majority of parasites belong to one of these four phyla: Protozoa, Platyhelminthes, Nemathelminthes, and Arthropoda.

Protozoa.—Of the four classes in this phylum, one, Sporozoa, is entirely parasitic; the other three (Sarcodina, Mastigophora, In-

fusoria) also contain a number of parasitic forms. Examples of parasitic Sarcodina are the three common human amoebae, *Endamoeba histolytica,* which invades and destroys the intestinal lining,

To cerebrospinal fluid causing sleeping sickness and death.

A

Trypanosomes in human blood causing Trypanosome fever.

Transmission by bite of tsetse fly.

↑ Man, Antelope, etc.

Tsetse Fly

Transmission by bite of tsetse fly.

E

Forms in salivary glands ready for re-infection. (20th–30th day)

Crithidial forms in salivary glands (2 or 3 days later)

B

Forms in mid gut (48 hrs after infective meal).

D

newly arrived form in salivary gland. (12th to 20th days.)

Long slender forms in proventriculus. (about 10th to 15th days)

C

Fig. 181.—*Life history of Trypanosoma gambiense.* (Reprinted by permission from *Introduction to Human Parasitology* by Chandler, John Wiley and Sons, Inc.)

thus causing amoebic dysentery; *Endamoeba coli,* a harmless commensal in the intestine; and *Endamoeba gingivalis,* a very common parasite in the human mouth, usually harmless but sometimes apparently injurious to the gums. Examples of parasitic **Mastigophora**

are the human intestinal flagellate, *Giardia lamblia*, and the blood-inhabiting trypanosome, *Trypanosoma rhodesiense*, causative agent of African sleeping sickness which is carried by the tsetse fly. Examples of parasitic Infusoria are the human intestinal ciliate, *Balantidium coli;* the various species of *Opalina*, and related genera found in the excretory bladder or cloaca of frogs and toads. Of the thousands of species of Sporozoa, all of which are parasitic, probably the best known are the three species of the genus *Plasmodium*, which cause human malaria, and *Babesia bigemina*, which produces Texas tick fever of cattle.
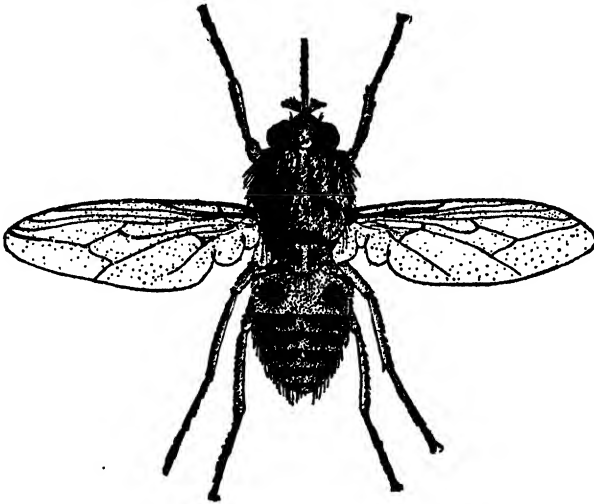
Fig. 182.—Tsetse fly, *Glossina*, the transmitting agent for trypanosoma, which causes African sleeping sickness. (Reprinted by permission from *Introduction to Human Parasitology* by Chandler, John Wiley and Sons, Inc.)

Platyhelminthes.—This phylum also contains four classes, two of which, Trematoda (flukes) and Cestoda (tapeworms), are all parasitic, while the other two, Turbellaria and Nemertinea, are mainly free-living but contain some species which are parasitic on aquatic invertebrates. Among the best known examples of Trematodes are *Fasciola hepatica*, the sheep liver fluke; *Clonorchis sinensis*, the Chinese human liver fluke; and *Schistosoma haematobium*, one of the three species of human blood flukes. Probably the best known tapeworms are *Taenia saginata*, the beef tapeworm, *Taenia solium*, the pork tapeworm and *Diphyllobothrium latum*, the broad fish tapeworm, all three common parasites of the human intestine, and *Echino-*

coccus granulosus, a dog and wolf tapeworm whose larval stage is the cause of a horrible human disease.

Nemathelminthes.—The single class Nematoda includes at least 95 per cent of the species in this phylum; most of them are free-living, but there are also thousands of parasitic species. Examples of parasitic species are the human hookworms, *Necator americanus,* the American hookworm, and *Ancylostoma duodenale,* the Old World hookworm; *Ascaris lumbricoides,* the large intestinal roundworm of hog and man; *Dracunculus medinensis,* the Guinea worm, often over a yard long, which crawls around under the human skin (believed by some to be the "fiery serpent" mentioned in Exodus); *Trichinella spiralis,* which causes the often fatal human disease, trichinosis, when

Fig. 183.—*Balantidium coli,* an infusorian parasite of the intestine. Active form from intestine. *c.v.,* anterior contractile vacuole; *cyt.,* cytostome; *f.v.,* food vacuole; *n,* nucleus. (Reprinted by permission from *Introduction to Human Parasitology* by Chandler, John Wiley and Sons, Inc.)

its larvae, encysted in pork, are eaten by man; and *Wuchereria bancrofti,* the filaria which is injected into the human blood by certain tropical mosquitoes and causes elephantiasis, a disease in which the infected limbs may become larger than the body of the victim. *Onchocerca volvulus,* transmitted by certain biting flies, is a common cause of blindness in some parts of Mexico. Besides the human nematodes there are thousands of others parasitizing lower animals, both vertebrates and invertebrates. The other two classes of the phylum Nemathelminthes are entirely parasitic; the Acanthocephala, or thorny-headed worms, are common intestinal parasites of many vertebrates, including the hog and occasionally man; the Gordiacea

or horsehair worms are parasites of insects until nearly mature; they crawl out of their insect hosts when the latter fall into water, become sexually mature, and lay their eggs.

Arthropoda.—All of the classes in this phylum are predominantly free-living, but several classes also include parasitic species. The class Hexapoda or Insecta contains, besides several hundreds of
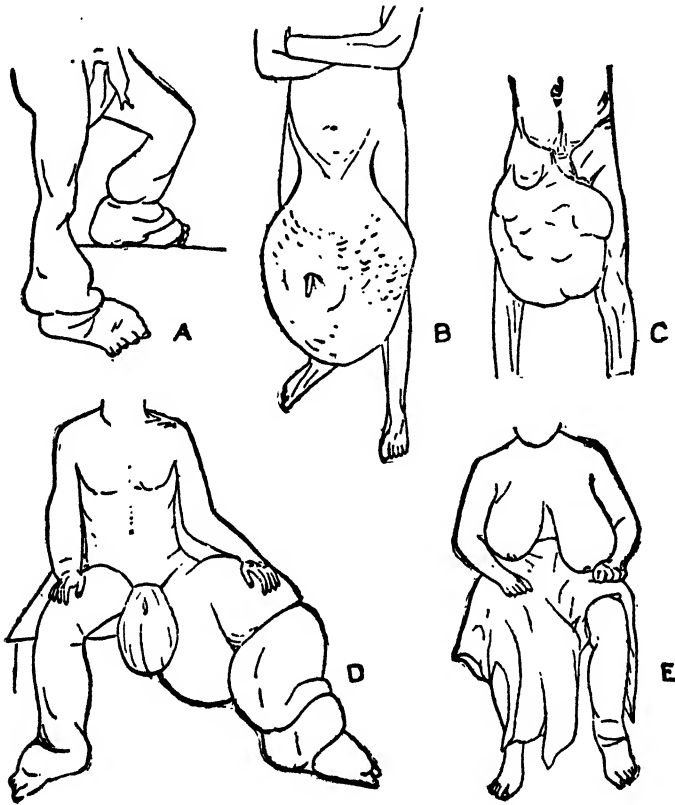
Fig. 184.—Elephantiasis, some extreme cases. *A*, of legs and feet; *B*, of scrotum; *C*, varicose groin gland; *D*, of scrotum and legs; *E*, of mammary glands. (Reprinted by permission from *Introduction to Human Parasitology* by Chandler, John Wiley and Sons, Inc. *A* and *B* sketched from photographs from Castellani and Chalmers; *C*, *D*, and *E* from Manson.)

thousands of free-living insects, the parasitic fleas, lice, and bedbugs; the class Arachnida, characteristically free-living, contains the parasitic ticks and mites, and the class Crustacea, though mostly free-living, includes a number of species parasitic on fishes and other aquatic animals. While most of the parasitic arthropods are ectopara-

sites, there are also a few endoparasitic species. For example, the horse bot, *Gastrophilus*, which is the larva of a fly, is parasitic in the stomach of horses; long wormlike arachnids known as Linguatulids or tongue worms are found in the intestines of some reptiles and mammals; and *Sacculina*, a crustacean, parasitic on crabs and lobsters, sends rootlike outgrowths all through the body of its host, although the saclike body remains on the outside.

Some Representative Parasites

Protozoa.—The very small amoeba-like protozoans of the genus *Endamoeba* are examples of parasites only slightly modified for parasitic life. There are two distinct stages in the life cycle, the
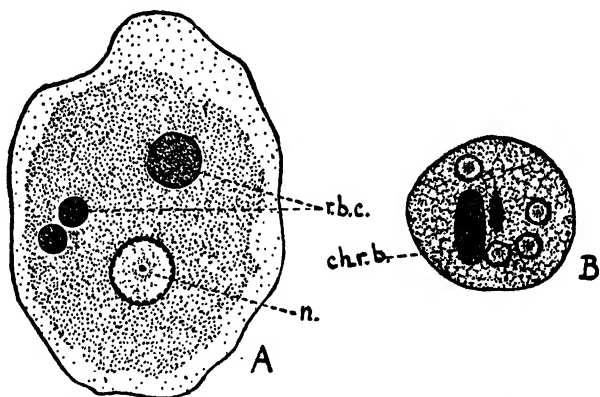
Fig. 185.—*Amoeba histolytica*, one of the important protozoan parasites. It is the causal agent of amoebic dysentery. *A*, Stained vegetative amoeba; *B*, cyst with four nuclei; *n*, nucleus, showing peripheral chromatin granules and central karyosome; *r.b.c.*, ingested red blood corpuscles; *chr.b.*, chromatoid body. (Reprinted by permission from *Introduction to Human Parasitology* by Chandler, John Wiley and Sons, Inc., after Dobell.)

active form being much like a small amoeba except that the pseudo-podia are shorter and move more slowly; these active forms finally round up and become surrounded by a semirigid, resistant cyst wall. In this encysted condition the Endamoeba is passed from the host with the feces or other body excrements. While in the encysted condition the parasite divides by binary fission into first two, then four, and finally (in *E. coli*) eight little amoebae. If the cyst is swallowed by another host, the cyst wall is dissolved and the four or eight young amoebae come out to begin the active stage again. The common Endamoebae of man are *E. gingivalis* which lives in the mouth

and is usually transmitted by kissing, and the two intestinal species *E. coli* (nonpathogenic) and *E. histolytica*. The latter species breaks down the cells of the intestinal lining by means of enzymes which it secretes, and then ingests the broken cells in the same way that the common free-living amoebae take in their food. The disease caused by *E. histolytica* is known as "amoebic dysentery." Infection occurs as the result of eating food or drinking water which has been contaminated by the feces of infected people, as in the case of the Chicago hotels where contamination of drinking water by water siphoned up from the toilet drains into the water pipes caused a serious outbreak in 1933.
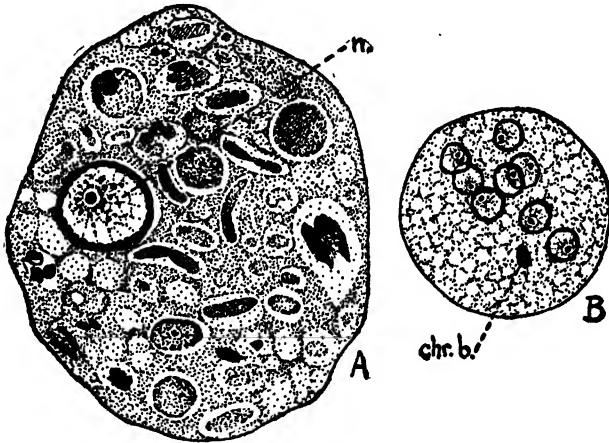
Fig. 186.—*Endamoeba coli. A*, stained vegetative amoeba; *B*, cyst with eight nuclei; *n.*, nucleus, showing coarse peripheral chromatin granules, chromatin granules in "clear zone" between periphery and karyosome which is eccentric in position; *chr.b.*, remnant of chromatoid body. Numerous food vacuoles in vegetative form. (Reprinted by permission from *Introduction to Human Parasitology* by Chandler, John Wiley and Sons, Inc., after Dobell.)

The malaria parasites, of which there are three species infecting man (*Plasmodium vivax, P. falciparum*, and *P. malariae*, each causing a different form of malaria), are Protozoa belonging to the class Sporozoa, and are very highly modified for parasitic life. The adaptations for parasitism and for transmission from host to host involve a very complex life cycle. The two main phases of the life cycle are the vegetative or *schizont* stage (merozoites) and the sexually reproductive or *sporont* stage. The biology of this parasite has been discussed in the earlier chapter on *Protozoa* under class Sporozoa and Economic Relations of Protozoa.
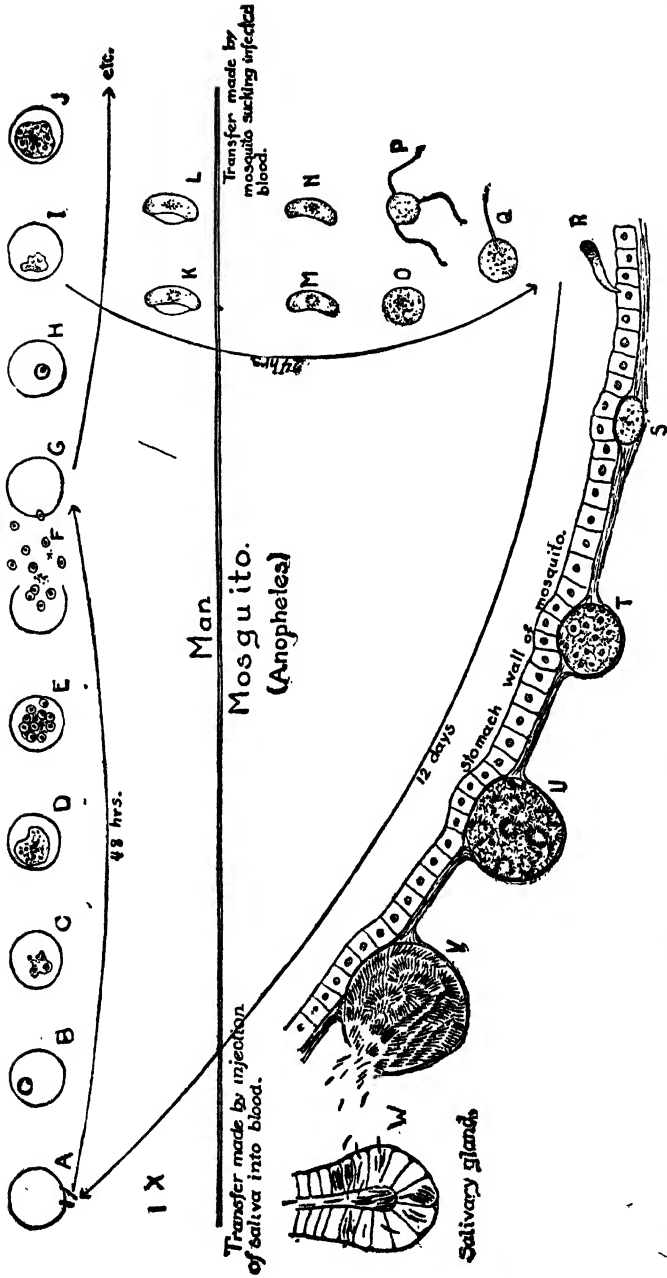
Fig. 187.—Life cycle of *Plasmodium*, the protozoan malaria parasite. *A*, spore from salivary gland of mosquito entering red blood corpuscle: *B*, young "ring" stage: *C*, later amoeboid stage: *D*, adult parasite ready to sporulate: *E*, young parasites in corpuscle, resulting from sporulation (note residual pigment granules): *F,G*, liberation of young parasites and attack of new corpuscle: *H*, *I*, and *J*, repetition of growth, sporulation, etc.: *K* and *L*, female and male cells (gametocytes), respectively, in blood stream: *M* and *N*, same, in stomach of mosquito, remnants of blood corpuscles digested: *O*, mature female gamete: *P*, formation of "flagellated body," i.e., extrusion of male gametes from male gametocyte: *Q*, fertilization: *R*, young wormlike body, developed from fertilized egg, penetrating wall of mosquito's stomach; *S*, *T*, and *U*, stages in development of spore-filled capsule on outer wall of mosquito's stomach; *V*, mature capsule burst, liberating spores into body cavity: *W*, penetration of spores into salivary glands: *X*, injection of spore into human blood. (Reprinted by permission from Chandler, *Introduction to Human Parasitology*, John Wiley and Sons, Inc.)

Nematodes.—Of the thousands of species of parasitic nematodes, space permits mention of only a few which are particularly important because of their danger to man.

Hookworms.—In the United States the most important human nematode parasite, from the public health viewpoint, is the American hookworm, *Necator americanus.* Although called the "American hookworm" this species probably came originally from Africa and was introduced into America by the negro slaves. The pioneer work on hookworm in the United States was done by Dr. Charles W. Stiles in 1901. Hookworms are slender threadlike nematodes about one-half inch long; the females are tapered to a point at each end, while the slightly smaller males have on the posterior end a fanlike expansion, the copulatory bursa, with curved riblike supports. Both sexes have a large mouth containing hooklike chitinous *teeth* by means of which they tear holes in the walls of the intestine and start blood flowing from the wounds. A muscular esophagus leading back from the mouth cavity gradually broadens into a large muscular bulb; by means of rhythmic contractions and expansions of the bulblike esophagus blood is drawn into the mouth and forced down into the straight intestine where some of it is digested and the rest passes on through and out of the anus near the posterior end. Because of the large number of worms present there is a serious loss of blood, resulting in anemia and lack of energy; in children the growth is stunted or retarded by hookworms, and often there is also a lack of proper mental development. Individuals, very heavily infected during childhood and early youth, may fail to develop sexually. Treatment is fairly easy, hookworms being easily killed by doses of anthelmintics, such as carbon tetrachloride and hexylresorcinol (which are poisonous and should be taken only under doctor's supervision).

Each female hookworm produces 9,000 eggs per day; these eggs pass out with the feces of the host; if the infected person defecates on the ground, the eggs hatch and the larvae crawl around in the soil; there they develop into infective larvae which live for several months on the surface of the ground. If bare human skin comes in contact with these microscopic worms they bore through it to the blood vessels, are carried by the blood to the lungs, then migrate up to the trachea and pharynx, into the esophagus, then down through the esophagus and stomach to the small intestine, meanwhile increas-

ing in size, so that on arrival in the small intestine they are ready to attach themselves to the wall of the intestine, feed on the blood of the host, and become adults.

Since the larval hookworms must go through part of their development in the soil, and a person can become infected only by direct contact with contaminated soil, the distribution of hookworm in the United States is determined by the following factors: (1) freezing of soil in winter (kills the larvae); (2) texture of soil (hookworm larvae live best in light, sandy loams); (3) moisture (hookworm larvae can live only in damp soil); (4) customs of the people in disposal of feces; the bad hookworm districts are sections in which sanitation is very primitive and sanitary toilets are not in universal use; deposit of feces on the ground is particularly conducive to spread of these animals.

From the public health standpoint hookworm disease is a social problem rather than a medical problem. Few if any people are killed by hookworm, and infected individuals are easily cured if they go to a physician for treatment. On the other hand, such a large proportion of the population, in hookworm territory, are kept in bad health and a listless condition that the social welfare of the whole community is injured. Prevention of hookworm disease is theoretically easy: hookworms could be killed out of a community in a few months if everyone would defecate only in sanitary toilets, if everyone would take treatments for hookworms at the same time, or if everyone would wear good shoes; but so far, it has been impossible to get the cooperation of all the people in hookworm districts. The work of the medical profession, with the help of certain state agencies, has reduced hookworm disease in the United States, but there are still considerable districts in which over 20 per cent of the population are infected. In parts of East Texas 33 per cent of the people examined have hookworm, even now.

Trichina.—*Trichinella spiralis,* commonly known as Trichina, is an example of a nematode with an alternation of hosts and a passive means of transmission. The microscopic larvae are encysted in the muscles of various meat-eating animals, being particularly common in hogs and rats; within the cyst, the larva is coiled in a tight spiral, which gives the species its name. If pork containing trichina cysts is eaten by a man, the cysts are digested off in the stomach, the larvae become active and penetrate the mucosa of the small intestine to
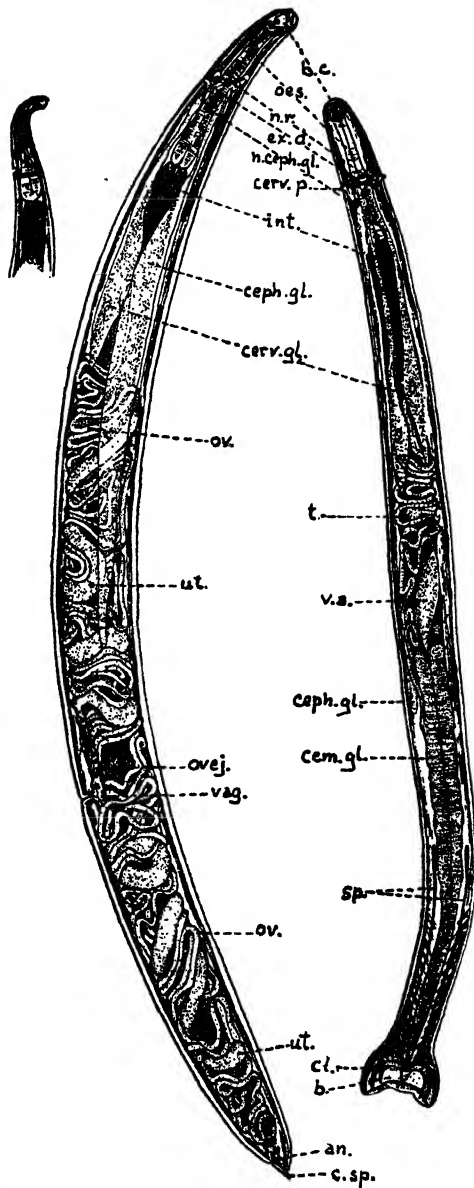
Fig. 188.—*Ancylostoma duodenale*, female and male, with head of *Necator americanus* drawn to same scale. *an.*, anus; *b*, bursa; *b.c.*, buccal capsule; *cem.gl.*, cement gland; *ceph.gl.*, cephalic gland; *cerv.gl.*, cervical gland; *cerv.p.*, cervical papilla; *cl.*, cloaca; *c.sp.*, caudal spine; *ex.d.*, so-called excretory duct; *int.*, intestine; *n.ceph.gl.*, nucleus of cephalic gland; *n.r.*, nerve ring; *oes.*, esophagus; *ov.*, ovary; *ovej.*, ovejector; *sp.*, spicules; *t.*, testes; *ut.*, uterus; *vag.*, vagina; *v.s.*, vesicula seminalis. (After Looss from Chandler, *Hookworm Disease*. Reprinted by permission from Chandler, *Introduction to Human Parasitology*, John Wiley and Sons, Inc.)

moult. They soon become full grown, sexually mature adults, some-
times beginning copulation only forty hours after being swallowed.
The adult worms are short-lived and are not harmful to the host, but
each fertile female, about a week or ten days after the infected meat
was swallowed, begins to produce thousands of microscopic larvae
which she deposits in the walls of the intestine, usually directly into
a lymph vessel or blood vessel. The larvae are carried by the blood
or lymph to the heart, and from there they are carried by the blood
to all parts of the body. The larvae which reach voluntary muscle
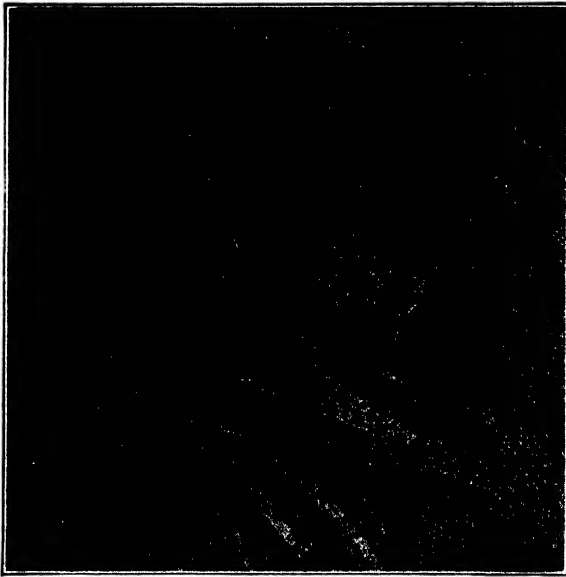
Fig. 189.—Larvae of *Trichinella spiralis*, encysted in voluntary muscle. The
adults are parasites in the intestine.   (Photomicrograph by Albert E. Gallgher,
Inc.)

enter the muscle fibers and coil up into spirals, grow rapidly to a
length of about 1 mm., and in a few weeks become enclosed in a cyst
of connective tissue which grows around them. Trichina larvae are
likely to be most abundant in active muscles, such as the diaphragm,
the intercostals, and the muscles of the larynx, tongue, and eye. The
symptoms of trichinosis (the disease caused by trichina worms) vary
according to the stage of the infection. In the first week, when the
adult females are burrowing into the walls of the intestine to de-
posit their larvae, the symptoms are so much like those of typhoid

fever that many cases are diagnosed as typhoid by good physicians. Nine or ten days after the beginning of infection, when the larvae are migrating to the muscles, there are severe muscular pains and aches (sometimes diagnosed as rheumatism), and the inflammation of the muscles used in breathing, chewing, etc., may interfere with these functions. As the parasites become encysted, about six weeks after infection, pains become worse and swelling of the infected parts occurs, accompanied by anemia and skin eruptions. If the victim survives this period he usually recovers, as the parasites are now walled off by cysts of connective tissue formed by the host; later calcium carbonate is deposited in these cysts, walling off the parasites so completely that they die, but the calcified cysts remain as hard grains in the muscles and may cause some rheumatic pains for years. Until the worms are completely walled off fever is caused by poisonous substances produced by the larval worms. Recent studies of the cadavers used in medical schools have revealed that about 20 per cent of the American population probably have cases of trichinosis in some degree at some time during life, since about this proportion of the cadavers had trichina cysts in the muscles.

All danger of trichinosis can be avoided by cooking pork thoroughly before eating it, as the larvae are killed by a temperature of 55° C. (131° F.). Investigations of the United States Bureau of Animal Industry, in which the author assisted, indicate that prepared sausages seldom contain living worms, most of them being killed by the salts and seasoning or by long-continued cold storage; the greatest danger is from fresh pork. Contrary to popular impression, Federal inspection does not guard against trichina, as there is no effective way to inspect meat for trichina on the large scale that would be necessary.

Trematodes.—*Schistosoma haematobium*, a Human Blood Fluke.— The blood flukes (Family Schistosomatidae) are distinguished from all other trematodes by having separate sexes. The male has a thick body with the lateral edges bent ventrally, thus forming a long groove on the ventral surface, the *gynecophoric canal*. The female is long and slender, almost threadlike in some species; when an adult male and female happen to come in contact, the male folds his body around the female so that she is held fast in the gynecophoric canal, and the pair begin copulation. After once becoming paired they remain in copula during the rest of their lives. Three species of the genus

Schistosomum are human parasites: *Schistosoma mansoni,* found in Africa and the tropical parts of the New World, *S. japonicum* of Japan and China, and *S. haematobium,* the Egyptian blood fluke found in north Africa and southwestern Asia. *Schistosoma haematobium* is a parasite in the large blood vessels of the rectum and urinary bladder. The female lays an enormous number of eggs, which collect in the capillaries of the bladder and intestinal walls and block the flow of blood, causing the infected parts to become swollen and ulcerlike. Eventually the eggs are released into the lumen of the rectum or bladder and pass out of the host's body in the feces and urine, along with considerable quantities of blood from the torn tissues. Aside from the pain caused by the egg-filled swellings, the loss of blood is the most serious effect of blood-fluke infection. Infected individuals are kept in a run-down anemic condition. The parasite is a serious public health problem in Egypt, where 80 per cent of the population of the Delta region is infected.

The egg must fall into water for the embryo to develop into a ciliated larva, the *miracidium*. When the miracidium is fully developed, the cap or *operculum* on the end of the egg shell is pushed open and the liberated miracidium begins to swim around in the water. Certain species of snails seem to emit a chemical which attracts schistosome miracidia; if a snail of the right species is in the vicinity, the miracidium swims to it and enters its body. If no suitable snail is available, the miracidium dies after swimming a few hours. After penetration into a snail the miracidium loses its cilia and develops into a long sausage-shaped sac, the *sporocyst,* without any recognizable organs. Germ cells within the sporocyst develop into a number of young sporocysts, which escape from the mother sporocyst into the tissues of the snail, grow to full size, and then in turn give birth to a new generation of sporocysts, or, under some conditions, these sporocysts may give rise to a different kind of larva, the *cercaria,* which has a long, forked, muscular tail, a pair of eyespots, two suckers (one anterior and one midventral), and a rudimentary digestive system. When fully developed, the cercaria forces its way out of the snail and begins to swim through the water. If unsuccessful in finding a host, the cercaria dies in a few hours, but if it comes in contact with the skin of a man, or any other mammal, the cercaria enters the skin, with the aid of glands in the head region which seem to be used in digesting or destroying the skin tissues. After penetrating the skin the cercaria soon finds its way into a blood vessel

and begins a voyage through the circulatory system, carried along by the current of the blood stream, meantime growing into an adult fluke. The mating of males and females usually occurs in the larger veins, and the pair moves to the veins in the walls of the rectum and bladder, where egg-laying begins.

Irrigated districts, such as the Nile Delta, are especially favorable for the development of blood.flukes because the eggs have more chance of getting into water and because the field workers often get into the water while working around the irrigation ditches. The chances of infection are increased by the customs of defecating and urinating into the water, and using water from irrigation ditches for drinking and washing. In Japan the number of human blood fluke cases has been greatly decreased by improved sanitation and by killing the host snails. In Egypt, public clinics (by injecting fuadin
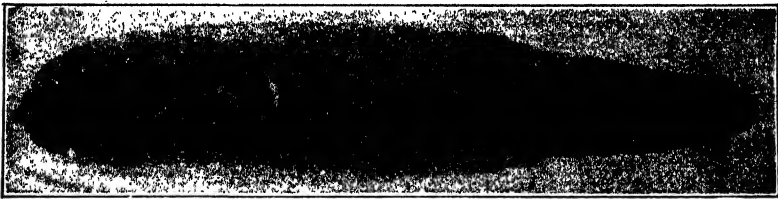
Fig. 190.—*Clonorchis sinensis.* Oriental human liver fluke, showing male and female reproductive organs. (Photomicrograph by Albert E. Galigher, Inc.)

into the blood) treat thousands of cases of this disease, but it will probably remain a public health problem for years because of the refusal of the Egyptian peasants to change their old customs.

Clonorchis sinensis, the Chinese Liver Fluke.—This is an important human parasite in parts of the Orient. *Clonorchis sinensis* also occurs in other fish-eating mammals, including dogs, cats, and pigs. The adult worm lives in the bile passages of the liver. In man it often causes enlargement of the liver, diarrhea, jaundice, anemia, and extreme weakness, sometimes resulting in death. Hundreds of worms may be found in a badly infected man. The eggs laid by the adults pass from the liver to the intestine of the host by way of the bile duct, then pass from the body in the feces. Snails probably become infected by swallowing the eggs, while feeding on fecal matter in the water. After hatching, the miracidia migrate into the lymph spaces of the snail and develop into elongated *sporocysts,* each of which gives birth to a number of *redia* (differing from sporocysts by

possessing a pharynx and a rudimentary gut). Each redia gives birth to six or eight *cercariae,* which emerge from the snail and swim around in the water by means of a very large, undivided tail. When a cercaria comes in contact with a fish, it enters the skin and encysts either in the skin or in the muscles just below the skin. It is now called a *metacercaria,* or *agamodistomum.* Man becomes infected by eating these metacercariae in poorly cooked fish. When swallowed, the cysts are dissolved by digestive juices of the host, the larva escapes into the duodenum, migrates up the bile duct to the liver, and there develops into an adult. There is evidence that the adult Clonorchis may live as long as twenty years in the liver of man.

Treatment of clonorchiasis is not very satisfactory. Prevention is simple: avoid eating fish which are not thoroughly cooked.

It will be noted that the Clonorchis life cycle involves three hosts: a mammal as the final host, a snail as the first intermediate host, and a fish as the second intermediate host. Infection of the fish is by active invasion of the cercariae, and infection of the final host is passive.

Other Trematodes.—One of the best known parasites of domestic animals is the sheep liver fluke, *Fasciola hepatica,* which occurs in all sheep-raising countries in which wet pastures are common. It is also a common parasite of goats and cattle. Like Clonorchis, Fasciola lives in the bile passages, and its eggs pass out with the feces of the host, but unlike Clonorchis, the eggs hatch in water and the free-swimming miracidium actively seeks and penetrates the snail host. *Sporocysts* in the snail give rise to *rediae* which produce *cercariae,* but the cercariae encyst on any surface, including grass blades and even the surface film of the water. Sheep become infected by eating grass bearing encysted larvae or by swallowing floating cysts while drinking water. *Fascioloides magna,* the large liver fluke of cattle and sheep in Louisiana, Arkansas, and Texas, is very similar in structure and life history.

Other important flukes are the human intestinal fluke, *Fasciolopsis buskii,* which is common among the Chinese, who become infected by eating the cysts on various aquatic food plants; the human lung fluke, *Paragonimus westermanii* of eastern Asia, where the natives become infected by eating the encysted larvae in fresh-water crabs and crayfishes; *Cotylophoron cotylophorum,* a stomach parasite of cattle in Louisiana, and *Dicrocoelium lanceatum,* a common liver fluke of herbivorous mammals in Europe and Asia.

Numerous ectoparasitic trematodes, of the Subclass Monogenea, occur on the skin and gills of fish and are often of economic importance because they kill goldfish and other aquarium fishes, and also young fishes in state fish hatcheries.
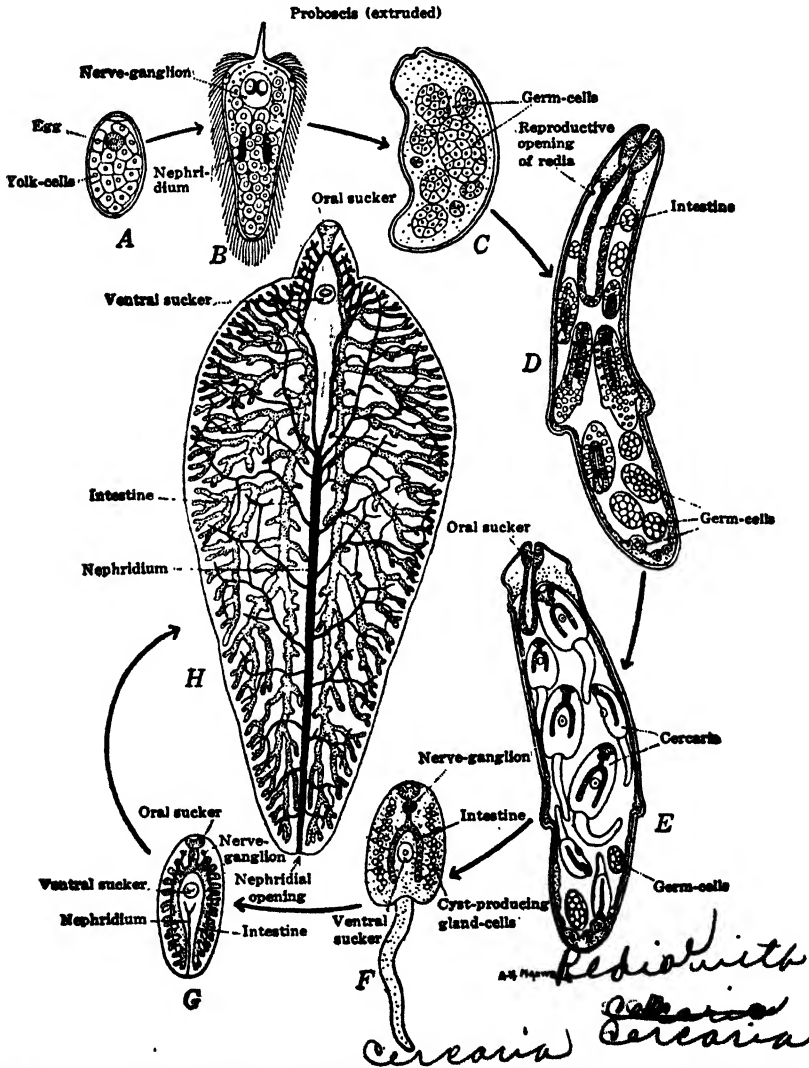
Fig. 191.—The liver fluke, *Fasciola hepatica*. *A*, egg; *B*, miracidium; *C*, sporocyst; *D* and *E*, rediae; *F*, cercaria; *G*, encysted stage; *H*, adult (showing digestive and excretory systems). (From Hegner, *College Zoology*, The Macmillan Company.)

The Tapeworms (Class Cestoda).—Cestoda differ from Trematoda in the complete lack of a digestive system. In fact, cestodes never have any sign of a digestive organ at any time during life; they receive their nourishment by absorbing through the surface of their bodies the food already digested for them by the host. Most cestodes
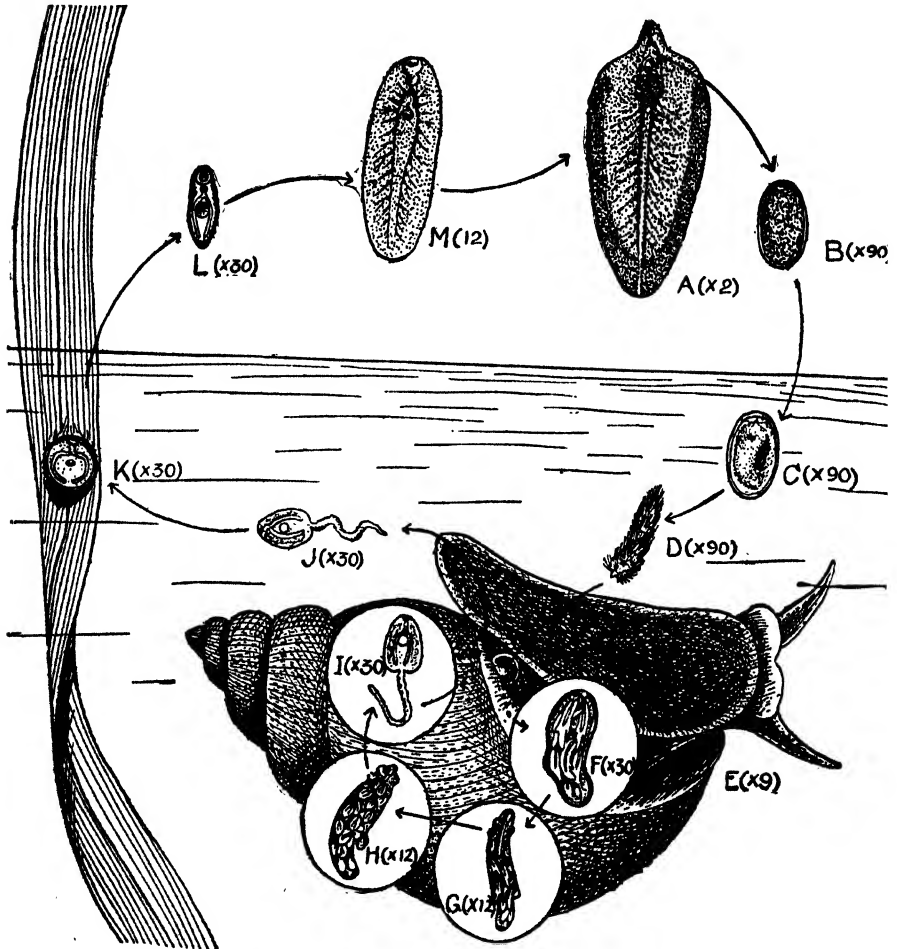
Fig. 192.—Life history of the liver fluke. *Fasciola hepatica.* *A*, adult in liver of sheep; *B*, freshly passed egg as it leaves the body of the host; *C*, developing embryo, ready to hatch in the water; *D*, ciliated miracidium embryo in the water and about to enter the pulmonary chamber of snail *E*; *F*, sporocyst containing rediae; *G*, redia containing daughter rediae; *H*, redia of the second generation containing cercaria; *I*, cercaria; *J*, same having emerged from snail into water; *K*, cercaria encysted on blade of grass; *L*, cercaria liberated from cyst after ingestion by sheep; *M*, young fluke developing in liver of sheep. (Reprinted by permission from Chandler, *Introduction to Human Parasitology*, John Wiley and Sons, Inc.)

also differ from trematodes by having the body divided into a series of segments, one behind the other, each segment having a complete set of reproductive organs. This structure characteristic of tapeworms is usually referred to as segmentation of the body, but it is
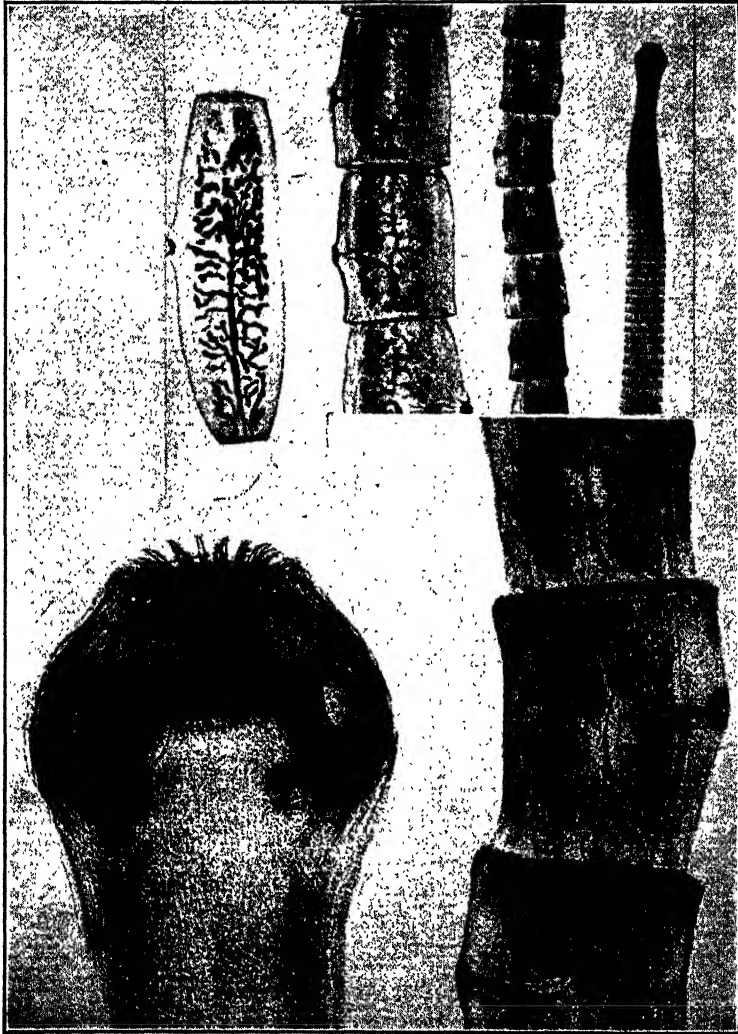
Fig. 193.—Structure of tapeworm to show different stages of maturity. At lower left, *Taenia pisiformis* scolex with hooks and sucker discs. At lower right, mature proglottids. Above, scolex and proglottids of three ages. The reproductive organs and pore are shown in most proglottids. (Courtesy of Ward's National Science Establishment, Inc.)

probably more correct to consider a tapeworm as a linear colony, in which the *segments* are really individuals in various stages of maturity.

Taenia solium, the pork tapeworm of man, may be taken as an example to illustrate the structure and life history of a cestode. The adult tapeworm consists of a *scolex* or *head* provided with four muscular *suckers* and a snoutlike *rostellum* surrounded by a row of chitinous *hooks,* which serve as means of attachment to the wall of the human intestine; a narrow unsegmented *neck* behind the scolex, and then a series of several hundred *proglottids* (the segments) becoming progressively larger as they get farther from the scolex. The
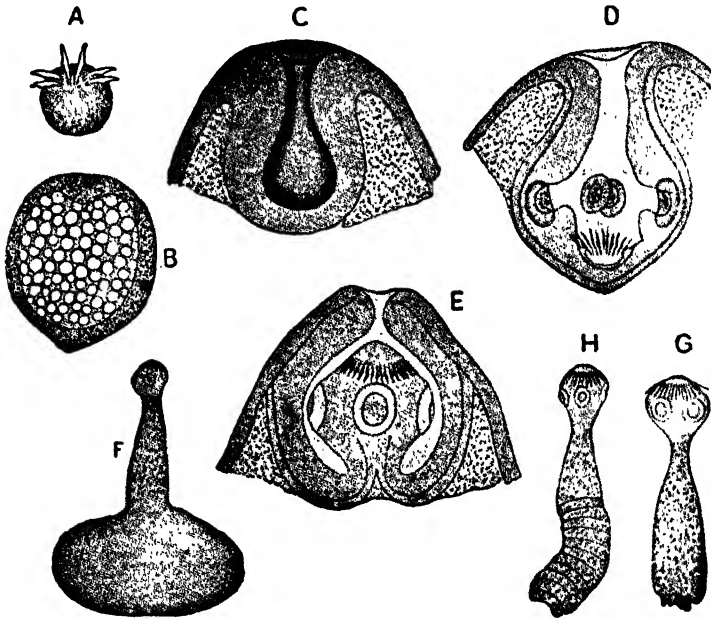
Fig. 194.—Development of tapeworm. *A,* six-hooked embryo ready to become embedded in muscle; *B,* cysticercus, or bladder worm as encysted; *C,* section through developing scolex in cysticercus; *D,* later stage; *E,* scolex everting as it protrudes from bladder; *F,* extension of scolex from bladder; *G,* later stage; *H,* formation of proglottids. (From Parker and Haswell, *Textbook of Zoology,* The Macmillan Company, after Jijima and Hatschek.)

whole chain of proglottids is called the *strobilus.* New proglottids are constantly budded off from the neck; consequently, the youngest proglottid is the first one back of the neck and the oldest one is the one at the end of the strobilus farthest from the scolex. The youngest proglottids contain no recognizable structures, except the paired longitudinal nerve cords and longitudinal excretory vessels

which run the full length of the strobilus, and a transverse excretory vessel in each proglottid. As the proglottids become older and are pushed farther away from the scolex, the reproductive organs begin to develop; each proglottid develops a complete set of both male and female reproductive organs; when these become mature and ready to function, the proglottid is a *mature proglottid*. Each mature proglottid is capable of copulating with itself, by bending the cirrus down into its own vagina, or it may copulate with another mature proglottid of another tapeworm if one is present close by.
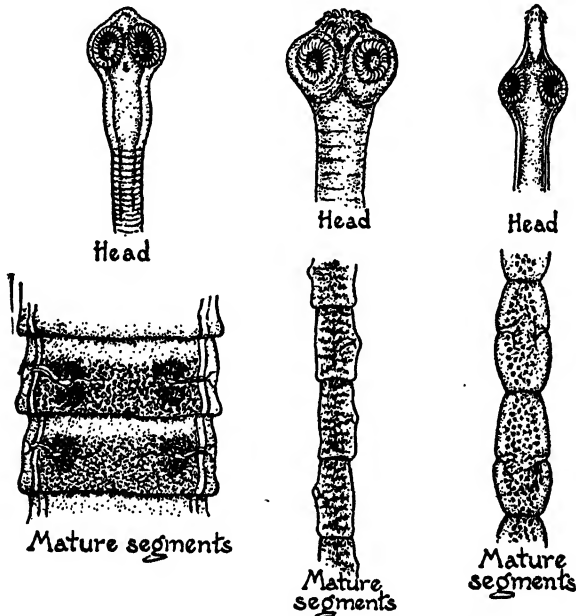
Fig. 195.—Common tapeworms, showing different regions of the body. At the left above—scolex of *Taenia saginata*, beef tapeworm; left below—proglottids of *Moniezia*, sheep tapeworm; middle—scolex and proglottids of *Taenia solium*, pork tapeworm; right—scolex and proglottids of *Dipylidium caninum*, a dog tapeworm. (Courtesy of General Biological Supply House.)

After copulation the male organs begin to degenerate, the uterus becomes filled with fertilized eggs and takes up more and more space, then the ovaries, vitellaria, and other female organs degenerate and leave the uterus to occupy nearly the whole proglottid; in this condition the proglottid, now hardly more than a sack of eggs, is called a *gravid proglottid*. The gravid proglottid at the extreme end of the strobilus breaks off and passes out of the host's

intestine with the feces. It continues to live and crawl slowly through the feces like an independent animal for a few hours, then usually dies, but the embryos within the proglottid remain alive much longer. If gravid proglottids or separate eggs are eaten by a hog, the six-hooked *hexacanth larva* hatches in the hog's intestine, bores through the intestinal wall, and migrates to other parts of the body where it changes into a bladder-worm or *cysticercus,* which is a saclike larva with an inverted scolex. The cysticerci remain in the flesh of the hog until the pork is eaten by man; under the influence of human digestive juices the cysticerci become everted so that the scolex is on the outside of the saclike part, then the scolex attaches itself to the wall of the human intestine, proglottids begin to bud off from the neck, and an adult tapeworm is formed within a few weeks.

Taenia saginata, the beef tapeworm, has a similar life history, but uses cattle instead of hogs as intermediate hosts. *Taenia serrata,* a common dog tapeworm often used as a laboratory specimen, is very similar to the two human species in structure and life cycle.

Other important cestodes are *Hymenolepis nana* of man and mice; the broad fish tapeworm, *Diphyllobothrium latum,* which man gets by eating raw or poorly cooked fish; the peculiar *Echinococcus granulosus,* adult in dogs, whose cysticercus stages are dangerous parasites of man (man being the intermediate host in this case); and many tapeworms of domestic animals, such as *Dipylidium caninum* of dogs, Thysanosoma and Moniezia of sheep, goats, and cattle, and many others.

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CHAPTER XXV

THE ANIMAL AND ITS ENVIRONMENT

(By A. O. Weese, University of Oklahoma)

Ecology is that division of biology which has to do with the relations between organisms and their environment. The environment of an organism, for convenience, may be divided into two parts, the nonliving, including physical, chemical, and climatic factors, and the living, including other organisms of the same and of different kinds. The science of ecology, in a sense, is as old as man, because from the very beginning of his conscious existence it was necessary that man take cognizance of the fact that his environment was made up in part of plants and animals and that these organisms in turn had relations to their environment. It was not until comparatively recently, however, that ecology came to be recognized as a separate department of biology. Modern ecology may be said to have begun with the recognition of the community. Plants and animals are distributed as they are over the surface of the earth, not because of any chance coincidence, but because of a combination of circumstances, one of which is the fitness of the physical environment for the proper completion of their life histories and another of which is the presence of such other organisms as are necessary to furnish food and to provide other requisite conditions. We can think of a community of organisms in much the same way as we think of a community of human beings. The analogy cannot be followed too closely, for, after all, human beings are much alike while the organisms in an ecological community are of many different kinds, having different requirements in detail as to food and environmental conditions. We shall arrive at a better concept if we think of a human community as made up, not only of butchers and bakers and candlestick makers, each with their particular functions as producers and as consumers, but also of the domestic animals which furnish materials for food or clothing or which perform labor, the household pets and pests, the cultivated plants which are utilized in the manufacture of food, clothing or shelter, and the host of wild animals and plants which enter into some relation with those previously

mentioned. The characteristics of such communities vary from time to time and from place to place. A difference in climate may be sufficient to change almost every component of the community. The domestic animals and plants associated with man in the tropics are quite different from those in arctic regions. Perhaps one species, the dog, almost as adaptable as man himself, might be considered as a member of both communities. The removal of a single species or the addition of a new one may alter profoundly the aspect of the community. Consider, for example, a human society from which
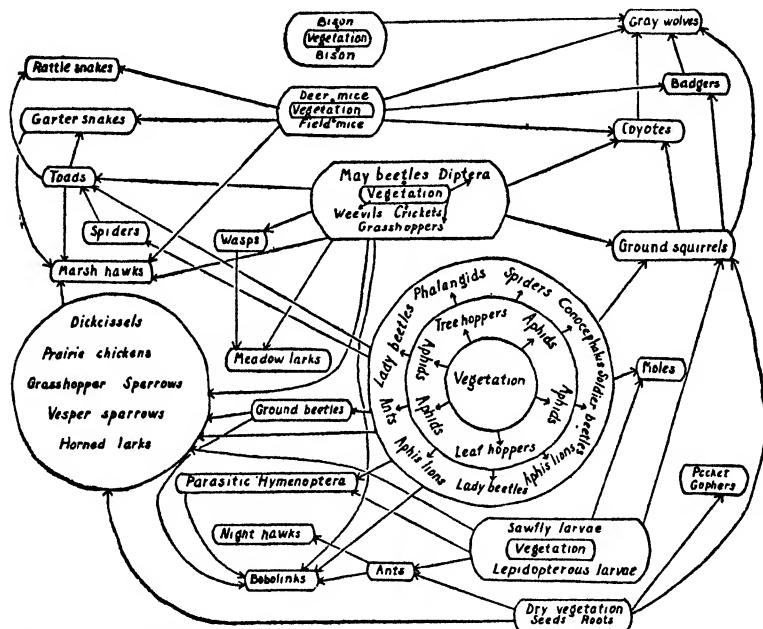
Fig. 196.—Diagram to show food relations in a hypothetical prairie community. (Redrawn and modified from Shelford, *Animal Communities in Temperate America*, University of Chicago Press.)

all cows were removed, or the changes made in the life of certain sections of the United States with the introduction of the cotton boll weevil.

Some idea of the complexity of the relationships involved in a community of organisms may be gained by citing Charles Darwin's example of the dependence of clover on cats, or Thomas Huxley's extension of the chain of cause and effect to the responsibility of the old maids of England for the supremacy of that nation on the

seas. Obviously, since old maids are fond of cats, the number of the latter is greater when old maids are numerous. Cats eat field mice, which in turn prey upon the nests of bumblebees. Thus, a large cat population is favorable for the development of clover which is fertilized by the bumblebee. Clover is fed to cattle and it is well known that Britain's sea power is due to "the roast beef of old England."

Most of the relationships suggested in this series have to do with food. It is often possible to gain a better idea of relations within a community by the use of a diagram indicating the more obvious influences. The accompanying figure, modified from Shelford (Fig. 185), represents food relationships only in a hypothetical prairie community and may be called a "food chain diagram." Many very obvious food chains are omitted in order to avoid a complexity
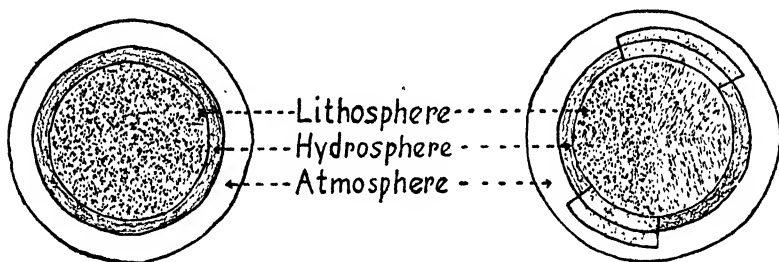
Fig. 197.—Diagram to show the relationship of the general areas of our planet.

too great for easy reading, and, of course, any real community would include many more kinds of animals. The chart is very incomplete, also, in that no relations other than those directly concerned with food are indicated.

Life exists on the earth only in a relatively very limited space. We might represent the relationship of the various parts of the planet on which we live by a series of concentric circles, the area within the inner circle corresponding to the "solid" portion of the earth, the lithosphere. If the lithosphere were uniform in diameter, it would be covered by a layer of water, the hydrosphere, which is in turn surrounded by a gaseous layer, the atmosphere. It is only where the components of these three layers interact that life is possible. Living organisms cannot exist in the lithosphere without the presence also of water, and of oxygen from the atmosphere. Similarly life in water is possible only where it contains in solution both

solids and oxygen. Air is habitable only temporarily and animals spending time there must return frequently to water or soil. Free interaction between the three components of the earth is made possible by the fact that the lithosphere is not of exactly uniform diameter so that certain portions project above the hydrosphere, forming continents (and islands). These elevated areas constitute a rather small proportion of the whole surface of the earth, but it is with these areas that we shall be concerned, not because there
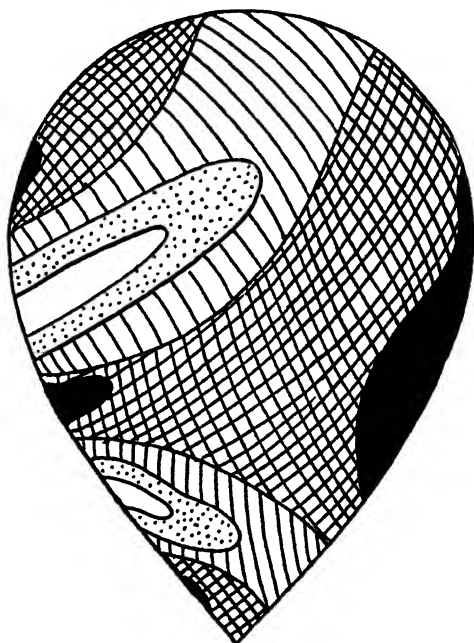
Fig. 198.—Distribution of "precipitation effectivity" on an ideal continent. (Modified after Thornthwaite. Drawn by Edward O'Malley.)

is no life in the submerged areas, but because the space available in this chapter is too small for us to consider the great subject of marine ecology.

The inclination of the earth's axis of rotation to the plane of the earth's orbit about the sun and the relative positions of the continents are factors which influence the distribution of climates. The two principal climatic factors are, of course, temperature and moisture. If the effect of altitude is not considered, the former is distributed rather uniformly, so that the familiar torrid, temperate, and

frigid zones express rather well the comparative temperature conditions on a continent. Many factors, however, operate in the control of the amount of precipitation and its distribution. In general, the distribution of available rainfall on an "ideal" top-shaped continent without mountain ranges might be expected to follow the plan of Fig. 198, in which the darker areas indicate maximum rainfall and the unshaded areas represent very arid regions. Each climatic type makes possible the occupancy of the region concerned by a

Perpetual snow or ice
Tundra
Evergreen forest
Deciduous forest

Grassland
Scrub (sagebrush)
Desert
Tropical forest & savanna
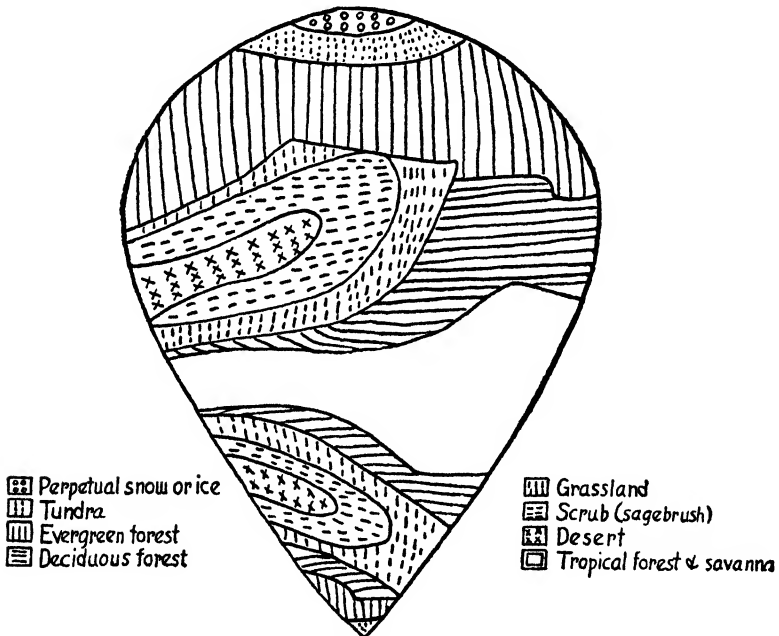
Fig. 199.—Hypothetical distribution of biotic communities on an ideal continent.

definite type of biotic community which can be most easily designated by the character of the conspicuous or dominant vegetation. Taking into consideration the seasonal distribution of available moisture and the annual variations in temperature, the "ideal continent" might be expected to present an aspect something like that represented in Fig. 199. It will be seen at once that in the regions of deficient temperature heat is the determining factor, and that in warmer regions the amount of moisture is the major influence. How closely this expectation is realized in the case of North America may be seen by a comparison with Fig. 200. As will be seen later,

the animals of a climatic region are as distinctive as the plants. The soil, which is the result of interaction between the climate, the plants and animals, and the rock substratum, also is characteristic of each climate. Thus, in the area influenced by each climatic type, there is a definite biotic community or formation, characterized by plants and animals whose relations to their environment are similar or equivalent.

The Principal Biotic Formations

A rough classification of the climatic formations of North America includes the following:

1. The Tundra Formation
2. The Coniferous (Evergreen) Forest Formation
3. The Deciduous Forest Formation
4. The Grassland Formation
5. The Sagebrush Formation
6. The Desert Formation

In addition there are transitional communities difficult of representation on a map because of their discontinuous distribution or small area. Some of these may be referred to, provisionally, as Woodland, Desert Scrub, Chaparral, and Swamp communities.

1. The Tundra Formation (Sedge-Musk Ox Biome).—This is the community of the arctic "barren grounds," beyond the northern limit of trees and between it and the polar region of perpetual snow and ice. Included, also, is the region above timber line on high mountains, where climatic conditions are similar to those of the far north. The vegetation of the tundra is composed mainly of grasses, sedges, and lichens (e.g., reindeer moss), although there are also patches of dwarf willows and other woody plants from a fraction of an inch to a few feet in height. Typical animals of the Arctic tundra are the musk ox and the Arctic caribou which feed on the low vegetation. Here, also, are found great hosts of rodents, including lemmings, whose enormous increases in numbers and periodic migrations in Europe have been known for many hundreds of years. Arctic hares and Arctic ptarmigan, with those animals previously mentioned, furnish food for the Arctic fox and the Arctic wolf. Many of these animals, including the Arctic fox, the Arctic hare, the ptarmigan, and the collared lemming, are adapted to the climatic rhythm of their environment by changing in color from

white in winter, when the entire landscape is snow-covered, to a darker color during the summer. On the tundra nest vast numbers of migratory birds, some of which, like the golden plover, fly to winter homes in South America.

2. **The Coniferous Forest Formation (Spruce-Moose Biome).**— South of the Arctic tundra and below the high mountain tundra along the Rockies and the Sierras is the great coniferous forest whose dominant vegetation is evergreen, composed chiefly of spruces,

Legend:
- Perpetual snow or ice
- Tundra
- Evergreen forest
- Deciduous forest
- Grassland
- Scrub (sagebrush)
- Desert
- Tropical forest and savanna
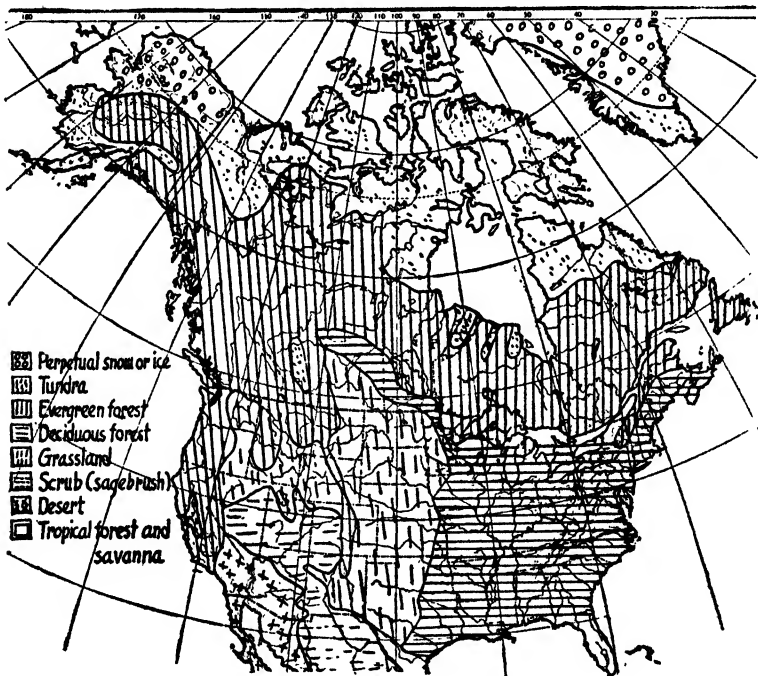
Fig. 200.—Distribution of the major biotic regions in North America.

firs, and pines of many species. The moose and the woodland caribou are characteristic animals over the greater part of the area. They feed upon grass and shrubs, chiefly in open areas near streams or lakes. The principal carnivore is the timber wolf. The Canada lynx is also a creature of the evergreen forest. Black bears are numerous but are widespread, also, beyond the borders of this formation. The wolverine and the red fox are lesser carnivores. The varying hare is similar to the Arctic hare but lives in more protected situations.

3. The Deciduous Forest Formation (Oak-Deer Biome).—Most of the United States lying east of the Mississippi River is characterized by deciduous forest. In this area the dominant vegetation consists of trees whose leaves are shed during the unfavorable winter season, such as oaks, beech, maple, hickory, and elm. The most widespread large herbivorous animal is the Virginia deer, although the wapiti (elk) was formerly of frequent occurrence. The wolf and the cougar were once widely distributed but are almost extinct now. The bay lynx, a close relative of the Canada lynx, preys upon the numerous rodents and birds. Other characteristic animals are the opossum, the raccoon, the flying squirrel, and the woodchuck. Many of these inhabit open areas in the woods rather than the dense forest.

4. The Grassland Formation (Grass-Bison Biome).—No single grass is included in the ''common'' name of this community because it is probable that the name of no single genus of grass is sufficiently familiar. Important grasses in the great central grassland area are the bluestems (or beard grasses), June grass, porcupine grass, grama grass, and buffalo grass. The grassland region was the habitat of the bison which once ranged over the prairies from Texas to Saskatchewan in enormous numbers. It is estimated that at the coming of the white man there were over 75 million of these animals, upon which the plains Indians depended for food, clothing, and shelter. The American pronghorn or antelope was also abundant. Both were held in check by the gray wolf. The black-tailed jack rabbit is an animal of the open grassland while the cottontail occupies wooded or at least bushy areas. In the drier western portion of the grassland the prairie dog and the badger are common. There are many small rodents, including the pocket gopher, the ground squirrels, and prairie deer mice.

5. The Sagebrush Formation (Sagebrush-Jack Rabbit Biome).—This community is centered in the Great Basin of Nevada, Utah, and neighboring states. It is an area of deficient rainfall, and sagebrush is a prominent constituent of the vegetation. Most of the larger animals belong to groups which are also found in neighboring formations, although the smaller mammals are mostly of different subspecies. Rabbits and rodents are especially abundant.

6. The Desert Formation (Creosote Bush-Kangaroo Rat Biome).—It is difficult to characterize this community by the name of a dominant plant and an important mammal, as there are many types of

desert associations. They have, however, one characteristic in common—a great deficiency in available water. Plants must guard against water loss and conserve water between the infrequent moist periods. Some of the adaptations which meet such conditions are: reduction of leaves (thorns), fleshy stems, thick cuticle, extensive underground organs, etc. Animals conserve water by remaining underground or in sheltered places during the hotter parts of the day and coming out only at night or at dusk. Reptiles and birds are able to reduce water loss by the absence of sweat glands and by giving off their nitrogenous excretion in the form of uric acid which does not need to be dissolved in water.

Adaptation

From what has been said above, it appears that each particular set of climatic and other environmental conditions accommodates a particular group of plants and animals. The activities and structure of these animals are such as enable them to survive best under the conditions in which they are found. The barren ground caribou is not fitted for life on the central grassland area nor is the bison able to survive on the tundra. Each is said to be adapted to the particular conditions under which it exists. Many so-called adaptations, however, seem to be worthless. One might think, for example, that the shovellike brow tines of the caribou would be a remarkable *adaptation* for shoveling snow from the vegetation on which the animal must feed during the winter—but the antlers are shed in the late autumn and do not grow out again until the following spring. One must be careful not to assign adaptive functions to animal structures without careful consideration of the habits and life histories of the animals concerned.

Succession

It must not be thought that, within the areas of the great climatic formations, there is entire uniformity in the communities of plants and animals. This is far from true. There exist minor differences of climate, soil, and physiographic conditions and of biological history which result in differences in plant and animal population. There are always areas which, for example, have been denuded by physiographic or other processes. Fire, flood, and human utilization are among the more common influences which may cause partial or

total destruction of the biotic communities of a region. When denudation occurs, a region does not long remain unpopulated, but the slow process of redevelopment of a community characteristic of the existing climate begins as soon as the destructive force has ceased its action. This process of development is called *succession* because it is characterized by the appearance, first, of pioneers, which give way to other groups of organisms which, in turn, alter conditions in such a way that still others find conditions favorable for their existence. The final result, after a long time, is the development of a community which is in equilibrium with its environment and will not change unless the environment changes. Such a community is called a *climax community*. An analogy might be sought, again, in human experience. The human pioneers who first penetrated into the broad plains of the "old west" conquered the wilderness to such an extent that some who required more of the comforts of civilization were able to find suitable homes. Many of the original pioneers, however, moved on to new frontiers when the land became too thickly settled. The "climax human community" has not yet been attained, as man is forever seeking more perfect adjustment to his environment.

It is often possible to study the stages in the development of a community without waiting for the entire process to take place in one locality. For example, the broad flood plains of many of our rivers are subject to frequent inundations. Such inundations may remove all living things from their paths, but since the flood plains are so broad and the course of the river is never the same from year to year, the same tracts are not covered each spring, and areas may be found which have been undisturbed for a few weeks, a few months, a year, two years, five years, fifty years, etc. In the flood plain of the Canadian River (in Oklahoma) mud flats from which the water has receded recently are soon occupied by an assemblage of organisms including blue-green algae, two small beetles, and a fly. Tiger beetle larvae come a little later, and then seedlings of willow and cottonwood. During the course of a year or so blowing sand is deposited so that the level of the ground is raised several feet, willows and cottonwoods increase in size, and other plants are added. Soil and sand continue to be deposited, the trees increase in size, and the ground becomes more thickly covered by vegetation. Finally, after a hundred years or so, a still higher level is attained and the willows and cottonwoods give way to oaks and

elms.   The table below indicates some of the insects to be found in each stage of this developmental series.   After the name of each insect is given, in parentheses, its principal food.

SUCCESSION ON THE CANADIAN RIVER FLOOD PLAIN.   (DATA FROM HEFLEY.)

STAGE IN DEVELOPMENT	1	2	3	4	5	6
Paralimma appendiculatum Fly	x*					
Heterocerus pallidus Beetle (Algae and detritus)	x					
Bendidion laevigatum Beetle (Algae and detritus)	x	x				
Cincindela hirticollis Tiger Beetle (small insects)	x	x	x			
Cinindela cuprascens Tiger Beetle (small insects)	x	x	x			
Cinindela punctulata Tiger Beetle (small insects)		x				
Mutillidae Velvet ants (insects and spiders)			x			
Apion pennsylvanicum Weevil (cocklebur)			x			
Haltica bimarginata Beetle (willow)			x	x	x	
Phalacrus politus Beetle (willow)				x		
Stictocephala lutea Tree hopper (willow, cottonwood)				x		
Cicadella gothica Leafhopper (willow)					x	
Dorytomus squamosus Weevil (willow)					x	
Strongylocornis stygicus Bug (coral berry)						x
Epitrix brevis Flea Beetle (Miscellaneous plants)						x

Brief descriptions of stages:
1. Mud flat with blue-green algae, later liverworts.
2. Sedges, willow and cottonwood seedlings in addition to 1.
3. Second level. Sand, sedges, willows, cottonwoods, cockleburs.
4. Third level. Grasses, willows, cottonwoods.
5. Third level. Cottonwoods, fewer willows.
6. Fourth level. Elm-oak forest with shrub undergrowth.

*x indicates the presence of the species as an important member of the community.

Animal Populations

A great deal can be learned about the relations of organisms by quantitative methods making possible an estimate of the numbers of various species present in a given community at any one time.
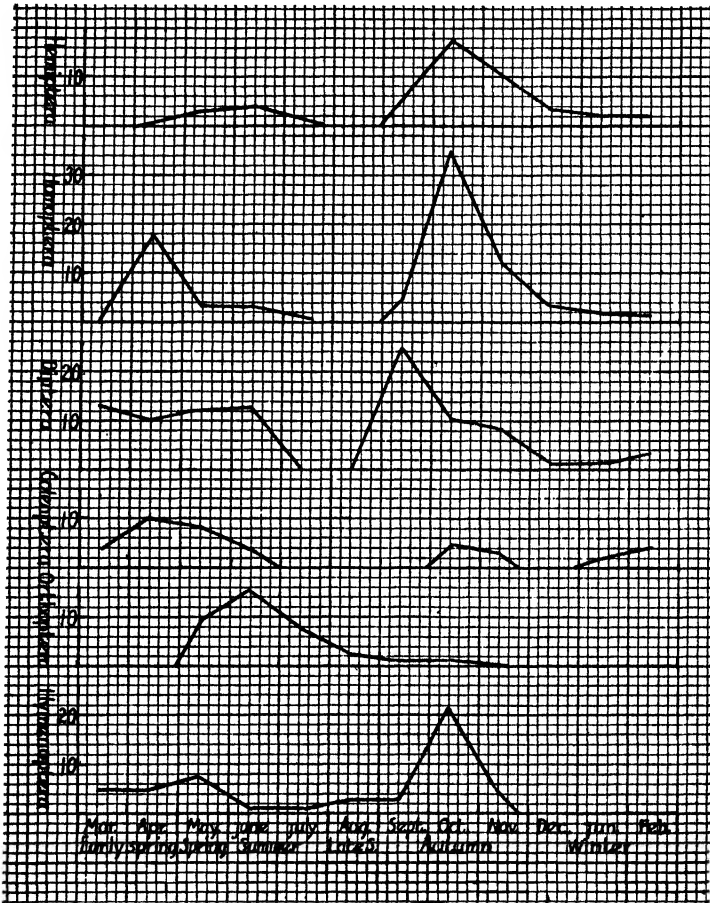
Fig. 201.—Numbers of insects collected in average catch with 100 sweeps of an insect sweep net in a prairie ravine (Oklahoma) arranged according to orders through the season of the year. (Data from Carpenter.)

Comparisons may then be made between the populations of communities differing in some observable respect, or between the population of the same community at different times of the year. It is comparatively easy, although somewhat tedious, to determine the

relative numbers of various plants in a given region by blocking off sample areas and counting the plants. Most animals, however, will not remain stationary while a census is being taken, and various less exact methods of obtaining population data must be employed. Some of these methods may be suggested. The number of birds may be estimated by the number seen within a given area or during a certain time, or a census of nesting pairs may be taken by counting nests. Larger mammals may be counted by experienced observers, burrows of rodents may be counted (but it is also necessary to determine the average number occupying a burrow) or the relative frequency of tracks, fecal pellets, or other evidences of the presence of the animals may give an idea of their numbers. The relative number of rodents is often estimated by the frequency with
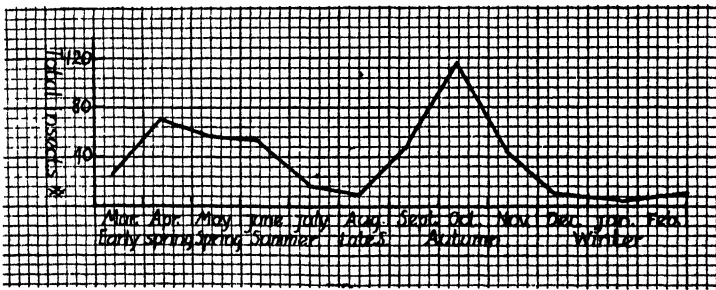
Fig. 202.—Total number of insects collected in average catch with 100 sweeps of insect net in prairie ravine (Oklahoma). (Data from Carpenter.) The scale for this graph is one-fourth of that in the preceding figure.

which they are caught in traps. The most frequently used method of estimating the number of insects is the use of the insect net. A net is swept through vegetation a definite number of times and all insects caught are counted. While all such methods are necessarily inaccurate, a great deal of valuable information may be obtained.

A list of the ten most abundant groups of insects found in two adjacent areas, one heavily overgrazed and the other lightly grazed, is given in the following table. The figures indicate their relative abundance in ten collections of fifty sweeps of the insect net, each. These collections were taken over a period of a month and indicate a very real difference in the insect populations of the two areas.

RELATIVE NUMBERS OF TEN MOST ABUNDANT INSECTS FROM OVERGRAZED AND NORMAL GRASSLAND. (WICHITA MOUNTAINS WILDLIFE REFUGE.)

GENUS	COMMON NAME	NORMAL	OVERGRAZED
Melanoplus	(grasshopper)	11.0	220.0
Campylenchia	(tree hopper)	0.5	144.0
Mermiria	(grasshopper)	14.0	138.0
Scolops	(plant hopper)	10.0	120.0
Elleschus	(weevil)	0.9	80.0
Poeciloscytus	(leaf bug)	1.2	54.0
Agallia	(leaf hopper)	8.0	38.0
Harmostes	(plant bug)	0.5	17.0
Deltocephalus	(leaf hopper)	8.0	3.4
Bruchomorpha	(plant hopper)	11.0	0.4

Seasonal Changes

It is a matter of common observation that the animals observed in any one place differ greatly from season to season during the
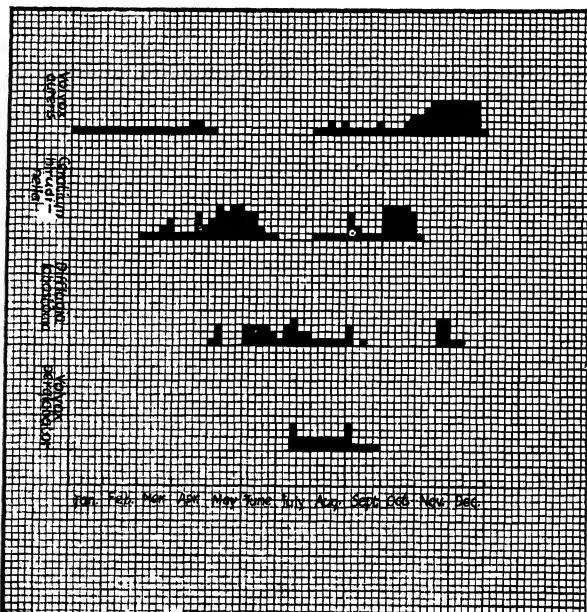
Fig. 203.—Fluctuations in populations of four Protozoa in an artificial lake in Oklahoma during the months of the year.

year. This is not only true of those animals which, like many birds, migrate southward on the approach of winter and return to northern climates for nesting. Some animals hibernate or aestivate, and

others spend a part of the year in an inactive stage, such as the egg, or the pupa. The life cycle of an organism must be adjusted to the annual climatic cycle of the climate in which it lives. Some idea of the variations in the number of insects during the year may be gained from a study of the accompanying charts (Figs. 201 and 202) giving the average catch with one hundred sweeps of an insect net at different seasons.

A study of the abundance of Protozoa in an artificial lake (Fig. 203) shows a similar difference in the time of abundance of the various species.

Summary

This chapter has considered very briefly the distribution of the biotic communities of North America in relation to climate. The phenomena of succession and seasonal fluctuation of populations have been discussed, with examples. Attention has been directed toward the community rather than toward the individual organism or the species. Similarly the sum total of physical environment as expressed in climate has been stressed rather than single factors, such as moisture, temperature, light, etc. The animal in nature is subject always to the action of a complex environment and its distribution and reactions are the result of its response to the whole.

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CHAPTER XXVI

ANIMAL DISTRIBUTION

(By Willis Hewatt, Texas Christian University)

Life Regions and Zones of the Earth

Every area of the earth has its animal and plant life. The apparently barren sun-baked desert, the ice-capped polar regions, the highest mountain tops, and the tropical rain forests are all inhabited by their faunas and floras. Life in the seas extends from the shore line to the greatest depths. After extensive taxonomic surveys have been made in practically all areas of the earth and these data are studied, it is found that the earth can be divided into fairly definite horizontal regions and vertical zones. These two phases of the distribution of organisms on the earth are very closely related to each other but are usually studied separately as *geographic* or horizontal distribution and *bathymetric* or vertical distribution, respectively.

Geographic Distribution.—Many attempts have been made to divide the earth into horizontal life regions based upon the distribution of various groups of animals and plants. The exact boundaries of the regions are not fully agreed upon since several groups of animals have been used as criteria for the division into life regions. P. L. Sclater (1829-1917), the earliest zoogeographer, worked with the perching birds. These forms were well adapted to such a study since they have little power of flight, they are widely distributed, and they had been very closely studied. The early (1876) classic work of the Englishman, Alfred Russell Wallace, in which the earth was divided into six primary regions, is the one most commonly followed by modern biologists. Wallace based his divisions upon the distribution of the mammals. Other significant studies in geographic distribution have been based upon the geographic ranges of mollusks, earthworms, moths, butterflies, spiders, fresh-water fishes, reptiles, and many others. From works dealing with such varied groups of animals it is readily understood that any classification of the regions of the earth will depend greatly upon the group of animals used as a criterion. On the other hand, there are many correlations found in the studies of the geographical ranges of all of these groups of animals. The zoogeographical regions of Wallace and the

general boundaries of these areas are given below.   The boundaries of the regions do not necessarily follow the outlines of continents as will be seen in Fig. 193.

· **1.** *The Palaearctic Region* includes all of Europe, Africa north of the Sahara, and all of Asia north of the Himalaya Mountains.

2. *The Nearctic Region* embraces the North American continent as far south as Mexico.

3. *The Ethiopian Region* consists of Africa south of the Sahara, southern Arabia, and Madagascar.
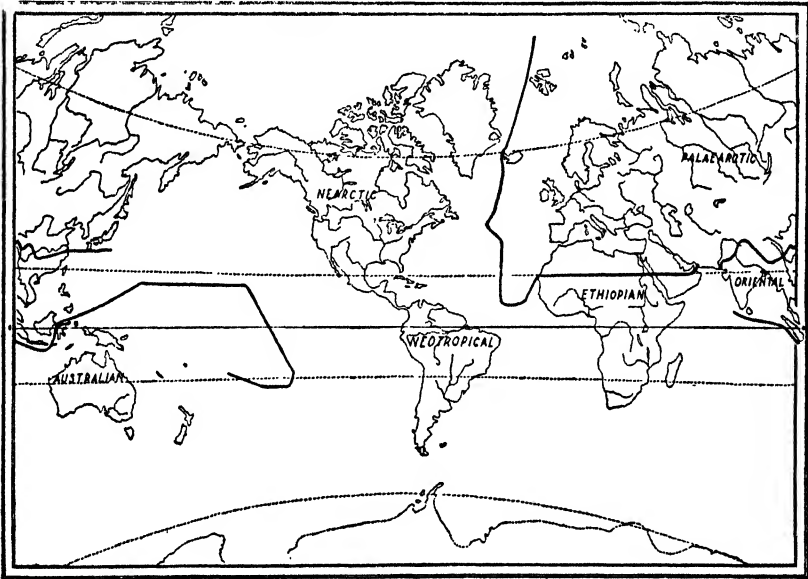
Fig. 204.—Map showing the life regions of the earth.   (Base by permission of A. J. Nystrom Company.)

4. *The Oriental Region* includes Asia south of the Himalayas, and that portion of the Malayan Archipelago which lies northwest of *Wallace's line*.   This famous line dividing the Oriental and Australian Regions passes east of the Philippines between the islands of Bali and Lombok, and between Borneo and Celebes.   Bali and Lombok are separated by a very narrow but deep strait, and there is a very remarkable contrast between the faunas of the two islands.

5. *The Australian Region* is made up of Australia and the neighboring islands as far west as Wallace's line.   It includes the great number of small islands east of Australia.

6. *The Neotropical Region* consists of Mexico, Central America, and South America.

The present distribution of animals on the earth gives us many evidences concerning the past history of the earth. The North American fauna is notably different from the South American fauna. This fact apparently indicates that North and South America were completely separated from each other by an extensive water barrier until a relatively recent period. The great contrast between the faunas of the islands of Bali and Lombok indicates that the Australian continent and its neighboring islands have been separated from the Asiatic mainland for a relatively long period of time. The study of distribution also gives many clues to the ancient changes of climate on the earth.

Bathymetric Distribution.—In discussing the vertical or altitudinal distribution of animals two fundamental types of habitats must be considered; namely, the water habitat or *Hydrobios* and the land habitat or *Geobios*. The inhabitants of these two realms differ greatly, but some few forms occupy both regions.

The hydrobios includes both fresh- and salt-water realms. The variation in vertical distribution of fresh-water animals is relatively insignificant when compared to that of marine animals. The seas have been variously classified into vertical zones. The divisions most commonly recognized are:

1. The *Littoral* which is the area between tide marks. It is characterized on rocky shores by growths of barnacles, mussels, and snails. Life in sandy littoral regions, such as that along the Texas Gulf Coast, is relatively scarce and consists chiefly of annelid worms and other boring forms.

2. The *Sublittoral* includes the subtidal region to a depth of approximately 100 meters. This is about the lowest depth at which plants can grow abundantly. It is the most productive region on the earth as far as variety and numbers of animals are concerned.

3. The *Abyssal* zone is marked by the absence of light and extends to the greatest depths of the oceans. Life is not very abundant in this zone. Plants cannot live at such depths, therefore, the animals which live in the abyssal region are dependent upon other animals as a source of food, or they subsist upon the floating plant life which is continuously dying and sinking to lower levels.

The vertical or altitudinal distribution of terrestrial animals depends primarily upon the vertical distribution of the vegetation. The variation in the kinds of plants found at different altitudes depends to a large extent upon the climatic belts which extend around the earth between the equator and the poles. The vertical belts of plants encountered in traveling from a lowland to a high mountain top correspond very closely to the climatic zones surrounding the poles of the earth. The communities of animals and plants found in each vertical zone are similar throughout the world.

The seven vertical life zones and a few of the characteristic animals and plants found in each zone, as it is represented in the Southwest, are here given.
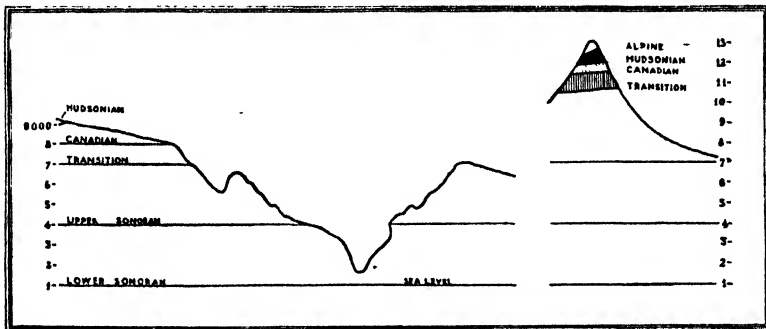
Fig. 205.—Diagrammatic sections of the Grand Canyon and San Francisco peak showing the vertical life zones. (After N. N. Dodge and Merriam.)

1. *The Alpine zone* (usually above 10,500 feet) is the area above the timber line. This highest zone is represented in the Southwest on the top of San Francisco Mountain in Northern Arizona and in the Sangre de Cristo range of the Rockies in Northern New Mexico. This zone is characterized by the presence of few plants, such as saxifrages and dwarf willows. Among the fauna are found the golden eagle, some weasels, and mountain sheep.

2. *The Hudsonian zone* (9,000-10,500 feet) consists of a forest of spruces and some firs, and harbors the dusky horned owl, bears, shrews, and red squirrels. The Hudsonian zone is found in the same region as the Alpine zone.

3. *The Canadian zone* (8,000-9,000 feet) is distinguished by the presence of the Douglas fir and the aspens. Common animals of this zone are the three-toed woodpecker, one species of shrew, and two

species of field mice. This zone is found in the Rockies as far south as southern New Mexico. There is some evidence of Canadian fauna in the Chisos Mountains of Texas.

4. *The transition zone* (7,000-8,000 feet) is found in the same regions as the above zones. It is also found in the Davis and Chisos and Guadalupe Mountains of Texas. It is covered with pine trees
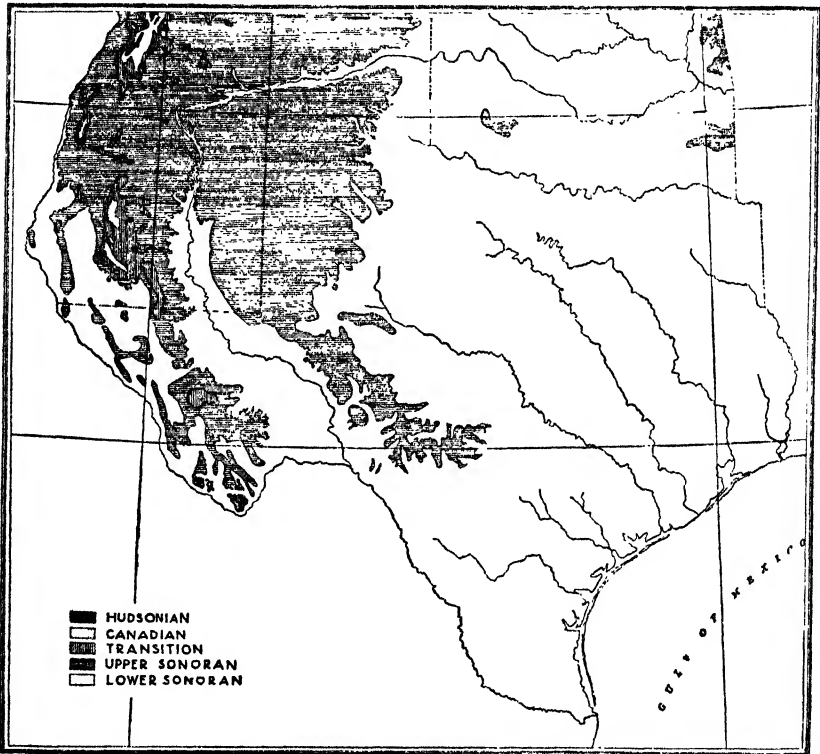
Fig. 206.—Map of the vertical life zones of Texas and adjacent areas. (After Bailey.)

(mainly *Pinus ponderosa*). Abert's squirrel is found in the Transition zone as is one species of horned lizard.

5. *The Upper Sonoran zone* (6,000-7,000 feet) is the piñon belt distinguished by the nut or piñon pine and cedars. The zone extends from western Texas through New Mexico, Colorado, Arizona, and into southern California. Characteristic animals are the piñon jay bird, and the large rock squirrel.

6. *The Lower Sonoran zone* is less homogeneous in its flora and fauna than are the other zones. In the Southwest it includes most of Texas, Oklahoma, southern New Mexico, southern Arizona, and southern California. The eastern third of Texas is typical of the lower Sonoran of the southeastern states which are characterized mainly by long-leafed pines, magnolia, and live oaks. Some animals of the eastern portion are mockingbirds, painted buntings, and wood rats. The western lower Sonoran is inhabited by typical desert and semidesert flora and fauna.

7. *The Tropical zone* is of very little significance in the southwestern United States, but many tropical plants, such as the Texas palms and bananas, grow in a narrow strip of the lower Rio Grande Valley.

Migration of Animals

The migrations of many animals are not well understood but in most cases they involve breeding habits, food, or shelter. Most of these migrations are seasonal, but many permanent changes of location have been made by groups of animals as a result of permanent changes of climate on the earth.

The seasonal migrations of the North American caribou and the bison are among the most noted examples of migrations of animals which move about in search of food. The caribou migrate southward in Canada during the winter and follow the melting snow northward in the summer.

The remarkable migrations of the eels of the Mediterranean area and of the eastern coast of the United States are among the best known examples of breeding migrations. The eels from the rivers of these two regions migrate into the Caribbean Sea and spawn. Although the two spawning territories overlap, the young eels of each species journey hundreds of miles back to the rivers inhabited by their ancestors. A great many species of birds migrate from the tropics and semitropics and breed in northern regions. The scarlet tanager spends the winter in northwestern South America and migrates across the Gulf of Mexico into northeastern United States and southern Canada and breeds during the summer months. The upland plover is familiar in the Southwest, since it migrates through this region twice each year on its journeys between Argentina and British Columbia.

Means of Dispersal and Barriers

The wide distribution of species of animals on the earth depends largely upon their means of dispersal or means of being carried from one place to another and upon the barriers which they encounter. Among the members of a species as well as among the related and nonrelated species of animals there is a continuous struggle for existence. Those forms which, by some means, are able to enter new environments where competition is less severe will have the better chance at survival.

In practically all marine organisms there exists a means of locomotion during some stage of the life history. In a great number of the forms, especially those which are sessile in the adult stage, there is a free-swimming larval stage: planula larva of the coelenterates; trochophore larva of annelids; and the various free-swimming larvae of mollusks, echinoderms, and crustaceans. The planktonic larvae and adults, i.e., those which swim or float free of the bottom, depend greatly upon oceanic currents for their wide dispersal.

The dispersal of oceanic animals is also greatly enhanced by the large numbers of eggs and larvae produced by these forms. For example, one investigator found that a "sea hare," a marine gastropod, deposited 478 million eggs during one four-month spawning period. The eggs were laid at the rate of 41,000 per minute.

Marine animals are limited in their distribution by such barriers as temperature, land masses, and salinity of the water. The marine animals on each side of the narrow Isthmus of Panama are entirely different. The extreme changes in temperature prevent most of these species going around the southern tip of South America. Littoral animals are often limited in their distribution by large river mouths which empty great quantities of fresh water into the oceans. Only specially adapted forms can live in these brackish waters.

Fresh-water faunas are restricted in their distribution by land barriers which usually separate the bodies of water in which they live. These forms depend mainly upon other animals, such as birds and insects, for the dispersal of their eggs and dormant stages. Many fresh-water animals, such as snails and clams, attach themselves to the bodies of birds or insects and are carried into new habitats.

Among land animals the birds and flying insects appear to be least restricted in their ranges. Even these, however, are often

limited by mountains, deserts, and large rivers which act as the most effective barriers to the wide distribution of land animals. Many of the birds and mammals found on the south rim of the Grand Canyon of the Colorado River are not able to reach the north rim of the Canyon. For example, the Abert squirrel is found in New Mexico and Arizona, south of the Canyon, while the Kaibab squirrel occurs only north of the Canyon. Small islands, which are located great distances from the mainland, are often inhabited by small mammals and reptiles similar to those found on the mainland. Such forms have probably reached the islands by way of floating rafts of vegetation, and hollow trees which are known to be carried several thousands of miles by oceanic currents.

Wind currents may carry birds across the Atlantic Ocean. It is not uncommon for American birds to land on the coast of England after severe storms. These same currents also carry spores of Protozoa, small insects, and the eggs of many invertebrates.

Effects of Man Upon Distribution

The advent of man upon the earth and the development of his more efficient means of travel have greatly enhanced the wide distribution of many species of animals. Marine invertebrates attach themselves to the bottoms of ships (ship fouling) and are carried to practically all parts of the earth. Rodents and insects are accidentally distributed from one country to another by ships. During the past man has purposely transported animals from one country to another. In some instances the animals multiply more rapidly in the new environment than they did in the original habitat. English sparrows were introduced into North America in 1859, and since that time they have become so numerous as to be a great pest in this country. The starling, which was introduced at about the same time, is rapidly increasing in numbers and in recent years has been reported as far south and west as Central Texas. By cultivating extensive prairie lands, man has created insurmountable barriers to grazing animals which once roamed these areas. Deforestation of wooded regions has destroyed the shelter necessary for such animals as deer, foxes, wolves, bears, and many others.

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CHAPTER XXVII

THE THEORY OF EVOLUTION

It is likely that no student of modern biology has gone far before he has realized something of a progressive relationship between the various groups of animals in the animal kingdom. Phylogeny refers to the background of what has gone before in producing a race or phylum and incorporates the thought that different species have arisen from common ancestors. The general idea of it, as now accepted by most biologists, is that all living organisms have been derived through normal reproduction and variation by adaptation from simpler, more generalized ancestors. Phylogenetic relationships of organisms and the origin of species have long been topics of exceptional interest to biologists. Two questions which have intrigued the thought of many are: first, whence came living material? and second, what has been its course of events since the time of origin? The theory of organic evolution provides the history of living things as interpreted by the biologist.

The observations and thought of Charles Darwin gave the first substantial support to the idea of all modern species originating from preexisting organisms. Results of his careful studies were presented in 1859 in his book *The Origin of Species,* which is now a classic in the field. There is still lack of agreement among scientists concerning the details of origin of life and species, but there seems to be little doubt that species, genera, and even larger groups have progressively developed since life originated on earth. The ideas of continuity, development, and differentiation of living organisms are quite generally accepted by those who have studied these problems. The lines of kinship of animal groups are traced only through common ancestry, and it is not ordinarily assumed that direct relationship exists between representatives of modern groups.

Sources of evidences of relationships are quite widespread, coming from such studies as zoogeography, comparative anatomy, embryology, physiology, paleontology, and even others. By combination of information gained from such sources much has been learned of the past history of many groups of organisms. Even these available

sources give incomplete and sometimes inconclusive evidence of the history of any particular organism. The individuals are recognized as being only points on a long line of modifications. The two ends of this progressive line are seldom recognized with any finality. Darwin, and many others since his time, recognized three fundamental facts that bring about a progressive continuity among living things: *heredity,* with the tendency for organisms to resemble their parents; *variation,* in that no two organisms are exactly alike, hence the resemblance between parent and offspring is not absolute; and *constant production of more offspring* than can survive. The phylogenetic relations of animals show all indications of having been brought about by the operation of the above-mentioned factors in an orderly, evolutionary progress.

Variation is one of the most obvious facts and consistent phenomena in the animal kingdom. Darwin held that variability is axiomatic among living things. As long as differences among individuals of a group are minor or are irregularly distributed, the group is likely to be considered a species. However, the species is not rigidly bounded, and it must be remembered that continuous variation is in progress within this group as one generation follows another. It is becoming apparent to man that new groups have arisen and are arising within old groups of animals, also that old groups have broken up, some to become new ones and others to become extinct. These new groups were separated by small differences at first but gradually they attained greater and greater divergence from the common form. This is particularly likely where the different groups have become widely separated geographically or exist under distinctly different conditions of life. Frequently, it is only the widely separated extremes of the group which carry on the posterity, the intermediate forms having died out. In this way rather widely separated species may have arisen from common stock, and the lack of intermediate forms may accentuate the wide divergence between them. During the millions of years which life has existed on earth, it seems evident that this process of divergence between groups has been in operation until there now exist many definable groups with distinct lines of relationship. Our natural system of classification is based on the relations and differences established for the different animal groups. Comparative studies of numerous animal groups will help to show some of the relationships.

Colony Formation in Certain Protozoa

Due to incomplete separation of cells following division in Protozoa, colonies are begun. In some instances groups of cells in some such colonies, e.g., *volvox*, become specialized as gametes for reproductive purposes and the other cells remain as somatic cells. Because of the similarity between various mastigophoran colonies and blastula stages in metazoan development, this group has frequently been cited as the predecessors from which Metazoa at some time originated.

Development of the Gastrula

The primitive gastrula is thought to have had its origin from a spherical colony of Protozoa by a more rapid growth of the cells at one pole which brought about an infolding or invagination to produce a new cavity from the exterior. This development establishes a body composed of two general layers. Modern adult coelenterates, like the hydra, and others demonstrate precisely this condition today, with the outer ectoderm and the inner endoderm, each composed of cells serving vital general functions. This allows all cells surface exposure either directly on the exterior or to the cavity. By this means larger and more complex organisms were developed and have lived.

Trochophore Larva

In Platyhelminthes, Annelida, Molluscoidea, Trochelminthes and Mollusca there occur larval forms of the trochophore type. Although the surface ciliation and some other superficial features differ somewhat, a direct relationship among these forms is trace-
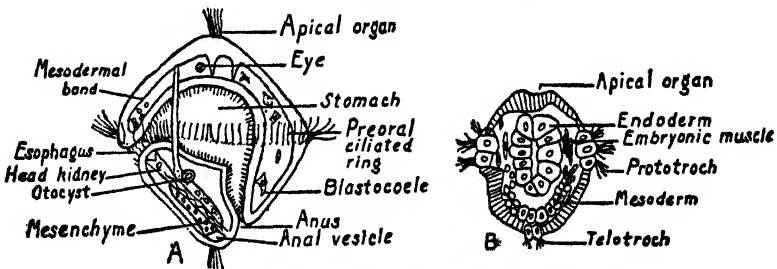
Fig. 207.—*A*, Trochophore larva of *Eupomotus* (a polychaete annelid), side view. (After Shearer.)

B, Veliger larva of *Patella* (a marine snail), frontal section. (After Patten.) (Drawn by Joanne Moore.)

able through the larva. The fundamental morphology of the cteno-
phore is similar to that of the trochophore larva, and the Platy-
helminthes are generally thought to have been derived from Cteno-
phores. The regular arrangement of gonads and the even, orderly
distribution of the diverticula from the intestines of the flatworms
are interpreted by many to indicate preparation for segmentation
as it appears in annelids.

Peripatus and the Wormlike Ancestry of Arthropoda

Peripatus, the only representative genus of class Onycophora, was
considered a segmented worm for a long time because of its shape, its
even, conspicuous segmentation, and possession of nephridia for ex-
cretion. But later it was discovered that the respiration is carried
on by tracheae, and the body cavity serves as a blood space, both
of which are typical arthropod features. In addition, the paired
legs are jointed, although similar in appearance to paropodia of
Annelida. There are two jointed antennae on the head and some

Fig. 208.—*Peripatus capensis.* Natural size. (After Moseley from Folsom's
Entomology. Redrawn by Nelson A. Snow.)

jawlike plates in the mouth. Situated as it is, midway between
annelids and arthropods, this form seems to show an immediate
transition from the one group to the other. Upon this basis it is
usually held that the arthropods have a wormlike ancestry.

Interestingly enough, there exists another idea of arthropod an-
cestry from the fact that all of the lower forms of Crustacea pass
through a characteristic stage known as the *Nauplius* (Fig. 167).
This larva does not correspond very closely to any strictly annelid
stage, but with its short body and three pairs of appendages it re-
sembles a modified trochophore larva. The nauplius larva has some
features in common with the rotifers which authors feel may have
arthropod tendencies.

Echinoderms and Their Larval Relations

Although the adult echinoderms possess radial symmetry, that
seems not to have been in the immediate phylogenetical background.

.The larvae of all echinoderms possess bilateral symmetry. These larvae all have definitely arranged bands of cilia over the body. Embryologists have pointed out the fact that these larvae are not directly related to the trochophore. They show more resemblance to the Tornaria larva of Balanoglossus than to any of the nonchordate forms.

Ancestry of the Vertebrates

The establishment of relationships between the chordate and nonchordate animals has been one of the perplexing problems in the study of phylogeny. Different students of this problem have investigated the possible relationships of such nonchordate groups as the flatworms, nemertine worms, annelids, arachnids, insects, and echinoderms. Their investigations have resulted in the formulation of a number of theories putting forth the various ones of the abovementioned groups as the progenitors of, or claiming common ancestry with, chordates.

Some authors insist that the chordates have arisen from some segmented form; others conclude from their evidence that this is not necessarily true or essential. All of the theories establish their relationships to the vertebrates through the protochordates, which are represented by Amphioxus, the tunicates, and Balanoglossus. Each of these has been considered as ancestral stock, which has contributed to the origin of vertebrates. It is usually conceded by authorities in this field of study that Amphioxus is a modified ancestor of the vertebrates, due to the clear-cut and well-defined condition of the distinctive characteristics of the chordates and the presence of a midventral endostyle. Next in the line of thought would come the possibilities of ancestors of Amphioxus. The tunicates have been given this distinction by some. The adult has lost most of its typical primitive characteristics, but the larva possesses the distinctive characteristics of chordates and also the ventrally located endostyle, very similar to these structures in adult Amphioxus. It has been suggested that probably the adult tunicate once existed as an animal similar to its larva of today, and that its forebear was not only the ancestor of modern tunicates but also the form from which the Amphioxus group has descended.

Balanoglossus, which is usually considered the most primitive of chordates, is regarded as a possible ancestor of, or as possessing common ancestral stock with, tunicates and Amphioxus. As will

be remembered from the previous study of *Balanoglossus,* it possesses gill slits, a support in the base of the proboscis which may be homologous to the notochord, and four longitudinal nerve cords of which the dorsal is the most highly developed. The above proto-chordate relations are rather generally conceded, but there is much less agreement concerning their origin, and several theories have arisen of which the following are important.

Annelid Theory.—The segmental condition of this group, the re-lationship of the digestive system to other circulatory and nervous systems, and presence of the coelom with related nephridia, present a close comparison to what is found in the embryonic development of the vertebrates. It has been suggested by some scholars that by inverting the body of the nonchordate annelid, the fundamental systems are brought to resemble their relative locations in verte-brates. A fibrous cord has been found in some groups of the an-nelids, and this structure is held to take the place of a notochord in function and position. These fibers are found just dorsal to the chain of ganglia in the annelids.

Arachnid Theory.—Such forms as scorpions, Limulus, and other arachnids have been favorably compared to vertebrates. By com-parison of these arachnids with the extinct, fishlike ostracoderms, an elaborate theory of the possible origin of the vertebrates from this ancestry is derived.

Echinoderm Theory.—This theory of vertebrate descent goes again to the Balanoglossus. The developing egg of this animal becomes a larva known as Tornaria (Fig. 47), which floats in marine waters, has bilateral symmetry, is almost transparent, and possesses bands of cilia used in locomotion. This larva is almost exactly like that of the starfish and other echinoderms which live in the same habitat (Fig. 140). The close correspondence of features of these two groups of larvae has suggested the conclusion that these two types of ani-mals have descended from a common ancestor which was similar to these larvae. The line of descent of one branch of this stock has presumably passed through *Balanoglossus,* Tunicata, *Amphioxus,* and Vertebrata. The nonchordate ancestors are not yet conclusively determined, but the foregoing theories suggest the thinking and evi-dence along that line.

Within the class Vertebrata the relations are somewhat more evi-dent, but the phylogenetic sequence is rather obscure at some points.

Cyclostomes, the simplest vertebrates, are most closely related to Amphioxus, which has been suggested as the protochordate most similar to vertebrates. These very primitive fish have an eellike body without paired fins and without jaws. They have from seven to fourteen branchial (gill) apertures in different species, and all of them possess skeletons composed of cartilage. The cartilaginous skull is not entirely closed dorsally but resembles a trough with bars over the roof. The anterior end of the nerve cord has expanded to become a brain. Next in order of complexity are the Elasmobranchii, which possess well-developed, paired appendages (fins) and jaws. They also have a cartilaginous skeleton, but the skull is much more complete dorsally. The number of gill arches is reduced to five, but the apertures are uncovered as in cyclostomes. The number of aortic arches has been reduced from the sixty to ninety pairs of Amphioxus or seven pairs of lamprey to five pairs. The group of ganoid fishes, which was the dominant Devonian animal, is generally conceded to have Elasmobranch ancestry. Most ganoids have more or less cartilage along with the bony structure of the skeleton. Their gills are covered with an operculum, and there are only four aortic arches. The bony ganoids are usually thought to be the ancestors of true bony fish.

There is an extinct form of Amphibia, *Stegocephalia,* which shows relations to the ganoid fishes and for this reason the ganoids are usually named as ancestors of Amphibia. Some authors hold that the lungfishes, which represent an independent branch of the Elasmobranch group, are the ancestors of Amphibia because of their ability to breathe air and live out of water. However, the former view of the phylogenetic relation between fish and amphibia is most commonly held. Amphibia have well-developed bony skeleton with paired appendages for locomotion on land. Lungs have appeared as a means of aerial respiration, and the aortic arches have been reduced to three.

Reptiles are supposed to have descended from *Stegocephalia* also, with most modern reptiles coming by way of *Rhynchocephalia* which is represented by one living species, *Sphenodon punctatum.* The snakes, lizards, crocodiles, and the extinct dinosaurs have probably branched from this group, while the turtles are thought to have descended through *Theromorpha,* another extinct branch of *Stegocephalia.* The dinosaurs are credited with the ancestry of birds by

way of a toothed, feathered, extinct form known as *Archaeopteryx*. It was essentially a flying reptile. The mammals probably descended from the reptilian group *Theromorpha* by way of our modern monotremes which lay eggs, hatch them out, and then suckle the young with milk from mammary glands. The marsupials, such as kangaroos and opossums, are next in order, and from these it is thought the Placentalia have arisen. Within this group some authorities hold the view that the Primates, the order including man, have arisen from Insectivora. The apes and monkeys belong to the Primate group, and there has been some misunderstanding among laymen generally in regard to the possible relationship of man and the apes. Most people have the misconception that this is a linear descent in which the most advanced member of the lower group represents the immediate ancestor of the next higher group. As a matter of fact, the theory is not that the higher monkeys are in the process of becoming apes and the higher apes becoming men, but that all three of these groups have had origin as different lines from a common primitive form.

Recapitulation Theory.—In the early part of the nineteenth century von Baer observed that the early stages of vertebrate embryos of different classes had a very close resemblance to each other. He did not subscribe, however, to the recapitulation theory when it was formulated later. Haeckel, coming a little later, became convinced that the developing embryo lives over again the stages through which its whole race has passed, and he formulated the recapitulation theory or biogenetic law from this idea. In other words, the organism in its individual life tends to recapitulate the different stages through which its ancestors have passed in their racial history. Briefly this same statement is, *ontogeny recapitulates phylogeny*. The rehearsal of the phylogeny is in rather slurred form in some details, but the basis for the idea is readily seen. In brief, the theory is applied by comparison. Nearly all metazoan organisms begin life by the union of the two germ cells to form a single-celled zygote which is the new organism. At this time it is comparable to the Protozoa. During the ensuing cleavage divisions a colonial form is represented. Following this, when one side infolds to form a gastrula with two germ layers, the embryo is almost identical to the diploblastic coelenterates as represented by Hydra. Following this, the third germ layer forms between the others and results in the triploblastic metazoan.

Basis for the Theory of Evolution

One who has thoughtfully studied the field of zoology soon realizes many relationships or homologies in structural make-up of certain different groups of animals; much similarity of embryonic developmental processes, and fundamental coincidences in physiological activities in all living material. Too, it is recognized that fauna and flora are not the same in all parts of the earth at the present, and have not been the same in the past as now. These realizations and other similar ones have been based on scattered sources of evidence, much of which is indirect. The evidences which have been discovered, however, have led to the formulation of the theory of evolution and its rather general acceptance as a working hypothesis among biologists. There has been confusion regarding this subject through failure to distinguish between the *existence* of progressive *evolutionary changes,* the *course* of these changes, and the *cause* of such a progressive series of events. The latter point has been the basis of most of the questions concerning the whole idea, and it is the most speculative of the three. These three are separate though related factors.

In general, scientists are convinced, according to the evidence they have examined, that organic evolution exists in the form of a progressive change, which has generally proceeded from simpler to more complex organization through a long period of time. Although some sections of the course of this series of developmental events cannot be charted as completely as a ship's course at sea, numerous landmarks serve to indicate what has taken place. Biologists are free to admit that the causes of this process are not understood, and treat it strictly as a scientific problem.

Most estimates of the time when living organisms first came into existence range between 60,000,000 and 1,200,000,000 years ago, coincident with Pre-Cambrian deposits. The manner of origin of protoplasm is purely hypothetical. It is suggested that when conditions became suitable, as to chemical elements present, temperature, pressure, etc., a relatively simple colloidal, protoplasmic mixture arose, having properties of life though perhaps in a very elementary way. It is assumed that all organisms which have lived are descendants of this simple origin. Cellular organization, with division of labor between nucleus and cytoplasm, is taken to be a first step in the development of protoplasm. It is the simplest vital

unit now recognized. If this speculation is followed further, it may be supposed that the unicellular organisms of modern times have descended from such early cells without changing from the simple-celled state, but have developed many specializations as individual types, while metazoans have advanced from certain of these simple forms to a more complexly organized cellular condition.

From the nature of protoplasm and from the evidence in the geological records, it is usually assumed that organisms first appeared in the water near the shores of the primitive oceans. Presumably the first oceans were boiling hot, and the land at that time was a molten volcanic mass. If this is true, there must have been a long period after the formation of the atmosphere, seas, and land before protoplasm, as we know it, could have existed. After these cooled and became favorable for life the seas are thought to have supported an abundant life before the land became suitable for its existence. Along with these several speculative aspects of the subject there have been offered several forms of evidence to support the existence of an evolutionary progress of development in organisms.

Geological Evidence.—Paleontology is the study of fossil remains of organisms deposited in the strata of the earth's crust. Shells and other hard parts are mineralized or petrified; in other cases mud impressions, or tracks, or pitch-preserved individuals, such as insects, and a few frozen forms constitute the majority of fossils. It must be kept clearly in mind that the geologist is able to determine quite accurately the sequence of time or chronological succession of the layers of the earth's crust. The geological time scale shows a long period before any life existed, then the appearance of unicellular plants, then unicellular animals, then colonial forms, simple many-celled forms, and then the more complex ones. Such a timetable estimates the relative period of time during each era and shows some fusion and overlapping of certain types of life. Certain types of unicellular forms are continuous through the entire scale.

The principal facts shown by the fossil record may be summarized: (a) The fossil forms are not strictly identical with any living species, and the remains of plants and animals of each geologic stratum are at least specifically different from the forms in any other stratum, but they may belong to the same genus; (b) the oldest strata containing fossils have represented in them most of

Fig. 209.—Geologic time scale, estimated to cover at least 1,200,000,000 years. (From Newman, *Outline of Zoology*, The Macmillan Company, after Osborn.)

the simple forms of nonchordate animals, while the upper strata
contain fossils of all groups more nearly like modern forms, includ-
ing chordates; (c) in studying these in sequence, there may be ob-
served a gradual progression from simpler and generalized types
toward more specialized and complex forms as one proceeds from
the older toward the upper or newer strata; (d) only the more gen-
eralized varieties have persisted within the groups that, as a whole,
have become specialized; many of the others have long since reached
their climax of specialization and have become extinct; (e) many
of the dominant groups of organisms have arisen near the close of
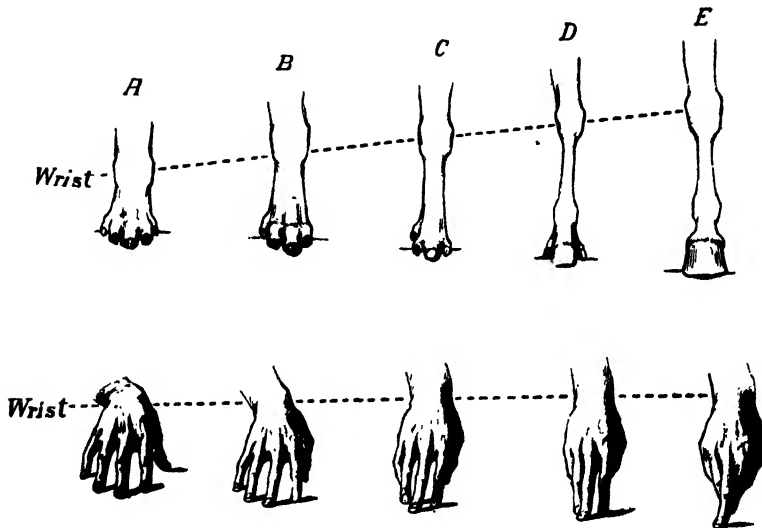
Fig. 210.—Positions of the human hand to show the comparative stages of
elevation of the horse's foot to the tip of the middle toe. (Courtesy of American
Museum of Natural History.)

a period during which great climatic changes were taking place and
have enjoyed dominance during the following period because such
a group probably arose in response to the conditions; (f) although
many nonchordate phyla had reached an advanced stage of develop-
ment in the early Cambrian period, where early fossil records occur,
many ancestral sequences have been observed, and these have sup-
plied information making possible the detailed description of the
course of events that has led to the surviving animals of modern
times; (g) the developmental changes of the chordate groups are
more completely read in the fossil record, with the history of the

mammals in fullest outline, partly because they are relatively recent and partly because the mammalian skeleton is readily fossilized. The most complete pedigree in fossils has probably been worked out for the horse, and a great deal of its material has been located right in the southwestern part of the United States.

The Rise of the Horse.—Primitive horselike animals are thought probably to have arisen from an extinct group called *Condylarthra,* which had five toes on each foot and a large part of the sole resting on the ground. The first unquestionable horselike form found in America is the small *Eohippus* which was about one foot tall and the fossils of which came from the rocks of Eocene times. It had the outer four digits complete on the forefoot, but no trace of the thumb, while the hind foot had three complete digits with vestiges or *splints* of the first and fifth. Following the foxlike Eohippus, later in the Eocene period came the *Orohippus* with an enlarged central digit in the forefoot and the loss of the splints in the hind foot. *Mesohippus,* about the size of a large dog with a three-toed foot both in front and behind but with the side toes much reduced and a trace of the fifth digit in the forefoot, appeared during the Oligocene epoch. *Merychippus* of Miocene times and *Pliohippus* of the Pliocene epoch show a continuation of this reduction to a one-toed type which leads to *Equus caballus* of modern times. The modern horse walks on the tip of the middle toe of each foot with the vestiges of digits 2 and 4 persisting as splints.

Arthur Dendy, in 1911, wrote that the horse is an example of the adaptation of a lowland type to become a plains type, as the extensive, dry, grass-covered plains developed. The adaptation has proceeded along two lines. The limbs have become elongated by the elevation of the heel, thus putting the animal on tiptoe and fitting it for rapid flight from its enemies on the grass-covered open prairie. At the same time the neck and head became elongated to enable the animal to graze the ground without bending the legs. Along with this the teeth changed from a carnivorous form to a complex, broad grinding type for feeding on grass. In addition to these changes the brain advanced.

These changes took place gradually through millions of years and the intermediate forms give the paleontologist a graphic picture of the history of this modern species. The sequence of these stages seems to fit in exactly with the theory that each has been derived
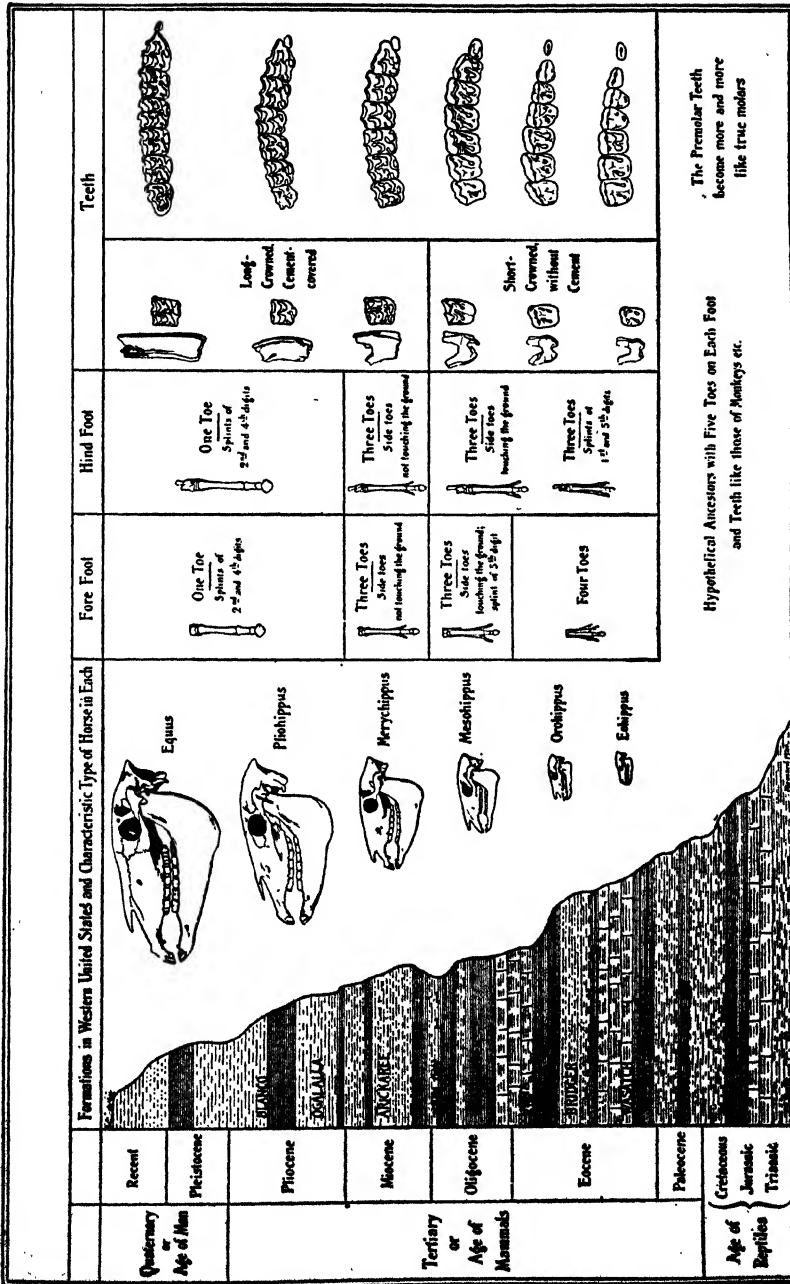
Fig. 211.—Phylogenetic development of the horse, showing changes in skull, feet, and teeth according to geologic eras. (Courtesy of American Museum of Natural History.)

from the preceding by a continued adaptation to the changing conditions of life. The horse's pedigree is essentially similar to that of numerous other forms, such as the elephant, camel, and certain birds, which have been worked out.

The Rise of Man.—The human group constitutes one of the groups of the class *Mammalia* along with many of the common larger animals which are well known. In fact, all of the vertebrate animals which have hair and mammary glands fall in this same class. Man is classified in the order *Primates* in which is grouped also the apes and their relatives. There can be no question but that the structure of the human body is that of a mammal or even a Primate. The suborder is *Anthropoidea;* the family, *Hominidae;* the genus, *Homo;* and the species, *sapiens.* According to studies and discoveries coming from many parts of the earth, it seems quite evident that there has been a long progressive development of manlike animals for hundreds of thousands and possibly millions of years to produce the being known as modern man.

The oldest known representative of the human family is *Sinanthropus pekinensis* (Peking man). His remains were found in a cave of Pleistocene times approximately forty miles from Peiping, China. A complete cranium of this form was found in 1929 and since that time parts of approximately a dozen others have been located. They are always found along with the remains of the type of elephant, rhinoceros, horse, saber-toothed tiger and others of the Pleistocene epoch which is estimated to have been between 500,000 and 1,000,000 years ago. Anthropologists have agreed that this chinless apelike skull with a receding forehead, heavy brows, and heavy jaw, belonged to a primitive man who could use tools and build fires. Another important discovery was made in Java in 1891 when a skull, a jaw bone, a few teeth, and a femur were found. This specimen is now known as *Pithecanthropus erectus* (Java man), and from the shape of the femur, it is definitely indicated that he walked erect. The brain cavity is intermediate in size between that of the largest apes and savage man. It is estimated that this form is somewhat less than a million years old. In 1907 a jaw bone found near Heidelberg, Germany, was determined as having come from a primitive man. A few years later, in England, the remains of *Eoanthropus dawsoni* (Piltdown man) were discovered. The brain cavity was larger than that of Java man and the forehead was

wider and higher. The Heidelberg and Piltdown men are considered as contemporaries of about 500,000 years ago.

A more recent type of European man is known from remains (skullcap and several long bones) found near Dusseldorf, Germany, about the middle of the last century. A rather complete collection of the skeletal parts has since been made. This form is called *Homo neanderthalensis* (Neanderthal man) and is thought to have descended from the Heidelberg man. There is division of opinion as to destiny of this man. One group holds that he became extinct sometime between 100,000 and 200,000 years ago, during the Great Ice Age in Europe. Another group of anthropologists contends that the negroid and Australoid races of men are the descendants of this man.

There is a more recent Asiatic group known as the Cro-Magnon man dated with the Old Stone Age of perhaps 40,000 years ago. Some students of early man hold that modern races have originated from this group. Some even suggest that Eskimos may be rather direct descendants. There are fewer of the apelike features in this type than in any of the others and apparently there have been no striking changes in human features since the time of this group.

From the paleontological evidence which remains, it seems in all probability that the more primitive prehistoric man was apelike. Too, it seems likely that men and apes have originated from a common ancestor. The heavy jaws, receding forehead, strong orbital ridges over the eyes, pointed ears, presence of hair over the ears and parts of the body are exhibited in some groups of modern primitive men. There is a close resemblance between the skeleton of the gorilla and the human skeleton. Other notable features of comparison may be seen in that the arms of the human infant are proportionally long and the grasp of the hand is exceptionally strong. Also the large toe is freer and more prehensile in the infant human than in the adult.

Man is a rather generalized type of animal as compared with some other mammals. Most of the parts of the body have remained relatively unspecialized, and as a result there is a high degree of adaptability, making it possible for men to live under many diverse conditions and climates. However, man has advanced among animals to a greater degree than others because of the development and use of intelligence. This development of the brain and its func-
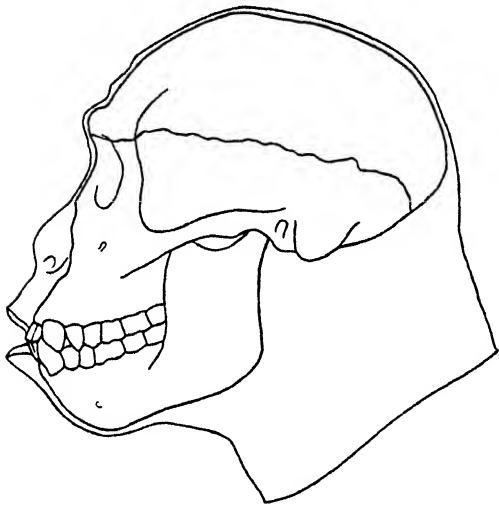
A.
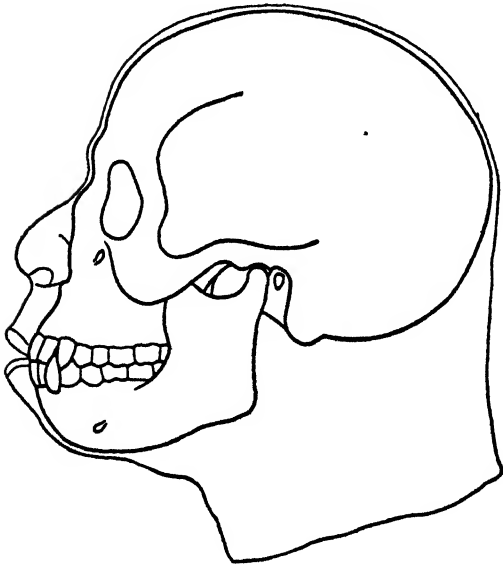
B.

Fig. 212.—*A*, Face and skull of *Pithecanthropus erectus*. *B*, Face and skull of *Eoanthropus dawsoni*. (Adapted from McGregor. From, *The Evolution of Earth and Man*, edited by G. A. Baitsell and published by Yale University Press.)
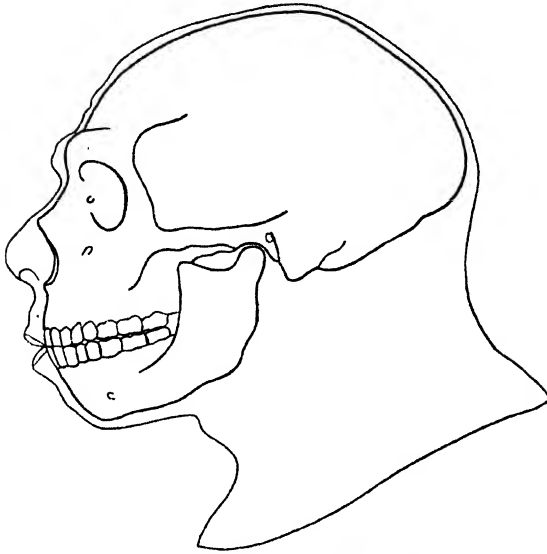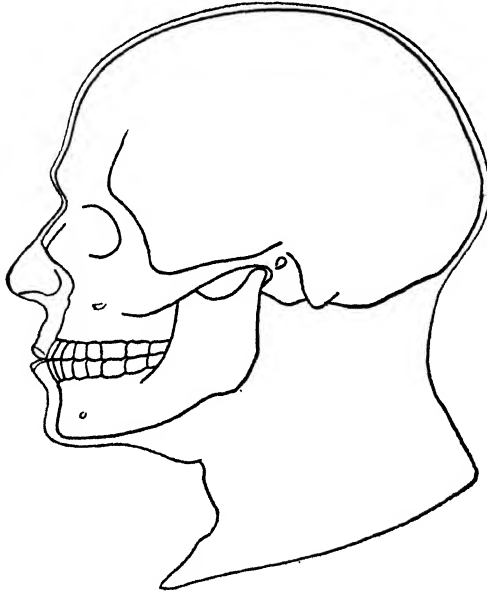
Fig. 213.—*A*, Face and skull of *Homo neanderthalensis*. *B*, Face and skull of *Homo sapiens* (Cro-Magnon man). (Adapted from McGregor. From *The Evolution of Earth and Man,* edited by G. A. Baitsell and published by Yale University Press.)

tions has even given man the advantage of being able to make use of other animals for his own needs. The use of fire, tools, weapons, clothing, shelter, and storage of food is all contemporary and corollary to the development of the human brain. As development along this direction progressed, the power of speech and later the ability to write have become exclusively human traits. Through the development of intelligence the human kind has been able to control certain forces in nature to his own advantage. This superiority of brain and intelligence is man's direction of specialization, and it distinguishes him from the other animals.

The molluscan, echinoderm, and arthropod fossils give similar stories among invertebrates. The numerous fossils of fish, Amphibia, Reptilia, particularly dinosaurs, and birds with the famous *Archeopteryx,* all have their testimony to contribute.

Distributional Evidence.—The paleontological distribution of animals is considered vertically while geographic distribution is in horizontal plane. It is impossible to separate these two completely. The study of geographical distribution gives essentially a cross section of the vertical distribution, thus giving a sort of "still picture" of the complex developmental relations of animal groups at one moment in geologic time. In studying this subject, it is necessary to have in mind two fundamental conceptions. The first is that the ancestors of related genera first appeared or originated in a locality which is designated as the *common center of origin.* A second conception is that as the ancestral form became established and multiplied, migration in search of food and more suitable conditions occurred. Barriers, many of which were geographic, determined the direction and extent of this migration. Large bodies of water blocked the passage of terrestrial animals, as of course land was a barrier to aquatic animals. High mountains or deserts were barriers to all animals unable to withstand low temperatures and altitudes on the one hand, or high temperature and dryness on the other. These forces, and others, are believed to account for the natural distribution of animals. There are the cases of the camel group, originating in North America, migrating to South America and Asia by the land connections of the Eocene to Pliocene epoch, and the tapirs, which are represented by distinct species in two widely separated regions, South Asia territory, and the Central America-South American territory. Here again paleontological data show that in

the Pliocene epoch tapirs were distributed over nearly all of North America, Northern Asia, and Europe. Following that time they were gradually decreased due to discontinuous distribution until the one-time world-wide distribution is now isolated in two widely separated regions. Long isolation of genera in different environments will bring about definite specific differences. As an example, a litter of foreign rabbits was introduced to the islands of Porto Santo during the fifteenth century and by the middle of the nineteenth century the descendants had become so distinct from the original ancestors that they were described as a new species. There are numerous instances of this effect, demonstrated by isolation on ocean islands. The islands are either continental, with fauna similar to those of the nearby continent from which the animals have come, as the British Isles, or they are oceanic, with a very bizarre assemblage of animals which have either drifted in or have been carried there, as the Hawaiian Islands. Many of the animals on these oceanic islands are peculiar and are found nowhere else on earth. Australia has a group of animals which are very different from those of Asia because the two have been so long separated. Europe, Asia, Africa, and North America have been connected with each other by land bridges in recent enough times that the mammals show similarity. The distribution of the species of a genus often radiates from the more generalized species which occupy the center of the range of the genus, and the more specialized species are found in the scattered outskirts of the range.

From the preceding statements concerning distribution it seems that any given species originates in a definite locality, that it multiplies there and migrates in all possible directions. It modifies as it goes in response to the various new conditions prevailing and becomes divided into local varieties which in the course of time become species. Thus the working method of animal distribution, as it has been presented, is the principle of descent from preceding generations with modification.

Morphological Evidence.—Classification of the animals shows in fact something of the morphological evidence, since current classification is based chiefly on anatomical features and comparative anatomy. The groups of the classification are established largely on anatomical similarities. The differences existing among the representatives of all the classes of vertebrates are relatively slight

when set over against the fundamental similarities. Closely related groups show numerous similarities in the form of homologies. The flipper of the whale, the wing of the bat or the bird, the foreleg of the cat and the arm of man all show the same general type of structure in spite of certain specific differences. There is seldom any question of their phylogenetic relationship.

The presence of series of similar parts on different segments of the same animal and the various specializations of these parts show a progressive development. The highly specialized walking legs, uropod, claws, and feelers of crayfish, for example, have all developed from the simple swimmeret type of appendage. They form a serial homology and are also homologous to the appendages of all other Crustacea as well.

In higher forms of animals, such as man, there are numerous structures which seem to be useless and are even harmful in some instances. These are spoken of as *vestigial structures.* Such parts correspond in structure and plan to functional parts in other related forms, but are reduced morphologically and without the original function. In man, one probably thinks first of the *vermiform appendix* of the colon as such a structure. This is apparently functionless in human beings and can be removed with no loss, but this same organ in rabbits, some birds, and other animals is an extensive and functional digestive organ. Man has a *coccyx* or vestigial tail, and the frog has the *urostyle.* Pythons and porpoises, neither of which has the least use for them, have vestigial hind limbs similar to the functional ones of their relatives. The salivary glands of certain snakes have become adapted as poison glands, certain sweat glands have become milk glands, and gill arches have become supporting structures of the tongue, larynx, and throat of adult terrestrial animals. The blood supply and nerves both follow the phylogenetic changes of these organs.

Most animal types seem not to have originated in their present forms, but they seem to have undergone changes through the long periods of geologic history. The explanation offered by modern biologists for the anatomical relations and resemblances between animals is that the individuals in any group have inherited a similar plan of structure from the ancestors which were common to all members of the group. In a group, such as the vertebrates, there have been numerous modifications of various fundamental structures in

different subdivisions in relation to the particular habits of life; still they remain fundamentally alike because they have developed from the underlying plan of organization found in the ancestors. The seal and the bird, although quite different, show similarities in habits and otherwise because of common ancestry long ago. The conclusion of biologists of today is that all of the animals in a group, such as the vertebrates, have arisen by descent with change from a primitive organism which possessed the fundamental organization as shown from cyclostomes to man.

Embryological Evidence.—Evidences from this field really continue directly from the previous discussion. The animal is to be thought of as an individual from the single-celled zygote stage to the mature stage of old age, no matter what its complexity is. Intimately related types of animals parallel through a large portion of their development to diverge somewhat in adult condition, more remotely related forms take separate developmental courses rather early in life, and unrelated forms may be different almost from the beginning. In numerous instances the developing stages of more advanced forms resemble very closely the mature stages of the less advanced types in a serial fashion. The history of the individual animal often corresponds in a general way to the history of the advances of the animal kingdom, up to its state of development. This apparent repetition of the ancestral development in individuals was what led Haeckel to formulate the *recapitulation theory*, expressed briefly: *ontogeny repeats or recapitulates phylogeny*, as has been discussed earlier in the chapter.

In the vertebrate group these apparent relations are much shown. Most of the embryos of this group are so similar that it is nearly impossible to distinguish them. They pass through the identical stages of development. Systems, such as the circulatory, nervous, digestive, and respiratory, follow the same course of development in all of the vertebrates, no matter how simple or complex. In earlier stages the similarity is strikingly close.

The course of development and the modifications shown in the aortic arches or main arteries leaving the heart and passing through the gill regions is a specific example of the manner in which a specific set of structures follows out a repetition of ancestral stages in the development of the individual. Fig. 204 shows a comparison of the arrangement of the branchial (aortic) arches from the primi-
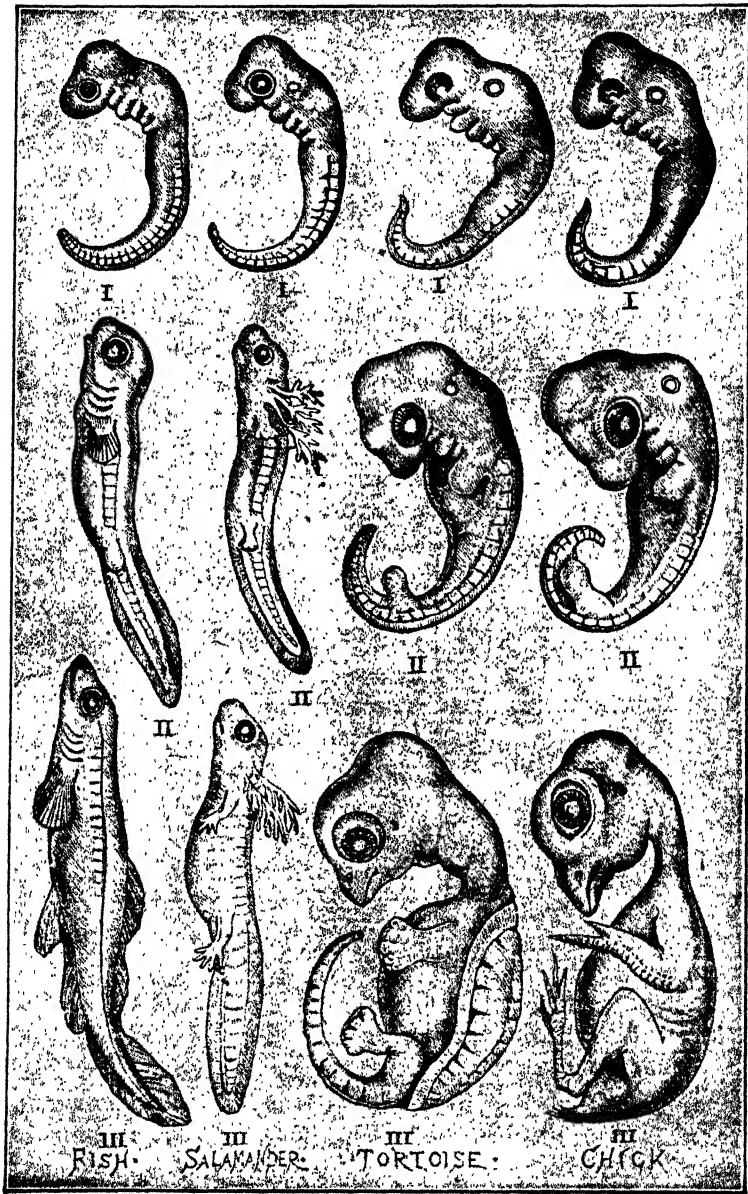
Fig. 214.—The development of several vertebrate animals shown in three parallel stages. Notice the close similarity of the first two stages for all the species shown. (From Romanes, *Darwin and After Darwin*, Open Court Publishing Company.)

(*See opposite page for legend.*)

tive set of six through the fishes, Amphibia, reptiles, to the birds and mammals, with a modified condition of three arches.

Along with the aortic arch situation are other examples of similar stages of development in all forms of the group. Gills are present in all chordates at some time. In the, primitive ones the gills are functional throughout life; in the more advanced types they are
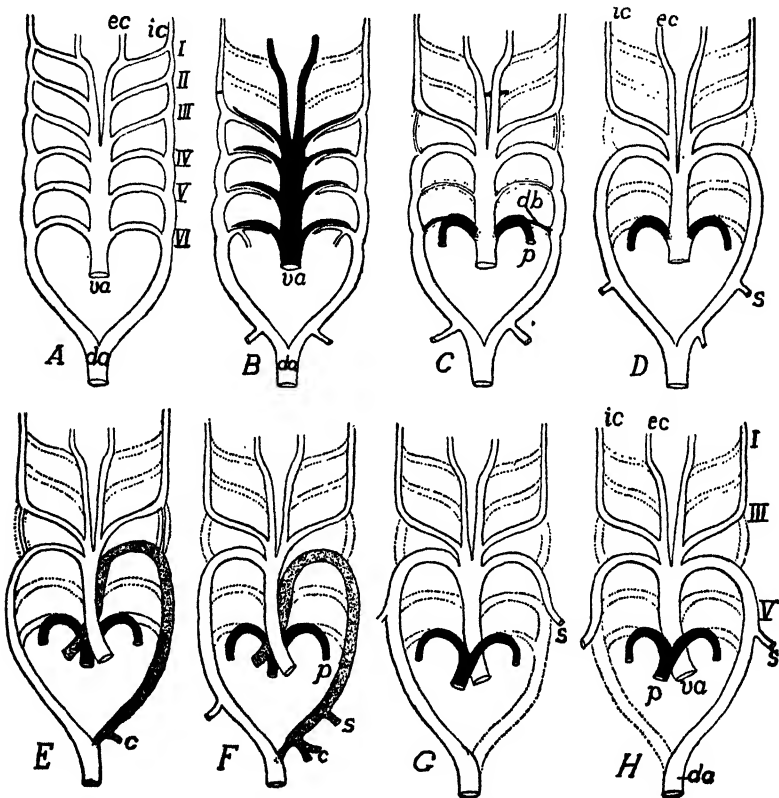
Fig. 215.—Diagram to show the modifications of aortic or branchial arches in different vertebrate types. *A,* primitive scheme; *B,* lungfish; *C,* primitive amphibian (urodele); *D,* frog; *E,* snake; *F,* lizard; *G,* bird; *H,* mammal, *ec, ic,* external and internal carotids; *va,* ventral aorta; *da,* dorsal aorta; *db,* ductus Botalli; *p,* pulmonary artery; *s,* subclavian; *c,* coeliac. Vessels carrying venous blood are black; those with mixed blood are shaded; those which disappear are dotted outlines. (After Boas. Reprinted by permission from Kingsly, *Comparative Anatomy of Vertebrates,* P. Blakiston's Son and Company.)

only transitory gill structures. In frogs and toads, the tadpole stage is essentially fishlike, and they become amphibian at metamorphosis. The notochord is a definite structure throughout the life of the

primitive chordates, but is present as such in only the embryo stage of all others. The development of the heart from the tubular condition through the two-chambered, three-chambered, and finally four-chambered condition, illustrates the same progressive development.

Physiological Evidence.—The fact that all protoplasm possesses the same set of fundamental properties or capacities as contractility, irritability, metabolism, etc., is in itself a definite indication of relationship of all organisms, since they are all composed of protoplasm. Too, all protoplasm acts under similar laws and conditions.

Such natural substances of animal bodies as the hormones, or antibodies or even enzymes are almost universal in their reactions among chordates and even among nonchordates. Most of them are interchangeable from one animal group to another. A deficiency of pepsin or adrenalin in man may be supplied from a cow, a hog, a cat, a rat, or a dog. The blood of all vertebrates has certain physiological similarities and some specific differences. The blood of large groups of human beings will mix without agglutination and is said to "match." Other individuals' blood may not "match" in this type but will mix with blood from another group. The agglutination (clumping of red corpuscles) when blood from two individuals is brought together is due to the reaction of two substances produced by the corpuscles in one or both of the blood samples. The designation of the blood groups depends upon the presence or absence of one or both of these substances. One blood group (O) contains neither, another (A) contains one substance, a third (B) the second substance only, while a fourth group (AB) contains both substances. Serum of the first group will agglutinate corpuscles when mixed with any of the other three. The groups with the single substance will agglutinate corpuscles in blood having only the other substance or blood with both substances. The serum from blood with both substances will not cause agglutination in any of the others.

In lower mammals some similar blood groups have been found, but it is only in the apes that the groups correspond to those in the human being. This is an indication of the rather close relationship of these animal groups. In the human being and in other animals, this blood characteristic is permanent in the individual, and it is hereditary.

Serum (blood minus corpuscles and fibrinogen) studies also establish certain relationships among animals. If small quantities of

human blood serum are introduced at intervals into the blood stream of a rabbit, in time there will be developed in the blood of the rabbit a substance (antibody) which, when mixed with normal human blood will cause precipitation of the proteins here. Serum from such a rabbit is called *antihuman serum*. When this serum is mixed with serum in a certain dilution taken from human, chimpanzee, gorilla, or monkey, it will cause precipitation. If the dilution is increased, there is no precipitation when mixed with monkey serum; at still higher dilution there is no precipitation when mixed with gorilla blood; and higher none for chimpanzee blood, until finally none for human blood. On the basis of these sera precipitation tests the chimpanzee is closest in its relationship to man, then the gorilla, and then the monkeys.

In making similar tests on other vertebrate groups, it is found that crocodiles are more closely related to birds than are the other reptiles; also among reptiles, that snakes and lizards are more closely related to each other than to turtles. Too, crocodiles show a closer relationship to turtles than to the other groups of reptiles. Blood studies of the various groups of vertebrates indicate that there is more similarity in blood of closely related forms than of others. At the same time, it is seen that a chemical relationship persists in the blood throughout the chordate phylum.

The *breeding* of plants and animals through long series of generations of domestication and laboratory experiments has yielded much information concerning the ways of adaptation and phylogenetic development. A significant result is the demonstration of changes occurring in animals and plants. From such studies it seems quite obvious that organisms now living have come to be what they are by gradual change from generation to generation through a course of descent from preexisting and varied ancestors, rather than by a sudden and completely new development. Most of the various breeds of cattle, chickens, dogs, horses, sheep, crops, etc., have been developed in each case from a preexisting common ancestor.

Darwin and Studies of Evolution.—Most discussions of organic evolution usually begin with mention of Darwin's monumental work on this subject, and difficult it is to get away from his fundamental basic thinking on the subject. He was the first to survey thoroughly the fields of morphology, embryology, and paleontology, and to relate logically the data found there to the theory of evolution. From

his studies, many of which were done along the east and west shores of South America while he was naturalist of a British Naval expedition on the ship *Beagle,* Darwin formulated a clear-cut and definite argument for evolution on the basis of *natural selection.* Beginning with Malthus' law of population, published in 1838, which stated that since man reproduces in a geometric ratio, the earth would be overpopulated in a few generations except for such checks as the arithmetic ratio of increase in food production, disease, war, flood, earthquake, fire and other natural catastrophes reducing population, Darwin formulated the theory of natural selection. This theory includes among other things the application of Malthus' law to all living organisms. The four basic points on which this theory is developed may be named in order as follows: (1) *overproduction,* (2) *struggle for existence,* (3) *variation and heredity,* and (4) *survival of the fittest* (natural selection).

Overproduction is in operation in all thriving normal species. A single codfish will produce several million eggs in one season. If every codfish egg were to be fertilized, to reach maturity, and to reproduce with no loss from one generation to the next, it would not be more than a dozen years until the entire face of the earth would be covered with codfish and all other animals would be crowded out of existence completely. Even a form like the elephant, which lives to be ninety or a hundred years of age and averages only six progeny, could soon occupy all of the standing room on the face of the earth. Beginning with one pair of elephants and providing every individual lived and reproduced even at the slow average rate mentioned above, 19,000,000 individuals would be produced in 750 years. If every elephant alive today were to enter into a program like that, both food and space would become quite scarce before many generations. However, this doesn't happen on a large scale. All plants and animals tend to produce more offspring than can ever reach maturity and reproduce.

The struggle for existence is ever present because there are more individuals produced than the habitat will support. The two most fundamental needs for which organisms struggle are (1) food and (2) opportunity to reproduce and rear young. Of these two, the struggle for food is very immediate and the food supply is an important limiting factor on population from season to season. Since the food supply, on the average, remains quite constant, it is evident that

only a limited number of the increase in individuals can be supported in a particular habitat; thus a struggle ensues with each individual attempting to secure the necessities of life. Not only is there a struggle for food but also with many factors in the environment like climate, geographic changes, etc.

Survival of the fittest was the outcome which Darwin saw resulting from such a struggle. Those individuals which were best adapted to the environment into which they were born have been the ones to win out in the struggle and leave offspring for a future generation. The inheritance of favorable or unfavorable characters influences very strongly the success of the individual in maintaining itself. The survivors in any generation are those which inherit the most favorable combination of variations. Many variations, both favorable and unfavorable to the success of the individual, are hereditary.

When changes in environment come and bring about new living conditions, the animals in the particular habitat must either meet these changes, be able to migrate, or perish. The standard for fitness has changed under such circumstances, and animals with somewhat different characters and adaptations may now be the "fittest." The individuals whose variations have brought them to most nearly fit the requirements for life in their particular habitat will be the ones most likely to obtain sufficient food supply and adequate provision for reproduction to increase their population rapidly. As one group is able to do this, it invariably reduces or perhaps entirely eliminates other species in the locality. Evolutionary changes result from survival of the fittest, since those individuals which succeed have done so because of an accumulation of favorable variations in each of successive generations. Those individuals or races which have not been as well adapted to conditions of the habitat have become inconsequential or extinct. The appearance of characters in an animal is a matter of chance as far as the individual is concerned. Natural selection may act as an eliminating agent and may determine whether the character or trait shall survive after it appears.

Mutation Theory.—Hugo de Vries is the name most prominently connected with the origin of this theory. He was a Dutch botanist and in 1886 found some evening primrose plants *(Oenothera lamarkiana)* which exhibited discontinuous variation or sudden appearance of new characters. These sudden, sharp variations came to be known as *mutations*. There are two types of variations which have been

recognized: (1) *continuous* or fluctuating variation, such as height of individuals of a species where they are expected to fall within a normal range thus allowing a degree of variation among individuals of the species, and (2) *discontinuous* or sport variation (mutation) where the variation falls outside the normal range of variation and not connected with it by intermediate changes.

In the course of seven generations of this primrose and involving approximately 50,000 individuals, six different mutations were found. The new characters which appeared were quite different from those of the typical species and were hereditary as well. Since this was the case, de Vries concluded that he was observing the origin of new species. He was sufficiently convinced of this to discount Darwin's conception of the development of new species by the gradual accumulation of continuous variations through natural selection. He pointed out that mutations are due to changes occurring in the germ plasm while the continuous variations, individually, are due to changes in somatic cells.

Following de Vries' work there has been much study of mutations, and numerous ones have been found in nature. Too, it has been found that spontaneous mutations could be produced in Drosophila (fruit fly) by x-ray radiation. It is thought that mutations come as the result of physiological changes in the chromosomes or genes.

While this mutation theory of origin of new species has prompted much study and thought on evolution it seems not to have displaced Darwin's general conception of the origin of new species. So far as Darwin's theory is concerned, the occurrence of mutations only hastens the process of evolution since they produce quick, abrupt variations instead of the slower, smaller, continuous variations. Natural selection will operate with either. Biologists now consider both small and large variations as mutations, and have turned back to Darwin's idea of natural selection as the most likely explanation of the development of new kinds of animals.

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GLOSSARY*

Abdomen (ăb dō'měn), the portion of the trunk posterior to the thorax of an animal.

Aboral (ăb ō'răl), opposite the mouth.

Absorption (ăb sôrp'shŭn), the process of taking in soluble foods by the circulatory medium or by the protoplasm directly.

Accommodation (ă kŏm ŏ dā'shŭn), the power of adjustment of the eye to near and far objects.

Acetabulum (ăs ē tăb'û lŭm), the socket in each side of the innominate bone of the pelvic girdle into which the femur fits.

Achromatic figure (ăk rō măt'ĭk), the mitotic figure without chromosomes.

Aestivation (ĕs tĭ vā'shŭn), state of torpidity induced by heat and dryness.

Allelomorphs (ă lē'lŏ môrfs), a pair of corresponding genes in homologous chromosomes, but each produces a different character.

Allergy (ăl'ĕr jĭ), acute sensitiveness to a foreign substance, as foreign protein in the body.

Alternation of generation (ăl tĕr nā'shŭn of jĕn ĕr ā'shŭn). (See Metagenesis.)

Altricial (ăl trĭsh'ăl), in reference to birds which are hatched without feathers and in a helpless condition.

Alveolus (ăl vē'ŏ lŭs), a small cavity or pit, such as the air sacs in the lung of a higher vertebrate.

Ambulacral (ăm bŭ lā'krăl), area of echinoderm related to tube feet.

Amino acids (ăm'ĭ nō), organic acids with a (NH_2) radical, and derived from complex proteins.

Amitosis (ăm ĭ tō'sĭs), direct cell division, occurring without chromosomal activity.

Amnion (ăm'nĭ ŏn), inner embryonic membrane of terrestrial vertebrates.

Amoeboid movement (à mē'boid), the streaming of protoplasm in a cell to extend the cell in some direction with the formation of pseudopodia.

Amphiaster (ăm'fĭ ăs tĕr), the complete mitotic figure of a dividing cell.

Amphiblastula (ăm fĭ blăs'tû là), the free-swimming larval form in sponges.

Amphimixus (ăm fĭ mĭk'sĭs), union of nuclear material from two different cells, as in fertilization.

Ampulla (ăm pŭl'à), a bulblike dilatation.

Amylopsin (ăm ĭ lŏp'sĭn), a pancreatic enzyme capable of converting starch into sugar.

Anabolism (ăn ăb'ŏ lĭz'm), the building up of living protoplasm.

Analogous (à năl'ŏ gŭs), differing in structure and origin, but similar in function.

Anaphylaxis (ăn à fĭ lăk'sĭs), acute reaction of the body to foreign protein materials which have a toxic effect; this may be an increased sensitivity to the material because of previous contact with it.

Anatomy (à năt'ŏ mĭ), the science that treats of the structure of organic bodies.

Anus (ā'nŭs), the posterior opening of the alimentary canal.

Appendicular skeleton (ăp ĕn dĭk'û lár), skeleton of the paired fins of Pisces.

Archenteron (är kĕn'tĕr ŏn), the cavity of the gastrula which is the primitive digestive cavity.

Artery (är'tĕr ĭ), the larger blood vessels leading away from the heart.

Asexual reproduction (à sĕk'shŭ ăl), reproduction without sex cells.

Assimilation (ăs sĭm ĭ lā'shŭn), the transforming of digested food into protoplasm.

Asymmetry (à sĭm'ĕt rĭ), a condition in which the two sides of an animal are dissimilar.

*Phonetics according to Webster's New International Dictionary.

Autonomic nervous system (ô tô nŏm'ĭk), that portion of the nervous system controlling the involuntary muscles.

Autotomy (ô tŏt'ô mĭ), self-mutilation.

Axial gradient (ăk'sĭ ăl grā'dĭ ĕnt), the graduation of the rate of metabolism along the principal axis of an axiate animal.

Axone (ăk'sŏn), a nerve fiber serving to conduct impulses away from a nerve cell body.

Barrier (băr'ĭ ēr), any physical, chemical, or biological obstruction that prevents migration of animals.

Benthos (bĕn'thŏs), life of the deep sea bottom.

Binary fission (bī'nà rĭ fĭsh'ŭn), division of a cell into two daughter cells.

Biramous (bī rā'mŭs), a two-branched condition.

Bisexual (bī sĕk'shŏo ăl), a condition in which both male and female organs are present in one individual.

Bivium (bĭv'ĭ ŭm), one side of an echinoderm including a pair of ambulacra.

Blastocoele (blăs'tô sēl), the cavity present in the blastula stage of development; also cleavage of segmentation cavity.

Blastomere (blăs'tô mēr), one of the segments first formed by the division of the ovum.

Blastula (blăs'tū là), a sphere of cells with a hollow cavity resulting from cleavage of the zygote.

Blepharoplast (blĕf'à rō plăst), the body in a cell from which a flagellum arises.

Brachium (brā'kĭ ŭm), arm.

Branchial (brăng'kĭ ăl), pertaining to gills or branchiae.

Buccal (bŭk'ăl), pertaining to the mouth cavity.

Budding (bŭd'ĭng), reproduction involving the branching of new individuals from the external surface of the old one.

Byssus (bĭs'ŭs), a tuft of fiberlike threads which attach certain mussels to the substratum.

Caecum (sē'kŭm), a blind pouchlike pocket of the intestine; usually at the junction of the small and large intestines.

Calcareous (kăl kâr'ê ŭs), composed of lime or calcium salts.

Calciferous (kăl sĭf'ēr ŭs), glands which are thought to secrete an alkaline secretion into the esophagus of the earthworm.

Canaliculus (kăn'à lĭk' û lŭs), one of the tiny canals extending from lacuna to lacuna to distribute nutriment in bone.

Capillary (kăp'ĭ lēr ĭ), a microscopic branch of an artery which extends into a tissue and finally joins a small vein.

Carapace (kăr'à păs), shell-like external covering.

Carbohydrate (kär bō hī'drăt), organic compound of carbon, hydrogen, and oxygen, such as starch or sugar.

Cardiac (kär'dĭ ăk), pertaining to the heart.

Carnivorous (kär nĭv'ô rŭs), flesh eating.

Caste (kàst), any group of distinct forms within a species, as found in some insects.

Catabolism (kà tăb'ô lĭzm), process of oxidation or break-down of protoplasm; destructive phase of metabolism; dissimilation; the oxidation of organic substances of the body to release kinetic energy and heat.

Catalysis (kà tăl'ĭ sĭs), the initiation or acceleration of a chemical reaction by the presence of a substance which itself does not enter into the reaction, as an enzyme.

Caudal (kô'dŏl), pertaining to the tail.

Cell theory (sĕl thē'ô rĭ), the theory that all living things are composed of cells.

Centimeter (sĕn'tĭ mē'tēr), one-hundredth of a meter and the equivalent of 0.393 inch; or 1 inch equals 2.54 centimeters.

Central nervous system (sĕn'trăl), that portion of the nervous system composed of the brain and the spinal cord.

Centriole (sĕn'trĭ ōl), a small granule within the central part of the aster in the mitotic figure; also known as centrosome.

Centrolecithal (sĕn'trō lĕs ĭ thăl), refers to the type of egg with the yolk mass in the center, as the egg in insects.

Centrosome (sĕn'trō sōm), usually considered synonymous to centriole.

Cephalic (sē făl'ĭk), pertaining to the head.

Cephalothorax (sĕf'å lō thō'răks), a fusion of the head and thorax or chest, as in crayfish.

Cerebellum (sĕr ĕ bĕl'lŭm), the large lobe of the hind brain, in front of and above the medulla.

Cerebrum (sĕr'ĕ brŭm), the anterior division of the brain.

Cercaria (sûr kā'rĭ å), a tailed larval stage of the liver fluke.

Ctenoid scale (tē'noid), a type of fish scale with spines at the free margin.

Cervical (sûr'vĭ kăl), has reference to the neck region.

Chaeta (kē'tå), one of the bristlelike structures in the body wall of many annelids, used as organs of locomotion.

Chelicera (kē lĭs'ĕr å), an anterior pair of appendages in arachnids.

Cheliped (kē'lĭ pĕd), most anterior thoracic leg of crayfish; large pincher.

Chemotropism (kē mŏt'rō pĭz'm), response of an organism to chemical changes.

Chlorophyll (klō'rō fĭl), the green coloring matter in plants and a few animals which is active in photosynthesis.

Chromosomes (krō'mō sōmz), bodies formed in the nucleus during mitosis which constitute the physical basis of inheritance.

Chitin (kī'tĭn), the hard material composing the exoskeleton or shell of Crustacea, insects, and others.

Chloragogue cells (klō'rå gŏg), compose the outer layer of the intestine of the earthworm.

Chondrin (kŏn'drĭn), the material of which cartilage is composed.

Chorion (kō'rĭ ŏn), the outer embryonic membrane of mammals.

Chorioid (kō'rĭ oid), middle or vascular coat of vertebrate eyeball.

Chromatin (krō'må tĭn), dark-staining substance of the nucleus of the cell.

Chromatophore (krō'må tō fōr), a colored pigment cell.

Chromidia (krō mĭd'ĭ å), scattered chromatin granules through the cytoplasm of some cells.

Chromonemata (krō mō nĕm'å tå), threads of chromatin distinguishable within chromosomes during mitosis; seen in the resting phase of some.

Chyme (kīm), partially digested food material which is in semiliquid condition.

Cilia (sĭl'ĭ å), hairlike cytoplasmic processes, used by certain protozoans for locomotion.

Cirrus (sĭr'ŭs), a bristlelike appendage.

Cleavage (klĕv'ĭj), the cell divisions changing the zygote into an organism of many cells.

Clitellum (klĭ tĕl'ŭm), a broadened area in the earthworm about one-third of the length of the body back from the head. It is glandular and serves in producing the cocoon.

Cloaca (klō ā'kå), the common chamber into which the intestine, and urinary and genital canals discharge in some forms.

Cnidoblast (nĭ'dō blăst), the type of cell of the coelenterate in which the sting cell or nematocyst develops.

Cochlea (kŏk'lē å), a coiled structure of the inner ear in which is located the sensory ending of the auditory nerve.

Cocoon (kŏ kōōn'), a covering which protects a larva, pupa, or even the adult stage of certain animals.

Coeloblastula (sē lō blăs'tū lå), blastula having a hollow center.

Coelom (sē'lŏm), or **coelome** (sē'lōm), the space between the walls of the body and the inclosed viscera.

Commensalism (kŏ mĕn'săl ĭzm), an association of different species of animals in which at least one benefits without injury to the other.

Commissure (kŏm'ĭ shŏŏr), a strand of nerve fibers or nerves joining two centers or ganglia.

Conditioned reflex (kŏn dĭsh'ŭnd), a reflex action which is modified or established by previous experience.

Conductivity (kŏn'dŭk tĭv'ĭ tĭ), the power of conducting or of receiving and transmitting.

Congenital (kŏn jĕn'ĭ tăl), conditions existing at birth.

Conjugation (kŏn jŏŏ gā'shŭn), a temporary union of two individuals with exchange of nuclear material.

Copulation (kŏp ū lā'shŭn), union of genital regions of two individuals during which spermatozoa are transferred from one to the other.

Corium (kō'rĭ ŭm), the deeper layer of the skin or dermis.

Cornea (kôr'nê å), transparent coat of modified epithelial tissue over the front of the eye.

Cortex (kôr'tĕks), superficial portion or outer layer, as of the brain or kidney.

Cranial (crā'nĭ ăl), pertaining to the portion of the skull enclosing the brain.

Cretin (krē'tĭn), a defective individual due to abnormality of the thyroid gland.

Cutaneous (kŭ tā'nê ŭs), pertaining to the skin.

Cuticle (kū'tĭ kl), the outer surface of the skin of many animals.

Cycloid scale (sī'kloid), a scale which is thin and shows concentric lines of growth without serrated margin.

Cyclosis (sī klō'sĭs), the rotation of the endoplasm of protozoan forms.

Cyst (sĭst), an organism enclosed by a resistant wall.

Cysticercus (sĭs tĭ sûr'kŭs), the bladder worm or encysted stage in the life history of the tapeworm.

Cytology (sī tŏl'ô jĭ), the science that treats of the minute structure of cells.

Cytopharynx (sī tô făr'ĭnks), channel from surface to endoplasm in Euglena.

Cytoplasm (sī'tô plăz'm), the protoplasm of the cell not including the nucleus.

Dactyl (dăk'tĭl), refers to finger.

Daughter cells (dô'tēr sĕlz), the two cells resulting from a division of one cell.

Delamination (dê lăm ĭ nā'shŭn), the formation of a new layer of cells parallel to the old by the division and migration of cells of the primary germ layers.

Dendrite (dĕn'drĭt), a nerve fiber which carries impulses toward the nerve cell body.

Dermis (dûr'mĭs), same as corium.

Dialysis (dī ăl'ĭ sĭs), separation of dissolved materials in crystalloids and colloids by means of semipermeable membrane.

Diaphragm (dī'å frăm), a muscular partition between the abdominal and thoracic cavities in mammals.

Diastase (dī'å stās), the class of enzymes capable of bringing about conversion of starches to sugars.

Diencephalon (dī ĕn sĕf'å lŏn), a region of the brain just posterior to the cerebrum.

Differentiation (dĭf ĕr ĕn shĭ ā'shŭn), the formation of special parts, tissues, or cells from the primitive unspecialized layers.

Diffuse (dĭ fūs'), to mix with or to spread through completely and thoroughly another substance.

Digestion (dĭ jĕs'chŭn), the conversion of complex unabsorbable food materials into a form capable of bodily absorption.

Dihybrid (dī hī'brĭd), progeny or offspring of parents differing in two characters.

Dominance (dŏm'ĭ năns), a condition in which one of two characters present in the individual appears to the exclusion of the other.

Dimorphism (dī môr'fĭzm), difference of form between members of the same species.

Dioecious (dī ē'shŭs), the male and female germ cells being produced by different individuals.

Diploblastic (dĭp lŏ blăs'tĭk), composed of two germ layers.

Diploid (dĭp'loid), having the base number or double number of chromosomes, as in somatic cells.

Dissimilation (dĭ sĭm ĭ lā'shŭn). (See Catabolism.)

Diurnal (dī ûr'năl), active by day.

Diverticulum (dī vĕr tĭk'ù lŭm), a blind tube branching out of a larger one.

Duodenum (dū ō dē'nŭm), the part of the small intestine between the stomach and the jejunum.

Ecdysis (ĕk'dĭ sĭs). (See Molt.)

Ecology (ē kŏl'ŏ jĭ), the science of the relation of an organism to its environment.

Ectoderm (ĕk'tŏ dûrm), the outer cell layer of the wall of a gastrula and its later derivatives.

Ectoplasm (ĕk'tŏ plăz'm), substance of the outer layer of cytoplasm or ectosarc of a protozoan animal.

Ectosarc (ĕk'tŏ särk), the superficial layer of cytoplasm of a single-celled animal.

Egestion (ē jĕs'chŭn), the casting out by the body of indigestible food material.

Electrolyte (ē lĕk'trŏ līt), a substance whose molecules dissociate into ions.

Electrotropism (ē lĕk'trŏt'rŏ pĭz'm), response of an organism to electric currents.

Embryology (ĕm brў ŏl'ŏ jĭ), the science of the origin and development of the individual.

Endocrine system (ĕn'dō krĭn), a system including those ductless glands which secrete hormones.

Endoderm (ĕn'dō dûrm), the inner cell layer of the wall of the gastrula and its later derivatives.

Endomixis (ĕn dŏ mĭk'sĭs), nuclear reorganization within a protozoan which does not involve conjugation.

Endoplasm (ĕn'dŏ plăz'm). (See Endosarc.)

Endopodite (ĕn dŏp'ŏ dīt), the internal or principal branch of a biramous appendage of Crustacea.

Endosarc (ĕn'dŏ särk), the area of cytoplasm within a cell which is surrounded by ectoplasm; substance of this is endoplasm.

Endoskeleton (ĕn dŏ skĕl'ĕ tŭn), the bony, cartilaginous, or other internal framework of an animal.

Endothelium (ĕn dŏ thē'lĭ ŭm), the mesodermic lining layer of such closed spaces as blood vessels and lymph spaces.

Enteric (ĕn'tĕr ĭk), adjective form of enteron.

Enterocoele (ĕn'tĕr ŏ sēl), a portion of the coelomic cavity that arises by outgrowth from the enteric cavity.

Enteron (ĕn'tĕr ŏn), a digestive cavity or tube.

Entomology (ĕn'tŏ mŏl'ŏ jĭ), the branch of zoology that deals with the study of insects.

Entozoic (ĕn'tŏ zō'ĭk), forms which live within the bodies of other animals.

Enzymes (ĕn'zīmz), substances that bring about chemical transformation.

Ephyra (ĕf'ĭ rá), the free-swimming larval form of the Scyphozoa.

Epiboly (ē pĭb'ŏ lĭ), posterior growth of a fold of the blastoderm over the surface of an embryo in the formation of the enteron during gastrulation.

Epigenesis (ĕp ĭ jĕn'ĕ sĭs), the conception that the parts of the organism arise from an undifferentiated germ cell.

Epithelium (ĕp'ĭ thē lĭ ŭm), a sheet of cells covering an internal or external surface of the body.

Equatorial (ē kwȧ tō'rĭ ăl) **plate,** the platelike arrangement of chromosomes lying in the plane of the equator of the mitotic spindle during cell division.

Erepsin (ĕ rĕp'sĭn), an intestinal enzyme which splits peptones into amino acids.

Estivation (ĕs tĭ vā'shŭn), a dormant condition adopted by certain animals during summer.

Eugenics (û jĕn'ĭks), the science of genetics applied to human kind, usually for the purpose of improvement.

Euglenoid (û glē'noid), resembling a Euglena, as euglenoid movement.

Eustachian (û stā'kĭ ăn) **tube,** the tube extending from the middle ear to the pharynx.

Evagination (ē văj'ĭ nā'shŭn), the unequal growth outward of a surface layer, one of the processes by which differentiation of organs is produced.

Eviscerate (ē vĭs'ẽr āt), to remove or cast out the internal organs.

Exopodite (ĕks ŏp'ō dīt), the external branch of the appendages.

Exoskeleton (ĕk sŏ skĕl'ē tŭn), the hardened parts of the external integument of an animal.

Expire (ĕk spīr'), to expel water or air in the process of respiration.

Factor (făk'tẽr), one of several interacting elements in a complex process. Agency influencing the development of an individual, as those carried in the genes of chromosomes.

Fauna (fô'nȧ), a term referring to animal life.

Feces (fē'sēz), the indigestible portion of the food which passes through the alimentary canal and is discharged by way of the anus.

Fertilization (fûr tĭ lĭ zā'shŭn), the union of a mature ovum and a mature spermatozoon to produce a zygote.

Fetus (fē'tŭs), an advanced stage of the embryo of a mammal before birth.

Fibrin (fī'brĭn), the fibrous material in a blood clot; formed when fibrinogen of the blood is exposed to air.

Filtrable virus (fĭl'trȧ b'l vĭ'rŭs), an organism too small to be seen with the microscope and usually within cells of other organisms.

First filial (fûrst fĭl'ĭ ăl) **generation,** the individuals arising from a particular mating.

Fission (fĭsh'ŭn), division of an organism into approximately equal parts.

Flagellum (flȧ jĕl'ŭm), a whiplike locomotor structure of a cell or single-celled animal.

Follicle (fŏl'ĭ k'l), a cellular sac or pocket.

Fragmentation (frăg mĕn tā'shŭn), a process by which individuals of certain Protozoa and simple Metazoa may divide internally to form several new individuals.

Freemartin (frē'mär tĭn), a modified female member of a pair of cattle twins which shows certain male features.

Gametes (găm'ēts). (See Germ cells.)

Gametogenesis (găm ē tō jĕn'ē sĭs), the series of cell divisions in the development of germ cells.

Ganglion (găng'lĭ ŏn), a group of nerve cell bodies outside the central nervous system.

Ganoid scale (găn'oid), rhombic in shape, composed of an inner layer of bone and outer layer of enamel.

Gastrula (găs'troõ lȧ), the two-layered stage in the development of an embryo.

Genes (jĕnz), the units of material which function in the transmission of characters in heredity.

Genetics (jē nĕt'ĭks), the science that treats of variation, resemblances, and their inheritance from parent to offspring.

Genotype (jĕn'ō tīp), the genetic constitution of genetically identical organisms.

Genus (jē'nŭs), *pl.* **Genera** (jĕn'ẽr ȧ), a division of the classification, a subdivision of a family, and is divided into species.

Geotropism (jê ŏt'rŏ pĭz'm), response of an organism to gravity.

Germ cells (jẽrm) (gametes), cells specialized for reproduction.

Germ layer (jẽrm), one of the primary cell layers in an embryo.

Germ plasm (jẽrm plăzm), the hereditary material of an organism, the chromatin.

Gills (gĭls) (pharyngeal clefts), a series of paired slits in the wall of the pharynx and body.

Gonads (gŏn'ăds), reproductive organs.

Gonophore (gŏn'ŏ fōr), a reproductive individual which bears gonads, as in Hydroids.

Glochidium (glŏ kĭd'ĭ ŭm), the larva of a fresh-water clam.

Glomerulus (glŏ mẽr'û lŭs), a body of capillaries enclosed at the end of each kidney tubule of the mesonephric and metanephric types of kidneys.

Glycerol (glĭs'ẽr ōl), one of the alcohols which enters into the composition of fats; glycerin.

Glycogen (glī'kŏ jĕn), a form of carbohydrate food material as formed and stored by the liver.

Habitat (hăb'ĭ tăt), the place or area in which an animal or species lives.

Haploid (hăp'loid), the reduced or half number of chromosomes of the mature germ cells.

Heliotropism (hē lĭ ŏt'rŏ pĭz'm), a response of an organism to light.

Hemoglobin (hē mŏ glō'bĭn), a protein pigment substance of the blood which is capable of absorbing oxygen and is red when combined with it.

Hemolysis (hê mŏl'ĭ sĭs), disintegration of red blood corpuscles.

Hepatic (hê păt'ĭk), pertaining to the liver.

Herbivorous (hûr bĭv'ŏ rŭs), herb- or plant-eating animals.

Hermaphroditic (hûr măf rŏ dĭt'ĭk) (monoecious), having both male and female germ cells produced in one individual.

Heterozygote (hĕt ēr ŏ zī'gŏt), an organism which is carrying sets of unlike characters in its genetical constitution.

Hibernation (hī bẽr nā'shŭn), the cessation of activity or dormancy of an animal during the winter season.

Histogenesis (hĭs tô jĕn'ê sĭs), the development and differentiation of tissue cells.

Histology (hĭs tŏl'ŏ jĭ), the science that treats of the microscopic structure of the various parts of the animal body.

Holoblastic (hŏl ŏ blăs'tĭk), having the type of egg structure in which cleavage divides the entire egg.

Holozoic (hŏl ŏ zō'ĭk), the animal nutrition, the ingestion and digestion of organic material.

Homoiothermal (hŏ moi'ŏ thûr'măl), having a temperature regulation.

Homolecithal (hŏ mŏ lĕs'ĭ thăl) (isolecithal), eggs having a uniform distribution of the yolk.

Homologous (hŏ mŏl'ŏ gŭs), similar in structure and origin, but different in function.

Homonomous (hŏ mŏn'ŏ mŭs), slight or no differentiation of body segments.

Homozygote (hŏ mŏ zī'gŏt), a zygote or resulting organism in which the corresponding genes are alike.

Hormone (hôr'mōn), the essential substance of an internal secretion which serves to help in metabolism regulation. Produced by endocrine glands and carried by the blood.

Hyaline (hī'à lĭn), semitransparent or glassy.

Hybrid (hī'brĭd), a cross, or offspring of parents differing in genetical constitution.

Hydrolysis (hī drŏl'ĭ sĭs), chemical rearrangement of a substance by combining with water.

Hydrostatic (hī drŏ stăt'ĭk), a type of organ which regulates the specific gravity of an aquatic animal.

Hypertonic (hī pẽr tŏn'ĭk), possessing greater osmotic pressure than some related substance.

Hypostome (hĭ'pŏ stōm), a conical projection around and below the mouth in coelenterates.

Hypothesis (hĭ pŏth'ĕ sĭs), an idea as it first develops as the result of preliminary observation and experiment.

Ileum (ĭl'ĕ ŭm), the posterior and longest part of the small intestine.

Ilium (ĭl'ĭ ŭm), dorsal bone of pelvic girdle of terrestrial vertebrates.

Immunity (ĭ mū'nĭ tĭ), freedom of susceptibility to disease.

Ingestion (ĭn jĕs'chŭn), the taking in of food material by an organism.

Insectivorous (ĭn sĕk tĭv'ŏ rŭs), insect-eating animals.

Inspire (ĭn spīr'), the drawing in of water or air in the respiration.

Instar (ĭn'stär), the period between molts in insect development.

Insulin (ĭn'sŭ lĭn), a hormone produced by the pancreas and essential to the proper metabolism of carbohydrates.

Integration (ĭn tĕ grā'shŭn), development and correlation to give unity in an organism.

Integument (ĭn tĕg'û mĕnt), the outer covering of the body.

Intracellular (ĭn trä sĕl'û lẽr), within the cell.

Intracellular differentiation (ĭn trä sĕl'û lẽr dĭf ẽr ĕn shĭ ā'shŭn), the presence of a variety of cells within one body.

Invagination (ĭn-văj ĭ nā'shŭn), the unfolding process by which the primary endoderm is withdrawn into the blastular cavity and becomes enclosed by the primary ectoderm.

Irritability (ĭr ĭ tä bĭl'ĭ tĭ), the capacity of protoplasm for responding to changes in environmental conditions or to external stimuli.

Isolecithal (ī sŏ lĕs'ĭ thăl). (See Homolecithal.)

Isotonic (ī sŏ tŏn'ĭk), possessing the same osmotic pressure in related substances.

Jejunum (jĕ jōō'nŭm), the middle division of the small intestine, between the duodenum and the ileum.

Karyokinesis (kăr ĭ ŏ kĭ nē'sĭs), mitotic cell division.

Karyolymph (kăr'ĭ ŏ lĭmf), the more fluid material of the nucleus.

Karyoplasm (kăr'ĭ ŏ plăz'm), the protoplasm which constitutes the nucleus.

Karyosome (kăr'ĭ ŏ sōm), a "net knot" or a part of the chromatin which forms a distinct body in the nucleus.

Katabolism (kå tăb'ŏ lĭz'm). (See Catabolism.)

Keratin (kĕr'å tĭn), a nitrogenous substance forming the chemical foundation of hair, horn, feathers, nails, claws, etc.

Kinetic energy (kĭ nĕt'ĭk), energy inherent in motion of a body.

Labium (lā'bĭ ŭm), posterior boundary or lower lip of an insect's mouth.

Labrum (lā'brŭm), the exoskeletal anterior boundary or upper lip of the insect's mouth.

Lacrimal (lăk'rĭ măl), pertaining to tears.

Lacteal (lăk'tĕ ál), pertains to milk; refers to lymphatics of the intestinal region because of their light color following absorption of fat.

Lacuna (lå kū'nå), a cavity or space, particularly that of bone, which contains the bone cells.

Lamella (lå mĕl'å), a thin layer or plate.

Larva (lär'vå), the young stage of an animal, which changes form during life.

Larynx (lăr'ĭnks), the expanded upper end of the windpipe or trachea; voice box.

Lethal (lē'thăl), capable of producing death.

Leucocyte (lū'kŏ sīt), a white blood corpuscle.

Ligament (lĭg'å mĕnt), a band of white fibrous connective tissue connecting structures other than muscles; particularly joining bones at the joints.

Limpet (lĭm'pĕt), a small type of gastropod (Mollusca) with a simple uncoiled shell.

Linin (lī'nĭn), the delicate threadlike structure which supports the chromatin granules in the nucleus.

Linkage (lĭngk'ĭj), the constant association of particular genes in certain chromosomes.

Lipase (lī'pās), a fat-splitting enzyme.

Lipin (lī'pĭn), fatty substance.

Lipoid (lĭp'oid), fatlike substance.

Lophophore (lō'fō fōr), a disc which surrounds the mouth and bears the tentacles of the Bryozoa.

Lumbar (lŭm'bĕr), pertaining to the region usually known as the small of the back.

Lumen (lū'mĕn), internal cavity of a tubular duct, gland, vessel, etc.

Luminescence (lū mĭ nĕs'ĕns), the emission of light from the body.

Lymph (lĭmf), the blood plasma and white corpuscles in the lymph spaces about the tissues.

Lymphatic (lĭm făt'ĭk), a vessel which carries lymph. In general, pertaining to lymph.

Macronucleus (măk rō nū'klē ŭs), the large nucleus of certain protozoans supposed to control vegetative functions.

Madreporite (măd'rē pō rīt), the strainerlike external aperture of the water-vascular system of echinoderms.

Malpighian (măl pĭg'ĭ ăn) body, a structure in the cortex of the kidney, composed of a glomerulus and Bowman's capsule which serves to take urine from the blood.

Mantle (măn't'l), a fold of the body wall which partially envelops the body; present in most mollusks and here secretes a shell.

Marsupial (mär sū'pĭ ăl), having a pouch for carrying the young.

Marsupium (mär sū'pĭ ŭm), an external pouch used in carrying the young, as in the kangaroo or opossum.

Matrix (mā'trĭks), the mother substance, such as that which encloses anything; the intercellular material of cartilage or other sustentative tissue.

Maturation (măt û rā'shŭn), the series of changes occurring in the development of germ cells before fertilization, including a reduction in the number of chromosomes in the cells.

Maxilla (măk sĭl'à), the major bone of the upper jaw of vertebrates or the accessory mouth part just back of the mandibles in many invertebrates.

Medulla (mē dŭl'à), posterior portion of the vertebrate brain; also the median area of many organs.

Medullary (mĕd'ŭ lĕr ĭ), pertaining to the medulla.

Medullated (mĕd'ŭ lāt ĕd), term used in reference to a nerve fiber which possesses a fatty or myelin sheath.

Medusa (mē dū'sà), a free-swimming individual coelenterate, such as a jellyfish.

Meiosis (mī ō'sĭs), the reduction division in maturation of germ cells.

Meridional (mē rĭd'ĭ ō năl), a condition in which planes extend from pole to pole of a spherical body.

Meroblastic (mĕr ō blăs'tĭk), having the type of egg structure in which cleavage is only partial, owing to the accumulation of yolk in the egg.

Mesencephalon (mĕs ĕn sĕf'à lŏn), the third region of the vertebrate brain, commonly called midbrain.

Mesenchyme (mĕs'ĕng kĭm) (Parenchyma), undifferentiated mesoderm composed of large cells.

Mesoderm (mĕs'ō dûrm), the middle germ layer and its later derivatives.

Mesoglea (mĕs ō glē'à), a jellylike substance found in Coelenterata between the ectoderm and endoderm.

Mesonephros (mĕs ō nĕf'rŏs), the vertebrate kidney of forms from lamprey to amphibians inclusive.

Mesorchium (mē sôr'kĭ ŭm), the mesentery or membrane supporting a testis.

Mesothelium (mĕs ô thē'lĭ ŭm), the mesodermic, membranous lining of the peritoneal cavity.

Mesovarium (mĕs ô vā'rĭ ŭm), the mesentery in which the ovary is suspended.

Metabolism (mĕ tăb'ô lĭz'm), the building up of living protoplasm and its concurrent oxidation.

Metagenesis (mĕt à jĕn'ē sĭs), an alternation of sexual and asexual generation in the life cycle of an organism.

Metameres (mĕt'à mērs), one or a series of similar parts that follow one another in a vertebrate or articulate animal.

Metamerism (mĕ tăm'ēr ĭz'm), serial symmetry or succession of segments.

Metamorphosis (mĕt à môr'fô sĭs), the transformation of one developmental stage into another without intermediate steps.

Metaphase (mĕt'à fāz), the phase of mitosis involving the longitudinal splitting of the chromosomes on the equatorial plate.

Metazoa (mĕt'à zō à), animals whose bodies consist of few or many cells functioning as a unit.

Micronucleus (mī krô nū klê ŭs), the small nucleus of certain protozoans supposed to control reproduction.

Micropyle (mī'krô pĭl), the small opening in the egg where sperm enter in certain forms of animals.

Milt (mĭlt), the light-colored spermatic fluid of male fish.

Miracidium (mī rà sĭd'ĭ ŭm), the early larval stages in the flukes.

Mitochondria (mĭt ô kŏn'drĭ à), small structures in the cytoplasm of animal cells; their significance is not entirely understood.

Mitosis (mī tō'sĭs), indirect cell division, involving the formation and splitting of chromosomes and their equal distribution to daughter cells.

Molt (mōlt), a complete or gradual shedding of the outer covering.

Monodelphia (mŏn ô dĕl'fĭ à), having a placenta.

Monoecious (mô nē'shŭs). (See Hermaphroditic.)

Monohybrid (mŏn ô hī'brĭd), an offspring of parents which differ by only one character.

Morphology (môr fŏl'ô jĭ), the science that treats of the form and structure of the bodies of animals.

Morula (mŏr'û là), a type of blastula characterized by the absence of a segmentation cavity.

Mucosa (mû kō'sà), a cellular membrane lining such cavities as those of the digestive tract.

Mucus (mū'kŭs), a viscous secretion which contains **mucin** (mū'sĭn). **Mucous** is the adjective form.

Mutation (mû tā'shŭn), a heritable change in an organism due to changes in one or more genes of germ cells.

Mutualism (mū'tû ăl ĭz'm), animals of different species associating together for the mutual advantage of each.

Myelencephalon (mī ĕ lĕn sĕf'à lŏn), the fifth or most posterior division of the vertebrate brain; the medulla oblongata of the adult.

Myelin (mī'ê lĭn), fatty substance surrounding the axone in medullated nerve.

Myoneme (mī'ô nēm), contractile fiber or strand in the cytoplasm of certain protozoans.

Myotomes (mī'ô tōms), segmental divisions of the muscles.

Nares (nā'rēz), the openings into the nasal chambers in vertebrate animals.

Nauplius (nô'plĭ ŭs), a larval stage of certain Crustacea.

Nekton (nĕk'tŏn), the pelagic aquatic animals which are independent of the effect of wind and waves.

Nematocysts (nĕm'à tô sĭsts), stinging bodies found in the tentacles of certain coelenterates.

Nematode (nĕm'à tōd), a roundworm belonging to class Nematoda of phylum Nemathelminthes.

Neoteny (nē ŏt'ê nĭ), the indefinite persistence of the immature condition of an animal.

Nephridium (nē frĭd′ĭ ŭm), a form of excretory organ, as found in the earthworm.

Nephrostome (nĕf′rŏ stōm), the funnel-shaped aperture at the medial end of a nephridium.

Neural (nū′răl), pertaining to the nervous system or to a nerve.

Neurilemma (nū rĭ lĕm′ȧ), the membranous outer coat of a nerve fiber.

Neuroid transmission (nū′roid), primitive transmission of impulses from cell to cell.

Neuron (nū′rŏn), a nerve cell together with its processes.

Notochord (nō′tŏ kôrd), a flexible rod extending anterior to posterior in the longitudinal axis of the body dorsal to the digestive tube and ventral to the nerve cord in chordates.

Nocturnal (nŏk tûr′năl), reference to night. Contrasted to diurnal which pertains to daytime.

Nodes of Ranvier (rän vyā′), constrictions in medullated nerve where the myelin sheath is interrupted.

Nomenclature (nō′mĕn klā tûr), a system of naming objects or ideas.

Nondisjunction (nŏn dĭs jŭngk′shŭn), the failure of homologous chromosomes to separate after synapsis and both go to one daughter cell with none to the other.

Nucleolus (nū klē′ŏ lŭs) (Plasmosome), a body within the nucleus containing material that is not chromatin.

Nucleus (nū′klē ŭs), a typically spherical body within the cell that contains the chromatin.

Nymph (nĭmf), the larval stage of an insect which undergoes incomplete metamorphosis; also the larval stage of a few vertebrates.

Ocellus (ŏ sĕl′ŭs), a simple type of eye, as in some insects.

Ommatidium (ŏm ȧ tĭd′ĭ ŭm), one of the numerous rodlike units of the compound eye.

Ontogeny (ŏn tŏj′ĕnĭ), the entire development and life history of an individual organism.

Oocyte (ō′ŏ sīt), the female germ cell before maturation is completed.

Oogenesis (ō ŏ jĕn′ĕ sĭs), the maturation of the female germ cell.

Oogonium (ō ŏ gō′nĭ ŭm), the female germ cell during the multiplication and growth stages of maturation.

Operculum (ŏ pûr′kŭ lŭm), a fold of skin, bone, and scales, which covers the gills of fishes and certain Amphibia; also the bony structure closing the aperture of certain snail shells.

Organ (ôr′găn), an arrangement of two or more tissues as a part of the body which performs some specific function or functions.

Organism (ôr′găn ĭz′m), any independent living being.

Orthogenesis (ôr thŏ jĕn′ĕ sĭs), the theory which holds that animals tend to develop along lines leading constantly in the same direction because they are determined by internal factors.

Osmosis (ŏs mō′sĭs), diffusion of substances dissolved in fluid, through a semipermeable membrane.

Ossicle (ŏs′ĭ k′l), a small bony structure.

Ostium (ŏs′tĭ ŭm), a mouthlike opening or entrance.

Otocyst (ō′tŏ sĭst), the primitive organ of hearing.

Ova (ō′vȧ), mature female germ cells. *Sing.*, **ovum** (ō′vŭm).

Ovary (ō′vȧ rĭ), the female gonad.

Oviduct (ō′vĭ dŭkt), the duct for the passage of ova from the ovary to the exterior of the animal.

Oviparous (ŏ vĭp′ȧ rŭs), pertaining to those animals which lay eggs that hatch after exclusion from the body.

Ovipositor (ō vĭ pŏz′ĭ tẽr), an organ of female insects and others which serves in helping to deposit the egg.

Ovoviviparous (ō vô vī vĭp'à rŭs), a condition of retention of the egg in the mother's body where it is nourished by the yolk of the egg.

Ovulation (ō vû lā'shŭn), the process of discharging mature eggs from the ovary.

Oxidation (ŏk sĭ dā'shŭn), a chemical combination of oxygen with another element.

Paleozoology (pā lē ô zô ŏl'ô jĭ), the science that treats of the animals of the past as represented by fossil remains.

Parasite (păr'à sīt), an organism that lives on or within and at the expense of another organism.

Parenchyma (pà rĕng'kĭ mà). (See Mesenchyme.)

Parietal (pà rī'ē tăl), pertaining to the walls of the coelom.

Parthenogenesis (pär thē nō jĕn'ē sĭs), the development of an egg without fertilization.

Pathology (pà thŏl'ô jĭ), the study of abnormal structures and abnormal functioning of life processes.

Pedal (pĕd'ăl), pertaining to the feet.

Pedicellaria (pĕd ĭ sĕ lā'rĭ à), pincherlike structures found over the surfaces of sea urchins and starfishes.

Peduncle (pĕ dŭng'kl), the stemlike attachment of certain shells and barnacles to other objects.

Pelagic (pĕ lăj'ĭk), floating near the surface of water.

Pericardial (pĕr ĭ kär'dĭ ăl), situated around the heart.

Periosteum (pĕr ĭ ŏs'tē ŭm), the membranous covering of bone.

Peripheral nervous system (pĕ rĭf'ēr ăl), that part of the nervous system exclusive of the brain and spinal cord.

Peristaltic (pĕr ĭ stăl'tĭk), forcing the food along the intestine by rhythmical contractions of the intestinal wall.

Peritoneum (pĕr ĭ tō nē'ŭm), the membrane that lines the coelom of vertebrates.

Phagocyte (făg'ô sīt), a white corpuscle which engulfs and destroys bacteria and other foreign material.

Pharynx (făr'ĭngks), the region between the mouth and the esophagus.

Pharyngeal (fă rĭn'jē ăl), pertaining to the pharynx.

Phenotype (fē'nô tīp), a type of organism possessing a complex of characters in its external features.

Phenotypic (fē nô tĭp'ĭk), pertaining to phenotype.

Photosynthesis (fō tô sĭn'thē sĭs), the process by which green plants manufacture starch from raw materials.

Phototropism (fô tŏt'rô pĭz'm), response of an organism to light.

Phylogeny (fī lŏj'ē nĭ), the study of the origin and relationships of the different groups and races of organisms.

Physiology (fĭz ĭ ŏl'ô jĭ), the study of the function of the parts of an organism as well as its living processes as a whole.

Pia mater (pī'à mā'tĕr), the membrane which is the immediate covering of the brain and spinal cord.

Pilidium (pī lĭd'ĭ ŭm), helmet-shaped larva of certain forms.

Pineal (pĭn'ē ăl) body, a dorsal projection from the diencephalon and thought to be the vestige of a third or median eye in vertebrates.

Pituitary (pĭ tū'ĭ tĕr ĭ) body, a glandular structure attached to the neutral side of the diencephalon of the vertebrate brain. It is an endocrine organ.

Placenta (plà sĕn'tà), the vascular membrane which connects the embryo with the parent.

Placula (plăk'û là), a type of blastula in which the animal and vegetative halves are somewhat compressed toward each other.

Plankton (plăngk'tŏn), the small pelagic organisms which are at the mercy of the waves.

Plasma (plăz'mà), the fluid portion of the blood.

Plasmagel (plăz'mà jĕl), the viscous or semisolid portion of protoplasm.

Plasmasol (plăz'mà sŏl), the more fluid phase of protoplasm.

Plasmosome (plăz'mô sōm). (See Nucleolus.)

Pleural (plōōr'ăl), pertaining to the cavity which contains the lungs.

Plexus (plĕk'sŭs), a network.

Polar (pō'lẽr) body, a small nonfunctional cell or oocyte produced during the maturation divisions of the female germ cell.

Polarity (pô lăr'ĭ tĭ), referring to a condition in which points or poles of concentration or dominance are established in a body.

Polocyte (pō'lô sīt), a technical name for a polar body.

Polyandry (pŏl'ĭ ăn drĭ), the practice of one female mating with several males.

Polygamy (pô lĭg'à mĭ), having more than one mate at the same time.

Polygyny (pô lĭj'ĭ nĭ), the practice of one male mating with several females.

Polymorphism (pŏl ĭ môr'fĭz'm), the occurrence of two or more forms of individuals within a species.

Polyp (pŏl'ĭp), the attached phase of the life history of a coelenterate animal.

Precocial (prê kō'shăl), type of bird which leaves the nest and has downy covering at time of hatching.

Predaceous (prê dā'shŭs) animal, one which preys on others.

Predatism (prĕd'à tĭz'm), the practice of one animal preying on another.

Primordial (prī môr'dĭ ăl), the first or primitive form.

Proboscis (prô bŏs'ĭs), an extension of the head or mouth parts. May be nose, as in elephant; mouth parts, as of moth; or pharynx, as of planaria.

Proctodeum (prŏk tô dē'ŭm), the pocket in the ectoderm ventral to the posterior part of the enteron of the embryo; primordium of the anus.

Proglottid (prô glŏt'ĭd), one of the sections or individuals of the chain making up the body of a cestode, such as the tapeworm.

Pronephros (prô nĕf'rŏs), the first kidney structure to form in the developing vertebrate.

Pronucleus (prô nû'klê ŭs), one of the two nuclei within a fertilized egg before cleavage occurs.

Propagation (prŏp à gā'shŭn), the production of new individuals.

Prophase (prō'fāz), the preparatory stages of mitosis during which the formation occurs of spindle, spireme, and chromosomes.

Proprioceptor (prō prī ô sĕp'tẽr), the receptor or end organ of the nervous system located within a certain tissue receiving stimulations in reference to bodily position or orientation.

Prostate (prŏs'tāt) gland, one of the male reproductive organs producing part of the semen.

Prostomium (prô stō'mĭ ŭm), portion of the anterior segment of annelids which overhangs the mouth.

Protein (prō'tê ĭn), one of the organic compounds found in protoplasm. It contains the elements carbon, oxygen, hydrogen and nitrogen.

Protoplasm (prō'tô plăz'm), the living matter of which all organisms are composed.

Protopodite (prô tŏp'ô dīt), the proximal section of the crustacean appendage. It includes coxopodite and basipodite.

Prototroch (prō'tô trŏk), the band of cilia extending around the equatorial region of trochophore larva.

Protrusible (prô trōō'sĭ b'l), the ability to be put out or extended from the body.

Proventriculus (prō vĕn trĭk'ū lŭs), the anterior, secretory portion of the stomach in certain animals, as the bird.

Pseudopodia (sū dô pō'dĭ à), protoplasmic processes (false feet) formed by certain protozoans and used for locomotion.

Ptyalin (tĭ'à lĭn), the starch-digesting enzyme of saliva; a diastase.

Pupa (pū'pà), the encased, inactive stage between the larva and adult condition in many insects and other animals.

Pyloric (pĭ lŏr'ĭk), pertaining to the pylorus.

Pylorus (pĭ lō'rŭs), the junction of the posterior portion of the stomach with the small intestine.

Radial symmetry (rā′dĭ ăl sĭm′ĕ trĭ), applied to a body that can be equally divided by several radial planes.

Radiant energy (rā′dĭ ănt ĕn ẽr jĭ), inherent power or energy transmitted through space, as that from the sun, radium, or x-ray.

Radula (răd′û là), the sheetlike rasping structure of the mouth of gastropods; used in mastication of food.

Recessive (rė sĕs′ĭv), in reference to a gene which is carried in the cell without expressing its character unless there is absence of its dominant mate.

Recapitulation (rē kả pĭt û lā′shŭn), repetition in development of an individual organism of its phylogenetic history.

Redia (rē′dĭ à), second phase of the life history of the fluke.

Reflex (rē′flĕks) action, automatic reaction to a stimulus from a receptor neuron and passed on to an adjustor neuron; performs an involuntary, appropriate act.

Regeneration (rē jĕn ẽr ā′shŭn), the replacement of mutilated parts or an entire animal from a portion of one.

Renal (rē′năl), pertaining to the kidney.

Rennin (rĕn′ĭn), an enzyme constituent of gastric juice of mammals and capable of coagulating the protein portion of milk.

Reproduction (rē prṓ dŭk′shŭn), the production by an organism of others of its kind.

Respiration (rĕs pĭ rā′shŭn), the exchange within an organism of oxygen entering the protoplasm and carbon dioxide leaving it.

Response (rė spŏns′), the reaction of an organism to a stimulus.

Rete (rē′tė), a limited meshlike arrangement or network.

Reticulum (rė tĭk′û lŭm), a fibrous or tubular network.

Retractile (rė träk′tĭl), that which can be withdrawn.

Retrogression (rĕt rŏ grĕsh′ŭn), going behind or moving backward.

Rhabdites (răb′dīts), special structures found interspersed among the epidermal cells of flatworms.

Rheotropism (rē ŏt′rŏ pĭz′m), response of an organism to mechanical currents.

Roe (rō), ovary and eggs of fish.

Rudiment (rōō′dĭ mĕnt), partially developed or embryonic structure; usually without function.

Rugose (rōō′gōs), possessing many ridges and folds.

Ruminants (rōō′mĭ nănts), animals which chew the cud.

Saprophyte (săp′rō fīt), an organism which absorbs nonliving organic matter in solution directly through the surface of the body.

Sarcolemma (sär kŏ lĕm′à), the delicate membrane immediately enclosing the striated voluntary muscle cell.

Sarcoplasm (sär′kŏ plăz′m), the cytoplasm of muscle cells exclusive of the sarcostyles or fibrils.

Sarcostyles (sär′kŏ stīls), cytoplasm fibrils in the structure of cytoplasm of voluntary muscle cells.

Schizogony (skī zŏg′ŏ nȳ), asexual reproduction.

Sclerotic (sklė rŏt′ĭk), the dense fibrous outer coat of the vertebrate eye.

Scolex (skō′lĕks), knoblike ''head'' on anterior proglottid of cestode.

Scute (skūt), a plate on the ventral side of the body of the snake.

Sebaceous glands (sė bā′shŭs), small subcutaneous glands, usually connected with hair follicles.

Sedentary (sĕd′ĕn tẽr ĭ), unattached forms which remain in one place.

Semen (sē′mĕn), fluid which carries the spermatozoa in the males of most animals.

Seminal (sĕm′ĭ năl), pertains to semen.

Semipermeable membrane (sĕm ĭ pûr′mė à b′l), one which permits the passage of solvents through it but not solutes, unless they dissolve in the membrane.

Senescence (sė nĕs′ĕns), period of old age and its effects.

Septum (sĕp′tŭm), a wall dividing two cavities.

Serial homology (sēr'ĭ ăl hŏ mŏl'ō jĭ), presence of structures of similar origin and form in different segments of the same animal.

Serosa (sē rō'sȧ), membrane covering peritoneal surface of internal organs; one which secretes a watery fluid.

Sertoli cells (sĕr tō'lē sĕls), modified, supporting or nurse cells for forming spermatozoa in the testes.

Serum (sē'rŭm), the fluid part of the blood which remains after clotting.

Sessile (sĕs'ĭl), attached directly and incapable of locomotion.

Seta (sē'tȧ), hairlike spine or bristle, found in animals.

Sinus (sī'nŭs), a cavity in a bone or other part, or a dilated vessel or canal.

Siphon (sī'fŏn), a canal or passageway, as the waterways in clams or tunicates.

Somatic cells (sō măt'ĭk), the cells of the body exclusive of the germ cells; body cells.

ᵼ **Somites** (sō'mīts), segments of the body of a segmented animal.

Spermatogonium (spûr mȧ tô gō'nĭ ŭm), a male germ cell during the period of multiplication and growth in maturation process.

Spermatocyte (spûr'mȧ tô sīt), the male germ cell before its maturation is completed.

Spermatogenesis (spûr mȧ tô jĕn'ê sĭs), the maturation of the male germ cells.

Spermatozoa (spûr mȧ tô zō'ȧ), mature male germ cells.

Sphincter (sfĭngk'tẽr), a muscular band surrounding a tube or aperture which, by its contraction, closes the lumen.

Spicule (spĭk' ūl), one of numerous needlelike, solid structures found supporting the tissues in the body wall of sponges.

Spiracle (spĭr'ȧ k'l), openings of air tubes in insects, or modified opening of first gill slit of certain fish.

Spireme (spī'rēm) thread, the coiled bead-like string of chromatin material that appears during the prophase of mitosis.

Splanchnic (splăngk'nĭk), has reference to the visceral organs.

Spongin (spŭn'jĭn), the skeletal material of a sponge.

Sporulation (spŏr û lā'shŭn), production of spores by division of a protozoan while encysted.

Statoblast (stăt'ô blăst), an encased, asexual winter bud of a bryozoan.

Statocysts (stăt'ô sĭsts), sense structures assisting in maintaining equilibrium in certain forms.

Steapsin (stê ăp'sĭn), one of the pancreatic enzymes which is capable of changing fats to fatty acids and glycerin.

Stereoblastula (stĕr ê ō blăs'tû lȧ), a blastula in which all the cells are in close contact and no blastocoele is formed.

Stigma (stĭg'mȧ), a sensitive pigment spot of Protozoa or the opening of a spiracle of insects.

Stomatodeum (stō mȧ tô dē'ŭm), the opening of the developing alimentary tract in an embryo.

Stratum (strā'tŭm), a layer of a series.

Striated (strī'āt ĕd), a type of muscle with more dense areas across the fibers.

Strobila (strô bī'lȧ), a series of individuals produced by linear budding, as certain Scyphozoa and tapeworms.

Succession (sŭk sĕsh'ŭn), the successive occupation of a given area by several species, either hourly, daily, or seasonally.

Sustentative tissue (sŭs'tĕn tä tĭv), binding together or supporting the various parts of the body.

Suture (sū'tûr), to sew together; a line of junction.

Symbiosis (sĭm bī ō' sĭs), the living together of two organisms for their mutual benefit.

Synapsis (sĭ năp'sĭs), the pairing of the chromosomes in the germ cells at one stage of maturation.

Syncytium (sĭn sĭsh'ĭ ŭm), a mass or layer of protoplasm with numerous nuclei but without distinct cell boundaries.

Syngamy (sĭn'gȧ mĭ), union of mature gametes to form a zygote.
System (sĭs'tĕm), an aggregation of organs to perform some general function of life.

Taxis (tăk'sĭs), a tropismal response involving movement of an organism as a whole.
Taxonomy (tăks ŏn'ȯ mĭ) (systematic zoology), the classification or orderly arrangement of organisms according to their natural surroundings.
Tegumentary (tĕg û mĕn'tȧ rĭ), referring to the skin.
Telencephalon (tĕl ĕn sĕf'ȧ lŏn), the anterior division of the vertebrate brain.
Telolecithal (tĕl ȯ lĕs'ĭ thăl), type of egg with abundant yolk unequally distributed.
Telophase (tĕl'ȯ fāz), the final stage in mitotic divisions.
Tentacle (tĕn'tȧ k'l), flexible, armlike extension of the body of many nonchordates.
Terrestrial (tĕr rĕs'trĭ ăl), a land form; living on or in the ground.
Testis (tĕs'tĭs), male gonad.
Thermotropism (thẽr mŏt'rȯ pĭz'm), response of an organism to temperature.
Thigmotropism (thĭg mŏt'rȯ pĭz'm), response of an organism to contact.
Thoracic (thȯ răs'ĭk), of or pertaining to the thorax or chest.
Thorax (thō'răks), the middle region of the body.
Threshold (thrĕsh'ōld), the minimum strength of stimulus necessary to get a response.
Thrombin (thrŏm'bĭn), the substance of the blood which plays an important part in clotting.
Thyroxin (thī rŏk'sēn or -sĭn), the hormone which is produced by the thyroid body.
Tissue (tish'ū), an organization of similar cells into a layer or group for the performance of a specific function.
Toxin (tŏk'sĭn), any poisonous substance.
Trachea (trā'kė ȧ), the windpipe or a tube for conveying air to the lungs; air tubes in insects.
Trichocyst (trĭk'ȯ sĭst), saclike structure in the ectosarc of Paramecium.
Triploblastic (trĭp lȯ blăs'tĭk), composed of three germ layers.
Trivium (trĭv'ĭ ŭm), the three anterior ambulacra of Echinodermata, collectively.
Trochophore (trŏk'ȯ fōr), a semispherical type of larva with cilia; found among flatworms, annelids, mollusks, etc.
Tropism (trō'pĭz'm), the movements of an organism in response to a stimulus.
Trypanosome (trĭp'ȧ nȯ sōm), genus of parasitic Protozoa (Mastigophora) including the causal agent of African sleeping sickness.
Trypsin (trĭp'sĭn), a pancreatic enzyme which converts proteins to amino acids.
Tsetse (tsĕt'sė) **fly,** a species of fly which serves to transmit the causal agent of African sleeping sickness.
Tundra (tŏon'drȧ), level plains region of the arctic region.
Tympanum (tĭm'pȧ nŭm), cavity of the middle ear or more generally any organ serving to receive sound waves.

Umbilical (ŭm bĭl'ĭ kăl) **cord,** the cordlike connection between the fetus and the placenta.
Umbilicus (ŭm bĭl'ĭ kŭs), the navel or the point of attachment of the umbilical cord to the abdomen.
Uncinate (ŭn'sĭ nȧt), in the shape of a hook.
Ungulate (ŭng'gû lȧt), hoofed.
Unguiculate (ŭn gwĭk'lȧt), having claws.
Urea (ū rē'ȧ), a nitrogenous compound which is produced as a protein by-product in metabolism.
Ureter (û rē'tẽr), the duct which conveys urine from the metanephric kidney to the cloaca or bladder.

Urethra (û rē'thrȧ), the duct which leads from the urinary bladder to the exterior of the body.

Uropods (ū'rō pŏdz), the sixth pair of abdominal appendages of a crustacean.

Vacuoles (văk'û ōlz), small cavities in a cell filled with water, gases, or oils.

Vagina (vȧ jī'nȧ), the cavity between the uterus and the external genital aperture of the female in many animals.

Vascular system (văs'kû lēr), the circulatory system.

Vascular tissue (văs'kû lēr), fluid tissue consisting of cells known as corpuscles in a fluid medium, plasma.

Vein (vān), the larger blood vessels leading to the heart.

Ventral (vĕn'trăl), side away from the back; literally belly; opposite to dorsal.

Villus (vĭl'ŭs), a fingerlike, vascular process of the internal lining of the small intestine.

Vitamins (vī'tȧ mĭns), substances which occur in small amounts in numerous foods and are essential regulatory substances for the animal body.

Vitelline (vĭ tĕl'lĭn), the outer membrane of an egg.

Vitreous (vĭt'rē ŭs), glassy in appearance.

Viviparous (vī vĭp'ȧ rŭs), the retention and development of the egg in the mother's body and nourishment of the embryo from the blood of the mother.

Volant (vō'lănt), able to fly.

Zoogeography (zō ȯ jē ŏg'rȧ fī), the study of the geographical distribution of animals.

Zoology (zō ŏl'ŏ jĭ) (animal biology), the study of the science which treats of animals.

Zygote (zī'gōt), a fertilized egg, or embryo, after fertilization.

Zymogen (zī'mȯ jĕn), a pre-enzyme; a substance which is produced in a gland cell and becomes an enzyme when it is discharged and activated by some other substance, perhaps another enzyme.

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