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TEXTBOOK
OF
GENERAL ZOOLOGY

BY THE SAME AUTHORS

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LABORATORY DIRECTIONS IN GENERAL
ZOOLOGY

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TEXTBOOK OF GENERAL ZOOLOGY

BY

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DEDICATED
TO
Ethan Allan Andrews

WHO, MORE THAN ANYONE ELSE, INFLUENCED THE EARLIER
WORK OF THE SENIOR AUTHOR AS A TEACHER OF
GENERAL ZOOLOGY, AND WHOSE INFLUENCE
DESCENDED TO THE JUNIOR AUTHOR
THROUGH GEORGE LEFEVRE
AND D. H. TENNENT.

PREFACE

ALTHOUGH prefaces are commonly forgotten, if indeed they are read by teachers, it seems that one must say something regarding the origin and nature of a new textbook, particularly in a field that is already well occupied. The present volume is the outcome of a work projected some years ago by the senior author as a formal organization of the course in General Zoology that has been developed at the University of Missouri during the past twenty-five years. Historically, it is the descendant of the course in General Biology that was introduced at the Johns Hopkins University by Huxley's student, Newell Martin, and later developed in that institution by E. A. Andrews. From Johns Hopkins and also from its original source in Huxley and later teachers in England, like T. J. and W. N. Parker, this early attempt to teach the principles of biological science has influenced instruction in many American institutions.

At the University of Missouri the course began as General Biology, but was restricted to the field of Zoology with the establishment of a separate department of Botany. The essential feature of this instruction in General Zoology is that a limited number of animals are selected to illustrate certain biological principles and only incidentally as representatives of particular phyla. This is in contrast with what may be called the "phylum" scheme of instruction, which has been widely prevalent during the past twenty years and is represented by well-known textbooks. The later form of instruction seems to have originated in the old-time courses in Natural History, represented by books like Tenny's "Manual of Zoology," and to have been transformed into modern garb through the influence of Louis Agassiz and his students. In both the "principles" and the "phylum" courses, the method of instruction by "types" has been utilized; but in one case the type illustrates principles, while in the other it shows the morphology and physiology typical of a given phylum.

Recent discussion of methods of teaching General Zoology has largely centered upon the relative merits of these two systems, and has been influenced by certain extreme departures in the attempt to teach principles. Another influence that is being felt is the "Project Method" which has been developed in many high school textbooks. While much is claimed for the Project Method, it seems to be the opinion of most college teachers that the product of the high schools in which this method flourishes is not such as to inspire full confidence in it, whatever may be the current educational theory of the learning process. It may be that the Project Method is the method of the future; but it has not yet arrived in the colleges, and the writers of the present volume have yet to be convinced that good teachers are not principally "born" and relatively little "made," when it comes to instruction of a serious intellectual content. Good teachers arouse the interest of their students, and to be a good teacher one cannot be forever thinking how it is done, else "the letter killeth." When all is said, intellectual work is for the intellectually competent; and, whatever may be the present population of our colleges, one questions whether the Project Method does not tickle the incompetent into temporary activity more often than it stimulates the competent to the work necessary in sustained intellectual effort.

This leads one to consider how a textbook of college Zoology should be written; whether it should give the student what he thinks he wants to know and can obtain in a way that takes little effort; or give him what he must know in order to understand something of the subject. The authors incline to the belief that college and university instruction must have a certain regard for the existing organization of subject-matter, for example, for Zoology as conceived by zoologists. As to phraseology, they have attempted to write clearly, but not with undue simplification of vocabulary or expression. It is part of a college training to learn how to read and understand writing that is understandable by educated adults. The only way to learn this is to read such writing. It is better for a student to find places in a textbook a bit difficult than to find it all easy. Whether the authors have succeeded in their attempt to write on a level above primary English, without using a style that is hopelessly beyond those for whom it has been intended, others must say. They profess only the intention.

To a certain extent they have been influenced by the idea that

is back of the Project Method. The senior author has always been conscious that such teaching of General Zoology as he has done effectively has been largely influenced by a sense of the "humanistic" aspects of the subject. The broader aspects of this "Humanism" of science have been discussed in a popular volume.¹ Zoology is full of human interest—not merely bread-and-butter interest, but interest that may be dignified by the term "humanistic." This is better developed individually by the teacher than formally in a textbook, since its effect upon the student depends so much upon the conviction of the teacher. On the other hand, the approach to Zoology through a study of vertebrate structure and physiology, as in the present work, recognizes the desirability of introducing the subject by means of the facts most familiar and interesting to the student. These are to be found in the body of a familiar animal and in the student's own body. To begin with the frog is to begin with man, since all vertebrates are so much akin in structure and function. The purpose of the first half dozen chapters is to review the knowledge of human anatomy and physiology that should be part of the training of every high-school graduate, although such is not the case. With this accomplished, and, one hopes, with interest aroused by the human problems involved, the facts and principles of animal life are presented in the formal manner that is current in most textbooks. The "project" in the first part of the work is to teach the student something of the principles of Zoology as illustrated in his own type of animal body; and the "project" in subsequent chapters is to teach him how other animal bodies may be compared with his own and to impart some of the many interesting facts about animals. If many of these facts do not interest him, the authors believe he is hopeless. In the final chapters on Development, Genetics, and Evolution, there is a return to more human problems. Here again, the attempt is made to state the facts and principles as clearly and fully as space permits, in the conviction that the origin of the individual and of the race, and the mode of inheritance are of such compelling interest that the teacher's energy should be directed toward clear presentation of facts and problems, rather than toward overworked schemes for stimulating intellectual laggards. This smacks of a take-it-or-leave-it doctrine in teach-

¹ Curtis, W. C., "Science and Human Affairs."

ing; but we take it or leave it all our lives, and perhaps the principal trouble with college teaching is that we do not make our students feel that college work is a serious enterprise.

As it stands, the present volume represents a temporary crystallization of the course in General Zoology as developed in the University of Missouri, although it contains more than the authors are able to offer in a course extending through but one semester. In the Laboratory Directions,² designed to accompany the present volume, it was possible to include work upon flatworms, molluses, and echinoderms. These have been omitted from the text, since it is obviously impossible to deal so largely with principles and at the same time present types of all the phyla. A chapter upon the History of Zoology has been omitted in favor of the inclusion of historical references in connection with special topics, since it is the authors' experience that historical chapters are not very effective with students.

In general, the aim has been to include the substantial body of well-established facts concerning the structure and functions of the animals described and to avoid undue inclusion of very recent details, however interesting. The authors hope that the book is not out of date in regard to recent biological investigation, but they have not tried to make it so "up to the minute" that it would soon be found to contain premature conclusions from very recent work. Such details are always better left to the teacher as a means of vivifying his instruction. For example, it is well to explain in a text the salient facts of "endocrine secretion," but not to include very recent extensions that have not been verified. It has been assumed throughout that the laboratory work of the course should be definitely related to lectures and text, and not given as though it were a separate course, as is done in some institutions. The authors' view of laboratory study has been discussed at some length in the Remarks to Instructors as printed in the Laboratory Directions. It is the belief of the authors that a textbook should contain a fundamental body of subject-matter that is correlated with the laboratory work and that may be extended by lectures at the discretion of the teacher. If laboratory work means anything, it should mean some measure of first-hand contact with the facts. On this foundation the text

² Curtis, W. C., and Guthrie, M. J., "Laboratory Directions in General Zoology."

becomes intelligible, and on the basis of laboratory study and text should rest the lectures and other oral discussion. The trouble with "principles" textbooks is that they have no foundation in accounts of representative types of animals; and the trouble with "phylum" textbooks is that they have no space for an outline of principles upon which the teacher can build his own superstructure.

The junior author is primarily responsible for the chapters on Metabolism, Irritability, the Cells of Vertebrates, and Genetics, and has collaborated, by critical editing and by advising, throughout the preparation of the remaining chapters as originally projected or written by the senior author. It is hoped that this united effort has resulted in a better textbook than could otherwise have been produced.

It is impossible, in a work of this nature, to acknowledge all the sources from which assistance has been received. There are the more remote influences, such as the authors have acknowledged in the dedication, and those of former colleagues, including G. S. Dodds and George Lefevre. The entire manuscript, as written before the final revisions, was read critically by Professor E. A. Andrews. Others who have read certain chapters are R. H. Wolcott, E. A. Martin, F. L. Hisaw, and J. A. Dawson. Thanks are due to the authors' colleagues in the department at the University of Missouri, who have collaborated in other ways, and to George T. Kline and Helen Woelfel, biological artists. Other acknowledgments of figures and of permission to use figures appear in the legends.

UNIVERSITY OF MISSOURI,
Columbia, Missouri,
March 1, 1927.

W. C. CURTIS
M. J. GUTHRIE.

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TEXTBOOK OF ZOOLOGY

CHAPTER 1

INTRODUCTION

An introduction to the science of Zoology may be secured in a variety of ways. One may become interested in the life of field and stream as a hunter and fisherman, or as an amateur naturalist through the collection of specimens. The farmer's son who watches the insects that devour the crops and who protects insect-eating birds may become something of a zoologist unawares. The boy or girl who studies Anatomy and Physiology in school becomes familiar with structure and function as found in the bodies of higher animals. A high-school course in Zoology or in Biology offers a more comprehensive introduction. Whatever may have been the student's previous experience with zoological science, it is desirable that he make the most of it throughout the study outlined in the present volume.

The Biological Sciences. — The term *science* may be applied to any body of exact knowledge. The *Natural Sciences* are those dealing with the facts of nature, in contrast with the *Social Sciences*, which deal with the facts of human nature. According to such a classification, the Social Sciences are contrasted with the Natural Sciences, as though the two were distinct. But the human relationships with which the Social Sciences deal are facts of nature no less than the phenomena of Chemistry or Physics. Hence it is better to say that the Social Sciences are conveniently set off, as dealing with human relationships, over against all other sciences, which are called the Natural Sciences. These Natural Sciences may be divided into two groups: the *Physical Sciences*, which are concerned with non-living bodies; and the *Biological Sciences*, which are concerned with organisms, or living things. Thus *Chem-*

istry, *Physics*, and *Astronomy* are Physical Sciences; while *Zoology*, *Botany*, and *Physiology* are Biological Sciences. In its narrower sense, the term *Biology* includes *Zoology*, *Botany*, and the closely related sciences that deal with particular phases of animal and plant life. In its broader sense, the term may include everything related to living organisms and their activities. The division of the sciences into a physical and a biological group is arbitrary. Even the Social Sciences may be grouped as "biological," if we choose to regard them as such, because they are concerned with the activities of living beings. The list of Biological Sciences is, therefore, extensive; and what, if anything, is to be excluded depends upon the point of view of the person making the classification.

Zoological Science. — Biology is, therefore, the science of living things, both plant and animal. Botany is the science of plants. Zoology is the science of animals. The term *Animal Biology*, which is sometimes used, means the study of animals *as living forms* illustrating the principles often common to both plant and animal life, rather than the principles related to animals alone. The term Plant Biology might be similarly applied, but has not come into general usage. The accompanying table (p. 3) indicates the larger groupings of problems and subject matter within the field of zoological science. It should be studied in connection with the definitions that follow. If the reader understands the justification for the groupings thus exhibited, he has mastered the definitions and their application.

Form and Function. — The science of *Morphology*, which deals with the structure of animal bodies, may be considered independently, although it is really inseparable from *Physiology*, which deals with their functions. Gross morphology, as studied in the dissection of the human body by medical students or in the dissection of the bodies of animals by students of Zoology, is commonly called *Anatomy*. *Embryology* has likewise its morphological and physiological aspects. The problem of form and function further includes microscopic organization and activities. *Histology* deals with the more general features of microscopic structure, the forms of the living units or cells, and their arrangement in *tissues* and in *organs*. *Cytology* deals with the internal structure of cells in their finer details. Like *Anatomy* and *Embryology*, *Histology* and *Cytology* began principally with descriptions of structure, but they have become increasingly physiological

PROBLEMS AND INTER-RELATIONSHIPS OF ZOOLOGICAL SCIENCES

Problems	Sciences	Related Sciences
Form and Function	Morphology Physiology	Anatomy Embryology Histology Cytology Pathology Psychology
Origin of the Individual	Embryology	Anatomy Histology Cytology Physiology
Organism and Environment	Ecology	Taxonomy Zoögeography Morphology Physiology Pathology
Classification	Taxonomy	Morphology Physiology Embryology Zoögeography Paleontology
Variation and Heredity	Genetics	Morphology Physiology Embryology Taxonomy
Origin of the Race	Organic Evolution	Morphology Physiology Zoögeography Embryology Paleontology Ecology Taxonomy

as the structural features of cells and tissues have been ascertained and it has seemed desirable to know more regarding functions. *Pathology*, or the science of abnormal structures and functions, and *Psychology*, or the science of the mind, are naturally included here.

The science of *Physiology* was first concerned with the activities of adult bodies. These activities are dependent upon structure to the same extent that the activities of a machine, such as a steam-engine or an automobile, are related to the structural relationships of its parts. Physiology and Morphology must, therefore, be studied together as the problem of function and structure, if one desires an adequate knowledge of living bodies. The animal is "something happening" rather than an actionless piece of machinery. One may infer how its parts "work" by an examination of their structure, just as the operation of an engine might be inferred from an examination of its mechanism; but complete knowledge can be obtained only when an understanding of the engine's "morphology" is correlated with observations and experiments upon its "physiology," or manner of action. Since Anatomy, Embryology, Histology, and Cytology have their morphological as well as their physiological aspects, the sciences of Morphology and Physiology are everywhere related as the structural and functional aspects of living organisms. To understand fully the problem of form without considering that of function is a manifest impossibility.

Origin of the Individual. — Although it might be included under the head of Morphology and Physiology, the study of *Embryology*, or the process of development by which individual animals come into existence, must be ranked as one of the major problems of biological science. Embryology is a phase of Anatomy, since it deals with the origin of structure. In studying it from this aspect, one examines embryos in their successive stages and likewise their histological and cytological organization. However, the more important aspect of the origin of the individual is not the description of successive stages, but rather an account of what "happens" in development. Now that the successive stages have become well known in so many animals, Embryology is becoming more of a physiological than a morphological science. There is the same relationship between structure and activities as in the problem of form and function. Psychology and Pathology might likewise be included here. The origin of the individual is, in fact, only the problem of form and function as it appears in other than adult phases.

Organism and Environment. — The relation of the animal to its surroundings, or environment, presents many complex problems.

Broadly speaking, the environment consists of the entire universe outside the animal's body, and a great deal that may be internal, such as chemical substances circulating in the blood, or the body heat of a higher animal. Narrowly speaking, it comprises the more immediate surroundings; but factors remote in their origin, such as the sun's light and heat, and even the light of the moon, may be important. In recent years the study of organisms in relation to their environment has come to be designated *Ecology*. To study animals as thus related to their surroundings, it is necessary to classify them. Hence, *Taxonomy*, or the science of classification, is related to *Ecology*, as the table shows. *Zoögeography*, or the distribution of animals over the surface of the earth, is likewise important; and one might include the distribution of organisms in geologic time as shown by the study of *Paleontology*. Since functions are everywhere important in relation to environment, *Physiology* is also concerned, and with it *Morphology* and *Pathology*, for the reasons indicated in a preceding paragraph.

Classification. — The problem of arranging the various kinds of animals in some orderly manner must have presented itself ever to primitive peoples. The "beasts of the earth," the "fowls of the air," the "fish of the sea," and "everything that creepeth," represents an early attempt of this nature. Advancing knowledge rendered a more satisfactory organization of the many kinds of living things imperative. Thus the science of *Taxonomy*, or classification, had its origin. In the past, classifications have been based upon various features of animals and plants. To-day the standard form is that based upon *structure*, because structural resemblance seems to be the most constant and significant feature in animal organization. Hence, *Morphology* and *Embryology*, and with them *Physiology*, are important to *Taxonomy*. *Zoögeography*, or the distribution of animals over the earth's surface, and *Paleontology*, or the science of fossils, are not branches of *Taxonomy*; but the classifier must consider the localities in which existing animals are found and must have some knowledge of the animals of the past. Beginning as a local effort to classify the plants and animals of a neighborhood, classification was progressively extended and developed into the science of *Taxonomy*.

Variation and Heredity. — Variation may be defined, for preliminary purposes, as the differences between the individuals of a species, and heredity as the resemblance between parents and

offspring; although neither of these definitions is quite accurate. From the time when his attention was first directed to such matters, man must have noted these facts of difference and resemblance and considered their significance as applied to his own offspring or to his domesticated animals. In recent years, however, variation and heredity have come to be studied by themselves in what is known as the science of *Genetics*, which may be said to have originated when the Mendelian laws of heredity were rediscovered and became generally known, about the year 1900. The relationship of Genetics to other biological sciences is very extensive, as will be apparent upon reflection. Variations of form are frequently studied, and hence an aspect of *Morphology* is involved. There are also functional variations, which involve *Physiology*. *Embryology* reveals the manner in which hereditary features are passed from one generation to another. *Taxonomy* is involved, because variations determine the limits of species in classification. Moreover, Genetics is the key to the causes of Organic Evolution, since evolutionary changes must originate in variations and be perpetuated by heredity. As with the other groupings of related sciences shown by the table, the list of those bearing upon the science of Genetics might be greatly extended.

Origin of the Race. — In ancient times the origin of the many different kinds of animals was commonly ascribed to some form of creation by which they were produced in their existing states, unless indeed it was believed that each individual arose spontaneously. With the advance of knowledge concerning animal and plant life, belief in an evolutionary process became inevitable. *Organic Evolution* is the term applied to the transformations of living things since they appeared upon our planet. It may be compared with *Inorganic Evolution*, which describes the history of non-living things in theories concerning the transformations of solar systems or of chemical elements, or in the more certain theories of geologic evolution.

Organic Evolution is the biologist's answer to the question of the historical development of the many and varied forms of life. Within the past century it has come to be supported by overwhelming evidence as the most reasonable explanation of this historic course of events. The sciences of *Morphology*, *Physiology*, *Embryology*, *Zoögeography*, *Paleontology*, *Ecology*, and *Taxonomy* are important to the student of Organic Evolution. Comparative

Anatomy and Embryology tell of relationships that are often unsuspected. Paleontology tells the history of these relationships. Ecology and Zoögeography enable one to interpret the past in terms of the present, which is a cardinal principle in Paleontology as in the related science of Geology. Taxonomy is a summary of all the conclusions regarding racial origins, since classification, based on structure, indicates the degree of relationship that exists among various forms of life and thus reveals their evolutionary history.

Definitions like those given in the preceding paragraphs are less interesting than many scientific matters-of-fact, but they are desirable for purposes of introduction. An attempt has been made to give greater significance to these definitions by means of the tabulation (p. 3), which shows how the more important zoological sciences are related to one another and to the broader problems of Zoology. If, after examining the table, the reader understands why each of the sciences listed in the right-hand column is cited in a particular place, he has mastered the definitions and has secured an outline of zoological science.

In such a tabulation it is evident that each subdivision of the right-hand column might contain the names of additional sciences. One's understanding of the definitions may be further tested by considering what other sciences might be so listed. The unity of life is such that every one of these right-hand subdivisions might contain the names of all the other biological sciences and of the principal physical sciences as well. This is a less striking way of saying that if one could know any single field of nature in all its ramifications one would understand the world in its entirety. Consider, for example, what it would mean to know everything one might conceivably know regarding a single animal: how light from the sun and moon is related to its activities; what physical and chemical changes occur within its body; the nature and origin of the material from which its organs are formed; the process of growth; what makes it, perhaps, an object of beauty in the eyes of man; these and similar questions touch the great problems of the material universe on the one hand and those of the human mind on the other.

The subdivisions of zoological science above enumerated find parallels in the science of Botany. While it is desirable at the outset to obtain the comprehensive survey of subject matter that

such definitions imply, it would be unfortunate if too much defining should give the impression that Zoology consists of many isolated fields of knowledge. An understanding of the table corrects such an impression. Anatomy, Embryology, Physiology, and the other sciences are merely different angles from which the study of animal life may be approached. Reflection will show that each overlaps others and that none is isolated by the nature of its subject matter. The problems and sciences defined in the foregoing paragraphs and illustrated by the tabulation will all be considered in the present course of study.

NOTE.—Italics are used throughout the present volume, as in Chapter 1, to emphasize the names of important parts or processes. Unfortunately, the font of type used for these italics does not show without close inspection the difference between the diphthongs *æ* (æ) and *æ* (æ). The student should, therefore, bear in mind this difficulty, and when in doubt as to the spelling of an italicized word containing one of these diphthongs should note the spelling where the word is printed in the regular type.

CHAPTER 2

NATURAL HISTORY OF VERTEBRATE ANIMALS

Everyone knows something concerning the human body and the bodies of related animals. The more complete this knowledge, the easier is the approach to many phases of zoological science. Because the great majority of students thus possess some knowledge of their own bodies, we shall examine first the structure and activities of an animal that is like ourselves. The frog has the advantage of being familiar in its natural surroundings, interesting in itself, large enough to handle, and man-like to a degree that can be appreciated only upon careful examination. It is sufficiently complex to illustrate the most important features of higher animals, and its structures and functions are relatively well known to science. By studying the frog it is possible to review and extend one's present knowledge and to discover certain biological principles which will be elaborated in subsequent chapters.

The term Natural History has no precise definition at the present time. It was formerly used to designate the study of natural objects, not only animals and plants but also non-living things like minerals. During the eighteenth and early nineteenth centuries, many naturalists were primarily concerned with the collection and classification of animals, although their studies afield brought knowledge regarding habits and distribution. In recent years the science of Ecology has taken over and refined some of the diffuse subject matter of natural history; but the word Ecology, which may be defined as the relation of organisms to their environment, conveys too restricted a meaning to serve as a title for the present chapter, in which an attempt is made to review the principal types of backboned animals, or *Vertebrata*, and to indicate some of the more general features of their organization, behavior, and general relationships. While this may seem an impossible task within so brief a compass, we shall, nevertheless, be able to consider certain facts of general biological interest by way of

introduction. As in the ensuing chapters on Morphology and Physiology, the frog and man will be most frequently cited for purposes of illustration.

The Frog as a Representative Vertebrate

Classification.—It is a familiar fact that animals fall into restricted groups called *species* (singular, *species*, not “specie”).

FIG. 1.—Representatives of the Sub-phylum *Vertebrata* (cf. Figs. 2 and 3).

Since the most effective manner of explaining what is meant by the term *species* is through concrete examples of such animal groups and their place in classification, we may proceed at once to

illustrations. This may be done either by following a larger group of animals through its lesser subdivisions until the individuals comprising the smallest groups, or species, are reached; or by proceeding in the reverse order. The existence of the group known as the *Vertebrata* (Figs. 1, 2, 3) was recognized only after it had been discovered that a great array of animals all possessed a backbone composed of vertebræ and hence could be called "vertebrates."

FIG. 2.—A representative of the Class *Aves* of the Sub-phylum *Vertebrata*: the ostrich in silhouette showing endoskeleton of bones and exoskeleton of feathers (cf. Figs. 1 and 3).

(After Pander and d'Alton.)

FIG. 3.—A representative of the Class *Mammalia* of the Sub-phylum *Vertebrata*: the lion in silhouette showing endoskeleton of bones and exoskeleton of hair (cf. Figs. 1 and 2)

(After Pander and d'Alton.)

These vertebrates have been found, in turn, to possess features that lead one to include them, along with certain other simpler animals (Fig. 4), in one of the major divisions, or *phyla* (singular, *phylum*), of the Animal Kingdom, the *Chordata* (cf. Table, p. 36), which are so called because they all possess, at some stage in their development, a *notochord*, or primitive skeletal axis. In the vertebrates the notochord appears in the embryo, but is later replaced by the segmented vertebral column, or backbone (cf. Fig. 40, p. 69, and Fig. 213, p. 405.)

The frog, as shown by the table of classification (p. 36), is a member of the Class *Amphibia*, a subdivision of the *Vertebrata*, which includes also the toads and salamanders. The classification of *Amphibia* is as follows:

Class, *Amphibia*Sub-class, *Labyrinthodonta* or *Stegocephali*

Fossil forms, long extinct; bodies of very large size in some instances and commonly covered with scales (Fig. 5).

Sub-class, *Lissamphibia*

Existing forms; no well-developed scales; mostly a soft moist skin, as in frog; none of very large size.

Order, *Gymnophiona* or *Apoda*

Worm-like creatures without limbs; burrowing in moist ground; not found in temperate America (Fig. 6).

Order, *Urodela*

Tailed amphibians; the salamanders, etc. (Fig. 1 B).

Order, *Anura*

Tailless amphibians; the frogs and toads (Fig. 7).

Following the *orders*, as one proceeds in classification, come *families*, then *genera*, and finally *species*. Thus, the Order *Anura* contains, along with some half dozen others, the Family *Ranidæ*, which in turn includes the Genus *Rana* and others. For example:

Order, *Anura*Family, *Ranidæ*Genus, *Rana*

Species, *pipiens*, the "leopard" frog (*Rana pipiens*)

In speaking of a species, it is customary to use both the generic and the specific names, much as we use a given name and a surname in referring to human individuals, for the purpose of more accurate designation. To be more definite, we say "*Smith, John,*" instead of saying merely "John" or "Smith." In like manner, we refer to the leopard frog as *Rana pipiens* or *R. pipiens*, writing the generic name with a capital and the specific name with a small letter. The following are common species of the genus *Rana*: *R. catesbiana*, the "bullfrog"; *R. clamitans*, the "green frog"; *R. sylvatica*, the "wood frog"; *R. palustris*, the "pickerel frog"; and *R. pipiens*.

FIG. 4.—Other representatives of the Phylum *Chordata*.

A, an attached tunicate, Sub-phylum *Urochordata*. a, larval free-swimming stage of same. B, *Amphioxus*, Sub-phylum *Cephalochordata*. C, *Balanoglossus*, Sub-phylum *Hemichordata*.

A species may be divided into *varieties*, if it shows different types that do not warrant specific distinction. The amount of difference between the individuals composing any species can be appreciated only if one examines specimen after specimen and makes exact comparisons. For such a purpose, collections of shells, containing large numbers of individuals, present convenient illustrative material. In general, the intra-specific differences that constitute varieties are slight, as are also the differences between species. Whether a given group shall be a variety of an existing species, a new species, or even a new genus, depends upon the judgment of the individual taxonomist making the classification. Some tend to make many species, others few species, of the same material. Taxonomists exhibiting these tendencies are termed "splitters" and "lumpers," respectively, by those who pursue the opposite course.

The foregoing catalogue of unfamiliar names is less interesting than many phases of Zoology, but it illustrates the principles of classification that are consistently fol-

FIG. 5.—Skeleton of a Permian stegocephalian, *Eryops*, an extinct type of the Class *Amphibia*.

(Photo. by courtesy of the American Museum of Natural History.)

lowed at the present time. Beginning with any small group of animals, such as a species of frog or grasshopper, one can follow it into larger and larger groupings until the *Phylum* is reached, and finally to the *Animal Kingdom*, which is coördinate with the other great group of living things, the *Plant Kingdom* (cf. Fig. 117 and p. 241). Conversely, if one should begin with the *Animal Kingdom*, one might conceivably follow it to every subdivision until all the species were reached, and thus pass in review all the varied forms of animal life that are known to exist. Our present knowledge of classification is the result of an enormous amount of study, by virtue of which hundreds of thousands of species have become

FIG. 6.—A footless amphibian, *Cæcilia*, one of the Order *Gymnophiona* or *Apoda*. a, anus.

described and arranged in the manner indicated. This grouping of species is necessary as a means of cataloguing the multitudinous organisms that make up the *Animal Kingdom*; but classification is further significant because it attempts to follow the lines of evolutionary relationship and hence becomes equivalent to a “family tree” of living beings.

Distribution.—With few exceptions, the *Amphibia* are confined to water and its immediate vicinity, or to a moist atmosphere. It is this characteristic that has given the name amphibian, which means “leading two lives,” to this class of the *Vertebrata*. Many of the salamanders pass their entire lives in water. Most species of frogs are amphibious. The common toad, *Bufo americanus*, passes the greater part of its life away from the water, but is quite sensitive to atmospheric moisture. The reader may have noticed that toads are seldom seen in exposed localities in times of drought but will appear after a heavy rain. During the dry inter-

vals, they either remain in shaded places, in which there is a maximum of moisture, or return to their "holes" as they do in the day time. The Amphibia are thus dependent upon water, for two obvious reasons: because their respiration is in part effected through the skin; and because their skins are not adapted to prevent evaporation. If a frog escapes in the laboratory, particularly if the room is artificially heated, it will usually be found shriveled and dead some hours later. On the other hand, many reptiles,

FIG. 7.—The American toad, *Bufo americanus*, a male with buccal sacs expanded in "singing."

(From Dickerson, "Frog Book," copyright, 1920, by Doubleday, Page & Co., reprinted by permission.)

including most lizards and snakes, are adapted for a hot, dry atmosphere and react accordingly under artificial conditions.

In this connection it may be mentioned that frogs and toads do not "drink" water through the mouth as do many familiar animals. They absorb through their skin such water as enters the body uncombined with their food. This can be demonstrated by exposing a frog first to a dry and later to a moist atmosphere, and weighing at proper intervals.

Among the species of frogs common in the eastern and central portions of the United States, the "bullfrog," *Rana catesbiana*, and the "green frog," *R. clamitans*, have similar habits and are

confined rather closely to the vicinity of water. The "leopard frog," *R. pipiens*, on the other hand, may wander far from water and thus is sometimes called the "grass frog" when found in meadows. The "pickerel frog," *R. palustris*, may also wander from the water, although it lives mostly in spring beds and in cool, damp places. A more extreme example is the "wood frog," *R. sylvatica*, which is regularly found in damp woods. In New England this frog is common in beech woods, often a long distance from water. Like the toad, it must come to the water at the breeding season, and in wet weather it has access to temporary ponds.

FIG. 8.—The common tree frog, *Hyla versicolor*, showing mottled coloration that matches its backgrounds in nature.

(From Dickerson, "Frog Book," copyright, 1920, by Doubleday, Page & Co., reprinted by permission.)

Acris gryllus, the "cricket frog," is another pond and stream-dwelling species, occurring often in swampy places and in small bodies of water. *Hyla versicolor*, the "tree frog" (Fig. 8), comes to the water in numbers only at the breeding season, and at other times frequents damp places, climbing tree trunks to feed upon insects. Its changes in color to match the background are remarkable in their rapidity and diversity, and probably account for the fact that these animals are difficult to locate; although their presence is often made known by their croaking, particularly under stimulation by the moist atmosphere preceding rain.

The general distribution of Amphibia is, therefore, conditioned by certain peculiarities of the body surface that have been described. They cannot live in arid regions or in regions where the ground remains frozen throughout the year, because they must hibernate during cold weather. They are, so to speak, tied to the water by the nature of their organization and activities and by

the fact that, with few exceptions, they must lay their eggs in water at the annual breeding season.

Food and Feeding. — The feeding habits of frogs and toads must be observed to be appreciated. A toad in a garden at dusk, or one

FIG. 9.—Feeding habits of the American toad, showing the sudden protrusion and retraction of tongue in capture of a flying insect and a toad walking around an earthworm preparatory to seizing head first.

(From Dickerson, "Frog Book," copyright, 1920, by Doubleday, Page & Co., reprinted by permission.)

found squatting near a street lamp to which it has been attracted by the insects, will often furnish an amusing as well as an instructive demonstration.¹ Insects flying near the head are snapped into

¹ The popular prejudice against toads is quite unreasonable. They do not produce warts and may be handled with impunity. Certain of their skin glands secrete a fluid which is irritating if brought in contact with the mouth or the eyes but has no effect upon the human skin. This fluid is discharged only when the animal is violently handled or is in grave danger, as when seized by a snake. It is presumably protective. Toads compare with the best of our insect-eating birds in their destruction of garden pests, and they should receive the protection afforded to all harmless and useful animals. In a garden or a field they should be welcome guests and not objects of persecution and destruction by adults as well as children. They have a marked sense of locality, and individuals appear to return year after year to the same foraging grounds.

the mouth by a sudden movement of the tongue (Fig. 9), which is almost as sticky as fly paper. An object crawling on the ground, such as an earthworm, is approached by jumping, and as it is gulped into the mouth the two front feet may alternately comb the wriggling prey away from the head. Frogs in the laboratory may be fed upon crayfish or similar animals. In nature their food is of wide variety. Almost anything that is small enough may be devoured, and sometimes, as in the case of crayfish, the size and number of the objects swallowed is amazing. Insects flying in the air; spiders, insects, snails, and earthworms crawling on the ground; insect larvæ, crayfish, and other animals in the water; even other frogs and tadpoles — all are eaten with avidity.

The writer once observed that some large bullfrogs had devoured a number of English sparrows, which had been inadvertently left in a caged aquarium and had fallen an easy prey with the approach of night. In nature, the bullfrog may devour young chicks and ducklings if they blunder within reach. Generally, only living food is taken by frogs and toads, the animals responding to the moving object, although a frog will sometimes swallow the bodies of dead animals if they are placed in its mouth. For this reason a frog will snap at a fishhook dangling near its head, although such a response usually means a speedy end. Similar responses to objects in motion are typical of many other carnivorous animals. They have doubtless been observed by the reader in fish, which "rise" to the bait that falls across the water with just the right imitation of the natural food; in the lizard, which darts forward only when the fly begins to crawl; or in the stolid barnyard fowl, which eyes suspiciously the insects lying motionless for a second or two after they have been uncovered by scratching, but seizes them as soon as they begin to make off. Motion of this sort is so invariable a sign of something alive, and hence good to eat, that carnivorous animals have come to respond automatically to such stimulation, yet they can learn to make nice distinctions, as with the wily old trout that feeds all day on his natural prey but never takes the most cleverly thrown fly.

Movements and Locomotion. — In contrast with the salamanders (Fig. 1 B), which are more typical as four-footed vertebrates, the frogs and toads exhibit a specialization of the limbs comparable with that seen in kangaroos, rabbits, the entire class of birds, and in human beings. These animals are not closely related as

vertebrates, but they have developed independently in the direction of more specialized uses for their two pairs of limbs than is commonly found. In the familiar hopping of frogs and toads, the hind legs are responsible for the strength of the spring while the front legs serve mainly as guides in pointing the body in the desired direction. The animals are frequently seen crawling in a clumsy fashion, but only for short distances, or to shift the position of the body. In water, likewise, the frog swims by means of its powerful hind limbs, while the fore limbs perform the function of balancers.

In the squatting posture which it assumes on the bank, the frog is in a position to leap at a moment's notice, like an athlete ready for the pistol shot. In the "floating" attitude, the animal is no less able to retreat suddenly. At first glance it seems so awkwardly placed that it must be at a great disadvantage, but observation shows that the floating individual actually "dives," with surprising rapidity. The reason for this appears when the series of movements is carefully observed. The animal hangs obliquely in the water with eyes and tip of nose exposed, the fore limbs projecting from the body and the hind limbs moderately extended. When diving from this position, it first withdraws from the surface by bringing the hind legs into their folded position, thus carrying the body backward beneath the water. While this is happening, the fore limbs give a stroke upward and backward, which, together with the bending of the body, directs the head downward. The hind legs are then extended with their powerful stroke, and the frog shoots away, the whole process occurring so rapidly that it is impossible to recognize the successive changes without repeated observations.

Like other active animals, the frog has a well-developed "sense" of its position. It "knows" when it is wrong side up. If placed on its back the animal rights itself without delay. It may roll either to the right or to the left, but the response is immediate unless the individual has been fatigued by repeated demonstrations. With the onset of fatigue, the process occurs more slowly and is readily observed. In this connection a peculiar mode of reaction may be mentioned. If a frog is seized in the hands, laid upon its back, and held a few moments until it has ceased its struggles, it will usually remain motionless for a time, sometimes for hours (cf. Fig. 10). The exact significance of this behavior, in relation to

death-feigning and to the hypnotic state in man, is a matter of doubt.

The use of the limbs in other vertebrate animals shows many interesting features. Relationships between structure and function are everywhere apparent. Typically, the skeleton of each limb consists, as in the human body, of an upper portion supported by a single bone, the *femur* in the leg and the *humerus* in the arm; a portion containing two bones, the *tibia* and *fibula* of the leg, and the *radius* and *ulna* of the arm; a group of smaller bones at the ankle or wrist; and the bones of foot or hand. This plan of structure, which appears in the generalized condition in man and some

FIG. 10.—Death feigning in young toads that have been seized and held for a moment, sometimes called hypnotism but probably not comparable with the hypnotic state in man.

(From Dickerson, "Frog Book," copyright, 1920, by Doubleday Page & Co., reprinted by permission.)

of the less specialized of the terrestrial vertebrates (Fig. 18, p. 39), is modified in a variety of ways for different uses, but persists throughout as a type to which the most specialized forms can be referred. Parts suppressed in the adult are often found in the embryo. Hence, it is in general supposed that limbs like those of the horse or the bird, with their smaller number of bones, have reached their present state by loss or fusion of parts in the course of evolution (*cf.* Fig. 277, p. 517). Often these fusions are readily seen, as in the radio-ulna or tibio-fibula of the frog (Fig. 40, p. 69).

Miscellaneous Activities.—Sound production by frogs and toads is more diversified than is commonly supposed. One who has trained himself in this regard can distinguish the notes of different species as he can those of birds, although there is much less range

and diversification. In *R. pipiens* there is a slight difference in the *croak* of the two sexes, and, in addition to its croaking, the animal gives forth a grunting sound under conditions that seem unusually agreeable. When seized by an enemy it may utter a cry called the *pain scream*. The croaking is produced by forcing air back and forth between lungs and mouth cavity across the vocal cords, which are stretched on either side of the larynx, or laryngo-tracheal chamber. The latter name is sometimes given to the larynx of the frog (Fig. 23, p. 43) because it is equivalent to both the larynx and trachea, or windpipe, in higher vertebrates. A frog can croak even though it is completely submerged in water, because there is only a slight loss of air through the nostrils during the process and the air may be driven back and forth a number of times before being expelled. It has been generally assumed that this sound production by means of the vocal cords functions primarily as a *sex call*, by means of which the males and females find one another at the breeding season. This is undoubtedly one of its uses, if not the only one, although the croaking is more or less in evidence at other times. Among the sounds uttered by frogs are community signals, like the *alarm cry*, which causes other individuals to seek safety in the water.

Vocal cords are, of course, present only in air-breathing vertebrates. The fishes have no such organs. It is interesting to find in the Amphibia, which are the simplest of the land vertebrates, structures and activities that suggest the origin of the human vocal organs (Fig. 24, p. 44). It may also be remarked that a well-developed sense of hearing appears only in terrestrial vertebrates, and that eardrums, like vocal cords, do not occur in fishes. In general, it appears that sound production and the ability to perceive sounds go hand in hand. The ear of a mammal, with its external portion and its drum sunken into a protected position (Fig. 68, p. 125), in correlation with a more delicate sense of hearing, is paralleled by the greater specialization of the sound-producing apparatus which mammals exhibit.

Some of the diverse activities of the frog seem to be adaptive, that is to say, useful, to the extent that they tend to protect the individual in time of danger. When threatened by an enemy, a frog or toad often folds the limbs close against its sides and inflates its body by filling the lungs to their maximum capacity. In this condition the animal is almost egg-shaped, and the moist

slippery surface makes it a difficult object for an animal like a snake to hold between its jaws and begin swallowing. Sometimes, instead of endeavoring to escape, the frog will crouch close to the ground and remain motionless, thus tending to evade capture by hiding. When diving into the water, it sometimes circles about and comes up to one side of the observer, near the bank, among the weeds. Or it may hide on the bottom by crawling under some object. The tree frog, *Hyla versicolor*, which possesses such unusual powers of changing its color to blend with surrounding objects (Fig. 8), is perhaps aided by this reaction in its struggle for life.

While it would be difficult to prove beyond a doubt that these varied activities of the leopard frog and its relatives are "adaptive" in the sense that they are frequently of life and death importance, such responses are similar to the forms of behavior exhibited by many other animals which, like the frog, possess no special means of defense. Adaptation in animals has no doubt been over-emphasized at times in the history of Biology; but the fact remains that living organisms, both animal and plant, exhibit a degree of adjustment to the necessities of their existence which has impressed the biologist ever since Aristotle said that the essence of a living being was "fitness."

Enemies and Parasites. — Being entirely without weapons or defensive armor, save the tough and slippery skin, frogs are preyed upon by many other animals and can find safety only in hiding or flight. Next to man, snakes are undoubtedly their greatest enemies, for, despite their lack of limbs, the snakes that frequent banks of ponds and water courses are very adept at capturing frogs and swallowing them, usually head foremost. Shore-feeding birds such as cranes and herons, the common crow, turtles, such fish as bass and pickerel, skunks, and many other animals all prey upon frogs. Were it not for their rapid multiplication, these Amphibia could hardly survive in the face of such destruction.

Like most animals that have been carefully studied, the frog is the "host" for a great number of parasites. Among those likely to be met with even in a single frog are fluke worms of the genus *Pneumonæces*, in the lungs; *Clinostomum*, encysted on the inner surface of the body wall; *Gorgoderina*, in the urinary bladder; and various other flukes within the intestine. In the lungs may also be found a species of roundworm, *Rhabdias*, and

immature worms of this type are often found in the intestine and the body cavity. In the large intestine of almost every specimen examined, there will be found, in addition to many bacteria, several species of single-celled parasites belonging to the group of animals known as *Protozoa*. The list might be still further extended. It is not uncommon to find a dozen or more different species of parasites in a single frog taken at random. Since most parasites are specialists, to the extent that they infest but a single species of host or a few closely related species, and since most well-

FIG. 11.—Development of the frog.

A, eggs. B, C, D, and E, cleavage, gastrula, and neural fold stages. F, newly hatched tadpoles. G and H, later tadpole stages. I, J, and K, metamorphosis to juvenile frog.

known animals have many parasites, it is not impossible that the total number of parasitic species of animals exceeds those that are free-living. Parasitism is, therefore, of widespread occurrence and presents many interesting biological problems. There are few, if any, true cases of parasitic vertebrates, probably for the reason that most vertebrates are animals of some size, while parasites are, of necessity, smaller animals.

Seasonal Changes and Life Cycle. — Following its breeding season in early spring, the leopard frog leads an active life, feeding voraciously to restore the loss entailed by its "winter sleep" and

by reproduction. There seems to be a less active period in the late summer, followed by further activity preceding the hibernation. With the lowering of the temperature in the fall, the animal goes to the bottom and works its way into the mud or under the bank, where it remains dormant until spring. Shortly after its emergence, the mating occurs. The eggs are laid by the female during sexual union, and fertilized by the sperm of the male as they pass into the water. At first each egg is surrounded only by a thin layer of sticky substance. In a few hours, however, this imbibes water and becomes the capsule of jelly surrounding the individual eggs, which lie massed together and lightly attached to submerged objects near the surface (Fig. 11 A). Development proceeds, in the course of three or four months, through the familiar tadpole stages to the miniature adult. The rather sudden change from the tadpole to the young frog is termed the *metamorphosis* (Fig. 11 I-K). In the tadpoles, gills like those of fishes constitute the primary organs of respiration, although well-developed lungs are present and assume an increasing importance in later tadpole stages. With metamorphosis, the gill apparatus in part disappears and is in part converted into other organs. The frog tadpole thus resembles a fish, since it develops in the open water and possesses certain fish-like organs.

Adaptation.—As has already been indicated, certain activities of the frog are so well fitted to the needs of the animal in its struggle for life as to attract our attention. A like condition prevails in other organisms. The leaves of a plant are adapted to perform certain functions; the stems and roots, others. Animals are adapted for many differing modes of life, each to its own set of conditions. While it is sometimes argued that non-living things also exhibit what may be termed *adaptation*, as when we find hydrogen “adapted” to combine with oxygen in the formation of water, the earth adapted to revolution about the sun, or the stones in the bed of a stream adapted to their particular places, this adaptation, or fitness, of inanimate objects is far less complicated than that observed in living bodies.

For convenience, the adaptations of organisms may be grouped as: (1) Anatomical, or structural; (2) Physiological or functional; and (3) Related to behavior. This, however, represents no hard and fast distinction. It would perhaps be better to say that structure and function are everywhere inter-related,

and are together adapted to the more obvious needs of the organism. Thus, the limbs of a vertebrate animal and those of an insect (Fig. 22, p. 42) are structurally adapted to function in a manner that is advantageous for the life of their possessor. A familiar example of what is generally regarded as an adaptive feature is the coloration and bodily shapes of many animals, notably birds and insects, which so resemble the surroundings that the animal seems likely to escape the observation of many enemies (Fig. 8). The behavior of an animal as a whole, as shown in actions like eluding an enemy or seizing a victim, is, therefore, adaptive insofar as it tends to preserve the life of the individual under the normal conditions of its environment. Such adaptation is not perfect, but only sufficient for the needs of the particular case. The snake that swallows a hen's egg profits by the experience, but should it swallow a china nest-egg it might die of indigestion. Frogs and toads snap at objects moving in the air near their heads. In nature, motion of this sort is almost invariably a sign of something good to eat. Behavior in frogs and toads is adapted accordingly. If the moving object happens to be a fish-hook, the animal may lose its life.

In general, it may be said that the behavior of animals is adapted to the conditions which they and their ancestors have commonly experienced. They are not adapted to untried situations, unless by accident. When animals come in contact with such situations, one of two things seems likely to happen: either the species is exterminated through its inability to cope with these conditions; or, after a period of wholesale destruction, the survivors become adapted. This adaptation may involve the development of new structures as well as new functions and modes of behavior, and hence may effect what is clearly an evolutionary modification. By such modifications in relation to changes of the environment, it is believed that species have reached their present state of fitness.

Charles Darwin (1809-1882) designated as "Natural Selection" this action of the environment whereby the individuals of a species are selected by nature according to their ability to meet the demands of an intense struggle for life. Granting the reality of adaptation as a widespread phenomenon among animals and plants, his theory remains the best scientific explanation of the manner in which such fitness has reached its present degree of excellence.

Adaptation in the Human Species. — The case of man appears to be somewhat different from that of the rest of the animal world. While it appears that animals must become adapted to their environment, must change with the changing demands of existence, or perish, man has succeeded to a surprising extent in altering his environment instead of becoming himself modified by the forces of nature. The beaver that builds a dam and constructs

FIG. 12.—American beaver and “house.” A beaver pond in background with dam to left.

(Photo. by courtesy of the American Museum of Natural History.)

its “lodge” by felling trees and cutting them in pieces (Fig. 12), or the colony of bees with its nest, alters the environment to suit its needs; but even these extreme cases show relatively little control of the environment when compared with that secured by mankind, unless one accepts a view of the purposeful actions of animals with which many biologists are not in agreement. Civilized man has created for himself conditions that may be characterized as “artificial” in contrast with those of nature. He does this by virtue of his intelligence, by understanding nature and by modifying natural conditions to suit his needs. By contrast, other animals must conform to changes in environment or perish. Having persisted in his present manner of life, man cannot return

to the order of nature, even if that were desirable. It is only possible to go forward to an increasing control. If men are to live herded together in cities, to traffic up and down the seas, to cultivate the soil, and to solve the problems of increasing population, it must be through an ever more effective control of their surroundings. The material problems of human beings are, biologically speaking, the problems of an organism that is struggling to control an environment from which much has been secured, but from which much remains to be wrested if the species is to be made safe in its present position or to reach higher levels. Because scientific knowledge is the key to this situation, science assumes an increasing importance in the life of mankind.

The Vertebrates and their Environment

Habits, Habitat, and Distribution.—Having examined the natural history of the frog as a representative vertebrate, we

FIG. 13.—The climbing perch, a fish that can leave the water and travel for some distance on land by means of an adaptation for storing water above the gills.

The fish on land and head dissected to show structure of gill region; *b.a.*, first branchial arch; *l.o.*, labyrinthiform organ; *op.*, operculum; *sb.c.*, suprabranchial cavity. (Left, courtesy of *Nature Magazine*; right, from *The Cambridge Natural History*, copyright, 1920, by Macmillan and Co., Ltd., reprinted by permission.)

may next consider the natural history of the vertebrates as a diversified group of animals. In connection with the classification of vertebrate animals (p. 36), reference will be made to the habits and habitats of the several types. The fishes (Fig. 1 C, D, E) are aquatic, and breathe by means of gills, although certain species are adapted for brief excursions from the water. Among these may be mentioned the climbing perch (Fig. 13),

the flying fish, and a few species that remain on the moist seaweed between tides or are capable of short journeys on land. These, however, are quite exceptional. The whole organization of fishes shows their fundamental adaptation to an aquatic life. The Amphibia (Fig. 1 B) are animals whose early stages, the tadpoles, are fish-like in structure and thoroughly adapted for life in the open water, save in a few species where some form of brooding the young occurs (Fig. 14); and even in such instances the embryo is surrounded by a fluid during its development. In its final stages the animal may live permanently in the water; but most forms become "amphibious," breathing air by means of lungs, although the skin is also used in respiration (*cf.* p. 91). Hence,

FIG. 14.—A tree frog, *Hyla goeldii*, which carries the eggs in an incipient brood-pouch on its back until the hatching stage, which is probably as late as the time of metamorphosis.

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the Amphibia, as a class, are confined to the vicinity of water, as with the frogs, or to regions of moist atmosphere, as with the toads.

The Reptilia, on the other hand, possess fully developed lungs and a skin that protects their bodies from excessive evaporation, and are true land animals. The developing embryo is enclosed in an egg shell which is leathery like that of a turtle, not brittle like that of a bird (Fig. 220, p. 423). Since these egg shells resist evaporation sufficiently to allow development in a moist atmosphere, the reptiles find it unnecessary to lay their eggs in water as do the Amphibia. They are thus "emancipated" from the water. There are a few cases among the reptiles, for instance, in some of the snakes, where the young are born "alive" (*cf.* p. 423). Birds are similar to reptiles in their manner of development, save for the difference in the egg shell and for the care given the young after hatching.

Of all vertebrates, the mammals are the most highly specialized for terrestrial life. In most species, the early stages of development are passed within the body of the female parent but the most primitive mammals (Fig. 15) lay eggs that resemble those of birds and reptiles (*cf.* Fig. 224, p. 428). In some

cases, as with the mare's colt, the young can stand and run almost at birth. In others, as in dogs and cats, there is a period of greater dependence. Adult mammals are adapted for a wide range of terrestrial conditions. The chamois, mountain sheep, and goats inhabit the heights; deer and wolves, the forests and open country; members of the horse and cattle families, the great plains; other mammals range along the shores of streams, lakes, or oceans. Among the most interesting cases are those of such mammals as whales, porpoises, and seals, which show varying degrees of adaptation to life in the water. The same peculiarity is shown, in a

FIG. 15.—The duckbill or platypus, *Ornithorhynchus anatinus*, an Australian mammal that lays eggs.

(From Parker and Haswell, "Textbook of Zoology," copyright, 1921, by Macmillan & Co., Ltd., reprinted by permission.)

lesser degree, by beavers, muskrats, and many others. These animals are obviously mammals; they have hair and give birth to well-developed young which are nourished by means of mammary glands. They are able, in extreme cases like that of the whales, to spend their entire lives in the water, coming up at intervals for air when not swimming at the surface. Others, like the fur seal, may spend most of their lives in the water save for the breeding seasons. The fur seals arrive at the seal islands of Bering Sea early in the summer; they give birth to their young on land at the so-called "rookeries" (Fig. 16); the young pass their early life in and out of the water; and in the late summer the seals "haul back to the sea and no man knows their track," although they return to the beaches year after year. A seal is a very clumsy animal on

the land, but very graceful in the water. It is "tied" to the land by its manner of breathing and producing young, just as the toads, among Amphibia, are "tied" to the water by the necessity of a moist atmosphere and by their breeding habits.

The foregoing examples enable us to understand something of the diversification in habits and habitats of the vertebrate group as a whole. The oceans in all their depths, the land surface even to the poles, and the air constitute the limits of distribution. No other one of the large animal groups, unless it be the *Arthropoda*

FIG. 16.—American fur seals at rookery, and adult male and his "harem" of females. Other similar groups are seen in the background. These seals come to the rookeries in summer, giving birth to the young on land. During the remainder of the year they live in the open waters of the North Pacific.

(Photo. by courtesy of the American Museum of Natural History.)

(cf. Fig. 117, p. 240), ranges so widely. This much can be said in general. To go further would necessitate detailed references to individual species, some examples of which have been given in the Amphibia. Of all the types of vertebrates, the human kind has ranged most widely. No other single species can compare with man in this particular, unless it be some of the animals associated with him, such as rats and other vermin. Taken as a whole, therefore, the vertebrates show a great range of habitat. The fishes, which are the simplest vertebrates, are adapted for aquatic life;

the reptiles, birds, and mammals, which are more complex, are adapted for life on the land and in the atmosphere; the Amphibia represent an intermediate state in both structure and habits.

Feeding and Food Supply. — Like other large groups of animals, the vertebrates present examples of varied types of diet. Some vertebrates are plant-feeding, or herbivorous; others, flesh-feeding, or carnivorous; while still others are omnivorous, thriving upon a diversified food supply. The differing foods and the differences in

FIG. 17.—Timber wolves. Typical of the adaptations that enable such mammals to range from the high mountains to the plains and even from the Arctic circle to the tropics.

(Photo. by courtesy of the American Museum of Natural History.)

feeding habits which they imply are, of course, related to the habits and habitat of each species.

The vertebrates, taken as a whole, show a wide range in feeding habits and in adaptations related to feeding. The sources of food supply may be considered in this connection, with reference not only to vertebrates but to animal life in general. Animals take into their bodies masses of material, the *food*, which is digested and becomes a part of their protoplasm (*cf.* p. 81). Green plants, on the other hand, take in simple compounds, such as water, carbon dioxide, and mineral salts; with these alone they are able, in the presence of sunlight, to maintain and increase the bulk of their bodies. Closer analysis shows that, strictly speaking, the difference between plant and animal nutrition is not so great as might be supposed; but for the present we are considering only the fact

that plants are able to maintain themselves upon non-living materials, whereas animals are dependent for their existence either upon the bodies of other animals or upon plants.

When the food of animals is traced to its source, the green plants are found to support not only themselves but also the vast majority of animals. Herbivorous animals feed directly upon green vegetation; carnivorous animals are usually but one step removed, because they feed upon other animals that are herbivorous. Examples will occur to the reader. Since the green plants depend upon sunlight for the energy by which they combine simple chemical compounds into the complex ones necessary for a living body, the maintenance, from day to day, of every living thing upon the land is dependent upon the light of the sun and the green substance, *chlorophyll*, in plants. If the green plants should be suddenly wiped out of existence, the animals would soon perish, for at the best they could do no more than "eat each other up," like the gingham dog and the calico cat. It is true that plants derive much of their available food from the decomposition of the bodies of animals, but this does not alter the general fact that animals depend upon plants for their food, whereas plants are not so obviously dependent upon animals. Even more fundamental than this difference in the source of their energy is the contrast between the chemical synthetic powers of plants and animals. Green plants make their own nutrients; animals digest and recombine theirs. The colorless plants, or *Fungi*, get their energy from organic matter, as do animals, but they are closely related to plants rather than to animals.

In the foregoing pages, the reader's attention has been directed to the life that is found upon the land. The relationships that exist in the ocean are similar, although at first glance there seems to be nothing there to correspond to the mass of verdure that clothes the fertile portions of the land.

If we try to call before the mind a picture of the land surface of the earth we see a vast expanse of verdure stretching from high up in the mountains, over hills, valleys, and plains, and through forests and meadows, down to the sea, with only an occasional lake or broad river to break its uniformity.

Our picture of the ocean is an empty waste, stretching on and on with no break in the monotony except now and then a flying-fish or a wandering sea-bird or a floating tuft of vegetable life. It contains plant-like animals in abundance, but these are true

animals and not plants, although they are so like them in form and color. At Nassau, in the Bahama Islands, the visitor is taken in a small boat, with windows of plate glass set in the bottom, to visit the "sea-gardens" at the inner end of a channel through which the pure water from the open sea flows between two coral islands into the lagoon. Here the true reef corals grow in quiet water, where they may be visited and examined.

When illuminated by the vertical sun of the tropics and by the light which is reflected back from the white bottom, the pure, transparent water is as clear as air, and the smallest object forty or fifty feet down is distinctly visible through the glass bottom of the boat.

As this glides over the great mushroom-shaped coral domes which arch up from the depths, the dark grottoes between them and the caves under their overhanging tops are lighted up by the sun, far down among the anthozoa or flower animals and the zoöphytes or animal plants, which are seen through the waving thicket of brown and purple sea-fans and sea-feathers as they toss before the swell from the open ocean.²

It appears, however, that what seem to be plants attached to the bottom are in reality attached animals feeding upon other animals that swim freely in the water. In these sea gardens the bottom is like one vast mouth, or rather it is carpeted with innumerable mouths. Even further examination seems to show that the animal life of the ocean possesses no visible means of support, unless one examines the open water with the aid of a microscope. In this way one discovers that in the ocean, as well as on land, *the green plant is the primary source of food supply*. In the ocean, however, the green plants consist of microscopic forms. Although the number of species is relatively small, such an enormous number of individuals are present in all the oceans that these organisms furnish an abundance of food for the teeming animal population. The inter-relationships whereby the material from this primary source becomes available for larger animals are no more complicated than those by which a similar elaboration of the food supply is effected upon the land, beginning with the green plants and ending with the largest carnivorous animals. A similar condition exists in the life of inland waters (*cf.* Fig. 305, p. 550), although the amount and importance of the larger aquatic vegetation is relatively much greater than in the ocean. The conditions that have been described for land, ocean, and fresh water, constitute a fundamental

² Brooks, W. K., "Foundations of Zoology," pp. 220-21.

nutritional relationship, upon which have developed all the multitudinous interactions and special devices by which animals and plants maintain themselves upon our planet.

Inter-relations between Species. — In concluding this discussion of the vertebrates in relation to their environment, reference may be made to the manner in which both animals and plants are inter-related in their daily existence. It is well known that animals depend upon other animals and upon plants for food. The relation of "eater" and "eaten" is almost universal. A host of other relationships also obtain, whereby species depend upon other species for their very lives; and the chain of events often ramifies in so many directions that we can only imagine its ultimate possibilities. Among many examples of such relationships are those cited by Darwin in discussing the "checks to increase" in his "Origin of Species." The relation between cats and clover is one of his most famous cases. Stated in Darwin's own language, this runs as follows:

I have also found that the visits of bees are necessary for the fertilization of some kinds of clover; for instance, 20 heads of Dutch clover (*Trifolium repens*) yielded 2290 seeds, but 20 other heads protected from bees produced not one. Again, 100 heads of red clover (*T. pratense*) produced 2700 seeds, but the same number of protected heads produced not a single seed. Humble-bees alone visit red clover, as other bees cannot reach the nectar. It has been suggested that moths may fertilize the clovers; but I doubt whether they could do so in the case of the red clover, from their weight not being sufficient to depress the wing petals. Hence we may infer as highly probable that, if the whole genus of humble-bees became extinct or very rare in England, the heartsease and red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends in a great measure upon the number of field-mice, which destroy their combs and nests; and Col. Newman, who has long attended to the habits of humble-bees, believes that "More than two-thirds of them are thus destroyed all over England." Now the number of mice is largely dependent, as every one knows, on the number of cats; and Col. Newman says, "Near villages and small towns I have found nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice." Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district. (Darwin, Chas., "Origin of Species," pp. 90-91.)

In examining such a chain of events, one should remember that it is no stronger than its weakest link. If the connection breaks at any one place, the conclusion does not follow from the premises. It is quite possible that the foregoing relationship between cats and clover may not obtain, because one or more links of the sequence do not actually occur. Probably in no such case can we ever be sure that the relationships we observe are in reality matters of life and death in a large number of cases. Nevertheless, in view of the many glimpses of such relationships that are everywhere disclosed by organic nature, we can be sure that living beings are frequently inter-related in ways that are of the utmost importance to the organisms concerned; and that such interdependence of life upon life is one of the major factors in the complex of animate nature.

As explained under the head of definitions in the preceding chapter, the biological science that deals with the relationship of organisms to their environment, both living and non-living, is known as *Ecology*. The ecological study of vertebrate animals presents many problems that are intimately related to problems of human existence. Thus, man, although no longer preyed upon by the larger animals, falls a victim to the attacks of parasites in the form of the germs of disease, or is tortured by insect pests which secure food from his body. Insects prey upon the plants that he cultivates for food. Insect-eating birds in turn devour the insects and are themselves destroyed by their enemies. From a state in which he lived by dint of holding his own physically with other forms of life, man has come to live by his wits, and in this way has become the dominant species among those now in existence. Within a very brief space of time, this single species, *Homo sapiens*, has upset the balance of power which had previously existed in the inter-relationships of living things throughout the earth and had continued throughout geologic time. A new and terrible thing has come upon the world of living beings. Because of man, forests have given place to fertile fields or to bare and eroded hillsides, the larger forms of animal life that do not serve for domestication are fast becoming extinct, and introduced animals and plants are supplanting native stocks in many localities. The zoologist can but feel that the world will be a far less satisfactory place for man, to say nothing of the animals, if the birds become mostly English sparrows and the mammals rats and mice,

while coincidentally the virgin forests are largely converted into Sunday newspapers.

Classification

The Vertebrates and their Next-of-kin. — As shown by the accompanying table of classification, the vertebrates belong to a larger group of animals, the Phylum *Chordata*. All chordates agree in certain fundamental points of structure, notably in the possession of the *notochord* (cf. p. 11), as their name implies. Other distinguishing features are the *gill slits*, and a *dorsal, tubular, central nervous system*. The *Hemichordata* (Fig. 4 C) are worm-like marine animals which are simple and yet have gill slits resembling those of vertebrates. The *Urochordata*, or "sea squirts" (Fig. 4 A), are usually modified for an attached mode of life in the adult; but some are free-swimming, and in early stages (Fig. 4 a) they possess a notochord and other unmistakable chordate features. The *Cephalochordata* are represented by the individuals of several genera, including *Amphioxus* (Fig. 4 B), which do not possess a skull; in other respects they are much like the *Vertebrata*, which possess a skull and vertebral column, as seen in familiar backboned animals (Figs. 1, 2, 3).³ Members of the Phylum *Chordata*, therefore, exhibit a wide range of organization, being represented at one extreme by very lowly animals, like the tunicates, and at the other by the most complex of all animals, the mammals.

Phylum, *Chordata*.

Sub-phylum, *Hemichordata*.

Balanoglossus, etc. (Fig. 4 C).

Urochordata.

Tunicates, or sea squirts, etc. (Fig. 4 A).

Cephalochordata (Acrania).

Amphioxus, etc. (Fig. 4 B).

³ It is sometimes convenient to distinguish between "vertebrate" and "invertebrate" animals, the vertebrates being sufficiently important, because of their complexity as well as from a human standpoint, to be placed over against the rest of the animal world. This distinction was originally made by Aristotle. As a matter of scientific classification, however, such a division of the animal kingdom into vertebrates and invertebrates is unwarranted.

*Vertebrata or Craniata.*Class, *Cyclostomata*.

Primitive, aquatic forms without jaws and paired appendages, and with circular mouths, e.g., Lampreys, etc. (Fig. 1 E).

Class, *Pisces*.

Aquatic forms with paired appendages, true jaws, and with scales in the skin, e.g., the Fishes.

Sub-class, *Elasmobranchii*.

Fishes with cartilaginous skeletons, e.g., Sharks, Skates, etc. (Fig. 1 D).

Sub-class, *Teleostomi*.

Fishes with bony skeletons, e.g., the more familiar fresh-water fishes (Fig. 1 C).

Class, *Amphibia*.

Semi-terrestrial and aquatic forms with soft moist skin and tadpole stage in development, e.g., Salamanders, Frogs, Toads, etc. (Fig. 1 B).

Class, *Reptilia*.

Terrestrial forms with scaly bodies, well developed lungs, and other adaptations for terrestrial life, e.g., Lizards, Alligators, Turtles, Snakes, etc. (Fig. 1 A).

Class, *Aves*.

Terrestrial forms adapted for flight, covered with feathers, e.g., Birds (Fig. 2).

Class, *Mammalia*.

Animals with hair and mammary glands, and in most cases giving birth to well-developed young, e.g., Mammals (Fig. 3).

CHAPTER 3

MORPHOLOGY OF THE VERTEBRATE BODY

An understanding of scientific facts, in Zoology as in other sciences, must rest upon a basis of first-hand knowledge. Little knowledge is required for an understanding of the preceding chapter, beyond the acquaintance with common animals that is possessed by most readers of a book of this character. In the present chapter, more depends upon what the student may be presumed to have seen in the laboratory, but he must also utilize such general information as he may have concerning the structure of the human body and that of familiar animals. As has been explained in the introductory chapter, the various fields of biological science are closely inter-related. This is particularly true of Morphology and Physiology. The study of structure may interest us, because of the intricacies or the beauties of form that it reveals; yet structure never can become meaningful unless we possess some knowledge of the way in which the parts work. The morphology of an automobile is interesting, but the parts have meaning only in relation to their manner of action. For this reason, the present chapter, which deals primarily with structure, will in many places explain functions as well. Likewise, in Chapters 4 and 5, which deal with functions, we shall find it necessary to explain structure in some detail. All these chapters are intended to serve as a review and extension of the knowledge concerning the functional organization of the vertebrate body which is given in elementary textbooks of human physiology, but which experience shows has not been properly comprehended by the majority of students before entering upon the study of General Zoology.

External Features and Related Structures

Head, Body, Tail, and Appendages.—Reference has been made in the preceding chapter to the external features of familiar

vertebrates. Head, body, and tail regions are recognizable, with few exceptions. In all but the lowest subdivision of the Vertebrata, the Cyclostomata, there are two pairs of appendages, the *fins* of fishes and the *limbs* of amphibians, reptiles, birds, and mammals (Fig. 1, p. 10). A neck, distinguishable externally as a constriction between head and body, is found in certain reptiles and in birds and mammals. Modifications occur (Figs. 1, 2, 3, p. 10), but the same general organization persists throughout. Compare the head, body, and tail in a fish, salamander, lizard, turtle, snake, ostrich, sparrow, seal, elephant, horse, and man. In the snakes and in a small subdivision of the amphibians (*Apoda*, Fig. 6, p. 14), limbs are absent in the adult, although present as rudiments in the embryo. In a few vertebrates the tail is rudimentary, as in frogs and toads, the higher apes and man; or it may be greatly developed as in the kangaroo and alligator.

Modifications of the appendages are of particular interest, since these organs are so closely related to the habits of the animal. Thus, the paired fins of fishes are usually paddle-like organs but, in special cases they are modified in whole or in part for other purposes, such as crawling on the bottom (sea-robin), "gliding" in the air (flying fish), and as copulatory organs (sharks and skates). More familiar examples of modification in appendages appear in the limbs of terrestrial vertebrates. The five-toed plan of structure (Fig. 18), from which all the varied types seem to have evolved by the loss or specialization of parts, is modified to fit particular functions in appendages so diverse in their external appearance as the fore limbs of man and the elephant, the flipper of a seal, the wings of bats and birds, and the fore limbs of horses and such familiar animals. Underlying an endless variety in detail, there appears a unity in essential organization. Such modifications of an animal's body are of interest as examples of

FIG. 18.—Skeleton of typical vertebrate appendage.

f, femur; *fi*, fibula; *mt*, metatarsals; *p*, phalanges; *t*, tibia; *ta*, tarsals. (Redrawn from Wiedersheim, "Comparative Anatomy of Vertebrates," copyright, 1907, by the Macmillan Co., printed by permission.)

the adaptation to environment that is so characteristic of both animals and plants; and also as evidence for organic evolution, since anatomical resemblance is regarded as evidence of evolutionary relationship.

The Skin and its Derivatives.—The skin of vertebrates is variously modified in relation to the conditions of life. Coloration of the skin or its derivatives occurs in all save exceptional cases. The skin glands are often important. Peculiar external modifications of the skin are characteristic of the several classes (*cf.*

FIG. 19.—Transverse section of the frog in region of kidneys and reproductive organs.

ab.v., abdominal vein; *cœ*, cœlome; *d.a.*, dorsal aorta; *d.c.*, digestive cavity; *kd*, kidney; *l.s.*, subcutaneous lymph sinuses, separated by septa; *m*, muscles; *ms*, mesentery; *ov*, ovary; *p.p.*, parietal peritoneum; *p.c.*, post-caval vein; *sk*, skin; *sp.cd.*, spinal cord; *sp.cl.*, spinal column; *sv.l.s.*, subvertebral lymph sinus; *t*, testis; *vs.p.*, visceral peritoneum. The specimen is shown as a male on one side and as a female on the other.

table of classification, p. 37, and Fig. 52, p. 95). The elasmobranchs have one type of scale, the teleosts another; the cyclostomes and most Amphibia possess a slimy surface; reptiles are covered with scales peculiar to the class, birds with feathers, mammals with hair. These characteristics are so distinctive that they serve, with few exceptions, as features by which one may determine at a glance the class to which a given vertebrate belongs.

In most instances the skin is tightly fastened to the muscles so that the "skinning" of the animal necessitates a cutting or tearing of the resistant connective tissue that unites skin and flesh. In contrast to this condition, the skin of the frog is like a glove, fit-

ting the body exactly, but fastened only along certain lines of attachment, or *septa* (Fig. 19). The spaces partitioned off by these septa contain a colorless fluid, the *lymph*, and are known as *subcutaneous lymph sinuses*. They are part of a system of cavities and vessels extending throughout the body of the vertebrate animal (*cf.* Fig. 20) and draining into the circulatory system.

General Internal Organization

Flesh and Skeleton.—It is a familiar fact that beneath the skin of a vertebrate animal lies the so-called “flesh,” composed mainly of muscles, which are attached to a supporting framework, the *skeleton*. This relationship is illustrated by a transverse section of the human arm (Fig. 21). So familiar is this type of organization, as found in well-known animals, that it is

FIG. 20.—Superficial and some deeper lymphatics of the hand.

(From Hough and Sedgwick, “Human Mechanism,” copyright, 1918, by Ginn and Co., reprinted by permission.)

FIG. 21.—Transverse section of upper arm.

b.v., blood vessel; *h*, humerus; *m*, muscle; *n*, nerve; *s*, skin.

not always realized that such an internal or *endoskeleton*, with its overlying muscles, is far less common in the animal kingdom than are *exoskeletons* like the external coverings of a locust or a crayfish or the shell of a snail. As a matter of fact, only three of the great animal groups, the Chordata, the Porifera, and the Echinodermata (p. 241), possess an endoskeleton that is charac-

teristic of the group as a whole. Endoskeletons and exoskeletons alike serve as protective and supporting devices to which muscles may be attached; but here the similarity ends (Fig. 22). In the one case, the muscles are attached to the outer surface of the skeleton; in the other, to the inner surface of a tubular covering. Hence the mechanics of the two systems are alike only insofar as

FIG. 22.—Endoskeleton and exoskeleton in relation to soft parts of the body, as shown by leg of man and of the grasshopper.

(Redrawn from Pearse, "General Zoology," copyright, 1917, by Henry Holt and Co., printed by permission.)

the contraction of muscles causes movement in the parts to which they are attached. In addition to muscles, the flesh contains nerves and blood vessels and, in places, glands, the whole being bound together by the so-called connective tissue.

Mouth Cavity.—Passing to internal features, we see that the mouth region of the frog (Fig. 23) offers some interesting contrasts with the conditions occurring in man and the familiar mammals (Fig. 24). The most obvious difference is that the nostrils of the frog lead directly into the anterior end of the mouth, whereas in man they lead into an extensive nasal chamber communicating with the

mouth cavity proper at its posterior end. This latter relationship may be seen by looking into the widely opened mouth of another person, or into one's own mouth by means of a mirror. The *Eustachian tubes* (Fig. 23), which lead from the mouth cavity of the frog to the cavity of the ear just inside the eardrum, have a similar relationship in man, save that they communicate at their inner ends with the nasal cavity (Fig. 24). Again, the long axis of the frog's mouth is in line with that of the body, while in man this axis of the mouth is at right angles to the body axis; but this is not a profound difference, and intermediate conditions are found in some of the higher animals. The most important dissimilarity that needs explanation is, therefore, the existence of the nasal

FIG. 23.—Median section of the frog.

a, auricle; an, anus; bl, urinary bladder; br, brain; cl, cloaca; *E.t.*, Eustachian tube; g.b., gall bladder; int, intestine; kd, kidney; l, liver; la, larynx; lg, lung; mes, mesentery; no, nostril; ovd, oviduct; p, pancreas; pc, pericardium; sp, spleen; sp.c., spinal cord; t, testis; ur, ureter; v, ventricle.

cavity in vertebrates such as man. As is the case with many other seeming differences of anatomy between the members of the Phylum *Vertebrata*, this is understandable by reference to their development. In the early stages of a human embryo, as with the embryos of reptiles, birds, and other mammals, there is a single mouth cavity with which the nostrils are connected as in the adult frog. In subsequent development there occur ingrowths from the right and left sides of the upper jaw. These finally meet in the mid-line and divide the mouth cavity into two portions, one of which becomes the nasal cavity. The latter is thus an upper portion of the general mouth cavity of the embryo. The adult frog

may, therefore, be said to possess a mouth cavity comparable with that occurring at an early stage in the development of air-breathing vertebrates, the mouth region of these higher vertebrates being, as it were, a "two-story" affair derived in the manner indicated.

Another point of difference is the attachment of the *tongue*, which extends backward and not forward into the mouth of the

FIG. 24.—Median section of human head for comparison with that of frog.

e, epiglottis; *es*, esophagus; *E.t.*, Eustachian tube; *f.s.*, frontal sinus; *gl.*, glottis; *h.p.*, hard palate; *n.*, nostril; *n.c.*, nasal cavity; *s.p.*, soft palate; *sp.cl.*, spinal column; *sp.s.*, sphenoidal sinus; *t*, tongue; *tb.*, turbinal; *tr.*, trachea; *v.c.*, vocal cords.

frog, in contrast with the condition existing in most of the familiar vertebrate animals. This difference, however, is easily explained. The tongue is a thickened portion of the floor of the mouth. In most cases where it is well developed, it grows out anteriorly, but in a few instances, including the frogs and toads, it extends posteriorly. Correlated with the posterior growth in these animals is their habit of suddenly "flopping" the tongue outward in the

capture of food, as described in the previous chapter, in contrast with the "running" out of the tongue by a snake and its "licking" action in the mammals.

An exact comparison can, therefore, be made between the mouth and related parts in frog and man if one understands the mode of development of the human embryo. When the mouth cavity of a frog is compared with that of a fish, the nostrils of the fish (Fig. 25) are seen to open into blind pits, which are not connected by internal nostrils with the mouth. There is, of course, no glottis, or opening from mouth to larynx, since the fish has no lungs; but the higher fishes possess a structure called the air bladder

FIG. 25.—Gill region and air bladder of fish.

a. b., air bladder; *g*, gill slits; *op*, outline of operculum; *st*, stomach.

which is probably homologous with the lungs of air-breathing vertebrates and becomes an actual lung in lung fishes (Fig. 26). Again, the Eustachian tubes found in air-breathing vertebrates are seemingly absent in fishes. In this region the fish exhibits a series of clefts, the *gill slits*, lying between what are called *gill bars*, or skeletal rods that bear the *gills*; through these clefts the water taken in by the mouth passes to the outside. Each one of the gill slits is a lateral opening from the mouth cavity in the region between head and neck. In the familiar bony fishes the external gill openings are covered by a flap-like *operculum* (Fig. 1 *C*, p. 10). In simpler fishes, like the sharks, the gill slits are visible externally (Fig. 1 *D*, p. 10).

At first glance these gill clefts of the fish appear to have no relationship to the Eustachian tubes of other vertebrates, save that

both are openings from the back of the mouth cavity. When, however, the development of the mouth region in a frog or other air-breathing vertebrate is examined, an explanation of this seeming diversity of structure in frogs and fishes is discovered. In the early stages of its development, the frog possesses gills and gill slits exactly comparable with those of a fish (Fig. 25). When the tadpole changes into the miniature frog, the gills disappear, and the gill slits, with a single exception, become closed, while the bony gill bars degenerate or become incorporated into portions of the skeleton in this region. The most anterior slit, however, remains as an opening extending laterally from the back of the mouth, and later becomes closed externally by a membrane, the

FIG. 26.—Lung fish, *Protopterus annectens*. About one-half natural size.

(After Dean, from Parker and Haswell, "Textbook of Zoology," copyright, 1921, by Macmillan and Co., Ltd., reprinted by permission.)

drum of the ear. Thus, in the development of every individual frog, the Eustachian tubes arise by the "making over" of a pair of the gill slits possessed by the embryo. The most anterior pair of gill slits of a fish and the Eustachian tubes of a frog are, therefore, homologous, that is, they are structurally similar. A like mode of development occurs in all the higher vertebrates. In the human embryo there is no swimming stage like the tadpole; but early in the development (Fig. 287, p. 531) there are vestigial gill slits, which later disappear or are made over into other structures, notably the Eustachian tubes. The latter are survivals of the anterior pair of gill slits in man as in the frog.

The mouth and related structures are thus seen to be built on the same anatomical plan in all vertebrate animals. The differences are explained when one understands the modifications in development, whereby parts have been lost or so changed that

their identity can only be recognized by a thorough study of Comparative Anatomy and Embryology.

The Cœlome and Viscera. — When the ventral body wall of the frog is opened, there is disclosed a spacious cavity, the *cœlome*, containing the digestive organs, heart, lungs, and other viscera (Figs. 23 and 27). The digestive tract enters the anterior end of the cavity as the *esophagus*, leading directly into the *stomach*, which is followed by the *small intestine*, the *large intestine*, and the *cloaca*. The *liver* is connected with the beginning of the small intestine by the *bile duct*. The *pancreas*, which secretes the pancreatic juice used in digestion, lies around the bile duct into which open the *pancreatic ducts*. The kidneys and their ducts, the *ureters*, lie on the dorsal side of the cœlomic cavity, separated from the body wall by an extensive lymph space, the *subvertebral lymph sinus* (Fig. 19). The reproductive organs, *ovaries* or *testes*, are attached to the ventral face of either kidney. Attached to the body wall at the anterior ends of the kidneys are masses of finger-shaped structures known as the *fat-bodies* which have the function of storing a reserve of nutrient material. They have no known functional relation to the urino-genital system. Along the ventral face of each kidney are elongated strips of tissue, the *adrenal bodies*, which have the function of producing a chemical substance, *adrenalin*, that passes into the blood. Like the fat-bodies, the adrenals have no known

FIG. 27.—Viscera of frog from ventral view.

ab.v., abdominal vein; *b.m.-c.*, brachial musculo-cutaneous vein; *b.w.*, body wall; *bl.*, urinary bladder; *c.a.*, carotid artery; *e.j.*, external jugular vein; *in.*, internal jugular vein; *int.*, small intestine; *l.a.*, left auricle; *l.i.*, large intestine; *l.p.-c.*, left pre-caval vein; *lg.*, lung; *lv.*, liver; *mh.*, mylohyoid muscle; *p.-c.a.*, pulmo-cutaneous artery; *pc.*, pericardium; *r.a.*, right auricle; *s.a.*, systemic artery; *sp.*, spleen; *st.*, stomach; *t.*, testis; *t.a.*, truncus arteriosus; *th.*, thyroid gland; *tm.*, thymus gland; *v.*, ventricle. (Redrawn with modifications from Howes, "Atlas of Zootomy," copyright, 1902, by Macmillan and Co., Ltd., printed by permission.

functional relation to the kidneys. The *heart* lies in its sac-like *pericardium* in the anterior ventral region of the coelome. The *spleen*, an organ whose function is not entirely certain, lies within the membrane, or *mesentery*, that holds the digestive tract in position, but has no special connection with the tract, as have the liver, pancreas, and urinary bladder. The *lungs*, which lie right and left in the dorso-lateral region, project into the coelome. Their connection with the digestive tract is through the *glottis* at the posterior end of the mouth.

For the complete understanding of these organs, comparisons should be made between the lateral view (Fig. 23) and a diagrammatic transverse section (Fig. 19), together with the ventral view as seen by dissection (Fig. 27). In the schematic section through the region of the kidney and reproductive organs the liver is omitted, and instead of showing the digestive tract cut in several places and at irregular angles, a single transverse section is indicated. With these ventral, lateral, and transverse views in mind, one can understand the nature of the *peritoneum*, which is the shiny membrane covering all the organs of the coelome and lining the coelomic walls as wall paper lines a room. The *mesenteries*, which are also a part of the peritoneum, and which have the function of holding the digestive tract and other organs in position, appear as delicate sheets of tissue containing nerves and blood vessels. The relationships of the peritoneum in these various regions can be understood by reference to the transverse section, where the peritoneum is seen on edge and, therefore, appears as a line. If its course is followed in such a section, the *parietal peritoneum*, which lines the coelomic cavity, is continued dorsally across the ventral faces of the kidneys, save where it passes ventrally as a two-layered membrane, the mesentery of the testis or the ovary. At the mid-dorsal region these right and left layers of parietal peritoneum unite to form the mesentery, which is thus composed of two layers of peritoneum and supports the digestive tract. Upon reaching the digestive tract, the ovary, or the testis, the layers of the mesentery separate and extend around these organs as the *visceral peritoneum*. Hence, if one begins on the ventral body wall and traces the line of the peritoneum right or left, the line is continuous, since the peritoneum is *an unbroken membrane, lining the coelome, passing ventrally as the mesenteries, and covering each of the coelomic organs*. The mesen-

teries assume greater complexities, through fusions and obliterations, as the coiling of the digestive tract becomes more extensive. An example of the disappearance of the greater part of a mesentery is seen in the stomach region of the adult frog. The simple relationship described is that which occurs in the early stages of development and persists to some extent in the adult.

When the cœlomic region of the frog is compared with the corresponding portion of the human body (Fig. 28), the most obvious difference is the presence in man of the *diaphragm* separating the region of lungs and heart from that of the abdominal viscera. The diaphragm is peculiar to mammals among the vertebrates, as the reader may have observed by noting its absence in the domestic fowl, the fish, and any reptile that he may have examined. The other anatomical features of the frog's body that appear in this connection have been sufficiently explained.

The Vertebrate Plan-of-body.—

What is found in the body of a frog is illustrative of what exists in other vertebrate animals. It is possible to construct a generalized diagram that does not represent any one vertebrate exactly but shows the essential relationships

in all vertebrates (Fig. 29). As a subdivision of the Phylum *Chordata* (p. 36), the vertebrates possess, at some stage in development, a dorsal, tubular, central nervous system; a notochord; or primitive axial skeleton, and gill slits. As vertebrates, they possess a skull, a segmented vertebral column, and two pairs of appendages. They are quite unlike such a group as the *Arthropoda*, to which the insects and crayfish belong (Fig. 117, p. 240), and in which the greater portion of the central nervous system is ventral, the cœlome is rudimentary, the heart dorsal, the skeleton external, the appen-

FIG. 28.—Thoracic and abdominal viscera of man from ventral view.

di, diaphragm; h, heart; in, small intestine; l, liver; lg, lung; st, stomach. (Redrawn from Hough and Sedgwick, "Human Mechanism," copyright, 1918, by Ginn and Co., printed by permission.)

dages numerous, and the organization wholly different, save for the segmentation, the elongation of the body, the bilateral symmetry, and other very general features that arthropods and vertebrates possess in common.

FIG. 29.—Diagrammatic longitudinal section of a vertebrate, with female reproductive organs.

b.d., bile duct; *br*, brain; *cl*, cloaca; *coe*, coelome; *g.s.*, gill slits; *g.d.*, genital duct; *h*, heart; *l*, liver; *lg*, lung; *m-n*, mesonephros; *n.t.*, neural canal; *no*, notochord; *p*, pancreas; *pc*, pericardium; *p-n*, pronephros; *r.g.*, reproductive gland; *s*, spleen; *s.c.*, spinal cord; *u.bl.*, urinary bladder; *u.d.*, urinary duct. (Redrawn from Wiedersheim, "Comparative Anatomy of Vertebrates," copyright, 1907, by the Macmillan Co., printed by permission.)

The Structural and Functional Systems of Vertebrate Animals

Organs and Systems.—In the terminology of Anatomy, the body of an animal is composed of parts known as "organs," which are grouped into "systems" according to their functional relationships. Thus, one speaks of the *muscular system*, composed of muscles, each of which can be regarded as an *organ*, although one more commonly thinks of "organs" as parts like the eye, the stomach, or the heart. Again, there is the *nervous system*, comprising the brain, spinal cord, and nerves, with the associated sense-organs; the *digestive system*, composed of the digestive tract and its appended glands, the liver and the pancreas; the *skeletal, circulatory, respiratory, excretory*, and *reproductive systems*, with their respective organs. Other systems might be included, but the foregoing are the more familiar ones. The principal features of these various systems may now be considered insofar as knowledge of their structure is necessary for the discussion of functions given in subsequent chapters. Since we are considering, in the present chapter, the organization of the body from the standpoint of func-

tion as well as structure, some account of the manner of action will be included.

The Digestive System. — The features of the digestive system that are important for the present purpose may be indicated by a brief elaboration of what has been said under the head of *Cœlome and Viscera* (p. 47). The digestive "tract" is a tube leading from mouth to anus and extending through the cœlome, within which it is coiled about and differentiated into the *esophagus*, *stomach*, *small intestine*, *large intestine*, and *cloaca*. In a schematic representation, as shown by Fig. 23, the tract may be drawn running straight through the cœlome or with a minimum of folding, as it actually does in the simplest vertebrates (*Cyclostomata*; Fig. 1 E, p. 10) and in the embryonic stages of more complex forms like the frog and man. Attached to the tract by ducts, and originating as outgrowths during its development (*cf.* Fig. 217, p. 413), are the *liver* and the *pancreas*, which are digestive glands. The connections which these organs have with the digestive cavity, by means of their ducts, are survivals of their origin as outgrowths from the gut cavity of the embryo. Their linings are modified portions of the embryonic digestive canal. Externally, they are covered with peritoneum like all the other organs within the cœlome.

The mesenteries of the digestive tract have been described in connection with the peritoneum. They perform the two-fold function of holding the parts in position and serving as a bridge by which nerves and blood vessels pass between the digestive canal and the body wall (Fig. 19, p. 40). The finer structure of the intestinal and stomach walls will be considered in connection with the processes of nutrition and the microscopic organization of the body, which will be discussed in later chapters.

The Urino-genital System. — In vertebrate animals, the *kidneys* and their ducts, the *ureters*, are so intimately related to the *reproductive organs* that it is customary to speak of these two sets of organs as the urino-genital system. While this is justifiable on anatomical grounds, it is obvious that such a system includes organs of widely different functions. The kidneys might be classed, along with the skin and lungs, as belonging to an *excretory system* composed of organs located in different parts of the body, and not connected as are the parts of other systems with which we are familiar. The reproductive organs would then be taken as the *reproductive system*.

In its ventral aspect, as seen from dissection (Fig. 30), the urino-genital system consists of the paired *kidneys* and their ducts, the *ureters*; the *ovaries* in the female, and the *testes* in the male, with their respective connections to the outside; and certain accessory parts like the *urinary bladder*. The kidneys are flattened organs lying dorsally but separated from the

FIG. 30.—Urino-genital organs of frog from ventral view, showing ovary and oviduct to left as in female, and testis and rudimentary oviduct to right as in male.

an, anus; *cl*, cloaca; *f.od.*, funnel of oviduct; *k*, kidney; *m.t.*, mesentery of testis; *od*, oviduct; *ov*, ovary; *p-c.v.*, post-caval vein; *r.od.*, rudimentary oviduct; *r.v.*, renal vein; *s.od.*, ovisac; *te*, testis; *u.bl.*, urinary bladder; *ur*, ureter.

dorsal body wall by the *sub-vertebral lymph sinus* (Fig. 19, p. 40), and having their ventral surfaces covered with peritoneum after the manner shown. The *ureters*, which convey the urine from the kidneys, leave the outer edge of either kidney and enter the dorsal surface of the *cloaca*. The *urinary bladder* is a bi-lobed sac connected with the ventral surface of the cloaca opposite the openings of the ureters. The urine, which flows from the ureters into the cloaca, enters the bladder as the only place available, because the large intestine is closed or filled with faeces and the anus is never open except when the faeces or urine is being extruded. From the bladder the urine is periodically discharged by way of the anus. These conditions in the frog are simpler than those found in mammals, where the

ureters lead directly to the bladder and the latter discharges by a separate opening instead of by the anus.

Microscopically, the kidneys of any vertebrate animal are composed of numerous *tubules* (Fig. 31 B), each of which begins blindly as an enlarged cup-like portion, known as *Bowman's capsule* and containing a coil of small arteries, the *glomerulus*. These tubules wind about somewhat irregularly, but each one empties

at its outer end into the *ureter*. In the frog, the arrangement of arteries and veins in the kidneys is such that blood from the hind limbs enters by the two *renal portal veins* (Fig. 31 A), and leaves by several renal veins which unite to form the single *post-caval vein*, lying medially between the kidneys. Blood also enters the kidneys from a number of small *renal arteries* which are given off by the *dorsal aorta* or principal artery in this region of the body. Fig. 31 B shows how the blood from

FIG. 31.—Blood vessels and circulation of kidney.

A, kidney and its principal blood vessels. B, schematic representation of circulation through capillaries of kidney. *c.k.*, capillary of kidney; *d.a.*, dorsal aorta; *g*, glomerulus; *i.a.*, iliac artery; *k*, kidney; *p.c.*, post-caval vein; *r.a.*, renal artery; *r.p.v.*, renal portal vein; *r.v.*, renal vein; *u*, ureter; *u.t.*, urinary tubule.

the renal portal veins and the renal arteries passes through the kidneys in relation to the kidney tubules. The branches of the renal portals break up into *capillaries*, which are the smallest divisions of the blood vessels, and these form a network about the tubules before uniting in the renal veins which pass to the post-caval vein. The branches of the renal arteries form the coil of minute arteries called the *glomerulus* before they join the more general capillary system. The course of the blood through the microscopic vessels of the kidneys is shown by the arrows in Fig. 31 B. As seen in sections under the microscope, the kidney shows

only tubules and blood vessels cut at various angles. The function of the kidneys is to remove certain waste materials, or *excretions*, brought to them by the blood from all parts of the body.

The **male reproductive organs** of the frog consist of a pair of *testes* which are suspended from the ventral face of either kidney by mesenteries (Fig. 30). Within these testes, the male germ cells, or *spermatozoa* (Fig. 212, p. 402), are produced. Small ducts, the *vasa efferentia*, lead through the mesenteries of the testes to connect with the kidney tubules. In this manner the spermatozoa pass through the kidney tubules and ureters to the cloaca. In some species of frogs there are pocket-like outgrowths of the ureters, forming *seminal vesicles* in which spermatozoa are stored in advance of the breeding season.¹ At the time of sexual union, the spermatozoa are passed from the anus and fertilize the eggs just after the latter leave the female. Lying along the body wall, lateral to the kidneys, and extending posteriorly beside the ureters to the cloaca, are the rudimentary *oviducts* of the male, which are structurally comparable with the functional oviducts of the female. In the leopard frog they persist as conspicuous organs even in the adult male, but in many other species they are recognizable in such proportions only during an earlier stage of development. As rudimentary structures, they may be compared with the mammary glands of a male mammal, since they have a known use in only one sex.

The **female reproductive organs** (Fig. 30) consist of the *ovaries*, which produce the female germ cells, the eggs or *ova*; and the *oviducts*, by which these ova are conveyed to the cloaca. Each ovary is a many-lobed mass, so much larger than a testis that it seems upon superficial examination to be wholly different in its relationship to neighboring parts. When, however, one examines the actual relationship, or better a younger stage in which the ovary is small, it is seen that the ovaries, like the testes, are attached to the ventral face of either kidney by mesenteries. There are, of course, no ducts through the mesenteries to the kidneys comparable with the *vasa efferentia* of the male, since the female system has its oviducts; but in other respects the ovaries and testes are similarly related to the other organs of the urino-genital system. The

¹ In the bullfrog, *Rana catesbiana*, and the leopard frog, *R. pipiens*, the seminal vesicles are inconspicuous. In the European form, *R. fusca*, they are well developed.

mesenteries of the ovaries are necessarily more extensive than those of the testes, since they must support much larger organs and also carry the many blood vessels that are necessary in providing the blood supply for the growing ova. The oviducts are a pair of much-coiled tubes communicating anteriorly with the coelome by funnel-shaped openings, and posteriorly with the cloaca, as indicated in the figure. The eggs leave the ovary by a rupture of its surface and are thus, for a brief period, free within the coelomic cavity. The action of microscopic structures known as *cilia* (Fig. 77 F, p. 141), aided perhaps by contractions of the body wall, convey the ova to the anterior openings of the oviducts. As they pass slowly along the oviducts, a fluid, which swells into the jelly surrounding the eggs after they have reached the water, is secreted about each individual ovum. It is believed that before the actual laying can be accomplished all the eggs must have reached the thin-walled sacs at the posterior ends of the oviducts, which thus become greatly distended. During sexual union, the ova pass from these *ovisacs* to the cloaca and out by the anal opening, where they meet the spermatozoa that are being emitted from the anus of the male. The union of one ovum with one spermatozoön constitutes *fertilization*. After the eggs have thus reached the water in which they are laid and have been fertilized, the fluid secreted by the oviducts becomes swollen to its final dimensions and forms the jelly that surrounds the eggs and embryos in the early stages of development. (Fig. 11, p. 23.)

In Fig. 30 the female organs are represented on the left and those of the male on the right, a condition which, of course, does not occur normally in the animal, since the sexes of frogs are separate. Such a figure, however, shows by direct comparison the resemblance between the male and female organization. The ovaries are larger than the testes and of different structure, since they produce ova and not spermatozoa. The ova reach the outside by special ducts and not through the kidney tubules and ureters. Since the functional oviducts of the female are represented by non-functional, rudimentary oviducts in the male, it appears that, aside from the differences between ovaries and testes, the only structures in the male frog that are not present in the female are the vasa efferentia, conveying the spermatozoa from testes to kidneys, and the seminal vesicles which are present, in some species, on the ureters of the male.

The Circulatory System. — Any well-developed circulatory system, like that of the frog, includes a “pump,” the *heart*, by which blood is forced through *arteries* to all parts of the body. The blood passes from these arteries to the *capillaries*, which are the smallest of all the blood vessels, and is thence returned to the heart through *veins*. The heart of a frog (Fig. 32) consists of two thin-walled *auricles* that function as “charging” chambers for the single *ventricle* which, by the contraction of its

FIG. 32.—Heart of frog with principal outgoing blood vessels, from ventral view and with part of ventricle removed.

au-v.v., auricular-ventricular valve; *c.a.*, carotid artery; *l.a.*, left auricle; *p-c.a.*, pulmonary artery; *s.a.*, systemic artery; *r.a.*, right auricle; *t.a.*, truncus arteriosus; *v*, valve of truncus arteriosus; *ve*, ventricle.

thick muscular wall, drives the blood into the arteries and thus around the circuit. The arteries may be traced outward from the ventricle to all parts of the body (Fig. 33). The veins (Fig. 34) parallel the arteries although they do not branch in a manner that exactly follows the divisions of the latter. The connection of arteries and veins by means of capillaries, which is essentially the same in all parts of the body, may be represented diagrammatically as in Fig. 60, p. 104. Circulation in the frog consists in the passage of the blood around such a circuit of heart, arteries, capillaries, and veins, complicated by the addition of the lesser circuit through the lungs.

The chief peculiarity of the frog's circulation consists in the three-chambered condition of the heart, whereby the unoxxygenated blood from the body and the oxygenated blood from the lungs pass through a single ventricle. In a four-chambered heart they are kept separate in the right and left ventricles respectively and never mixed. The manner in which a partial separation of the blood from body and lungs may be brought about in the frog appears when the structure and manner of action of the heart is examined. The structure of the frog's heart and its principal outgoing blood vessel is shown in Figs. 32 and 33. The two *auricles*

FIG. 33.—Arterial system of the frog, from lateral view.

1, common carotid artery; 2, systemic artery; 3, pulmo-cutaneous artery; *c.a.*, cutaneous artery; *c.g.*, carotid gland; *c.m.*, coeliac-mesenteric artery; *d.a.*, dorsal aorta; *ex.c.*, external carotid; *i.a.*, iliac artery; *i.c.*, internal carotid; *int*, branches to intestine; *kd*, kidney; *l*, hepatic veins from liver; *l.a.*, lingual artery; *la*, left auricle; *lg*, lung; *l.i.*, large intestine; *lpc*, left precaval vein; *l.s.a.*, left systemic artery; *pcv*, post-caval vein; *r.a.*, renal artery; *ra*, right auricle; *t.a.*, truncus arteriosus; *sc.a.*, subclavian artery.

FIG. 34.—Venous system of the frog, from lateral view.

ab.v., abdominal vein; *br.v.*, brachial vein; *d.l.*, dorso-lumbar vein; *f.v.*, femoral vein; *h-p.v.*, hepatic portal vein; *i.j.*, internal jugular vein; *in.v.*, innominate vein; *int*, branches to intestine; *kd*, kidney; *la*, left auricle; *lg*, lung; *l.i.*, large intestine; *liv*, liver; *lpc*, left precaval vein; *l.p.v.*, left pelvic vein; *l.v.*, lingual vein; *m-c.v.*, musculo-cutaneous vein; *p-c.v.*, post-caval vein; *p.v.*, pulmonary vein; *ra*, right auricle; *r.p.*, renal portal vein; *r.p.v.*, right pelvic vein; *r.v.*, renal vein; *s.sc.*, subscapular vein; *s.v.*, sinus venosus; *st*, stomach; *t.a.*, truncus arteriosus; *v*, ventricle.

lie dorsal and anterior to the single *ventricle* and open by a common aperture provided with valves. The ventricle connects with an outgoing vessel, the *truncus arteriosus*, the opening to which is again protected by valves leading in one direction. The truncus arteriosus divides, right and left, into three large arteries, the *carotid*, *systemic*, and *pulmo-cutaneous arteries*, passing to the head, to the body, and to the lungs and skin, respectively. Within the truncus is another valve, guarding the openings of the *systemics* and *carotids*. This does not appear in the figure. If one watches the contractions of the heart in a freshly killed frog, it is seen that the two auricles contract simultaneously, then the ventricle, and lastly the truncus. By gently lifting the ventricle it will be seen that the *sinus venosus*, which connects with the right auricle and contains blood returned from all parts of the body save the lungs, also contracts an instant before each contraction of the two auricles. The "contraction" of the heart in the frog is, therefore, a series of contractions, including not only the auricles and ventricle, but also the sinus venosus and the truncus arteriosus. Appropriate valves guard the several openings, and a periodic repetition of the contractions results in circulation.

From the structural and functional relationships, it would appear that the separation of oxygenated and unoxygenated blood can be effected in the following manner. When the two auricles contract they force their contents simultaneously into the single ventricle. The left auricle contains oxygenated blood from the lungs, and the right auricle contains unoxygenated blood from the body. By referring to Fig. 32, it will be seen that, roughly speaking, the side of the ventricle on the observer's left is now occupied by unoxygenated blood, and the side on his right by oxygenated blood. If the two remained for even a brief time in the ventricle, complete mixing would occur. But the ventricle contracts at once; and, since the opening to the truncus is located on the side containing the unoxygenated blood, it is this blood that leaves the ventricle first of all. Blood from the middle region follows, and, last of all, the blood from the side of the heart on the observer's right enters the truncus. The mechanism of the valves within the truncus and the conditions of pressure are such that the unoxygenated blood that enters first flows at once into the two pulmo-cutaneous arteries and thence reaches the lungs and skin. Blood delivered to the truncus from the middle region

of the ventricle, where a certain amount of mixing has occurred, in general enters the systemics, or the second pair of arterial vessels, and passes to all parts of the body save the head. The oxygenated blood from lungs and left auricle, which was emptied into the side of the ventricle on the observer's right is the last to enter the truncus, and passes into the carotids, or anterior pair of arterial trunks, to be distributed to the brain and spinal cord. Hence, by the arrangement of the parts and the timing of their contractions, the oxygenated and the unoxygenated portions of the blood, after being together for an instant in the ventricle and truncus, are actually distributed to suitable parts of the body with a minimum of mixture. The mechanism is less effective than that of the four-chambered device in birds and mammals. Nevertheless, the heart of the frog is the more remarkable, because a separation of oxygenated and unoxygenated blood is fairly well accomplished, under conditions that make this result seem impossible when the structural relationships are first examined.

Another factor of the frog's circulation is the existence of what are called the *portal systems*. Blood passing from the capillaries of the digestive tract goes by the *hepatic portal vein* (Fig. 34), to the liver, where it is again distributed through capillaries, which combine to form the *hepatic veins* leading from this organ. Similarly, in the *renal portal system* of a vertebrate like the frog, blood that has passed through capillaries in the hind limbs passes to the kidneys by the *renal portal veins* (Fig. 34). These break up into the capillaries of the kidneys, which in turn form the *renal veins* leading from the kidney to the *post-caval vein*.

We may consider briefly the circulatory systems of other classes of vertebrates for comparison with that of the frog and other Amphibia. In the fishes (Fig. 35), where there are no lungs, the gills with their capillaries are merely inserted at one place in the general circuit, so that, diagrammatically, the blood may be shown passing from the heart to the gills where oxygenation occurs, and thence to all parts of the body, returning through the veins to repeat the process. The heart of the fish is two-chambered, consisting of a single auricle, which is thin-walled since it serves only to "charge" the ventricle, and a ventricle, which is heavy-walled since its contraction must force the blood through the entire system. The only further complexity is the presence of an additional set of capillaries where the blood flowing from the digestive

tract passes through the liver, and the connections, as shown, through the kidneys and the posterior extremities. In such a system there is no such problem of the separation of oxygenated from unoxygenated blood as appears in the frog.

FIG. 35.—Schematic representation of circulation in a vertebrate having a two-chambered heart as in fishes.

a, auricle; *d.t.*, digestive tract; *kd*, kidney; *l*, liver; *s.v.*, sinus venosus; *v*, ventricle.

The circulatory systems of birds and mammals (Fig. 36) have four-chambered hearts, consisting of two auricles and two ventricles, and two entirely distinct circuits, one through the body and another through the lungs. The blood is forced by

FIG. 36.—Schematic representation of circulation in a vertebrate having a four-chambered heart as in mammals.

d.t., digestive tract; *f.b.*, fore body; *h.b.*, hind body; *kd*, kidney; *l*, liver; *l.a.*, left auricle; *ls*, lungs; *l.v.*, left ventricle; *r.a.*, right auricle; *r.v.*, right ventricle.

the left ventricle into the general arterial system and so to the capillaries in all parts of the body. Returning by the veins, it goes to the right auricle and thence to the right ventricle, which forces it through the lesser circuit of the lungs, whence it is returned

to the left auricle, and is again delivered to the left ventricle. The separation of oxygenated and unoxygenated blood is thus complete, since the two circuits are distinct and there is no mingling in a common ventricle. A blood corpuscle, for example, may pass to one part of the body or to another, but it cannot make its "next trip" to any region without first making the circuit of the lungs. Hence, every drop of blood passes once through the lungs and once through some other part of the body in completing its circulation.

Reference has been made to the *lymph spaces* that lie beneath the skin of the frog and to the large *lymph sinus* that lies dorsal to the kidneys (Fig. 19). These are part of an extensive system of irregular vessels and spaces extending throughout the body and are filled with a colorless fluid, the *lymph*, which is essentially the same as blood minus the red blood cells, or corpuscles, that give the blood its color. In the frog, the lymph is pumped into the blood by four *lymph hearts* (Fig. 50, p. 90) which are connected with lymph spaces and empty into four of the principal veins. The lymph originates largely by diffusion from the blood capillaries in all parts of the body and thus circulates as lymph in its own vessels and also as part of the fluid portion of the blood. In man, the lymph vessels, or *lymphatics*, consist principally of vessels rather than spaces, so that a part of the body, such as the hand, has lymph vessels so extensive that they resemble a second set of veins (Fig. 20, p. 41). These communicate with the blood vessels by two large lymphatic trunks which empty, by a larger connection on the left and a smaller on the right side, into the great veins of the neck. There are no structures in man comparable with the lymph hearts of the frog, and no such lymph sinuses beneath the skin.

The circulatory system, therefore, consists of a series of vessels through which the blood is caused to circulate by the action of a specially modified area, the heart. In the course of its circulation, the blood is distributed to all parts of the body, including organs like the lungs, kidneys, and digestive tract, where it gives off and takes up the substances that it carries to and from the various regions (cf. Fig. 50, p. 90). Consideration of the blood as a "common carrier" presents many interesting problems, some of which will be examined in the next chapter; but these do not properly belong with the present discussion, which is principally concerned with the structure of the circulatory system.

The Respiratory System.—By respiratory organs one commonly means such parts of an animal as the *lungs* or *gills*, where oxygen enters the blood, although the essential fact of respiration is the utilization in all parts of the body of the oxygen carried from the respiratory organs by the blood. A frog can live for some months after its lungs have been removed, if it is not kept at too high a temperature. The skin of this animal is, in fact, a part of its respiratory system, although we shall consider only the lungs in this connection. The lungs of the frog consist of two simple sacs connected with the mouth cavity by means of the *larynx* and the *glottis*. Unlike the lungs of man and other warm-blooded animals, they are not subdivided into many complex outpocketings, the *alveoli*, but exhibit simpler foldings of their inner surfaces.

The mechanism which causes the air to pass in and out of the lungs differs in man and the frog, because of the absence of a diaphragm in the latter animal. In man, the mechanics of the process would resemble the sucking of air in and out of a pipette, if the single rubber bulb of the pipette were lined with another more delicate bulb, fused with the outer bulb at its neck and lying close against it in every expansion and contraction. In such a comparison the outer bulb would then represent the body wall of the chest; the inner bulb, the lungs; and the glass tube of the pipette, the trachea leading to the mouth. Expanding the cavity of the outer bulb draws air into the cavity of the inner bulb; contracting the outer bulb forces this air outward. There is never any space between the two bulbs. In like manner an expansion of the chest cavity, whether by elevation of the ribs or by a downward movement of the diaphragm, draws air into the lungs, while contraction of the chest forces the air outward.

In the frog, the mechanism is wholly different. If one watches the respiratory movements of the living animal, it will be observed that the nostrils open and close in relation to a rhythmic beating of the floor of the mouth, and that each beat of the mouth corresponds to a slight movement of the walls of the body. While not observable externally, it can also be shown that the glottis opens and closes in relation to these other movements. When observed for a brief period, the walls of the body are seen to swell by almost imperceptible stages and then suddenly to collapse, at which time a considerable amount of air is discharged from the opened nostrils.

When the respiratory mechanism is examined as it appears in a longitudinal section (Fig. 23), the mouth cavity is seen to connect with the outside by means of the nostrils, which can be opened and closed by valve-like action. The glottis is capable of a similar opening and closing in relation to the incoming and outgoing air. The jaws are always pressed close together except during the taking of food, and the same is true of the walls of the esophagus. Hence, for purposes of breathing, the mouth is a closed cavity opening only by nostrils and glottis. If the reader will now compare the mouth of the frog with a pump guarded at its outer end by a valve, comparable with the nostrils, and the lungs with a tire guarded by its valve, the glottis, he can, by a proper manipulation of such a mechanism, imitate the "pumping up" and sudden "emptying" by which the air enters and leaves the lungs in this animal.

A further structural difference between the frog and the more familiar birds and mammals is the absence of a windpipe or *trachea*. The glottis of the frog obviously corresponds to the glottis of man (*cf.* Figs. 23 and 24). The cavity containing the vocal cords would naturally be called the *larynx* in the two cases.

If we now compare the respiratory organs of the frog with the structures found in vertebrates below the Amphibia, the fact that fishes breathe by means of gills renders impossible an exact comparison of the adult stages in such water-breathing and air-breathing types. However, the fishes possess a structure called the *air bladder* (Fig. 25), which lies dorsal to the esophagus and ventral to the backbone in the familiar bony fishes (*Teleostomi*), and which is probably homologous with the lungs of air-breathing vertebrates. In such fishes the air bladder has a hydrostatic function; but in one small group, the *Dipnoi*, or lung fishes (Fig. 26), it has actually become a lung and functions in respiration.

The Nervous System. — When considered in its anatomical aspects, the nervous system of a vertebrate animal may be divided into two parts: the *central nervous system*, including the *brain* and *spinal cord* (Fig. 37); and the *peripheral nervous system*, consisting of the *nerves* by which the central system is connected, on the one hand, with the *sense organs* and, on the other, with the *muscles* and *glands*. From its functional aspect this division is less important, because the system works *as a whole*, and because its

functional units are arranged in such a manner that the anatomical

FIG. 37.—Nervous system of frog from ventral view, after Ecker.

b.n., brachial nerve; *br*, brain; *e*, eye; *f.t.*, filum terminale; *na*, nasal sac; *r.c.*, ramus communicans; *s.c.*, spinal cord; *s.g.*, sympathetic ganglion; *s.n.*, 1–10, spinal nerves; *sym*, sympathetic trunk; *va*, vagus nerve. (Redrawn from Wiedersheim, "Comparative Anatomy of Vertebrates," copyright, 1907, by The Macmillan Co., printed by permission.)

divisions, as here indicated, have only a superficial significance. Indeed, the sense-organs, which receive the external stimuli, and the nervous system, which transmits the impulses from these sense-organs to the muscles that are thus called into action, are all so intimately related that they may even be regarded as a single system carrying out the combined sensory-neuro-muscular functions of the body. Or better, the term *sensory-neuro-muscular* may be used for the sense-organs that receive the stimuli, the nervous system that transmits and adjusts impulses, and the muscles that effect the forms of bodily activity controlled by the nervous mechanism. In like manner one may speak of the *sensory-neuro-glandular* system.

The nervous system of the frog is a good example of what exists among vertebrates in

general, since its organization is intermediate between the simpler conditions found in the fishes and the more specialized relationships existing in reptiles, birds, and mammals. As seen by dissection from its dorsal aspect, the brain of the frog (Fig. 38 A) is composed of five main parts. The anterior portion of the brain consists of the paired cerebral hemispheres, or *cerebrum*, from which the *olfactory lobes* are incompletely separated. Posterior to the cerebrum is a narrowed area, the *diencephalon*, from the dorsal surface of which there arises a rudimentary structure, the *pineal body*, which is of interest because it is developed

FIG. 38.—Brain of the frog.

A, dorsal. *B*, in horizontal section to show internal cavities or ventricles. *C*, ventral. *cbl*, cerebellum; *cbm*, cerebrum; *ch.p.*, posterior choroid plexus; *di*, diencephalon; *inf*, infundibulum; *l.v.*, lateral ventricle; *md*, medulla oblongata; *o.c.*, optic chiasma; *ol.l.*, olfactory lobe; *ol.n.*, olfactory nerve; *op.l.*, optic lobe; *op.v.*, optic ventricle; *pin*, pineal gland; *pit*, pituitary gland; *s.c.*, spinal cord; *s.n.1*, 1st spinal nerve; *sp.c.*, spinal cord; *v.3*, 3d ventricle; *v.4*, 4th ventricle; 3, 4, 5, 7, 8, 9, 10, cranial nerves.

as a simple eye lying on the dorsal midline in some of the reptiles. The *optic lobes* are a pair of conspicuous rounded bodies behind the diencephalon. Posterior to these is a narrow transverse ridge, the *cerebellum*, followed by the *medulla oblongata*, which is continuous with the spinal cord.

When the brain is viewed from the ventral side (Fig. 38 *C*), one finds, in addition to the parts above mentioned, the *optic chiasma*, or region of the crossing of the optic nerves, in the anterior ventral wall of the diencephalon; and the *infundibulum*, extending downward from the posterior ventral wall of the diencephalon to meet the *hypophysis*, which is not a part of

the nervous system but originates from the roof of the mouth. The infundibulum and the hypophysis together form the *pituitary body*, an endocrine gland which pours its secretion into the blood. The ventral part of the brain below the optic lobes is known as the *crura cerebri*. As on the dorsal side, the most posterior region is the *medulla oblongata*. On the dorsal surface of the medulla and just posterior to the cerebellum, is a mass of blood vessels, the *posterior choroid plexus*; and on the dorsal side of the diencephalon, a similar mass, the *anterior choroid plexus*. The *spinal cord* exhibits a *brachial* and a *lumbar enlargement*, in correlation with the larger nerves of these regions, and tapers posteriorly as the terminal filament, or *filum terminale* (Fig. 37).

Internally, the brain and cord contain a continuous cavity (Fig. 38 B), which is expanded as the *ventricles* of the brain and reduced to a microscopic canal in the cord. The choroid plexuses, which are located at places where the roof of the neural tube is very thin, are masses of small blood vessels included in the roof of the third and fourth ventricles and projecting downward into these cavities.

In the frog there are ten pairs of *cranial nerves* arising from the brain (Fig. 39 B), all of them passing to the head and neck region, with the single exception of the tenth pair, or *vagus nerves*, which have branches running to the lungs, heart, and digestive tract. These ten pairs of cranial nerves occur with slight modifications in all vertebrate animals. In addition, an eleventh and twelfth pair are differentiated as cranial nerves in reptiles, birds, and mammals.

The *spinal nerves* of vertebrates vary in number according to the length and development of the spinal cord and its protective spinal column. In general, one expects to find a pair of spinal nerves for each well-developed vertebra in the body region. In the human body, there are some thirty pairs of spinal nerves, if we include the rudimentary nerves at the posterior end of the cord. In the adult frog, the vertebræ are reduced to nine and there are nine well-developed spinal nerves and a smaller tenth nerve which is readily seen in dissection (Fig. 37). In the frog tadpole, however, there are rudimentary structures, which correspond to the vertebræ and spinal cord of this posterior region in other animals; but, as the frog develops, these become a single terminal bone, the *urostyle* and the terminal filament of the spinal cord (Figs. 37 and 40 B).

In addition, there are the *autonomic nerves*, of which the *sympathetic nerves* (Fig. 37) are a part, and which connect with both cranial and spinal nerves. These innervate the blood vessels and viscera.

The relative development of the nervous system of vertebrate animals, particularly of the brain, may be mentioned here. If

FIG. 39.—Brains of representative vertebrates from dorsal view (cf. the lateral views shown in Fig. 288, p. 532).

cbl, cerebellum; *cbm*, cerebrum; *dien*, diencephalon; *md*, medulla oblongata; *oll*, olfactory lobe; *opl*, optic lobe.

one examines the brains of a fish, an amphibian, a reptile, a bird and a mammal (Fig. 39), one sees that the cerebrum exhibits a progressive increase in size and complexity in passing from the lower to the higher types. The intelligence of the animals in question may likewise be arranged in an order that parallels

their brain development, particularly that of the cerebrum. In man the cerebrum is so large that it overlaps and completely hides all other parts except a portion of the cerebellum and the spinal cord. It is known that the cerebrum is the part of the brain associated with such functions as memory and the more complex mental processes. Without a well-differentiated cerebrum, no animal seems capable of these higher nervous activities. Defects of the human cerebrum are correlated with defective mental functions. If the matter is considered from an evolutionary standpoint, one can hardly examine such a series of brains, each correlated with the degree of intelligence exhibited by its possessor, without believing that the nervous system of the higher vertebrates has gradually acquired its present complexity of structure, and that in the course of this evolution the intelligence of these animals has increased by gradual stages.

The Muscular and Skeletal Systems.—It is impossible to understand either the muscular or the skeletal system when considered separately, because the two are so intimately related. The skeleton of the frog or any vertebrate constitutes a framework, which supports the softer parts and offers firm places of attachment for the muscles. The relationship between muscles and skeleton may be illustrated by typical examples. In bending and straightening the arm at the elbow, one observes that the movement is in one plane, like that of a hinge, and that a thickening, and hence a contraction, of the muscles can be felt in the upper arm as the joint is “flexed” by the biceps and “extended” by the triceps muscle. Dissection reveals that the mechanical arrangement involved consists of two “antagonistic” muscles which, acting against each other, move the bones in the manner indicated. Thus, muscles “pull,” and never “push” to any appreciable extent. Antagonistic muscles are found throughout the body, as is well shown by the mechanism used in maintaining the erect posture in man (Fig. 41).

Similar relationships exist in the bodies of all animals possessing a well-organized musculature. In some instances the extension of a part is due to its elasticity, following compression by the contraction of a muscle; but commonly extension, as well as flexion, is caused by the “pull” or contraction of a muscle or muscles. Complex movements, like the swinging of the ball-and-socket joints of the human hip and shoulder, or rotation of the forearm, necessi-

tate joints that permit motion in more than one plane and a complex of muscles working together in a coordinated fashion. When one understands the principles involved, many interesting demonstrations may be obtained merely by moving various parts of the body and observing the tightening and slackening as the muscles

FIG. 40.—A. Axial skeleton of man in lateral view, with skull and spinal column cut in median section. B. Skeleton of frog from dorsal view.

as, astragalus; c.b., cartilage bone; ca, calcaneus; cr, cranium; f, femur; h, humerus; i, ilium; m.b., membrane bone; pl, pelvic girdle; r-a, radio-ulna; s, scapula; sa, sacrum; t-f, tibio-fibula; th, thoracic region; u, urostyle; v.c., vertebral column; v.1, 1st vertebra or atlas; v.9, 9th or sacral vertebra. (A, redrawn from Hough and Sedgwick, "Human Mechanism," copyright, 1918, by Ginn and Co., printed by permission. B, redrawn from Parker and Haswell, "Textbook of Zoology," copyright, 1921, by Macmillan and Co., Ltd., printed by permission.)

contract and relax beneath the skin. Although the mechanical arrangements are many and varied, the muscular movements recognizable in the bodies of animals are all dependent upon the fundamental phenomenon observed in the shortening and thickening of any single muscle and its effect upon the skeleton and surrounding parts. The same principle appears in the movements of an animal like an insect, with its external skeleton (Fig. 22),

FIG. 41.—Diagram showing action of antagonistic muscles which keep the human body erect.

Arrows indicate the direction of the pull, the feet serving as a fixed basis of support. The muscles *A*, *B*, *H*, and *C* keep the body from falling forward; *D*, *E*, *F*, and *G* keep it from falling backward.

(After Huxley, redrawn from Hough and Sedgwick, "Human Mechanism," copyright, 1918, by Ginn and Co., printed by permission.)

although the exoskeleton reverses the manner of attachment of the musculature. In some animals, like the earthworm, there is no skeleton whatsoever.

The vertebrates thus possess the external features which have been described and which are seen in many familiar animals. They differ externally from animals like insects and other invertebrates in such features as the skeleton, appendages, and sense-organs. Internally, the vertebrate plan-of-body has its own peculiarities, notably the type of skeleton, and the circulatory, respiratory, and urino-genital systems. It also exhibits features like the dorsal, tubular, central nervous system, which are characteristic of the *Chordata*. The schematic representation of a vertebrate (Fig. 29) illustrates this structural organization that all vertebrates possess in common. In studying the frog or any backboned animal, one may observe this fundamental organization. Since man is a vertebrate, the essentials of human anatomy may be illustrated by the study of another vertebrate animal like the frog. Since structure has meaning only in the light of function, we have, by the various references to functional activities in the present chapter, secured an introduction to the problems of physiology which are discussed in the chapters that follow.

CHAPTER 4

PHYSIOLOGY OF THE VERTEBRATE ANIMAL: METABOLISM

In the preceding chapter it was shown that, structurally, vertebrate animals are made up of systems of organs. These systems are named according to the functions they perform, and it is to an account of these functions that we must now turn our attention. Since structure and function, morphology and physiology, are so closely correlated, the student must keep clearly in mind the facts of morphology as the discussion of physiology progresses. In this account we shall deal with the physiology of the human body in particular, although other forms will be mentioned in special cases, and the discussion in general is applicable to all vertebrates.

The Nature of Protoplasm. — It is necessary, in order to understand and appreciate the significance of the functioning of the animal as a whole, that we should look more closely at its structure. One of the fundamental generalizations of biological science is that all living organisms are composed of *cells*, which are the units of structure and function, and of cell products. This is known as the Cell Doctrine. Cells are microscopic masses of *protoplasm*. A detailed account of their grosser structure and variations in kind will be given in Chapter 6. At this point it is necessary to gain some ideas concerning the protoplasm that occurs in all types of cells. The physico-chemical nature of protoplasm is very complex, but upon its organization depend the reactions that characterize living organisms.

Physical Nature of Protoplasm. — After many attempts to explain protoplasm as a "living compound," investigators are now agreed that, physically, protoplasm is a *colloidal system*. The term colloid is derived from *colla*, meaning glue, and the name was first applied to types of solutions which do not diffuse through parchment or similar membranes, and which, upon evaporation, yield formless masses of material. Such mixtures differ from crys-

talloid solutions, such as those of salt and sugar, which readily diffuse through parchment-like membranes, and yield crystals or definitely formed masses when evaporated. Colloidal systems are a subdivision of what are known as "disperse systems," examples of which are familiar to all. Fog is a disperse system in which water in small droplets is dispersed in the air. In this instance the air is known as the "dispersion medium" while the water droplets constitute the "dispersed phase." Foam is a disperse system in which air bubbles are the dispersed phase and water the dispersion medium; smoke, a disperse system in which the disperse phase is made up of soot particles and the dispersion medium is air. A muddy stream, in which the water is a dispersion medium for solid particles like soil, is a suspension type of disperse system.

When both disperse phase and dispersion medium are liquid, we have an emulsion, as, for example, when oil and water are shaken

FIG. 42.—Diagrams to illustrate relation of dispersed phase to dispersion medium in a disperse system.

In the diagram on the left the dispersed phase is shown in black and the dispersion medium in white; on the right, the dispersed phase is white and the dispersion medium is black. If in both diagrams black represents the fatty substances of milk and white the solution of the other constituents in water, the diagrams illustrate the "reversal of phases" that occurs when milk is churned to form butter.

medium formed by the solution of the other constituents in water. When milk is churned, what is known as "reversal of the phases" occurs, and in butter we find droplets of whey making the dispersed phase in a dispersion medium of butter-fat (Fig. 42). The "setting" of gelatine may also be interpreted as a reversal of phase in an emulsion.

These examples indicate the conception of disperse systems.

together so that fine droplets of oil are dispersed in the water. Such an emulsion may be temporary, but by appropriate methods small amounts of oil can be held in permanent emulsion in water. Another emulsion commonly made is mayonnaise salad dressing, in which oil is dispersed in egg yolk. A familiar natural emulsion is milk. In this instance, cream, in the form of very fine fat droplets constituting the dispersed phase, is held in a dispersion

Colloids are disperse systems of the "solid in liquid" and "liquid in liquid" types, that is, suspensions and emulsions, in which the particles of the disperse phase are extremely minute. The dispersal of material in minute masses produces a very great increase in the surface of the dispersed phase. Since many phenomena, both chemical and physical, are dependent upon surfaces, it may be said that the characteristic properties of colloids are due to the enormous surfaces present in such systems.

Chemical Nature of Protoplasm. — When protoplasm is analyzed chemically it is found to contain carbon, hydrogen, oxygen, nitrogen, phosphorus, sodium, chlorine, magnesium, iron, potassium, sulphur, calcium, and sometimes other elements, such as silicon, copper, aluminum, manganese, iodine, fluorine, and bromine. These chemical elements are combined to form the four great groups of organic compounds, carbohydrates, fats, lipins, and proteins, in addition to organic substances known as enzymes, inorganic salts, and water. Organic compounds are so called because they occur in nature only as the products of the chemical activities of living organisms.

Carbohydrates are compounds of carbon, hydrogen, and oxygen, and are so called because, typically, the hydrogen and oxygen occur in the proportion of two to one, as in water. The great majority of the carbohydrates are made up of structural units known as the simple carbohydrate or saccharide groups, which have the empirical formula $C_6H_{12}O_6$. The starches and sugars are the most commonly known representatives of this class of substances, although cellulose, gums, dextrines, and glycogen are widely distributed members. The simplest carbohydrates are easily oxidized, and furnish, indeed, the ultimate source of protoplasmic energy.

Among organic compounds is found a very heterogeneous group, soluble in ether, alcohol, and chloroform, and having a greasy feeling. This is the class of *lipoid substances* and may be subdivided for our purposes into fats and lipins. Fats, under which we include neutral fats and fatty oils, are composed of carbon, hydrogen, and oxygen, but contain much less oxygen in proportion to the carbon than is found in the carbohydrates. These three elements occur in the form of structural units known as glycerol (glycerine) and fatty acids, which are combined in different ways to give rise to the different fats. Examples of fats are to be

found in butter, lard, tallow, olive oil, and cottonseed oil. Fats are readily oxidized in protoplasm, with the production of much heat. *Lipins* differ chemically from fats chiefly in the fact that they contain phosphorus and nitrogen, or nitrogen only, in addition to carbon, hydrogen, and oxygen. The structural units in the majority of cases are glycerol, fatty acid, phosphoric acid, and some nitrogen base. Examples of lipins are lecithin, which is abundant in the yolks of eggs, and the cerebrosides found in nervous tissue.

Proteins are very complex compounds of carbon, hydrogen, oxygen and nitrogen, with traces, in almost all cases, of sulphur and phosphorus, and sometimes of magnesium and iron. The protein molecule is very large, and is composed of structural units known as amino acids, which are organic acids containing nitrogen in an amino group (NH_2). There are at least twenty different amino acids, which are combined in different amounts and groupings with one another and with other molecules, to form many different types of proteins. Chemists have not yet succeeded in determining the exact composition of any protein molecule, but by certain methods it is possible to estimate the empirical formulæ of some of them. For instance, fibrin, the protein of clotted blood, has the approximate formula

while casein, the characteristic protein of milk, is

Gelatin and the albumin of eggs are examples of protein. In animal protoplasm, proteins are the most abundant of the organic constituents.

Enzymes are substances whose chemical composition has not been determined, but which act in the nature of organic catalysts. Catalysts are substances that affect the rate of a chemical reaction but do not appear among the end products of the reaction. The classic example of inorganic catalysis is the effect of a minute quantity of finely divided platinum upon the rate at which hydrogen and oxygen combine to form water. Enzymes are produced in all cells and are responsible for the autocatalysis which is characteristic of protoplasmic reactions. Some cells, known as gland

cells, specialize in the production of enzymes, which are passed out to catalyze external reactions, as in digestion.

The *inorganic salts* of the protoplasmic system include the ones found in sea water, chiefly sodium and calcium chloride. *Water* constitutes 60 to 90 per cent of protoplasm and holds the inorganic salts in crystalline solution. This watery solution is the dispersion medium for the very finely divided masses of carbohydrates, fats, lipins, and proteins, which are the coexisting dispersed phases. The ionization of the dissolved salts is responsible for the electrical phenomena that protoplasm exhibits.

It cannot be too strongly emphasized that protoplasm is not a *living compound* but a highly organized colloidal system. Under the conditions of enormous exposure of surface of the dispersed phases and the intimate associations of these ultramicroscopic masses, are made possible the multitudinous autocatalyzed chemical reactions and the physical phenomena which are characteristic of living organisms. These chemical reactions and physical processes are interdependent, and in normal protoplasm a very delicately balanced equilibrium between these processes gives rise to the visible manifestations that we call life. Life is not a property of any single constituent of protoplasm, or of all of them taken together, or of their manner of organization, but is the result of the reactions made possible under the physico-chemical conditions which have just been explained. As Hopkins puts it, the life of a cell, and, therefore, of organisms, "is the expression of a particular dynamic equilibrium which obtains in a polyphasic system," known as protoplasm.

Distinguishing Capacities of Living Organisms. — Living organisms differ from lifeless things in three fundamental respects. These distinguishing capacities are metabolism, irritability, and reproduction. Under *metabolism*, as a distinguishing characteristic of living organisms, are included all the chemical reactions that occur in protoplasm. These reactions group themselves under the headings of assimilation and dissimilation. Assimilation includes those reactions by which suitable materials are taken in by protoplasm and built up into the constituent parts necessary for its normal functioning. Dissimilation is, on the other hand, the sum of the disintegrative changes, chiefly oxidations, which occur in protoplasm, resulting in the transformation of energy, with

production of heat, and certain waste products. Growth occurs in living organisms when assimilation goes on at a more rapid rate than dissimilation. Organisms grow by the method of intussusception, or growth from within; they differ in this respect from inorganic crystals, which grow by the process of accretion, or the deposition of additional material on the surface of that already present. Metabolic reactions are catalyzed by the enzymes typical of protoplasm, and are made possible by the fundamental physico-chemical organization of that system. The results of the reactions of the cells of the body and their interactions are apparent as the normal functioning of the animal, and all bodily functions may be understood, in the final analysis, by reference to metabolism.

Irritability is the term applied to the capacity which protoplasm possesses of responding by internal reaction to a stimulus, or change in its environment. It is well known that non-living things react in certain definite ways to certain changes in their surroundings, as when a metal undergoes a particular amount of contraction for a particular decrease in temperature. The reactions of living organisms, however, involve both chemical and physical factors, and, as we shall see later, are so much more complicated as to be distinctive.

Reproduction is that capacity upon which depends the continuity of living organisms. Under varied conditions, certain parts of organisms detach themselves, and, either alone or after union with protoplasm of another organism of the same kind, give rise to a new individual in all essential respects like the parent or parents. Nothing comparable with reproduction is known to occur among inanimate objects.

Assimilation. — *Nutrition.* — A discussion of nutrition involves consideration of the needs that food must supply and of the nature of food. Food is necessary in order to enable the protoplasmic system to replace those constituents that are constantly being removed in dissimilative reactions, some of which are for the transformation of energy and production of heat; that is, food is necessary for maintenance or repair. In young organisms, food also supplies the materials for growth. Food, therefore, is the source of the raw materials necessary for the normal functioning of the protoplasmic system.

Consequently, the nature of food becomes clear. It must

contain the elements or compounds needed by the protoplasm for its upkeep and normal functions. If we recall the chemical nature of protoplasm, it will be evident that food must contain carbohydrates, fats, lipins, proteins, water, and inorganic salts, or materials from which these constituents can be made. Certain organic compounds known as vitamins are also necessary. In addition, atmospheric oxygen becomes a food, since it is essential for the oxidative reactions that are characteristic of protoplasmic functions. The chemical composition of carbohydrates, fats, lipins, and proteins has been indicated, and their occurrence in typical foodstuffs is shown by the following table:

EXAMPLES OF COMPOSITION OF FOOD
(Adapted from Bulletin 28, U. S. Dept. Agriculture)

	Water	Protein	Carbohydrate	Fat	Organic Accessories ("vitamins")	Mineral salts (ash)	Fuel value per pound
Milk.....	87.0	3.3	4.0	5.0	present	0.7	325
Egg.....	74.0	15.0	0.0	10.0	abundant	1.0	720
Steak.....	67.0	20.0	0.0	12.0	present	1.0	900
Fish (fresh mackerel).....	73.0	19.0	0.0	7.0	present	1.0	645
Butter.....	11.0	1.0	0.0	85.0	some abundant—others absent	3.0	3605
Honey.....	20.0	trace	80.0	0.0	present	trace	1520
Sugar.....	0.0	0.0	100.0	0.0	absent	absent	1810
Corn flour.....	13.0	7.0	78.0	1.0	nearly absent	1.0	1645
Wheat flour.....	12.0	11.0	75.5	1.0	deficient	0.5	1665
Macaroni.....	10.0	13.0	74.0	1.0	deficient	1.0	1665
Dried peas.....	9.5	24.5	62.0	1.0	deficient	3.0	1635
Peanuts.....	9.0	26.0	24.0	39.0	deficient	2.0	2560
Tomatoes.....	94.3	0.9	3.9	0.4	very abundant	0.5	105
Asparagus.....	94.0	1.8	3.3	0.2	abundant	0.7	105
Cabbage.....	71.5	1.6	5.6	0.3	present	1.0	145
White potatoes.....	75.5	2.5	20.9	0.1	present	1.0	440
Squash.....	88.3	1.4	9.0	0.5	present	0.8	215
Sweet potatoes.....	69.0	1.8	27.4	0.7	abundant	1.1	570
Green peas.....	74.6	7.0	16.9	0.5	abundant	1.0	465
Oranges.....	86.9	0.8	11.6	0.2	very abundant	0.5	240
Apples.....	84.6	0.4	9.0	0.5	abundant	0.3	290
Bananas.....	75.3	1.3	22.0	0.6	present	0.8	460

Early workers in the field of nutrition came to the conclusion that the average adult man needed 500 grams of carbohydrates,

56 grams of fat (including lipins), and 120 grams of proteins daily, the so-called "balanced ration." It will be recalled that all carbohydrates are composed of structural units, the simple sugars, of which glucose is the most universal; that the fats and lipins have relatively simple and constant structural components; but that the proteins are built up of amino acids, of which there are at least twenty, combined in many different ways. It has been determined that certain proteins in our foodstuffs are lacking in certain amino acids that are necessary for the compounding of our proto-

FIG. 43.—The rations of these two rats had the same composition as shown by chemical analysis. They differed only in the source of the protein which they contained.

The rat on the right grew up on a mixture of proteins from the corn kernel and wheat gluten; that on the left, on a mixture of corn proteins and gelatin. The difference in size, and remarkable difference in appearance is solely the result of the difference in the quality of the proteins in the two diets. Corn proteins and gelatin do not supplement each other's amino-acid deficiencies. These animals were the same age when photographed, and had been confined for the same number of days to the experimental diets. (From McCollum, "Newer Knowledge of Nutrition," copyright, 1922, by the Macmillan Co., reprinted by permission.)

plasm. Thus, the characteristic protein of corn is lacking in three of the amino acids that are necessary for maintaining human protoplasmic proteins (Fig. 43). Therefore, even if one were to eat 120 grams of corn protein daily, this food would not fulfill the requirements for upkeep. Also, lean-meat proteins contain from 12 to 14 per cent of a particular amino acid, while wheat proteins contain 40 per cent of the same acid. The proteins of our foodstuffs differ widely in their content of particular amino acids. Without going further into this matter, it may be said that kidney, liver, milk, and wheat contain proteins of unusual value which should be used in all diets to insure the presence of the

requisite amino acids. The necessity of including water in a diet is altogether obvious in view of what has been said of its importance as a constituent of protoplasm. It is also clear that mineral salts are necessary to maintain the supply of chemical elements used in metabolism. These inorganic salts are present to a greater or lesser extent in the water we drink, but the best single source of these materials is milk, which contains potassium, calcium, phosphorus, chlorine, sodium, and magnesium.

Our knowledge of the importance of *vitamins* as dietary necessities has developed rapidly since 1910. Vitamins are organic

FIG. 44.—The rations of these two rats from weaning time were exactly alike except in the character of the fats which they contained. The one on the left was given 5 per cent of sunflower seed oil. The one on the right was given 1.5 per cent of butter fat.

Butter fat, egg yolk and the leaves of plants contain a dietary essential, the chemical nature of which is still unknown, which is necessary for growth or the maintenance of health. This substance is known as fat-soluble A, and is not found in any fats or oils of vegetable origin. The animals were the same age when photographed. (From McCollum, "Newer Knowledge of Nutrition," copyright, 1922, by the Macmillan Co., reprinted by permission.)

compounds, of unknown composition, which must be present as such in foods, since it is apparently impossible for the protoplasm to build them up. Three different vitamins, known respectively as fat-soluble A, water-soluble B, and water-soluble C, have been found to be essential in human nutrition, and it is possible that others will be identified as knowledge progresses. Fat-soluble A is present in milk and butter but not in butter substitutes like oleomargarine; it is also present in egg yolk, in cod-liver oil, and in leafy vegetables such as spinach and lettuce (Fig. 44). Water-soluble B occurs in oranges and other citrus fruits, prunes, milk, egg yolk, whole wheat, yeast, and thin-leaved vegetables. Water-soluble C is found in citrus fruits and in many fresh leafy vegetables, in young carrots, and in tomatoes. Heating reduces

the effectiveness of vitamin C, but not of A and B. The complete absence of these dietary factors produces specific abnormal conditions (Fig. 45). For example, scurvy results from the absence of water-soluble C; beri-beri, from the elimination of water-soluble B; and xerophthalmia, resulting in blindness, from deficiency in fat-soluble A.

In the light of modern investigations on the nutritional requirements of animals, it becomes evident that in order to obtain a proper balancing of the diet one must do more than obtain a cer-

FIG. 45.—Tadpoles of *Rana pipiens* showing general effect of absence of vitamins in diet.

The tadpoles of each pair are the same age and the period intervals are one week. The larger member of each pair had received a complete diet. The smaller one had no vitamins in its diet which was otherwise complete. (From Emmet and Allen, *Jour. Biol. Chem.*, 1919.)

tain ratio between carbohydrates, fats (lipoids), and proteins. It is essential that the proteins eaten contain the amino acids needed by the protoplasm, that the inorganic elements be present in proper concentrations, and that vitamins be furnished in abundance. The abnormal functioning produced by inadequacy of food with respect to single vitamins, and the conditions, such as rickets and pellagra, that are recognized as due to more complex deficiencies, are very serious factors in human welfare (Fig. 46). On the whole, however, it is the very numerous cases of borderline malnutrition, predisposing to various diseased conditions and general lack of physical and mental efficiency, that are of more vital importance to society as a whole.

It is characteristic of the nutrition of animals that they cannot build their foods from the constituent chemical elements, but must take compounds produced by the protoplasm of other animals or of plants. The protoplasm and the products of metabolism of one

type of organism are not ordinarily usable as such by another kind of animal. Therefore, food, in addition to containing the necessary elements as outlined, must be utilizable by the form eating it. That is, it must be possible for the food to be made available for use in the building of the protoplasmic system of the animal using it. The changes which food undergoes, in the body of a vertebrate, before it is assimilated, are well known and will be discussed under the headings of digestion and absorption.

Digestion. — Digestion may be defined as the series of chemical changes which food undergoes in the digestive tract in the presence of digestive enzymes. It is necessary that the majority of foodstuffs have their complex molecules broken down into their simple structural units in order that they may be absorbed from the digestive tract and distributed to the cells of the body; and also in order that they may be transformed into substances that can be

FIG. 46.—This picture illustrates the emaciated appearance of a middle-aged rat after being fed about four months on a diet consisting of bolted flour, degerminated corn meal, rice, sugar, starch, pork fat, molasses, sweet potato, and cabbage.

This diet affords wide variety and consists of wholesome food products, yet fails to maintain normal nutrition because it contains too little of the *protective foods*, milk, eggs and the leafy vegetables. (From McCollum, "Newer Knowledge of Nutrition," copyright, 1922, by the Macmillan Co., reprinted by permission.)

assimilated by the protoplasm. Digestion, then, is a chemical process. Closely associated with the chemical phenomena are certain mechanical factors which will be indicated as the discussion progresses, but which must not be confused with the essential digestive reactions.

Food enters the digestive tract at the *mouth* by a process known as *ingestion*. In the mouths of the higher vertebrates the food may be torn apart or ground into fine particles by the teeth, but in lower forms the food is merely held by the teeth and no mechanical disintegration occurs. The frog, for instance, merely retains its food with the teeth until it can be swallowed, and no digestive

changes take place in the mouth. However, in man, the sight, the odor, or even the thought of food induces the flow into the mouth of *saliva*, a digestive juice secreted by the salivary glands. As the food is chewed it is mixed with the saliva, which is almost neutral or slightly alkaline. This results in the softening of the food, which aids swallowing, and also in the initiation of the digestive changes. Saliva is largely water and mucin, but contains a digestive enzyme known as *ptyalin*, in the presence of which starchy foods are partially digested. Starch, if it has been cooked, enters the mouth in the soluble form; if not, it is changed to that form by the ptyalin. This soluble starch in the presence of ptyalin reacts with water to form erythrodextrine and maltose, one of the compound sugars. Certain investigators believe the reactions to occur as follows:

This reaction, which is a splitting of the starch and dextrine molecules by the addition of water, continues until the action of the ptyalin is halted by the acidity of the juices in the stomach. The food mass, softened by the water and mucin of the saliva, mixed by chewing, and with its starch components partially digested, is carried down the esophagus by the muscular movements known as swallowing. No digestive changes occur in the esophagus; it is merely a passageway.

The digestive juice of the *stomach* is known as *gastric juice* and is thoroughly mixed with the food mass by muscular movements of the stomach wall. Because of the contraction of the pyloric sphincter, a circular band of muscle located between the stomach and the small intestine, the materials are retained in the stomach for a time. Gastric juice is secreted by the gastric glands in the lining of the stomach, and is strongly acidic because of the presence of hydrochloric acid. It contains three enzymes, pepsin, rennin, and lipase. *Pepsin*, the action of which is dependent on the presence of the hydrochloric acid, starts the digestion of some of the protein foods and brings about their distintegration into proteoses and peptones. *Rennin*, which is present chiefly in the

stomachs of young milk-feeding animals, has a coagulating effect upon milk, and also digests milk protein or casein. The *lipase* of the gastric juice acts principally upon lipins and emulsified fats, splitting them into glycerol and fatty acids. As the acidity of the stomach contents increases, the pyloric sphincter relaxes at intervals, permitting the expulsion of the partially digested food mass from the stomach into the small intestine.

The muscular activities of the *small intestine* are of two types, known as peristalsis and segmentation (Fig. 48). In *peristalsis*, a contraction begins at the upper end of the intestine and passes with wave-like effect toward the lower end. This motion has a tendency to cause the passage of the food mass toward the large intestine. *Segmentation*, on the other hand, consists of a series of contractions occurring close together and simultaneously at different levels of the intestine. This results in the pinching of the food mass into segments; and since these segmentation contractions disappear and reappear at alternate levels they cause a very thorough mixing of the intestinal contents. Food in the small intestine comes in contact with three digestive juices: *bile*, which comes from the liver by way of the bile duct; *pancreatic*

FIG. 47.—The digestive tract and appended structures of the frog.

b.c., buccal cavity; b.d., bile duct; bl., urinary bladder; c.d., cystic duct; cl., cloaca; du., duodenum; e., position of eye; es., esophagus; E.t., Eustachian tube; g.b., gall bladder; gl., glottis; h.d., hepatic duct; i.n., internal nostril; int., small intestine; lg., lung; li., large intestine; lv., liver; mx.t., maxillary teeth; ovd., opening of oviduct; p., pancreas; p.d., pancreatic duct; pyl., pyloric sphincter; sp., spleen; st., stomach; t., tongue; ur., opening of ureter; vt., vomerine teeth. (Redrawn with modifications from Howes, "Atlas of Zootomy," copyright, 1902, by Macmillan and Co., Ltd., reprinted by permission.)

juice, entering from the pancreas through the pancreatic duct; and *intestinal juice*, from glands in the lining of the duodenal region

FIG. 48.—To illustrate the muscular activities of the small intestine.

The three upper drawings represent a particular region of the intestine at successive periods during segmentation. The three lower drawings show a particular region of the intestine at successive periods during peristalsis. Arrows within the tube show direction of movement of food contents. Arrows between drawings call attention to changes in wall of intestine. The vertical dotted lines in upper drawings indicate places of following contractions.

of the small intestine. The reactions of this region occur in an alkaline medium, owing to the presence of alkaline salts in the three juices. Bile contains no digestive enzymes and serves chiefly as an emulsifying agent for the fats. That is, fat drops in the presence of bile become divided into very fine droplets, thus offering a much greater surface for the activities of the fat-splitting enzyme. Pancreatic juice contains three digestive enzymes: steapsin, or intestinal lipase; trypsin; and amylopsin, or intestinal amylase. *Steapsin* brings about the digestion of the emulsified fats into glycerol and fatty acids. *Trypsin* is a protein enzyme and acts to split the undigested or partially digested protein molecules into simpler compounds known as polypeptids. *Amylopsin* continues the digestion of starch, begun in the mouth by ptyalin and interrupted in the stomach, and converts starch into maltose, a compound sugar. The intestinal juice contains enterokinase, erepsin, and the sugar-splitting enzymes. Without *enterokinase*, trypsin is inactive and has no effect upon proteins. *Erepsin* is the enzyme that finally completes the digestion of proteins into their component amino acids. Of the sugar-splitting enzymes, *maltase* acts upon maltose or malt sugar; *sucrase*, or invertin, upon sucrose or cane sugar; and *lactase* upon lactose or milk sugar. The effect of these enzymes is to produce simple sugars, principally glucose or grape sugar. The final stages of digestion of all foods occur in the small intestine.

Some of the materials taken in with the food cannot be changed, or for some reason are not changed. These are carried by peristaltic contractions toward the *large intestine*, which is separated from the small intestine by the ileo-cæcal valve. In man, about four hours elapse from the time of eating until the first part of the food mass enters the large intestine, and the discharge continues for about two hours. After being retained in the lower part of the large intestine for from ten hours to two days, this undigested and undigestible material, now known as fæces, is discharged from the digestive tract upon relaxation of the anal sphincter. This process is known as defecation, or *egestion*. The amount of food-stuff egested is about 10 per cent of the amount ingested.

In the large intestine of some animals there are many bacteria which digest cellulose, a carbohydrate present in the walls of plant cells, and produce simple sugars from it. While some of this sugar is absorbed, it must be kept in mind that the bacteria digest this

material for their own nutrition, and it is only incidentally that it affords nourishment for the animal harboring the bacteria. Bacteria in the large intestine of man also cause the putrefaction of protein elements, forming products many of which are toxic, or poisonous, and which, when absorbed into the body, cause headaches, drowsiness, and a general feeling of depression, or auto-intoxication. Some idea of the great number of bacteria present may be had when it is stated that from one-quarter to one-half of the dry weight of the faeces consists of bacteria.

In summarizing the essential processes of digestion, it may be recalled that in some animals, which possess salivary glands, the digestion of starchy carbohydrates is started in the mouth by the action of ptyalin. This action on starch is continued in the small intestine by the amylase of the pancreatic juice, with the result that the starch is converted into maltose, a compound or disaccharide sugar. The digestion of the maltose, together with other compound sugars, is completed by the sugar-splitting enzymes of the intestinal juice, with the formation of the simple sugars or mono-saccharides. Protein digestion, started by pepsin in an acid medium in the stomach, is continued in the small intestine in an alkaline medium, by trypsin of the pancreatic juice, and completed by erepsin of the intestinal juice, with the formation of amino acids. Emulsified fats and lipins are split by gastric lipase; and, in the small intestine, after the emulsification of fats by bile, the steapsin from the pancreas is effective in producing glycerol and fatty acids as the end products of fat and lipin digestion. The entire result of digestion is the decomposition of complex food materials into their structural units, which are simple sugars, amino acids, and fatty acids and glycerol. These components are thus made available for absorption and assimilation in the maintenance of the protoplasmic system.

Absorption. — By the process of digestion, complex food materials are chemically changed into the simpler compounds that can be assimilated by the cells. Before assimilation can occur, the simple nutrients must be absorbed from the alimentary canal into the circulating fluids and be distributed to all cells. Absorption may be defined as the passing of simple food compounds through the mucous membrane of the digestive tract into the blood or lymph. Examination of the wall of the digestive tract reveals that the cavity is lined with a single layer of compactly placed

cells, known as the mucous membrane. Between this layer and the muscular coats of the tract is a region of loosely arranged cells with interlacing fibers, which make up the submucous layer

FIG. 49.—Schematic representation of blood and lymph vessels of the digestive tract.

A, blood and lymph vessels in relation to entire wall of tract. *B*, blood capillaries in a single villus of the human intestine. *C*, lymph vessel from center of same. *a*, artery; *b.c.*, blood capillaries; *l*, lymphatic vessel; *l.c.*, lymph capillaries; *m.l.*, muscular layers of intestine; *m.m.*, mucous membrane; *mes*, mesentery; *s.m.*, submucosa; *v*, vein.

or submucosa. It is in this region, separated from the digestive cavity by the mucous membrane, that the delicate lymphatics and the thin-walled capillaries that connect arteries and veins are

found (Fig. 49). Substances, in being absorbed, pass through the cellular membrane and into the fluid of these vessels.

Although certain foods, such as grape sugar, water, and the inorganic salts, require no change before they are ready for absorption, there is practically no absorption in the stomach. In the upper part of the small intestine the exposed surface of the mucous membrane is greatly increased by the projection of numerous finger-like *villi* into the cavity. Each villus is covered by mucous membrane and has a core of submucosa containing capillaries and lymphatics. It is in this region that by far the greatest amount of absorption occurs. Simple sugars, amino acids, and mineral salts pass directly into the blood stream and are found there and transported as such. The presence of a great deal of ammonia in the cells of the mucous membrane would seem to indicate that some of the amino acids had undergone a chemical change there, but the significance of this is not clear. The fats and lipins are digested into fatty acids and glycerol in the presence of bile, and the fatty acids combine with certain alkaline constituents of the bile to form soaps. In this form they enter the cells of the mucous membrane along with the glycerol. There the soaps are broken down and the fatty acids recombine with the glycerol to form neutral fat droplets, the presence of which can be demonstrated in the protoplasm of the cells of the mucous membrane. This fat is discharged into the lymph vessels of the submucosa. Water is absorbed throughout the length of the small and large intestine.

No satisfactory theory to account for absorption has yet been formulated. Such a theory must explain the phenomena by which the digestive juices are passed into the cavity of the tract while solutions of the digestion products are passed in the opposite direction into the blood or lymph. Osmosis, or the passing of water through a membrane to equalize concentration of solutions on the two sides of the membrane, would account for the passing of water into the digestive cavity to decrease the concentration of the food mass, but not for the reabsorption of water in other regions of the tract. Diffusion, which is the mixing of substances in such a way that regions of higher and lower concentrations tend to become equal in concentration, would explain the passage of digestion products from the tract, where they are very concentrated, into the circulating fluids which are constantly changing so that equilibrium is not established. However, it has been found that if the

fluid portion of the blood of an animal be introduced into its digestive cavity, this blood serum will very soon be absorbed into the circulating fluid, which must have the same concentration. It is, therefore, evident that factors other than osmosis and diffusion must be considered. In the absorption of fat, it is clear that the cells of the mucous membrane are not passive. The fact that the glycerol and fatty acids are resynthesized is evidence of protoplasmic activity. Indications of such activity are not so obvious in the absorption of other substances, but it must not be forgotten that in protoplasm we are dealing with a complex colloidal system about which we are still seeking knowledge.

The enormous surfaces present in colloidal systems make possible a great deal of *adsorption*, a well-known physical principle which is responsible for the use of finely divided charcoal in gas-masks. The gases in passing through the charcoal are adsorbed on the surface of the finely divided particles. A consideration of this phenomenon, along with other properties of colloidal systems, is engaging the attention of some investigators who seek to explain the physico-chemical basis for absorption. It is safe to say that no explanation will be found satisfactory that does not take into consideration the metabolism and organization of the cells of the mucous membrane.

Fate of the Nutrients Absorbed from the Digestive Tract. — The fat absorbed into the lymph vessels in the submucosa passes, in man, by way of the lacteals running in the mesentery to the thoracic duct which empties into the left jugular vein. From there the finely emulsified fat is carried in the blood, and with the amino acids, simple sugars, water, salts, and vitamins is distributed to all the cells in the body by way of capillary networks. The veins carrying blood from the digestive tract unite to form the hepatic portal vein, which empties into the capillary system of the liver. Here the greater part of the simple sugars absorbed from the intestine leave the blood and are synthesized in the liver cells to glycogen, a complex carbohydrate known as animal starch. As glycogen, carbohydrates are stored in the liver, and to a lesser extent in the muscles of the body. According to the needs of other cells of the body, glycogen is converted into glucose, passed into the blood stream, and distributed. Interference with this control of the amount of sugar in the blood stream results in abnormal conditions, of which diabetes is the best known. The nature of this control will be discussed in a

FIG. 50.—Diagram of circulatory system of the frog.
(Explanation continued on opposite page.)

Explanation of Fig. 60

By means of blood and lymph vessels nutrients and oxygen are distributed to all cells of the body, while excretions and endocrines are collected and transported from place to place. The arrows indicate the direction of flow of the blood.

Ab.V., abdominal vein; *Au.*, right auricle, *Au'*, left auricle; *B.D.*, bile duct; *Bl.*, urinary bladder; *C.A.*, carotid artery; *C.M.*, coeliaco-mesenteric artery; *Cp.D.T.*, capillaries of digestive tract; *Cp.F-l.*, capillaries of fore-leg; *Cp.H-d.*, capillaries of head; *Cp.H-l.*, capillaries of hind-leg; *Cp.K-d.*, capillaries of kidney; *Cp.Sk.*, capillaries of skin; *Cu.A.*, cutaneous artery; *C.V.*, cutaneous vein; *D.A.*, dorsal aorta; *D.T.*, digestive tract; *F.V.*, femoral vein; *G.*, gonad; *Gl.*, glottis; *Glm.*, glomerulus; *H.A.*, hypogastric artery; *H.P.V.*, hepatic portal vein; *Hp.V.*, hepatic vein; *I.A.*, iliac artery; *J.V.*, jugular vein; *L.H.*, lymph heart; *Lg.*, lung; *Liv.*, liver; *L.S.*, lymph sinus; *L.V.*, lymph vessel; *P.A.*, pulmonary artery; *Pa.*, pancreas; *P-c.A.*, pulmo-cutaneous artery; *Pcr.*, pre-caval vein; *P-c.V.*, post-caval vein; *P.D.*, pancreatic duct; *Pel.V.*, pelvic vein; *P.V.*, pulmonary vein; *R.P.V.*, renal portal vein; *S.*, sinus venosus; *S.A.*, systemic artery; *Sb.A.*, subclavian artery; *Sb.V.*, subclavian vein; *Sk.*, skin; *Sk.Gl.*, skin gland; *Sp.*, spleen; *T.A.*, truncus arteriosus; *Ur.*, ureter; *V.*, ventricle. (Redrawn with modifications from Parker and Parker, "Practical Zoology," copyright, 1916, by Macmillan and Co., Ltd., reprinted by permission.)

later section (p. 101). Fat, also, may be stored in certain regions of the body, such as the subcutaneous fascia, a layer between the skin and muscles; in the mesentery; between the muscles; and, in an animal like the frog, in special organs, the fat-bodies. As is the case with stored carbohydrate, this fat can pass back into the blood for distribution in case of cellular need. So far as we know, amino acids are not stored in any part of the body but are taken from the blood, as required, by all cells.

Because of the ingestion of food, its digestion, absorption, and distribution, the protoplasm of all cells of the body receives a supply of the materials that are necessary for its metabolism. The substances brought to the cells are synthesized under the influence of cellular enzymes, to form the constituents characteristic of the particular protoplasm in which the synthesis occurs. Then, finally, we have assimilation of the foods that enter the body by way of the digestive tract.

Respiration. — The term respiration has been widely used to cover the so-called gaseous metabolism of an organism. It seems unnecessary, and perhaps unwise, to try to separate the metabolism of oxygen from that of other substances, since all metabolic reactions are so closely inter-related. If food is to be defined as any substance necessary for the normal functioning of the organism, oxygen becomes a food, just as water and mineral salts are foods. Respiration, then, is used here as a term covering the delivery of oxygen to the protoplasmic system.

As was pointed out in the discussion of the structure of vertebrates, respiratory systems are of two types, depending upon

the environment of the animal. Water-dwelling forms have structures known as gills, which are richly supplied with blood, covered by a thin layer of cells and exposed to a constantly changing current of water. Air-dwelling forms, by the process of breathing, draw air, by way of the air passages, into their lungs, which are cavities separated from a rich capillary network by a cellular membrane (Fig. 51). In both types, oxygen passes into the blood stream; but in one case it is dissolved in water, while in the other

FIG. 51.—Diagram of a section through a portion of the lung.

The capillaries, which have been cut across, are shown in black. (From Hough and Sedgwick, "The Human Mechanism," copyright, 1918, by Ginn and Co., reprinted by permission.)

it is free in the air. This is known as *external respiration* and is analogous to the absorption of nutrients from the digestive tract. As is the case with alimentary absorption, there is no agreement as to the physical explanation of the process. Here, also, simple diffusion has been proposed as the underlying principle. The concentration of oxygen in the water or air being greater than that in the blood, from which the oxygen is constantly removed by the cells of the body, the oxygen would diffuse in the direction of the blood to establish equilibrium. However, the fact that the membrane is composed of protoplasmic units cannot be ignored, and all the factors governing the absorption of oxygen into the blood are not understood. In the blood stream the oxygen enters into a loose combination with *hæmoglobin*, an iron compound carried by the red blood cells, and is distributed throughout the body in that way. This combination with hæmoglobin, which is responsible for the red color of oxygenated blood, is unstable, and, in the

from which the oxygen is constantly removed by the cells of the body, the oxygen would diffuse in the direction of the blood to establish equilibrium. However, the fact that the membrane is composed of protoplasmic units cannot be ignored, and all the factors governing the absorption of oxygen into the blood are not understood. In the blood stream the oxygen enters into a loose combination with *hæmoglobin*, an iron compound carried by the red blood cells, and is distributed throughout the body in that way. This combination with hæmoglobin, which is responsible for the red color of oxygenated blood, is unstable, and, in the

regions of the capillary networks, free oxygen leaves the blood and passes into the cells. This assimilation of oxygen is designated *internal respiration*.

The bodily processes preliminary to assimilation have now been discussed. These include ingestion, digestion, and absorption of the foods that enter the blood by way of the digestive tract, as well as external respiration, which supplies oxygen to the blood and is dependent, in terrestrial animals, upon breathing. In addition to the incorporation and synthetic processes that maintain the protoplasmic system, assimilation, in a wide sense, includes also the utilization of reserves or stored materials, such as glycogen and neutral fat, and storage products which may be more temporary and present in all cells. It is possible, also, that the production of certain secretions should be classed under assimilative metabolism.

Dissimilation. — *Oxidation.* — Dissimilative metabolic activities include those reactions by which protoplasmic constituents are chemically decomposed for the transformation of energy and production of heat, and probably, in some cases, for the elaboration of certain secretions. The reactions that transform energy and produce heat are in the nature of oxidations, that is, reactions in which oxygen unites with compounds of the protoplasmic system. Oxidation is commonly known as combustion, or burning. When fuel burns, oxygen from the air is combined with the chemical compounds that make up the fuel, producing heat and liberating energy which can be made to do work. It was Lavoisier, in 1777, who first recognized the exact similarity between the combustion of fuels and oxidation as it occurs in the bodies of animals. The statement is sometimes made that "food" is oxidized in our bodies to produce heat and energy. It is well to keep in mind that this is true only in the sense that our organic foods, broken down into their simple structural units, are assimilated by the protoplasm of our cells. The protoplasmic constituents, synthesized from nutrients delivered to the cells, are the compounds that unite with the oxygen. Oxidation of carbohydrates and fats goes to completion in the body and results in the liberation of energy, some of which is converted into heat. The combustion of these classes of compounds is the chief source of animal energy. Proteins are also oxidized to some extent, but the incompleteness of the reaction makes it

impossible to regard them as primary sources of energy. These oxidations, in addition to the transformation of energy, result in the formation of chemical compounds which are of such a nature that they are no longer of use in the protoplasmic system. The combination of oxygen with carbohydrates, fats, and lipins gives rise to carbon dioxide and water, while in the case of proteins the end products are carbon dioxide, water, and a variety of nitrogen-containing compounds. These materials are the waste products of metabolism and are known as *excretions*.

Excretion. — The waste products of the oxidations of carbohydrates, fats, lipins, and proteins are carbon dioxide, water, and various compounds containing nitrogen. These excretions must be constantly removed from the cells in order that the normal oxidation reactions may continue. It is well known that if ashes are permitted to accumulate, a fire will be put out by these waste products of its burning; and the continuity of all chemical reactions depends upon the removal of end products. The process of removal of the waste products of metabolism is *excretion*, and the places of removal are chiefly the lungs, skin, and kidneys. The waste products are carried from cells all over the body by the blood stream. In air-dwelling vertebrates, as blood passes through the lung capillaries, the carbon dioxide passes into the cavity of the lung and is exhaled. In aquatic forms, this waste gas is eliminated into the water surrounding the gills. This excretion of carbon dioxide is often included under the heading of respiration. Carbon dioxide is, however, one of the metabolic wastes and it seems more logical to include its discharge under the heading descriptive of the removal of water and nitrogenous excretions. Exhaled air is moist, because the lungs also excrete water. From the skin of man, carbon dioxide, water, certain salts, and minor quantities of nitrogenous substances are excreted as perspiration (Fig. 52). In the frog, the amount of carbon dioxide excreted by the skin is relatively large and the loss of water is considerable.

The kidneys are usually spoken of as the organs of excretion, and through them about 50 per cent of the water, traces of carbon dioxide, and the principal part of the nitrogenous waste, in the form of urea, are discharged as urine. Urea is not produced, as such, in the cells throughout the body or in the kidney. It is compounded from ammonia in the liver, from which it is carried to the kidneys. It will be recalled that the kidney is made up of tubules

surrounded by capillaries and ending in a cup containing a knot of small arteries (Fig. 31, p. 53). Evidence as to the function of the various parts of the tube with reference to the elimination is conflicting, and final conclusions have not been reached. Some hold that, from the glomerulus, water and inorganic salts filter through

FIG. 52.—Diagram of section through the skin of man showing characteristic structures.

B, bulb or root of hair, where growth occurs; *C.N.*, capillary net surrounding sweat gland; *D*, duct of sweat gland; *M*, erector muscle of hair; *P*, papilla of hair, where blood vessels and nerve endings associated with hair are found; *S*, shaft of hair which extends beyond surface of skin; *Sb.G.*, sebaceous or oil gland from which secretion passes to the surface by way of the hair follicle; *Sw.G.*, sweat gland from which perspiration is eliminated.

Bowman's capsule, and that the nitrogenous compounds are passed in through the walls of the convoluted tubules. An older view was that all the constituents were filtered out at the glomerulus and that some water was reabsorbed from the tubule. Here again, the physical factors governing the passage of materials through living cells are not completely understood.

In conclusion, it may be stated that excretion is the elimination of compounds that have resulted from metabolic reactions of cells. The materials appearing as excretions have been a part of the protoplasmic system. Excretion, as a process, should not be confused with egestion, which is the elimination of undigested or undigestible substances from the digestive tract by way of the anus. Most of the egested materials have never been within the cells of the animal from which they are discharged, but some water and the substances giving odor and color to the faeces may have been.

Secretions. — It has been pointed out that the protoplasmic constituents are produced, within cells, from the end products of digestion by the reactions of assimilation. Oxidations that break down compounds in the protoplasm liberate energy, furnish heat, and give rise to waste products known as excretions. In addition to these types of reactions, certain substances that are necessary for the performance of bodily functions are formed in protoplasm. These substances are called *secretions*, and the process of elaborating and passing them out of cells is termed secretion. There is no evidence to indicate whether these compounds are made from food materials entering the cells or from intermediate products in dissimilation. It is possible that both types of reactions occur. Secretions, in the nature of enzymes catalyzing protoplasmic reactions, are formed within all cells and used within the cell where they are formed. Certain cells, however, produce secretions that go out of the cells to be used elsewhere in the body. The juices that are secreted into the digestive tract have already been mentioned. These contain materials that serve to soften the food, to render it acid or alkaline, to change its physical state, as in the case of emulsification of fat by bile, and to catalyze the chemical reactions of digestion. These juices are produced in groups of cells composing the digestive glands, and the secretions are emptied into the digestive tract by way of ducts or slender tubes (Fig. 53). The oil glands of the skin likewise discharge their secretions by way of ducts. Sweat glands and kidney tubules are often said to secrete perspiration and urine; but since the substances passed out are not built up in these regions, and also since they are in the nature of waste products, the processes are not functionally comparable. It is, therefore, better to say that the kidney excretes than to say it secretes urine.

There are a number of glands which do not have ducts by which to discharge their secretions, but which pass their products into the blood stream. Such glands are known as the *ductless glands*, glands of internal secretion, or endocrine glands; and their secretions are called internal secretions, or *endocrines*, because they are never passed out on surfaces such as the digestive canal or skin (Fig. 54). A well-known example of the way in which endocrines function in coördinating bodily processes is the control

FIG. 53.—Diagram of a gland with a duct which passes to some surface where the secretion is discharged.

(From Hough and Sedgwick, "Human Mechanism," copyright, 1918, by Ginn and Co., reprinted by permission.)

of the flow of pancreatic juice. This fluid is not passed into the small intestine continually but only when food is present to be digested. It was for a long time supposed that this was due to nervous control. Experimentation revealed the fact that the nerves leading to the pancreas could be cut without affecting the control of flow of the pancreatic juice. It was then discovered that if the blood vessels were tied so that blood did not flow into the pancreas the digestive juice was not discharged when food entered the intestine. Further study revealed that when the

contents of the stomach enter the small intestine the hydrochloric acid stimulates certain cells in the intestinal mucosa to discharge into the blood an endocrine substance known as *secretin*. The secretin, reaching the pancreas by way of the blood, serves to stimulate the pancreatic cells to secrete pancreatic juice, which then passes into the small intestine by way of the pancreatic duct.

Endocrinology is a relatively new field of study and information is incomplete concerning many of its phases. The results of investigations are rather confusing in many cases, because of the

FIG. 54.—Diagram of a section through the thyroid gland, which does not have a duct.

cp, blood capillary which carries the thyroxin secreted by the cells of the follicles; *c.t.*, connective tissue; *se*, secretion stored in follicle; *t.f.*, follicle or secretory portion of thyroid.

great difficulty in identifying abnormalities in structure or function as being directly due to particular substances. The glands of the endocrine system seem very closely inter-related, and normal function is secured when all are acting in a state of balance. Certain effects are, however, particularly referable to individual glands. The nature of the function of these endocrine glands is determined by removing them from experimental animals, by injection of endocrine extracts into the circulating fluid, by feeding, and by clinical observations in cases of diseased glands. The most important endocrine glands, as now known, are the thyroid, adrenals, pituitary, pancreas, gonads, pineal, thymus, and para-

thyroids. In addition, there are more or less isolated cells, such as those that produce secretin.

The *thyroid gland* is located on the sides of the trachea posterior to the larynx (Fig. 55). Its removal causes death in all cases after a few weeks. However, death can be prevented, and normal function secured after removal, by grafting in a thyroid from another animal. This grafting can be done successfully in any region of the body that affords an abundant blood supply. Injection of *thyroxin*, as the endocrine of this gland is called, or feeding of thyroid will also prevent death after thyroidectomy, but must be repeated at regular intervals in order to maintain life. Extreme deficiency of thyroid secretion in children results in the disease known as *cretinism* (Fig. 56) in which neither physical nor mental development is normal. Cretinism can be remedied by administration of the endocrine from other animals if this treatment is started before the individual is too old. Subnormal thyroid secretion in adults causes a condition known as *myxedema*, strikingly characterized by swollen, distended, dry skin, and resulting in mental impairment. Here again, administration of extracts is helpful in some cases. On the other hand, the thyroid may over-secrete; in extreme cases this results in *exophthalmic goiter*, characterized by enlarged thyroid, rapid pulse, moist skin, protruding eye-balls, and nervous symptoms of excitability and restlessness. This condition may be remedied by removal of a part of the gland so that the amount of secretion is reduced to normal.

Fig. 55.—The thyroid gland of man showing its position with reference to the larynx and trachea.

L, larynx; T, trachea; Thy, thyroid.

The *adrenal bodies*, which in the frog lie on the ventral surface of the kidneys, and in higher vertebrates come to lie anterior to the kidneys, are composed of two regions, a central medulla and a surrounding cortex (Fig. 57). These two regions differ in function, but both are seats of endocrine secretion. The secretion of the medulla, known as *adrenalin*, is important in increasing the flow of blood carrying augmented sugar supply in cases of

FIG. 56.—Individuals suffering from thyroid deficiency.

The effect of thyroid treatment on the cretin to the left is shown in the central figure. An untreated cretin is shown at the right: age 28, height $34\frac{1}{2}$ inches. (Figures to left and in center from Schäfer, "The Endocrine Organs," copyright, 1916, by Longmans, Green and Co., reprinted by permission. Figure to right from Murray, "Diseases of the Thyroid Gland," copyright, 1900, by H. K. Lewis and Co., reprinted by permission.)

FIG. 57.—Portion of the medulla of the adrenal gland.

cap, blood capillary which carries the adrenalin secreted by the medullary cells; *m.c.*, medullary cells.

muscular emergency. This is due to its effect upon the smooth muscle in the walls of the blood vessels. The cortex secretion is concerned with the regulation of the secondary sexual characteristics, notably the growth of hair.

Like the adrenals, the *pituitary gland*, located ventral to the diencephalon, is composed of two parts, the anterior lobe being formed from the hypophysis, and the posterior lobe from the infundibulum (cf. p. 65). The secretion of the anterior lobe, known as *tethelin*, is active in regulating growth, particularly that of the long bones. Abundant over-secretion results in *gigantism* in youth and *acromegaly* when it occurs in adults (Fig. 58). The secretion of the posterior lobe is called *pituitrin*, and has a marked effect upon smooth muscle fibers, similar to that of adrenalin.

The *pancreas* is composed of cells differing in their functions. The pancreatic juice, which has already been mentioned, is passed into the small intestine by way of the pancreatic duct and is important in digestion. In addition to the cells elaborating this secretion, there are, scattered throughout the pancreas, groups of cells, known as the *islands of Langerhans*, producing the endocrine *insulin* which is discharged into the blood (Fig. 59). Insulin has the important function of regulating the storage of sugar by the liver cells. If this secretion is absent, sugar is present in excessive amounts in the blood and conditions of *glycosuria* and *diabetes* result. Injections of insulin have been effective in correcting diabetic symptoms, and its isolation and the technique of its use constitute a recent

FIG. 58.—Individual in which gigantism has resulted from over-secretion by the pituitary gland.

Note the narrow chest, length of arms and legs, and large size of hands and feet. Height, 8 ft., 3 in. (From Cushing, "The Pituitary Body and its Disorders," copyright, 1912, by Lippincott and Co., reprinted by permission.)

medical achievement. As is the case with all endocrine injections, the dosage must be continued as long as results are desired.

In the case of the *gonads*, or sex organs, there is evidence of the production of endocrine secretions by both ovaries and testes. These secretions are responsible for the control of the secondary sex characteristics, but as yet there is too much confusion for assignment of definite functions. Although the effect of other endocrine secretions in association with those of the gonads is

FIG. 59.—Section through pancreas showing an island of Langerhans surrounded by acini.

A, pancreatic acinus, the cells of which secrete pancreatic juice; C, blood capillary which carries the secretion of the cells of the island; I, cells of the island of Langerhans which secrete insulin; L, lumen of acinus by way of which pancreatic juice passes to the pancreatic duct.

established, the exact relationships are still to be solved. The confusion in data makes it impossible to draw definite conclusions.

From this brief sketch, in which some of the glands have been treated individually, the student should not get the impression that each member of the endocrine system acts alone. In cases of "imbalance" a number of glands are always concerned, possibly the entire chain. It is well to remember that the examples given are the result of serious divergence from the normal. A vast series of deviations from the typical human reactions seem

explicable as disturbances of function in a delicately balanced endocrine system. It is probably true that these effects are in the last analysis due to disturbances in the metabolic reactions of the protoplasm, which are dependent in some way upon the presence in certain amounts of the several endocrine secretions.

Blood as the Common Carrier.— In this chapter the main topic of consideration has been metabolism, or the chemical phenomena characteristic of the protoplasm found in the cells making up the bodies of animals. In complex multicellular animals, such as the vertebrates, it is impossible for each cell to obtain its food materials directly from the animal's surroundings, or to discharge its excretions into the external environment. Consequently, we find cells organized into organs and systems which function in such a way that the individual cells may be able to carry on the metabolic reactions that are responsible for the animal's life. The digestive system serves to prepare nutrients, other than oxygen, so that they can be assimilated by the protoplasm; respiratory organs obtain oxygen for the organism; excretory organs are the places of discharge for the waste products of metabolic reactions; and endocrine glands produce secretions essential for metabolic balance. Blood and lymph, the circulating fluids of the body, place these systems in intimate relationship with the individual cells in which assimilation and dissimilation occur.

The blood, circulating in a system of closed tubes, is composed of a liquid, the plasma, in which float two kinds of cells: red blood cells, or *erythrocytes*; and white blood cells, or *leucocytes*. Lymph consists of blood plasma that filters out of the thin-walled capillaries into spaces between the cells. White blood cells migrate out through the capillary walls and are found in the lymph. Reference to the diagram (Fig. 60) will show that lymph is collected by the delicate vessels known as the *lymphatics* (Fig. 20, p. 41). These finally discharge their contents into the veins. The individual cells of the body are surrounded by lymph which is derived from the blood, and, by means of these two fluids, materials are transported to and from all cells. When the simple sugars, amino acids, vitamins, water, and mineral salts are absorbed from the small intestine they pass into the plasma of the blood. Fats and lipins, absorbed into the lymph, are soon discharged by way of the great veins into the blood plasma for distribution. Oxygen,

from the organs of external respiration, enters into combination with the hæmoglobin of the red blood cells. These materials, which are necessary for maintenance of the chemical reactions of the protoplasm, are carried into capillary networks all over the body, and pass from the blood into the lymph and so into the cells where they are used. Carbohydrates and fats may be left in large amounts at storage depots, to be picked up later for distribution.

FIG. 60.—Schematic figure of blood capillaries and lymphatic vessels in relation to cells throughout the body. A maximum of intercellular space is shown.

a, artery; *b.c.*, blood capillaries; *c*, cells; *i.c.l.s.*, intercellular lymph spaces; *l*, lymphatic vessel; *l.c.*, lymph capillaries; *v*, vein.

Carbon dioxide, water, and nitrogenous wastes, produced by oxidations within the cell, pass out into the lymph and so into the blood plasma in the capillaries. Water and carbon dioxide are carried directly to places of excretion; nitrogenous wastes are transported to the liver where the urea is formed, to be taken to the kidneys. The exchange of foods and excretions between blood and cells by way of the lymph can apparently be adequately

explained on the basis of diffusion from regions of higher to those of lower concentration. Toxic products of intestinal putrefaction are carried in the blood plasma to the liver, lungs, and skin, from which they are discharged. Secretions of the endocrine glands are distributed throughout the body to produce chemical coördinations between metabolic processes in different regions. Finally, in passing through parts where oxidations are occurring rapidly with production of heat, the blood becomes heated, and thus acts, in warm-blooded animals, as the agency for heat transmission and equalization.

In summary, the blood as a common carrier performs four functions: first, it carries the nutrient substances, including simple sugars, amino acids, fats, lipins, vitamins, water, inorganic salts, and oxygen, to all the cells of the body; second, it removes the waste products of metabolism, carbon dioxide, water, and nitrogenous compounds, from all cells; third, it distributes the endocrine secretions, the chemical coördinators, to all body cells; and fourth, it transfers heat from regions of rapid oxidation to those of a lower rate.

An understanding of the functions that have been discussed in the present chapter must be based on an understanding of the necessities of cells as units of function. Complicated systems of organs exist for the maintenance of metabolism in cells throughout the body. If the physiology of metabolism in vertebrate animals is considered and mastered from the point of view of the chemical reactions occurring in its individual cells, the study of function in other types of animals will be merely a reaffirmation of the facts brought out in this chapter. The protoplasmic requirements and reactions are assumed to be in general the same throughout the animal kingdom. Another important fact to keep in mind is that, while the cell is the unit of function, the reactions of the animal as a whole depend upon the coördinated activities of all cells—upon what we shall call the physiological balance of the organism.

CHAPTER 5

PHYSIOLOGY OF THE VERTEBRATE ANIMAL: IRRITABILITY

Metabolism in the vertebrate animal has been discussed in terms of the chemical reactions in the protoplasm of cells. In such a complex organism there are systems of organs, each specialized and functioning in some particular way to make metabolism possible in all the cells of the body. Thus, in the digestive system, food is disintegrated into its simple compounds by means of secretions from various glands, and is absorbed into the vascular system, by way of which it is transported to all parts of the body. The respiratory system and the circulation of the blood provide for oxygen intake and distribution. Again, the blood, together with the organs of excretion, eliminates waste products of metabolism. An organism cannot live if any one of these systems ceases to function, and it becomes abnormal if the activities of its organs are not correlated in the usual way. That is, the manifestations of life by the animal depend upon the coördination of its many systems.

We have seen that in some cases the unification of functions is brought about by endocrines secreted by certain glands and carried in the blood. This is to be thought of as a chemical coördination. Another and a far more important integrating mechanism is the nervous system. Both chemical and nervous coördinations are dependent on irritability, which has been defined as the capacity of protoplasm to respond by internal reaction to stimuli or changes in the environment. All protoplasm is irritable. One problem of the multicellular animal is that of keeping individual cells in touch with the environment of all the cells. This has been solved by means of the sense organs, with their highly differentiated capacities for sensitivity to changes in the environment; and by the nervous system, which is specialized for conductivity. The nervous system of a vertebrate may be divided into two

main parts, the peripheral nervous system and the central nervous system. These regions are, of course, continuous, since the peripheral nervous system, which consists of the cranial, spinal, and autonomic nerves, serves to connect the central nervous system, or the brain and spinal cord, with other systems and organs of the body. The structure and relationships of the divisions of the nervous system have been described in Chapter 3 and should be reviewed in this connection. As our consideration of this phase of physiology progresses, the student must not lose sight of the fact that we are discussing the activities of the nervous system both with respect to the irritability of individual cells and with respect to the coördination of the animal as a whole.

Reflex Action

Simple Reflexes. — Every nervous coördination is the result of a reaction by some part of the body to a stimulus received by some other region. The simplest type of response is that known as *reflex action*. This term is derived from the analogy that can be drawn between the most primitive reflexes and the reflection of light from a mirror. When one touches a hot stove with one's finger the muscles of the arm react to withdraw the hand. Something passes from the point stimulated to the central nervous system, and is passed back to produce the contraction of the arm muscles. Another case is that of the knee-jerk reflex in which the leg is extended as the result of a sharp tap below the knee cap. In both of these examples the response to the stimulus is apparent in the same general region that received the stimulus. This is somewhat comparable with the reflection of light by a mirror, in that the central nervous system seems to reflect the effect of the stimulus. Complete analysis of these simple reflexes shows that they are but the expression of a nervous mechanism which some investigators believe explains all nervous coördination. The original meaning of the term reflex has, therefore, been extended.

The cellular structure within the nervous system that furnishes the mechanism for reflex action is known as the *reflex arc*. A nerve cell, or *neurone*, has a nucleus surrounded by cytoplasm as have most cells, but this cytoplasm is extended as two or more processes (Fig. 82, p. 148). The processes from two or more cells meet one another at their ends, but do not fuse. The places of con-

tact are known as *synapses* and furnish the basis for what is known as functional continuity in the nervous system. Extensions of one cell may have synapses with those of many other cells so that nervous connections become very complicated, as will be shown later. However, in the simplest reflex arc (Fig. 61 A) there may be only two neurones involved. The stimulus is received by some specialized group of cells constituting a *receptor*, which is a general term for any type of sense-organ. As a result of the reception of the stimulus, what is known as a *nervous impulse*, or excitation, is transmitted from the place of stimulation toward the central nervous system, over a nerve-cell process. In the simplest reflex arc, the impulse will travel to the spinal cord. The neurone over which the impulse enters the spinal cord is a *sensory* or *afferent neurone*, and is one of the nerve cells that are located in the *dorsal root ganglion* of the *dorsal* or *sensory root* of a spinal nerve. One of the processes of the afferent neurone enters the gray matter of the spinal cord and comes in contact with processes of other nerve cells located there. In the case under consideration the impulse would pass through the synapse between the process of the sensory and a process of a *motor* or *efferent neurone* and leave the spinal cord by way of a nerve fiber in the *ventral* or *motor root* of the spinal nerve. The process of the efferent neurone extends to a muscle on which it terminates. The place of contact between a nerve fiber and a muscle is known as a *neuro-muscular junction* (Fig. 70, p. 127). It is by way of such a contact that the impulse is discharged and produces a reaction in the protoplasm of the muscle cell. This reaction is the result of, or the effect produced by, the stimulus received. The muscle is, therefore, known as the *effector* in the reflex arc. The parts of the simplest type of reflex are the receptor, where the stimulus is received; the afferent neurone, over which the impulse passes to the spinal cord; the efferent neurone, over which the impulse passes from the spinal cord; and the effector, where the reaction to the stimulus occurs.

When acid is applied to the skin on a frog's back the first response is a contraction of the muscles of the body wall in that region. This is a simple reflex action. The receptor in this example consists of certain cells in the skin; the afferent neurone is one of the nerve cells lying in the dorsal root ganglion of the spinal nerve that supplies this particular region of the skin; the efferent neu-

FIG. 61.—A. Diagram of a cross-section of the spinal cord showing a pair of spinal nerves and the essential parts of a reflex arc. The neurones necessary for the simplest type of reflex action are present on the left, while those of a typical reflex arc are represented on the right. B. Diagram of spinal cord to show some relations of neurones in reflex arcs. The brain would lie to the right as the diagram is constructed. Arrows in both diagrams indicate the direction of transmission of the nervous impulses.

a.n., afferent or sensory neurone; ad.n.₁, adjustor neurone, transmitting impulses ventrally; ad.n.₂, adjustor neurone, transmitting impulses longitudinally; ad.n.₃, adjustor neurone, transmitting impulses from one side of the cord to the other; d.r., dorsal or sensory root; d.r.g., dorsal root ganglion; E, effector; e.n., efferent or motor neurone; g.m., gray matter; R, receptor; s.n., spinal nerve; v.r., ventral or motor root; w.m., white matter.

rone is one of the nerve cells of the gray matter of that part of the spinal cord; and the effector, a certain muscle lying under the region of stimulated skin. The knee-jerk reflex in man is perhaps even simpler. When the tendon of the muscle that extends the knee is tapped sharply just below the knee cap, the stimulus is received by receptors in the tendon. The impulse is transmitted to the spinal cord over an afferent neurone, and, passing through a synapse in the gray matter, is carried back by way of an efferent neurone to the muscle of the region. This effector, by its reaction to the discharge of the impulse, produces the extension of the knee. In both of these examples the impulse is transmitted to an effector which is in the same region as the receptor. The analogy to light reflection is apparent.

In the great majority of cases of reflex action, we find the effect produced at some part of the body other than that at which the stimulus is received. If the skin of a dog's back be rubbed with a pointed implement, the animal will respond by attempting to scratch the place of stimulation with its hind leg. The receptors in this instance are located at the roots of the hairs of the region of the back that is stroked. The afferent neurone carries the impulse to the spinal cord over the dorsal root of the spinal nerve that supplies the skin region involved. Within the gray matter of the cord, the sensory neurone has a synapse with a neurone of which both the cell body and the processes lie entirely inside the spinal cord. Over the processes of such a neurone the nervous impulse passes posteriorly along the spinal cord to the level of exit of the nerves of the hind legs. Here a synapse occurs with an efferent neurone and the impulse leaves the spinal cord over the ventral root of a spinal nerve, passing to muscles (effectors) that produce the scratching motion.

In this type of reflex there are three neurones concerned (Fig. 61 A). The neurone along which the impulse passes within the spinal cord is known as the *adjustor neurone*. Adjustor neurones are very numerous in the central nervous system and make possible the varied reactions that a single stimulus can produce. For example, when acid is applied to the skin of a frog's back, the first reaction, as has been pointed out, is a contraction of the body-wall muscles in the region stimulated. Very soon, however, this is followed by other reactions which can be easily observed in a frog from which the brain has been removed (Fig. 61 B). The fore leg on the side

stimulated will move toward the location of the acid, and this will be quickly followed by movements of the hind leg on the same side. These movements, tending to remove the source of stimulation, are made possible by the passage of the impulse over adjustor neurones that transmit it posteriorly to efferent neurones leading to muscles of the hind leg. The reactions described occur on the side of the animal to which the acid has been applied. If, under such conditions, the hind leg that is contracting be prevented from moving, the hind leg of the opposite side will respond to the original stimulus by contracting. This effect is the result of adjustor neurones that carry impulses from one side of the spinal cord to the other and make possible bilateral coördination.

Compound Reflexes.—In the examples given we have been concerned with isolated reflexes. That is, particular reflex arcs have been discussed as if they were separable from the remainder of the nervous system. Such is obviously not the case. In fact, if any reflex reaction is completely analyzed it is found to be dependent upon many reflex arcs. This compounding of reflexes, or the interaction between reflex arcs, is the principal method of nervous coördination (Fig. 62).

Any organism at any particular moment is being subjected to many different kinds of stimuli; yet its reactions are orderly and exhibit correlation. One may say, without becoming involved in too theoretical a consideration, that if more than one reflex are stimulated at the same time one of two things may happen. The reflexes may combine for the production of a harmonious effect, in which case they are said to be *allied reflexes*. In contrast to this condition, cases are found where stimuli that occur simultaneously do not produce reflexes that reinforce one another. Instead, one of the reflexes may prevent the others from becoming effective, that is, it may inhibit the others. Such a reflex is said to be *antagonistic* with respect to the others. When an antagonistic reflex or group of reflexes occurs, such reflexes dominate the animal's reactions until they in turn are inhibited or their stimulus is removed. The succession of reflexes, or their occurrence in sequence, is very well understood in some situations and must be a very important factor in reflex coördination. The procedure by which a frog obtains its food involves a sequence or chain of reflexes which has been analyzed. The visual stimulus produced by a moving insect brings about the protrusion of the tongue. If the insect

is captured, its contact with the lining of the mouth stimulates the closure of the mouth. This, in turn, sets in operation the swallowing reflexes, which occur in sequence.

In the cases considered so far, the response to the stimulus has been studied with respect to the usual external conditions that

FIG. 62.—Diagrams showing relations of neurones in different reflex arcs. *A*. A simple reflex arc. *B*. A typical reflex arc showing possibility of longitudinal transmission. *C*. A chain of reflex arcs. *D*. Compound reflex arcs. If the two effectors produce similar action the reflexes are allied. If the action of the effectors should be opposed one or the other is inhibited and the reflexes are antagonistic. *E*. Compound reflex arcs. Here impulses from two receptors use as a "final common path" the efferent neurone to a single effector.

A.N., afferent neurone; *AD.N.*, adjustor neurone; *C*, central nervous system; *E*, effector; *E.N.*, efferent neurone; *R*, receptor. (Redrawn with modifications from Herrick, "Introduction to Neurology," copyright, 1915, by W. B. Saunders Co., printed by permission.)

produce the effect. Pavlov discovered that it was possible to produce what he termed "conditioned" reflexes. For instance, the flow of saliva is a reflex action stimulated normally by the sight of food. Under experimental conditions, a bell may be rung whenever food is given to an animal. After a number of such experiments, the mere ringing of the bell, without the sight of food,

will result in the secretion of saliva. In this way a stimulus that originally had no effect upon the salivary glands has been associated with one to which the glands did respond. As a result of this association, the previously indifferent stimulus becomes effective in producing the reaction. A conditioned reflex has been established. Experiments and analysis of conditioned reflexes make it clear that a very large number of our adjustments are the result of such correlations. Our responses to warning colors, signals, and nationally used signs and symbols are all conditioned reflexes. The same explanation holds for many more subtle and less widely understood adjustments.

This compounding of simple reflexes into allied, antagonistic, and chain reflexes, any or all of which may apparently be conditioned, constitutes what is known as the "behavior" of the animal. The study of certain fields of animal reactions has indicated that behavior is dependent upon the "pattern" and "order" of the reflexes. Pattern is used to indicate the number of simple reflex arcs involved in the compounding and their localization in the nervous system. A study of pattern is essentially one of the "morphology" of behavior, or the tracing of possible pathways of transmission of impulses. The study of order uncovers the time relations that exist in the succession of the pattern elements or simple reflexes.

It is generally recognized that certain forms of behavior, known as *instincts*, are inherited. The nest-building and migratory instincts of birds, for instance, can be explained only on the assumption that both the pattern and the order of the reflexes involved are inherited. Defense instincts of many young animals furnish other examples of inherited behavior. Reactions called *emotions*, such as fear, rage, and love, seem also to be illustrations of the inheritance of both pattern and order.

The consideration of behavior also involves a discussion of *habit*. In habits, both the pattern and the order of reflexes are acquired during the individual's lifetime. Habits of walking, dressing and undressing, eating, and talking are examples in which the pattern and order of reflexes may be determined very early in life. In learning to manipulate a machine one establishes reflexes of a particular kind and order. One has to make only a superficial analysis of the routine procedure of operating an automobile, or writing on a typewriter, to trace the formation and

seriation of the reflexes involved. Learning is the putting together of a series of reflexes which, when they are finally established, become a habit. The retention of habits involves memory of some sort.

In any detailed discussion of behavior that takes account of the distinctions between emotions and instincts, the formation and retention of habits, and the inter-relations that exist between these divisions, the student must follow the investigations and arguments of the psychologists in order to form his opinions. It can be said, however, with an increasing degree of certainty, that analysis of nervous coördination in all its complications depends on knowledge and understanding of the reflex arc.

Principle of the Common Path. — The examples of reflex action that have been given are representative. It can be seen that, beginning with the simplest type of reflex arc, in which one specific response occurs as the result of a stimulus, the series becomes increasingly complex as the result of the interpolation of one or many adjustor neurones between the afferent and efferent neurones. Both simple and complex reflexes may enter into allied and antagonistic combinations or form chains for purposes of coördination. Patterns and orders of compound reflexes are transmitted from generation to generation and give rise to instinctive correlations. The mechanism of the reflex arc obviously makes possible the highest degree of coördination. Sherrington has generalized the facts of nervous coördination in his "principle of the common path." Each afferent neurone is a special pathway by which impulses from its particular receptor enter the central nervous system. Within the central nervous system the impulse may travel over varied paths, formed by synapses between adjustor neurones, and, theoretically, may produce a reaction in any of the effectors. The efferent neurones, over which impulses travel from the central nervous system to the effectors, differ from the afferent neurones in that they are not private paths for particular impulses. It is a commonplace that many different kinds of stimuli can produce the same reaction or effect. Consider, for example, the many and varied stimuli to which man responds by walking. The efferent neurone is, therefore, a "common path" over which impulses from receptive regions all over the body can be discharged at a particular effector (Fig. 62 E). By means of the adjustor neurones of the central nervous system, connections are made pos-

sible between all the special paths that lead from receptive areas and these final common pathways to effector regions. The conduction of impulses according to this principle of the common path furnishes the mechanism for the complicated and varied responses that characterize nervous coördination. By means of this mechanism the animal is enabled to behave as a unit in its reactions to the numerous and changing conditions of its environment.

Localization of Function in the Nervous System

Up to this point, the analysis of nervous coördination has been made in terms of the reflex arc. No particular emphasis has been placed on the position of the neurones involved in these arcs with reference to the morphology of the nervous system. It now becomes interesting to understand the functions of the different parts of the vertebrate nervous system.

Peripheral Nervous System. — The peripheral nervous system consists of spinal, cranial, and autonomic nerves. The general function of these parts of the peripheral system is the transmission of nervous impulses to the central system from receptive regions, and from the central system to the effector organs. In the case of the spinal nerves, it was pointed out that processes of afferent neurones entered the spinal cord over the dorsal roots of spinal nerves, while the processes of efferent neurones passed out along the ventral roots. Such nerves are called "mixed nerves" and may be considered to represent the primitive condition of nerve trunks. Certain of the cranial nerves, as the third or oculomotor, also carry fibers of both sensory and motor neurones. Others carry processes of but one type of neurone. The eighth cranial nerve is made up entirely of processes of afferent neurones from the auditory receptor; while the eleventh and twelfth cranial nerves, found in the higher vertebrates, contain only efferent or motor fibers to striated muscles. Finally, the autonomic nerves, which include the sympathetic system, are entirely efferent, and constitute the "final common paths" to glands and to the muscles of the blood vessels and viscera.

Central Nervous System. — The central nervous system is composed of the spinal cord and brain. As has been repeatedly implied in the discussion of the reflex arc, the general function of the central nervous system is the adjustment of incoming to out-

going impulses. It is in the central system that afferent neurones have synapses with adjustor neurones and these in turn with efferent neurones. The multiplicity of connections thus made possible furnishes the most important part of the mechanism of integration. It is desirable to consider the nature of the adjustment in the different regions of the central nervous system (Fig. 63).

Adjustor neurones in the spinal cord are concerned with the simpler and less complicated of the reflex arcs. In the "scratch" reflex, for instance, adjustor neurones carry the impulse down the spinal cord or may transmit it from side to side. Impulses entering the cord over spinal nerves can also pass upward to the medulla, cerebellum, and diencephalon. The cell bodies of these adjustor neurones are located in the gray matter of the spinal cord, while their processes, which transmit impulses up and down the cord, are to be found in the fiber tracts of the white matter. The white matter also contains groups of nerve fibers which arise from adjustor neurones located in the cerebral cortex, mesencephalon, and medulla. The gray matter of the cord is, therefore, the seat of adjustor neurones which connect different levels of the cord with one another and with parts of the brain, and which carry impulses from one side of the cord to the other. In addition, the efferent neurones, which send processes out through the ventral roots of spinal nerves, are found in the gray matter of the cord. The spinal cord adjusts simple reflexes and transmits impulses to and from the brain.

The primitive brain in vertebrates is composed of the telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon. These parts constitute the so-called "brain stem." The changes in the direction of greater brain complexity occur chiefly in the region of the telencephalon and metencephalon. The cerebral hemispheres arise from the dorsal wall of the telencephalon and, by outgrowth and folding, become the most conspicuous part of the brain in mammals (*cf.* Figs. 39, p. 67, and 288, p. 532). The cerebellum is the dorsal development from the metencephalon. The cerebral hemispheres and cerebellum are the parts in which new functions are added; while the functions of the brain stem remain, for the purposes of this discussion, constant throughout the vertebrate group. In contrast to the arrangement of the white and gray matter of the spinal cord, within the brain the gray matter, which consists of groups of adjustor neurones, occurs in masses,

FIG. 63.—Diagram to illustrate some of the possibilities of nervous coördination. No attempt is made to indicate specific reflex arcs. Impulses travel from receptors to central nervous system and thence to effectors as indicated by the lines and arrows.

A, adjustor neurone; *E*, effector; *R*, receptor.

known as *centers*, which are completely surrounded by white matter, as in the medulla, or form a continuous peripheral layer, as in the cerebrum (Fig. 64). It is impossible to give here a detailed account of the functions of the parts of the brain, but the more important localizations may be given.

The medulla, into which the spinal cord merges, serves as a

FIG. 64.—Diagrams of cross-sections of different regions of the central nervous system to show the distribution of white and gray matter. The regions of gray matter are stippled.

A, spinal cord; B, medulla; C, cerebrum.

pathway between the cord and other parts of the brain. It also contains the centers that control the reflexes of the tongue and of breathing. In the case of the tongue reflexes, afferent neurones enter over the fifth and ninth cranial nerves, and motor neurones pass out along the twelfth nerve. The adjustor neurones lie within the medulla. The respiratory reflex depends upon the sensitivity of the respiratory center in the medulla to the amount

of carbon dioxide in the blood. Efferent neurones pass to the muscles between the ribs and those of the diaphragm. The rhythm of breathing is likewise controlled in the medulla by way of afferent neurones from the walls of the lungs. The medulla also controls other reflexes of the viscera, pharynx, and larynx. At the level of the auditory nerve, certain reflex adjustments of the head and neck to the reception of sound stimuli are made in the medulla.

The ventral part of the metencephalon consists of fiber tracts that transmit from side to side as well as those connecting lower and higher levels. In the cerebellum, or dorsal part of the metencephalon, there are important muscle-coördinating centers. These include adjustments involving the body as a whole, such as the reactions occurring in response to stimuli received by the organs of equilibration, the semicircular canals. The adjustments that result in bilateral muscular coördinations are also made in the cerebellum. Such bilateral coördinations are chiefly those of the voluntary movements of the limbs, although the muscles of the eyes, facial expression, and mastication are also believed by some investigators to be bilaterally correlated by centers in the cerebellum. Finally, the normal tension of voluntary muscle, or what is known as "muscle tonicity," is governed by cerebellar centers.

On the dorsal surface of the mesencephalon are found the optic lobes. In all vertebrates, the optic tracts, which extend from the optic chiasma, end here. Centers are present which control certain important visual reflexes, such as the constriction of the pupil of the eye in response to the stimulus of light on the retina. In the higher vertebrates, certain reflexes following sound stimuli are controlled in the roof of the mesencephalon. The lateral and ventral regions of the midbrain contain many groups of neurones that provide for numerous connections, and fiber tracts over which impulses are relayed from one level to another.

In the diencephalon are many fiber tracts connecting various centers in other parts of the brain with the cerebral cortex. The optic nerves and tracts, carrying impulses from the retinae to the optic lobes, form the floor and part of the lateral walls of the diencephalon (Fig. 67). In the lower vertebrates, all the fibers from one retina cross the optic chiasma to enter the opposite optic lobe. The crossing in higher vertebrates involves only the medial half of the fibers of each retina (Fig. 65), while the fibers of the lateral halves do not cross. Correlations resulting from olfactory stimuli are

made in the diencephalon, and pain sensations are received there. Other centers are in the nature of important relay stations in the compounding of reflexes.

Among the lower vertebrates, the most important parts of the telencephalon are the centers for correlation of impulses transmitted from the olfactory organs. The olfactory centers in mammals occupy the same relative position, but are overshadowed by the very great growth of the roof of the telencephalon to form the cerebral hemispheres. In the cerebral hemispheres, as in the

FIG. 65.—Diagram of the optic chiasma in higher vertebrates. Notice that only the medial nerve fibers cross.

o.c., optic chiasma; *o.n.*, optic nerve; *o.t.*, optic tract which ends in the optic lobe; *r*, retina.

cerebellum, the neurones that make up the gray matter are found in a continuous superficial layer known as the cerebral cortex. Although the cortex is continuous, certain areas are known to be concerned with special functions. Impulses producing movements of the voluntary muscles are sent out to opposite sides of the body from the motor centers of the cortex; that is, if these particular areas of the cortex are destroyed the animal is unable to

use the voluntary muscles on the opposite side of the body. In man, the regions that control movements of the principal parts of the body, from the toes to the face muscles, are known. Another major division of the cortex is concerned with sensory functions, and contains the sensory centers, to which impulses are transmitted from visual, auditory, and olfactory organs, as well as from receptors of pressure, pain, temperature, and taste. These areas have been almost completely mapped out for the human cortex. Surrounding and connecting the motor and sensory centers which occupy a relatively small part of the cortex, are the association centers. These regions are filled with adjustor neurones which are responsible for the complicated pathways of learning processes and which are involved in memory.

"Intelligence," which is a very vague expression for something almost intangible, is dependent upon the degree of development of the cerebral cortex and especially upon the neurones of the association areas. The ability of an animal to profit by experience, which involves analysis of a situation and memory, and which enables the individual to react in a way that is advantageous in a new situation, is determined by its degree of intelligence. This, in turn, is limited by the number of adjustor neurones and the synapses possible between them. It is well known that all the neurones that an animal possesses are present at a very early stage of its development. New synapses are, however, formed throughout the life of the individual and probably depend upon the variety and intensity of the stimuli received by that individual. For example, it has been found that if light be prevented from stimulating the eyes of an animal, such as a dog, the adjustor neurones in the optic lobes do not grow and send out processes in the usual manner (Fig. 66). The sensory impulses that reach the cerebrum, the motor impulses that pass out from it, and the associations made in it constitute our so-called "consciousness." Sleep and anaesthetics in some way lessen or completely block the functioning of the cortex and produce unconsciousness. It is sometimes said that the cortex "initiates" or controls "voluntary" movements. While there is no necessity of entering upon a discussion of the "will," it must be remarked that, so far as the physiology of the nervous system is understood, the motor centers of the cerebrum transmit impulses produced by stimuli, just as do other parts of the central system. The sources of the stimuli may be difficult to locate, but that does not seem to be a sufficient reason for departing from the neurone mechanism as an explanation.

In order to make clear the functions of the nervous system, the analogy to a telephone system is sometimes employed. The various lines that place individual telephones in connection with one another would correspond roughly to the peripheral system. "Central" occupies a position similar to the central nervous system. If we had in our telephone system certain lines that connected one central office with another central office, these would correspond to the adjustor neurones.

It is also possible to compare the nervous mechanism of the vertebrate to the administrative organization of any efficiently managed commercial enterprise. There are the different phases

of buying, selling, financing, crediting, personnel, etc. In each of these departments, adjustments that concern it alone are constantly being made. If one makes a cash-and-carry purchase in a large department store, the process can be compared to a simple reflex action. The clerk making the sale has the package wrapped, obtains the change, and returns these to the purchaser. No other part of the sales department is concerned. If, however, the buyer wishes to shop in several parts of the store and pay when the list of purchases is complete, the floor managers concerned must

FIG. 66.—A. Undeveloped adjustor neurones in the optic lobe of a dog, the eyelids of which had been sewed together immediately after birth. B. Fully developed adjustor neurones in the same region of a normal dog of the same age.

(From Verworn, "Irritability," copyright, 1913, by Yale University Press, reprinted by permission.)

approve the transactions, and payment is finally made in a special part of the sales department. Such a situation can be compared to a series of reflexes adjusted by the spinal cord. The several departments are not independent of one another. Let us suppose that clerks in a certain sales division report to the floor manager that customers are inquiring for some product that is not in stock. The floor manager may relay this information through certain intermediate officials to the sales manager of the establishment. The sales manager may consult with the purchasing manager, who will be aware of the source of supply of the desired material and will

start the proper movements to acquire some of it, to satisfy the customers' demands. This series of events corresponds in a way to the allied and chain reflexes that are controlled by centers of the brain other than those of the cerebral cortex.

We may next assume that the sales and purchasing managers cannot adjust the situation that is presented to them until the points involved have been passed on by higher officials. A general policy of the firm may have to be considered. In that case the

FIG. 67.—A. Section of a bird's retina showing all the cell-layers. The rods and cones are the blackened cells in layers 6 and 7. The inner ends of their processes have synapses, in layer 5, with processes of the bipolar neurones that pass across layer 4. In layer 3 the bipolar neurone processes have synapses with dendrites of the neurones of layer 2. The axons of the nerve cells of layer 2 make up the optic nerve and pass out from layer 1. B. Showing three outer layers of retina. The middle cell is a cone, the three on each side are rods.

(Both figures from Schäfer, "Essentials of Histology," copyright, 1916, by Longmans, Green and Co., reprinted by permission.)

information would finally be carried to the directors, who with all the details before them would adjust the situation, with reference to previous circumstances, in the way that was best for the company's affairs. This decision of the directors would be placed in effect by the lesser officials who handle many matters without the directors' immediate consent. The actions of the directors can be thought of as being comparable with conscious cerebral adjustments in the higher vertebrates, where previous experience based on many types of stimuli results in intelligent coördination

of the animal in a given situation. It should be clear to the student that in any organism the vast majority of adjustments are not conscious, and that, in general, the simplest of these adjustments occur in the spinal cord, the more complex in the brain.

In summarizing the details of functional localization, it may be said that the central nervous system has the general function of adjustment of impulses, while the peripheral system furnishes transmission paths between all parts of the body and the central system. By the combined functions of the nervous system as a whole, the activities of the organism are correlated so that it behaves as a unit. This result is also known as coördination or integration. The degree of integration of which an animal is capable determines its ability to react successfully to the environment, which is the most important factor in its survival. The increase in the complexity and specialization of the nervous system has therefore been said to be the chief factor in evolution. As Gaskell puts it, "The law of progress is this: The race is not to the swift, nor to the strong, but to the wise."

Reception, Transmission, and Discharge

It has been pointed out that nervous coördination depends essentially upon three factors. In the first place, the organism must be able to be aware of changes in its environment, that is, to receive stimuli. The stimulus sets up an impulse which must be transmitted. And, finally, the animal responds to the stimulus because the impulse is discharged at some effector. Theories of reception, transmission, and discharge are rather complicated, and the processes are not well understood. However, certain statements can be made.

Animals like the vertebrates possess sense-organs which are specialized for the reception of stimuli. These sensory areas, or receptors, are sensitive to special kinds of stimuli. The retina of the eye is a receptor for changes in the environment brought about by light waves (Fig. 67). In the lower fishes, the ear is primarily a receptor for stimuli produced by changes in the animal's equilibrium. The semicircular canals of the ear in higher vertebrates retain this function, while the cochlea becomes specialized to receive sound waves (Fig. 68). Chemical substances in solution stimulate the olfactory epithelium of the nose and the taste-buds of the

mouth (Fig. 69). Certain areas of the skin are sensitive to changes in temperature, others to pressure. In addition to these receptors, by means of which the organism is made aware of external environmental changes, there are receptors in all the internal organs of the body. The nature of the specialization involved in receptor surfaces is not understood, but their specificity is well known. Sound waves will not start an impulse in the retina. On the

FIG. 68.—Diagram of human ear.

A, the auditory canal leading from the external ear to the tympanic membrane at B; C, cavity of the middle ear containing the "ear-bones" that transmit vibrations from the tympanic membrane to the inner ear; D, the pharynx with which the cavity of the middle ear is connected by the Eustachian tube; E, semicircular canals of the inner ear; F, cochlea; G, auditory nerve. (From Hough and Sedgwick, "Human Mechanism," copyright, 1918, by Ginn and Co., reprinted by permission.)

other hand, if the optic nerve is stimulated mechanically, the impulse started results in a visual sensation. The person who says he "sees stars" when he gets a "black eye" has scientific foundation for his assertion. Receptors normally are sensitive to only one type of stimulus, and if they are stimulated by unusual methods the impulse produces the typical sensation. This latter effect may be due to the specificity of reaction of the brain center to which the impulse is conveyed.

The reception of a stimulus by a sensory area is followed by the

transmission of a nervous impulse along the afferent neurones associated with the area. Nerves were at first thought to be tubes that conducted the "animal spirits," which were supposed to be like gas. Later the material carried by the tube was believed to be more like water and was called "animal juice." The nature of the nervous impulse and its transmission still remains a puzzle in many respects and engages the attention of many investigators. Some workers have believed that the transmission of the nervous impulse is a wave of chemical reactions along the nerve fiber. The analogy

FIG. 69.—*A*, Cells of olfactory epithelium from human nose. *B*, Cells of a taste bud in epithelium of tongue. In both cases the sensory cells terminate externally in hair-like processes that are able to receive the chemical stimuli of olfaction or smell, and gustation or taste.

ep, epithelium of tongue; *gc*, gustatory cell; *oc*, olfactory cell; *p*, pore or external opening of epithelial cup in which the taste bud is located; *sc*, sustentacular or supporting non-sensory cell.

to the burning of a path of gunpowder is often made. This idea involves metabolic activities of a destructive kind in the neurone process. Such metabolism uses oxygen and liberates carbon dioxide and heat. It also is limited by the amount of combining constituents of the protoplasm. The production of carbon dioxide and heat in sufficient quantities to justify a chemical interpretation of transmission has not been demonstrated. The fact that it is almost impossible to detect signs of fatigue, or loss of capacity to transmit in a bundle of nerve fibers, is also an argument against the metabolic theory. Opposed to the chemical interpretation is the physical theory, which explains transmission as the passage of an electric current. The velocity of nervous transmission varies from 27 to 125 meters per second in the cases measured. This is, of

course, much slower than electrical transmission through metals or air. That an electric current occurs simultaneously with the transmission of an impulse has been clearly established, although it must be granted that that does not prove they are one and the same. It may well be that the process is dependent upon both chemical and physical factors.

An interesting feature of transmission is that the direction of conduction in the fiber is not reversible. Afferent fibers always carry impulses toward the central nervous system; efferent fibers always carry impulses away from the central system. No fundamental difference in the morphology of these fibers has been found. It was stated above that it was impossible to fatigue a nerve trunk, that is, to diminish its capacity to transmit impulses. However, fatigue occurs when the impulse is permitted to pass over the entire reflex arc and produce an effect. Conduction through the central nervous system includes transmission through synapses that connect neurones. The evidence indicates that changes occurring in the synapses are responsible for nerve fatigue.

When the impulse reaches the effector cell, it passes through the neuromuscular junction, or end organ, to the protoplasm (Fig. 70). This is the discharge of the impulse, and little is known of its nature. It has been mentioned before that the same response can be obtained in an effector by impulses coming from many different types of receptors. Nervous control may be said to be of two kinds, excitation and inhibition. The effector reacts as a result of excitation. Its reaction ceases as the result of inhibition. Inhibition might be brought about by blocking the transmission of the exciting impulse, by altering the mechanism of reaction in the protoplasm of the effector, or by making the neuromuscular junction non-functional. Some evidence indicates that inhibition

FIG. 70. — Neuromuscular junction of a medullated nerve and striated muscle. Note that the medullary sheath does not cover the branches of the nerve fiber that come into intimate contact with the muscle cell.

ms, medullary sheath; *n*, neurilemma; *nf*, nerve fiber. (From Schäfer, "Essentials of Histology," copyright, 1916, by Longmans, Green and Co., reprinted by permission.)

results from an alteration of cell metabolism which affects the junction between the nerve and the effector. It therefore appears that, like receptors, effectors are highly specialized and react in a particular way or not at all.

Coördination and Irritability

It must not be forgotten that coördination in any organism depends in the last analysis upon the irritability of protoplasm. The unicellular animals respond directly to changes in their environment which are received and become effective in the protoplasm of the same cell. That certain of the individual cells of multicellular organisms retain the capacity to respond directly to changes in their immediate surroundings is clear from the nature of chemical coördination. It will be recalled that endocrines carried in the blood and lymph produce reactions by direct stimulation. However, it is impossible for each cell in a highly organized multicellular animal to be directly stimulated by changes in the environment of the organism as a whole. Integration of the many-celled animal is accomplished by means of the mechanism of the neurone arcs of the nervous system, connecting receptors and effectors according to the principle of the common path. This coördination of higher forms is associated with great specialization of cells and regions. A particular receptor receives only a certain kind of stimulus; neurones conduct impulses in only one direction; and effectors respond in a distinctive manner to discharged impulses. The question of the fundamental nature of this specialization is one that cannot be answered at present. Nor, for that matter, can the essential character of irritability be clearly explained. Certain facts point to a close association between metabolism and irritability. In other words, if the metabolism of a cell is altered its irritability may be changed. Metabolism, in turn, depends in some way upon the physico-chemical nature of protoplasm. The complete explanation of irritability and coördination, therefore, awaits further knowledge of the physics and chemistry of protoplasm. It is, fortunately, quite possible to understand to a greater or lesser degree the outward expression of protoplasmic irritability in the behavior of animals.

REPRODUCTION

Protoplasm has three distinguishing capacities: metabolism, irritability, and reproduction. Protoplasm always occurs in units called cells. A single cell may be a complete organism, or a group of cells may be associated to form an individual. Reproduction can therefore be defined as the capacity, under varied conditions, of certain parts of organisms to detach themselves, and, either alone or after union with protoplasm of another organism of the same kind, to give rise to new individuals in all essential respects like the parent or parents. The function of reproduction differs from metabolism and irritability in that it is not necessary for the maintenance of the life of the individual; it is the capacity upon which depends the continuity of the race or species.

To understand the physiology of reproduction, one must have a knowledge of the differentiation of the gametes or germ cells, the problems of fertilization or the union of gametes in pairs to form zygotes, the development of zygotes in characteristic ways, and heredity and variation in the new individuals. Much more is known of the morphology than of the physiology of these phases of reproduction. As these topics are considered in the special chapter on Reproduction and in the chapters on Development and Genetics, no further discussion of reproduction will be undertaken at this point.

CHAPTER 6

CELLS OF THE VERTEBRATE BODY

In the preceding chapters the functions of metabolism, irritability, and reproduction in the vertebrate organism were discussed. Such a consideration of function, together with that of the structure or anatomy of the vertebrate, conveys a rather definite idea concerning the animal as an individual, possessing the complex and highly coördinated organization that is familiar in the higher types. It is evident, however, that in order to explain the outward manifestations of life one must understand the activities that are characteristic of protoplasm as it occurs in the animal cell. The individual organism is an association of cells, which make up its structure and determine its functions by their correlated interdependence. A fundamental understanding of cells is necessary for the explanation of the normal morphology and physiology of the individual. It is also true that the appearance of cells furnishes the evidence that enables us to analyze and classify the abnormal conditions which exist in diseased organisms, and which are determined by the science of Pathology.

As will be pointed out in the chapters on development, the processes whereby the adult individual arises from the germ cells, through all the stages of cell division and differentiation, are, essentially and without exception, cell phenomena. Embryology is best understood as the behavior of cells during the development of organisms. In addition, the subject of Genetics, or the study of heredity and variation, can be explained satisfactorily only when one makes clear the cell phenomena that are correlated with the inheritance of characteristics from generation to generation. Hence, the science of Cytology, which deals with all aspects of cell structure and activity, explains phenomena in all fields of biological investigation. For the student of General Zoology, this fundamental knowledge of cells is best obtained through the detailed consideration of a particular subject. In the present chapter the

general facts about cells will be explained, the expansion of these facts and their relation to particular fields being left for later chapters on these topics.

FIG. 71.—A and B. Leeuwenhoek's microscope (about 1673). C. Hooke's compound microscope (1665).

(From Carpenter, "The Microscope and its Revelations," copyright, 1891, by J. and A. Churchill, reprinted by permission.)

Historical Development of the Cell Doctrine

The discovery of cells was made possible by the use of the microscope, which was invented about 1591. This instrument was first used as a toy, but about 1650 it began to be utilized in scientific

studies (Fig. 71). Robert Hooke, one of the early English microscopists, discovered that cork was composed of small spaces, surrounded by firm walls, and in 1665 he gave the name *cell* to these compartments (Fig. 72). The development of microscopic instruments was very slow, and it was not until 1833 that Robert Brown observed, in certain plant structures, that each cell contained a small body, which he called the nucleus. In 1838, Schleiden, a

FIG. 72.—A. Diagram of cork to show cell walls of plant cells. B. Squamous epithelium to show nucleus and protoplasm in the animal cell. There are no cell walls.

cw, cell wall; *n*, nucleus; *p*, protoplasm.

German botanist, proposed the interpretation that cells were the units of structure in plants, and Schwann in 1839 extended this conception to the structure of animals (Fig. 73). This was the first formulation of the *Cell Theory*.

The founders of this theory, and other scientists of that time, believed that the walls that surround plant cells were the essential part of these units. The contents of cells had been observed, but were regarded as unimportant or as waste products. Purkinje, in 1840, and von Mohl, in 1846, gave the name *protoplasm* to the cell contents. Through a series of researches, it became apparent that protoplasm was the essential part of cells, since walls were found only in plant cells. Likewise, the presence of a *nucleus* was discovered in almost all types of cells, and a cell came to be described as a mass of protoplasm containing a nucleus.

As knowledge became more complete it was ascertained that in certain parts of the animal much material which is not in the form of cells lies between them. This material, examples of which will be given later, was shown to be produced by cells, and the Cell Theory was modified by saying that organisms are composed of structural units, called cells, and of cell products. Further study of animals with reference to their activities has revealed the fact that all physiological processes must be understood in terms of the functions of cells. That is, the cell is the unit of function. The Cell Theory has, therefore, been extended and

confirmed, and now stands as one of the fundamental generalizations of biological science, being known as the *Cell Doctrine*. A complete statement of this unifying conception of Biology would be that all living organisms are composed of cells, which are the units of structure and function, and of cell products. In complex organisms these units are not isolated; but the coördination, both structural and functional, between the different kinds of cells, is ex-

FIG. 73.—M. Schleiden, 1804–1881 (on the left); and Theodor Schwann, 1810–1882 (on the right).

(From Loey, "Biology and its Makers," copyright, 1908, by Henry Holt and Co., reprinted by permission.)

pressed in the well-known fact that the animal, as a whole, constitutes a higher type of unit, the individual. This is sometimes called the Organismal Theory. It is based upon the observed fact that cells associated in a complex organism are coördinated, by their own activities, in such a way that the animal is an individual.

Structure of a Typical Cell

A cell may be correctly defined, in a general way, as a mass of protoplasm containing a nucleus. It is true, however, that certain cells, notably the red blood cells of mammals, do not contain nuclei after they reach the final stage in their development. If

the definition is to hold for all cases, it must be modified to the effect that a cell is a mass of protoplasm which, at some stage in its development, contains a nucleus. This statement, together with the definition of a cell as the unit of structure and function, is of fundamental importance in further consideration of cells. Structurally, cells are divided into two main parts, the *cytosome*, or cell body, and the *nucleus*. In the following account these parts will

FIG. 74.—Diagram of a typical animal cell.

c.m., cell membrane; *c.r.*, cytoplasmic reticulum; *cso*, centriole or centrosome; *csp*, centrosphere; *f*, fat; *g.b.*, Golgi elements; *l*, linin; *m*, mitochondria; *n.k.*, net knot of chromatin granules; *n.m.*, nuclear membrane; *nu*, nucleolus; *v*, vesicles; *y*, yolk.

be considered as they occur in what may be called a typical cell (Fig. 74).

The Cytosome.—The cytosome is limited externally by the *cell membrane* or plasma membrane, which is generally regarded as a firmer layer of the *cytoplasm*. In some cases a reticulation is indicated in the cytosome, but this is not a constant feature. Lying near the nuclear membrane, a differentiated,

rounded area of cytoplasm, the *centrosphere* encloses one or two small granules, the *centrioles* or centrosomes. The centrosphere and centrioles are conspicuous structures during mitotic cell division (*cf.* p. 137). A number of bodies found more or less commonly in the ground substance of the cytoplasm are grouped under the name of *cytoplasmic inclusions*. *Mitochondria* are the most universal members of this group. These are small granules, isolated or arranged in rows; they are typically scattered throughout the cytosome but may be more numerous in some regions. *Golgi elements* have been observed in many cells. *Fatty products* of metabolism are stored as larger or smaller drops in the majority of cell bodies. *Yolk*, built up in the cytoplasm, is stored in the form of yolk plates or spheres in egg cells. In many cases, *vesicles*, filled with solutions of unknown composition, are present. When the contents of these vesicles are lost they may appear as vacuoles. Secretions produced in gland cells are stored as *secretion granules* until they are passed from the cells. Granules of *pigment* characterize many cells. These cytoplasmic inclusions constitute a rather diversified group, and full understanding of their origin and function is dependent on information, much of which is yet to be gained, concerning the metabolism of the cell.

The Nucleus. — The nucleus, which is usually round and centrally located, is everywhere surrounded by the cytosome. It is separated from the cytoplasm by a continuous bounding membrane, the *nuclear membrane*, and typically exhibits a fine framework known as the *linin net*. Scattered on the linin are fine granules which are called *chromatin*, because with some stains they color very intensely. These chromatin granules are frequently aggregated on the nuclear framework to form *net knots*. Chromatin is the material that has been shown to be closely correlated with the mechanism of heredity. Further description of its behavior will be given in the accounts of cell division and maturation. Lying in the meshes of the linin net are found one or more rounded bodies, the *nucleoli* or plasmasomes. Nucleoli have been interpreted as waste products of nuclear metabolism, but a growing mass of evidence seems to indicate their more fundamental importance as perhaps temporary storage products of such metabolism. The nuclear components described above are embedded in the ground substance of *nucleoplasm*.

Both nucleus and cytosome are necessary for the normal activities of the cell. It is not entirely possible to define the part each plays in the metabolism of the whole. Cells that are deprived of their nuclei are unable to carry on assimilation, although dissimilation goes on until the cytoplasm is exhausted. This fact and other types of experimental evidence would seem to indicate that the nucleus may be a place where enzymes necessary for assimilation are produced, but that the cytosome is the principal region of synthetic activity and energy transformation in the cell. Whether or not such a distinction can be sharply drawn, it cannot be doubted that there is very close interdependence between these two morphological divisions, and that the life of the cell depends upon balanced interactions between nucleus and cytosome.

Cell Division

When cells were first discovered they were thought to arise spontaneously by a sort of crystallization. The nucleus was interpreted by some early investigators as a new cell in process of formation. As the microscope was perfected and more observations were made, it was found that new cells were formed as the result of the division of previously existing cells, and in no other manner. It will be recalled that the amount of protoplasm increases when assimilation exceeds dissimilation. During this period the cell is said to be in the vegetative or nutritive stage. The cell is sometimes referred to, at this time, as a "resting" cell, but nothing could less adequately describe it during this period of metabolic activity. When the cell has reached a certain size it divides. Whether or not cell size is the only factor governing cell division, it is certainly a very important one. Cells divide by two different methods: *amitosis*, or direct cell division; and *mitosis*, or indirect cell division. Mitosis is by far the more common method.

Amitosis. — In amitosis or direct cell division, the nucleus of the cell becomes somewhat elongated and is pinched into two parts which are about equal in volume. The nuclei of certain types of cells may divide amitotically without division of their cytosomes and thus give rise to multinucleate cells. In complete amitosis, after the nucleus is constricted the cytosome divides and two new cells are formed. In this direct process of division the distribution of cell components is only approximately equal. Such a type of

division apparently occurs only in cells that are very specialized, very old, or in some abnormal or degenerating condition (Fig. 75).

Mitosis. — Mitosis is the typical method of cell division. It is called the indirect method because it involves changes that are more complicated than the simple constriction of amitosis. The process is divided, for purposes of description, into four stages, which are continuous.

These are the *prophase*, the *metaphase*, the *anaphase*, and the *telophase*.

The structure of a typical vegetative cell should be recalled (Fig. 74). Among the earliest changes in the **prophase** of mitosis are those of the centrosphere and centrioles. If the cell contains

FIG. 75.—Amitosis in tendon cells of a newborn mouse. (After Nowikoff.)

nc., nucleolus. (From Kellicott, "General Embryology," copyright, 1913, by Henry Holt and Co., reprinted by permission.)

only one centriole, this divides and the two halves begin to separate, passing toward opposite sides of the nucleus (Fig. 76). The centrosphere elongates and gives rise to fine fibers, the *spindle fibers*, which extend between the centrioles as they migrate, and also to delicate strands, the *astral rays*, which radiate freely from the centrioles. Collectively, these structures are called the *mitotic spindle* because of the arrangement of the fibers, the *amphiaser*, because of the resemblance to a double star, or the *achromatic figure*, because these structures do not stain. Within the nucleus the chromatic granules become associated in delicate threads which form what is known as the *spireme*. It is the formation of these threads that gives the name mitosis (from *mitos*, thread) to this kind of cell division. As the prophase progresses, the chromatin threads condense to form bodies known as *chromosomes*. These chromosomes are constant in number, size, and shape for the cells of any particular species of animal. As migration of the centrioles, formation of the amphiaser, and condensation of the chromosomes progresses, the nuclear membrane and nucleolus disappear. When the nuclear membrane is broken down, the spindle comes to lie in the region of the nucleus and the chro-

FIG. 76.—Diagram of mitosis, or indirect cell division, showing four chromosomes.

a.r., astral ray; *as*, aster; *ce*, centriole or centrosome; *chr*, chromatin; *chs*, chromosome; *cs*, centrosphere; *d.c.*, daughter cell; *d.chs.*, daughter chromosome; *e.p.*, equatorial plate; *ne*, nucleolus; *n.m.*, nuclear membrane; *s*, mitotic spindle; *sp*, spireme.

mosomes take up a position in the spindle, halfway between the centrioles, to form the so-called *equatorial plate*.

During the **metaphase**, the longitudinal division of each chromosome into halves becomes conspicuous. This splitting of the chromosomes occurs at different periods in the prophase, but is more easily observed during the metaphase as the half-chromosomes lie side by side on the equatorial plate of the division spindle. The fact that the chromosomes divide in this manner is of theoretical significance, because regions of chromosomes are believed to differ from one another along the longitudinal axis. The genes, or determiners of hereditary characteristics, located in the chromosomes are believed to be arranged like beads on a string. The longitudinal division of chromosomes is, therefore, thought to be equal with respect to quality as well as quantity of chromatin. The importance of the chromosomes and their behavior in correlation with the mechanism of heredity will be more fully discussed in the chapter on Genetics.

Following the period of inactivity of the chromosomes as they lie on the equatorial plate, the halves of each chromosome begin to separate and move toward opposite centrioles. This migration constitutes the **anaphase**. No satisfactory explanation of the physical principle underlying the movement of the half-chromosomes toward the ends of the spindle has been proposed. That certain of the spindle fibers are attached at specific points to the chromosomes is an established fact.

The **telophase**, or reconstruction of nuclei, begins when the half-chromosomes approach the centrioles. The chromosomes more or less reverse the process of their formation during the prophase. They become irregular in outline, and are redistributed as chromatin granules on the linin network of the new nucleus, which is set off by the appearance of a nuclear membrane. In this way, daughter nuclei, containing chromatin equal in amount and kind, are established at each end of the mitotic spindle. As nuclear reconstruction goes on, the astral rays and spindle fibers disappear, and in some types of cells each centriole divides. At the same time the cytosome becomes constricted so as to form approximately equal halves, each of the daughter cells containing one of the daughter nuclei and a centrosphere with one or two centrioles.

This process of indirect cell division is regarded as essentially a mechanism for insuring equal qualitative and quantitative dis-

tribution of the chromatin of a cell to its two daughter cells. In particular instances, variations in certain features may occur, but the essential significance of mitosis is the same throughout the animal kingdom.

Histology

Tissues. — In the preceding section a so-called typical cell has been described. If the body of a vertebrate is examined microscopically, it will be found that no cell conforms to the diagram of a typical cell. In other words, cells differ among themselves although they all contain certain features in common. Cells differ in respect to size, shape, position in the body, and also in the functions that they are especially fitted to perform. Cells that are similar in structure and function make up groups known as tissues. *Tissues*, then, are groups of cells specialized in the same way for the performance of the same function, and are classified on the basis of the structure and function. There are four principal classes of tissues: *epithelial*, *sustentative*, *contractile*, and *nervous*.

Epithelial Tissue. — The cells of epithelial tissues are compactly placed with but a small amount of intercellular material, and function for the covering and protection of body surfaces, both internal and external, and in secretion and excretion. According to the predominating form of cells, this class is subdivided into *squamous* and *columnar epithelium*, each of which is again divided into *simple* or *stratified*, depending upon whether it exists in single or multiple layers. The cells of simple squamous epithelium, when viewed from the surface, resemble tiling-blocks, and on edge they are very thin (Fig. 77 A). Such epithelium, sometimes called endothelium, is found lining the coelome, that is, forming the peritoneum; it also forms the lining of blood vessels (Fig. 77 B). In stratified squamous epithelium only the outermost layers are typically flattened cells, while the cells of the deeper layers are progressively more cuboidal (Fig. 77 C). Since blood vessels do not penetrate epithelial layers, it is only the cells of the deeper layers that receive abundant nourishment and consequently divide and replenish the outer layers, which die and are cast off. Stratified squamous epithelium is found in the outer layer of the skin and in the lining of the nasal and mouth cavities of many vertebrates. In simple columnar epithelium, such as that lining the digestive tract, the

cells are longer than they are wide and are arranged side by side (Fig. 77 D). Stratified columnar epithelium is not abundant, but a modified type is found lining the trachea (Fig. 77 E). Columnar epithelial cells are sometimes modified by having their free surfaces, that is, the surfaces exposed to the cavity that they line, covered with *cilia*, which are fine, hair-like cytoplasmic processes

FIG. 77.—Epithelial tissues. A. Simple squamous epithelium from human mouth. B. Simple squamous epithelium (endothelium) from peritoneum. C. Stratified squamous epithelium from lining of nasal canal. D. Simple columnar epithelium from mucous membrane of digestive tract. E. Pseudostratified ciliated columnar epithelium from lining of trachea. One cell is shown secreting a drop of mucus. F. Simple ciliated columnar epithelium. G. Glandular epithelium from the pancreas. H. Goblet cell with drop of mucus.

(A, B, and C from drawings by D. F. Robertson.)

(Fig. 77 F). The cilia are vibratile and, by their motion, act to keep the surfaces clean. The epithelium of the air passages in higher vertebrates and the roof of the frog's mouth offer examples of this variation.

In the retina and in other places, epithelial cells are sometimes characterized by pigment granules and known as pigmented epi-

thelium. In organs of secretion, columnar epithelium is modified as glandular epithelium for the production of certain types of secretions (Fig. 77 G). Epithelial cells, temporarily modified as gland cells, occur as *goblet cells* (Fig. 77 H), so called because distended by a drop of mucus, in the mucous membrane of the digestive tract. Sometimes glandular epithelial cells occur in groups, and these cell groups may sink below the general surface (Fig. 78). Such groups of cells may form simple tubes, constituting *simple tubular glands*, like the gastric glands; or flask-shaped struc-

FIG. 78.—Diagrams of glands. A. Unicellular glands. The one to the left is shown extending below the surface epithelium. B. A group of gland cells remaining in the surface epithelium. C. A simple alveolar gland. D. A simple tubular gland. E. A compound tubular gland. F. A compound alveolar gland.

d, duct; *gc*, gland cell; *se*, cells of surface epithelium.

tures, making *simple alveolar glands*, such as those of the frog's skin. Secretion may occur in all cells of these glands; or it may be confined to the basal cells, while those leading to the surface form the *duct* or tube by way of which the secretion leaves the gland. A *compound tubular gland*, like the liver, or a *compound alveolar gland*, such as the pancreas, is formed by outpocketings from an original simple type (Fig. 78).

Sustentative Tissue.—The sustentative tissues are a very heterogeneous group, classed together because they are all derived during development from the same source—the stellate mesen-

chyme cells (Fig. 79 B). In general, they function in supporting the body and connecting or binding together its parts. Sustentative tissues are characterized by a large amount of intercellular material, which is produced by the cells. In the vertebrates, it is, for the most part, this intercellular material that furnishes the supporting and connecting qualities. Sustentative tissue may be divided into five sub-classes: *connective*, *cartilage*, *bone*, *adipose*, and *vascular*.

Connective tissues are of three kinds: *mucous*, in which the intercellular material is gelatinous, and which is found in the umbilical cords of mammals (Fig. 79 A); *reticular*, in which there is a mesh-work of connective tissue cells with the interspaces filled with other types of cells, and which forms the groundwork of organs like the spleen (Fig. 79 C); and *fibrous*, in which the intercellular material is composed of fibers, and which is widely distributed as a binding tissue in many organs. The intercellular fibers of fibrous connective tissue are of two kinds, white and elastic. *White fibers* are very fine and occur in bundles, while *elastic fibers* are thicker and occur singly. Fibrous connective tissue in which both white and elastic fibers occur is found in the submucous layer of the digestive tract and in the dermis of the skin (Fig. 79 D). Fibrous connective tissue in which white fibers predominate is found in tendons, and that containing chiefly elastic fibers is found in the walls of larger arteries and in certain ligaments (Fig. 79 E). The cells of fibrous connective tissue are spindle-shaped or irregular in outline and possess relatively little cytoplasm.

The second sub-class of sustentative tissues is *cartilage*, which is a supporting tissue. The intercellular material in cartilage is usually hardened by impregnation with mineral salts, chiefly those of calcium. Here the cells are more or less rounded and lie in spaces known as *lacunæ*. Where the matrix between the cells is translucent and apparently structureless, the tissue is called *hyaline cartilage*, or gristle (Fig. 79 G). Such tissue is found at the ends of long bones, at the ends of ribs, and in the cartilages of the nose and trachea. The cartilage of the external ear contains elastic fibers in its matrix and is, therefore, known as *elastic cartilage* (Fig. 79 H), while that found between the vertebræ has white fibers in its matrix and is *fibrous cartilage* (Fig. 79 I).

Bone, or osseous tissue, is characterized by its very hard matrix, which is impregnated with lime salts. There is twice as much inor-

FIG. 79.—Sustentative tissues. *A*. Cells of mucous connective tissue which occurs in the umbilical cords of mammals. The gelatinous intercellular material is not represented. *B*. Mesenchyme cells. *C*. Reticular connective tissue from the spleen. *D*. Fibrous connective tissue from the submucosa showing both white and elastic fibers. *E*. Elastic fibers of fibrous connective tissue from the nuchal ligament of the ox. *F*. Adipose tissue showing various stages of storage of fat drops in the cells. *G*. Hyaline cartilage from the end of a rib. *H*. Elastic cartilage from the external ear. *I*. Fibrous cartilage from an intervertebral disc. *J*. Bone cell lying in a lacuna. *K*. Bone lacunæ and canaliculi from dried bone. *L*. Haversian system in which lacunæ are arranged concentrically around a central or Haversian canal.

Canaliculi connect lacunæ and canal.

cc, cartilage cell; *cl*, lacuna in which cartilage cell lies; *ef*, elastic fiber; *fd*, fat drop; *hc*, capsule of hyaline cartilage, surrounding cells of elastic and fibrous cartilage; *wf*, white fiber. (*A*, *E*, *H*, *K*, and *L* from drawings by D. F. Robertson.)

ganic material as organic in bone. The long bones of the body, such as the femur, have a central marrow cavity filled with bone marrow, where red blood cells are formed. This marrow is, however, not osseous tissue but is merely contained in the cavities of bones. The bone cells (Fig. 79 J and K) lie in lacunæ within the matrix. A very typical arrangement is that of the *Haversian system*. This consists of a central Haversian canal, containing an artery, a vein, and a nerve, surrounded by concentrically arranged rows of lacunæ which are in communication with one another and with the central canal by means of minute spaces, the *canaliculi* (Fig. 79 L). Lymph circulates in these canaliculi and furnishes a passageway for foods and wastes between blood and cells.

In *adipose tissue* there is no intercellular material, and the stellate mesenchyme cells become transformed into rounded cells which serve as storage depots for fat (Fig. 79 F). In fully developed adipose cells there is a very large drop of neutral fat with only a film of cytoplasm surrounding it and containing the nucleus. The large drop of fat is formed during the specialization of fat-storing cells, by the coalescence of numerous finer drops that are deposited in the cytoplasm.

Vascular tissue, which is subdivided into *blood* and *lymph*, is characterized by its fluid intercellular material, the *plasma*. In blood, two kinds of cells are suspended in the plasma. Of these the red cells, or *erythrocytes*, contain the iron-bearing hæmoglobin, in combination with which oxygen is carried in the blood (Fig. 80 A and B). In mammals, the red blood cells lose their nuclei at maturity, are consequently very short-lived, and must be constantly replaced. The chief source of red cells is the bone marrow, but some are apparently formed in the spleen. Of the white blood cells, the *leucocytes* are granular, irregular in form, and move by changing their shapes, in the same manner as the amœba, one of the single-celled animals (Fig. 80 C). Hence, they are said to possess amœboid movement. In this way they are able to migrate through the walls of the capillaries. Leucocytes are also able to take solid particles, like bacteria and other foreign bodies, into their cytoplasm and so remove them from other tissues. They so function in the case of infections in any part of the body. *Lymphocytes* are non-granular white blood cells (Fig. 80 D). The source of white blood cells is chiefly the lymph glands and spleen. Blood plasma is believed to be the carrier for all substances transported by the blood, save

oxygen. It possesses the capacity of clotting when drawn from the vessels. During clotting, a mass of fine fibers, composed of a simple protein material, the *fibrin*, appears, and the cells are held in its meshes. The plasma that is left can be separated from fibrin and cells and forms the *serum* that is used in immunizing against certain diseases. Lymph differs from blood in that it does not contain erythrocytes but is composed of plasma and colorless cells. The importance of lymph as the pathway between blood and tissues should be recalled.

Contractile Tissue. — Contractile tissues are known as muscles, and are of three kinds: *non-striated*, *cardiac*, and *striated*. The

FIG. 80.—A. Mammalian erythrocytes arranged in rouleaux. B. Single mammalian erythrocyte. C. Leucocytes with polymorphic nuclei. D. Lymphocytes.

cytoplasm of muscle cells is characterized by the presence of numerous fine fibers which are longitudinally placed. It is the shortening and thickening of these muscle *fibrillæ* that produces contraction of the individual cell and is therefore responsible for the particular function of this kind of tissue, the production of motion. *Non-striated muscle* cells are typically spindle-shaped with the nucleus centrally placed (Fig. 81 A and B). These cells usually occur in sheets, which are formed by many of the cells lying side by side and held together loosely by fibrous connective tissue. This kind of muscle is sometimes called involuntary muscle, because it is found in the wall of the digestive tract, in the urinary bladder, and in blood vessels, where it is not under conscious nervous control. *Cardiac muscle* is found only in the heart and is capable of rhythmical contractions (Fig. 81 F). The cells are arranged in the

form of a syncytium, which means that the cylindrical cytoplasmic units containing the nuclei are not separated from one another by membranes where they meet at their ends. These units branch and unite in such a way that a network of cells is formed. The fibrillæ of cardiac muscle are made up of regions of different density

FIG. S1.—Contractile tissues. *A*. Non-striated muscle cells in cross-section. Note that many cells are not cut through the region of the nucleus. *B*. Isolated non-striated muscle cell from wall of digestive tract. *C*. Cross-section of a voluntary muscle. The striated muscle cells are held together in bundles by fibrous connective tissue. *D*. Portion of striated muscle cell showing multinucleate condition and cross-striations. It has been injured near its right end in order to show the cell membrane. *E*. Striated muscle cells showing blood supply. *F*. Cardiac muscle cells from human heart.

bv, blood vessel; *c*, cytoplasm; *cm*, cell membrane; *fc*, fibrous connective tissue; *mb*, muscle bundle; *n*, nucleus. (*A*, *B*, *C*, and *E* from drawings by D. F. Robertson; *F*, from Schäfer, "Essentials of Histology," copyright, 1916, by Longmans, Green and Co., reprinted by permission.)

so that the cytoplasm presents an irregularly striated appearance. *Striated muscle* is sometimes known as skeletal muscle because it is attached to the bones and by its contractions produces motion of body parts which are supported by bone (Fig. S1 *D* and *E*). Since these muscles are under conscious control they are also termed voluntary muscles. They are called striated because of the fact that the regions of different density in the fibrillæ occur at such regular

intervals as to give a distinct cross-striped appearance to the cytoplasm. The cells are cylindrical, sometimes very long, and each contains many nuclei. Fibrous connective tissue serves to bind together striated muscle cells, and forms sheaths that enclose great numbers of cells and so produce the visible muscles, such as the gastrocnemius or the biceps (Fig. 81 C). These connective tissue sheaths are continuous with the tendons by which muscles are attached to bones.

Nervous Tissue.—Nervous tissue is specialized in the direction of irritability. Its cells are differentiated for the purpose of

FIG. 82.—Nervous tissues. *A.* Typical bipolar neurone from olfactory epithelium. *B.* Showing transformation of bipolar neurone into type found in dorsal root ganglia of spinal nerves. *C.* Multipolar neurone. *D.* Bundle of medullated nerve fibers surrounded by fibrous connective tissue as in spinal and cranial nerves. *E.* Portion of single medullated nerve fiber. The sheath of myelin is interrupted at the nodes of Ranvier. The neurilemma is continuous. *F.* Portion of non-medullated nerve fiber characteristic of autonomic nerves.

a, axon; *cb*, cell body; *d*, dendrite; *fc*, fibrous connective tissue; *ms*, medullary sheath of myelin; *n*, neurilemma or nerve sheath; *nf*, nerve fiber; *nn*, nucleus of neurilemma; *Rn*, node of Ranvier.

receiving stimuli, or changes in the environment; for transmitting nervous impulses from one part of the body to another; and for discharging these impulses to other kinds of cells in nerve-controlled organs. The general functions can, therefore, be stated as reception, transmission, and discharge. The result of these activities of nervous tissue is the coördination of the organism as a whole. A nerve cell, or *neurone*, is composed of a nucleus sur-

rounded by a relatively small mass of cytoplasm which is prolonged into two or more processes of varying lengths, the *nerve fibers*. Where there are only two cytoplasmic extensions, the cell is called a *bipolar neurone* (Fig. 82 A and B). The process by which nervous impulses travel toward the cell body is called a *dendrite*, while the one over which impulses pass away from the cytosome is the *axon*. There is never more than one axon, but there may be many dendrites. Where there is more than one dendrite, the cell is *multipolar* (Fig. 82 C). The cell bodies of neurones are found in groups, forming *ganglia*, outside the central nervous system; they also constitute the gray matter of the central system. Nerve fibers, bound together and surrounded in bundles by fibrous connective tissue, form the visible *nerves* of the peripheral nervous system (Fig. 82 D) and make up the white matter of the central nervous system. Certain nerve fibers are intimately covered by a layer of myelin, which contains much lipin, and are known as *medullated fibers* (Fig. 82 E). A nerve fiber is always a process of a neurone. As will be recalled, neurones are named according to their position in the reflex arc, but these names do not indicate subdivisions of the main class.

Organs and Systems. — The tissues that have been described exemplify the various types of specialization that cells undergo in the vertebrate body. Each particular tissue is capable of performing its special function alone, but they usually occur grouped in *organs*. Thus, organs are groups of tissues associated together for the performance of a special function. For example, if the wall of the small intestine is examined microscopically, it is found to consist of layers known as the *peritoneum*, *longitudinal* and *circular muscle layers*, *submucosa*, and *mucous membrane* (Fig. 83). The peritoneum consists of simple squamous epithelium and functions as a covering membrane. Both longitudinal and circular muscle layers are of non-striated muscle tissue, bound together by fibrous connective tissue, and their contractions produce the muscular movements that mix the food contents of the intestine and push them along toward the lower parts of the tract (*cf.* Fig. 48, p. 84). Fibrous connective tissue, containing both white and elastic fibers, is the distinguishing tissue of the submucosa and serves to support the numerous vessels carrying blood and lymph. This layer also provides the elasticity necessary for the expansion of the canal, in addition to carrying the circulatory fluids necessary for absorption.

The mucous membrane is composed of simple columnar epithelium which forms the lining of the tract and functions in secretion and absorption. These several tissues are associated to form the small intestine, in which digestion and absorption occur, and each tissue contributes its part of the function of the whole.

In addition to the grouping of cells to form tissues, and of tissues to form organs, organs are associated to form the systems described in the discussions of morphology and physiology. An understanding of the vertebrate body as a whole is to be had in

FIG. 83.—Wall of small intestine (semi-diagrammatic).

cap, capillary; *c.m.*, circular muscle; *g.c.*, goblet cell; *i.g.*, intestinal gland; *l.m.*, longitudinal muscle; *l.v.*, lymph vessel; *m.m.*, muscularis mucosae, a more or less distinct layer of non-striated muscle cells lying beneath the mucous membrane; *mu*, mucous membrane; *p*, peritoneum; *s-mu*, submucosa; *v*, villus

terms of the cells, which are the units of both structure and function.

Let us consider briefly, for the purpose of illustrating this statement, some of the activities of a common vertebrate, such as a frog. The structure of such an animal is familiar, and the general relations of parts and their functions are well understood. If we consider a frog that has not recently fed, sitting on the bank of a stream, we know that, as a result of metabolism and the consequent using up of the protoplasmic constituents, it will be necessary for the animal to obtain food. At such a time, if an insect comes within the frog's range of vision, the cells of the frog's retina receive

the stimulus produced by the appearance of the insect. Within these retinal cells nervous impulses are set up and pass along nerve-cell processes toward the brain (*cf.* Fig. 67, p. 123). In the visual centers of the brain, the impulses are transmitted to other cells of the nervous system, and eventually go out along nerve fibers leading to the muscle cells of the frog's tongue. The effect produced is the contraction of certain muscle cells, resulting in the movement of the tongue for the capture of the prey. The contact of the insect with the lining of the frog's mouth causes the closing of the mouth, and this in turn stimulates the act of swallowing. These activities, of course, result from muscle-cell reactions. In the stomach and intestine, the insect is digested by the juices secreted by gland cells occurring in the wall of the tract and in the pancreas and liver. These juices are secreted at the proper time because of the coördinating mechanism of nerve cells and their processes, or because of the production of endocrines by certain cells and their effect upon other cells (*cf.* p. 97). After digestion and absorption have occurred, the simple foods are carried in the blood plasma to capillary networks where they pass out through the endothelial walls of the capillaries to the many different kinds of cells that compose the organs of the body. In the cells throughout the animal, assimilation occurs and certain types of food may be stored, as is glycogen in liver cells and fat in adipose tissue.

During its stay out of water, the frog is carrying on respiratory movements of the nostrils, floor of mouth, and glottis. These movements are the results of muscular cell activities, and are produced and controlled as a result of nerve-cell reactions which are dependent, in turn, upon the production of carbon dioxide by cells in all regions of the organism. Oxygen is forced into the lungs by these respiratory movements and passes through the walls of the lungs into the blood, where it enters the red corpuscles and combines with hæmoglobin. In capillaries throughout the body, oxygen leaves the red cells and the blood stream to enter the protoplasm of all types of cells, where it produces the oxidative reactions of metabolism. As a result of metabolism, excretions are produced and, reaching the blood by diffusion, are eliminated from the body through cells in the liver, kidney, lungs, and skin. A continuation of this discussion would only add further examples of the same kind. Thus we see that the general activities of ani-

imals are to be explained in terms of simple cell and tissue reactions, built up into complex activities as a result of the coördinations that produce the phenomena of individuation.

The emphasis placed upon the activities of individual cells as the basis for the interpretation of bodily processes as a whole, and the analysis of all structures in terms of cells and cell products should make clear how fundamental is the generalization embodied in the Cell Doctrine. As animals other than the vertebrates are studied, it will be seen that cells, and their requirements and responses, are essentially the same throughout the realm of living organisms. The Doctrine of Organic Evolution alone takes rank with the Cell Doctrine as a unifying conception in biological science.

CHAPTER 7

REPRESENTATIVE SINGLE-CELLED ANIMALS

The preceding chapters are essentially an extended introduction to the subject of zoology. An attempt has been made to review and expand the student's knowledge of familiar zoological subject matter, namely, the structure and functions of higher animals, with a view to making this the point of departure for a survey of further aspects of zoological science.

The *Protozoa*, or unicellular animals, are naturally chosen to serve as an introduction to this more comprehensive study; although their organization and activities are not so simple as might be supposed from superficial examination. The *Protozoa* are often referred to as "animals reduced to the lowest terms." This is a good characterization, because of their unicellular state; but when we examine the more specialized *Protozoa* we see that they are more complex than any single cells that occur in many celled animals. The *Protozoa* are of further interest because in classification (p. 240) they may be placed over against the rest of the animal world. If we proceed to the classification of animals by asking what is the most fundamental difference between the animals of different kinds, the greatest difference, in the opinion of many zoologists, lies between the unicellular and the multicellular state. The Animal Kingdom may be divided into two great groups: (1) the *Protozoa*, or unicellular animals; and (2) the *Metazoa*, or multicellular animals. While this distinction cannot be sharply drawn, because of the existence of certain intermediate types which are "colonies" of cells, it is good for practical purposes; although it may seem to over-emphasize the Cell Doctrine and to disregard the organization of animals as individuals irrespective of their cellular state (*cf.* p. 194).

Classification of *Protozoa*

The *Protozoa* have been variously classified into groups comparable with the classes in other phyla of the Animal Kingdom

(cf. p. 241). The scheme most commonly used separates them into the four groups indicated in the following paragraphs.

FIG. 84.—Representatives of the four classes of protozoa.

A, *Amaba*, Class Sarcodina. B, *Chilomonas*, Class Mastigophora. C, *Frontonia*, Class Infusoria. D, *Podophrya* feeding on small ciliate, Class Infusoria. E, *Gregarina* attached to cell of host's intestine and stages within such cells, Class Sporozoa.

Class Sarcodina.—These are forms in which the cell exhibits more or less temporary processes termed *pseudopodia*, or “false feet.” In one subdivision, the *Rhizopoda* (Fig. 84 A), which are typically creeping forms, these processes are lobed or root-like and sometimes branching. In another, the *Actinopoda*, which are typically floating forms like *Actinophrys* (Fig. 85), the pseudopodia are stiff and more permanent. The name Sarcodina was originally applied to this class of the protozoa, because of their resemblance to the *sarcode* or “flesh,” as the protoplasm of animal cells was called in the early days of the cell theory.

Class Mastigophora.—In these forms the cell possesses, in the dominant phase of its life cycle, one or more *flagella*, or whip-like processes, which are used for locomotion, and in some instances for feeding. The number of flagella is relatively small. The Mastigophora (Fig. 85) are a very diversified group, repre-

sented on the one hand by species that are animal-like, the *Zoömastigina*, and on the other by plant-like types, the *Phytomastigina*. Mastigophora means "whip-bearers."

Class Infusoria.—This class consists of forms in which the cell has cilia during the whole or a part of the life cycle (Fig. 84 C and D). With few exceptions, the nuclear material is represented by a larger "vegetative" macronucleus, and a smaller, "generative" micronucleus (Fig. 95 E). The infusoria include many highly specialized protozoa. They were so named because many species of this class are often abundant in "infusions."

FIG. 85.—Representative Sarcodina (upper row) and Mastigophora (lower row.)

Mastigamöbea, which has a flagellum and pseudopodia, is classified as a mastigophoran.

(Drawn by C. W. Wilson.)

Class Sporozoa.—These are parasitic forms in which the cell often shows marked degeneration in the locomotor and other structures necessary for free life (Fig. 84 E). Spores or seed-like encysted stages give the group its name, "seed animals."

The Sarcodina

Structure of Amöba.—The class *Sarcodina* includes the simplest forms that are found among Protozoa, although there are

reasons for believing that some of the Mastigophora are more primitive from an evolutionary standpoint. Notable for their simplicity are the members of the genus *Amœba* (Fig. 86). The following descriptions of the structure and activities of *Amœba proteus* and related species are intended to supplement observations which are presumed to have been made in the laboratory. The amœba is composed of a gelatinous, semi-fluid substance, with an outer portion, the *ectoplasm* or ectosarc, which is almost homogeneous even under the highest powers of the microscope, and an inner portion, the *endoplasm* or endosarc, which contains vacuoles and particles of various sorts in addition to the *nucleus*. The ectosarc appears as a firmer substance, in spite of its manner of flowing as the amœba moves, and the endosarc as a more fluid region in which the endosarcular particles are suspended. Some investigators have claimed that there is an outermost layer, so thin that it cannot be seen, but demonstrable because objects which stick to the surface move at a different rate from that of the underlying ectoplasm. Others question the existence of this outermost layer.

Like other cells, the amœba, therefore, possesses a *nucleus* and *cytosome* or cell body, but the cytosome is differentiated into ectoplasm and endoplasm. The nucleus contains *chromatin*, arranged in a characteristic manner in different species. The cytosome is composed of cytoplasm, in which may be recognized inclusions of various sorts, as is the case with most cells in other animals. The larger bodies suspended in the endoplasm are of several kinds: the *food vacuoles*, in which the digestion of ingested food occurs; the *contractile vacuole*, connected with the ectoplasm; ordinary *water vacuoles*; various *granules*; and, particularly, *crystals* of definite shapes, which are perhaps distinctive for particular species of amœba. The significance of these several parts will be discussed in connection with their activities.

Movements, Locomotion, and Behavior.—The apparently simple manner in which an amœba effects locomotion by the “flowing” of its irregularly shaped body has attracted attention since the animal was first observed by the early microscopists, who called it the “*proteus animalcule*,” meaning “changing little animal.” We seem to have before our eyes, in the amœba, the simplest of all forms of protoplasmic movement, and one, perhaps, reducible to physico-chemical phenomena. However, the simpler

explanations that have been given fail to account for certain complexities in behavior which are disclosed by more thorough study. For example, it was at one time supposed that the movements of an amoeba were caused by the same physical phenomena as the changes visible in a drop of clove oil when placed on a slide in a mixture of 3 parts glycerine and one part 96 per cent alcohol. Such a drop will change its form, send out "pseudopodia," and move about much as does an amoeba. Or, a mass of glycerine,

FIG. 86.—Locomotion in amoeba as recently described by Mast.

According to this account, the amoeba consists of an inner granule-containing fluid substance, the plasmasol, surrounded by a more solid layer of similar composition, the plasmagel, which are together equivalent to what is ordinarily termed the endosarc. Outside there is a hyaline portion of the plasmagel, which is almost homogeneous optically, and an outermost layer, the plasmalemma. These last together constitute the ectosarc. During locomotion the plasmasol and plasmagel become transformed into one another after the manner shown in the figure. The plasmasol moves forward and at the end of the advancing pseudopod becomes transformed into the layer of plasmagel, which in turn is becoming plasmasol at the posterior end, "much as a chimney might be extended by carrying brick and mortar up through it and depositing them on the wall surrounding the opening."

g, region of gelation of plasmasol resulting in forward extension of the granular layer of the plasmagel; *g'*, region of gelation resulting in formation of hyaline layer of plasmagel; *n*, nucleus; *pg*, plasmagel; *pl*, plasmalemma; *ps*, plasmasol; *s*, region of solation resulting in transformation of plasmagel into plasmasol. (Reproduced from the original drawing by courtesy of S. O. Mast.)

placed in a watchglass of rather thick lubricating oil, can be made to roll about in a suggestive manner. If soot particles are added to the glycerine they are held in suspension much as are the bodies in the endoplasm of an amoeba, and the movements have an even greater resemblance. These simple imitations now appear to offer inadequate explanations of amoeboid movement, although it may be that the phenomenon is capable of physico-chemical explanation in more complex terms.

Within the past fifty years a number of different interpretations have been placed upon the processes to be observed in the movements of various species of amœba. Thus, amœbas have been supposed to send out pseudopodia, like jets from a fountain with a current flowing outward in the center and backward on all sides (Berthold, 1886, and others); again, it has been thought that the amœba flows by a rolling motion (Jennings, 1904); or "walks" on stiff pseudopodia (Dellinger, 1906) (Fig. 87). According to the most

FIG. 87.—Outlines of successive stages in the movements of a single amœba as seen laterally. Such "walking" upon the pseudopodia, which can flow out and be retracted, is apparently a method of locomotion in some species.

A marks a fixed point on the surface. (Outlined from the photographs by Dellinger.)

recent theory (Mast, 1923), an amœba moves by contractions of the body, which cause a flow of the central fluid portion out into the pseudopodia. This movement is accompanied by characteristic changes of the protoplasm from a sol to a gel state and from gel to sol. Further explanation appears in the legend of Fig. 86. While Mast's theory supersedes many of the earlier interpretations, one hesitates to accept it as final in the absence of confirmations in various species. It is an interpretation of observations upon *Amœba proteus* alone and may not be applicable to all amœbas. It seems, however, to be an important step forward in the understanding of what actually happens in amœboid movement.

The term *behavior* is used to designate the activities of an organism as a whole in relation to external and internal conditions. Fundamentally, we are dealing with *irritability*, or sensitivity, which is one of the important properties of protoplasm; but the unicellular amœba is an individual and hence may be studied as any other animal that "behaves" in certain ways under given conditions. The feeding reactions are of particular interest in this connection. The amœba captures living prey in the form of smaller unicellular animals and plants, which are abundant wherever there are many amœbas. The various species differ in

their selection of food. A wide variety of microscopic organisms may be utilized, and even many-celled animals and plants, if they are small enough for the amœba to lay hold upon, may serve as its food. Under ordinary laboratory conditions, unicellular and other minute green plants among the fresh-water algæ are common food for certain species of amœbas and are often seen within the cell in various stages of digestion. *Amœba proteus* normally feeds upon such green plant cells and also upon motile prey such as ciliate or flagellate protozoa and the minute multicellular animals known as rotifers (Fig. 88). As with amœboid movement, investigators have made repeated attempts to reduce the process of ingestion to a basis that can be imitated by non-living bodies, as when a drop of chloroform is placed in a watchglass of water and made to "ingest" bits of shellac or paraffin. The majority of observations, however, indicate that the feeding reactions are complex and variable according to the nature of the prey and the state of the amœba. It is found that food bodies that are motionless, like many of the green plant cells, call forth reactions that differ from those induced by active prey, like ciliates and flagellates. Moreover, the two types of reaction are not fixed, but each varies with the particular conditions. The reactions, like those of higher animals, tend to be "qualitative" and "in the interests of" the reacting amœba in a way that does not seem to occur in non-living bodies. Amœbas have been carefully studied with reference to other forms of behavior, such as their responses to light, to contact, and to chemicals. These reactions cannot be discussed here, but it may be said in general that the behavior is not so simple as might be supposed.

Metabolic Processes. — In common with other animal bodies, the unicellular amœba carries on the activities related to waste, repair, and growth in a living organism. Food is ingested, digested, and assimilated. Waste products resulting from dissimilation are excreted. At first glance, these metabolic processes in the protozoa seem much simpler than the complex series of events that have been described under metabolism in a vertebrate animal (p. 71). In reality, the metabolism of the amœba is fundamentally the same as that of the many-celled organism when its essential features are alone considered. The amœba ingests the smaller organisms which serve as food, it digests this food within its cytoplasm, and then assimilates the fluid products of digestion in the same manner that

a cell in the body of a many-celled organism assimilates the food it receives from the blood.

The exact methods employed in the *ingestion* of food differ considerably in different species of amœba, and even in the same species, according to the conditions. In general, the outer surface of the cell flows around the prey, either as finger-like pseudopodia or by the formation of a cup-shaped depression in which the

FIG. 88.—Feeding habits of amœbas.

A and B, ingesting motile prey like small flagellate by means of pseudopodia with formation of large food vacuole. C, ingesting non-motile prey like filamentous algæ without formation of food vacuole. D and E, "cornering" a paramœcium against a bit of debris. F, G, and H, cutting a paramœcium into two pieces either by mechanical pressure or perhaps by stimulating the paramœcium so that it cuts itself into two. I, 1, 2, and 3, ingesting an encysted protozoan. (A to E, after Kepner, Taliaferro and Whitlock; F and H, after Mast and Root.)

prey is finally enclosed (Fig. 88). Thus the food, surrounded by a drop of the external water, becomes included within the endoplasm, forming a food vacuole. The mechanics of the process are usually such that a portion of the outer surface of the cell is folded in, loses its connection with the surface, and becomes a part of the endoplasm. The process varies somewhat, but such is the

more common relationship. Food bodies like the elongated filaments of certain green plants (Fig. 88 C) may be included in the endoplasm without the surrounding mass of water. Active prey, like another protozoan, is usually enclosed in a conspicuous vacuole, formed either during ingestion by the inclusion of external water or by the secretion of fluid into the vacuole after the capture (Fig. 88 A and B).

Digestion occurs within the food vacuole as is indicated by the disintegration of the soft parts of the ingested food. The case of green plants, which undergo color changes similar to those observed in masses of such material when subjected to digestion in a test-tube, is instructive. Since enzymes are necessary for digestion wherever it can be studied on a large enough scale, it may be inferred that enzymes are secreted into the digestive vacuoles from the surrounding cytoplasm. It is claimed that, in some protozoa, bodies, like the secretory granules of the gland cells in a vertebrate animal, surround the vacuole at a certain stage and disappear as they are converted into the enzyme which enters the vacuole.

After digestion, the food vacuole undergoes a shrinkage in bulk which is supposed to indicate the passage into the cytoplasm of the products of digestion. This corresponds to the *assimilation* of nutrient material by the cells of a higher animal. In such a manner, nutrients, consisting certainly of proteins, and perhaps of fats and sugars, but apparently not including starch, are digested and become incorporated into the protoplasm of the protozoan cell. The non-nutrient portions of the food, such as the siliceous skeletons of the green plants known as diatoms, and the shells of animals, are *egested* when the food vacuole, with what remains of its original contents, comes to the surface and breaks through the ectoplasm, so that the amœba flows away and leaves the contents of the vacuole behind. In some cases the indigestible contents of several vacuoles unite and are egested together.

As with the vertebrates, the more important story is that of the nutrients that become incorporated into the protoplasm upon their passage outward from the food vacuoles. It is supposed that in the single-celled amœba, just as in each cell of a many-celled organism like the human being, metabolic changes are constantly taking place. Like other cells, the amœba receives nutrients, incorporates these into its protoplasm by a process of *assimilation*,

and gives off the waste materials that are produced by *dissimilation*. The contractile vacuole is commonly described as effecting *excretion* by receiving water containing in solution the chemical products of metabolism and discharging these to the outside, somewhat as does the kidney in a vertebrate animal. However, many protozoa are without contractile vacuoles, and some investigators regard this structure as serving to regulate the water content of the cell and only incidentally for purposes of excretion. In protozoa that do not possess contractile vacuoles, like the majority of both marine and parasitic species, excretion must be supposed to take place in a manner similar to the passage of waste products of metabolism from the cells of a many-celled animal with a well-developed circulatory system (*cf.* p. 104). Like a cell in the body of a vertebrate (Fig. 60, p. 104), the protozoan cell is surrounded by fluid. If the outer portions of the cell are permeable to substances in solution, an accumulation of such substances within the cell will result in a diffusion outward, into the intercellular lymph in the one case, and into the surrounding water in the other. The process will continue as long as the outer cell region remains permeable and the strength of solution is greater within the cell than on the outside. Thus the mechanism for the continual removal of the waste products of dissimilation is provided alike in protozoa and in metazoa. Even in protozoa having contractile vacuoles, such diffusion of excretory material from the entire surface may be the more important means of excretion.

Respiration in amœba is similar to internal respiration in the cells of higher animals (*cf.* p. 93). Oxygen consumption can be demonstrated in such protozoa by means of delicate micro-chemical tests. As with the cells of a man or a frog, which are surrounded by their intercellular lymph (Fig. 60, p. 104), so with the amœba surrounded by water (Fig. 86), it may be supposed that oxygen diffuses into the cell as fast as it is consumed by chemical combinations within the cytoplasm. The amœba will die if deprived of oxygen, as will the cells of higher organisms.

When one recalls the various processes of ingestion and egestion, digestion, absorption, circulation, assimilation, dissimilation, and excretion, as described for the vertebrate, it becomes apparent that the amœba lacks only those steps of the process that are necessitated by the size and complexity of the multicellular organism. The essential steps in metabolism occur in amœba in the same

manner as in man, namely, by assimilative and dissimilative changes within the individual cell.

Reproduction and Life Cycle. — Up to the present time, amœbas have been rather difficult forms to maintain for long periods in

A. Binary Fission in *A. proteus*

B-2. Endogenous budding

B-1. *Naegleria gruberi*, binary fission

B-3. Exogenous budding

B-4. Encystment and emergence from cyst through pore

B-5. Flagellate stages

C. Flagellulæ, *Sp.?*

FIG. 89.—Phases in the life cycles of amœbas.

A, *A. proteus*, a common fresh-water species. B, 1 to 5, *Naegleria gruberi*, one of the soil amœbas, various phases not necessarily in sequence as shown. C, flagellulæ of an unknown species apparently in conjugation. (A, after Botsford; B, after C. W. Wilson.)

laboratory cultures. It is probable that the cells are very minute during part of the cycle and hence difficult to follow with certainty by the methods of pedigreed cultures now used in the study of protozoa. In the large active phase of *Amœba proteus*, it is well

known that reproduction occurs by *cell division* or binary fission, by which the cell divides into equal halves (Fig. 89 A). *Encystment*, or the enclosure of the cell in a *cyst* formed as a secretion after the amœba has contracted into a sphere and become quiescent, also occurs in some species of amœba that have been studied (Fig. 89 B 4). The formation of flagellated cells and their union in *conjugation*, a process comparable with the union of egg and sperm cells in many-celled animals, is known in some of the Sarcodina (Fig. 89 C). However, the details of the life cycle in all its particulars have not yet been established in any one instance for *Amœba proteus* and similar fresh-water species. While more is known regarding some of the parasitic species in this subdivision of the Sarcodina, it is not safe to conclude that the same stages occur in free-living forms, although there is doubtless some parallelism.

If we now summarize what has been learned concerning the amœba in the foregoing paragraphs and in the laboratory study which is presumed to accompany this account: The three great bodily functions are no less important for the amœba than for the vertebrate animal. The unicellular organism cannot exhibit the complexities of the many-celled state, but it does exhibit *metabolism*, *irritability*, and *reproduction*, within the limits of a single cell, comparable with these activities in the cells of the metazoan. Waste and repair of protoplasm, growth, and reproduction of the cell thus appear to be fundamentally alike at the two ends of the animal kingdom. Response to stimulation in an amœba may be as complex as it can be demonstrated to be in a majority, if not all, of the cells of more complex animal bodies. The activities of protoplasm and hence of cells are, therefore, similar in the simplest and in the most complex animals.

Other Sarcodina.—In the subdivision of the Sarcodina known as *Rhizopoda* (cf. p. 154), there are many forms that resemble the amœba. Others, like the genera *Arcella* and *Diffugia* (Fig. 85), possess shells into which the animal can withdraw and from the mouth of which issue pseudopodia. In another type, called the *Foraminifera*, there is a shell composed of carbonate of lime, through which pseudopodia pass by one or by numerous openings. These pseudopodia form networks in which the food particles are ingested. With few exceptions, the Foraminifera are marine, occurring in the open ocean in unbelievable numbers.

As the animals die their shells sink to the bottom, forming the "foraminiferal ooze" found at great depths in regions like the North Atlantic (Fig. 90). In spite of their small size, and the slow rate at which they accumulate upon the bottom, such protozoan skeletons have become a part of sedimentary rocks in the same manner as the shells of larger animals. The chalk formations in

FIG. 90.—Shells of marine Foraminifera.

Left, foraminiferal ooze from bottom of ocean at 1900 fathoms. Right, piece of nummulitic limestone, showing fossil shells of the foraminiferan *Nummulites*. (From Shipley, "Invertebrate Zoology," copyright, 1903, by A. and C. Black, reprinted by permission.)

various parts of the world, like those of England and France, as seen in the chalk cliffs of the English Channel, are composed almost exclusively of the shells of Foraminifera that once lived at the surface of the ocean, died, and "rained" down upon the bottom, to be later consolidated into rock and raised up as part of the dry land, where they are now exposed as layers, sometimes hundreds of feet in thickness. Among the *Actinopoda*, two representative types deserve mention: the "sun animalcules," like *Actinophrys sol* (Fig. 85), which is common in fresh water; and the marine forms known as *Radiolaria*, which are famous for their beautiful siliceous skeletons. These, like the Foraminifera, have contributed to the formation of sedimentary rocks.

In conclusion it may be remarked that the Sarcodina are the simplest of the protozoa in their internal organization and external differentiation. There are, however, reasons for believing that they are less primitive, from an evolutionary standpoint, than the Mastigophora. Many of the Sarcodina, for example, have a

flagellated stage in their life cycles. The Mastigophora are more primitive in their metabolic activities, since they may combine the modes of nutrition of both animals and plants even within the same individual. Nevertheless, the amœbas and their relatives are fairly called the simplest of all organisms that exhibit the typical animal functions.

The Mastigophora

Structure of Euglena. — The Mastigophora include types that are distinctly plant-like in their appearance and manner of nutrition, and others that resemble animals. The genus *Euglena* (Fig. 91) is representative, because in a measure it combines the characteristics of the plant-like and the animal-like mastigophorans. What follows applies to *Euglena viridis* and *E. gracilis*, two of the commonest forms, and also to the other species of this genus that are abundant in fresh water. The cell in typical euglenoids, as members of the Family *Eugenoidina* are often called (Fig. 91 A), is covered with an outer layer of *ectosarc*, sufficiently stiff to preserve the contours of the organism as it swims through the water, but flexible enough to allow the extensions and contractions that are termed “euglenoid movements” (Fig. 91 B). It is quite characteristic of the euglenoids to have spiral markings of various sorts upon the outer surface of the ectosarc. In some species these are highly developed. When seen in what might be termed the “lateral” view (Fig. 91 C), the anterior end of the euglenoid shows a mouth-like opening, the *cytostome*, with one side suggesting a projecting upper lip. However, the cytostome is not so much a slit between the lips as it is an oval opening leading into the *gullet*. The *flagellum*, a whip-like structure used in locomotion, extends from the gullet into the water. At one side of the gullet is a vacuole system consisting of a *reservoir* which drains into the gullet and is surrounded by *contractile vacuoles* (Fig. 91 A). An excretory function can perhaps be ascribed to these vacuoles, as with the vacuoles of the Sarcodina. Also near the anterior end, is a mass of red pigment (Fig. 91 C and C'), called the *eye-spot* because it is probably the part that is most sensitive to light; although it would be difficult to prove this beyond question. Euglenoids that regularly ingest food particles and pass them into the cell in food vacuoles have a more highly developed gullet region than *Euglena viridis*.

The inner protoplasm of the cell, which may be referred to as the *endosarc*, is of a semi-fluid consistency, but sufficiently stiff to hold the various inclusions in place without the obvious flowing that occurs in many other protozoa. The *nucleus* lies near the center. Embedded in the *cytoplasm* are found structures characteristic of green plants, the *chromatophores*, containing chlorophyll, and masses of the carbohydrate *paramylum*, a substance allied to starch.

FIG. 91.—Structure and activities of euglena and related flagellates.

A, typical euglenoid. B, 1-3, euglenoid movements of *Astasia*. C and C', gullet and stigma or eye-spot of euglena. D, spiral course of swimming euglena. E, ingestion of bacteria by euglena. F, ingestion of another protozoan by *Peranema*. G, euglena feeding upon mass of bacteria. H, euglena completing longitudinal fission.

b, mass of bacteria; c.e., food; ch, chromatophore; f, flagellum; f.v., food vacuole; g, gullet; n, nucleus; p, paramylum body; r, reservoir surrounded by contractile vacuoles; r.o., pharyngeal rod; s, striation; st, stigma, or eye-spot. (A, after Walton; C, after Wager; E to H, after Tannreuther.)

Movements, Locomotion, and Behavior.—Expansions and contractions of the cell are frequently observed in euglenas that

are not in active locomotion by means of the flagellum. In some euglenoids there are also movements that resemble peristaltic waves as they traverse the cell body. All such activities are termed "euglenoid," since they are commonly seen in the genus *Euglena* (Fig. 91 B). Some of the larger euglenas regularly lose their flagella and crawl about by a peculiar motion which is not fully understood, although it has been ascribed to the existence of a surface film of flowing protoplasm. This film is invisible but its presence may be demonstrated by the movements of fine particles adhering to its surface. The most characteristic movements, however, are those effected by means of the flagellum.

The *flagellum* is a cylindrical structure composed of an axial filament surrounded by a sheath. This filament arises from the *blepharoplast* or basal granule, an enlargement within the cell, and is the contractile portion (Fig. 91 A). The sheath apparently functions as an elastic covering that tends to keep the flagellum in an extended position. The action of such a flagellum as that of euglena may be compared with the spiral waves which can be made to pass along a rope that is tied at one end and held in the hand at the other. The flagellum, however, is free at one end and makes its own spiral waves, which cause the cell to move through the water.

Careful observation reveals that the euglena pursues a spiral course (Fig. 91 D) which consists of three factors: (1) It moves forward, *progression*; (2) it turns on its long axis, *rotation*; and (3) it swings away from the axis of the spiral, *swerving*. One can understand what happens by taking an object like a cane or a larger cylinder and marking one side to indicate the shorter lip of the euglena which is kept turned toward the axis of the spiral. If the cylinder is then made to describe a cone and rotated to keep this lip toward the axis of the cone, the factors (2) and (3) above will be represented. By walking in the direction of the axis and continuing to describe the cone, the factor (1) is added. In this manner a euglena pursues a spiral path, always keeping the shorter lip toward the axis of the spiral, and proceeding in a course, which, if not a straight line, nevertheless enables it to steer what amounts to a straight course "across the trackless deep." The spiral movement of the organism is, of course, a result of the spiral beating of the flagellum. This mode of locomotion is the common one in asymmetrical organisms, whether protozoa or other minute forms that swim through the open water. By such means, an

asymmetrical body is able to move in what is approximately a straight line.

FIG. 92.—*Euglena* sp. (?) in crawling state, showing details in process of orientation.

a-c, positions of euglena with light from *n* intercepted; *c-m*, positions after light from *n* is turned on and that from *o* cut off so as to change the direction of the rays; *es*, eye-spot; *n, o*, direction of light; *v*, contractile vacuole. (From Mast, "Light and the Behavior of Organisms," John Wiley and Sons, copyright, 1919, reprinted by permission.)

By its movements of crawling and contracting, and by its spiral swimming, the euglena responds to a variety of stimuli. The *behavior* in response to light has been most thoroughly studied since it can be easily observed. Euglenas depend upon sunlight for one type of their nutrition, and hence, like green plants, they respond positively to light of optimum intensity. The reactions of a crawling euglena with respect to light are shown by Fig. 92.

which is sufficiently explained by the legend. It will be noted that the individual rotates slowly on its long axis as it proceeds, and that the response is a rather complicated one; although the cell may seem to swing into line with the new source of illumination without much delay. A similar positive response to light occurs in the free-swimming individual (Fig. 91 D). Just how the euglena brings itself into the new position, whether by what might be termed a "trial and error" method or by a more direct means, as when a boat swings directly in response to a "stimulation" of the rudder, is a disputed question among investigators. This can best be discussed for the protozoa as a whole in connection with a species like *Paramecium*, which is larger and more easily observed (cf. p. 178). It is thus apparent that the euglenoid cell responds to stimulation as does all protoplasm and hence gives evidence of an *irritability* comparable with that shown by the cells of higher organisms.

Metabolic Processes.—The term *holozoic nutrition* is applied by zoologists to the nutritive processes that occur typically in animals and that have been described in a preceding chapter, as they occur in the vertebrate, and again in the protozoan *Amoeba proteus*. Food, in the form of living prey or material derived from the bodies of animals and plants, is ingested, and then digested to simpler compounds, which are incorporated into the protoplasm by assimilation. The green plants, on the other hand, exhibit such a relationship to their surroundings that they are able to take in simple compounds, such as oxygen, carbon dioxide, water, and the mineral salts of the soil, and, by the process known as photosynthesis because it is dependent upon sunlight, followed by other synthetic processes, to build up the nutrients upon which their existence depends. The substance known as *chlorophyll*, which gives the green color to plants, is necessary for photosynthesis, which is the initial step in this synthetic process. Nutrition of this kind is referred to as *holophytic* in textbooks of zoology, although this term is not in common use among botanists.

What is known to occur in higher plants can be assumed to take place in any cell that contains chlorophyll, and its occurrence can in part be demonstrated by appropriate experiments upon unicellular organisms. Euglena can be shown to liberate oxygen in the presence of sunlight, as a result of photosynthetic processes carried on by virtue of its chlorophyll. Starch, in the form of paramylum,

is formed by the euglenoid cell, and the other constituents of protoplasm must be synthesized when euglenas grow and multiply. In this manner the euglena carries on the holophytic nutrition characteristic of all living bodies that possess chlorophyll.

But the euglena is further interesting because this is not its sole mode of nutrition. Small organisms, such as bacteria, may be ingested through the gullet (Fig. 91E-G) surrounded by vacuoles, and digested in the cytoplasm as in the feeding of an amoeba or of other *holozoic* protozoa. Respiration, comparable with internal respiration in the cells of higher animals, as well as excretion of carbon dioxide, can be shown to occur.

A third type of nutrition, according to zoological terminology, is known as *saprophytic*. In this case the organism is unable to synthesize its food from such simple compounds as do the chlorophyll-bearing organisms. It must depend upon the decomposition products of other plants and animals, after the manner of the moulds and many bacteria that grow upon organic material. When certain species of euglenas are kept in a low illumination and in a medium rich in decomposing organic matter, they lose most of their chlorophyll; and, since they grow and multiply without other nutritive activities, it may be presumed that they carry on their nutritive processes saprophytically. Such is known to be the case with many other Mastigophora.

Reproduction and Life Cycle. — As an example of the conditions in one of the common euglenoids, the life cycle of *Euglena gracilis* may be described. This species is well suited for purposes of illustration, because its cycle includes an unusual range of possibilities (Fig. 93). As with the majority of fresh-water protozoa, there is an alternation of "active" and "encysted" phases. In the *active phase*, the euglenas usually multiply by longitudinal division of the cell, but transverse division may also occur. In the former case (Fig. 93, 2), the pigment spot, the reservoir, and the enlargement at the base of the flagellum divide, to form these parts for the two daughter cells, while the division of the nucleus is in progress. The external part of the old flagellum is always cast off before division begins, and a new one formed by each daughter cell as division proceeds. As these internal changes advance, a division of the cytosome begins at the anterior end and proceeds posteriorly until separation is accomplished. The nucleus divides by a peculiar type of *mitosis* (cf. p. 137). In

transverse division (Fig. 93, 3 and 4), the pigment spot and reservoir also divide, and one member of each migrates to form the

FIG. 93.—Phases in the life cycle of *Euglena gracilis*.

(After Tannreuther.)

pigment spot and reservoir of the posterior cell. While this is taking place the nucleus divides, and a transverse constriction of

the cell body is begun. A new gullet and flagellum are formed on the posterior cell. The old flagellum may persist on the anterior cell, or it may be dropped and a new one produced. Separation of the cells finally occurs. *Euglena gracilis* thus reproduces itself either by longitudinal or by transverse division of the cell during its active phase.

Under various external conditions, and perhaps as a result of internal changes, euglenas may undergo *encystment* by secretion of material that hardens as a thin covering, or cyst, enclosing the cell. In *E. gracilis*, temporary encystment may occur at the surface of ponds during hot days as shown in Fig. 93, 5. Later, the individuals escape from these cysts without reproduction. Apparently, cysts may also be formed for the purpose of cell division, which in this instance is transverse (Fig. 93, 4). The euglena becomes quiet, loses its flagellum, remains extended, and secretes the cyst. Transverse division now occurs in the same general manner as in the active stage. When all the structures are completely formed for each cell, the individuals escape from the cyst without further division. In the more common form of encystment, however, there may be numerous divisions that are longitudinal. In this instance the euglena casts off its flagellum, becomes spherical, and secretes a delicate cyst. Division then occurs longitudinally. If the culture is kept in sunlight the cells grow as the result of holophytic nutrition, and repeated divisions may ensue, resulting in great distention of the original cyst. Sometimes this is ruptured, the liberated cells form new cysts about themselves, and each repeats the process (Fig. 93 6). When the active phase is to be resumed, flagella are produced, and the euglenas break from the cyst and swim away.

A process of *conjugation*, by which cells unite in pairs and become permanently fused into a single cell, having its single nucleus and cytosome derived from this double parentage, is well established in many flagellated protozoa. In the genus *Euglena* it has been described by some investigators but is questioned by others. Unpublished observations by Tannreuther on *E. gracilis* indicate what is evidently conjugation of free-swimming euglenas (Fig. 93, 7). The cells unite in pairs, and as they fuse a union of the two nuclei occurs. Thus, one cell is formed by the union of two as in *fertilization*, which is the term applied to the union of ovum and spermatozoön in many-celled animals. Such

conjugating cells of protozoa are collectively termed *gametes*, as are also the sex cells, *ova* and *spermatozoa*, of metazoa. Likewise, conjugation and fertilization, or union of ovum and spermatozoön, are collectively termed *syngamy*, meaning union of gametes. The single cell formed by syngamy is termed the *zygote*, which means something "yoked." In the case of euglena above mentioned, the gametes are all alike and hence are called *isogametes*. In some protozoa (Fig. 108, p. 208) they are dissimilar, like the spermatozoön and ovum of metazoa, and are therefore called *anisogametes*. Syngamy may thus be a process of *isogamy*, by the union of isogametes, or a process of *anisogamy*, by the union of anisogametes. Such smaller and larger conjugating cells in protozoa are called *microgametes* and *macrogametes*, respectively, and are comparable with spermatozoa and ova (*cf.* Fig. 212, p. 402). The phenomenon of *sex*, which consists in the production of two kinds of gametes, is recognizable in protozoa wherever there are microgametes that are smaller and more active, like spermatozoa, and macrogametes that are larger and tend to be food-laden, like the ova of metazoa. Thus in the euglena and other protozoa, *reproduction*, which may be defined as the formation of a new individual, may be *asexual*, by means of cell division, or *sexual*, by means of conjugation.

Other Mastigophora. — The flagellated protozoa are difficult to subdivide into lesser groups because of the diversified habits and structures of various species. On the one hand, there are flagellates, the *Phytomastigina*, so plant-like that many of them are classified as plants; on the other, there are forms, the *Zoömastigina*, that are distinctly animal-like in their nature. In addition there are forms, like the genus *Mastigamæba* (Fig. 85), in which the cell is amœboid and resembles the Sarcodina, although the presence of a flagellum leads to the classification of such genera with the Mastigophora. There are also many instances of amœboid stages in the life cycles of species that are typical flagellates throughout the greater portion of the life history, a condition which may be compared with the occurrence of flagellated stages in the life cycles of certain Sarcodina. These facts suggest an evolutionary relationship between Mastigophora and green plants on the one hand and Mastigophora and Sarcodina on the other.

Turning to specific examples of Mastigophora that are of interest, there are many simple flagellates occurring in fresh water

(Fig. 85). Of these the euglenoids are perhaps the most common, but others are frequently observed. In forms like *Trachelomonas* it seems that the cell wall is very firm, and in others, like *Peranema*, the cell exhibits surprising mobility. An interesting type is the choanoflagellates like *Monosiga*, in which there is a delicate collar surrounding the flagellum. Another is the marine genus *Noctiluca*, the "nocturnal light," a very large species having one finger-like flagellum, another smaller one in the region of the buccal groove, and cytoplasm which is highly vacuolated. In this instance the cells produce brilliant luminescence throughout large areas of the ocean.

Many of the Mastigophora are parasitic. The posterior region of the digestive tract in man often harbors such forms, and almost any frog or tadpole will show more than one species of these parasites in its large intestine. A most interesting type is the *trypanosome* (Fig. 109, p. 210), many species of which occur in the blood of vertebrates and in the digestive tracts of invertebrates. These are elongate cells with an *undulating membrane* along one side, on the edge of which is attached a flagellum that becomes free posteriorly and arises anteriorly within the cell. One famous species is *Trypanosoma gambiense*, the parasite causing one type of the sleeping sickness that is so fatal to man in equatorial Africa. Among the plant-like Mastigophora there are some striking examples of colonial organization which suggest a transition from the unicellular to the multicellular state. Some of these are considered in Chapter 8.

The Infusoria

Structure of *Paramœcium caudatum*.—The ciliated Protozoa, or Infusoria (Fig. 94), are grouped into two main subdivisions: the *Ciliata*, which possess cilia throughout the life cycle; and the *Suctoria*, in which cilia are present for only a limited period, and are later replaced by the so-called tentacles, which are used in the capture of food (Fig. 84 D). Among the Ciliata, the species *Paramœcium caudatum* (Fig. 95) is one of the simpler types and is a common object of laboratory study. If any one kind can be said to be the omnipresent protozoan of fresh water, it is paramœcium, since no other type occurs more commonly in cultures and under a wider range of circumstances in nature. It is, so to speak, adapted to "slum" conditions, and hence can be main-

tained in the laboratory during long periods, so long in fact that it may be regarded as an animal that can be thoroughly "domesticated."

The size of *Paramæcium caudatum* varies greatly, because, like all other species of plants and animals that have been exhaus-

FIG. 94.—Common ciliated and other protozoa from fresh water.

(Drawn in part by Wiley Crawford.)

tively studied, the species is really composed of many races which breed true among themselves but may differ widely when one race is compared with another (*cf.* Fig. 308, p. 559). The body is spindle-shaped with the anterior end bluntly rounded and the posterior end more pointed. The older microscopists called paramæcium the "slipper animalcule" because its shape seemed to them to resemble the outline of a slipper. At one side is a depression, the oral or *buccal groove*, passing diagonally from the anterior end to about the middle of the body and ending in a tunnel-like cavity, the *cytopharynx*, or gullet. The outer end of the gullet is the *cytostome*, or cell mouth. The *cilia* that clothe the body are of uniform length, save at the extreme posterior end

FIG. 95.—Structure and activities of paramoecium.

A, spiral path of paramoecium. B, paramoecium at rest, showing cilia motionless against a cotton fiber. C, paramoecium at rest against a mass of bacteria (a) showing currents produced by the cilia. D, *P. calkinsi*, external contours and buccal groove. E, *P. calkinsi*, internal structure. F, *P. caudatum*, section perpendicular to surface. G, surface of pellicle showing cilia and trichocysts. H, section through cytostome and gullet. I, trichocysts before (left) and after (right) discharge.

c, cilia with basal granules; cv, contractile vacuole; ec, ectoplasm; en, endoplasm; fv, food vacuole; ma, macronucleus; mi, micronucleus; n, nucleus; t, trichocysts which form in endoplasm and migrate to ectoplasm; um, undulating membrane. (A, B, and C from Jennings, "Behavior of the Lower Organisms," reprinted by permission of Columbia University Press; D and E, after Woodruff; F to H, after Maier; I, after Khainsky.)

and in the buccal groove, where they are slightly longer. Within the gullet, the cilia are fused together in a plate to form the *undulating membrane*, which aids in the passage of food to the interior of the cell. Since the egestion of faecal material occurs at but one point on the surface of the cell, there is a *cytopyge*, or cell anus, as well as a cell mouth. In this regard the paramœcium is more specialized than the amoeba, in which ingestion and egestion occur at any place on the surface.

The outermost layer of the cell is a thin *cuticle*, or pellicle, which is like an elastic membrane. This cuticle is striated to correspond to the distribution of the cilia along definite lines (Fig. 95 F and G). Beneath the cuticle is a thicker, non-granular layer, the *ectoplasm*, from which the cilia arise (Fig. 95 E and F), and which contains the numerous *trichocysts*. The latter are apparently defensive structures since they are discharged as threads upon appropriate stimulation (Fig. 95 I). It is the ectoplasm that gives to the paramœcium its permanent shape, for the internal portion, or *endoplasm*, of the cell is semi-fluid. The paramœcium may be pressed out of shape mechanically, but resumes its former outline because of the elastic ectoplasm. The endoplasm contains a *macronucleus*, which is related to the vegetative processes of the cell; and a *micronucleus*, which is the part of the nuclear apparatus that is most intimately related to heredity and reproduction. The endoplasm also contains the two *contractile vacuoles*, with their radiating canals, and the *food vacuoles*. Larger masses of various sorts may also be found, in addition to the very fine inclusions of the cytoplasm.

Movements, Locomotion, and Behavior. — The cytosome in paramœcium has a constant shape, unless it is temporarily distorted by external pressure. Locomotion and other movements are effected by the cilia, which beat in such a fashion that the animal pursues a spiral course (Fig. 95 A). The same factors of *progression*, *rotation*, and *swerving*, as described for euglena (*cf.* p. 168), are to be found in the locomotion of paramœcium. In paramœcium, however, these factors are more easily recognizable. The progression is caused by the backward beat of the cilia, and the rotation by the fact that they strike diagonally. It has been supposed that the swerving results from a stronger beat of the cilia in the buccal groove, but there are some ciliates that follow a spiral course without having any such differentiated area, and hence the stroke of the buccal cilia may not be the only factor. These three

factors operating together bring about the spiral course that is pursued in locomotion. There is, however, much more to the behavior than mere forward progression.

The various responses to stimuli that constitute the behavior of paramœcium are effected by modifications of the three factors just mentioned. Thus, if a paramœcium is swimming forward and comes in contact with a chemical solution that stimulates the cell

FIG. 96.—Reactions of paramœcium.

A, avoiding reaction. 1-6, successive positions occupied by the animal, not showing the rotation on the long axis. *B*, path followed by an individual trapped in a drop of acid. *C*, paramœcium approaching a region containing ludia ink (shown by the dots). A cone of ink is drawn toward the anterior end and oral groove of the animal. *D*, paramœcium swinging its anterior end about in a small circle, in a weak avoiding reaction. 1, 2, 3, 4, successive positions occupied. (From Jennings, "Behavior of the Lower Organisms," reprinted by permission of Columbia University Press.)

strongly but does not injure it, the animal responds by reversing its course and may swim backward spirally for a considerable distance before the normal progression is again resumed. The more common reaction, however, is that seen in the responses to less violent stimulation. When, for example, the animal strikes an obstacle (Fig. 96 *A*), it responds by backing off a short distance, stopping the backward movement, describing a cone by continuing to rotate and swerve dorsally (Fig. 96 *D*), and

proceeds forward by a resumption of the spiral course. A complete cone-shaped figure is not always described, but there is always a portion of such a figure. The angle of the cone may vary to such an extent that in extreme cases the animal swings about almost in one plane, as would be the case if a cone became flattened out to form a plane surface. Under mild stimulation, however, the response is not so extreme. The paramœcium backs away from the obstacle, stops, describes part of a cone by continuing to swerve and rotate, and starts forward once more on a spiral course but with the axis of the spiral at a new angle. If this line of progress brings it again in contact with the obstacle, it repeats the process of backing off, describing the cone-shaped figure, and proceeding in a new direction. Thus, by a series of what may be called "trials," some of which may be "errors," the paramœcium may eventually succeed in finding its way around an obstacle. This automatic and reflex-like response has been called the "avoiding reaction." The same kind of reaction occurs in response to other situations, as when the animal is confined within the trap-like meshes of the cotton fibers sometimes used in laboratory study, or in response to other forms of stimulation likely to be encountered in nature. With electrical and other stimuli not encountered in nature, the responses may be different.

When many paramœcia are crowded together, the individuals seem to be merely darting backward and forward in aimless fashion. When, however, the response of isolated individuals is studied with reference to particular stimuli, the behavior is found to be as above described. The avoiding reaction is given in response to mechanical, thermal, and chemical stimuli, water currents, gravity, and centrifugal force. This form of activity so much resembles the "trial and error" behavior of higher organisms that it seems justifiable to extend this term even to the protozoa. The use of such a phrase does not imply that the paramœcium acts with any degree of intelligence, that it "tries" and "errs," and recognizes its mistakes; but only that it responds mechanically with a stereotyped form of behavior, which, if repeated a sufficient number of times, will usually bring the individual under conditions that are favorable for its normal activities.

As the animal swims through the water or swerves in giving the avoiding reaction, the beat of the cilia in this region draws a cone of fluid against the buccal groove, which thus "samples" the water

in advance of its contact with the entire body. As a result of this, responses may be made before the cell becomes wholly surrounded by new conditions, as when it approaches an area containing different chemical compounds in solution. The possibility of such "advance information" may be demonstrated by watching a paramœcium as it approaches a drop of India ink (Fig. 96 C).

FIG. 97.—Reactions of paramœcium to salts, acids, and heat.

A, method of introducing a chemical into a slide of infusoria. B, slide of paramœcia four minutes after the introduction of a drop of $\frac{1}{2}$ per cent NaCl. The drop remains empty. C, a slide of paramœcia is heated to 40 or 45 degrees C., then a drop of cold water (represented by the outline a) is placed on the upper surface of the cover-glass. The animals collect beneath this drop, as shown in the figure. D, collection of paramœcia in a drop of $\frac{1}{30}$ per cent acetic acid. (From Jennings, "Behavior of the Lower Organisms," reprinted by permission of Columbia University Press.)

The power of receiving stimulation by "sampling" in advance is no doubt useful to the animal in nature, and is presumably utilized under conditions of experimentation when the cell responds (Fig. 97 B) by keeping out of a drop of $\frac{1}{2}$ per cent salt solution, or, having entered a drop of acid (Fig. 97 D), remains trapped therein because it responds negatively whenever it again comes in contact with the surrounding water. The avoiding reaction is, of course, the means by which all such responses are effected.

Responses to stimuli such as those described above are usually known as *tropisms*; although, like the term "instinct," this word has been used in so many ways that some investigators would prefer to abandon it entirely. Thus, a response to light is positive or negative *phototropism*; a response to mechanical contacts,

stereotropism; a response to chemicals, *chemotropism*; and so on. The word *taxis* is sometimes used in place of tropism, and thus we have *phototaxis*, *chemotaxis*, etc. If one attempts to define a tropism, not much more can be said, in view of the present disputed use of the term, than that almost any response of an animal to a stimulus may be called a tropism; but in practice the word is not so often used for complex responses as for simple reactions. We speak of the phototropism of a protozoan, of a moth flying into the flame, even of a fish reacting to a fisherman's "flare"; but not so commonly of the phototropism of dogs and other higher animals. The important things to understand, in the present state of our knowledge, are the visible manner in which each form responds to a given stimulus, and, where a nervous system is present, the internal processes. Any general theory of "tropisms" must rest upon particular cases. There is still considerable disagreement as to how these responses are brought about, whether, for example, by trial and error or by a simpler means.

In the case of paramœcium it therefore appears that response to the kinds of stimulation which the organism meets in nature occurs by means of a form of behavior known as the avoiding reaction. This can be modified only within limits; but by performing it a sufficient number of times, no matter how blindly, a suitable adjustment to existing surroundings may be effected if any such is possible. Thus the paramœcium gives evidence of the same underlying phenomenon of *irritability*, or response to stimulation, that is observed in amœba and euglena and in higher organisms.

In view of the complexities of behavior in this species, it is of interest to know that certain structures recently discovered in *Paramœcium caudatum* are interpreted as a miniature *neuromotor system*, comparable in function with the nervous system of a many-celled animal. There is an area near the anterior end of the cytostome, called the motor center or *motorium*, from which minute fibers extend to the peripheral parts of the cell (Fig. 98 A). The ends of these fibers are described as connected with granules at the bases of the cilia and with the trichocysts (Fig. 98 B). Connected with the motorium are two lesser centers in the wall of the cytopharynx (Fig. 98 C). Similar systems of more complicated nature have been found in some other ciliates (Fig. 102, p. 194, and Fig. 153, p. 315). If these systems are correctly interpreted as

having the function of transmission of impulses within such protozoan cells, they constitute a mechanism by which coordinated action of parts of the cell may be accomplished. The function of such a mechanism may be compared with that of the nervous

FIG. 98.—Neuromotor mechanism of *Paramæcium caudatum*.

A, showing fibers radiating from motorium (*m*); B, showing fibers connected with cilia and trichocysts; C, showing lesser centers of coordination in region of cytopharynx. (After Rees, University of California Publications, 1922.)

system in a multicellular animal. Since it lies within the limits of a single cell, its structure cannot be so compared; unless one is more impressed by the Organismal Theory (*cf.* p. 194) than by the Cell Theory in making comparisons between single-celled and many-celled animals.

Metabolic Processes. — In feeding, the cilia of paramœcium draw a current of water against the buccal region (Fig. 95 C), and thus masses of fine particles, such as bacteria, smaller protozoa, and organic débris, which constitute the food, are passed through the mouth into the gullet. By means of the undulating membrane and by a gulping movement of the protoplasm, such masses of food are passed into the endoplasm, included in a drop of water, and are *ingested*. Within the endoplasm these food vacuoles move

along a definite course (Fig. 95 E). As with *amœba*, it is presumed that *enzymes* are secreted into the vacuoles, and that the products of *digestion* undergo *assimilation* by the surrounding cytoplasm. Finally, *egestion* of the indigestible remnants contained within the vacuoles takes place at the anal spot, or cytopyge. As in the many-celled body, the assimilated material becomes a part of the protoplasm. *Dissimilation* is, of course, always occurring; and *excretion* of the end products of metabolism may take place by diffusion over the entire surface of the cell or by means of the contractile vacuoles. While the latter have been commonly regarded as having an excretory function, it is possible that they are primarily for the purpose of regulating the water content of the cell. Even so, we should expect the extruded water to contain any soluble wastes that might be in solution in the water within the protoplasm. Under suitable conditions the storage of nutrient materials, such as starches and fats, may take place in the cytoplasm. *Respiration*, as in other protozoa, is the passage into the cell of oxygen from the surrounding water and is comparable with internal respiration in the cells of metazoa.

Reproduction and Life Cycle. — As with *amœba* and *euglena*, the life cycle of paramœcium consists principally of *asexual reproduction* by cell division (Fig. 99, E and F). *Sexual reproduction* occurs by *conjugation* (Fig. 100). The animal seldom, if ever, encysts under laboratory conditions, but *encystment* has been observed (Fig. 99 A to D). Perhaps it takes place more frequently in nature, since it is difficult to understand how any protozoan can be so universally distributed in fresh water without undergoing at least occasional encystment as a means of tiding over adverse conditions. It is true, however, that encysted stages are rarely observed, and some investigators have doubted whether encystment ever occurs. As seen in the laboratory, the life cycle consists apparently of an endless *active stage* with frequent cell division and occasional conjugation. There also occurs a process of internal nuclear reorganization, termed *endomixis*.

Aside from the problem of encystment, the life cycle is very well known, because of the ease with which the common species of paramœcium can be reared under laboratory conditions. Woodruff, for example, has maintained *P. aurelia* in the laboratory, *without conjugation*, from May 1, 1907, until the present time, and this race can no doubt be thus maintained indefinitely with-

out conjugation. The technique by which such results are obtained consists of isolating single paramœcia in a suitable culture medium, like hay infusion, leaving each individual until it has divided once or twice, and then isolating as many of the progeny as it is desirable to retain. As division of the cell usually occurs

FIG. 99.—Encystment and binary fission in paramœcium.

A to D, sketches by Curtis from living material observed by McClendon, showing problematical encystment and emergence a few days later. The animal folded itself together (A) and rotated as shown by arrows. Gradually a covering appeared (B). Within this the paramœcium seemed to have a truncate outline (C) that persisted for a short time after emergence (D), but disappeared in the course of one or two cell divisions as the paramœcium resumed its normal activities. E and F, binary fission, with dedifferentiation of old gullet and redifferentiation of a new one for each daughter cell, and with mitosis of the micronucleus and amitosis of macronucleus.

from one to four times in twenty-four hours, the multiplication is very rapid. If all could be preserved, they would soon produce an inconceivably large mass of protoplasm (*cf.* p. 548). Although such increase cannot actually occur either in the laboratory or in nature, it is always a possibility as shown by the rapidity of multiplication often observed in a culture jar that has been “infected” with paramœcia and allowed to stand for several days in the laboratory. *P. caudatum*, as well as *P. aurelia*, lends itself to “domestication” by the cultural methods above described.

In the cell division by which *asexual reproduction* is accomplished, the macronucleus divides by a simple elongation and constriction (Fig. 99); the micronucleus, by a special kind of mitosis (*cf.* Chapter 6, p. 137). As division of the two nuclei nears completion, the cell body becomes constricted near its middle and finally separates into two daughter cells. Meanwhile, one

new contractile vacuole is formed for each "daughter," and new gullets arise in each from the material of the original buccal region. After separation, the daughter cells normally grow to full size before a new division occurs. Under favorable conditions there

FIG. 100.—Schematic representation of conjugation in *Paramecium caudatum*.

(Redrawn from Jennings, "Life and Death, Heredity and Evolution in Unicellular Organisms," copyright, 1920, Richard G. Badger, printed by permission.)

may be as many as four such divisions, with the production of sixteen individuals in twenty-four hours. The rate of this division is determined by external conditions, such as food and temperature, and by certain internal factors. This production of "orphan twin sisters" continues until interrupted by conjugation or endomixis.

Although *P. aurelia* and probably other paramœcia may continue to live indefinitely without the *sexual reproduction* that is effected by conjugation, this process apparently occurs at more or less frequent intervals under natural conditions as well as in the laboratory. In some cultures that were long continued (Calkins, *P. caudatum*), it was observed that the need for conjugation occurred at intervals of some two hundred generations. In others (Woodruff, *P. aurelia*), it was found that conjugation need not occur even in many thousands of generations, if at all. The details of conjugation in *P. caudatum*, after the two cells have come in contact in the region of their buccal grooves, are shown in Fig. 100, the explanation of which should be consulted in this connection. The process differs markedly from the permanent fusion of cells that occurs in Sarcodina and Mastigophora. In such protozoa, conjugation consists in the complete and permanent union of two cell bodies and of their nuclei, and is thus comparable with the union of egg and sperm in the fertilization of higher animals (cf. Fig. 116, p. 233). The type of conjugation that occurs in paramœcium is found only among the Infusoria.

However, the net results are the same in both cases. Conjugation in one of the Sarcodina, such as amœba, or in one of the Mastigophora, such as euglena, results in a single cell of biparental origin, which is a *zygote*, comparable with the zygote formed by union of egg and sperm in many-celled animals. From two cells one is formed. In paramœcium a similar condition is brought about, since there arise, as a result of conjugation, zygotes, or cells of bi-parental origin (Fig. 100). The conjugation of paramœcium and other Infusoria may be said to be more efficient, however, because two zygotes, instead of one, result from each conjugation. Although the term "sexual reproduction" is commonly applied to the conjugation of paramœcium, it will be noted that the conjugating cells are *isogametes* and hence there is no evidence of sexual differentiation. Attempts are sometimes made to compare the migratory nucleus of conjugation with a sperm nucleus,

and the stationary nucleus with the nucleus of an egg. In this way conjugation is compared with reciprocal fertilization by two hermaphroditic animals. This is a most confusing comparison unless one has an extensive knowledge of the process of syngamy in both protozoa and metazoa.

In addition to conjugation, there has been discovered, first in *Paramœcium aurelia* and later in *P. caudatum*, the process of *endomixis*, which involves nuclear reorganization within the limits of a single cell, whereas conjugation involves two cells (Fig. 100). As with conjugation, however, there occurs during endomixis a disappearance of the macronucleus and of a considerable portion of micronuclear material. From the single micronucleus that remains in each cell, a new macronucleus and the two micronuclei characteristic of *P. aurelia* are then formed. Endomixis has, therefore, some resemblance to conjugation, although only one cell is concerned. Its significance in the life cycle is probably somewhat the same as that of conjugation.

There has been much discussion among investigators regarding the significance of conjugation and endomixis. It was originally supposed (Maupas) that conjugation must occur periodically among the Infusoria and that it exercised a "rejuvenating" effect upon paramœcium, since the rate of cell division was described as more rapid just after conjugation and gradually declining until the animal was rejuvenated by another conjugation. Later work has shown that conjugation is not necessary in the life cycle of paramœcium, since *P. aurelia* has been carried for many thousands of generations without such union of the cells (Woodruff). Endomixis has also been shown to be unnecessary, since *P. calkinsi* has been carried for four years (Spencer) during which time neither endomixis nor conjugation has occurred.

What, then, is the significance of conjugation in these ciliated protozoa? The present state of our knowledge seems to justify the following general answer: The ciliate *Uroleptus*, as studied by Calkins, does seem to be rejuvenated, in the sense that a declining rate of cell division is restored to normal by conjugation. Endomixis seems also to have this effect in some cases. But varied environmental conditions, such as changes in food supply, may also maintain a species at a proper level of cell division and hence normal metabolism. Moreover, there is the case of *P. calkinsi*, just cited, where neither conjugation nor endomixis seems neces-

sary. Ciliates without micronuclei, and hence possibly without conjugation or endomixis, are also known. It therefore appears that such rejuvenescence as may be necessary in these protozoa can be accomplished by more than one means. The one factor in conjugation that is unquestionable is the union of two diverse lines of descent; for, just as the fertilized egg of a many-celled animal is a single cell derived by union of two different germ cells (Fig. 116, p. 233), so the ex-conjugants of paramœcium are cells of double parentage. Thus, the basis for bi-parental inheritance exists among Infusoria as in other protozoa. Conjugation in the ciliated protozoa, and presumably in other unicellular forms, is, therefore, significant (1) as a means of uniting two diverse lines of descent with the result that variation may be increased; and (2) apparently, under some conditions, as a means of stimulating cell division and other cell functions and hence rejuvenating lines that might otherwise perish.

Other Infusoria. — Since the ciliated Infusoria, or *Ciliata*, include most of the species of Protozoa that are likely to be seen by the student, it will be useful to indicate the more important subdivisions and the names of representative genera. Ciliata are classified, according to the nature and distribution of their cilia, into the following groups:

- I. **Aspirigera.** — Forms without a spiral zone of oral cilia or membranelles.
 1. Order, *Holotricha*. — Having the cilia of about equal length and evenly distributed in the simpler forms; and with cilia having more complex arrangements in the more specialized forms. With a cytostome, except in some of the parasitic types. *Opalina*, *Prorodon*, *Cotaps*, *Didinium*, *Amphileptus*, *Lionotus*, *Loxodes*, *Dileptus*, *Colpoda*, *Frontonia*, and *Paramœcium* are among the genera of this order that are common in fresh water (cf. Fig. 94).
- II. **Spirigera.** — Forms with a conspicuous spiral zone of larger cilia or vibratile membranelles leading to the mouth.
 2. Order, *Heterotricha*. — Usually swimming, sometimes attached. Body cilia small or reduced in

- contrast to the well-developed cilia of the oral region. *Spirostomum*, *Stentor*, and *Halteria* are common genera (cf. Fig. 94).
3. Order, *Hypotricha*. — Typically creeping forms with a marked dorso-ventral differentiation. Cilia of ventral surface modified to form large leg-like cirri. *Oxytricha*, *Stylonichia*, and *Euplotes* are the most common genera (cf. Fig. 94).
 4. Order, *Peritricha*. — Typically attached forms. Oral cilia are continued into a depression in which open the cytopyge and the contractile vacuole, and at the base of which is the mouth. Locomotor cilia are present only during certain phases of the life cycle. *Vorticella*, and the colonial forms, *Carchesium* (Fig. 103 G), *Epistylis*, and *Zoöthamnium*, are the most common genera in fresh water.

The *Suctoria*, or *Tentaculifera*, which constitute the other subdivision of the Infusoria standing on a par with the *Ciliata*, may be mentioned here. Few of these occur in fresh water, but they are not uncommon at the seashore where they are found attached to various objects. In the adult phase of their life cycle the Suctoria are attached and capture food by means of *tentacles* to which the prey becomes attached distally and through which its contents are slowly sucked into the body of the suctorian. The fresh-water *Podophrya* is an example (Fig. 84 D). *Suctoria* are classed with the *Ciliata* as *Infusoria*, because they have a ciliated phase in their life cycle. This leads us to believe that in their evolutionary history they have arisen by modification of ciliated forms.

The Sporozoa

Monocystis. — The Sporozoa are a large group of Protozoa, all of which are parasitic. Like other parasites, they show a degeneration of the structures necessary for free life, and a specialization of structure and function and of the life history, wherever necessary to meet the demands of parasitic existence. The genus *Monocystis*, which inhabits the seminal vesicles of earthworms, is a sporozoan that is easily obtainable, and one that exhibits within its host all the important stages of its life cycle. In structure, the adult monocystis (Fig. 101) is a simple elongated cell with a single

nucleus. Living as it does under rich nutrient conditions, the cytoplasm of the cell at this stage is able to assimilate and store up an abundance of food material to be used in later stages when nutritive processes are in abeyance. Such powers of rapid assimilation, and hence of rapid growth, are common in parasites during favorable periods of their life cycles.

FIG. 101.—Life cycle of the gregarine, monocystis.

A, spore consisting of a spore case enclosing eight sporozoites. B, transverse section of same. C and D, liberated sporozoites. E, sporozoite after entering multicellular sperm sphere of earthworm. F and G, growth in sperm sphere until the fully formed trophozoite is formed surrounded by the degenerate remains of sperm sphere with flagella of spermatozoa. H, two trophozoites that have become free of the degenerate sperm sphere and united as gametocytes. I, encystment of gametocytes. J, division of nuclei and cytoplasm to form gametes. K, union of the gametes in isogamous conjugation to form zygotes, residual cytoplasm of gametocytes in center of cyst. L, cyst containing many sporozoites formed by secretion of a spindle-shaped spore case around each zygote, which then divides to form eight sporozoites. These eventually become arranged as in A and B, in which stage they are transferred to another host. (Drawn by Wiley Crawford.)

Excretion of the waste products of dissimulation must occur, in monocystis, by diffusion from the cell into the surrounding fluid of the host. Hence, the parallel between a monocystis, living sur-

rounded by the fluid of the earthworm's seminal vesicles, and the cell of any higher animal (*cf.* Fig. 60, p. 104), surrounded by intercellular lymph, is a close one. Presumably, the same kind of constructive and destructive metabolic changes occur in either case. Very little can be said regarding the cell behavior in such a form. By expanding and contracting its body, the monocyctis effects a slow locomotion, but, living as it does, it has no need for any complexity of behavior or for locomotor structures. The life cycle is shown by Fig. 101 and its legend.

Metabolism, Irritability, and Reproduction in Protozoa

The types of protozoa that have been described illustrate the manner in which the three great capacities of metabolism, irritability, and reproduction are exhibited by the protoplasm of unicellular animals. While comparisons can be made between the protozoan cell as an individual animal and the individual composed of many cells as in higher animals, the more exact comparisons are to be made between cell and cell. Thus, in parasitic protozoa, the unicellular organism bathed in the fluids of its host's body, from which it assimilates nutrients and into which it excretes the waste products of its dissimilation, presents a close parallel with the cell of a higher animal as it lies surrounded by its intercellular lymph. If one examines the more representative protozoa with holozoic nutrition like that of the amœba and paramœcium, it appears that they exhibit all the metabolic processes that it is possible for them to possess in view of their organization. Ingestion, digestion, egestion, assimilation, respiration, dissimilation, and excretion are all present on essentially the same basis as in many-celled forms (*cf.* p. 103). In the nature of the case, absorption through the mucous membrane of a digestive tract, circulation in the blood, and excretion by excretory organs cannot be present in the protozoan. Metabolism is the same, however, whether in an amœba or in a human being.

Likewise, the response to stimulation, which constitutes irritability, appears to be the same kind of process whether in protozoa or metazoa. If we consider the cells of the frog or man individually, they respond to a variety of stimuli: mechanical, chemical, thermal, electrical, photic, etc. To all these a protozoan cell may respond equally well, and sometimes to a more marked degree,

because metazoan cells are limited by their specialization. Even the cells of sense-organs, which are *par excellence* the cells of irritability, have limited powers in the metazoa, for they respond only to particular forms of stimulation — the auditory cells only to sound waves, the retinal cells only to light, the cells of the taste-buds to certain chemicals. Nerve cells may respond more widely, as when one stimulates a nerve by heat, by chemicals, or by electricity; but when a nerve impulse reaches other nerve cells in the central system, the effect may be similar, because the cells seem able to respond only in a limited manner. While the responses of the metazoan body as a whole may be far more complex than those of any protozoan, it is, nevertheless, difficult to make out for the majority of cells in the metazoan even as wide a range of response to stimulation as occurs in the more active protozoa, for the reason that the cells of metazoa are specialized for particular functions while the protozoan cell is specialized for all the functions of an individual. In any event, it is clear that irritability is the same kind of a process in both protozoa and metazoa.

The exact manner in which the reproductive process may be compared in protozoa and metazoa is described in a subsequent chapter. In this connection, however, it may be repeated that conjugation, as it occurs in a majority of the protozoa, by a permanent fusion of two cells to form one, is comparable with fertilization, or the union of egg with sperm, in the metazoa. From a zygote arising in this manner, many independent protozoan cells are formed by division; while in metazoa the zygote produces, by cell division and differentiation, a many-celled body. Hence, there is a remarkable parallelism between the cellular cycles even in the extremes of animal life (*cf.* Fig. 110, p. 215). Reproduction, like metabolism and irritability, is a similar process whether in the highest or the lowest animals. The essential nature of the cell and its protoplasm and the universality of the distinguishing capacities of protoplasm become increasingly apparent as we proceed.

The foregoing comparison of cell with cell in protozoa and metazoa perhaps does injustice to the protozoan as an individual animal. Protozoa are "cells," but they are also "individuals." As such they may be compared with individuals composed of many cells. In extreme cases (Fig. 102) the single-celled organism may present features that parallel structures in higher animals and thus may

show an astonishing complexity. Comparisons can be made even in forms as simple as paramœcium, in which, although there is no digestive canal, there is a region in the cytoplasm along which

vacuoles move from "mouth" to "anus."

Again, the paramœcium "behaves as a whole" in the action of its cilia during the avoiding reaction and in swimming forward or backward. These considerations have led some students of the group to emphasize the individuality of the protozoan instead of its cellular state, and to disregard the comparisons that may be made between colonial protozoa and metazoa as colonies of cells. This idea of *the individual as more important than the cell*, has been called the *Organismal Theory* in contrast to the Cell Theory of organisms. The more reasonable position seems to be a recognition of the protozoa as physi-

FIG. 102.—A complex ciliate, *Diplodinium caudatum*, showing highly developed organelles.

caec., caecum or rectal canal; cut., cuticle; c.v., contractile vacuole; cytop., cytopyge or cell anus; cytost., cytostome or cell mouth; d.m., dorsal membranelle; ect., ectoplasm; end., endoplasm; mac. n., macronucleus; mic. n., micronucleus; myon. (str. retr. oes.), myonemes, strands for retracting oesophagus; neur. m. ap., neuro-motor apparatus; oes., oesophagus; or. cil., oral cilia; sk. lam., skeletal laminae. X750. (After Sharpe.)

ologically balanced and independent cells, which in some instances have undergone extreme specialization of structure within the limits of their unicellular nature; and of the metazoa as multicellular organisms in which the cells are physiologically unbalanced because of their mutual dependence.

CHAPTER 8

GENERAL PROBLEMS RELATED TO SINGLE-CELLED ANIMALS

It is evident from the special accounts in the preceding chapter that many important biological problems are intimately related to single-celled organisms. The existence of colonial species among unicellular animals and plants suggests the transitional steps that probably occurred in the development of various organisms from the primitive unicellular forms of life that are supposed to have existed at a very remote period and to have been the ancestors of many-celled animals. The manner in which individuals come into being at the present time, whether by reproductive processes, *biogenesis*, or by processes of spontaneous generation, *abiogenesis*, may be considered here, since unicellular organisms were the last stronghold of the advocates of spontaneous generation. Again, many diseases are caused by protozoa living as parasites in the bodies of men and animals, thus linking the protozoa with medical problems.

Colonial Protozoa and the Comparison of Unicellular with Multicellular Organisms

The Colonial Organization. — Although the typical protozoan is an independent and self-sustaining cell, there are many colonial species. These *protozoan colonies* are produced when the cells arising from the single cells, which occur at one or more phases of the life cycle, remain together, instead of separating after division as in non-colonial forms. During this colonial phase the group of cells constitutes an individual of a slightly higher order, which is the colony. Such colonies are called *gregaloid*, if their cells are arranged irregularly (Fig. 103 A); *linear*, if in a line (Fig. 103 B); *arboroid*, if branching (Fig. 103 G); or *spheroid*, if in a spherical or globular mass (Fig. 103 E). The cells of a colony are associated but independent, since each cell can reproduce a new colony by division

FIG. 103.—Types of colonial protozoa.

A, *Microgromia*, a gregaroid colony. B, *Ceratium*, a linear colony. C, *Codonosiga*; an arboroid colony. D, *Spondylomorum*, a spheroid colony. E, *Synura*. F, *Uroglena*. G, *Carchesium*. H₁ and H₂, portions of *Anthophysa* colony. (Figs. redrawn as follows: A, from Calkins, "Protozoa," copyright, 1901, by The Macmillan Co., printed by permission. C, from Minchin, "Introduction to Study of Protozoa"; copyright, 1912, by Edward Arnold and Co., printed by permission. D and E, after Blochmann; G, after Kent; H₁ and H₂ after Blochmann.)

or become a gamete at the time of sexual reproduction, and is self-sustaining in its metabolism and irritability. The colony may have a definite shape and size and move as a whole in locomotion, but otherwise its cells are as independent as those of non-colonial species. Their colonial organization is only the remaining together of similar cells to form a mass of characteristic size and appearance. Some coördination may exist, as when the colony swims in a particular direction or contracts as a whole; but the colony is not a many-celled organism in the true sense, because there is no division of labor, as in the metazoan, where there are different kinds of cells and corresponding specializations in function.

Colonial Mastigophora. — The comparison of unicellular with multicellular organisms may be pursued through certain of the

FIG. 104.—*Chlamydomonas*, a non-colonial protozoan, and two simple colonial types.

A, *Chlamydomonas*. B and B', two views of *Gonium sociale*, a colony with only four cells. C and C', two views of *Gonium pectorale*, a colony with sixteen cells.

plant-like Mastigophora, particularly the family *Volvocidae* and closely related forms. The members of the genus *Chlamydomonas* (Fig. 104 A) are simple non-colonial protozoa consisting of a single spherical or oval cell with two flagella, a red pigment spot like that of *Euglena*, a prominent chromatophore, two contractile vacuoles, and a cell wall. Reproduction is effected by binary fission with immediate separation of the two individuals thus formed. Conjugation takes place by the permanent union of isogametes. *Chlamydomonas*, therefore, resembles Type 3 of the series shown in Fig. 110, p. 215.

A very simple type of colony is seen in *Gonium sociale* (Fig. 104 B; and cf. Type 4, Fig. 110), one of the *Volvocidæ*. This consists of four cells arranged in a single layer and embedded in a gelatinous plate. Each cell has two flagella, a pigment spot, a chromatophore, and a contractile vacuole with one pyrenoid. Locomotion is by a revolution which shows first the surface and then the edge of the colony. The cells are physiologically self-sustaining, like those of non-colonial protozoa, since each can produce a new colony if they are separated. The colonies are produced asexually by division of the cells to form four daughter colonies, which separate, thus ending the existence of the parent colony as such; or sexually by separation of the cells of the colony to form isogametes (cf. p. 174). In the related species, *Gonium pectorale* (Fig. 104 C), there are sixteen cells in the colony, but otherwise the structure and life cycle resemble those of *G. sociale*.

Pandorina morum (Fig. 105; and Type 4, Fig. 110), which is slightly more specialized than *Gonium*, consists of eight or sixteen

FIG. 105.—*Pandorina morum*, a colonial protozoan.

A, fully developed colony composed of sixteen flagellated cells. B, formation of daughter colonies by division of each cell to form sixteen. B', daughter colony free of parent colony. C, formation of microgametes. d to g, union of microgamete (d) with macrogamete (d') to form zygote (g). (After Oltmanns.)

cells, rarely thirty-two, packed together in an oval mass and surrounded by a common envelope. Each cell has two flagella, a pigment spot, a chlorophyll body and a contractile vacuole. The colony swims as a whole, but otherwise its cells are physiologically independent. When fully grown, each cell divides to form miniature colonies of sixteen cells, each of which breaks through the envelope of the parent colony and grows to full size, repeating the

process. Preceding conjugation the cells of the colony separate and each cell becomes a gamete. These gametes are isogamous, or slightly anisogamous, thus showing the simplest form of sexual differentiation (cf. p. 174).

In *Eudorina elegans*, another species of the *Volvocidæ*, the colony consists of eight, sixteen, thirty-two, or even sixty-four flagellated cells resembling those of *Pandorina*. Daughter colonies are likewise formed by division of the individual cells of the parent colonies. Conjugation occurs by union of anisogametes, which are formed from all the cells of the colony as in *Pandorina*, but in different colonies, and fuse to form zygotes that produce new colonies by cell division. *Eudorina* is more complex than *Pandorina* because the colony is composed of a greater number of cells, and because there are "male" and "female" colonies as well as "male" and "female" gametes.

Thus in *Gonium*, *Pandorina*, and *Eudorina*, there are gametes; but there is no distinction between body cells and germ cells, because all the cells of these colonies give rise to germ cells at the time of conjugation. The cells of such colonies are, therefore, independent in all essential respects and exhibit the condition of physiological balance that characterizes the cells of non-colonial protozoa. In the examples that follow, the distinction may be drawn between *body cells*, which die a natural death by the disintegration of the colony, and *germ cells*, which are potentially immortal since they may unite in fertilization and so continue to future generations.

Pleodorina illinoisensis consists of a colony of thirty-two cells differentiated into twenty-eight larger cells, which give rise to *gametes* or *germ cells* like those of *Eudorina*, and four smaller *somatic* or *body cells*, which are located at one end of the ellipsoidal colony. There is another species, *P. californica*, in which there are either sixty-four or one hundred and twenty-eight cells, of which approximately one-half are body cells. Hence a division of labor exists among the cells of such a colony, as shown by their structural differences, and by the physiological differences that may be inferred to exist between cells having such different fates as do gametes and somatic cells.

In the various species of the genus *Volvox*, this fundamental division of labor between somatic and germ cells becomes more conspicuous, since the somatic cells of the *Volvox* colony greatly

outnumber the germ cells. For example, *V. perglobator*, a species common in the United States and very similar to the European form *V. globator* (Fig. 106), is a colony of several thousand cells arranged at the surface of a sphere the interior of which is occupied by a watery fluid. Each somatic cell consists of a central mass

FIG. 106.—*Volvox globator*.

A, one-half of the spherical colony. B, fertilized macrogamete or ovum, with male and female nuclei uniting, and protective shell secreted after entrance of the sperm nucleus into the cytoplasm of the ovum. C, microgamete or spermatozoön. Ov, ovum; S.C., somatic cells; Sp. 1-2-3, developing spermspheres.

of protoplasm containing a nucleus and connected with the protoplasm of neighboring cells by radiating strands that perforate the cell walls. Each somatic cell further possesses two flagella, by means of which the colony is propelled, a red pigment spot, and a contractile vacuole. The germ cells of the volvox, which are much less numerous than the body cells, become differentiated from the general mass of somatic cells as the colony develops. In their earlier stages they appear as cells of larger size, projecting from the inner face of the somatic layer but retaining their connections with the outer surface (Fig. 106 A). The *macrogametes*, or ova, as they are sometimes called, are formed by an increase in size which is principally due to the formation of nutrient material in the cytoplasm; the *microgametes*, or spermatozoa, arise by the

division of a single large cell to form many small ones, each with two flagella. In *V. perglobator* these male and female cells are produced in different colonies. In some of the other species, like *V. globator*, both male and female cells are produced in the same colony, which is therefore said to be *hermaphroditic*. At the time of fertilization, the microgametes are discharged from the colonies and swim by their flagella until they perish or come in contact with a colony containing ova. The ovum is fertilized as it lies in place within the colony. In addition to the somatic cells, and the gametes that take part in sexual reproduction, the *Volvox* colony contains cells known as *parthenogonidia*. A parthenogonidium, by repeated divisions, can give rise to a new colony. This is the asexual method of reproduction in *Volvox*.

These colonial Mastigophora are of interest because they show that the line between single-celled and many-celled forms cannot be sharply drawn in existing organisms. Since this is the case among the plants and animals now living, it is not unreasonable to suppose that many-celled forms may have arisen, during the early history of organisms upon the earth, by steps somewhat like those indicated by Fig. 110. This statement does not mean that *Volvox* and its plant-like relatives, *Pleodorina*, *Pandorina*, and *Gonium*, are the ancestors of animals. They are plants rather than animals, although classified in the Mastigophora (*cf.* p. 155). What the series shows is a transition, from the single-celled to the many-celled state, which is so gradual that one sees why distinctions cannot be sharply drawn, although the extremes of the series represent distinct conditions. In the protozoan the cell is an independent unit and therefore in a state of physiological balance with respect to its fundamental capacities of metabolism, irritability, and reproduction. In the metazoan it is the whole mass of cells that possesses a physiological balance comparable with that of the protozoan. In protozoa, the "individual" is the cell; in metazoa, it is the group of cells. These facts have a bearing upon the Organismal Theory as opposed to the Cell Theory (*cf.* p. 194). The series of colonial Mastigophora that form the basis of the comparisons here set forth between unicellular and multicellular organisms are further considered in the general discussion of reproduction in the next chapter.

Biogenesis *vs.* Abiogenesis

Historical.—As a result of investigations extending over a period of more than two hundred years, it was shown during the third quarter of the nineteenth century that spontaneous origin of protoplasm does not take place. Protoplasm seems to come from preëxisting protoplasm, by a process of detachment, as in reproduction, or by an increase of bulk as in growth. It was natural for the ancients to believe that animals like rats and mice, frogs, and insects, which suddenly swarmed in certain places, were produced from the mud of the fields under the influence of the sun's rays, or bred spontaneously within the decomposing carcasses in which they were found. It was even supposed that forms like the mammals, which developed within the female parent, arose spontaneously under the influence of the male's seminal fluid. The higher animals were, of course, known to have "parents," but there was no concept of the continuity between generations, save as "eggs" like those of birds and reptiles were observed to produce young, and mammals to give birth to living offspring. However, it was gradually established that smaller animals arose from eggs. The Italian naturalist, Redi, performed experiments (1688) that showed how maggots originated in meat from the eggs laid by flies. He placed pieces of meat in jars, covering some with wire gauze and others with parchment, and leaving others uncovered. Flies were attracted as the contents of the jars began to decompose, and laid their eggs directly on the meat or upon the wire gauze. Maggots were seen to hatch from these eggs and to develop as they consumed the meat. Eggs transferred from the gauze to the meat behaved in like manner. The meat in the parchment-covered jars merely decomposed without the appearance of any maggots. Redi made other observations upon the development of insects and reached the conclusion that all cases of "spontaneous" generation of living organisms were presumably due to the introduction of living germs from without. Had it not been for the discovery of protozoa, bacteria, and other micro-organisms during the latter half of the seventeenth century, the question would perhaps never have arisen again in the subsequent history of biological science.

In 1676, the Hollander, Anthony van Leeuwenhoek, discovered with the microscope, which had recently come into use as a toy and

source of amusement, what he described as "little animals observed in rain, well, sea, and snow water as also in water wherein pepper had laid infused." Among other things, he observed some of the larger bacteria, many protozoa, and the passage of blood from arteries to veins through the capillaries; and he was the first to describe, if not the discoverer of, the human spermatozoön. In one of his publications, Leeuwenhoek writes as follows:

In the year 1675 I discovered living creatures in rain-water which had stood but four days in a new earthen pot, glazed blew within. This invited me to view this water with great attention, especially those little animals appearing to me ten thousand times less than those represented by Mons. Swammerdam, and by him called water-fleas or water-lice, which may be perceived in the water with the naked eye. The first sort by me discovered in the said water, I divers times observed to consist of 5, 6, 7, or 8 clear globules, without being able to discover any film that held them together, or contained them. When these *animalcula* or living atoms did move, they put forth two little horns, continually moving themselves; the place between these two horns was flat, though the rest of the body was roundish, sharpening a little towards the end, where they had a tayle, near four times the length of the whole body, of the thickness (by my microscope) of a spider's web; at the end of which appears a globul, of the bigness of one of those which made up the body; which tayle I could not perceive, even in very clear water, to be mov'd by them. These little creatures, if they chanced to light upon the least filament or string, or other such particle, of which there are many in the water, especially after it hath stood some days, they stood entangled therein, extending their body in a long round, and striving to dis-entangle their tayle; whereby it came to pass, that their whole body lept back towards the globul of the tayle, which then rolled together serpent-like, and after the manner of copper or iron-wire that, having been wound about a stick, and unwound again, retains those windings and turnings. This motion of extension and contraction continued a while; and I have seen several hundreds of these poor little creatures, within the space of a grain of gross sand, lie cluster'd together in a few filaments.

The observations of Leeuwenhoek were greatly extended by other workers during the eighteenth century, until all the more important types of microscopic animals came to be recognized. Although it was supposed that larger organisms arose from eggs or seeds that were in the nature of living "germs," it was still possible to believe that micro-organisms arose spontaneously where conditions were suitable for their production. This belief was not

unnatural in view of the sudden appearance of innumerable minute forms of life as often observed in laboratory cultures. Some biologists, from Redi onward, reasoning by analogy with higher organisms, always believed that such micro-organisms arose from preëxisting forms, although many clung to the idea of spontaneous origin. The process by which life was assumed to arise spontaneously may be called *abiogenesis*, in contrast to *biogenesis* or the genesis of life from life. The persistent belief in the possibility of abiogenesis led Spallanzani, in 1775, and Schwann, in 1837, to perform extensive experiments, the results of which were against the theory of spontaneous origin. In spite of these repeated failures to find any positive evidence for abiogenesis, the question was reopened on theoretical grounds by Pouchet in 1859.

Final Establishment of Biogenesis. — The work of Pasteur and others was stimulated by this final recrudescence of the idea of spontaneous generation, as induced by Pouchet and his followers. Then came the series of brilliant researches by this great Frenchman, by the German, Koch, and by others, which finally showed how even the smallest organisms arise by cell division from parent forms. Encysted stages of protozoa and spore stages of bacteria were recognized and followed stage by stage until the life cycles of representative types were fully established alike in their active and in their resting stages. The English physicist, Tyndall, in the course of his investigations upon light, studied the "floating matter of the air" and showed that it teemed with spores and other resistant stages which needed only to settle upon a proper medium in order to germinate (Fig. 107). The English surgeon, Lister, and others who investigated the germ theory of disease as applied to surgery, established the fact that the germs found in wounds and in specific diseases were not generated spontaneously when conditions became right for them within the animal body, but were introduced into it as the spores or active stages of such minute organisms might be introduced into a sterile culture medium. The progressive extension of such demonstrations and the further extension of the Cell Doctrine to the origin of higher organisms completed the overthrow of abiogenesis and established biogenesis, or the origin of living organisms from preëxisting organisms, as the true explanation of the source of new individuals, although there will always remain the theoretical possibility that protoplasm may be synthesized under conditions of laboratory experi-

FIG. 107.—Tyndall's apparatus.

The apparatus consisted of a chamber with glass front and windows (*w*) and with test-tubes fitted tightly in the bottom. Air could enter the chamber by the tubes *a* and *b*, but the entrance of particles floating in the air, like dust and bacterial spores, was prevented by bending these tubes. A pipette (*c*) that entered the chamber through a rubber diaphragm could be moved to place material in the different test-tubes. This pipette was plugged with cotton at (*p*) when not in use.

In the experiments, the chamber was tightly sealed and left undisturbed for a few days until the particles floating in the air had settled to the bottom of the chamber, as indicated by the fact that an intense beam of light, when passed through the windows, failed to show its track within the chamber. Various nutrient fluids, like hay infusion, beef broth, etc., were then introduced into the test-tubes by means of the pipette. A brine or oil bath was placed under the chamber and the test-tubes boiled for five minutes. Although the chamber was thereafter placed in a warm room, there was not a single unexplained case in which such an infusion showed any signs of life. That the observed sterility was not due to any lack of nutritive power in the infusions was proved by opening the door of the chamber and permitting free entrance of the external air with its suspended particles, and by introducing contaminated material into individual test-tubes through the pipette. (From Tyndall, "Floating Matter of the Air," copyright, 1888, by D. Appleton & Co., reprinted by permission.)

mentation. Hence, the dictum of an earlier time, "*omne vivum ex ovo*," every living thing from an egg, and the later one, "*omnis cellula e cellula*," every cell from a cell, express the facts as now established. The manner in which unicellular organisms arise by processes of reproduction from parent organisms like themselves has been described. The origin of higher animals by reproduction and development is explained in subsequent chapters.

The long controversy over spontaneous generation, described in the foregoing paragraphs, was related throughout to the idea that certain diseases spread and multiplied like living organisms. When it was discovered that organisms did cause disease, this idea was confirmed. It is, therefore, appropriate to consider the Germ Theory of disease in the section that follows.

Protozoa and Disease

The Germ Theory of Disease. — What is known as the Germ Theory of disease postulates that certain diseases are produced by "germs," or minute organisms that live as parasites in the bodies of plants or animals and are the specific causes of particular diseases. The "symptoms" of the disease are, in general, the bodily reactions in response to such parasitic invasions. Some diseases, like the *hookworm disease*, are caused by larger parasites; others, like *malaria* and *typhoid fever*, by minute parasites which are protozoa or bacteria. In general, all "infectious" diseases are due to organisms which infect the body and whose normal existence in this phase of their life cycle is a parasitic one.

Malaria and the Malaria Parasite. — The disease called malaria has been known since ancient times. Some have even regarded it as one of the causes of the decline of ancient Rome. Certain it is that both Romans and Greeks, and probably other ancient peoples, suffered greatly from this pestilence. Early explorers of the Americas found it established in the tropical regions of both continents and brought back to Europe the South American Indian's medicine in the form of "Peruvian bark," from which quinine was later extracted. At the present time the seriousness of the disease in all the warmer parts of the world is a matter for statesmanship as well as medicine. In India alone there are over a million deaths per year, to say nothing of the uncounted thousands who are incapacitated. Other regions are not much better off,

save as restricted localities have become subject to sanitary measures. In 1907 it was estimated that there were some 12,000 deaths per year in the United States, principally in the South; and it has been estimated that there may be as many as three million cases a year, involving a financial loss of not less than \$100,000,000. This condition exists in a country in which there is full knowledge of the causation of the disease and of the preventive measures that have made such regions as the Panama Canal Zone safe habitations.

The word "malaria," which means bad air, was originally applied to a group of fevers known to be associated with the air of swampy regions. The idea that such air acts as the causative agent is still prevalent among the ignorant, but if there are no mosquitos to act as intermediate hosts for the parasite there is no malaria. The disease germ in this instance is one of the Sporozoa, a representative of which is the *Plasmodium malariae*, which causes the quartan type of malaria. In man the parasite lives in the blood, invading the red corpuscles (Fig. 108), where it forms merozoites that are liberated with the destruction of the corpuscles, and in turn invade new corpuscles in which the process is repeated. In this manner a very large number of the red blood cells may be destroyed and the numbers of the parasites greatly increased. Waste products, in the form of melanin granules set free in the blood stream with the liberation of the merozoites from the disintegrating corpuscles appear to be the specific substances that cause the chills and fever, since the liberation of merozoites and the ague both occur at intervals of about seventy-two hours. After a considerable period of such multiplication, the parasite begins the formation of male and female gametocytes which must be drawn from the blood of man by the bite of a mosquito if they are to undergo the process of conjugation which is necessary for their further development. In the stomach of the new host the final stages of the gametes and the conjugation occur. The resulting cell passes through the epithelium of the stomach wall and takes up a position as shown in the figure. Then division of the nucleus occurs repeatedly, and as the mass grows each nucleus is surrounded by cytoplasm and eventually becomes a spindle-shaped cell or sporozoite. The cyst bursts and the cells thus liberated migrate through the body spaces to the salivary glands, from which they are ejected with saliva when the mosquito bites a human being.

Life cycles in which there are similar primary and intermediate hosts are not uncommon among parasites. The present example

FIG. 10S.—Life cycle of the parasitic protozoan, *Plasmodium malarie*, that is the cause of quartan malaria.

1, the parasite, known as the sporozoite, as it is introduced into the blood of man by bite of mosquito; 2, 3, 4 and 5, sporozoite entering red blood corpuscle where the parasite grows and reproduces new individuals by sporulation; 6, destruction of corpuscle resulting in liberation of these new individuals, known as merozoites, and of excretory or melanin granules into blood plasma; 7, 7a, 8 and 8a, formation of male and female gametocytes in red blood corpuscle of man; 9, formation of macrogamete in stomach of mosquito; 9a and 9b, formation of microgametes in stomach of mosquito; 10 and 11, union of macrogamete with microgamete to form zygote in stomach of mosquito; 12, zygote after penetrating epithelium of mosquito's stomach; 13, sporozoites formed by divisions of zygote within its cyst; 14, female of mosquito that transmits malarial parasite; head of male below; 15, external surface of mosquito's stomach showing swellings produced by encysted stages formed by division of zygotes shown in 13; 16, section of salivary gland of mosquito, showing sporozoites which have been freed from cyst and have migrated through the body cavity to the gland cells. They lie ready to be discharged into the blood stream of man when the mosquito feeds. (After the Leuckart-Chun chart, from Hough and Sedgwick, "Human Mechanism," copyright, 1918, by Ginn & Co., reprinted by permission.)

also illustrates the relationship of insects to disease-producing organisms. The following are representative cases affecting man: yellow fever, the germ of which, like that of malaria, is carried by a mosquito; typhus fever and trench fever, transmitted through the body louse; Rocky Mountain spotted fever, transmitted by a wood tick; the Japanese flood fever, transmitted by a small mite; elephantiasis, in which the parasite is one of the thread worms, transmitted by mosquitos; relapsing fever in man, and Texas fever in cattle, transmitted by ticks; bubonic plague, by fleas. The list might be further extended. It is for this reason that the insects have assumed great importance to medicine, particularly in tropical countries, since the stages of the malaria parasite, the first life cycle of this nature to be discovered, were ascertained in 1898.

African Sleeping Sickness and Trypanosomes. — Another example of an insect-borne disease is the sleeping sickness, occurring in equatorial Africa and caused by one of the flagellated protozoa called *trypanosomes* (Fig. 109). By the bite of the blood-sucking tsetse fly, the stages of the parasites found in human blood are transferred to the intestine of the insect, which serves as an intermediate host. Here a series of stages occur, until some three to four weeks later the parasites appear in the salivary glands of the tsetse fly, from which they may be again transferred to the blood of man or some other mammal. In the final stages of the cycle, they invade the cerebro-spinal fluid, causing the sleep that characterizes this disease and finally ends in death. It is a curious fact that while they cause a fatal disease in human beings, they apparently produce no very serious effects when they invade the blood of some of the larger African mammals. Such a condition can perhaps be explained on the theory that the mammals in question have acquired an immunity through being subjected to the infection for many generations, whereas man has perhaps but recently come into contact with these parasites.

Protozoa, as well as bacteria, have thus become recognized as the germs of certain diseases, although the majority are harmless or even beneficial to man. A science of *Protozoology*, comparable with Bacteriology, has arisen in the past twenty-five years. Medical schools in which tropical diseases demand special consideration have established professorships in this subject. It seems unlikely that the protozoa will ever assume the importance of the

bacteria in this regard, since so many more bacterial diseases have now been discovered. Nevertheless, the fact that certain protozoa

FIG. 109.—Life history of *Trypanosoma gambiense*. × 1500.

(From Chandler, "Animal Parasites and Human Disease," John Wiley and Sons, copyright, 1922, reprinted by permission.)

are important as causes of infectious diseases, along with the relation of insects to disease, is among the great discoveries of medicine in recent years.

Reactions of Hosts to Parasites in Disease. — In the present connection we may consider some aspects of the host-parasite relationship that have a bearing upon the problems of infectious diseases. Similar relationships probably obtain in other cases of parasitism, although the knowledge of such conditions is mainly derived from the study of disease in man and the domesticated animals. One feature of general importance is that most parasites are specialists. One might think that a given species of parasite would invade many hosts. This is the case in some instances; but on the whole the parasitic species are remarkably limited in their range of habitat, since they are able to survive only in a single species of host or a few closely related species.

Many interesting reactions might be considered under the head of adjustments by the host to its parasites. The simplest of these is *mechanical protection* by the formation of barriers against further invasion or injury, as when cysts are developed by the connective tissue of a host in a way that walls off the parasites. Another important means of defense is that known as *phagocytosis*. The white blood cells, or phagocytes, and, to a lesser extent, other cells such as those of the mucous membrane and connective tissue, regularly ingest and destroy invading organisms like bacteria, as does the amoeba with its prey or the endoderm of a hydra during intracellular digestion (*cf.* p. 261). This relationship is so well adjusted in the higher animals that the number of white blood cells increases rapidly in response to infection by certain disease-producing organisms.

A more complex reaction is seen in what is termed *immunity*. It is a familiar fact that a patient who has recovered from typhoid fever, or certain other diseases, is immune to a subsequent attack of the same disease. In some manner the individual is not as he was before, because he has almost no chance of ever contracting disease again. Something, which we call immunity, has been acquired by his body. Apparently what has happened is a chemical change in the plasma of the blood and lymph, but the exact nature of this change is unknown.

That the relationships are complicated and far-reaching will appear from the most general enumeration of the types of immunity that are now recognized. Thus, immunity acquired by successfully withstanding the course of a disease is called *natural immunity*, in contrast to the *artificial immunity* acquired through artificial

agencies. Natural immunity may be inherited, as when a race of animals shows high resistance to a disease; or acquired during development by any individual having a disease at any period of life. Artificial immunity may be acquired by the various methods of vaccination and inoculation that are common practices in current medical treatment. For example, in typhoid vaccination the dead germs of the disease are injected into the individual. In response to the stimulus of the organisms introduced during vaccination, the individual produces substances by his own metabolism that protect him against such disease organisms. This is known as the establishment of *active artificial immunity* because the individual has built up his own protection. As a check against the progress of diseases such as diphtheria, blood serum, prepared from an animal, such as a horse, that has been inoculated with the germs, is injected into the patient. In such cases it appears that there is present, in the injected serum, a substance called the antitoxin, which counteracts the toxins or poisons liberated by the bacteria of the disease. This produces *passive artificial immunity*, so called because the metabolism of the patient takes no part in building up the antitoxin. Immunity thus implies the opposite of "susceptibility" and covers a wide range of phenomena. However, it is to be regarded as but an aspect of the whole series of metabolic events and of the responses of the animal body under stimulation.

CHAPTER 9

REPRODUCTION

The functions of metabolism and irritability have been examined in our study of a vertebrate animal and of unicellular organisms. There remains the third great bodily function, reproduction. We may now consider this in a similar manner, by examining the reproductive processes of protozoa and by extending the examination to multicellular animals. The protozoa arise from pre-existing organisms like themselves, as do higher types of animal life. Both sexual and asexual reproduction occur in protozoa, asexual reproduction being effected by cell division, and sexual reproduction by the union of gametes which may or may not be sexually differentiated as microgametes and macrogametes. In the metazoa, sexual reproduction also occurs by means of gametes, the ova and spermatozoa, while asexual reproduction, by processes of budding and fission, occurs in some many-celled animals. In addition, there is in metazoa the process called development, which may be distinguished from reproduction for purposes of definition, although the two are inextricably related. The union of ovum and spermatozoon is obviously comparable with the union of conjugating cells in protozoa to form a new individual; but nothing in the protozoan cycle is exactly comparable with the development of a many-celled body from the zygote by cell division and differentiation, except the division of the protozoan cell and the colony formation that appears in a few species. Hence development occurs only in metazoa, while reproduction occurs in both protozoa and metazoa. By making this distinction, the process of reproduction may be considered in the present chapter and the study of development deferred until we have completed our examination of representative many-celled animals.

The Reproductive Cycle

The Cell Cycle in Single-celled and in Many-celled Organisms.—The resemblances between the reproductive processes throughout the Animal Kingdom may be shown by a schematic represen-

tation of cell cycles in a series of unicellular and multicellular organisms (Fig. 110). **Type 1** of this tabulation is the cycle of a simple protozoan in which there is no process of conjugation. The cycle in this instance consists merely of asexual reproduction by cell division. Changes in the rate of division may occur, and there may be encystment; but these may be omitted for the purposes of the present discussion. There is nothing to compare with the cycle in a many-celled organism (Type 6), except the cells and their division.

In **Type 2** is shown a cycle that occurs in a few species of protozoa, in which there is a periodic reorganization of the nucleus, either by *autogamy* or by *endomixis*. Autogamy may be compared with the nuclear reorganization involving nuclear fusion that occurs during conjugation but not with the part of conjugation that involves a union of two cells, since it occurs within the limits of a single cell. Endomixis is a nuclear reorganization within a single cell but without nuclear fusion. The life cycle of such a protozoan consists of a series of cell divisions with occasional nuclear reorganization.

Type 3, in which conjugation occurs, is the most representative protozoan cycle. The species reproduces asexually by cell division, and at times sexually by conjugating cells, the *gametes* (cf. p. 174), which unite in *syngamy* to form a single cell, the *zygote*.¹ The reproductive cycle in such a protozoan thus consists of the asexual reproduction of new individual cells by division, and occasionally sexual reproduction of new cells by syngamic union or conjugation. The gametes are isogamous, and hence there are no structural differences between them that indicate sexual differentiation, although it is conceivable that functional differences may exist.

There are, however, many species among the protozoa, as might be shown by a **Type 3a**, in which the gametes are anisogamous and, therefore, called "male" and "female" cells because they resemble the spermatozoa and ova of metazoa. Hence, the essential feature of *sex*, which is the production of male and female gametes, is recognizable in the protozoa. The life cycle of such species differs from that of Type 3 only in the production of anisogametes.

¹ It will be recalled that conjugation by temporary union and mutual exchange of nuclear material, which occurs in ciliates like *Paramœcium*, is an exceptional form of syngamy even among protozoa (cf. p. 187).

In **Type 4** is represented the cycle of a simple colonial organism such as the plant-like Mastigophora,² *Gonium* or *Pandorina* (Figs. 104 and 105, p. 197). It will be recalled that such a colony consists of a number of cells which have been formed by the

FIG. 110.—Cell cycles in Protozoa and Metazoa.

division of a single cell and have remained together (*cf.* p. 195). Such a colony is an individual of a slightly higher order than the single cell of a simple non-colonial organism (Type 3), although it is not truly many-celled because its cells are structurally similar

² The authors are sensible of the fact that these organisms, *Gonium* and *Pandorina*, and also *Eudorina*, *Pleodorina*, and *Volvox*, are plants rather than animals. The inclusion of such plant-like forms as a subdivision of the Mastigophora, the Phytomastigina, has been explained (*cf.* p. 174). As the multicellular state has probably evolved from a unicellular one along parallel lines in animals and plants, the use of such plant-like organisms seems justifiable for the purposes of the present illustration.

and physiologically independent. In *Pandorina* (cf. p. 198), each of the sixteen cells divides into sixteen, forming daughter colonies, which separate, grow to full-sized colonies, and repeat the process. These processes are obviously comparable with similar ones in the preceding types. The only difference is the temporary association of the cells to form the colonies. At the time of sexual reproduction the cells separate and become gametes, which conjugate to form zygotes comparable with those of the non-colonial types. In Type 4 there is, therefore, a period in which the cells are associated in colonies and another in which the species is represented by isolated cells from which colonies again develop by cell division. The gametes of such a species may be isogamous or anisogamous. In *Pandorina* they are usually isogamous, but they may be slightly anisogamous (cf. p. 199), in which case they show the beginnings of sexual differentiation. In the related genus *Eudorina*, there are more cells in the colony and the gametes are markedly anisogamous. Moreover, the male and female gametes of *Eudorina* are produced in different colonies. We might include in the table a **Type 4a** which would be more specialized after the manner of *Eudorina*.

Type 5 represents the cycle in organisms like *Pleodorina* and *Volvox* (Fig. 106, p. 200), in which colonies arise by division of single cells as in *Pandorina*, but in which the cells are differentiated as body or *somatic cells* and gametes or *germ cells*. The unbalanced physiological state of the cell that thus arises has been mentioned in the special account of these colonial Mastigophora (p. 201). From the standpoint of reproduction, the important difference between these two kinds of cells in Type 5 of the table is that *the body cells die a natural death* with the disintegration of the colony, while *the germ cells are immortal* in the sense that they may live if they unite in conjugation. In the preceding types the cells may die, as most of them do, by the accidents of nature; but there is no death that is "natural" in the sense that it is inevitable for some of the cells at one phase of the life cycle. In Type 5 the body cells must perish while the gametes alone are immortal like all the cells in the preceding types. In this respect a form like *Volvox* can perhaps be called a many-celled rather than a single-celled organism, since the differentiation between body cells and germ cells is the most distinctive step in the series of cell cycles represented by the table.

In **Type 6** the conditions are shown for a simple many-celled organism like the animal hydra, or one of the lower plants. This differs from Type 5 only in the number of kinds of body cells. In Type 5 there is but one kind of body cell. In Type 6 there are several, as found in simple metazoa (Fig. 121, p. 250). In the higher plants and animals the difference consists only in the greater number of kinds of body cells and their organization as tissues, organs, and systems; until in an animal like a vertebrate or one of the flowering plants there are innumerable body cells of many sorts. Functional differences are, of course, correlated with these structural differences. The cell in the multicellular body is a unit that is largely dependent upon the life of the organism as a whole.³ We may thus distinguish between body and germ cells in many-celled animals and compare the germ cells with cells of protozoa, as the table shows (Fig. 110), without supposing that these two types of cells are always sharply distinguishable in the manner implied by extreme theories of the independence of the germ cells or *germplasm*, as they may be collectively termed in contrast with the *somatoplasm* which is the whole mass of body cells.

The foregoing comparisons of cell cycles in many-celled and single-celled organisms are, of course, made from the viewpoint of the Cell Theory. According to the Organismal Theory (cf. p. 194), the homologies of cells and cell activities that are here indicated should not receive so much emphasis, since the organism must be considered as a whole and not as a mere colony of cells differentiated for various functions. The existence of protozoa (Fig. 102, p. 194) so highly specialized that they are more complex than any other cells further emphasizes the importance of the individual as compared with the cell. As already stated, a more reasonable position would seem to be the recognition of organisms

³ In plants and in animals that are capable of regenerating the whole organism from a part (cf. p. 273), the body cells are dependent upon a certain mass of the whole, which may be capable of regeneration, rather than upon the entire organism. In tissue cultures, small masses of body cells may be cultivated for long periods, if not indefinitely. The cells of some sponges may be completely dissociated by squeezing through bolting cloth and will even then form new individuals. But in none of these cases have the single body cells been shown to be capable of reproducing the whole as do single germ cells. There is, however, no sound theoretical reason why such cells might not thus reproduce the whole if they could be placed under proper conditions.

as individuals composed of cells which may exist in a balanced physiological state, as in protozoa, or in an unbalanced state, as in metazoa.

Reproduction and Development.—The distinction between reproduction and development, to which reference was made in the introductory paragraph of the present chapter, is now apparent. Reproduction has been defined as *the formation of a new individual* (cf. p. 129). In protozoa reproduction may occur *asexually* by cell division of various sorts, and *sexually* by the conjugation, or syngamy, of gametes. In the latter process a new cell is formed by the permanent fusion of two cells, as in the fertilization of many-celled animals. In metazoa what is called *asexual* reproduction occurs by budding and fission, but is confined to the lower many-celled animals (cf. Fig. 121, p. 250); while *sexual* reproduction is effected by the syngamic union of ova and spermatozoa in fertilization. The *zygote*, or one-cell stage, which is thus formed, then produces the adult individual by the cell divisions and differentiations that constitute *development*. By making this distinction between reproduction and development, the sexual reproduction of protozoa and metazoa may be exactly compared; and it becomes clear that development in the metazoa has no exact parallel in the protozoa, although the cell division of protozoa and metazoa are obviously comparable as shown by the table (Fig. 110). To compare development, as thus defined, with the cell development that occurs when protozoan cells increase in size and undergo certain differentiations after fission, as in the growth and differentiation of the two cells resulting from division in a ciliate (Fig. 99, p. 185), is confusing, since one is comparing a single cell with a mass of cells. Yet something may be said for such a comparison along the line of the Organismal Theory. The comparison of cell cycles points to the origin of development as a necessary incident of the evolutionary change from the single-celled to the many-celled state. It is, therefore, possible to consider the reproductive processes of metazoa apart from those of development. This is desirable, because we have now become familiar with specific examples of reproduction in the protozoa, and because the related processes in metazoa are so similar in all many-celled animals that they may be described in general terms. In our subsequent study of animal types, the reproductive and developmental processes will be

further illustrated, and development will be examined in detail as it occurs in vertebrate animals.

Modes of Reproduction ⁴

Asexual Reproduction.—As the name indicates, this form of reproduction involves nothing that may be called sexual, since it concerns only one individual and is not dependent upon the existence of sexual differentiation. In the asexual reproduction of protozoa, the cell may either divide into two cells of the same size, *binary fission* (Fig. 99, p. 185); bud off smaller cells, *budding* (Fig. 89 B-3); or form many small cells by simultaneous division of the cytoplasm about nuclei that have been produced by division of a single original nucleus, *sporulation* (Fig. 101 J). The asexual reproduction of metazoa occurs by vegetative processes, like the budding of hydra (Fig. 121, p. 250) and the fission that occurs in some Platyhelminthes and Annulata. Modifications are seen in the budding of hydroids (Fig. 133, p. 275), where the new individuals remain attached to the parent and produce colonies; in the internal budding, known as *gemmulation*, which occurs in fresh-water Porifera and Molluscoida; and in cases of fission, where the individuals remain attached until completely developed, forming temporary chains which resemble linear colonies. In all these instances among metazoa, new individuals are produced without any relation to the phenomenon of sex, and hence such modes of reproduction may be called asexual.

Sexual Reproduction.—As the table shows (Fig. 110), the conjugating cells in protozoa are obviously comparable with the germ cells in metazoa, and conjugation is equivalent to fertilization insofar as it involves a union of two lines of descent in the production of a new individual. It is true that the gametes of protozoa may be isogamous and thus without the sexual differences that characterize the gametes of metazoa, but in many protozoa

⁴ The distinction that is here made between sexual and asexual reproduction is open to certain objections. Other classifications of the modes of reproduction might be used, for example: uniparental as compared with biparental reproduction; reproduction by syngamy as compared with reproduction by cell division. The authors have chosen the conventional distinction between sexual and asexual reproduction, because it is perhaps as good as any other and because confusion always results when an elementary presentation departs too widely from the usage in current books of reference.

they are anisogamous and thus show the beginnings of sex. The resemblance between the processes of sexual reproduction in protozoa and metazoa is, therefore, as obvious as the homology between cells that exists throughout the Animal Kingdom. For this reason the term *gametes* is applied to the conjugating cells of protozoa and to the ova and spermatozoa of metazoa; and the term *syngamy* is used to include both conjugation and fertilization. If anything be needed to complete the resemblance, the existence in some protozoa of processes resembling the maturation of gametes in metazoa presents conclusive evidence of the fundamental similarity of these sexual processes in all forms of animal life. As to the functional significance of conjugation and fertilization, it is clear that each furnishes a basis for biparental inheritance; but whether conjugation and fertilization have other features in common is uncertain (*cf.* p. 187).

The syngamic union of a male and a female cell to form a single cell, the zygote, which is a new individual, is, therefore, the essential feature of sexual reproduction. In the protozoan this individual remains an isolated cell. In the metazoan it develops into a many-celled organism by cell division and differentiation. As this development proceeds, the biparental nature of the original cell supposedly persists in all the cells of the individual; and in this manner the biparental inheritance that appears in an adult is based upon the bisexual origin of every cell of its body when traced back to the one-cell stage. Thus, sexual reproduction and development are inextricably related; but the comparison with protozoa is clarified if sexual reproduction in the metazoa is thus defined as the origin of a new individual by syngamy and distinguished from the development that follows.

Modifications of sexual reproduction appear as *parthenogenesis*, both natural and artificial (p. 235); and as *pædogenesis*, in which the organism becomes sexually mature in a larval stage in particular generations and may never reach the fully developed adult condition. Examples of *pædogenesis* are seen in the axolotl, an amphibian which reproduces sexually in a stage comparable with the late tadpole stages of other salamanders; in the liver fluke, which reproduces parthenogenetically through a series of larval generations; and in some insects.

Processes Related to Sexual Reproduction in Metazoa

Sexual Differentiation. — The males and females of many familiar animals are distinguishable by characteristics that may not be directly connected with the reproductive organs. There are, however, many other animals, like starfish and sea-urchins, the jelly-fish and polyps, the sponges, and many of the worms, in which there are no such characteristics by which the sexes may be recognized. In some instances, even ovaries and testes are wanting, and the sex cells are distributed throughout the body, as in sponges. It is evident, therefore, that sexual differentiation in the metazoa consists primarily in the production of male and female reproductive cells which are comparable with the microgametes and macrogametes of protozoa. The sexes are separate in the great majority of animals; but cases of *hermaphroditism*, or the production of both male and female gametes by the same individual, are not infrequent among certain classes. In the higher multicellular animals, the underlying maleness and femaleness, which is indicated by the sex cells, may be so extended to the structure and functions of the body that sex seems a matter of somatic organization. Nevertheless, the primary factor of sexual differentiation in metazoa, as in protozoa, is the production of male and female gametes.

From an evolutionary standpoint, sexual differentiation probably originated in the division of labor between gametes, whereby there came to be male cells, or microgametes, which were small and active with special powers of locomotion; and female cells, or macrogametes, which were large, inactive, and food-laden. The course of such an evolution is indicated by the gametes of protozoa, which illustrate all the stages from isogamy to a very specialized anisogamy (*cf.* p. 174). If the original forms of life were unicellular organisms, it is, therefore, probable that sex originated even before the appearance of multicellular animals, in the manner suggested by the comparison of cellular cycles (Fig. 110). Among metazoa, the primary sexual differentiation of male and female cells has been variously complicated by the evolution of reproductive organs and systems, which are known as *primary sexual characters* and by the appearance of *secondary sexual characters*, which are not directly related to the reproductive organs, although they are expressions of the underlying maleness or femaleness of

the individual. Examples of this latter type of characters are the color and size differences between the sexes of many birds, the antlers of deer, and even physiological characters like the greater pugnacity of the males in many of the mammals. Thus, the phenomenon of sex, as indicated by sexual differentiation, occurs in many of the simplest forms of animal life and in all many-

FIG. 111. — Diagram illustrating the Theory of Germinal Continuity.

A, B, and C represent successive generations; *g*, gamete (spermatozoön) produced by another organism; *z*, zygote. White circles indicate successive cell divisions within the somatic tissues, the existence of which terminates with the individual of the given generation. Solid black circles indicate the germ cells. Dotted circles indicate gametes which may perish, or may unite with those of another organism. (From Kelliecott, "General Embryology," copyright, 1913, by Henry Holt & Co., reprinted by permission.)

celled animals, as well as in the great majority of many-celled plants. Some students of unicellular organisms believe that it may exist as a physiological difference in the absence of visible structural differentiation. In any case, it is so nearly universal that it must have appeared at a very early period in the evolution of organisms. It is, therefore, not surprising that there should be important differences between the sexes in many animals.

The Germ-cell Cycle. — *Historical.* — Even in ancient times, the "seeds" of plants and the "germs," or embryonic stages, of animals were recognized as the material from which many organisms arose, although the general nature of development was a mystery. Eggs of larger size, like those of birds and reptiles, were observed to bring forth young; and the seminal fluid of the male was believed to be necessary for conception in the Mammalia. Aristotle (384–322 B.C.) wrote with remarkable acumen upon the problem, considering the facts that were then available. In later times the Italian naturalist, Redi, who showed in 1668 that flies

arose from eggs, and not spontaneously, in decaying meat, extended this concept of the egg as the initial stage of development, but such observations did not explain the action of the seminal fluid. After the spermatozoa and the microscopic ova of many animals had been discovered, between 1650 and 1700, the rôle

of each was long in dispute, the "spermatists" of the eighteenth century maintaining that the embryo arose from the sperm, the "ovists" that it came from the ovum. The answer to the riddle was found only as the result of two discoveries: the recognition that the ovum and spermatozoön are cells, following the establishment of the Cell Theory in 1838-39; and the discovery by Oscar Hertwig, in 1875, that fertilization consists in the entrance of a single spermatozoön into the egg and the union of egg-nucleus with sperm nucleus. An animal was thus shown to begin its existence as an individual at the time of fertilization, and development was recognized as a problem of cell division and differentiation. The gametes were seen to be the basis of the hereditary transmission of characters from one generation to another and the most remarkable of all cells because of their potentialities.

Confusion will be avoided if we recall the terms that must be used in this connection. The word *ovum* is applied to the female gamete of an animal in the final stages of its development and before fertilization, in contrast to the male gamete, which is called the *spermatozoön*. The word "egg" is used more loosely, as when one speaks of a hen's egg, which is a complex structure including the shell and "white," which are secreted by the oviduct, and the ovum or "yolk," which is a product of the ovary; or, biologically speaking, the word egg may mean the ovum. The word *gamete* is a general term for both male and female sex cells. The *germ cells* include not only the fully formed ova and spermatozoa, or gametes, but also the antecedent cells from which these gametes are differentiated. Since the germ cells may be recognized at early stages of development as the *primordial germ cells* that are seen in many animals (Fig. 112), the distinction that can be made on theoretical grounds between *germplasm*, or germ cells, and *somatoplasm*, or body cells, is actually recognizable in particular cases. What is known as the *germ-cell cycle* includes the entire history of the germ cells from the time they can be recognized in the embryo until they have become differentiated as ova and spermatozoa.

Origin of the Germ Cells. — The relationship between the germplasm and the somatoplasm is frequently illustrated by such a diagram as that shown in Fig. 111. According to the theory that is commonly associated with this representation, the germplasm is of primary importance, since it gives rise to both body cells and germ cells in each generation, while the somatoplasm is destined

to perish with the death of the body. As developed by Weismann in the last quarter of the nineteenth century, this theory regarded the germplasm as relatively stable and independent of changing conditions in the somatoplasm. It was, therefore, in opposition to the theory that the germ cells were a product of the body cells

FIG. 112.—Early differentiation of germplasm.

A, transverse section of late blastula stage of a lamellibranch, *Spharium striatinum*, showing segmentation cavity (s. c.) and the two primordial germ cells (g. c.) from which all the germ cells of the paired reproductive organs seem to originate; B, section of late ovarian egg of an insect, *Miastor americana*, showing covering of follicle cells, the nurse cells (n. c.), the nucleus of the ovum (n. o.), and a differentiated area of cytoplasm (p) that is traceable to the cytoplasm of the germ cells in the subsequent development. (A, from an unpublished drawing by F. H. Woods; B, after R. W. Hegner, *Jour. of Morph.*, Vol. 25.)

at the time of sexual maturity and subject to many of the influences that affect the somatoplasm. The individual is a "chip of the old block," but the "block" is the germplasm and not the parent's somatoplasm. Although this idea was originally elaborated by Weismann on theoretical grounds, it found concrete support in the later discovery that the germ cells of many animals may be identified at an early stage of the embryo before the reproductive organs have become differentiated as such. Thus, in many instances, it has been possible to trace the primordial germ cells of the individual from the late cleavage stages (Fig. 112 A), and in some instances to discover within the cytoplasm of the unfertilized ovum (Fig. 112 B) substances that become localized in the germ cells when these can be definitely recognized in the subsequent development. More recently, however, it has been found in a number of cases that these early germ cells degenerate; and that the

functional germ cells are differentiated at a later period. For example, in some vertebrates the cells that actually produce the germ cells may arise from the epithelial cells of the ovaries and tests even in the adult organism. As the matter stands, it calls for renewed investigation, although many instances of early differentiation appear to be well established. In general, it may be said that the germ cells are relatively stable, for all their dependence upon the body; and that in many instances they appear as a type of cell that can be recognized in the early stages of the individual's development.

In the reproductive organs of the adult animal the relationships of the germ cells are, of course, readily established. For example, in the ovaries of most animals there are germ cells surrounded by smaller cells which have a supporting and nutritive but not a germinal function. Thus, the ovary of the frog, as seen in the fall (Fig. 210, p. 401), shows cells of various sizes: the ova of the coming spring, which appear as large cells; other cells of intermediate size, representing approximately those of the next succeeding year; and many smaller cells, constituting the reserve from which the eggs of subsequent years will be differentiated. In addition to these there are other cells that form a matrix of tissue in which the ova are embedded. The ovary of a mammal presents similar relationships, except that fewer eggs are produced at each breeding season and hence the stock is relatively less extensive. Nevertheless, there are within the human ovary tens of thousands of potential germ cells from which mature eggs might be developed. The testis presents a similar condition, although the number of spermatozoa is so much greater than the number of ova that the multiplication of the primordial germ cells is accordingly increased.

The foregoing explanations of the early appearance of the germ cells and their relationships within the reproductive organs will render more intelligible the history of these cells. In the case of the male germ cells, the zygote, or oö sperm, from which an individual originates, is represented by the uppermost circle in Fig. 113. Within this are included outlines to represent chromosomes, which are taken as eight in this instance. The unshaded chromosome, which represents the single sex-chromosome of the male, need not be considered in the present discussion. From this zygote there arise many cells by mitotic division, all with the same

FIG. 113.—Diagram of maturation in male germ cells, spermatogenesis, showing eight paired chromosomes and a single "X" or sex chromosome.

The oöspere or zygote, which is the fertilized ovum, with its eight paired chromosomes, the autosomes, and a single "X" chromosome, is represented by the upper circle. Such a zygote produces by mitotic cell division, as shown schematically on the left, all the body cells or somatoplasm. The zygote also gives rise to the germ cells or germplasm, as shown

number of chromosomes; but sooner or later some of these descendant cells can be recognized as the early germ cells of the male, or the *spermatogonia*. Hence, the body cells, or somatoplasm, and the germ cells, or germplasm, are represented in the figure as two distinct lines of descent among the cells of the individual, although both originally came from the same zygote. The spermatozoa are differentiated from the spermatogonia by the nuclear changes of maturation and by the changes in size and shape of the cell body as described in the following section. The separation of germplasm from somatoplasm in a female is similarly shown in Fig. 114.

Maturation of the Male Germ Cells: Spermatogenesis. — The final changes in the maturation by which the spermatogonia and oögonia become transformed into the spermatozoa and ova are known respectively as *spermatogenesis* and *oögenesis*. In spermatogenesis (Fig. 113), there first occurs a union of the chromosomes in pairs, which is known as *synapsis*.

Following this union, there is a cell division known as the *first maturation division*, producing two cells as shown by the figure. These resemble the cell shown in synapsis, because each chromosome splits lengthwise, as is regularly the case in mitosis, and thus no change in number is produced. In the *second maturation division*, however, the mitotic cell division is unique; for the chromosomes do not split lengthwise as in all other mitotic divisions in both body and germ cells. Instead of this, the members of the pairs of chromosomes separate, producing cells in which there are only one-half the number of chromosomes that occur in all the other cells of the organism. In some instances reduction occurs in the first instead of the second maturation division. The final result in

on the right. Like the body cells, the early germ cells or spermatogonia undergo mitotic cell divisions in which the number of chromosomes remains unchanged. At the time of synapsis the paired chromosomes, or autosomes, unite in the manner shown, but the sex chromosome remains unpaired, since it has no synaptic mate. In the first maturation division there is no change in the number and relationships of the chromosomes, because each one splits lengthwise as in typical cases of mitosis. In the second maturation division, the pairs of autosomes, which united in synapsis, separate and pass without further division to the two cells that become the spermatozoa, while the sex chromosome passes undivided to one or the other of these cells. In this manner each spermatozoön receives one member of each pair of autosomes, and one-half of all the spermatozoa receive an "X" chromosome, while the remaining spermatozoa are without an "X" chromosome. Hence, at the time of fertilization (*c.f.* Fig. 114), one-half the oöspers or zygotes receive but one "X" chromosome and become males, while the other half receive two "X" chromosomes and become females (*c.f.* p. 448).

FIG. 114.—Diagram of maturation in female germ cells, oögenesis, showing eight paired chromosomes and two "X" or sex chromosomes, and fertilization of ova by spermatozoa to form male and female individuals.

As in Fig. 113, the oöperm or zygote, with its eight paired chromosomes, the autosomes, and two "X" or sex chromosomes, is shown giving rise to cells of the body and to the

such cases is the same, since the second maturation is then like any other mitotic division, with the chromosomes dividing lengthwise and producing the same number as in the parent cell. After this second maturation or "reducing" division, a spermatozoön, with this reduced or *haploid* number of chromosomes, is produced from each of the four cells by changes in the cytosome and condensation of the nucleus (Fig. 115). The essential significance of spermatogenesis is, therefore, the reduction in the number of chromosomes of the mature spermatozoön to one-half the number characteristic of the spermatogonia and all other cells of the animal.

Maturation of the Female Germ Cells: Oögenesis. — The maturation of the female germ cells, or oögenesis (Fig. 114), is comparable with that of the male cells so far as the nuclear changes are concerned, although only one of the four cells that are formed by the two maturation divisions becomes a functional ovum. The other three are small cells with the same number of chromosomes as the ovum, but with a minimum amount of cytoplasm. As these are formed at the so-called animal pole of the ovum and can be recognized as minute globules (*cf.* Fig. 148, p. 307), they were called the *polar bodies* by the earlier embryologists before their true significance was ascertained. This difference in the maturation of the male and female germ cells may be regarded as a device whereby the cytoplasmic materials that might have been distributed to four equivalent cells are given instead to one of the four, which thus obtains a proportionately greater amount of the nutrient material that is utilized in the early stages of development. The polar bodies might, therefore, be described as abortive ova that come to naught, because one of their fellows receives the cytoplasm that might have been theirs. Another difference in the development of the ovum and spermatozoön is the amount of

oögonia or early germ cells of the female. In synopsis the autosomes unite in pairs and likewise the "X" chromosomes. The two maturation divisions produce from each oögonium a single ovum and three abortive cells, the polar bodies (*cf.* Fig. 148, p. 307 and Fig. 211, p. 402). In the first maturation division there is no change in the number and relationships of the chromosomes, because each one splits lengthwise as in typical cases of mitosis. In the second maturation division the pairs of autosomes, which united in synopsis, separate and pass without further division to the resulting cells. In this manner the ovum and each polar body receives one member of each pair of autosomes and one "X" chromosome. The fertilization of an ovum by a spermatozoön that possesses an "X" chromosome gives an oöspERM or zygote with two "X" chromosomes and hence a female. Fertilization with a spermatozoön that does not possess an "X" chromosome gives a male (*cf.* p. 448).

growth that occurs in the female germ cell before the maturation divisions. By this means the greater size of the mature ovum is attained. In many animals only two polar bodies are found upon the surface of the egg (Fig. 211, p. 402). Examination shows

FIG. 115.—The spermatozoön.

A and B, human spermatozoön, two views showing flattening of the "head" (nucleus) region. C, stage in formation of spermatozoön of guinea-pig, showing what is more obviously a cell. D, diagrammatic figure of fully formed spermatozoön of a guinea-pig. *acs*, acrosome; *a.f.*, axial filament; *cy*, cytoplasm; *fl*, flagellum; *n*, nucleus; *m.p.*, middle piece. (A and B after Retzius; C and D after Meves. Reproduced from figure in Curtis, "Science and Human Affairs," by permission of Harcourt, Brace and Co.)

that these are cases in which the first polar body fails to divide, as shown by the schematic representation (Fig. 114). The time of polar-body formation also varies. In some animals both maturation divisions occur before the egg leaves the ovary and well in advance of fertilization; in others the first maturation division occurs when the egg is mature and the second only when the egg is stimulated by the entrance of a spermatozoön in fertilization. In still other cases, both maturation divisions are delayed until the time of fertilization. These differences in the time of maturation in no wise affect the fundamental nuclear behavior involved.

As a result of the nuclear changes in oögenesis and spermatogenesis, the mature ovum and spermatozoön each contain one-half the number of chromosomes characteristic of all other cells in the

animal. When ovum and spermatozoön unite in fertilization, the full or *diploid* number is restored by union of these two *haploid* groups. It will be recalled that the chromosomes of many cells are present in pairs (*cf.* p. 234). The members of such a pair in the cells of an adult animal are presumed to have descended, one from the ovum and the other from the spermatozoön, by this union of the two haploid groups in fertilization. Maturation might be characterized as a device whereby the number of the chromosomes is prevented from being doubled in each generation at the time of fertilization. It is believed to occur with minor variations in the germ cells of all metazoa, and comparable phenomena preceding conjugation can be recognized in many of the protozoa (*cf.* Fig. 110). As similar reductions in the number of chromosomes in the gametes and restoration of the diploid number by fertilization occur in plants, the phenomenon is well-nigh universal.

The Gametes.—The foregoing account of the history of the female germ cells explains the origin of the ovum. In contrast to the spermatozoa the distinctive characteristics of ova are the additions of nutrient material in the cytoplasm and of cell membranes that may be variously developed. Some ova are amœboid and can migrate for short distances by means of pseudopodia-like processes; but in most instances the egg of a metazoan is a non-motile, food-laden cell, comparable with the macrogamete of a protozoan and hence markedly different from the spermatozoön. The ovum is, indeed, a rather typical cell and easily recognizable as such (*cf.* Fig. 210, p. 401).

The history of the male germ cells likewise explains their cellular nature, but the mature spermatozoön is a much more specialized cell than the ovum (Fig. 115 A). In a schematic representation of a type that occurs in many vertebrate animals (Fig. 115 D), the following parts can be recognized. The "head," as it was called by the early microscopists in contrast to the "tail," consists of a *nucleus* composed principally of very dense chromatin and surrounded by a thin layer of cytoplasm. This cytoplasm is continuous with the "middle-piece," which contains a *centriole*. The "tail," or *flagellum*, contains an *axial filament* which extends into the middle-piece to a point near the centriole and is surrounded, except at its posterior end, by a sheath of cytoplasm. These peculiarities of structure do not appear in the male cells until the last stages of their development, following maturation (Figs.

113 and 115). When liberated in the proper medium, the spermatozoön swims actively until it dies or meets an ovum in fertilization. The structural and functional resemblances between spermatozoa and the more specialized forms of microgametes in protozoa are obvious (*cf.* Figs. 115 A and 108, 9b).

Fertilization. — The union of ovum with spermatozoön, which constitutes the "fertilization" of the egg, may be described in general terms, since it occurs in much the same manner in all animals. The process has been most thoroughly studied in eggs that are fertilized in water after discharge from the parent, as with many marine animals; but, so far as the observations go, there seems to be little difference between such cases and the fertilization of a grasshopper's or a mammal's egg in the fluid of an internal cavity of the female reproductive system. The present account has reference to the process as it occurs in the sea-urchin, *Toxopneustes* (Fig. 116), in which the maturation of the ovum is delayed until the time of fertilization. After being discharged into the water, the egg remains suspended or slowly sinks to the bottom while the sperm swim about actively by means of the lashing of their flagella. When such a spermatozoön comes in contact with the surface of an ovum and penetrates the egg membrane, the movements of its flagellum cease and the surface of the ovum forms the so-called entrance cone by which the head and middle-piece of the spermatozoön become enclosed. From this time on, the spermatozoön appears as though it were inactive and were being drawn into the ovum by the action of the latter's cytoplasm rather than by any movements of its own. In many animals the flagellum remains on the outside, and even where it normally enters, as in the birds, it takes no further part in the development. As the entrance cone develops, the egg produces on its external surface what is known as the *fertilization membrane*. This was formerly believed to be the mechanism by which the entrance of other spermatozoa was prevented, but is now regarded as the incidental result of changes produced in the ovum by the presence of the spermatozoön. These changes in some way render the surface of the ovum impervious to other spermatozoa within a few minutes, or even a few seconds, after the entrance cone has made its appearance. In this manner *polyspermy*, or the presence of more than one spermatozoön in the ovum, is prevented unless the sperm are so abundant that several reach the surface of the

egg simultaneously. The nucleus and middle-piece of the spermatozoön, having thus entered the egg, move very slowly toward the egg nucleus, gradually rotating through an angle of almost one hundred and eighty degrees, with the result that the centrioles of the zygote, which develop from the middle-piece of the spermatozoön, finally occupy a position between the male and female

FIG. 116.—Fertilization in the sea-urchin, *Toxopneustes*.

A, the spermatozoön showing "head" containing nucleus, "middle-piece," and "tail" or flagellum. B to F, entrance of head and middle-piece into cytoplasm of the egg, showing entrance cone and the rotation of sperm-head during development of aster about the middle-piece (the minute centriole in center of the middle-piece is not shown). G and H, beginning of enlargement of sperm-nucleus and its movement toward the nucleus of the ovum. I and J, development of amphiaser of first cleavage and union of male and female pronuclei. (From Wilson, "The Cell," copyright, 1897, by The Macmillan Co., reprinted by permission.)

nuclei, which are often called the *pronuclei*. Meanwhile, the male pronucleus has increased in size, and its chromosomes, which are not recognizable as such in the nucleus of the spermatozoön again become apparent in the haploid number seen at the close of its maturation (cf. Fig. 113).

While these changes are in progress, the maturation divisions

of the ovum are occurring in cases like *Toxopneustes* where the polar-body formation normally takes place at the time of fertilization. When this maturation has been completed, the centriole of the ovum disappears, and the egg-nucleus, with its haploid number of chromosomes, moves to a position beside the sperm-nucleus, while the centriole from the middle-piece of the spermatozoön divides and the mitotic spindle of the zygote is formed.

As a result of fertilization, the male and female pronuclei, therefore, come to occupy a position on either side of the first-division spindle and their chromosomes are distributed equally to each cell of the two-cell stage. If this process were continued throughout the development, the cells of the adult body would contain paired chromosomes arising in such a manner that one member of each pair would be descended from the corresponding chromosome of the ovum and the other member from that of the spermatozoön. As a matter of fact, such a paired relationship of the chromosomes can be observed in many animals, not only in the first division of the zygote but also in many subsequent cell divisions. Moreover, in the cells of the adult body the chromosomes are found to occur in pairs wherever their diversity of size and appearance renders such a distinction possible. These facts, together with the theoretical conclusions regarding the chromosomes that are drawn from their behavior in correlation with the inheritance of adult characters, are the basis for the generally accepted conclusion that the chromosomes, as they are found in their diploid condition in the cells of an adult animal, have descended one-half from the pronucleus of the ovum and the other half from the pronucleus of the spermatozoön. If this is correct, one can hardly escape the conclusion that the chromosomes furnish a mechanism for the inheritance that is observed in sexual reproduction.

In addition to this union of two lines of descent in the production of a new individual, the process of fertilization also involves the stimulus which causes the ovum to develop into the adult animal after its union with the spermatozoön. The term fertilization is sometimes restricted to this developmental stimulus, which may be called the *activation* of the egg, since the word fertilization suggests the act of making an egg fertile and hence a stimulation to development. In this discussion the authors have chosen to use the term fertilization to include both the

union of germplasms, or *amphimixis*, which is the basis of biparental inheritance, and the activation by which the egg is stimulated to develop instead of dying as it would do eventually if unfertilized.

Natural and Artificial Parthenogenesis.—In this connection, the phenomenon of *parthenogenesis*, in which an ovum develops without the entrance of a spermatozoön, may be described. Such a process occurs normally in a considerable number of the Arthropoda (cf. p. 241), like insects and spiders, in some Platyhelminthes and Trochelminthes, and perhaps in some of the lower Vertebrata. Males are known to exist in most of these cases, and fertilization of the eggs occurs in certain generations; or certain eggs may be fertilized while others are not, as in the honey bee. Where males are unknown, it is presumed that they have not yet been discovered, although it would be theoretically possible to have the male sex completely eliminated in the evolution of a species with such a mode of reproduction. Hence, it appears that species exhibiting *natural parthenogenesis* produce, under certain conditions, eggs that develop without fertilization and other eggs that develop only when normally fertilized as in the great majority of animals.

The occurrence of natural parthenogenesis suggests that eggs that develop in nature only after normal fertilization may be caused to develop parthenogenetically if suitable stimuli can be applied. This is found to be the case; and the phenomenon is known as *artificial parthenogenesis* in contrast to the parthenogenesis that occurs under natural conditions. Since the first successful experiments in artificial parthenogenesis were conducted, about 1900, it has been found that the eggs of many animals, among which are worms, molluscs, echinoderms, and vertebrates, may be caused to develop in the absence of fertilization. Development, which in some few cases has progressed to a late stage, ensues when such eggs are subjected to very dilute solutions of salts, acids, narcotics, and other substances, to changes in temperature, and in some instances even to simple mechanical stimulation. It is conceivable that there is no egg of any animal that might not be thus "artificially" started on its development by the application of a suitable stimulus.

The reproductive processes of animals, therefore, have certain fundamental resemblances. This is particularly true of sexual

reproduction, which is comparable from one end of the Animal Kingdom to the other, and also in plants. Not only do unicellular animals reproduce by means of cell division and conjugation; but every multicellular animal is, at one stage of its life cycle, circumscribed within the limits of a single cell, the zygote, which is formed by fusion of the ovum and spermatozoön, and from which the many-celled adult animal develops. One of the ultimate problems in Embryology is to discover how a thinking man can arise from a single cell that bears no resemblance to the adult organism. Reproduction, like metabolism and irritability, is reducible to cell activities. As a matter of convenience, reproduction has been separated from the process of development, which is described in later chapters, although the two are but different aspects of the reproductive cycle in metazoa.

CHAPTER 10

CLASSIFICATION AND GENERAL ORGANIZATION OF ANIMALS

The principles of classification have been illustrated in particular groups of animals in the accounts of Vertebrata and other Chordata, and in the Protozoa. The distinction between Protozoa and Metazoa has also been explained. The classification of Metazoa is indicated in this chapter in order that the student may understand something of the Animal Kingdom as a whole before undertaking the study of representative animals that is outlined in the chapters immediately following.

Classification

The Principal Types of Animals. — It is necessary to classify animals, if only for the purpose of listing the various types, and hence there have been many classifications in the history of Zoology. Gradually, however, these have been refined to a measure of agreement, until at present there is no wide diversity of opinion regarding the nature of the major subdivisions, or *phyla*. The Animal Kingdom may be divided, according to most zoologists, into a relatively small number of these larger groups, the *phyla*, which are in turn variously subdivided. As listed in most of the current texts, these *phyla* are as follows:

Phylum *Protozoa*, the single-celled animals.

Phylum *Mesozoa*, a small group of very simple organization.

Phylum *Porifera*, the sponges.

Phylum *Cœlenterata*, the polyps, jellyfish, corals, etc.¹

Phylum *Platyhelminthes*, the flatworms, and nemerteans.²

Phylum *Nemathelminthes*, the roundworms.

¹ The *Ctenophora*, or sea-walnuts, which would here be listed as a subdivision of the *Cœlenterata*, are classified by some zoologists as a separate phylum.

² The nemerteans may be placed in a Phylum, *Nemertinea*.

Phylum *Trochelminthes*, the rotifers.

Phylum *Molluscoida*, the polyzoa, brachiopoda, etc.²

Phylum *Echinodermata*, the starfishes, sea-urchins, sea-cucumbers, sea-lilies, etc.

Phylum *Annulata*, the earthworms and other segmented worms.

Phylum *Arthropoda*, the crayfish and other crustaceans, the insects, spiders, centipedes, etc.

Phylum *Mollusca*, the clams, snails, squids, etc.

Phylum *Chordata*, the tunicates, etc., and the vertebrates (cf. p. 36).

Within the limits of these major groups, and a few lesser ones that are commonly appended to particular phyla, are included all the manifold forms of animals. The diversity of animal life, which is so bewildering upon superficial examination, is thus seen to be unified by the existence of only a few principal types of organization.

In many textbooks of zoology no broader classification is attempted than this division of the Animal Kingdom into phyla. It is possible, however, to make further unifications, although some zoologists doubt the certainty of such relationships. To illustrate what may be done in this regard, let us proceed as follows:

Taking the Animal Kingdom as a whole and assuming a knowledge of its varied types, suppose one asks what is the greatest difference between the various kinds of animals. If all the animals were to be divided into two groups, on what basis would they be separated? As previously explained in introducing the Protozoa (cf. p. 153), one may answer that animals may be first subdivided into *Protozoa* and *Metazoa*, as shown by the accompanying tabulation (Fig. 117). Unicellular animals may thus be placed over against all others, and the Phylum *Protozoa* may be written in the right-hand column.

Proceeding further, one may ask a similar question for the Metazoa. What is the greatest difference between the kinds of many-celled forms? Some zoologists would not agree to the answer here given, but a majority would probably say that the Metazoa may be divided into two principal groups, according as they have or have not a *digestive cavity*. There is one large

² The Phylum *Molluscoida* is questioned because it includes forms so diverse. There is much justification for its division into at least two phyla, the *Polyzoa* and *Tentaculata*.

phylum, the Porifera, or sponges that seems to lack in its development and in its adult state anything that can be properly compared with the digestive tract as found in all higher many-celled animals. A similar condition exists in the small group of animals that is here designated as the Phylum *Mesozoa*. Hence the Metazoa may be divided into two groups, the *Parazoa*, which includes the Porifera and Mesozoa; and the *Enterozoa*, which includes all other Metazoa.

Again, if the same question be asked for the Enterozoa, it appears that the most fundamental difference between these forms is the presence or absence of another cavity, the *cœlome*, which surrounds the digestive tract. In some cases, as in the Trochelminthes and Molluscoida, the cœlome seems to have degenerated; while in others, the Platyhelminthes and Nemathelminthes, it may never have existed. In the more important phyla, the Annulata, Arthropoda, Mollusca, Echinodermata, and Chordata, there are either unmistakable signs of its former existence or it is well developed, as in the familiar vertebrates. For this reason, the Enterozoa may be divided, as the table shows, into the *Euterocœla*, including the Cœlenterata, and perhaps the Platyhelminthes, which have no cœlome; and the *Cœlomocœla*, which possess such a body cavity. The Nemathelminthes, the Trochelminthes, and the Molluscoida may be left as uncertainties; although they are presumably forms in which the cœlome has become modified beyond clear recognition. In this manner the phyla may be grouped in larger subdivisions according to the classifications maintained by many zoologists. A tabulation showing how the phyla of animals are divided into classes appears on p. 241.

The Basis and Meaning of Classification. — For practical purposes of listing and arrangement, the classification by phyla alone is sufficient; but classification has a significance in modern zoology apart from its convenience as a cataloging system. The basis of the classification here indicated is *structure*, and structural resemblances are believed to indicate evolutionary relationships. When one says that certain animals are all chordates, or cœlenterates, or annulates, one means that they are to be regarded as more akin to one another than to any other group. Hence, the "natural" classification, which zoologists are now attempting to ascertain upon the basis of structural resemblance, is in reality a *family tree of animal life*. If certain phyla are placed

FIG. 117.—Classification of the principal groups of animals
(cf Fig. 118 and list of phyla on opposite page.)

Sub-division of the Phyla into Classes

Kingdom, *Animalia*Phylum, *Protozoa*Class, *Sarcodina*Class, *Mastigophora*Class, *Infusoria*Class, *Sporozoa*Phylum, *Mesozoa*Phylum, *Porifera*Class, *Calcarea*Class, *Hexactinellida*Class, *Demospongia*Phylum, *Cœlenterata*Class, *Hydrozoa*Class, *Scyphozoa*Class, *Actinozoa*Class, *Ctenophora*Phylum, *Platyhelminthes*Class, *Turbellaria*Class, *Trematoda*Class, *Cestoda*Class, *Nemertinea*Phylum, *Nemathelminthes*Class, *Nematoda*Class, *Acanthocephala*Class, *Chaetognatha*Phylum, *Trochelminthes*Class, *Rotifera*Class, *Gastrotricha*Phylum, *Molluscoida*Class, *Polyzoa*Class, *Phoronida*Class, *Brachiopoda*Phylum, *Mollusca*Class, *Amphineura*Class, *Pelecypoda*Class, *Gastropoda*Class, *Cephalopoda*Phylum, *Echinodermata*Class, *Asteroidea*Class, *Ophiuroidea*Class, *Echinoidea*Class, *Holothuroidea*Class, *Crinoidea*Phylum, *Annulata*Class, *Archi-annelida*Class, *Chætopoda*Class, *Sipunculoidea*Class, *Hirudinea*Phylum, *Arthropoda*Class, *Crustacea*Class, *Onychophora*Class, *Myriapoda*Class, *Insecta*Class, *Arachnida*Phylum, *Chordata*Sub-phylum, *Cephalochordata*Sub-phylum, *Urochordata*Sub-phylum, *Hemichordata*Sub-phylum, *Vertebrata*Class, *Cyclostomata*Class, *Pisces*Class, *Amphibia*Class, *Reptilia*Class, *Aves*Class, *Mammalia*

together as the Enterozoa, it means that they are regarded as closely related in their ancestry. It is, therefore, possible to regard a table of classification like the one under discussion from the standpoint of evolutionary development.

Referring to the accompanying table (Fig. 117) as though it were a family tree and to Fig. 118, one may say that the first great step in evolution was the divergence between the forms of animal life that continued in a unicellular state and gave rise to the Protozoa, and those that acquired the many-celled state and produced the Metazoa. Within the latter line, the next great divergence was between forms that continued in a primitive state and without a gut cavity, the Parazoa, whose principal descendants are the Porifera; and those that acquired such a cavity and became the ancestors of the Enterozoa. Next came the acquisition of a coelome by forms that may be termed Cœlomocœla; while the more primitive state survived in the Enterocœla, from which the coelenterates, and perhaps the platyhelminthes, have descended without fundamental changes in their general organization. Among Cœlomocœla, there was then a divergence into the ancestors of the great phyla, and following this a specialization within the limits of the several phyla. Thus ended the most profound changes in evolution, as expressed by the classification indicated. If such changes occurred, they must have taken place at a very remote time, since the earliest fossil-bearing rocks that contain an abundance of life show representatives of all the larger groups except the Chordata (*cf.* Fig. 259, p. 491). If one desires to speculate upon the problem, some such answer as the one just given will probably be accepted by most biologists, although it is recognized that such conclusions regarding major evolutionary changes are speculative and not to be taken as clearly demonstrable.

The lesser phases of evolutionary history, for example, the evolution of lesser groups of vertebrates (*cf.* Fig. 276, p. 515), may be accepted with a higher degree of certainty. The table of cell cycles discussed in the preceding chapter may be consulted in this connection, since it shows how Metazoa might conceivably have arisen from a unicellular ancestry in common with the Protozoa, and since it explains the existence of a unicellular stage in the life cycle of every many-celled animal that reproduces by germ cells. The fact that so many members of the phyla that are grouped as

Cœlomocœla exhibit the *gastrula stage* (cf. Fig. 148 G, p. 307 and Fig. 209, p. 399) in their development may be taken as evidence for the course of evolution here indicated. The gastrula is a two-layered sac comparable with the Cœlenterata in its type of structure (cf. Fig. 121, p. 250), and perhaps reminiscent of an inheritance from an enterozoan ancestry. In other words, it may be that a gastrula stage occurs in these higher phyla because they have never completely lost this evidence of their primitive ancestry; and it may be that cœlenterates are two-layered because they have never evolved beyond what is fundamentally the enterozoan stage. Similar propositions could be laid down for the one-cell stage in all Metazoa (Fig. 110, p. 215), for the gill-slit stage in higher vertebrates (Fig. 287, p. 531), and for many features of development that are suggestive of ancestry in the various phyla. According to such an interpretation, the frog (Fig. 213, p. 405) arises from male and female gametes, which form a zygote, and later passes through its gastrula and gill-slit stages because it has never lost these vague evidences of its ancestral history as a vertebrate and as a member of the Metazoa. Classification upon a basis of structural resemblance has, therefore, a deeper meaning than convenience, since it is fundamentally the study of evolutionary relationships (cf. p. 506).

General Organization of the Animal Body

Forms of Symmetry.—In this connection the principal structural differentiations found among animals may be explained. Forms like *Volvox* (Fig. 106, p. 200) have a *universal symmetry*, since they are symmetrical around the center of a sphere. Any plane that passes through this center will divide the individual into halves that are symmetrical. A few of the protozoa are thus universal in symmetry, but there are no cases among Metazoa.

The *radial symmetry* that exists in animals like the fresh-water polyp, *Hydra* (Fig. 128, p. 266), and in the starfish (Fig. 118) is characteristic of Cœlenterata and Echinodermata. Such animals are symmetrical, like an umbrella or a cylinder, around a line that is the principal axis of the body. There are a number of planes through this axis that will divide the individual into equal halves. As with plants, radial symmetry is intimately related to an attached mode of life. Radially symmetrical animals that are free-living, like jellyfish and starfish, have

probably come from ancestors that were attached and hence radially symmetrical, if they do not have an attached stage in the life cycle. In many cases, animals that are essentially bilateral in type but are attached, like some of the segmented worms, Annulata, show a modification of bilateral organs in the direction of radial symmetry.

The *bilateral symmetry* that is characteristic of all the more highly developed animal types is a symmetry on either side of a plane, in contrast to radial symmetry which is through a line. A radially symmetrical body may become bilateral by modification in one of its radii, as when an umbrella has a curved handle or a glass cylinder is modified to form a beaker, and can then be divided into symmetrical halves by only one plane. Another way to define bilateral symmetry is to say that each of the halves separated by the median plane is a mirrored image of the other, or that the halves are "rights" and "lefts," like hands and feet. In general, bilateral symmetry is related to going "head-end first," and to the antero-posterior differentiation described in a subsequent paragraph. Some organisms are *asymmetrical*; that is, there is no plane that will divide them into symmetrical halves. The most familiar examples are Protozoa like paramecium.

Other Modes of Differentiation. — In addition to being organized according to the foregoing types of symmetry, animals may show *proximal* and *distal* differentiations, as in attached forms, where the base or proximal end differs from the distal end. An example is hydra, with its "foot" and tentacles (Fig. 121, p. 250). In other cases there is an *oral* side, which is differentiated from the *aboral*, as in a jellyfish (Fig. 127, p. 265) or a starfish. Such proximo-distal and oral-aboral modifications are most typical of radially symmetrical animals.

Bilateral animals, on the other hand, characteristically exhibit *dorso-ventral* differentiation into a "back" and a "belly" side; and *antero-posterior* differentiation into "head" and "tail" ends. *Metamerism*, or the segmental condition that appears so clearly in the earthworm (Fig. 137 A, p. 284) and other Annulata, is also characteristic of the Arthropoda and Chordata, as evidenced by the abdomen of the crayfish (Fig. 155, p. 323) and the vertebral segmentation of a vertebrate (Fig. 40, p. 69).

Types of Internal Organization. — The internal structure of many-celled animals may in turn be broadly classified as belonging

to one or another of the following types: the *protozoan* or unicellular type, which occurs only in the Phylum *Protozoa*; the *para-*

FIG. 118.—Principal types of animal structure and their probable relationships for comparison with Fig. 117.

zoan type, found only in the Phylum *Porifera* or sponges (Fig. 118), and differing from that of other many-celled animals principally in

the absence of a true enteron or gut cavity; the *enterocæalous-diploblastic* type in which there is an enteron with a single opening that functions as both mouth and anus, and in which there are only two principal cell layers, the ectoderm and endoderm, as in the Phylum *Cæloenterata* (Fig. 121, p. 250); the *enterocæalous-triploblastic* type, as with the Platyhelminthes (Fig. 118), in which the enteron has only one opening, although there is a middle cell layer, the mesoderm, between ectoderm and endoderm; the *cælomocæalous-triploblastic* type in which there is, in addition to the enteron, a cœlomic cavity, as in Annulata, Vertebrata, Mollusca, and Echinodermata (Fig. 118); and the *hæmocæalous-triploblastic* type, in which a cœlome is not present although there are extensive cavities, the hæmocœles as in the Arthropoda (*cf.* p. 331). Cœlomocœlous and hæmocœlous types are necessarily triploblastic, since cœlome and hæmocœle are cavities within the mesoderm cells which lie between ectoderm and endoderm.

Homology and Analogy. — Such classifications as the foregoing necessitate consideration of the resemblance in essential structure, which is termed *homology*; and the resemblance in function, termed *analogy*. The fore limbs of amphibians, reptiles, birds, and mammals are “homologous” whatever their functions, because all are constructed upon the same plan (*cf.* Fig. 18, p. 39). They may or may not be “analogous” structures since fore limbs may have different functions, like the wings of birds, the flippers of whales, the front legs of horses, and the arms of man (*cf.* Figs. 263 and 264, p. 500). The wings of a bird and those of an insect are analogous since they have the same function, but not homologous since they differ completely in structure. Again, the skeletons of insects and vertebrates (Fig. 22, p. 42) are analogous but not homologous. Since the classification commonly used in biological science is based upon structural resemblance, it is constantly necessary, in classifying animals, to distinguish between what is homologous and what is analogous. These principles are involved in evolutionary problems, since structural resemblance is supposed to indicate evolutionary relationship. For this reason classification is commonly cited as one of the lines of evidence for organic evolution (*cf.* p. 506).

CHAPTER 11

THE HYDRA, A SIMPLE MANY-CELLED ANIMAL

In preceding chapters the structure and functions of the most complex type of animal body were examined as a means of reviewing and extending our knowledge concerning the body of man and other animals. The organization and activities of the simplest animals were likewise examined with a view to understanding the resemblances between the highest and the lowest forms of animal life. As the next step, one of the simplest many-celled animals will be studied in order that we may determine the essentials of the many-celled state. The Metazoa, or many-celled animals, comprise the great bulk of the animal world, but there are many kinds of Metazoa. At the first survey there seems to be an endless diversity. When, however, one looks beneath the surface, there is more unity; for the structural plans among the Metazoa are restricted in the manner described in the preceding chapter. While the simplest type of metazoan is that represented by the Mesozoa and by the Porifera, a more usable type for the present purpose is that found in the Phylum *Cœlenterata*. Among cœlenterates the fresh-water organism called hydra is a form that is readily obtainable and one that is unusually well suited to illustrate the organization of a simple many-celled animal as well as that of a cœlenterate.

The Hydra as a Simple Metazoan

Occurrence and External Features of the Common Species of Hydra. — Three species of the genus *Hydra* are commonly found in the eastern and central portions of North America: *H. viridissima*, which is green; *H. vulgaris*, which is usually gray although at times orange or brownish; and *H. oligactis*, which is brown and has very long tentacles. The following account is sufficiently generalized to be applicable to any of these types unless otherwise stated. The green hydras are smaller and more active, have

shorter tentacles, and are likely to be found in greater numbers. The brown hydras are sluggish, but their larger size renders them more favorable for the study of the general organization. In nature, hydras occur in much the same manner as in laboratory aquaria. The individual is attached at the basal region, and extends into the water, tending to stand at right angles to its surface of attachment with tentacles outspread. As observed in an aquarium the green hydra extends its body and frequently changes its position, while the brown hydra is more likely to remain

FIG. 119.—Hydra with portion of body turned inside out in attempting to ingest a piece of beef.

with tentacles irregularly extended and almost motionless for much longer periods. These different degrees of activity are correlated with differences in the feeding habits of the two species. As may be observed in the laboratory, hydras devour small organisms, such as water-fleas and minute insect larvæ, sometimes overpowering and ingesting objects many times larger than themselves. If given opportunity, hydras will feed greedily upon bits of meat and similar materials (Fig. 119). Although there are no special organs of locomotion, the animal shifts its position from place to place by various simple movements of the body

(Fig. 120). Green hydras react positively to sunlight and thus tend to collect in regions of optimum illumination. Before undertaking a further description of habits and general behavior, it will be necessary to describe the structures involved.

General Structure and Body Plan.—The hydra, as shown by Fig. 121, consists of an elongated *body* normally attached at one end, the *base*, or “foot,” and surmounted at the other by a circle of *tentacles* enclosing a conical region, the *hypostome*, at the apex of which is the *mouth*. The tentacles vary in number in different

individuals as well as in different species. The body consists of but two layers of cells surrounding a central digestive cavity, the *enteron*, and this same organization extends to the tentacles, the cavities of which communicate with that of the body. Between the outer and inner layers of cells, which are known respectively as the *ectoderm* and *endoderm*, is the *supporting lamella*, which separates the two layers and may be regarded as a secretion formed by the basal ends of the cells. Functionally, this lamella is comparable with an elastic skeleton since it serves as a place of attachment for the cells and thus gives support and continuity to the entire organism. In contrast with most familiar animals, which are bilaterally symmetrical, the hydra is *radially symmetrical*, since its body is radially arranged about an axis of symmetry. This is one of the most obvious characteristics of the Phylum *Ctenophora* whether attached or free-living.

FIG. 120.—Locomotion in hydra.

(Redrawn from Borradaile, "The Animal and Its Environment," copyright, 1923, by Oxford University Press, printed by permission.)

Cellular Structures and Functions. — *General Organization of the Ectoderm.* — The cellular structure of the hydra is such that each layer of the body is largely composed of cells of one particular type with lesser numbers of cells of one or more other types. The *ectoderm* is made up primarily of large cells of the epithelial type (Fig. 122), having *muscular processes* extending laterally from the bases of the cells and attached to the supporting lamella. The muscular processes are further differentiated by the presence of a *fibril* which is presumably the essential contractile portion. Since they run lengthwise, these muscular outgrowths of the ectoderm cells are equivalent to a longitudinal muscular layer by

FIG. 121.—Cellular structure of hydra.

A, longitudinal section. *B*, cnidoblast with discharged nematocyst (cf. Figs. 123, 124 and 125). *C*, nematocyst as in *B* before discharge. *D*, nematocyst of another type before discharge. *b*, *b'*, bud; *e*, enteron; *ec*, ectoderm; *en*, endoderm; *f*, foot; *g.c.en.*, gland cell of endoderm; *g.c.f.*, gland cell of foot; *hy*, hypostome; *l.en.c.*, large endoderm cell; *mo*, mouth; *n.c.ec.*, nerve cell of ectoderm; *n.c.en.*, nerve cell of endoderm; *n.c.t.*, nerve cell of tentacle; *ne*, nematocyst; *n-s.c.*, neuro-sensory cell; *s.c.*, endodermal gland cell of hypostome; *s.c.ec.*, sensory cell of ectoderm; *s.c.en.*, sensory cell of endoderm; *s.c.f.*, sensory cell of foot; *s.c.t.*, sensory cell of tentacle; *s.l.*, supporting lamella; *t*, tentacle.

which the entire body may be shortened or bent in various directions. The mechanics of their concerted action can be understood when it is recalled that they are attached to the supporting lamella and hence all pull together upon this sheet-like membrane

FIG. 122.—Ectoderm and endoderm of hydra.

C, cnidocil; Cu, cuticle of ectoderm cell; EK, ectoderm; EN, endoderm; J, interstitial cells; JZ, intercellular space; K, cnidoblast; KB, nematocyst; KN, stalk of cnidoblast; M, muscle fibril of ectoderm; M', muscle fibril of endoderm; N, nerve cell; NF, process of nerve cell; P, striation of supporting lamella; S, sensory cell; SF, sensory process of neuro-sensory cell; SN, neuro-sensory cell; Z, supporting lamella; ZK, nucleus of epithelio-muscular cell. (After Hadzi, *Arb. Zool. Inst. Wein.*, Vol. 17.)

which is continuous throughout the animal. Since they possess the double function of covering the body and furnishing a muscular system, these *large ectoderm cells* are epithelio-muscular in character. At the base of the body they are modified as the *gland cells* of the foot by which the animal fastens itself to the substratum. The larger ectoderm cells in a typical region are

described by some investigators as divided toward their bases into prop-like structures connecting the outer portion of the cell with the region of the muscle processes that extend along the supporting lamella. According to this interpretation, the cavities that appear in the basal half of the ectoderm are, therefore, spaces between the larger cells and not so much vacuoles within the cells themselves as is often supposed. Partially filling these cavities, are smaller cells, the *interstitial cells*, and their derivatives, the *cnidoblast cells*; and, also, the *nerve cells*. The outer portions of the cnidoblast cells, and the *sensory cells* of the nervous system lie in the upper region of the ectoderm. If this interpretation is the correct one it is the peculiar shape of the large epithelio-muscular cells and their complex relationships with the other cells of the ectoderm that render the organization of this layer so difficult to demonstrate in ordinary laboratory study of sections or macerations. The structure and functions of the nerve cells and sensory cells will be considered in the account of the nervous system. The development of the germ cells, which arise from interstitial cells when the reproductive organs are produced, will be described along with the reproductive system. There remain for consideration here the interstitial cells and their derivatives, the cnidoblasts.

The Cnidoblast Cells and their Nematocysts.—Scattered over the body, but reaching their full development only upon the tentacles, are the *cnidoblast cells*, containing the *nematocysts*, or stinging capsules, by which the hydra paralyzes its prey (Fig. 125). The relationship of these to other cells can be understood if the history of the nematocysts and their cnidoblast cells is followed in connection with the schematic representation in Fig. 126. While it is difficult to ascertain the exact conditions in structures so minute, it appears that the relationships are as follows: An interstitial cell (Fig. 123) produces in its cytoplasm a structure which has at first the appearance of a vacuole and is later seen to be a minute capsule containing a thread that becomes surrounded by a stainable fluid. Apparently the thread originates as an ingrowth from one side of the capsule wall, much as a blind tube might be formed by pushing in a small area at one end of a football bladder, and gradually assumes the relationship of an elongated and turned-in glove finger. The *nematocyst is, therefore, not a cell, but a capsule*, containing a hollow inverted thread, and it is produced within the cytoplasm of an interstitial cell. When an interstitial cell thus

begins to form a nematocyst, it becomes a cnidoblast cell. The first steps in this process occur in cells lying near the supporting lamella. After the nematocyst is fully developed the cnidoblast attaches itself to the supporting lamella, grows toward the surface, and thus becomes exposed externally either between the larger ectoderm cells or embedded in their substance (*cf.* Fig. 122), but the connection with the supporting lamella is retained by means of a delicate stalk (Figs. 124 and 126). Upon reaching this exposed position, the cnidoblast develops a trigger-like projection, the *cnidocil*, which protrudes from the surface and is the part of the cnidoblast which is sensitive to the chemical stimuli that normally produce the discharge of the nematocyst. As may be

FIG. 123.—Formation of a nematocyst in the cytoplasm of an interstitial cell, which thus becomes a cnidoblast.

A to E, the successive stages. *ne*, nematocyst; *nu*, nucleus of cnidoblast; *se*, fluid within nematocyst that is supposed to cause the eversion of the thread by a sudden swelling due to imbibition of water. (After Hadzi, *loc. cit.*)

readily seen under the microscope, this discharge consists of a sudden eversion, by which the thread is turned right side out and is extended into the surrounding water or penetrates the prey (Fig. 125). When discharged, the nematocyst, therefore, resembles a football bladder with an elongated structure like an everted glove finger extending from one end (Fig. 121 B).

Although it is impossible to say that cnidoblast cells are never controlled by the nervous system, recent investigation indicates that they are what are known as *independent effectors* (Fig. 129), that is, structures responding like the nervous elements to stimulation, but not under nervous control. The cnidoblast cells of hydra seem to be little affected by mechanical stimuli, as when a tentacle is rubbed with a fine glass rod, or when the surface is brushed by the movements of the ciliated protozoans, *Trichodina*

and *Kerona* which often infest the outer surface of hydras. On the other hand, suitable chemical stimuli are very effective, as when dilute acetic acid is used to discharge the nematocysts in laboratory study. It seems, therefore, that under natural conditions the nematocysts become discharged by the stimulation of chemical substances given off by the water-fleas and other small organisms that are the common food of hydra. In contrast to this, the muscular responses of the tentacles, in the capture of prey and otherwise, appear to be controlled by the nervous system.

The mechanism by which the eversion of the nematocyst thread is brought about, following the chemical stimulation of the cnidocil,

FIG. 124.—Cnidoblasts of hydra.

A, B, and C, stages in formation of the stalk (*st*) of the cnidoblast after attachment to the supporting lamella (*sl*). The exposure of the nematocyst at its outer end is not normal, but due to shrinkage of the cnidoblast in the preparation. D, E, and F, cnidoblasts and their nematocysts as seen in macerated specimens. *cn*, cnidoblast; *n*, nematocyst; *nu*, nucleus of cnidoblast; *sl*, supporting lamella; *st*, stalk. (After Hadzi, *loc. cit.*)

is of interest. Experiments and observations indicate that the threads are everted by an increase of pressure inside the capsule. Before discharge, the cavity within the capsule and surrounding the thread contains a fluid (Fig. 123) having the property of swelling rapidly when it can imbibe water. Apparently, a chemical stimulation of the cnidocil brings about changes in the cnidoblast and its contained nematocyst such that water suddenly enters the cavity of the latter and causes a rapid swelling of the enclosed fluid. Thus the mechanical effect is similar to that which might be produced by blowing into the wrist of a rubber glove and causing the eversion of an intumed finger.

From the examination of animals paralyzed by a hydra and removed from its clutches before being swallowed, it appears that

there are at least two types of nematocysts, each with its special function. One type is like a grappling organ, since the threads wrap themselves about any fine hair-like processes (Fig. 125 B) and hold fast; the other is able to puncture the outer surface of the prey and drive its everting thread through the surface into the tissues (Fig. 125 A). How this penetration occurs is problematical, but it may perhaps be effected by the extreme rapidity of the eversion, or by means of the barbs at the base of the thread. These leave the capsule pressed together like a triple spear point (Fig. 121 C) and only assume their positions on the everted thread by spreading outward and backward as the eversion proceeds. The poisonous substance of the nematocyst, which is known as *hypnotoxin*, is seemingly contained within the cavity of the thread itself before eversion and, therefore, covers the outer

FIG. 125.—Use of nematocysts by hydra.

A, insect larva punctured by numerous nematocysts of the barbed type (redrawn from Jennings, "Behavior of the Lower Organisms," printed by permission of the Columbia University Press). B, part of an appendage of a water-flea showing another type of nematocyst that seems to function like a grappling hook. (Redrawn from Toppe.)

surface of the thread when it is finally turned right side out. If the thread penetrates the prey, one can understand that a poison so placed would be highly effective. Sometimes the discharged nematocysts, as seen in the laboratory, show a stainable coagulum about the thread which is the remains of the hypnotoxin.

The effectiveness of the nematocysts as weapons of offense and defense may be observed if hydras are watched in laboratory aquaria containing water-fleas and other small animals which are their common food. A water-flea blunders against the tentacles of a hydra and is held fast. Almost immediately it ceases to struggle, although flickering movements of the appendages may continue for a time. If the hydra has recently fed, the water-flea may soon be released and drop to the bottom, where it may gradually resume its activities much as though it were recovering from an anæsthetic. On the other hand, if the hydra has been without

food for a time, its tentacles and mouth begin to react in a characteristic fashion with the result that the prey shortly disappears into the mouth and the hydra resumes its watchful waiting, although it is now less responsive to such stimulation until it again becomes "hungry." The water-flea might as well have gripped an electric wire for all the help it receives from its protective skeleton or the hairs and spines upon its appendages. In spite of its apparent lack of weapons, the hydra has easily overpowered its armored prey. These deadly effects are produced by the hypnotoxin, which is brought into contact with the prey by the nematocyst threads in the manner described. Thus the hydra is a terrible enemy for such animals as water-fleas, although at first glance it appears wholly incapable of offensive or defensive actions. Because of its nematocysts, it is well equipped for this phase of its struggle for existence.

Such stinging capsules are found in all but one group of the coelenterates. In some of the jellyfishes their poison is so strong as to produce a violent reaction in the human skin. In all cases they are used for paralyzing active prey and incidentally for defense; so that a jellyfish, in spite of its soft body, may overpower active animals of small size, and even animals that are protected by external skeletons and defensive organs. When a nematocyst is discharged it is of no further use, and both capsule and thread are soon detached from the hydra. Often the cnidoblast cell is also torn from its position and lost. There are several types of nematocysts in hydra and many types in different coelenterates, but these must be studied at first hand to be understood. However, they are all constructed and seem to function in the same general manner. That the nematocysts are not "cells" is obvious. By suitable methods they may be extracted from a hydra without being discharged, and kept for days, to be discharged later upon appropriate stimulation. There are also some animals, like the flatworm *Microstoma* and certain molluscs, that feed upon coelenterates without causing a discharge of the nematocysts, and later use these stinging capsules for their own defense.

There is another feature in the behavior of the cnidoblasts with their contained nematocysts that presents further complications. If the various regions of a hydra are examined, almost no nematocysts in the developmental stages are represented upon the tenta-

cles. Only the fully developed capsules will be found in this region, along with many cnidocils indicating the presence of cnidoblast cells in their final stage of development. Since it is on the tentacles that most of the nematocysts are used, there must be some means by which such fully formed nematocysts and cnidoblasts can be supplied to replace those which are lost. In the body region, on the other hand, there are many developmental stages of nematocysts but few cnidocils. This indicates that while the nematocysts may reach their full development in the body, few of them reach their final location in the outer part of the ectoderm of the body where they can become functional. The problem thus presented is illuminated when we examine some of the marine relatives of the hydra.

In many hydroids (*cf.* p. 274) it has been demonstrated that the nematocysts are originally produced by cnidoblast cells in the region corresponding to the body of the hydra, and that these cnidoblasts migrate in an amœboid fashion through the spaces between the epithelio-muscular cells of the ectoderm (*cf.* Figs. 122

FIG. 126.—Origin and migration of cnidoblasts.

When its nematocyst is fully formed (*cf.* Fig. 123) the cnidoblast may either become attached to the supporting lamella in the body region and grow outward until it pierces the surface of the body where it lies with cnidocil exposed as shown in the lower part of this figure and in Fig. 122; or the cnidoblast migrates between the bases of the ectoderm cells as shown here until it reaches the tentacles, where it becomes attached to the supporting lamella and grows outward as shown in the upper part of this figure and in Fig. 122. Such a migration is demonstrable in hydroids like *Tubularia*, and probably occurs in hydra, since developmental stages of the nematocysts are found principally in the ectoderm of the body, while fully developed cnidoblasts and nematocysts are abundant only upon the tentacles. *cn*, cnidoblasts; *cn'*, cnidoblasts migrating; *ec*, ectoderm; *n*, nucleus of large ectoderm cell; *s.l.*, supporting lamella; *st*, stalk of cnidoblast; *st'*, stalk united with another at base. (Based upon the account by Hadzi, *loc. cit.*)

and 126) until they reach the places where they are used, upon tentacles or hypostome. Arriving at this region, they become attached to the supporting lamella and grow upward to pierce the "roof" of ectodermal cells (*cf.* Figs. 122 and 124), thus becoming exposed at the surface and finally developing their cnidocils in the manner previously indicated. In the hydroid *Tubularia* it seems that the cnidoblasts, after forming their nematocysts in the stalk of the hydroid, may even migrate through the supporting lamella and endoderm into the enteron, in which they are carried to the region of the tentacles. Here they reënter the endoderm and again pass through the supporting lamella to reach the ectoderm once more. In this layer they then migrate to their final position on the tentacles. It is impossible to observe such migration in hydra because the body is mobile and not enclosed by a skeleton-like perisarc as is the body of the hydroid, where the cnidoblasts can be observed to move past fixed points. But the lack of developmental stages on the tentacles of hydra where the nematocysts are used and the abundance of such stages on the body so parallels the conditions observed in hydroids, that there can be little question as to the similar conditions of origin and migration. There is no evidence that the path of migration is so complex as in *Tubularia*, but there is little doubt that nematocysts originate in the body ectoderm of hydra and are carried by the amœboid movements of their cnidoblast cells to their place of use upon the tentacles.

The justification for this extended account of these microscopic structures centers about the fact that so minute a "harpoon-gun" can be produced and function, not as a living cell but as a non-living mechanism produced within a cell. The nematocyst is capable of being discharged by the action of its cnidoblast cell, or it may be discharged by external agencies, days after the capsule has been separated from its cnidoblast. It may even be appropriated by another animal and put to the use that would have been made of it by the hydra. Just as we are awed by the immensity of space, as revealed by the telescope, so we are amazed by the minuteness of such a mechanism as the nematocyst. If one may modify the German of Röscl von Rosenhof, a student of microscopic life in the early eighteenth century,

Lies dieses Buch, und lern dabey,
Wie gros Natur im kleinem sey.

Organization of the Endoderm. — The endoderm, like the ectoderm, is composed mainly of large epithelio-muscular cells (Fig. 122). In these, however, the basal processes run transversely and thus provide a circular musculature for the body. The endoderm cells of the tentacles are without muscle processes, and hence these organs have no mechanism within themselves by which they may be elongated. They are extended by pressure of fluid forced into them from the enteron of the body. Around the mouth and at the base of each tentacle, the endodermal muscle processes are especially developed as *sphincters*. In green hydras these large endoderm cells are crowded with the bodies known as *zoöchlorellæ*, which are really a kind of unicellular green plant that has come to be associated with the hydra. There are similar symbiotic plants in the endoderm cells of some marine coelenterates, particularly the corals. In the staining of hydras by students in the laboratory, the nuclei of the zoöchlorellæ are sometimes recognizable. Being green plants, they must take in carbon dioxide and liberate oxygen in photosynthesis (*cf.* p. 170). In view of the needs of respiration, the presence of such organisms within the cytoplasm of an animal's cells would be advantageous. Likewise, the end products of oxidation in the animal cell would be useful to the plant. A relationship of this sort is termed *symbiosis*, or living together with mutual benefit, in contrast with the association known as *parasitism*, in which the advantage is all on one side; or with *commensalism*, in which the two organisms merely feed together without obvious advantages or disadvantages.

At a certain interval after the hydra has taken food, the endoderm cells are seen to be crowded with numerous particles of food which are enclosed in vacuoles of digestion like those of a protozoan such as *amœba*. In starvation, these cells become highly vacuolated; and when not overcrowded with food vacuoles they are likely to contain one or more larger vacuoles like those found in many plant cells, in addition to the spaces described (Fig. 122). At their inner ends, where they are exposed to the digestive cavity, the endoderm cells may have pseudopodia-like processes, by which the food particles mentioned are engulfed; and also flagella, by which the contents of the enteron are kept in motion in the absence of movements of the hydra as a whole. Scattered among these large endoderm cells are others having an elongated body and enlarged at the end that is exposed to the enteron (Fig. 121). As

the cytoplasm of such cells contains a frothy or granular material which can sometimes be seen in process of discharge, it is evident that they are *gland cells* and are presumably responsible for the digestive enzymes that act upon the food within the enteron. Just inside the mouth there is a circlet of cells producing another type of secretion which probably serves as a lubricant in the swallowing of food, or perhaps as a paralyzing agent in addition to the nematocysts. Aside from the endodermal *nerve cells* and *sensory cells*, described as part of the nervous system, no other types of cells are known to occur in the endoderm.

Hydra is, therefore, composed of two cell layers, the ectoderm and the endoderm. This is a very simple type of organization and one found only in the Coelenterata. In contrast with this, we shall see that all the higher groups of animals have another cell layer, or rather cell mass, the *mesoderm*, between the ectoderm and endoderm and composing the greater bulk of the body. This body plan of hydra and the coelenterates is called *diploblastic* in contrast with the *triploblastic* plan which is found in higher forms.

Metabolic Activities.—The capture and ingestion of food, to which incidental references have been made, is discussed in the section on behavior. After entering the mouth, the food is shifted by peristaltic contractions of the body to a position in the upper half of the enteron, where digestion occurs. As the food mass is never found at lower levels, there is apparently a physiological division of the enteron into a "stomach" portion and an "intestinal" or absorptive one, although no structural difference is recognizable, except the abundance of gland cells in the endoderm of the upper body. If the objects ingested as food by a hydra are examined during the earlier stages of digestion, it is found that they are undergoing a disintegration similar to that which takes place in the stomach of any carnivorous animal. The softer parts of a water-flea, for example, become liquefied and divided into smaller particles, while fragments of the indigestible skeleton remain as would bits of the skeleton of an insect or a crayfish within the stomach of a frog. Eventually, these indigestible portions are egested, slowly or by a violent contraction, through the mouth. It is thus evident that a digestive process takes place within the enteron. This is doubtless caused by enzymes, since these are present in all cases where digestive juices can be collected in sufficient quantity for experimentation.

We have seen that certain gland cells of the endoderm appear to be the source of such enzymes. Hence, there is a digestive process in hydra which occurs outside the cells and is therefore called *extracellular*. It appears also that during the latter stages of digestion the large endoderm cells ingest small particles in much the same way as does an amœba, and that such particles are then digested within food vacuoles by an *intracellular* process. If this is true, hydra carries on the type of digestive process characteristic of higher animals and also that of protozoa. This is not so strange, since white blood cells and certain others, even in our own bodies, exhibit intracellular digestion of ingested particles.

Since the hydra has no circulatory system, there can be no activities strictly comparable with "absorption" and "circulation" in an animal with a well-developed blood system. Something analogous to circulation is, however, accomplished by the movement of food within the enteron, as when material in the later stages of digestion passes from the cavity of the body out to the cavities of the tentacles, to be taken up by the cells of these regions. The enteron of the cœlenterate is sometimes called the *gastro-vascular cavity* on the ground that it possesses this circulatory function in addition to that of digestion. In the jellyfish and some other larger members of the group, this seems to be true, but in hydra there appears to be no special arrangement other than the shifting of the gut contents incidental to the various bodily movements and the beating of the flagella at the free ends of the large endoderm cells. It appears, however, that such transfer of nutrient material as exists must take place mainly within the enteron, since there is evidence that the lateral diffusion from cell to cell in endoderm and ectoderm is very limited. The step that follows digestion, either within the enteron or in the vacuoles of digestion, is therefore comparable with *assimilation* in a higher animal, since it consists of the incorporation and utilization, by cells of the endoderm, of the products of digestion, and their diffusion, as necessary, to the ectodermal layer.

It is supposed that the same metabolic changes occur within the cells as in those of higher animals, with the resultant excretory products. *Excretion*, in an animal like hydra, may take place by diffusion over the entire external surface, and perhaps, to a limited extent, into the enteron. There is some indication that granules of insoluble excretory matter may at times accumulate in the

endoderm cells. Since the individual cells are in the same intimate contact with the surrounding water as the independent cells of a protozoan, or the cells of a multicellular animal with their surrounding lymph (cf. Fig. 60, p. 104), similar exchanges of material can be postulated for each case. Likewise, the oxygen used in *respiration* in hydras without zoöchlorellæ is presumably taken directly from the surrounding medium in much the same fashion as the cells of a higher organism receive their oxygen from the neighboring intercellular lymph. If the metabolic processes of the frog and the protozoa be recalled and compared with those of hydra, it will, therefore, be seen that the phenomena of metabolism are essentially alike in all these animals. The differences are those incidental to the state of organization and not to any fundamental contrasts.

Irritability and Behavior.—*Movements and Locomotion.*—The more obvious movements of the hydra, whether the animal is attached or in locomotion, may be accounted for mechanically by means of the longitudinal and circular muscle processes of the ectodermal and endodermal cells. The fact that these processes can contract and relax locally and in a coördinated fashion is evidenced by the varied positions and outlines the animal may assume. Less obvious movements of sliding along on tentacles have been described as due to the protoplasmic flow of ectoderm, while gliding on the foot has been attributed to pseudopodia. In addition to extensions and contractions of body and tentacles as a whole, there are peristaltic pulsations by which the food is passed from one part of the enteron to another. These may be very slow, consuming from fifteen to thirty minutes in traveling over the length of the body; or they may be so rapid as to shift the mass rather suddenly, as when faecal matter is violently egested or food quickly shifted toward the middle of the hydra. There is also a sphincter, or special contractile area, formed by the circular muscle processes around the mouth. The sphincter at the base of each tentacle is capable of shutting off the tentacular cavity from that of the body. Detachment of the base during locomotion seems also to be due to muscular contraction.

Locomotion is effected in a variety of ways (Fig. 120). A hydra may move by imperceptible degrees, gliding upon its "foot" by amœboid extensions of this area. Under stronger stimulation, it may extend itself laterally until the tentacles are in con-

tact with the surface, release the foot, draw it to a new point of attachment, and extend the tentacles once more, repeating this process after the manner of caterpillars that move by "looping along." Again, the hydra may attach the tentacles, release the base, and move by slow somersaults. Under an increasing stimulus of hunger, these forms of locomotion appear in the order named. In some cases, the animal crawls clumsily upon its tentacles with the body free and contracted. Sometimes hydras float about and may be collected from the open water by a fine net in pond or aquarium.

Failing to find food after a long search, or under other unfavorable conditions, hydras may become contracted and remain without movement in one place. If this condition continues, the tentacles may be resorbed and later regenerated unless the unfavorable conditions result in death. Hungry hydras may go to the bottom of an aquarium and gorge themselves with ooze. This seems to be an alternative method of feeding not commonly recognized.

Feeding. — In feeding, the activities of green and brown hydras differ markedly. If a green hydra that has not fed for a time is carefully observed, it will be seen to extend its body and tentacles and remain in one position for only a short period. Failing to secure food, the body is contracted and reextended at a new angle. This process is repeated until the area within reach of any one point of attachment has been irregularly "covered." The almost imperceptible gliding on the base may occur during these activities and thus new territory may be reached. If no food is captured by these lesser activities, the hydra begins the looping movements (Fig. 120), and if still unsuccessful it begins to somersault, finally becoming quiescent if its quest is useless. In contrast with this, the brown and gray species of hydra, which have longer tentacles, remain motionless for considerable periods with all the tentacles widely extended, much as a party of fishermen might set out a number of lines in all directions from a boat and wait for a catch. If no food is secured they begin to move clumsily after the same general manner as the green hydras.

The function of the nematocysts in paralyzing the prey has been described. When a water-flea or some such organism has thus been caught by a tentacle, the remaining tentacles usually "go into action" in a coördinated fashion, although it is possible

for a very small animal to be caught by one tentacle alone and passed to the mouth without a disturbance of the other tentacles. In either case the prey is drawn toward the mouth, which may open in advance of the actual contact. When food begins to enter the mouth, the tentacles cease to function. In the case of large food masses, they may even become folded back away from the hypostome (Fig. 119), the final stages of ingestion being accomplished by a lip-like creeping of the mouth around the food. Hungry hydras will sometimes ingest the bodies of animals or bits of meat many times larger than themselves, or they may attempt the impossible with large masses of food, even turning the body wrong side out for a short distance. The process of feeding is so remarkable that it must be seen many times to be fully appreciated. The fact that the tentacles and the entire oral region of the body behave in a coördinated fashion can be accounted for by the presence of the nervous mechanism described in a later section. Another point that is of interest here is that hydras kept without food, and therefore "hungry," are much more responsive in their feeding reaction than individuals that have recently fed. This indicates that the internal physiological state of the animal may influence its responses to external stimuli.

Tropisms.—The complexities in the hydra's behavior show that it must respond with some delicacy to a considerable range of stimulation. This is found to be true upon observation and experimentation. *Stereotropism*, or reaction to contacts with external objects (cf. p. 181), is one of the most important forms of response, since the stimuli of contact with a substratum are recurrent whether the hydra is in locomotion or at rest. The animals are also very sensitive to touch, as may be demonstrated in the laboratory by bringing a glass rod into contact with the tentacles or the side of the body. They also respond to mechanical shocks, as when one jars the table on which an aquarium is standing. *Phototropism*, or the response to light, is particularly in evidence in green hydras, which will collect in the parts of an aquarium where the illumination is at an optimum. This response is sometimes complicated by the fact that water-fleas and similar animals may collect in such places in response to light or contact stimulation and the hydras may come to occupy the same territory in response to the presence of this food supply. The response to heat, or *thermotropism*, may be shown by heating one end and chilling the other

end of an aquarium and observing that the hydras will begin moving at a temperature of 31°C . There is, however, no definite movement toward or away from the source of heat, only a vague wandering that continues until a region of optimum temperature is reached in a wholly accidental fashion, unless the animal is killed by blundering into a region that is too hot. What evidently happens is that the rising temperature induces a changed internal state of the hydra which leads it to wander until this internal regulation is modified by new external conditions. At temperatures that are too high or too low the animal contracts and remains quiescent until it dies or is relieved by the restoration of a suitable temperature. Response to chemicals in solution, or *chemotropism*,

FIG. 127.—A young jellyfish, *Gonionemus murbachi*, resting upon the bottom with oral side uppermost.

(After Perkins.)

is also demonstrable, as when meat juice is squirted from a capillary pipette against the tentacles or hypostome, or when various chemicals like acetic acid, to which the hydra is probably not subjected in nature, are similarly used. Although it has no special sense-organs, but only sensory cells (*cf.* Fig. 129), the animal thus responds to as many fundamental types of stimuli as do many of the higher animals.

The more delicate responses are perhaps the result of a combination of stimuli, such as probably occurs in feeding. If the tentacles are touched gently with the end of a capillary tube there is not much reaction, nor is there a very marked response when meat juice is brought against them with the minimum of mechanical stimulation. When, however, these two stimuli are combined, the maximum reaction is obtained. The small size of hydra makes

it more difficult to observe, but there is apparently the same mode of response as in the jellyfish, *Gonionemus* (Fig. 127), where a combination of motile, mechanical, and chemical stimulations gives the maximum reaction, since this most closely imitates the kind of stimulus to which the animal normally responds in the capture of

FIG. 128. — Young hydra stained to show network of ectodermal nerve cells with ring-like arrangement in foot and hypostome.

(After Hadzi, *loc. cit.*)

its prey. The tentacles of a resting *Gonionemus*, for example, are moderately sensitive to the mechanical stimulus of a fine pipette when it touches them or moves slightly, or to the gentle ejection of meat juice against them without movement of the pipette; but when the mouth of the pipette is drawn rapidly along a tentacle as the meat juice is extruded the animal springs into action, as though a small fish or crustacean had come within its toils. The tentacles twist and turn, bending toward the mouth, and the hypostome bends toward the tentacles stimulated.

The Nervous System.—An animal exhibiting the complexities of behavior that have been described in the foregoing paragraphs may be presumed to possess a nervous system with some degree of organization. Such proves to be the case with hydra (Figs. 128, 129 and 130). In the ectoderm there is a network of *nerve cells*,

with which are connected, on the one hand, at least four different kinds of *sensory cells*, and on the other, the *muscle fibrils* of the large ectoderm cells. In the endoderm there is a much smaller number of isolated nerve cells and also a few cells that appear to be sensory. There is no microscopic evidence that the nervous elements of the ectoderm and endoderm of hydra are united by fibers passing through the supporting lamella. The absence of a nerve network in the endoderm and the independent muscular action of the two layers which this implies is further evidenced by experimentation; since the movements due to the longitudinal

muscles of the ectoderm are active and coördinated as compared with the sluggish and more diffuse contractions effected by the endodermal muscle fibers.

As the nervous system of hydra is quite representative of the conditions found in ccelenterates and other simple metazoa, its organization will be described in some detail. Extending throughout the ectoderm are *nerve cells* or neurones, which are connected with one another by their processes (Fig. 128). Although it is impossible to be entirely certain, it appears that these connections represent continuity and not mere contact of neighboring cell processes, as seems to be the case between the specialized nerve cells of higher animals. These nerve cells of hydra lie in the basal region throughout the ectoderm of body and tentacles and near the

FIG. 129.—Schematic representation of the ectodermal nervous system, including a cnidoblast shown as an independent effector.

cn, cnidoblast; ect, ectoderm; m.f., muscle fibril of large ectoderm cell; n.c., nerve cell; n-s.c., neuro-sensory cell; s.c., sensory cell; s.l., supporting lamella.

muscle processes (Fig. 129). Since they appear edgewise when the ectoderm is seen in profile, one does not appreciate their shape and connections until they are seen in surface views. In addition to these nerve cells, there are in the ectoderm three slightly different types of *sensory cells*, since they evidently receive the external stimuli at their outer ends. One type is present on the tentacles, one on the hypostome, and one on the foot (Fig. 130, A, E, and K). In the body there are nerve cells having sensory processes extending to the surface, and hence constituting a fourth type called *neuro-sensory cells* (cf. Fig. 129). It is probable that both the sensory cells and the neuro-sensory cells have some direct connections with the muscle processes; but in the main these sensory cells connect with the nerve cells, which in turn

FIG. 130.—Nervous system of hydra as shown by maceration.

A, sensory cell (s.c.) from ectoderm of tentacle, shown in its relation to supporting lamella (s.l.) and cnidoblast (cn). B, nerve cell of endoderm (n.c.), connected with large endoderm cell (en). C, sensory cell of endoderm. D, network composed of nerve cells (n.c.) and neuro-sensory cell (n-s.c.) from ectoderm of body (cf. Figs. 128 and 129). E, sensory cell from ectoderm of hypostome. F, lateral view of two nerve cells and the supporting lamella (s.l.). The processes do not pass through the lamella, although they seemed to do so in this bit of macerated material. G and H, sensory cells from ectoderm of body. I, part of the ring of nerve cells in ectoderm of foot (cf. Fig. 128). J, neuro-sensory cell from ectoderm of body. K, sensory cell (s.c.) and gland cell (g.c.) of foot. L, nerve cells (n.c.) and gland cells (g.c.) of foot. (After Hadzi, *loc. cit.*)

send processes to the muscle fibrils and thus mediate between the cells that receive the stimulation and those making the response. Taking such a mechanism as a whole, it is better called a *sensory-neuromuscular system* than merely a nervous system.

Hydra, therefore, exhibits in its ectoderm the machinery of what is known as a receptor-effector system (*cf.* p. 317), since the sensory cells, or *receptors*, receive the stimuli and transmit impulses to the nerve cells, which in turn transmit them to the muscle cells which are the *effectors*. If the gland cells of the foot are under nervous control, as may be the case although it has not been demonstrated, they constitute another type of effector (Fig. 130 K and L). This form of nervous organization is typical of coelenterates.

Within the endoderm there are only a very few cells that can be regarded as nerve cells (*cf.* Figs. 121 and 130 B). There is no evidence that these are connected with one another, although they probably have processes connecting with neighboring muscle cells. There are also cells that seem to be sensory and probably have connections with muscle processes (Fig. 130 C). The small number of such nerve and sensory cells in the endoderm and the sluggish nature of the movements involving the endodermal musculature, alike indicate that there is no unified nervous system in the endoderm comparable with that of the ectoderm. As we have seen, there is neither structural nor functional evidence for a connection between the ectodermal and endodermal nerve cells through the supporting lamella. It is probable, however, that the sphincter of endodermal muscle processes surrounding the mouth may be connected with the ectodermal nervous system of this region, a relationship that would account for certain coördinations of ectodermal and endodermal muscular action observed in ingestion and egestion.

At first glance it seems that the hydra has no centralization of the nervous elements, but only a diffuse distribution throughout the body. More careful examination reveals the existence of ring-like collections of nerve cells (*cf.* Figs. 128 and 130 I) and a corresponding abundance of sensory cells in the foot and hypostome, the two regions of the body that are most active. The processes of the nerve cells tend to run lengthwise on the tentacles and perhaps on the body, although contraction of the latter region makes the exact arrangement difficult to ascertain. In some other

coelenterates, like the jellyfish, which are more active animals than hydra, a similar primitive centralization of nerve cells has produced a definite nerve ring about the margin of the bell, and a similar development in the hypostome.

There remain the cnidoblasts (Fig. 129), which do not seem to be connected with the nervous system, although it is impossible to say that there are no such connections. Judged by its structural relationships and manner of functioning, the cnidoblast appears to be an *independent effector*, that is, a cell capable of direct response to stimuli. In the comparison of the nervous systems of various animals, in Chapter 13, it will be shown that such effectors probably represent the beginnings of the sensory-neuro-muscular mechanism of animals.

Reproduction. — *Asexual Reproduction.* — Hydra frequently produces new individuals by budding. As there is nothing involved in this process that can be identified as maleness or femaleness, it may be properly termed "asexual" (*cf.* p. 219). There first occurs an accumulation of nutrient material in the endoderm cells at some place toward the middle of the body and the interstitial cells in this region increase in numbers. Gradually a bud-like swelling develops, into which, at an early stage, there grows an extension of the enteron so that the bud becomes a blind outgrowth of the two layers of the body wall (Fig. 121). As the development proceeds, tentacles begin to appear as lesser outpushings of ectoderm and endoderm, and finally the mouth is formed. Usually, the bud closes its connection with the parent's enteron about the time the tentacles appear, and soon after pinches itself off, leaving no permanent scar at its place of origin. It thus drops to the bottom and becomes a new and independent individual. In some cases, however, the bud remains longer on the parent and may even re-bud so that there may be several generations in a branching system. This is comparable with the colonial state in hydroids (*cf.* p. 274), where the budding is so extensive that colonies are produced, containing hundreds of individuals originating from a single original hydra-like organism (*cf.* Fig. 134).

Sexual Reproduction — At certain seasons of the year, particularly in the fall, hydra reproduces sexually by means of male and female cells. The *testes* are usually located on the upper half of the body. The *ovaries* lie near the middle of the body. Testes may appear first and ovaries later, on the same animal, or both

may appear together. Thus the hydra is an *hermaphroditic* animal, or one producing both male and female cells in the same individual. If the early stages of a testis are examined it is found that a group of interstitial cells have multiplied to form the early germ cells, from which the spermatozoa, or male germ cells are

FIG. 131.—Formation of germ cells of hydra.

1, part of longitudinal section (cf. Fig. 132 A), showing two oocytes (*a* and *b*) in ectoderm. 2 to 4, sections through one of the compartments of the testes showing stages in development of interstitial cells into spermatozoa (*a*, *b*, *c*, *d*). 5 to 10, formation of spermatozoa. 11 and 12, optical sections of compartments of testes (cf. 2 to 4) in two different stages immediately after removal from living hydra. (After Tannreuther.)

differentiated (Fig. 131). When the spermatozoa are fully matured, they may be seen moving actively within the testis. They are discharged into the water by the opening of the apex of the testis, which thus liberates successive swarms of sperm. They swim about until they perish or come in contact with a ripe ovum, which is entered in fertilization. By far the greater

FIG. 132.—Development of hydra.

A, section showing two stages in formation of ovum within ovary. B, section of ectoderm showing early stage of ovary with several oocytes or female germ cells (*g.c.*) surrounded by yolk-forming cells (*y-f.c.*). C, four stages in development of the zygote, while still attached to parent, showing one-cell stage with polar bodies (*p.b.*) and membrane (*m*), two-cell stage, blastula with cleavage cavity (*c.c.*), and later stage in which ectoderm and endoderm have been differentiated. D, section of embryo soon after detachment from parent showing cyst-like covering formed by further development of membrane. E, portion of D showing inner and outer membranes of the cyst in relation to the ectoderm. F, young hydra emerging from the cyst. *c.c.*, cleavage cavity; *ec*, ectoderm; *en*, endoderm; *g.c.*, germ cells; *i.m.*, inner membrane; *m*, membrane; *o.m.*, outer membrane; *ov*, ovum; *p.b.*, polar bodies; *y-f.c.*, yolk-forming cells. (B and C, after Tannreuther.)

number of spermatozoa must perish, as the ova are produced in much smaller numbers and fertilization consists in the union of a single spermatozoön and a single ovum.

Like the spermatozoa, the ova arise from interstitial cells (Fig. 132 B). In the young ovary there are several dozen germ cells, the oöcytes, each formed from an interstitial cell. As the ovary develops, one of these cells outstrips the rest and begins to ingest its fellows much as an amoeba might devour other amoebas. Indeed, the ovum is actually amoeboid in shape during this stage of its development (Fig. 132 A). The process of ingestion continues until there remains only a single egg cell of large size. The ovary then consists of this one egg covered by a thin layer of ectoderm which ruptures at the time of maturity and exposes the surface of the ovum to the water. In this manner the spermatozoa have access to the ovum at the time of fertilization. Following fertilization, the zygote undergoes division and, after secreting about itself a cyst-like membrane, the early embryo drops to the bottom at a stage of development which differs in the various species of hydra. Development now proceeds slowly or rapidly, according to the season, until an outer layer of cells, the ectoderm, and a solid inner mass, the endoderm, are formed. Tentacles then develop and the embryo breaks from its cyst, elongates, becomes attached at one end, develops within the endoderm a cleft which forms the enteron, forms a mouth at the free end, and so becomes a young hydra. When the zygotes are formed in late fall, the developing individual passes the winter in the egg shell at the bottom.

The life cycle of hydra, therefore, is as follows: Two germ cells, or gametes, unite to form a single cell, the zygote, which by cell division and differentiation becomes the adult animal with its many-celled organization. From this adult, masses of cells may be detached to form new individuals by budding; or single cells, the germ cells or gametes, may unite in fertilization for the production of a new individual after the manner described. By comparison with the cell cycles previously described (Fig. 110, p. 215), it will be seen that, save for the budding, such a cycle is typical of all metazoa. The general comparison between cell cycles in protozoa and metazoa will be recalled in this connection.

Regeneration. — Related to the process of budding is the phenomenon known as regeneration, or the formation of new indi-

viduals from parts of an original one. If the hydra is cut in two transversely, a new basal portion is formed on the part having tentacles and new tentacles on the basal piece. In a few days two complete hydras are formed which gradually assume normal proportions. These changes may occur even when the hydra is cut into several pieces.

Other Cœlenterata

Classification. — The Phylum *Cœlenterata* is divided into four classes: the *Hydrozoa*, which includes the hydra, the forms known as "hydroids," and related jellyfishes; the *Scyphozoa*, types of jellyfishes that are usually larger and otherwise differ from the hydroid jellyfishes; the *Actinozoa*, including the sea anemones and true corals; and the *Ctenophora* or sea walnuts, forms which have long been classed as cœlenterates but are regarded by some taxonomists as belonging to a separate phylum. As the life cycle of hydroids presents an unusual mode of development, it will be considered at length, and other representatives of the Cœlenterata more briefly.

The Hydrozoa. — *Hydroid Colonies.* — With the exception of hydra and a few other genera, none of which are widely distributed, the Cœlenterata are marine animals. The Class *Hydrozoa* includes the *hydras*, the *hydroids* which are hydra-like in appearance, and the *hydro-medusæ* or jellyfish that are related to the hydroids. It is characteristic of most hydroids to form colonies, which often contain thousands of individuals, or *polyps* as they are sometimes called, connected as would be the buds of a hydra, if the latter were to re-bud many times without the individuals becoming detached. Thus, in the genus *Obelia* (Fig. 133), the units of the colony resemble many individual hydras all connected. The individuals have a greater number of tentacles than the hydra and there is a sheath-like skeleton or perisarc. The shape of the hypostome differs, and there are certain other minor differences between the two forms. Yet each polyp resembles a hydra in the fundamental organization of the body into ectoderm and endoderm surrounding a gut cavity, in the radial symmetry, and in the absence of an anal opening. Moreover, the colony arises from a single hydra-like polyp by budding and *division of labor* among the individuals thus formed (Fig. 133 B).

Organization of an Obelia Colony. — Obelia is representative in this particular. The colony consists of three types of individuals: (1) *hydranths*, or feeding individuals (Fig. 133 A), (2) *blas-*

FIG. 133.—Alternation of generations in a hydroid such as Obelia.

A, portion of an Obelia colony. B, development of colony following attachment of planula (Pl. 2).

a, zygote; b, two-cell stage; bl, blastostyle; bla, blastula; c, four-cell stage; h, hydranth; h.b., hydranth bud; m, medusa; m.b., medusa bud; o, ovum; Pl. 1 and Pl. 2, planula, or ciliated larvæ with ectoderm and endoderm (cf. Fig. 132 D).

lostyles, or non-feeding individuals that produce *medusa buds* which are set free as (3) the *medusæ* or jellyfish. As shown by Fig. 133, the hydroid colony arises from a single polyp which buds and re-buds until hundreds or even thousands of individuals are formed. These individuals are attached to the vertical stalks that arise from the *hydrorhiza* or root-like extensions of the mass along the substratum to which it is attached. In this way *Obelia* colonies often cover the surfaces of submerged woodwork, such as float-stages or the spiles under wharves, and may be collected in masses by removing thin slices of wood from such a surface.

As the colony approaches maturity, the blastostyles make their appearance, and, on their sides, the medusa buds. The process of forming all these structures, hydranths, blastostyles, and medusa buds, is essentially like that of bud-formation in hydra. The ectoderm and the endoderm grow out, carrying with them an extension of the enteron. In the blastostyle no mouth or tentacles are formed. Hydranths and blastostyles never separate from the parent colony, but medusa buds do become detached in a manner that may be compared with what happens to the buds of a hydra. Thus, for purposes of comparison, one may say that *Obelia* is like a colony of hydras formed by budding and by a corresponding division of labor among the units of the colony, such that three types occur: feeding individuals, or hydranths; mouthless individuals, the blastostyles; and sexual individuals, the medusæ, which are set free to swim away and produce male and female germ cells by which sexual reproduction is effected. The production of the colony with these three types of individuals is obviously comparable with the asexual reproduction in hydra. The medusa, with its reproductive organs, is like a hydra bud set free as a swimming individual, and producing either ova or spermatozoa, since the sexes are separate in the medusæ of *Obelia*. The structure of the medusa is complex (Fig. 127), but its adult structure, as well as its bud-like manner of origin, is homologous with that found in the other units of the colony. It is like a polyp modified for free-swimming life and for its special reproductive functions. It is instructive, after mastering the structure of the medusa, to consider the features of the jellyfish that are related to its free life, in comparison with the simpler organization of its sister units of the colony, the hydranths.

Alternation of Generations in Obelia. — We are now in a position to consider the unusual type of life cycle that is represented by such a hydroid as *Obelia*. The colony with its three types of individuals arises from a single parent polyp by the asexual process of budding. The medusæ, which arise as buds detached from the colony, are individuals, specialized for swimming, which upon reaching maturity develop either testes or ovaries. The ova and spermatozoa are shed into the water where they meet in fertilization. After producing its crop of medusæ, the colony dies; and after producing its ova or spermatozoa, the medusa dies. Thus one may say that there are two generations which alternate: the hydroid generation, reproducing asexually; and the medusa generation, reproducing sexually. To such life cycles in animals, the term *alternation of generations*, or metagenesis, has been applied.

Not all hydroid polyps and hydro-medusæ exhibit such a cycle. There are polyps like the hydra, with no medusa stage and no real colony formation; and medusæ, like *Gonionemus*, in which there is no well-developed hydroid colony. In some medusæ, as, for example, *Liriope*, the fertilized egg develops so directly that if the species were taken by itself one would never suspect the existence of an elaborate colonial stage in some of its near relatives. There are also hydroids such as *Clava* which, like hydra, have merely reproductive organs and produce no medusæ. To appreciate the many interesting comparisons that can be made, it is necessary to make a more extended study than is possible here. One can, however, get some understanding of the relationships by considering how the life cycle of *Hydra* could be modified to make it like that of *Obelia*; or how the life cycle of a medusa like *Liriope* could be modified to make it like that of *Obelia*.

Other Hydrozoa. — Related to the hydroids and the hydro-medusæ, as jellyfishes like *Gonionemus* are called, are the hydroid corals, or *Hydrocorallinæ*. These have a massive skeleton of carbonate of lime formed by the ectoderm, and thus when dried resemble somewhat the skeletons of the true corals. The extinct forms represented by the fossils called *Graptolites* probably belong to the Hydrozoa. Most interesting of all are the *Siphonophora*, of which the *Physalia*, or "Portuguese man-of-war" (Fig. 134), found floating in the Gulf Stream and occasionally blown upon the coast, is a familiar example. Its structure cannot be con-

sidered in detail, but the general nature of its organization and probable relationships may be indicated. The *Physalia* is a colony of highly specialized individuals having a gas-filled float

FIG. 134.—*Physalia* floating at the surface of the ocean.

cr, crest; *p*, polyp; *pn*, pneumatophore or float. (After Huxley. From Parker and Haswell, "Textbook of Zoology," copyright 1921, by Macmillan & Co., Ltd., reprinted, by permission.)

that supports the whole. The tentacles are laden with nematocysts which sting so powerfully that their effect on the human hand is like the stinging of many wasps. These capture such prey as small fishes and crustaceans, which are drawn up to the feeding polyps that lie nearer the float. There are also medusa-like units of the colony, which, however, are not set free, but produce the reproductive cells. For purposes of comparison, one might say that the siphonophore is like a hydroid colony that has "gone afloat" and become much specialized accordingly.

Scyphozoa, Actinozoa, and Ctenophora. — Most of the hydroid jellyfishes are of small size. *Gonionemus* is larger than the majority, although in a few instances such jellyfishes attain considerable dimensions, as in the case of *Æquorea*, which is some fifteen inches in diameter.

In contrast, the jellyfishes of the type known as *Scyphozoa*, or scypho-medusæ, are mostly forms of large size. In an extreme case, that of the *Cyanea arctica* of the New England Coast, there are records of individuals twelve feet in diameter and with tentacles one hundred feet in length. However, the amount of solid material in such an individual would be very small, since jellyfishes have been shown to be composed of as much as ninety-nine per cent water. The genera *Dactylometra* and *Aurelia* are also represented upon the Atlantic Coast. In

typical instances, the life cycle of a scyphozoan consists of an alternation of generations with an attached generation from which the free-swimming jellyfish arises by budding that is transverse to the long axis of the body. By this means saucer-like individuals are produced, become detached, and grow into adult jellyfishes.

FIG. 135.—Two divergent types among Cœlenterata.

Left, a sea-walnut, *Hormiphora plumosa*, a representative of the Class *Ctenophora*, illustrating one of the types of delicate-bodied, free-swimming cœlenterates. *c*, comb or swimming plate, a row of very large cilia; *m*, mouth; *s*, sense organ; *t*, tentacle. (After Chun.)

Right, the sea anemone, *Metridium dianthus*, a representative of the Class *Actinozoa*, illustrating a heavy-bodied, attached type of cœlenterate. (Photo. of Jewell Model, by courtesy of the General Biological Supply House, Chicago, Ill.)

The *Actinozoa* are represented by the familiar sea anemone, *Metridium dianthus* (Fig. 135), of the New England Coast, and by the true corals (Fig. 136) which abound in tropical seas. The latter are like small sea anemones to which a skeleton of carbonate of lime has been added and which have budded to form colonies containing innumerable individuals. The part that has been played by corals in the formation of coral islands and the coral limestone of various geologic formations has given these cœlenterates an important rôle in the history of some portions of our planet.

FIG. 136.—Coral polyps and a coral reef.

Above, a colony of *Astrangia danae*, the only species found as far north on our eastern coast as Cape Cod. The polyps arise from a skeleton of carbonate of lime similar to that seen in dried specimens of corals. The tentacles and radially symmetrical body are characteristic features of these coelenterates as in hydra.

Below, the Great Barrier Reef of Australia, showing prolific coral growths exposed at low tide. In the middle distance may be seen the lagoon separating the Barrier Reef from the distant shore. This great reef extends for more than 1200 miles along the Australian coast. (After Saville-Kent. Photos. by courtesy of the American Museum of Natural History)

The *Ctenophora*, or sea-walnuts (Fig. 135), are so specialized a type that their structure must be described at length to be understood. It will be recalled that they are sometimes classified as a separate phylum of the Animal Kingdom instead of a class within the Phylum *Cœlenterata* (cf. p. 237). In typical cases they swim by means of eight rows of swimming plates formed by modifications of cilia. They are far less common than the jellyfishes, but abound in some regions, including the Mediterranean Sea. *Mnemiopsis leidyi* and *Pleurobrachia pileus* of the Atlantic Coast are the forms most familiar to American students.

The Cœlenterate Plan of Body. — The body plan that occurs in cœlenterates is important for comparison with that existing in other phyla. Like hydra, the schematic cœlenterate is sac-like, with the walls composed of two cell layers, the *ectoderm* and the *endoderm*, and with a *mouth*, which combines the functions of mouth and anus in higher animals. The central cavity, or *enteron*, is comparable with the digestive tract in animals like the frog and the earthworm. If comparisons can be made between the cell layers, the ectoderm is comparable with the epidermal layer of the skin, and the endoderm with the mucous membrane of the digestive tract. Thus, the greater bulk of the body, derived from what is called *mesoderm* in an animal like a vertebrate, is not represented in the Cœlenterata, which are *diploblastic*, or two-layered, animals, in contrast with animals that are called *triploblastic* or three-layered, because they have ectoderm, mesoderm, and endoderm. The *gastrula stage*, which occurs in the development of many triploblastic animals, has been compared with the cœlenterate plan of body (cf. p. 242).

CHAPTER 12

THE EARTHWORM AND OTHER ANNULATA

In the preceding chapters we have studied the structure and functions of a familiar vertebrate animal, of the single-celled organisms, and of one of the simpler types of many-celled animals. The general biological problems that are most suitably illustrated by these forms have also been examined. In the work beginning with the present chapter, we shall extend this method to other representative types among invertebrate animals. The phenomena of metabolism, irritability, and reproduction will be further examined, but particular attention will be given to the structures and functions of various animals as representatives of their respective phyla, and to some of the general biological problems that each type naturally suggests. The earthworm, the crayfish, and various insects will be studied in detail; and other representatives of the phyla concerned will be described for purposes of comparison. Thus we shall complete a broad survey of the animal world before proceeding to the concluding chapters, which deal with certain problems of a more general nature, although two important phyla, the Mollusca and the Echinodermata cannot receive special consideration.

The division of the phyla of the Animal Kingdom into *Enterocæla*, or forms with no internal cavity other than the enteron, and *Cœlomocæla*, or those that have a *cœlome* in addition to an *enteron*, will be recalled (*cf.* Fig. 117, p. 240). In the Annulata, or segmented worms, which are the subject of the present chapter, the *cœlome* is highly developed and the body is divided into segments, the *somites*, or *metameres*. The same type of organization exists in modified form among the Arthropoda and Chordata. The Annulata constitute an important group from the structural standpoint, because they exhibit the simplest and most extensive development of these important features of organization.

The Earthworm

Occurrence and Distribution. — The common earthworm, *Lumbricus terrestris*, is selected as representative of the Annulata because it is a familiar animal and because it illustrates in a satisfactory manner the biological principles of structure and function which it is desired to present in connection with this phylum. It is, however, a more specialized type of annulate worm than some of its relatives that inhabit the ocean. Earthworms of various genera and species are found in most parts of the world, even on isolated oceanic islands, wherever the ground is sufficiently moist and where the temperature is not too low. In localities where they are abundant, the distribution is determined by the nature of the soil and its moisture. Heavy clay soils and thin soils in which the underlying rock is near the surface are not favorable, while rich loamy and sandy soils are the most advantageous.

External Features. — Before describing the burrowing and other general activities of the earthworm, it is desirable to review the more important external features (Fig. 137 A). The elongated cylindrical body is bluntly pointed anteriorly and somewhat compressed dorso-ventrally in its posterior region. The *mouth* is at the anterior end, surrounded by the first segment, or *peristomium*, and just ventral to a small protuberance, the *prostomium*. The *anus* is a vertical slit at the posterior extremity, in the terminal or *anal segment*. Dorsal and ventral surfaces may be recognized by the difference in color, the dorsal being darker as in most animals, and also by a slight flattening of the ventral region which appears throughout the greater portion of the length (cf. Fig. 140). The body is conspicuously marked off into a series of segments, or *metameres*, of which there are about one hundred and seventy-five in a full-grown specimen of *Lumbricus terrestris*. There is a swollen area, the *clitellum*, which, at the time of egg laying, secretes the egg capsules in which the young develop, and which is usually located in the region between segments twenty-nine and forty-one. Other special skin glands appear as lighter areas on certain of the anterior segments. The openings of the *vasa deferentia*, or male genital ducts, are found on the fifteenth segment as apertures surrounded by conspicuous lips. The openings of the *oviducts* are much smaller and located on the fourteenth segment. Between segments nine and ten and

FIG. 137.—Structure of the earthworm.

A, ventral view of anterior and posterior ends. B, diagram showing a seta and muscles by which it is directed anteriorly and posteriorly, and protruded (*cf.* retractor muscle of setae shown as *s.m.* in Fig. 140). C, internal organs in anterior portion of body as dissected from dorsal side. The nephridia are not shown (*cf.* Fig. 143, D). D, schematic longitudinal section showing body wall, digestive tract, coelome, and septa.

an, anus; *br*, brain; *c*, clitellum; *c.g.*, calciferous glands; *cr*, crop; *d.b.v.*, dorsal blood vessel; *e*, esophagus; *g*, gizzard; *h*, heart; *m*, mouth; *mu*, muscle fiber; *n.c.*, ventral nerve cord; *od*, opening of oviduct; *ph*, pharynx; *ps*, prostomium; *r.m.*, radial muscles of pharynx; *s*, septum; *se*, seta; *s.g.*, seminal groove; *s.i.*, stomach-intestine; *sn.v.*, subneural blood vessel; *s.r.*, seminal receptacles; *s.v.1*, *s.v.2*, *s.v.3*, seminal vesicles; *v.b.v.*, ventral blood vessel; *v.d.*, vas deferens; *w*, body wall. (From Sedgwick and Wilson "General Biology," copyright, 1914, by Henry Holt and Co., reprinted by permission.)

ten and eleven, on the ventral side, are the openings of two pairs of *seminal receptacles* in which the spermatozoa are stored after being received from another worm during sexual union. Paired *nephridiopores* open ventro-laterally from the nephridia or excretory organs, located in each segment except a few at the anterior end. There are no organs of locomotion such as the legs of many animals, since the worm moves by peristaltic extensions and contractions of its body. There are, however, on each segment four pairs of minute spine-like *setæ*, which function in locomotion by being extended at the proper angle to give the maximum hold upon a surface according to the direction of movement (Fig. 137 B).

General Activities. — The earthworm burrows in the earth and is found from a few inches to several feet beneath the surface. The burrows usually run straight down for several inches and then wind about irregularly, sometimes reaching a depth of seven or eight feet in soils of the right consistency. In winter the animals are always found below the frost line and are relatively inactive. Sometimes there is an enlargement at the lower end of the burrow in which several worms may be found coiled up in knots during this period of hibernation or winter rest. In loose soil the worms burrow down by forcing the pointed anterior end between the particles of earth, as may be seen when they are thrown upon the surface in the spading of a garden. In soil that is of normal consistency, however, they excavate the burrow by literally eating their way through the soil. The earth passes into the mouth and through the digestive tract, and is deposited on the surface of the ground as the faeces, or *castings*, which are always in evidence in places where earthworms abound. This toilsome method of excavation is not so wasteful as it might seem, because the soils that are most suitable for these animals contain a considerable amount of organic matter, which can be used as food, in addition to what is secured at the surface of the ground. In this manner earthworms bring about important changes in the soil wherever they are abundant.

In his book entitled "*Vegetable Mould and Earthworms*," Darwin showed how these animals, by constantly bringing to the surface the lower layers of the soil and thus tending to bury objects upon the surface, produce the same general effect as that accomplished by man in cultivating a field by turning the

soil with a plow. Objects like stones or a layer of gravel gradually sink below the surface, as soil is brought up from beneath and deposited above them, until they rest near the lower level of the worms' activities. Darwin showed by observations upon the fields near his home that this sinking occurred where layers of

FIG. 138.—Burial of objects by earthworms.

Above, section through a fallen stone of the Druids' "temple" at Stonehenge, England, showing how much it had sunk into the ground (scale $\frac{1}{2}$ inch to 1 foot).

Below, section of part of a Roman ruin at Silchester, England, showing a stone floor upon which was a mass of charred wood, represented in black, and rubbish twenty-seven inches thick, all covered by nine inches of fine soil.

(From Darwin, "Vegetable Mould and Earthworms," copyright, 1892, by D. Appleton and Co., reprinted by permission.)

foreign material had been spread upon the ground. He explained the settlement of great stones and even the burial of pavements and debris of Roman buildings (Fig. 138), that have been excavated in England as due to the worms bringing up soil year after year as they burrowed between and below the stones, until a structure that was originally at the surface came to rest at a lower level. In the localities observed by Darwin, it was found that

the average rate at which a layer of gravel or cinders would thus settle if left undisturbed was something over two inches in ten years. By weighing the castings brought up over a limited area in a given period, he further estimated that in ten years the bulk of such material deposited on the surface would make a layer one and one-half inches deep. The difference between the two estimates he accounted for by the fact that not all the castings could be collected and by the very conservative way in which the second set of observations were made. A uniform layer of fine soil one and one-half inches in diameter is equivalent, according to these calculations, to one hundred and fifty tons of earth to the acre in the ten-year period under consideration. Moreover, such soil is deposited at the surface in a finely pulverized condition and impregnated to some extent with waste products of the worms' metabolic activities. The bulk of such material seems not unreasonable, since it was conservatively estimated that there were some 26,886 worms to the acre in the fields that were being examined. In a garden plot, where it was estimated there might be 53,767 worms to the acre, the effects would be proportionately greater.

Darwin's mental attitude in accumulating facts and in reflecting upon their significance is nowhere better illustrated than in this little volume on earthworms, which was based upon observations extending over almost forty years. Other organisms that burrow in the soil, like the ants and various insects, have similar effects, and there are causes of a physical nature involved in the production of the fine surface layers of the soil; but the rôle of earthworms in the localities where they abound cannot be questioned.

Earthworms are nocturnal in their activities above ground, although they sometimes come to the surface in daylight following a shower. During the daytime they lie in the vertical part of the burrow near the surface, unless engaged in excavating at a greater depth. Often the mouth of the burrow is plugged with bits of grass or other materials that have been drawn in at the close of the night's activities. With the approach of darkness this plug is pushed aside and the worm extends its body preparatory to the nocturnal foraging. With the posterior end of the body retaining its place within the burrow, the animal now explores the surface in all directions. If disturbed, it can by a sudden contraction dash "like a rabbit into its burrow," as Darwin said, and thus

find a safe retreat. When the upper levels of the soil are moist and the worms can work at the surface night after night, they secure most of their food in this manner. In times of drought they avoid the surface and must depend upon such nutrient material as may be extracted from the soil that passes through the digestive tract as a result of their mining operations at the lower levels. Leaves, bits of grass, and other vegetable material are laid hold of by the mouth, which acts as a sucker, and dragged toward the burrow or devoured little by little. A small portion of a leaf, for example, is smeared with the saliva-like fluid secreted by the mouth, and after being thus softened is "nibbled" away by the sucking action of the lips. In this manner small bits of material are conveyed into the digestive tract. While most of its food consists of vegetation, the earthworm feeds also upon animal matter. In nature the bodies of insects and other small animals that have died at the surface attract earthworms, while in the laboratory bits of fresh meat, and even salt pork and bacon are attacked greedily.

Under favorable conditions, when the worms are coming to the surface nightly for weeks at a time, the burrow is relatively permanent and its uppermost portion may be strengthened by a lining of minute pebbles and other particles, much as the walls of an old-fashioned well are lined with stones. In times of abundant moisture or when the ground is suddenly flooded by a heavy rain, the worms may leave their burrows and be found free in great numbers on the surface, as is sometimes seen the morning after a shower. This accounts for the popular idea that they "come down in the rain," for they are observed on pavements or roadways where they have strayed in their nocturnal wandering and from which they have not found a retreat with the coming of daylight. The animal's negative responses to light, save in very low intensities as at twilight, and to a dry atmosphere are, therefore, the two most important factors in controlling its activities at the surface. Because of these responses it is nocturnal in its habits and is active at the surface of the ground only in times of normal moisture. The abundance of the worms in the evening after a heavy rain following a dry period may have been observed by the reader.

Internal Organization. — The general body plan of the earthworm is shown in Fig. 137 D. A tubular *body wall* encloses a

cavity, the *cœlome*, through which a smaller tube, the *digestive tract*, extends from end to end of the body. The *cœlome* is divided throughout, except in its most anterior region, by vertical partitions, the *septa*, which extend inward from the body wall to the digestive tract, thus holding the tract in position like so many transverse mesenteries. The *nervous system* consists of a ventral

FIG. 139.—Median sections of anterior end of earthworm.

Above, diagrammatic representation with parts labeled.

Below, the same as shown by a model.

br, brain; *c.g.*, calciferous gland; *cr*, crop; *e*, esophagus; *g*, gizzard; *m*, mouth; *n.c.*, ventral nerve cord; *ph*, pharynx; *s*, seta.

(The upper figure is redrawn with modifications from Marshall and Hurst, "Practical Zoology," copyright, 1895, by John Murray, printed by permission. The lower figure is from a photograph of the Jewell model of the earthworm, by courtesy of the General Biological Supply House, Chicago, Ill.)

nerve cord (Fig. 139) on the inner surface of the body wall and composed of right and left parts which separate anteriorly where they encircle the esophagus, to unite in the pair of cerebral ganglia, or *brain*, which lies dorsally in the third segment. There are *nerves* passing outward from the cord and brain as in higher animals. In each segment, except a few at the extreme anterior end, there is a pair of excretory organs, the *nephridia*, each consisting of a tubule having at one end an opening into the *cœlome*

and at the other a *nephridiopore* or external opening (Fig. 142). The *circulatory system* consists of a rather complex arrangement of vessels, of which the principal ones are the large *dorsal blood vessel* (Fig. 137 C), and the *ventral blood vessel*, lying beneath the intestine; and the five pairs of transverse vessels, called *hearts*, which pass from the dorsal to the ventral vessel in segments seven to eleven. Save in the anterior region, where the digestive tract is specialized into a *pharynx*, *esophagus*, *crop* and *gizzard* and where

FIG. 140.—Transverse section of earthworm in posterior region (cf. Fig. 141).

a.c., cavity of the alimentary canal; c, cuticle; c.m., circular muscles; coe, coelome; c.v., lateral intestinal blood vessel; d.v., dorsal or supra-intestinal blood vessel; hy, hypodermis or epidermis; l.m., longitudinal muscles; n.c., ventral nerve cord; p.e., peritoneal epithelium; s, seta; s.g., setigerous gland; s.i.v., ventral or sub-intestinal blood vessel; s.m., retractor muscle of seta; ty, typhlosole. (From Sedgwick and Wilson, "General Biology," copyright, 1914, by Henry Holt and Co., reprinted by permission.)

the *reproductive organs* are located, the body is relatively simple, since it is composed of a series of somites, or *metameres*, all of which possess a similar structure. With this general body plan in mind, we may now examine the special systems of organs.

Body Wall and Coelome. — The wall of the earthworm's body (Fig. 140) consists of several layers. Externally there is a delicate non-cellular cuticle covering an *epidermis* of low columnar epithelium. Beneath this is a layer of *circular muscle fibers* supported by connective tissue; a thicker layer of *longitudinal muscles*,

arranged in bundles which have a feathery appearance when cut transversely; and an innermost layer of *peritoneum* lining the *cælome*. The *setæ*, which are seen externally, are embedded in the *setigerous sacs*, which arise as invaginations of the epidermis and are lined with modified cells of this layer. The movements of the *setæ* are controlled by special muscles. Attached to the inner ends of each pair of setigerous sacs are muscles (Fig. 137 B) which extend anteriorly and posteriorly, and which cause a protrusion of the *setæ* by their united contraction, or a slanting in either direction, as the figure shows, by contraction on one side only. Attached to the two pairs of *setæ* in the side of each segment (Fig. 140) there is a muscle which by its contraction draws the inner ends of the two pairs closer together and thus retracts the *setæ* from their extended position. By the coördinated action of these muscles the *setæ* of any region of the worm can be retracted, thus avoiding friction as the body is extended along the surface or within the burrow; and then protruded with a slant in the proper direction to catch like minute claws upon the surface as the worm crawls forward or backward. Such a mechanism is well suited for locomotion in a burrow or upon the surface of the ground among grass and other objects, against which not only the ventral but also the lateral *setæ* can find a purchase.

The *cælome*, as has been pointed out in the general description, is divided into a series of compartments by the transverse partitions, or *septa*, which correspond to the external constrictions between the segments, except toward the posterior end of the animal. Where the digestive tract is modified into its special regions in the anterior end of the worm (Fig. 139), the arrangement of the *septa* is less regular. In the region of the pharynx, the *septa* are replaced by muscle fibers which radiate outward to the body wall. There is an opening in the ventral part of the septum above and around the nerve cord, so that the several compartments are not entirely isolated. The *cælotomic fluid*, which occupies all these cavities between the *septa*, contains colorless amœboid cells and might be compared with the lymph in one of the large lymph sinuses in the frog. The *cælome*, as in a vertebrate animal, is lined throughout with a *peritoneum* of squamous epithelial cells, except on the surface of the stomach-intestine where the peritoneum is modified as the *chloragogue cells*, which are columnar. The *septa* consist of two layers of peritoneum which enclose muscle

fibers, connective tissue, and small blood vessels, and which separate at the body wall like the two layers of peritoneum that form the mesenteries of a vertebrate animal (Fig. 19, p. 40).

Digestive System.—The *mouth* leads into a short *buccal* region (Figs. 137 C and 139). This is followed by the *pharynx*, which is the muscular organ concerned in the sucking action of the lips. There are numerous radial muscles extending outward from the walls of the pharynx to the inner surface of the body wall, and within its wall there are well-developed circular muscles. When the mouth is applied to an object the contraction of the radial muscles expands the cavity of the pharynx, so that the lips hold fast, like the edges of a vacuum cup. The circular muscles restore the pharynx again to its original dimensions. The effectiveness of this action may be judged from the way in which the worms can drag relatively large objects, like leaves, toward their burrows and “nibble away” the surfaces that have been softened by the saliva. The *esophagus* is a comparatively slender region of the tract that leads from the pharynx. On the walls of the esophagus, in segments eleven and twelve, are the paired *calciferous glands*, the secretion of which passes into the esophagus in segment eleven. The function of this secretion is somewhat problematical, although it has been supposed that the carbonate of lime neutralizes the free acid, which may be contained in the food, and thus enables the intestinal enzymes to function more effectively. Posterior to the esophagus in segments thirteen, fourteen, and fifteen is the *crop*, which, as its name implies, serves as a place of temporary storage, anterior to the muscular *gizzard*, where the food is reduced to a more finely divided state. The sand grains and minute pebbles that are swallowed with the food seem to be used in the gizzard as in the part of the digestive tract which is given the same name in birds. After being thus reduced to a finer condition and thoroughly mixed, the food passes through the valve-like aperture at the posterior end of the gizzard into the *stomach-intestine*, which is a thin-walled tube that is capable of much dilation between the septa when distended with food. A longitudinal fold, the *typhlosole*, which protrudes from its dorsal wall (Fig. 141) and which increases the surface area available for digestion and absorption, may be compared with the foldings observed in the mucous membrane of the stomach and intestine of a vertebrate animal (cf. Fig. 83, p. 150). The fæces of the earthworm consist

largely of undigestible mineral matter from the soil consumed in the excavation of the burrow. They are deposited on the surface of the ground as the castings, to which reference has been made in the account of the action of the worms upon the soil.

Circulatory System. — The circulatory system of the earthworm is more highly developed than might be expected in an animal whose general organization is not elaborate (Fig. 137 C and 141).

FIG. 141.—Transverse section of earthworm in posterior region, showing blood vessels and other features not shown in Fig. 140.

a, setæ; *b*, mucous membrane of intestine; *c.l.*, ventral nerve cord; *cm*, commissural blood vessel; *ea*, afferent intestinal blood vessel; *ep*, epidermis or hypodermis; *ex*, blood vessels of nephridium; *il*, lateral intestinal blood vessel; *i.s.*, supra-intestinal (dorsal) blood vessel; *m.c.*, circular muscle layer; *m.l.*, longitudinal muscle layer; *m.s.*, septum; *n.a.*, circum-neural opening in septum; *n.ig.*, interganglionic nerve; *n.l.*, lateral neural blood vessel; *n.s.*, sub-intestinal or ventral blood vessel; *n.s'*, sub-neural blood vessel; *r.m.*, retractor muscle of setæ; *s*, seta; *sg*, nephridium; *gs.e.*, nephridiopore or external aperture of nephridium; *t.c.*, chloragogue tissue; *tp*, typhlosole. (From Howes, "Atlas of Zootomy," copyright, 1902, by Macmillan and Co., Ltd., reprinted by permission.)

The blood is bright red from the presence of *hemoglobin*, contained in the plasma, and not in corpuscles as in vertebrate animals. The principal blood vessels are the *dorsal* and *ventral vessels* lying along the digestive tract, the *sub-neural* below the nerve cord, and two *lateral neurals*. These longitudinal trunks are connected by a complex arrangement of lateral vessels after the manner shown. There is no true heart, since the larger vessels contract by peristaltic waves, which, together with the valves

located at certain points, cause the blood to flow in appropriate circuits. There are, however, five pairs of so-called *hearts*, consisting of specially developed contractile vessels in segments seven to eleven inclusive, and running dorso-ventrally. By

FIG. 142.—Nephridium of earthworm.

Above, diagram of an entire nephridium, drawn with coils somewhat separated. Below (left), portion of nephridium showing blood supply; and (right) the nephridial funnel or nephrostome by which the nephridium communicates with the coelome.

bl, bladder-like muscular portion; *b.v.*, blood vessel; *c.t.*, connective tissue surrounding tubules; *d.l.*, dorsal lip; *e.p.*, peritoneal epithelium; *f*, funnel or nephrostome; *l*, lumen; *n*, nephridium; *n.p.*, nephridiopore or external opening of nephridium; *s*, septum; *t*, tubule; *v.l.*, ventral lip. (Redrawn with modifications from Howes, "Atlas of Zootomy," copyright, 1902, by Macmillan and Co., Ltd., printed by permission.)

means of this system the blood circulates through the larger vessels and the capillaries throughout the body. The terms "arteries" and "veins" are hardly applicable, because there is no specialization of blood vessels leading to and from a central heart.

Excretory System.—The excretory organs of the earthworm consist of paired tubules, called *nephridia* (Figs. 142 and 143 D), and located in every segment of the body with the exception of the most anterior region. At one end, each nephridial tubule opens from the coelome by a funnel-like *nephrostome*. At the other, it opens on the surface of the body by a *nephridiopore*. The nephrostome is a ciliated structure with lip-like edges. It projects anteriorly from the face of the septum on either side, in the ventral region near the nerve cord. From this point the nephridium extends posteriorly through the septum to the next compartment of the coelome, where it is folded upon itself in the parallel loops that compose the principal bulk of the organ. The terminal portion is enlarged as a bladder-like structure. The loops of the tubule, as thus formed, are held in place by connective tissue attached to the posterior surface of the septum, and the whole is covered with peritoneum. The tubule is ciliated for a short distance back of the nephrostome and again in one of the loops. Except for the terminal enlargement, the nephridial tubule is an intracellular duct. The terminal enlargement is lined with a non-stratified squamous epithelium, outside of which are muscle fibers. Each nephridium is well supplied with blood vessels, so that the relationship of the nephridium and the blood system resembles that of a single kidney tubule and its capillaries in a vertebrate animal (cf. Fig. 31, p. 53).

Reproductive System.—The earthworm is hermaphroditic, each individual containing a complete set of male and female reproductive organs. The female system (Fig. 143 D) consists of a pair of *ovaries* attached to the posterior face of the septum between segments twelve and thirteen and projecting backward into segment thirteen. Upon microscopic examination, the ovary (Fig. 143 A) is seen to contain at its posterior end ripe *ova*, which will soon be detached and passed into the *oviduct*; while anteriorly it contains eggs that are in earlier stages. Immediately behind the posterior end of each ovary is the oviduct, which is a short tube with a ciliated funnel opening from segment thirteen and thence leading through the septum to segment fourteen, where it passes diagonally outward to its external opening. A pocket-like outgrowth on each oviduct just posterior to the septum, functions as a receptacle in which the ova that have been detached from the ovary may be temporarily stored. The *seminal recep-*

tacles, in segments nine and ten, may be regarded as a part of the female system, since they receive the spermatozoa that

FIG. 143.—Reproductive organs of earthworm.

A, an ovary with ova in various stages of growth. B, a single ovum, on a slightly larger scale than the ovum shown in A, about ready for detachment from ovary. C, an egg capsule (*cf.* Fig. 147 C). D, dorsal view of reproductive system with seminal vesicles of right side dissected to show testes and sperm funnels. E, multinucleated cell that is detached from the testis and develops into spermatozoa within the seminal vesicles. F and G, development of spermatozoa, showing the spermatids, on the surface of a central mass of cytoplasm from the original multinucleated cell (E). H, two spermatids in a later stage as they appear attached to the surface of this spherical mass of cytoplasm.

bl, muscular bladder-like portion of nephridium; f, funnel or nephrostome of nephridium; n.c., ventral nerve cord; ne, nephridium; od, oviduct; ov, ovary; r.o., receptacle of oviduct; s.f., sperm funnel; s.r.1. and s.r.2, seminal receptacles; s.v.1, s.v.2, and s.v.3, seminal vesicles; t, testis; v.d., vas deferens; v.e., vas efferens.

are obtained from another worm during sexual union and used in the fertilization of the ova at the time of egg laying.

The male system (Fig. 143 D) consists of two pairs of *testes* located in segments ten and eleven, in which they are attached to the septa in the same relative position as the ovaries in segment thirteen. Posterior to each testis, in a position comparable with that of the funnels of the oviducts, are the *sperm funnels* at the inner ends of the male ducts. These are openings of relatively large size, having crumpled walls as though one took a funnel of filter paper and pleated its edges into many folds. From each funnel a single *vas efferens* leads diagonally outward to the *vas deferens*, which opens externally on the fifteenth segment. The arrangement of the testes and their ducts, therefore, somewhat resembles that of the ovaries and oviducts. The male system is further complicated by the development of large *seminal vesicles* in which the spermatozoa that have been detached from the testes in an immature condition complete their development. These seminal vesicles originate as three pairs of lobular bodies attached to the three septa between segments nine to twelve. As they increase in size the two anterior pairs become united in such a manner that the region of the coelome immediately surrounding the anterior pair of testes and their funnels becomes enclosed as a cavity which is extended outward into the lobes of these seminal vesicles. A similar relationship to the posterior pair of testes and their sperm funnels develops with respect to the third pair of seminal vesicles. Hence, when the immature spermatozoa become detached from the testes, they are not free in the coelome, but are confined to the cavities within the seminal vesicles. Instead of passing immediately into the funnels, they pass into these cavities of the vesicles, where they complete their development before entering the funnels (Fig. 143 E to H).

Nervous System.—The *brain* of the earthworm consists of a pair of cerebral ganglia that are fused together and located on the dorsal side of the pharynx in the third segment (Fig. 137 C). From these ganglia, the *circum-pharyngeal connectives* extend around the pharynx and unite to form the *ventral cord*, which extends to the posterior end of the body. The *nerves* arise in pairs from this central system (Fig. 143 D). There is some complexity in the region of the cerebral ganglia and circum-pharyngeal connectives, from which the sensitive anterior region of the body is innervated, but throughout the ventral region there are uniformly three pairs of nerves to each segment. Hence, the nervous system of each

segment is like that of every other. Upon first examination, the ventral cord seems to be a single structure with right and left sides like the spinal cord of a vertebrate animal. More careful study shows, however, that it is really double, since it is formed by the fusion of right and left cords on the median line. In some other members of the phylum these cords are separated, so that the ventral cord presents a ladder-like arrangement. As in other invertebrate animals, the term *ganglion* is applied to a region having a special collection of nerve cells, while *connectives* are parts that unite regions that are consecutive longitudinally, and *commissures* are the unions between symmetrical parts of the two

FIG. 144.—Ventral nerve cord of earthworm showing neurones of reflex arc.

ep., epidermis or surface epithelium; *g.c.2*, adjustor neurone; *g.c.2*, motor or efferent neurone; *m.c.*, muscle cell (effector); *s.c.*, sensory cell (receptor).

sides. The commissures are represented in the earthworm by the fusions that have occurred, but sections of the ventral cord show the right and left divisions. Anteriorly, the double condition becomes evident in the separation of the two sides to form the circum-pharyngeal connectives and the two cerebral ganglia.

To understand the functions of the nervous system, it is necessary to examine its cellular organization. In each segment, the ventral cord contains numerous nerve cells, the neurones, located principally in the ganglia (Fig. 144). In the epithelium of the body surface there are sense-organs consisting of groups

of *sensory cells* (Fig. 145) the inner ends of which extend as *axons* which enter the cord by way of the nerves. Following the terminology used in describing the nervous system of hydra (*cf.* p. 269), these sensory cells are the *receptors*. Within the ventral cord the end processes of the axons have contacts, or synapses, with processes of the neurones of the ganglion. Certain of these neurones, the *adjustors*, have their processes confined to the nerve cord, and are not represented in a nervous system like that of hydra (*cf.* p. 317). Others of the nerve cells, the *motor* or *efferent* neurones, have axons that pass out from the cord to the muscles. Comparisons should be made with the two similar types of cells found in the spinal cord of a vertebrate animal (Fig. 61, p. 109). The mechanism of response to stimulation within a single segment will now be apparent. The stimulus is received by the sensory cell, or receptor, and a nervous impulse is transmitted along its axon, either to adjustor neurones or directly to the efferent or motor neurones which have axons leading to the muscle cells which are *effectors* as in hydra. In this manner a stimulus applied to sensory cells brings about muscular contraction. As in the vertebrate, coördination is due to the many interconnections between the nerve cells of the central system. The coördination between segments may be effected by extensions of the sensory axons somewhat beyond the limits of the segment, but it seems to be principally effected by the extension from segment to segment of the processes of adjustor neurones. However, the longitudinal extent of this inter-segmental coördination is not so great as might be supposed, since many of the worm's responses give evidence of spreading from one segment to the next even when they seem to be transmitted with comparative rapidity from one end of the body to the other. Comparisons between the earthworm's nervous system and that of other animals are made in Chapter 13.

Microscopic Organization.—The cellular structure of the various organs has been described in the preceding paragraphs only so far as was necessary in explaining the general structure and functions of the several systems. We may now examine the microscopic organization of the earthworm as an illustration of the Cell Doctrine and as an introduction to a study of the physiological processes. In a transverse section of the intestinal region (*cf.* Figs. 140, 141, and 145), the *cuticle* is seen as a delicate non-

cellular covering of the outer surface, perforated for the openings of gland cells, nephridia, sense-organs, setæ, and dorsal pores, so that the number and location of these structures can be determined from surface views when the cuticle is stripped from the body. The *epidermis* is a layer of columnar epithelial cells, among which are *gland cells* that secrete the mucus which normally covers the body. *Sense-organs* appear as groups of modified epithelial cells, the inner ends of which are prolonged as the sensory axons that enter the ventral nerve cord (cf. Fig. 144). The *circular muscle layer*, by which the elongation of the worm's body is produced, lies immediately beneath the epidermis. The cells of this layer are simple non-striated muscle cells, among which there are capillaries of the circulatory system and connective tissue. The *longitudinal muscle layer* has a feathery appearance in cross section, because the non-striated fibers are somewhat flattened and attached on either side of sheets of connective tissue that divide the layer longitudinally. Lining the cœlome is the *peritoneum*, which is a layer of simple squamous epithelium. Within the *cœlome* are found the *nephridia* with their cellular organization and covering of peritoneum (cf. p. 296). The *cœlomic fluid*, which completely fills the body cavity and contains numerous amœboid corpuseles, may be compared with the lymph in the larger spaces found in the bodies of higher animals.

The intestine is covered externally with a layer of modified peritoneal cells, which are known as the *chloragogue cells* and which have been supposed to possess functions resembling in part those of liver cells in vertebrate animals. They are columnar and expanded at their outer ends. The center of the typhlosole is occupied by a mass of these chloragogue cells. Beneath this outermost layer of the intestine is a *connective tissue layer* containing longitudinal and transverse *muscle fibers*. This layer has a rich supply of capillaries at the bases of the elongated columnar epithelial cells that compose the innermost layer, or *mucous membrane*, the inner surface of which is covered by a delicate *cuticle*.

The structure of the larger blood vessels is such that a wall of contractile and connective tissue cells encloses the blood plasma containing the hæmoglobin and numerous blood cells or corpuscles. The ventral nerve cord (cf. Fig. 144), when seen in such a section, shows *nerve cells* and their processes. Dorsally there

are the three so-called *giant fibers*, the function of which is problematical. The entire cord is surrounded by a connective tissue sheath in which are included muscle fibers and the *sub-neural* and *lateral neural* blood vessels, which extend throughout the length of the body. The earthworm's body, therefore, consists of cells and cell products, as do the bodies of other animals. Epithelial, muscular, sustentative, and nervous tissues, with their various types of cells, are represented, although the modifications of these principal types are less diversified than in the bodies of higher animals. Likewise, the varied functions of the body are cell functions.

Metabolic Processes. — In the earthworm, the processes by which the nutrients are digested, absorbed, and conveyed to the cells of the body, and the excretions eliminated, resemble the corresponding processes in the frog, since there exists in each of these animals a circulatory system, in which the blood is everywhere confined to definite channels. Within the tissues of the earthworm there are likewise intercellular lymph spaces resembling those of vertebrate animals. While the arrangement of the blood vessels and the nature of the blood differ markedly in vertebrates and annulates, the fundamental relationships are alike: nutrient material is absorbed from the digestive tract into the blood and thence conveyed to all parts of the body, where the assimilation and dissimilation occur within the cells, the result being that the waste products of metabolism are returned to the blood, which conveys these substances to the excretory organs.

Irritability and Behavior. — Earthworms respond to various forms of stimulation. If the term "sense" may be applied to animals of such a lowly organization, they have "senses" of touch, taste, smell, and temperature; and, although lacking a sense of hearing like our own, they are extremely sensitive to mechanical vibrations in solid objects with which they may be in contact. They are also sensitive to light, as shown by their retreat into their burrows when a light is suddenly turned upon them, and by their nocturnal habits. In the volume on "Vegetable Mould and Earthworms," to which reference has already been made, Darwin described their responses to various forms of stimulation as observed in confinement and in nature. Despite the limitations of any study of animal behavior published so many years ago, the painstaking observations made by this great natural-

ist may still be used as an introduction to the behavior of the earthworm from the standpoint of the animal's activities under natural conditions.

Regarding the sense of *touch*, the whole body is very sensitive to mechanical contacts, as one may see by touching the animal at different places. Even a slight puff of air from the mouth may cause an instant withdrawal into the burrow. In general, the anterior region is the most sensitive, then the posterior, and the middle of the body least of all, as might be suspected from the

FIG. 145.

FIG. 145.—Epidermis of earthworm, showing the columnar epithelial cells, gland cells, and sensory cells of a sense organ.

b.m., basement membrane; *c*, cuticle; *c.c.*, one of the columnar epithelial cells that form sheath of sense-organs; *g.c.*, gland cell with secretion being exuded from pore in cuticle; *ep.c.*, epithelial cell; *s.c.*, sensory cells (receptors) with outer ends protruding through openings in cuticle and inner ends prolonged as sensory fibers; *s.f.*, sensory fibers or axons arising from sensory cells (*cf.* Fig. 144).

FIG. 146.

FIG. 146.—Light-perceiving cell in epidermis of earthworm.

b.m., basement membrane; *c*, cuticle; *l*, lenslike body in cell; *n*, nucleus; *o.n.*, nerve fiber from base of cell (*cf.* Fig. 145, *s.f.*); *r*, retinella or retina-like structure surrounding lens; *s*, sub-epidermal plexus of nerve fibrils. (After Hess, *Jour. of Morph. and Physiol.*, Vol. 41)

uses of these parts and their supply of sense-organs (Fig. 145). The *prostomium* appears to be the most sensitive portion of the animal. For example, when the worms first come out of their burrows in the evening they make exploratory movements in all directions, using the anterior end, and particularly the prostomium, as an organ of touch. In a similar manner, leaves and other objects that are used as food may be subjected to a preliminary examination by the prostomium.

Something that may be described as a sense of *taste* exists, since

there is some choice of food. Cabbage leaves and onion, for example, will be selected from among other bits of food. The location of this sense has not been determined experimentally, but it is probable that it is restricted to the mouth region. What could be called *smell* was evidenced in Darwin's experiments by the fact that the worms found and drew to the surface savory food, such as cabbage and onion, that had been buried under one-fourth of an inch of soil. Since, in vertebrate animals, taste and smell are to be regarded as modifications of a more primitive chemical sense from which both have originated, it is not unlikely that these two senses are closely related, if not identical, in the earthworm.

Darwin also studied the responses of the worms to light under conditions resembling those to which they are subjected in nature. In general, he concluded that, while the worms respond indefinitely to low and diffuse illumination, light does affect them both by its intensity and by its duration. A strong light flashed suddenly upon the anterior end will cause a retreat into the burrow, and light of moderate intensity may cause the worms to withdraw in some instances. What later investigators have called the varying "physiological state" was recognized by Darwin in his observation that when the worms were employed in dragging leaves into their burrows or in eating them, and even during the short intervals while they ceased from their work, "they either did not perceive the light or were regardless of it; and this occurred even when the light was concentrated through a large lens." The response to stimuli that are effective at other times is also inhibited during sexual union. Experiments conducted under the exacting conditions of modern laboratories, show that the worms respond negatively to strong light and positively to light of low intensity. The results are in harmony with their daily habits, since "during the daytime, while the light is of relatively high intensity, these animals retreat into their burrows because of negative phototropism. At night-time, however, they emerge from their burrows, not because of the absence of light, but by reason of their positive phototropism to light of low intensity, for even in the darkest night there is faint light." As with the tactile sensibility, the anterior end is the most sensitive, the posterior end is next, and the middle region of the body least of all.

It might be expected that special sense-organs would exist for the reception of the tactile stimuli, for the chemical stimuli that must act upon the senses of taste and smell, and for stimulation by light. It has been known for many years that sense-organs exist upon the surface of the earthworm's body, particularly at the anterior end, but all of these seemed to be of one sort (Fig. 145). Recently, however, sensory cells that appear to be those responsive to light have been discovered (Fig. 146), and some progress has been made in differentiating the common sense-organs previously mentioned into more than one type. It is, therefore, probable that the worms possess special groups of sensory cells for the senses above mentioned, after the manner of higher animals.

Certain other senses may exist in the absence of special sense-organs that can be recognized as such. For instance, earthworms are sensitive to *temperature*, at least to the extent that they are sluggish at low temperatures, as may be shown by their not coming out of their burrows during a frost, and as demonstrated by laboratory experimentation in which they can be shown to react to optimum temperatures. They also react to *mechanical vibrations*, as may be demonstrated by striking the receptacles in which they are kept for observation, or by stamping upon the ground where they are being collected at night by the dim light of a lantern. Since even the protozoa respond to these and other stimuli in the absence of special sense-organs, it is not necessary to postulate such structures for the earthworm, even though sense-organs adapted for receiving thermal and mechanical stimuli do exist in some of the higher animals.

If the foregoing very general account of the behavior of the earthworm be stated in the terms of laboratory experimentation upon animal behavior, one may say that the worms exhibit responses to gravity, *geotropism*, as shown by their behavior in relation to their burrows; to light, *phototropism*; to temperature, *thermotropism*; to contact, *stereotropism*; to chemicals, *chemotropism*; to moisture, *hydrotropism*. As with other animals, it is in general true that earthworms respond to stimuli such as normally affect them in nature, in a manner that is related to the conditions under which their lives are conducted. In other words, their behavior is *adaptive* to the extent that it fits the necessities of their environment fairly well. If this were not the case, earthworms would soon cease to exist.

Reproduction and Life Cycle. — In the earthworm, as in many hermaphroditic animals, *sexual union* consists in the temporary pairing of two individuals with a mutual exchange of spermatozoa. In *L. terrestris*, at the time of this union two individuals come together with their heads pointing in opposite directions and the ventral surfaces of their bodies in contact (Fig. 147 A), so that segments nine, ten, and eleven of each individual are opposite the

FIG. 147.—Sexual union and egg-laying in earthworm.

A, two worms encased in mucus secreted by skin glands, as they appear during passage of spermatozoa along seminal grooves as shown by arrows. B, transverse section showing encasing mucus and four seminal grooves (*g*) on each individual. C, formation of egg capsule and its passage anteriorly (*a* to *b*) until it is slipped off as the fully formed capsule (cf. Fig. 143 C).

clitellum, segments thirty-one to thirty-seven, of the other; while the ventral elevations about the openings of the vasa deferentia on the fifteenth segment of one worm lie opposite, or perhaps a little anterior to, the twenty-sixth segment of the other individual. The posterior ends of the worms usually retain their holds upon the burrow throughout the entire process. As the adjustment of the individuals to one another becomes more complete, mucus flows copiously from the clitellum and from other skin glands in this anterior region of the body. Also, a depression is formed

beneath the clitellum and opposite the openings of the seminal receptacles of each worm, by an expansion of the ventro-lateral edges of the bodies and a hollowing out of the median ventral regions. The mucus secreted on the surface stiffens and thus the two individuals become enclosed in a common tube extending from segment fifteen to a region posterior to the clitellum. The worms are now ready for the exchange of spermatozoa. In mature specimens there are two parallel lines on either side of the body and extending from the openings of the vasa deferentia to the clitellum (*cf.* Fig. 137 A). These are the superficial indications of muscular differentiations of the body wall which form, during the stages of sexual union that follow, channels for the passage of seminal fluid from one worm to the other, in the following manner. A ridge with a groove on its dorsal and ventral edges is formed on either side of each individual in the way shown by Fig. 147 B. The ventral grooves are mostly hidden by the close apposition of the bodies, but the dorsal ones are exposed (Fig. 147 A). It can be seen that the dorsal grooves extend from the openings of the vasa deferentia of one worm to the cavity beneath the clitellum and opposite the seminal receptacles of the other worm. Since the groove is roofed over by the mucus that encloses the individuals it is actually a closed tube extending from the opening of the vas deferens of one worm to the openings of the seminal receptacles of the other. Small masses of the seminal fluid containing sperm may now be seen, through the transparent mucus, being ejected at regular intervals from the vasa deferentia. As fast as one of these is emitted it is enclosed in a pit-like depression of the groove about the length of a single segment, which then passes posteriorly as a wave-like depression, carrying the mass of sperm slowly backward to the cavity beneath the clitellum. These masses appear as a row of white rod-shaped objects traveling along the line of the groove. When the seminal fluid of one individual has thus accumulated opposite the openings of the seminal receptacles of the other, it is forced into the latter, apparently by contractions of the clitellum, aided perhaps by a sucking action of the receptacle. In this manner the mutual exchange of spermatozoa occurs apparently without mixture of the seminal fluid derived from the two individuals. The worms now wrench themselves apart and are ready for egg laying at a later time.

At the time of *egg laying*, the clitellum exudes a secretion that becomes a girdle-like structure as it hardens by exposure to the air

FIG. 148.—Development of earthworm within egg capsule.

A to C, fertilization showing entrance of spermatozoön, approach and fusion of male and female nuclei (*cf.* Fig. 116, p. 233 and Fig. 213, p. 405). D, two-cell stage. E, early blastula stage showing cells which will give rise to ectoderm, endoderm and mesoderm in later development. F, late blastula showing beginning mesoderm formation. G, gastrula showing three primary germ layers and formation of enteron and coelome. H, embryo showing beginning of adult structures.

bp, blastopore; br, brain; ca, coelome; ec, ectoderm; en, endoderm; m, mesoderm; n, nephridia; p.b., polar bodies; s, spermatozoön; sc, segmentation or blastula cavity; v.m., fertilization membrane; v.n.c., ventral nerve cord. (Based upon figures and descriptions by Wilson, *Jour. of Morph.*, vol. 3.)

(Fig. 147 C). This is gradually slipped forward as a ring might be drawn from a napkin. During its passage toward the head, several ova pass from the opening of the oviduct on segment fourteen into

the space between the body and the girdle. At the openings of the seminal receptacles on segments nine and ten, spermatozoa derived from another worm enter the space containing the ova, and fertilization occurs. There is also included an albuminous secretion from the skin glands which later serves as nutrient for the developing embryos. When the girdle is finally "laid," by being slipped over the head, its two ends come together and it thus forms the egg capsule, or *cocoon*, in which the fertilized eggs develop (Fig. 143 C). The capsules of *L. terrestris* are deposited in the earth, usually a few inches below the surface. They are oval bodies, showing at either end the signs of their origin as a girdle-like structure. They are about 6-8 by 4-6 mm. in size and of a dark olive color. In *L. terrestris*, only one egg finally develops out of several that are originally included in the capsule. In a related species, *L. communis*, two worms arise from a single ovum, by division of the embryo at an early stage, in a manner comparable with the production of "identical" twins in some of the mammalia.

The earthworm, therefore, reproduces exclusively by the sexual method. The structure and mode of action of the reproductive organs have been described (*cf.* p. 295). The ova are formed in ovaries. The spermatozoa are detached from the testes in an immature stage and their maturation takes place in the seminal vesicles, from which they eventually reach the outside by way of the vasa deferentia. Sexual union consists in the mutual exchange of spermatozoa, which are then stored in the seminal receptacles. In this manner cross fertilization is insured at the time of egg laying. The fertilized eggs develop to young worms enclosed within an egg capsule, which contains an albuminous fluid that serves as nourishment for the embryo.

Development occurs as shown in Fig. 148. In addition to *ectoderm* and *endoderm*, as in a diploblastic animal like *Hydra* (*cf.* p. 260), *mesoderm* appears as in triploblastic animals. The *cælome*, which is differentiated in the mesoderm, is a new feature that is not found in the Cœlenterata. The earthworm is thus *triploblastic* and *cælomocælous* (*cf.* p. 240). The relationships between the germ layers of the earthworm and the cells of the adult organism are shown by the accompanying table (Fig. 149).

Germ Layers and their Derivatives in the Earthworm

Ectoderm	Epidermis Stomodæum and Proctodæum Nervous System and Sense-organs Reproductive Ducts in Part Outer Portion of Nephridia
Mesoderm	Muscles Connective Tissue Peritoneum Reproductive Organs in Part Blood Vessels Inner Portion of Nephridia
Endoderm	Mucous Membrane of the Digestive Tract, except Stomodæum and Proctodæum

FIG. 149.—Germ layers of the earthworm and their derivatives.

In the development of Metazoa, with the possible exception of the Porifera and Mesozoa, there appear at an early stage of differentiation what are known as the *germ layers*. In the Cœlenterata, which are diploblastic animals (*cf.* p. 260), there are only two germ layers, the ectoderm and the endoderm. In higher metazoa, a third germ layer, the mesoderm, develops between the ectoderm and endoderm. Thus the gastrula of an earthworm (Fig. 148, *G*) is like a hydra with its ectoderm and endoderm surrounding the enteron, with the addition of mesoderm, in which the cœlome is developing. The Platyhelminthes (*cf.* Fig. 117, p. 240 and Fig. 118, p. 245) represent a condition intermediate between Cœlenterata and Annulata to the extent that they possess ectoderm, mesoderm, and endoderm surrounding the enteron, and are thus triploblastic, but are not cœlomate animals, since they do not possess a cœlome within the mesoderm. Although there are many exceptions, the three germ layers may be identified in the development of the vast majority of metazoa, and they normally give rise to certain adult parts that may be broadly homologized in the several phyla (*cf.* Fig. 218, p. 417).

Other Annulata

Classification. — The Phylum *Annulata* includes four classes: the *Chatopoda*, which is the class to which the earthworms belong; the *Archi-annelida* (Fig. 150 A), a small group of segmented worms with either a very primitive or a somewhat degenerate organization; the *Sipunculoidea* (Fig. 150 B), a group of marine worms that are greatly modified from the fundamental segmented condition of the group; and the *Hirudinea*, or leeches (Fig. 150 C), another very specialized group in which the primary segmentation has become obscured by subdivisions of the original metameres and other modifications related to the mode of life, which is parasitic in many of the species.

The members of the Class *Chætopoda* are the most important of the Annulata for our present purposes, since they exhibit most clearly the segmental or metameric organization which seems to be the primitive condition of the phylum. This class is divided into two sub-classes: the *Oligochætata*, which includes the earthworms and closely related annulates, mostly fresh-water species; and the *Polychætata*, which are for the most part marine. These

FIG. 150.—Other Annulata.

A, *Polygordius*, one of the Archiannelida, from dorsal view. *B*, *Phascolosoma*, one of the Sipunculoidea, from lateral view. *C*, *Placobdella*, one of the Hirudinea, from ventral view showing sucker at posterior end.

an, anus; *h*, head; *m*, mouth; *n*, nephridiopore; *p. s.*, posterior sucker; *t*, tentacles.

two sub-classes of the Chætopoda, which means “bristle-footed,” are distinguished structurally by the fact that the Oligochætata (*oligos*, few; and *chætata*, bristles) have but few setæ, or chætæ, on a segment; while the Polychætata (*polys*, many) have a larger number. The four pairs of setæ on each segment of the earthworm, in contrast with the many in *Nereis* (Fig. 152), illustrate this difference. The further differences in the structure and activities of these two subdivisions of the Chætopoda are indicated in the descriptions which follow.

Oligochæta.— The individuals comprising this sub-class are found chiefly in moist soil and in fresh water. A very few species inhabit the ocean. They have a bodily organization similar to that of the earthworm, although they are of smaller size and variously modified. One thinks of the common earthworms as land animals, but they are not fully adapted for terrestrial life because of their dependence upon moisture in the atmosphere. In fact, some species of earthworms live in fresh water. Hence, the oligochætes as a group are primarily aquatic animals, which, in a few instances like that of the terrestrial earthworms, have become adapted for life upon land under conditions of sufficient moisture. As there are many species of fresh-water oligochætes, they are familiar objects in laboratory aquaria.

Polychæta.— Although there are many species and genera of Oligochæta, the most diversified and representative group among the Annulata is the Polychæta. These are almost exclusively marine and are abundant in all the oceans where they burrow in the sea floor in shallower water; or, in some instances, swim actively. In order to illustrate the structure and activities of the Polychæta, for comparison with what has been seen in the Oligochæta, we may consider a single representative example.

A Representative Polychæte.— The clam-worm, *Nereis virens* (Fig. 151), is a polychætous annulate, common along the Atlantic Coast of North America from Long Island Sound to Labrador. It lives buried in the sand and fine gravel or under stones between tide marks and just beyond low-water mark, without, however, forming very permanent burrows. If disturbed, it swims effectively

FIG. 151. — Anterior and posterior ends of *Nereis virens*, one of the Polychæta, from dorsal view.

In contrast to the earthworm (cf. Figs. 137 A and 152, A), *Nereis* has well-developed sense organs at the anterior end or "head," a pair of tactile cirri on either side of the anus; and on each somite, a pair of parapodia that serve as locomotor organs (cf. Fig. 152 B).

by undulations of its body and by the movement of its lateral appendages, or parapodia; but it soon burrows again into the bottom where it lies for the most part with only the head exposed. It is characteristically a form adapted for movement and light burrowing under stones, among seaweed, in clean, loose sand and fine gravel, or very soft mud, rather than for burrowing in close, hard material. At the breeding season, in the spring, the male and female worms swim freely near the surface, discharging their ova and spermatozoa into the open water where fertilization occurs. Their breeding habits are thus in marked contrast with those of the earthworm and other oligochaetes. There are many other species of *Nereis* at the seashore in all parts of the world.

The external features of *Nereis* (Figs. 151 and 152) are also noticeably different from those of *Lumbricus* (cf. Fig. 137 A). The body is worm-like, 30 cm. or more in length, tapering toward the two ends, but broader at the anterior end where there is a distinct *head*. The living animal is flesh-colored with a greenish sheen and some iridescence as it is seen shifting its position in the water. On the head are well developed sense-organs in the manner of a free-living animal. The *peristomium*, or most anterior segment, like that of the earthworm, bears a *prostomium* dorsally above the mouth, but this prostomium is terminated anteriorly by a pair of *tentacles*. In addition, there are on either side of the head four tentacle-like organs of touch, the *cirri*, and antero-ventral to these on either side, two *palps*. The *mouth* is ventrally placed below the prostomium, with wrinkled lips encircling its outline. In seizing prey the mouth is everted as a short *proboscis* at the free end of which is a pair of powerful *jaws*. On the dorsal surface of the prostomium are two pairs of simple eyes or *ocelli*. By means of these organs of the head and its powers of locomotion, *Nereis* is well equipped for the active existence which it leads in preying upon smaller organisms such as other worms and the small crustaceans that abound in its normal habitat.

The median portion of the body is composed of segments, or *metameres*, like those of the earthworm; but each of these segments, except the peristomium, bears a pair of lateral appendages, the *parapodia* (Fig. 152 B), which are paddle-like organs used in locomotion and respiration. Anteriorly, the parapodia are somewhat reduced; and posteriorly, where the new segments are added as the worm grows, they are somewhat undeveloped. There is,

however, a pair of parapodia on every segment of the body except the peristomium and the terminal segment. The latter bears the *anus* (Fig. 151) dorsally, and ventrally two *anal cirri* which project posteriorly.

Internally, the *digestive tract* is somewhat less differentiated than in the earthworm, since it consists only of pharynx, esophagus with a pair of digestive glands, and a stomach-intestine. The *circulatory* and *nervous systems* resemble those of the earthworm. The *reproductive system*, like that of all the polychaetes, is much

FIG. 152.—Head and parapodium of *Nereis virens*.

A, head in lateral view, showing sense organs. One of the eyes is seen as a small dot on the dorsal side posterior to the tentacles. B, a single parapodium.

ac, aciculum or specially developed seta; c, peristomial cirrus; m, mouth; p, palp. pr, peristomium; s, seta; t, tentacle.

simpler than in the earthworm, since the sexes are separate and ovaries or testes are formed on the coelomic walls at the breeding season as specialized regions of mesoderm in each somite except a few at the anterior end. The ova and spermatozoa pass out by the nephridia and not by special genital ducts. Fertilization and development occur in the open water, and there is a free-swimming larva, the *trochophore*, which settles to the bottom as it changes into the miniature adult.

Other Polychaetes. — *Nereis* represents a free-living type of polychaete to which the name *Errantia*, or “wanderers,” was applied in one of the older classifications. This was in contrast

with the *Sedentaria*, or forms that "sit down." The latter group included many polychaetes that build tubes and thus become more or less permanently fixed in one locality. Many sedentary polychaetes, like the tube-building species, *Hydroides*, and *Cirratulus*, have remarkably developed feeding and respiratory organs at the anterior end of the body. *Cistenides* forms a conical tube of sand grains cemented together. *Chaetopterus* produces a leathery U-shaped tube through which it causes a circulation of the water, thus bringing food and the oxygen within reach.

The Annulate Plan of Body. — In the body plan of the more representative types of the Phylum *Annulata* (cf. Figs. 137 D and 140), an outer tube, the body wall, surrounds a coelomic cavity and an inner tube, the digestive tract, which extends from end to end of the animal. The coelome is divided by septa between the segments or metameres. The paired excretory organs are segmentally arranged so that the inner opening is in one segment and the outer opening in the one just posterior. There are dorsal and ventral blood vessels, connected laterally in each segment. The nervous system consists of a double chain of ventral ganglia with their connectives, together with the circum-pharyngeal connectives, and the paired cerebral ganglia, which form the dorsally placed brain. In the simpler types the sexes are separate, there are reproductive organs in each segment, and the nephridia serve as ducts for the spermatozoa and ova. Certain segments may be specialized externally or internally, as is the case toward the anterior end of the earthworm and *Nereis*; but, in the general scheme of the body, every metamere is the equivalent of every other one, since it contains similar parts of each system of organs. Metamerism is, therefore, one of the distinctive features of the annulate body. Only two other phyla of the Animal Kingdom, the *Arthropoda* and the *Chordata*, exhibit this type of organization, the simplest form of which is shown by those annulates in which large portions of the body are merely repetitions of similar segments. Metamerism, the coelome, and a triploblastic structure, together with the nephridia and the arrangement of the nervous system, are thus the most important characteristics of the body plan in the Phylum *Annulata*.

CHAPTER 13

THE ANIMAL NERVOUS SYSTEM

Since the nervous system of the earthworm resembles, on the one hand, that of the hydra, and, on the other, that of higher animals, comparisons may now be made between the structure and

FIG. 153.—Neuromotor mechanism of *Euplotes patella*, one of the Infusoria.

A, diagram of an individual showing position of cut through the right margin which results in paralysis of the anal cirri. B, an anal cirrus which has become detached from its fiber plate and rotated on its axis 90 degrees to the left. C, diagram of the neuromotor apparatus.

a. c., anal cirrus; *a. c. f.*, anal cirrus fiber; *a. f. p.*, anal fiber plate; *ant. cyt. f.* and *mb. f.*, membranelle fiber; *b. p.*, basal plate; *c. v.*, contractile vacuole; *e. g.*, ectoplasmic granules; *f. c.*, frontal cirri; *mac.*, macronucleus; *m. c.*, marginal cirri; *mf.*, membranelle fiber; *m. f. p.*, membranelle fiber plate; *mic.*, micronucleus; *mot.*, motorium; *o. l.*, oral lip; *ph.*, cytopharynx; *v. c.*, ventral cirri. (After Taylor, Univ. of California Publications in Zoology, Vol. 19, 1920.)

functions of this system in representative animals. In the study of irritability in the frog and hydra and of related phenomena in protozoa, it has been pointed out that behavior is conditioned by

cell functions. Again, instead of speaking of the "nervous system," it is better to say the *sensory-neuromuscular system*, since the receptors of the sense-organs, the adjustors of the nervous system proper, and the effectors are intimately connected in a unified system. Glands are also effectors but they are less in evidence than muscles. The basis of function in this *receptor-adjustor-effector* mechanism is the irritability of the protoplasm. Similar phenomena occur in the protozoa, and in some species there is a miniature "nervous" mechanism within the limits of the cell (cf. Fig. 153 and Fig. 98, p. 183). The cell is the unit in both protozoa and metazoa. In the discussion that follows, the organization of this sensory-neuromuscular system will be compared in a series of animals with a view to tracing the probable evolution of the nervous system and related structures. As the behavior of animals is founded upon the nervous mechanism, we may in conclusion refer briefly to the evolution of nervous functions and of intelligence.

The Sensory-neuromuscular System

Porifera. — In the sponges, or Phylum *Porifera*, which are the lowest type among the principal phyla of many-celled animals (cf. Fig. 117, p. 240), there is nothing that can be called a nervous system and there are not even nerve cells. The sponge exhibits irritability, since it responds locally when stimulated, and there is a slow extension of the response in all directions from the original place of stimulation. Histological examination reveals that there are contractile cells, particularly those arranged

FIG. 154.—An apopyle, one of the openings in a sponge, showing contractile cells that function as independent effectors.

apo, the apopyle; *arc*, archæocytes or undifferentiated cells; *my*, myocytes or contractile cells.

around certain openings (Fig. 154). These cells are *independent effectors* like the cnidoblasts of hydra (cf. Fig. 129, p. 267), since they receive and react to stimuli independently of any other part. The extension of the reaction from an original region of stimulation is due to *neuroïd trans-*

mission, which supposedly occurs by passage from cell to cell in the general mass. The word "neuroid" is used in order to distinguish this process from *neural transmission*, which occurs in animals having a nervous system.

Cœlenterata. — The nervous system of the hydra (Fig. 129, p. 267) illustrates a further development. The sensory cells and the neuro-sensory cells are *receptors*, connected, directly in some instances, with *effectors* in the form of the muscle processes of the large ectoderm cells. Usually, however, there are nerve cells between these sensory and muscular elements. The sponge has only effectors, while hydra has a *receptor-effector system*, but lacks the adjustors, which are found in higher animals. It is of interest that cœlenterates also possess *independent effectors*, in the form of cnidoblast cells, since these seem to be stimulated directly and therefore to function independently of the nervous system. The merest beginning of centralization in the nervous system is seen in the hydra in the concentration of nerve cells in a ring about the hypostome at the bases of the tentacles and near the base of the body (Fig. 128, p. 266). In some of the jellyfishes such centralized rings of cells are further developed.

Annulata. — In segmented worms, like the earthworm, a *central nervous system* is well developed, but the cellular mechanism is comparable with that found in the hydra, with certain additions (Fig. 144, p. 298). The sense-organs in the epidermis are composed of groups of sensory cells, the *receptors*, from which processes extend as nerve fibers running in nerves to the central system. Here the processes may end in contact with the many finer processes, or dendrites, of motor neurones which are comparable with the nerve cells of a hydra (*cf.* Fig. 129, p. 267), and from which single processes, or axons, extend outward to the muscle cells or *effectors*. There is, however, another type of nerve cell, the dendrites and axons of which are restricted to the central system. To these the term *adjustor neurones* may be applied. In the longer reflex circuits such adjustor cells lie between the processes of the sensory cells and the dendrites of efferent neurones whose axons extend to the muscles. Communication from segment to segment is made possible by the processes of adjustor cells that extend longitudinally in the nerve cord. The development of the *central system* with its adjustor neurones constitutes the important advance of the earthworm's nervous mechanism

over that of the hydra. In comparison with the independent effector mechanism of sponges and with the receptor-effector mechanism of the coelenterates, the annulates possess the *receptor-adjustor-effector* mechanism which is characteristic of all the higher metazoa.

Vertebrata.—Comparisons between the nervous systems of vertebrate animals (Fig. 61, p. 109) and segmented worms show that the relationships are similar, except that the sensory neurones of the vertebrate, comparable with the sensory cells or *receptors* of the earthworm, have been shifted inward to the dorsal root ganglia, retaining connections with the skin by long processes. In correlation with this, special groups of cells in the skin have become differentiated as receptors that receive stimuli and transmit impulses to these receiving fibers of the afferent neurones. The mechanism of cells that function as *adjustors* within the central system is similar to that in the earthworm, but there are many more of these cells and hence a greater complexity of interconnections. Long-distance transmission of nerve impulses and the centralization of the system to function as a whole, instead of segment by segment, are conspicuous features of this development. The brain of the vertebrate illustrates this in particular, as does the enormous increase in adjustor cells in the spinal cord. Here, again, muscles constitute the greater mass of the effectors, but gland cells are also effectors. In general, the vertebrate nervous system is characterized by a greater specialization of receptors, a greater centralization in the brain, and a larger number of adjustor neurones. In this manner the receptor-adjustor-effector elements of the sensory-neuro-muscular system of animals, from the simplest to the highest, may be compared. Such comparisons indicate the probable course of the evolution of the nervous system.

Forms of Behavior in Animals

Tropisms.—The functions of the cells have been indicated in the foregoing account of the structure of animal nervous systems. Something may be said of the behavior, or the activities of the organism as a whole. We have seen that what are called “tropisms” have been defined as forced responses of lower organisms to simple forms of stimulation (*cf.* p. 181); but the term has

been used in so many senses that it is meaningless, and the study of animal behavior would be clarified if it could be eliminated. If the word could have been restricted to the protozoa, it would be convenient to use for the responses of unicellular organisms. The protozoa respond to a variety of stimuli and thus exhibit an obvious irritability; and the protozoan cell responds as a whole, since it is an independent organism. By contrast, the irritability of metazoan cells is less diversified, because of their unbalanced physiological state (*cf.* p. 128). We may, therefore, ignore the term tropism and say that the protozoa exhibit irritability or response to stimulation to an extent that is surprising. The trial-and-error responses of ciliates are examples.

Behavior in Animals like Hydra. — The existence of a nervous system in the Cœlenterata makes possible more effective response to stimulation than occurs in sponges, although there is a similar diffuse spreading of the reaction from the original point of stimulation. Such animals are said not to have reflexes, because there is no evidence of the passage of a nerve impulse in and out along an established reflex arc (*cf.* p. 107). There is, however, neural transmission in contrast with the neuroid transmission in sponges. Such a condition as exists in the hydra might be termed a *pre-reflex type* of response. From this, reflexes might be evolved by the establishment of definite paths in a more centralized nervous system, as in the earthworm.

Behavior in the Earthworm and in Higher Animals. — That *reflex action* occurs in animals like the earthworm and other Annulata may be inferred from the fact that the individual reacts as though the stimulus were "reflected" in the response. Such a conclusion from the visible effects that follow stimulation is supported by the existence of a *reflex arc* as pictured by the receptor-adjustor-effector mechanism (Fig. 144, p. 298). The behavior of such animals is composed of reflex actions, modified and compounded to some extent as in higher animals. The principal difference between the behavior of the earthworm and that of higher metameric invertebrates, such as crustaceans and insects, consists in complexity of reflexes and the modifiability of behavior by what is called *memory*, or the impress of past experiences, in spite of the high development of *instincts*. In the chapter on irritability, it was shown that instincts may be defined as inherited reflexes. The manner in which instincts grade into forms of behavior that are

more complex than simple reflexes was briefly considered in the same chapter. From the evolutionary standpoint, it is as difficult to draw a sharp line at any point between the different forms of behavior as it is between the different levels of structural organization in animal nervous systems.

CHAPTER 14

THE CRAYFISH AND THE ARTHROPODA

The crayfish is a member of the Class *Crustacea* in the Phylum *Arthropoda*. In studying the Arthropoda, we find again a type of structure resembling that of the Annulata, since the bilaterally symmetrical body is metameric and there are paired appendages. The general organization is, however, far more specialized than that which is found among the annulates. In two other great invertebrate phyla, the Mollusca and Echinodermata, which are not described in the present volume, the body is non-metameric. Crustacea are for the most part aquatic animals, although a few species are terrestrial in their mode of life. Taking the Crustacea alone among the Arthropoda, it appears that the members of this class present the same general conditions of structure and habitat as that indicated for the Annulata. The sea is the home of the vast majority of existing crustaceans and was presumably their original home. From this primæval habitat the ancestors of forms like the crayfish and other crustaceans now living in lakes and streams seem to have migrated into fresh water at various times in the past. The few species of land-dwelling crustaceans are clearly offshoots of a group that is primarily aquatic, just as the earthworms are fresh-water oligochætes which have become adapted for terrestrial life in moist soil. Two other great classes of Arthropoda, the Insecta, or insects, and the Arachnida, which includes the spiders and scorpions, are, however, thoroughly adapted to terrestrial life. The distinctive characteristics of the Arthropoda will become apparent during the study of the representative types that follows.

The Crayfish

Occurrence and Distribution.—Crayfish have been widely used in zoological study to illustrate certain general principles as well as the structure of a crustacean, since Huxley, in 1880, made

use of this animal in his classic volume entitled "An Introduction to the Study of Zoology, Illustrated by the Crayfish." They abound in the streams and smaller bodies of fresh water in the more temperate regions of North America, although, like other animals, their distribution is determined by past migrations as well as present conditions that may be favorable. In parts of New England they are entirely absent, but throughout most of the Mississippi Valley region, in the Pacific Northwest, and in the southeastern states they are familiar animals wherever a favorable environment presents itself. In many other parts of the world crayfish of various species and genera are likewise abundant. In Europe, in Asia, and in North America west of the Rocky Mountains, are found members of the genus *Potamobius* (*Astacus*), while the genus *Cambarus* is typical for the remainder of our continent. Other genera of crayfish are widely distributed in the southern hemisphere, in Australia, Tasmania, New Zealand, the Fiji Islands, Madagascar, and South America. The first reference to crayfish in scientific literature is found in Aristotle's writings, where he speaks of the "small *astaci* that breed in the rivers." *Astacus* was the Greek name for the lobster, and for a long time the crayfish were known as "river-lobsters." They are, in fact, closely related to the lobsters, although the latter are marine animals and must be placed in a different family. The common name "crayfish" is better scientific usage, although "crawfish" is the popular designation in this country and was used by the naturalist Say, in 1817, years before Huxley gave currency to the English name crayfish in the textbook above mentioned.

General External Features. — There are three principal regions of the body, the *head*, the *thorax*, and the *abdomen* (Fig. 155). The body is composed of segments, the *somites* or metameres, each having a pair of jointed appendages. In the abdomen these segments are in evidence dorsally, but in the head and thorax their dorsal portions are fused together as a continuous structure, the *cephalothorax*, which shows, however, the line of separation between head and thorax as the *cervical groove*. The cephalothorax is prolonged anteriorly as the pointed *rostrum* on either side of which are the *eyes*. Ventral to the eyes are two pairs of appendages, the *antennules*, which are smaller and biramous; and the *antennæ*, which are more elongated. Posterior to these sensory

appendages of the head are six pairs of oral appendages, including the *mandibles*, which lie on either side of the *mouth*. Posterior to these oral appendages are the great claws, or *chelæ*, which are followed by four pairs of walking legs, or *pereiopods*. The abdomen bears the *swimmerets*, which are small and delicate, except the most posterior pair, or *uropods*, which are modified as strong paddle-like structures. The uropods, together with the *telson*, or terminal portion of the body, constitute the *tail-fin* which is no less important than the pereiopods in locomotion. The *anus* is located ventrally on the telson.

In the special account of the appendages given on p. 325 it will be seen that there are five pairs of cephalic appendages, eight pairs of thoracic appendages, and six pairs of abdominal appendages.

FIG. 155.—Crayfish viewed laterally in the attitude assumed when the swimmerets are being waved gently in aëration of the eggs which are attached to these appendages. (After Andrews.)

Since there is a pair of appendages for each somite of the crayfish's body, there are six somites in the abdomen, in addition to the telson and eight somites in the thorax. In the head region there are five somites plus the part bearing the eyes, which are not true appendages. Thus the body has nineteen somites between the telson at the posterior end and the most anterior part of the head region. The structure of the internal organs, particularly the nervous and circulatory systems, and the development bears out this interpretation. The crayfish has, therefore, a greater degree of antero-posterior differentiation than the earthworm, although its metameric organization is clearly in evidence. Another feature of the external organization is the strict bilateral symmetry that is everywhere apparent, except in the slight difference between the *chelæ* of the two sides. The abdomen is broader in the female,

in correlation with the function of this part of the body in carrying the eggs and embryos attached to the swimmerets.

Other structures that are really external are the *gills*, and the *gill-cavity*, which is formed by the ventral and posterior extension of the thoracic skeleton as the *carapace* (Fig. 156). The skeleton extends from the dorso-lateral region, like a man's coat if it were sewed to his body along a line a few inches on either side of his

FIG. 156.—Transverse section through thoracic region of crayfish.

a, artery to appendage; *a.b.*, afferent branchial blood vessel; *c*, carapace; *e.b.*, efferent branchial blood vessel; *g.c.*, gill cavity; *g.f.*, gill filaments; *h*, heart; *m*, muscle; *n.c.*, nerve cord; *pc*, pericardial sinus; *s*, skeleton; *v.a.*, sternal artery. The arrows show direction of blood flow. (Redrawn from Lang, "Comparative Anatomy," copyright, 1891, by Macmillan and Co., Ltd., printed by permission.)

backbone and widely opened on the ventral side where paired appendages might be located.

The *skeleton*, which clothes the entire outer surface of the crayfish, is an exoskeleton that envelops even the smallest external parts and extends as a delicate lining for some distance into the digestive tract at the mouth and anus. It is composed chemically of an organic substance, *chitin*, to which is added carbonate of lime in the thicker portions. The *joints* of the appendages and those

between the segments of the abdomen are merely places where the skeleton is thin and flexible, not where it is absent. A similar skeleton composed of chitin without the carbonate of lime is found in other classes of the Phylum *Arthropoda*. Like the cuticle of an annulate (cf. Fig. 145, p. 302) this arthropod skeleton is secreted by the underlying epidermal cells. It is everywhere continuous and it cannot receive additions at its edges with the growth of the animal, as does the shell of a mollusc. Hence, the crayfish, like other arthropods, is confronted with the problem of increasing in size while it is encased in a skeleton that cannot be stretched. Crayfishes outgrow their skeletons as children outgrow their clothes, but they have the advantage that a new skeleton is secreted inside the old one, which is then "molted." Such a process is characteristic of the Arthropoda (cf. Fig. 169, p. 345).

Appendages. — Even the most superficial examination shows that the appendages are adapted for different functions in different regions of the body. The antennules and antennæ are sensory organs; the mandibles, maxillæ, and maxillipeds, organs of feeding; the chelæ, organs used for defense and offense and for the capture of prey; the pereopods, organs of locomotion. In the female, the abdominal appendages have the specific function of carrying the eggs (Fig. 155). In the male the two anterior pairs of swimmerets are modified as organs for the transfer of sperm to the seminal receptacles of the female. The uropods, together with the telson, function as the powerful tail-fin by which the animal darts backward through the water. There is, therefore, great functional diversity among the appendages of the various regions and there seem to be corresponding differences in structure. Yet all these appendages are constructed upon the same plan and are therefore *homologous*. This, of course, is but an expression of the metamerism, whereby the parts of each somite are formed according to a general plan which is modified in relation to its particular functions. Resemblances of this nature between the parts of a single animal are called *serial homologies*, as distinguished from the homologies between the corresponding parts of different animals. Thus, the fore limbs of all vertebrates are homologous, whereas the vertebræ, the ribs, and the two pairs of appendages of any vertebrate animal are serially homologous. The appendages of the crayfish and similar Crustacea have become a classic example of this form of homology, because there is no more convenient

material among metameric animals for illustrating this great principle of organization.

The simplest appendages of the crayfish's body are the *swimmerets* on the abdomen. A swimmeret (Fig. 157A) consists of a proximal segment, the *protopodite*, which bears two distal seg-

FIG. 157.—Appendages of American lobster, *Homarus americanus*.

A, second swimmeret. B, mandible. C, first maxilliped. D, third maxilliped. E, first pereopod.

en, endopodite; ep, epipodite; ex, exopodite; g, gill; pr, protopodite.

ments, the *endopodite* toward the median plane and the *exopodite* toward the outside, as the names imply. The endopodites of the swimmerets are further divided into proximal and distal segments. The *uropods*, which are borne on the most posterior abdominal segment, are much larger, yet they exhibit this same type of structure save that the exopodite, instead of the endopodite,

has two divisions. In the adult female the most anterior pair of abdominal appendages are reduced in size and are uniramous. In the larval stages of both sexes, however, they show the biramous structure, and by following their development it is seen that the exopodite is lost during the late embryonic stages with the result that only protopodite and endopodite remain.

The structure of the *pereiopods* and *chelæ* may be understood even without a knowledge of the development, if one examines first the *third maxilliped* (Fig. 157 D). This appendage is composed of two parts: a protopodite, divided into a proximal por-

FIG. 158.—Young American Lobster, *Homarus americanus*, at a stage when exopods are present on the pereiopods.

(After Herrick, Bull. U. S. B. F., 1895.)

tion bearing a gill, with which is fused a delicate outgrowth known as an *epipodite*; and a distal portion which bears the exopodite and endopodite. Of these, the exopodite is smaller and finger-like, with small divisions at the distal end, while in the endopodite five segments may be counted, the proximal one being fused with the outer portion of the protopodite. By comparison with the third maxillipeds, it will be seen that the pereiopods and *chelæ* lack exopodites. In the embryonic stages, however, they have exopodites somewhat in the manner of the larval lobster shown in Fig. 158. These five posterior appendages of the thorax are, therefore, constructed according to the fundamental

plan that was recognized in the appendages of the abdomen; but a part of the structure has disappeared in the course of the development, just as one or more digits may be present in the embryo and not in the adult of a vertebrate animal.

The homologies of the *first* and *second maxillipeds*, the *first* and *second maxillæ*, the *mandibles* and the *antennæ* may be similarly established by comparisons between their adult structure and development. The *mandible*, for example, is a biramous appendage in the embryo but the exopodite is lost during later stages, while the protopodite and endopodite become modified. The *antennules* are the only pair of appendages regarding which there may be question as to the fundamental structure. They are in fact biramous; yet it is possible that they are not body appendages, with protopodite, exopodite, and endopodite, like all the others, but were originally sense-organs of the head like the cirri of an annulate (*cf.* Fig. 152 A, p. 313). The *antennæ*, on the other hand, are probably a pair of appendages that were originally posterior to the mouth and have shifted anteriorly to function as sense-organs, while the next pair posteriorly have shifted to a position on either side of the mouth to become the mandibles.

Thus, within the body of a single animal, are found the modifications of a similar plan of structure to suit the needs of functions so diverse as sense-organs, jaws, walking legs, sexual organs, and tail-fins. Although this serial homology is confined to the single animal, it illustrates the same principle of structural resemblance underlying seeming diversity that is found in comparing the limbs of vertebrates (*cf.* Fig. 264, p. 501). In the one instance, the resemblance can be explained as due to the antero-posterior differentiation that has gradually arisen during the evolution of a metameric animal from ancestors whose somites were more nearly similar throughout the body. In the other, the resemblance is due to the descent of different types of animals from a common ancestral race from which they have inherited their common structural organization.

General Activities. — In its natural surroundings the crayfish is found crawling upon the bottom, or concealed among the rocks and within the burrows that it excavates in the banks of streams and ponds. It walks slowly forward by means of the pereopods, holding the great claws menacingly in front of the body; or swims

backward with sudden strokes of the fin-like uropods, which are pressed strongly against the water by contractions of the muscles that fold the posterior half of the abdomen in a ventral and anterior direction. One such powerful stroke of the tail-fin formed by the telson and uropods will carry the animal several feet backward and usually out of danger. As the crayfish thus shoots through the water, the folded abdomen offers little resistance; it expands gently as the animal comes to rest upon the bottom, ready for another stroke if the occasion demands. The antennules function as tactile organs, but the antennæ are more useful for this purpose, since they can be moved in all directions: forward, sidewise, and even backward along the abdomen. In the dark crevices under stones and in the burrows where little light penetrates, they must be one of the most important means the animal possesses of exploring its surroundings.

Although the crayfish is primarily an aquatic animal, there are times when it leaves the water. Observations made at night with a lantern often show crayfish in the shallow water near shore and upon the bank at short distances from the water. In a laboratory aquarium, they thrive better if they can spend part of the time, including some of the daytime, upon stones or other objects that may project from the water. In nature, they seem occasionally to make short nocturnal expeditions on the land in search of food, if there is sufficient moisture in the atmosphere; and they do this regularly in a laboratory vivarium having a sloping bank.

In spite of its means of defense and escape, the crayfish suffers from many enemies, both internal and external. It has a variety of parasites. Fresh-water oligochaete worms, of the genera *Branchiobdella* and *Bdellodrilus*, and certain nematodes parasitize the gills. Many fish, such as the black bass, hunt for crayfish and devour them greedily. Toads, frogs, salamanders, water snakes, and turtles prey upon them. Even birds, such as the eagle and kingfisher, have been observed with crayfish in their claws or the remains of crayfish found in their nests. Man, however, is the most serious enemy in well-populated countries, since he not only consumes many crayfish as food but may also destroy large areas of the natural habitat by drainage and similar projects. Wherever fairly normal conditions present themselves, however, the crayfish usually thrives even in the face of attempts at extermination.

In some localities, as along the lower Mississippi River, crayfish become a pest by burrowing into earthen dams and levees and starting leaks that rapidly enlarge. In Pennsylvania, Maryland, and West Virginia, one of the burrowing species is reported as being very annoying in lowland fields. The "chimneys" of mud excavated and placed at the air holes of the burrows clog the harvesting machines; and farmers claim that the crayfish come to the surface and destroy the young sprouts of buckwheat, corn, and beans. In attempts to combat them, it is customary to throw unslacked lime upon the fields, to pour carbon bisulphide into the air holes, or to drain the infested areas. None of these measures is efficacious, since the first two do not reach the animals in the water of their burrows while drainage merely lowers the water level and thus only abates the nuisance until the animals reestablish themselves in deeper burrows.

With the decline of the lobster and shrimp supply of the seashore, crayfish will probably assume increasing importance as an article of food. They have long been esteemed as delicacies in other countries, and in the United States there are many cities having a considerable foreign population that consume quantities of crayfish. Many of our streams furnish almost unlimited opportunities for "crayfish farming" such as has been carried on in Europe for years. Or the clear streams of less settled districts, like the Ozark region of Missouri and Arkansas, may yield a natural supply of clean and appetizing appearance. The small boy, who now boils "crawdads" in a tin can by the side of a stream, may, when he grows to be a man, pay a fancy price for them at a city restaurant. Even at the present time, "crawfishing" is an important item in the fishing industry of many localities in the United States.

Internal Organization. — The appearance of the internal organs of the crayfish bears little resemblance to that of the earthworm. The nervous and digestive systems are similarly related, but there is no true *cœlome* that is clearly recognizable, and the circulatory, excretory, and reproductive systems differ so widely that few comparisons can be instituted. Beneath the skeleton is an ectodermal epithelium similar to that of the earthworm, which, in turn, is underlain by the muscles and connective tissue. Between these muscles are cavities, so extensive that they might be mistaken for parts of a *cœlome*, but in reality they are

merely spaces through which the blood flows in the course of its circulation. To such a system of cavities the term *hæmocœle*, or blood cavity, may be collectively applied. The term *cœlome*, it will be recalled, is applied to a cavity of more definite limits and lined with a peritoneal epithelium as in the Annulata and the Vertebrata. If there is anything in the crayfish that has been derived from a true cœlome in the animal's ancestors, it is probably the cavity within the reproductive organs.

When the crayfish is viewed laterally (Fig. 159), the heart is seen in the dorsal region of the thorax, in a cavity that resembles

FIG. 159.—Digestive and arterial systems of the crayfish.

Instead of being continuous with veins, through capillaries as in a vertebrate animal (cf. Fig. 60, p. 104), the blood of the crayfish passes from the ends of the arteries into spaces between the internal organs, through which it flows slowly back to the pericardium. Such spaces are called *hæmocœles*, because they thus contain blood. The circulation of the crayfish is representative of what occurs in the Arthropoda. Blood from a pericardial sinus enters a dorsally placed heart through openings in its walls called ostia. From the heart it passes by arteries, that may be well developed as in the crayfish or consist of but a single aorta (cf. Figs. 178 and 179, p. 355) and is thence distributed to the body. The presence of ostia in the wall of the heart is a feature that is unique for the Phylum *Arthropoda*.

a.a., antennary artery; d.a.a., dorsal abdominal artery; g.gl., green gland; h, heart; md, mandible; o.a., ophthalmic artery; s.a., sternal artery; v.a.a., ventral abdominal artery. (Redrawn with modifications from Howes, "Atlas of Zootomy," copyright, 1902, by Macmillan and Co., Ltd., printed by permission.)

a pericardium, although it is only one of the larger sinuses of the *hæmocœle* and hence must be called a pericardial sinus. Arteries extend from the heart to all parts of the body, as the figure shows. The digestive system is as shown. The brain lies anteriorly near the eyes and antennæ and there are connectives around the esophagus to the nerve cords on the ventral side of the body. The muscular system is complex, particularly in the abdomen where there is a large ventral mass of flexor muscles which bends this part of the body in the powerful swimming strokes, and a much smaller mass of extensor muscles on the dorsal side. The various movements of the appendages are made by similarly

"antagonistic" muscle attached, like those of the abdomen, to the inside of the skeleton on either side of a movable joint (Fig. 160). Such a relationship of muscles to skeleton is characteristic of the Arthropoda and may be compared with that seen in an animal with an endoskeleton (cf. Fig. 22, p. 42). Since the locust will be studied intensively as another representative of the

FIG. 160.—First pereiopod of lobster cut open to show relation of muscles to skeleton.

Arthropoda, the internal structure and special activities of the crayfish will not be further described. The eggs of the crayfish are attached to the swimmerets of the female at the time of laying and remain in this position until the young are hatched (Fig. 155). The young remain attached to these appendages by means of their chelæ until a stage that resembles the adult in miniature (Fig. 161).

Other Crustacea

Classification.— In an older classification, based upon less knowledge than is now available, the Class *Crustacea* was divided into only two sub-classes, the *Entomostraca* and the *Malacostraca*. Such an arrangement is still useful, if we do not need to burden ourselves with too much terminology, because it separates the more highly developed types, like the crayfish, from the crustaceans of simpler organization. It is true that many of the *Entomostraca*, like the water-flea, *Daphnia* (Fig. 162), are greatly specialized; but some of them, like the "fairy shrimp," *Branchinecta* (Fig. 162) are the simplest of all Crustacea in their metamerism and in the arrangement of their appendages. Hence, one often speaks of the *Entomostraca* as the "lower," and the *Malacostraca* as the "higher" Crustacea.

The Malacostraca.— To these "higher" Crustacea belong the forms that are popularly known as the sow-bugs, scuds, shrimps, prawns, crayfishes, lobsters, and crabs (Fig. 163). Although the great majority are marine, many occur in fresh water;

FIG. 161.—Development of crayfish.

A and B, early embryonic stages showing origin of appendages and principal divisions of body as seen from ventral view on surface of the spherical egg. C, mass of young crayfish upon a swimmeret of the mother (*cf.* Fig. 155). D, second larval stage (2) attached by chelæ to hairs on swimmeret of mother. The molted shell of the first larval stage (1) is seen clinging by its chelæ. Notice, also, the remains of the egg shell and the stalk by which the eggs are fastened to the hairs of the swimmerets at the time of laying. When the first larval stage hatches it remains attached to this shell by a filament (*t.f.*) until the chelæ have secured their hold. After the first molt, the second larval stage is in turn held securely by another filament (*a.f.*) until its chelæ become attached. By means of these filaments the young remain fastened to the mother during the brief periods of development when they might easily become detached. E, first larval stage hatching through break in egg shell. F, second larval stage.

1, cast shell of first larva; 2, second larva; AB, abdomen; *a.f.*, filament of second larval stage; AN and AN', antennæ and antennules; LB, labrum or upper lip; *m*, membrane inside shell; MD, mandible; OP, eye; *p*, swimmeret; AB, papilla-like beginning of abdomen; *s*, hairs of swimmeret; *sh*, shell; *st*, stalk of egg; TAP, thoracic appendage; *t.f.*, broken filament of first larval stage; Y, yolk. (A and B, redrawn from Howes, "Atlas of Zootomy," copyright, 1902, by Macmillan and Co., Ltd., printed by permission; C to F, after Andrews, Smithsonian Contributions, Vol. 35, 1916.)

and a small number, like the sow-bugs and the land crabs of the tropics, have become adapted for terrestrial existence. A few are parasitic upon larger animals. Since the number of somites and the division of the body into three principal regions are constant for all Malacostraca, a schematic representation of a malacostracan shows an animal essentially like a crayfish. The body is

FIG. 162.—Representative entomostraca.

Above, a water-flea, *Daphnia pulex*, one of the Cladocera. Below, a fairy shrimp, *Branchinecta packardii*, one of the Phyllopoda; left, anterior view of male showing second antennae modified as clasper; right, lateral view of female with eggs in uterus and showing appendages. (After Dodds, University of Colorado Studies, Vol. XI.)

divided into *head*, *thorax*, and *abdomen*, which are composed, respectively, of five, eight, and six *somites*, each bearing a pair of *appendages*. The anterior part of the head bears the eyes, which are probably not homologous with the appendages; while posteriorly the abdomen terminates in a *telson*. There are thus nineteen somites with paired appendages, in addition to the most

anterior part of the head region and the telson. A *carapace*, resembling that of the crayfish, is variously developed in different species. The internal organization is likewise modified in accordance with the habits of particular species and the external features are highly specialized in many instances, yet the fundamental plan remains. There is, in fact, no better place in the Animal Kingdom for illustrating how an underlying unity of organization may pervade a seeming diversity of structure in adaptation to a wide range of functions. Just as the crayfish or any other mala-

FIG. 163.—A hermit crab encased in a sponge.

The crustacean, a species of *Pagurus* from Puget Sound, like other so-called "hermit crabs" appropriates the empty shell of a gastropod mollusc. The sponge becomes attached to this shell and grows completely around it, eventually destroying the shell itself and leaving the crab in a spiral cavity that was originally the cavity of the shell. The association seems to be a normal one and, therefore, a case of symbiosis or living together with mutual advantage, since the crab is protected while the sponge, which is a sessile animal, is dragged from place to place. A, the crab exposed as it appears during locomotion, and the encasing sponge in which there are two oscula or exhalant openings. B, the sponge cut open showing part of the spiral cavity occupied by the crab, the many small internal cavities of the sponge, and a single osculum. (Drawn by George T. Kline.)

costracan offers an unusual opportunity for study of the serial homology that finds expression in the body of a single animal, so the various types of Malacostraca offer remarkable examples of the homologies between corresponding parts in different animals.

The Entomostraca. — The Entomostraca include the simplest forms among the Crustacea, although many entomostracans are

highly specialized. There are five principal types, as represented by the Orders *Phyllopoda*, *Cladocera*, *Ostracoda*, *Copepoda*, and *Cirripedia*. Like the Malacostraca, the vast majority of these are marine, although the Phyllopoda and Cladocera are for the most part fresh-water animals.

Among the Phyllopoda, which are otherwise known as the "fairy shrimps," species of the genus *Branchinecta* are familiar representatives (Fig. 162). The animals swim upon their backs by means of their paddle-like thoracic appendages. The typical habitat is in the shallow pools of fresh water that are formed by the spring rains and become dry later in the season. Under such conditions the organism must be able to withstand rather rapid changes in the salt content of the water. This probably explains the habits of the phyllopod called the "brine shrimp," *Artemia*, which lives in salt lakes and in the evaporating basins of salt works, where the salinity far exceeds that of the ocean. Yet, strange to say, none of the fairy shrimps are marine. The males of *Branchinecta* are distinguishable from the females by their second antennæ, which are modified as organs by which the males clasp the females at the time of sexual union. The females have a brood pouch or uterus, on the ventral side of the abdomen, in which the eggs are carried for a time. After the eggs become free they can withstand prolonged dessication if the pools become dry. They are often carried for long distances by winds or by the mud adhering to the feet and legs of vertebrate animals. Eventually, the young emerge as free-swimming larvæ, with three pairs of appendages and a median eye. In this stage they are known as *nauplii* and are comparable with the nauplius stage that appears in the development of many higher Crustacea such as the crayfish (cf. Fig. 161 A). The adult arises from this nauplius by a series of molts, during which the characteristic features are gradually acquired.

The Crustacean Plan of Body. — We are now in a position to consider the general organization of the crustacean body. The simplest types of Crustacea are evidently forms in which the metamerism is recognizable externally, not only in the paired appendages but also in the well-marked constrictions between the metameres on the dorsal and lateral parts of the thorax and abdomen. A form like *Branchinecta* will serve to illustrate this condition. The head is always a single mass externally, but the

appendages and the paired ganglia show the existence of a metameric structure. The eyes are sense-organs rather than appendages, and it is also likely that the antennules were originally tentacle-like sense-organs of the head. The antennæ, however, are evidently comparable with the paired appendages upon the remaining somites of the body. It is possible that they were originally posterior to the mouth and have been shifted anteriorly during the evolutionary modification of the Crustacea.

One may thus picture the schematic crustacean (*cf.* Figs. 164 and 166) as an animal segmented throughout its body except in the head region, having the entire external surface covered by a cuticular exoskeleton, and with a pair of jointed biramous appendages attached to the ventral side of each somite. The mouth is near the anterior end, and the anus opens upon the terminal posterior

FIG. 164.—Hypothetical ancestor of the arthropods. The parts labeled kidneys correspond to the nephridia of the earthworm.

(From Pearse, "General Zoology," copyright, 1917, by Henry Holt and Co., reprinted by permission.)

segment. Such an arrangement recalls the type of organization made familiar by our study of the Annulata. For all one can see, the crustacean might be made out of the annulate by a thickening of the cuticle to form a skeleton and by specialization of the parapodia to form the biramous appendages. The resemblance is so obvious that zoologists have commonly assumed the ancestors of the Crustacea, and so of the Arthropoda, to have been closely related to those of the Annulata.

On the other hand, the internal structure offers little resemblance to the annulate plan of body. There is no clearly recognizable coelome, with its paired nephridial tubules communicating with the outside in each segment and serving as ducts for the reproductive organs. There is only an extensive system of cavities (*cf.* p. 331) which function as part of the circulatory sys-

tem and are therefore called a hæmocœle. When, however, all the facts of Comparative Anatomy and Embryology are brought together, it seems probable that the cavity within the reproductive organs, from the walls of which the germ cells originate, represents the degenerate remains of a cœlomic cavity; and that the reproductive ducts, which may open on different segments in different types of Crustacea, or on different somites in the two sexes, represent so many greatly modified nephridia. The excretory organs suggest a similar relationship, since there are two types, the green glands of the Malacostraca opening on the antennal segment, and the shell glands of the Entomostraca opening on the somite that bears the second pair of maxillæ. The nervous system closely resembles that of the annulate and is similarly related to the digestive tract. The musculature is too specialized for any comparison with the simple arrangement in the body wall of the worm; as is also the circulatory system, with its unique feature of ostia in the walls of the heart. In many Crustacea, however, the heart is an elongated tubular organ and thus suggests the pulsatile dorsal vessel of the segmented worms. The sternal artery, in such animals as the crayfish, resembles the sub-neural vessel of the worm as it extends along the ventral side of the body; while its vertical portion, which lies on one or the other side of the intestine in different individuals, is perhaps a survival of the lateral connections between dorsal and ventral vessels in the Annulata. The crustacean plan of body may, therefore, be compared with that of the Annulata, if we suppose that Crustacea are annulate-like animals that have been greatly modified in the manner indicated.

The Phylum Arthropoda

Other representatives of the great Phylum *Arthropoda* may now be considered. No other phylum of the Animal Kingdom approaches the arthropods in the number of species included. There are over 360,000 known species of insects alone, as compared with a total of some 35,700 species of the Chordata and 60,000 of the Mollusca, these two being the only other phyla containing many thousands of species. If to these 360,000 insects be added 16,000 crustaceans, 16,000 arachnids, and 2,000 myriapods, the grand total of 394,000 species is more than three times larger than that of all other species of animals added together (128,400). We are

accustomed to think of the chordates as the dominant forms of life upon the land surface at the present day, but they are far exceeded in numbers of species and individuals by the Arthropoda. In view of these facts, we may ask what are these Arthropoda, aside from the Crustacea, that so swarm upon the land surface as literally to contend with the terrestrial chordates for possession of the earth.

There are five classes within the Arthropoda: the *Crustacea*, as described in the preceding pages; the *Onychophora*, a small class which is especially important because of its primitive organization; the *Myriopoda*, or thousand-legged and hundred-legged animals; the *Insecta* or *Hexapoda*, which are the great terrestrial class of the phylum; and the *Arachnida*, or spiders.

FIG. 165.—*Peripatus* entangling a cockroach in sticky threads discharged from two papillæ beneath the head.

(From Pearse, "General Zoology," copyright, 1917, by Henry Holt and Co., reprinted by permission.)

Class Onychophora.—The members of the Class *Onychophora* are of interest because they appear to represent a type somewhat similar to the probable ancestors of the Class *Insecta*. In other respects they link the whole arthropod phylum with the Annulata. They are represented only by the genus *Peripatus* (Fig. 165) and several closely related genera. These are worm-like animals living in tropical regions, in moist places under bark or objects on the ground, much as do the larvæ of many beetles. The general resemblance to an annulate worm, with its terminal mouth and anus and a pair of appendages on each segment of the body is apparent.

Class Myriopoda.—In the Class *Myriopoda* are included the centipedes, or "hundred-legged worms" (Fig. 166), and the milli-

pedes, or "thousand-legged worms." These are familiar animals in all temperate and tropical countries, living in damp places under stones and timbers and in the upper layers of the soil.

FIG. 166.—The house centipede, *Scutigera forceps*.

(From Farmers' Bulletin, No. 627, U. S. Dept. Agr.)

There is a head region, but the worm-like shape of the body and the many appendages are primitive features. In the subdivision of the myriopods that includes the millipedes, there are two pairs of legs to each true somite. Respiration is carried on by a tracheal system (cf. p. 355). Hence, when all the facts of their structure and development are considered, it seems that they are the type of arthropod most closely related to the insects, although not specialized like the members of this class by a division of the body into thorax and abdomen, the loss of abdominal appendages, and development of the two pairs of wings that are characteristic of most insects.

Class Insecta.—The Class *Insecta* are to-day the dominant forms of life upon the land so far as number of species is concerned, although they are exceeded in size of individuals by most other types of terrestrial animals. With respect to their intelligence, they may also be compared more favorably with the Chordata than may any other class of animals, despite their specialization along the lines of inherited and unmodifiable reflexes in contrast with the capacity

for acquiring individual habit reflexes that characterizes the higher chordates.

Class Arachnida.—The most familiar examples of the Class *Arachnida* are the many species of spiders (Fig. 167); but the scorpions, the mites, and the ticks are all members of this class, which is, therefore, highly diversified. All these arachnids are

characterized by the exoskeleton typical of arthropods, and by jointed appendages, of which two pairs are mouth parts and four pairs organs of locomotion. Related to the spiders are the arthropods known as king crabs, represented by the genus *Limulus*.

FIG. 167.—A spider catching a fish.

Some of the spiders hunt their prey instead of spinning a web and lying in wait. This is an extreme instance but well authenticated. (After Abraham, from drawing by Smit in *Natural History*, 1925. Courtesy of American Museum of Natural History.)

These are of gigantic size as compared with other existing arachnids and are of special interest because they have persisted from very early times without important evolutionary changes.

CHAPTER 15

THE LOCUST

A survey of the several classes of the great Phylum *Arthropoda* was given at the close of the preceding chapter. The Insecta, or Hexapoda, are the most important class of land-dwelling arthropods. Their numbers, both in species and in individuals, far exceed those of all other terrestrial animals. While the grasshoppers and their allies are not the simplest type among the Hexapoda, they represent a more generalized condition than is found in such forms as the moths and butterflies, the bees and wasps, or the two-winged flies. They are, moreover, familiar animals, of large size as compared with the majority of insects; their mode of development is relatively simple; and their habits and life histories have been extensively studied because of their economic importance. Like the earthworm and the crayfish, the grasshopper is, therefore, representative of the class of animals to which it belongs, and illustrates the biological principles that are exemplified by that class.

The words "grasshopper" and "locust" are used indiscriminately in popular speech, as when one reads of locusts in the Bible or of the "grasshopper years" in the early days of Kansas. If any scientific distinction is to be made between the two terms, it is that the locusts are the "short-horned" grasshoppers, or those in which the antennæ are relatively much shorter than in the "long-horned" forms which have long and delicate antennæ. The roadside locusts are examples of the former type, and the meadow grasshoppers and katydids, with antennæ even longer than the body, are examples of the latter. Unfortunately, the name locust has also been applied in the United States to an entirely different type of insect, the periodical cicada, which is popularly called the thirteen-year or seventeen-year "locust." As there are many species among the locusts that may be used for the present study, the account that follows has not been confined to a single

species. The descriptions are generalized except where reference is made to species that are especially suited to illustrate particular structures or activities.

The Locust or Short-horned Grasshopper

Occurrence and Distribution. — The locusts or short-horned grasshoppers are typically inhabitants of dry fields and pastures, in contrast with the green grasshoppers which live upon the damp grass of meadows. As one follows the dusty roadway or tramps across the upland pastures in summer and autumn, they spring into the air. Their "shrilling" as they rest upon the ground and the "clacking" of their wings in flight are characteristic sounds of the noontide, just as the songs of their near relatives, the katydids and crickets, are among the most familiar sounds of night. As one American student of the insects puts it:

We do not shut up our singing insects in cages as the Japanese do, and bring them into the house to cheer or amuse us, but we do enjoy them, and were our summer and early fall days and nights to become suddenly silent of chirping and shrilling, we should realize keenly how companionable crickets and grasshoppers and katydids had been for us. A wholesome blitheness and vigor and ecstasy of living rings out in the swift and steadfast song of most of our field and wood insect singers, while the cheeriness of the cricket on the hearth is familiar in poetry and proverb.¹

Locusts are universally distributed on all the continents in all climates where the insect life of open fields abounds. Some species, like the common red-legged locust, *Melanoplus femur-rubrum*, are local in their habitat, being confined for their entire life cycle to a restricted locality. Others are migratory, like the mountain locust, *Melanoplus spretus*, which formerly bred upon the upland plateaus of the Rocky Mountains and in certain years swarmed eastward for hundreds of miles to settle upon the Kansas prairies. All crawl upon the grass of fields and similar vegetation, leaping into the air by means of the posterior pair of legs and sustaining their flight according to the development of the wings. In temperate climates the eggs of most species are laid in the ground during late summer and autumn, hatching as the innumerable wingless hoppers that can be collected in the early spring by sweeping an insect net across the grass.

¹ Vernon L. Kellogg, "American Insects," p. 123.

General External Features: (The Carolina locust, *Dissosteira carolina*; and the red-legged locust, *Melanoplus femur-rubrum*).—A division of the body into regions known as *head*, *thorax*, and *abdomen* is apparent in the locust (Fig. 168) as in the crayfish; although the number of *somites* in these regions cannot be exactly compared in types of arthropods that are so widely separated as

FIG. 168.—Representative locusts.

A, the New Mexico long-winged locust, *Dissosteira longipennis*, adult female, enlarged about one-third. B, southwestern lubber grasshopper, *Brachystola magna*, adult female, natural size. (From Farmers' Bulletin No. 747, U. S. Dept. Agr.)

insects and crustaceans. In like manner, the *metamerism* is obvious in the abdominal region of the locust, but obscure in the head and thorax. Ten somites can be easily recognized in the abdomen, and there are three thoracic somites, as indicated by the three pairs of legs. The number of somites in the head is a vexed question among students of insect anatomy. There is clear evidence of four, since there are three pairs of mouth appendages and the antennæ, and there are probably not less than five somites in this

part of the body. The *skeleton*, like that of other arthropods, is an external layer of firm consistency, thinning out at the *joints* and marked off by grooves into the so-called *plates*, but everywhere continuous over the outer surface and continued within the anterior and posterior ends of the digestive tract as a delicate cuticle. Unlike the skeletons of many Crustacea, that of the grasshopper and other insects is not hardened with carbonate of lime but only by additions of the chitinous substance that is characteristic of all arthropod skeletons. The relationship between this skeleton and the underlying epidermal cells, by which it is secreted, is similar to what has been described for the crayfish (*cf.* p. 325). Before the molting (Fig. 169), a new skeleton is secreted without becoming united with the older skeletal layer within which it is enclosed. The same principles of skeletal relationships and metameric organization that have been indicated for the Crustacea may, therefore, be applied to the locust. The animal consists of a series of somites which are

FIG. 169.—Molting of locust.

A, B, C, D, E, successive stages in process, slightly enlarged. (After Riley. Reproduced from Linville and Kelly, "General Zoology," copyright, 1906, by Ginn & Co., reprinted by permission.)

variously modified in different parts of the body in correlation with special functions. There is typically a pair of jointed appendages for each of these somites, although these may be absent in certain regions, and the body is completely covered by the exoskeleton.

The appendages of the head consist of a pair of sense-organs, the *antennæ* (cf. Fig. 168), and three pairs of oral appendages.

FIG. 170.—Mouth parts of a cockroach, *Ischnoptera pennsylvanica*.

Mouth parts of insects show great diversity of structure in relation to feeding habits. All seem to have evolved from simpler types with jaws and other parts such as are found in cockroaches and locusts.

A, labrum. B, mandible, C, hypopharynx. D, maxilla with basal portions (*s* and *c*), lacinia (*l*), galea (*g* and *sg*), and palp (*mp* and *pf*). E, labium with basal portions (*m* and *sm*), glossa (*g* and *pg*) and palp (*lp*). (From Folsom, "Entomology," copyright, 1906, by P. Blakiston's Son and Co., reprinted by permission.)

The compound eyes are primarily sense-organs, and not appendages modified for sensory functions as are the *antennæ*. What are called the mouth parts of the locust (cf. Fig. 170), include the following: an upper lip, or *labrum*, which is not formed by the fusion of right and left appendages as might be supposed; a pair of appendages known as the *mandibles*, which are the strong biting jaws on either side of the mouth; a tongue-like projection, the *hypopharynx*, which, like the labrum, is a single median structure

and not a fused pair of appendages; the *maxillæ*, which are clearly paired appendages; and the *labium*, which resembles a lower lip, although, unlike the labrum, it is composed of a pair of appendages sometimes called the second maxillæ, which are fused together on the mid-line. The three pairs of thoracic appendages, the *legs*, are similar in structure, although the most posterior pair is specialized for leaping. A minute pad and a pair of hooks at the end of the outer division function as grasping organs by means of which the animal secures a firmer hold during locomotion or when at rest upon the vegetation (Fig. 171). The abdomen of the locust is devoid of appendages and none appear in this region during development, although there are traces of such rudimentary appendages in the development of certain insects.

The posterior end of the abdomen differs in the two sexes, principally by the presence in the female of the large *ovipositors* (cf. Figs. 168 A and 180 A). Between these is the opening of the female reproductive ducts. In egg laying the ovipositors are thrust into the ground and then opened to form the cavity in which an egg is deposited (Fig. 186). In the male there is a thick, conical copulatory organ, or *penis*, which occupies a position between the anus and the external genital opening on the terminal segment of the abdomen (Fig. 180 B).

There are two pairs of *wings* attached to the latero-dorsal surfaces of the mesothoracic and metathoracic somites, as is typically the case in the majority of insects. The anterior pair is heavy and membranous in some species of locusts, thus assuming the nature of wing-covers rather than of wings. In the "lubber" grasshoppers, both pairs of wings are greatly reduced with corresponding reduction in the power of flight (cf. Fig. 168 A and B). The wings of insects are composed principally of exoskeleton with a very small amount of other material between the two layers.

FIG. 171. — Locust resting on stem of plant.

(From Farmers' Bulletin No. 747, U. S. Dept. Agr.)

They are stiffened by thickened portions, or "veins," between which the wing is thin and membranous. In the majority of flying insects the wings are much more delicate than in the locusts.

The external openings of the respiratory system appear as the paired *spiracles* (Fig. 177), on either side of the three thoracic segments and on the eight anterior abdominal segments. In many insects the margins of these openings are colored, appearing as conspicuous spots along the sides of the body. The number of spiracles differs in insects, but there is typically a pair for each segment of the thorax and abdomen. In life, they may be seen rhythmically opening and closing with the respiratory movements of the body.

The following sense-organs may be easily recognized in the locust: the *compound eyes*; the three simple eyes, or *ocelli*, forming a triangle on the anterior surface of the head; the *antennæ*, which are tactile and olfactory; and the *tympanic membranes*, supposedly auditory in function, which are located latero-dorsally on either side of the first abdominal somite (Fig. 177).

General Activities. — Grasshoppers are active only in the daytime, although their relatives, the crickets and katydids (Fig. 191, p. 373), are nocturnal like many other insects. With the coming of nightfall the grasshopper remains quietly attached to the vegetation until the sun warms it into the renewed activities of another day. Since the grasshoppers have been extensively studied in attempts to combat them as foes of growing crops (Fig. 172), a brief account of their habits and life cycles, as related to agriculture, will be given.

Along the eastern approaches to the Rocky Mountains, for example, injurious grasshoppers may be grouped into two types, the migratory and the non-migratory species. The more serious injury to vegetation is usually caused by the migratory forms. This latter type, of which the "warrior" grasshopper (*Camnula pellucida*) is the most important species now that the Rocky Mountain locust has become virtually extinct, breeds in one locality and migrates to another. The non-migratory type, which includes all the common species, usually spends its entire life within the radius of a single field or, at most, in a very restricted area. Thus, a farmer who knows nothing of grasshopper control, or one who is indifferent, may breed the local plague that consumes his own fields and also those of his immediate neighbors, whereas

the descent of the migratory grasshopper is a "visitation" that can only be controlled at a distance and over a wider territory.

Migratory and non-migratory grasshoppers appear periodically in large numbers because of the fluctuations in the abundance of their enemies and in the environmental conditions which are favorable to their development. In a "plague" year it usually happens that the enemies multiply to a corresponding degree, since there are many grasshoppers upon which they may feed. As a result, the number of enemies is larger the next season with corresponding decrease in the number of "hoppers" that can reach maturity. Such a decrease in food supply in turn acts as a

FIG. 172.—Corn ruined by locusts.

(After Dean, from Bulletin No. 215, Kansas State Agr. Col.)

check upon the numbers of the enemies until the number of grasshoppers again increases, as it is likely to do over a period of years or in any season that presents unusually favorable conditions. There are probably enough eggs laid each year to produce a plague if all came to maturity, but this can only occur under exceptional conditions. Thus, cold, wet weather in spring destroys countless young grasshoppers, while hot and dry weather allows almost every egg to hatch and almost every young grasshopper to develop. Hence, it usually takes two or three favorable years for the "warriors" to reach destructive numbers, and there is little danger of their appearing again in the year following a serious outbreak.

The life history and migratory habits of the warrior grasshopper are representative of other migratory types. In Utah, for exam-

ple, the young hatch in May or June, depending upon the season. Within a few hours the migration begins. The grasshoppers travel toward the sun as long as it shines. If a cloud passes, they stop and gather in clusters in the dryer places. In cold or rain, they crawl under anything available or into crevices in the ground, until they may seem to have entirely disappeared, but they reappear with the sun. In parts of the foothills where it rains lightly on many afternoons, they will, therefore, follow the morning sun more than that of the afternoon and tend to travel in a southeasterly direction; but the distance and rate of the migration and even its direction is indefinite. As the wings have not yet developed, locomotion at this stage is effected principally by crawling rapidly over the ground, although the air is filled with hopping individuals as the swarm moves forward. When they happen to cross a cultivated field the plants are eaten even to the roots, yet the swarm passes on its march to what may be barren territory beyond, without destroying the grain that may stand on either side. At the time of the final molt when the larvæ are ready to be transformed into the adult, the individual stops and clings to some upright stem until the skeleton is cast and the wings are sufficiently dried for flight. The possibility of a high rate of increase, which is ever present in the grasshopper as in other insects, is, however, reduced to a minimum by various checks that keep the numbers within bounds save in exceptional seasons. The factors of the physical environment that are thus effective as checks upon increase are moisture and temperature, since the young will not develop in large numbers except in a dry, warm season. Frequent freezing and thawing also destroys the eggs in winter. Large numbers are destroyed by enemies and parasites. Mice, ground squirrels, moles, and skunks dig for the eggs. Insectivorous birds and also toads, lizards, snakes, and skunks devour large numbers of the young and adults. The larvæ of blister beetles are by far the most important insect enemies of the grasshopper (Fig. 173). These beetles lay their eggs in the ground, where they soon hatch into active larvæ with powerful jaws which seek out the grasshopper egg-masses, burrow into them, and begin to devour the eggs. Larvæ of bee-flies are a less important enemy of the same sort.

Among the parasites of grasshoppers is an insect that lays its eggs with the eggs of the grasshopper. In accomplishing this, the

female clasps itself to the body of the female grasshopper until

FIG. 173.—Insect enemies of locusts.

To the left, egg-masses of locusts (cf. Fig. 186 B) are shown; to the right, larvæ of blister beetles (cf. Fig. 197, p. 383) and of bee-flies that were found in the distorted remnants of the egg-masses shown as larger bodies. (From Farmers' Bulletin No. 691, U. S. Dept. Agr.)

the latter lays her eggs. As the grasshopper digs the hole (cf. Fig. 186), the parasite thrusts her long abdomen into the opening and lays eggs that hatch into parasites which enter the eggs of the grasshopper and develop at their expense. Likewise, the adult grasshoppers are destroyed in large numbers by the larvæ of other parasitic insects. These larvæ which may be found developing within the body cavity of the adult grasshoppers are the young of certain parasitic flies (cf. Fig. 198 A, p. 385) that lay their eggs upon the bodies or wings. The maggot which hatches from such an

FIG. 174.—Young locust stung by a wasp, *Priononyx atrata* (cf. Figs. 201 and 202, p. 388), and on which a parasitic fly, *Sarcophaga kellyi* (cf. Fig. 198, p. 385), afterwards deposited an egg.

(From Bulletin No. 293, U. S. Dept. Agr.)

egg bores into the body of the grasshopper and feeds until it is ready to be transformed into the adult. It then forces its way to the outside, killing its host. Again, there are species of wasps that capture grasshoppers and paralyze them with their stings

(cf. Figs. 201 and 202, p. 388). The paralyzed "hopper" is then carried to the burrow, in which the wasp lays its eggs attached to the body of the victim which thus serves as food for the developing larvæ. Fungus diseases are often epidemic, destroying large numbers of the young and adults (Fig. 175).

FIG. 175.—Locusts killed by a fungus disease.

(From Bulletin No. 172, South Dakota Agr. Exp. Sta.)

In a season when some or all of these checks upon increase fail to function to the usual extent, a plague of grasshoppers may occur. At such times various methods may be employed to combat the outbreak, such as poisoning the adults or burning the grass in

which the young have hatched in the spring. None, however, is so satisfactory as destruction of the eggs in the soil. This may be accomplished by plowing in the late fall or early spring in order that the eggs, which lie near the surface, may be turned under so deeply that the young cannot escape even if they succeed in hatching. Deep harrowing in spring and fall is also effective.

Internal Organization.—The internal structure is much the same in all species of grasshoppers and locusts. What follows is applicable in general to any of the common species, but particularly to the Carolina locust, *Dissosteira carolina*.

Body Wall and Hæmocœle. — Removal of the dorsal skeleton and underlying tissue discloses the digestive tract and other internal organs lying in a cavity which is a *hæmocœle* and not a true body cavity or coelome. Within this cavity, or attached to the body wall, are the internal organs. The spaces of the hæmocœle between the organs are largely occupied in the adult insect by an irregular mass of tissue known as the *fat-body*, which is the principal place of food storage. In insect larvæ, such as the caterpillars of the moths and butterflies, the fat-body becomes greatly devel-

FIG. 176.—Anterior end of locust showing digestive and nervous systems.

an, antenna; *an.n.*, antennary nerve; *br*, brain; *c.e.c.*, circum-esophageal connective; *cr*, crop; *e*, esophagus; *f.g.*, frontal ganglion; *hy*, hypopharynx; *l.n.*, labral nerve; *md*, mandible; *oc.n.*, nerve to eyes and ocelli; *op.g.*, optic ganglion; *s.d.*, salivary duct; *s.e.g.*, sub-esophageal ganglion; *t.g.l.*, first thoracic ganglion. (After Snodgrass, Educational Publications No. 2, Washington Agr. Col.)

oped as the larva stores up food against the time of its metamorphosis. Parasites that invade the body cavity of such insects feed principally upon this accumulated food of their hosts.

Digestive System. — The alimentary canal is almost a straight tube, extending from mouth to anus (*cf.* Figs. 176 and 180), although it is modified in different regions. The *hypopharynx*, arising from the base of the labium and just posterior to the mouth, has been mentioned in the account of the mouth parts. Upon the inner surface of the labium is a slightly elevated area, on which is located the sense of taste. The space included by the cranial appendages might be called a *buccal cavity* since it contains the

tongue-like hypopharynx. It is, however, entirely outside the digestive tract, and the true *mouth* is the opening just anterior to the hypopharynx. Opening into this buccal cavity on the anterior face of the labium, and just posterior to the hypopharynx, is the *salivary duct*, which leads from the *salivary glands* located in the thorax. The mouth, which is surrounded by a membranous peristome, leads into the *esophagus*, which passes dorsally as a narrow tube and enlarges into the thin-walled *crop* which extends posteriorly in the thorax almost at right angles to the esophagus. The crop tapers posteriorly, and where it leads into the *proventriculus*, which is the next division of the tract, there are six slender outgrowths, the *gastric cæca*, extending anteriorly and posteriorly from their points of attachment. The gastric cæca secrete a digestive fluid resembling the pancreatic secretion of a vertebrate animal. Posterior to the proventriculus is a division of the tract known as the *ventriculus*, which is the true stomach of the insect. The beginning of the *intestine* is not sharply separated from the ventriculus, but the place is indicated by the *Malpighian tubules* which arise in a circle at the anterior end of the intestine. These tubules are supposedly excretory in function. Posteriorly, the intestine is continued as the terminal portion of the tract, which is the *rectum*.

The animal bites off pieces of the grass or other vegetation with its mandibles, using the labrum and labium as upper and lower lips, respectively, and the maxillary and labial palps as tactile organs. A salivary secretion which is emptied into the cavity enclosed by the mouth parts serves as a lubricant in the swallowing of the food and perhaps as a digestive fluid after the food has reached the crop. As the name implies, the crop functions principally as a storage region. Some digestive changes may occur in its posterior end, but the proventriculus and ventriculus are the principal regions of *digestion*. The "molasses" that is extruded from the mouth when a living grasshopper is handled is the contents of these anterior portions of the digestive tract mingled with the digestive fluid of the gastric cæca. *Absorption* in this instance would be defined as the passage of the diffusible products of digestion, through the walls of the digestive tract, into the blood contained in the hæmocœle which surrounds the digestive organs.

Respiratory, Circulatory, and Excretory Systems. — The external openings of the respiratory system have been noted as the *spiracles* that occur on the segments of thorax and abdomen. Leading from the spiracles are the *tracheæ* or tracheal tubes. These consist of a complex set of larger tubules from which arise innumer-

A

B

FIG. 177.—Respiratory organs of locust, *Dissosteira carolina*.

A, tracheæ branching from spiracles of third thoracic segment to digestive tract as seen dorsally. B, anterior end of abdomen showing spiracles and tympanic membrane from lateral view. *ab.2*, second abdominal segment; *g.c.*, gastric cæca; *sp*, spiracle; *th.*, first thoracic segment; *ty*, tympanic membrane. (After Snodgrass, *loc. cit.*)

FIG. 178.—Heart of locust.

ao, aorta; *br*, brain; *d*, membrane ventral to heart, sometimes called the diaphragm; *h*, heart; *t.m.*, thoracic muscles; *tr*, tracheæ. (After Snodgrass, *loc. cit.*)

able lesser ones (Fig. 177). In the abdomen there are sac-like enlargements of the tracheæ, the *air sacs*, that serve as reservoirs. The lesser tracheæ branch and re-branch until they end blindly as microscopic subdivisions in all parts of the body. So extensive is this branching that no bit of tissue is far removed from one of these tracheal tubules.

The fact that the blood has no part to play in respiration probably accounts for the simple organization of the circulatory system in the grasshopper and other Insecta. In the Carolina locust, the *heart* is a slender pulsatile tube extending along the dorsal mid-line in the abdomen (Fig. 178) and closely applied to the skeleton. Ventral to the heart is the *pericardial sinus*,

FIG. 179.—Diagram showing course of circulation in larva of a dragon fly, *Epitheca*.

The flow of the blood through the heart (*h*) and aorta (*a*), and its course through the hæmocœles may be seen in the living animal as shown by the arrows. (After Kolbe, from Folsom, "Entomology," copyright, 1906, by P. Blakiston's Son & Co., reprinted by permission.)

which is separated from the general space of the hæmocœle by a horizontal membrane called the *diaphragm*. The heart, like that of other arthropods, possesses *ostia*, or paired openings guarded by valves through which the blood enters from the pericardium (cf. Fig. 156, p. 324, and Fig. 159, p. 331). From the heart the blood is driven into the *aorta*, which is an anterior prolongation extending through the thorax to the head. On leaving this aorta, the blood enters the general cavity of the hæmocœle, just as it does from the ends of the arteries in the crayfish. Being thus continuously delivered at the anterior end of the body and drawn into the heart in the dorsal region of the abdomen, the fluid of the hæmocœle, which is the blood, circulates slowly through the body from the anterior to the posterior parts, and thence

passes dorsally to the pericardium where it again enters the heart through the *ostia* (Fig. 179). Such a circulatory mechanism is far less efficient than the closed system of vessels that occurs in vertebrate animals and in annulates like the earthworm. It is, however, effective enough for insects, with their special mode of respiration. What may be called the blood of the grasshopper is, therefore, the colorless fluid contained in all the spaces

between the body wall and the digestive tract and also in any spaces within the appendages. The products of digestion pass through the walls of the digestive tract into the blood and thence by diffusion to all parts of the body, aided by the circulatory mechanism and by the respiratory movements of the abdomen. There are colorless cells, or *leucocytes*, within the blood, but no colored cells comparable with the red corpuscles of vertebrates.

The excretory system of the locust, like those of the majority of insects, consists of the *Malpighian tubules*, which arise from the anterior end of the intestine. In section, such a tubule is seen to be composed of large excretory cells enclosed by a peritoneum-like outer covering and surrounding a cavity. The cuticular layer that lines this cavity is perforated by canals and is continuous with the cuticle of the intestine and thus with the external skeleton at the anal opening. The Malpighian tubules extend into the hæmocœle. Their cavities are in communication with the intestine but not with the hæmocœle. The relationship

of their cells to the surrounding fluids is, therefore, not unlike that of the cells in the kidney tubules of a vertebrate or the nephridia of an earthworm. It is supposed that nitrogenous wastes are taken from the fluid of the hæmocœle and passed into the cavity of the intestine. The existence of this function is further indicated by chemical tests which show the presence of relatively large amounts of nitrogenous wastes in the Malpighian tubules. In some insects the fat-body is in part concerned with excretion, since it becomes a permanent storage place for nitrogenous compounds that are relatively insoluble.

FIG. 180.—Sections of posterior end of locust showing digestive and reproductive organs.

A, the female with ovipositors expanded. B, the male. a, anus; a.g., accessory glands; e.d., ejaculatory duct; e.g., egg guide; od, oviduct; ovp., ovipositor; p, penis; r., rectum; s.r., seminal receptacle; v, vagina; v.d., vas deferens. (After Snodgrass, *loc. cit.*)

Reproductive System. — Reference has been made to the external differences between males and females in the account of external features. The two *testes*, which occupy a position dorsal to the intestine and rectum, are composed of many tubules closely bound together. The tubules of each testis open into the anterior end of a *vas deferens* which passes on either side of the body to the *ejaculatory duct* (Fig. 180 B). This duct lies in a median ventral position and extends posteriorly and dorsally to the external genital opening at the base of the *penis*. The *accessory glands*, which communicate with the system at the anterior end of the ejaculatory duct, secrete a fluid that is apparently necessary in the transfer of the spermatozoa from male to female during sexual union. The parts of the female correspond to those of the male. The two *ovaries* are composed of tubules, each containing eggs arranged in a linear series from the earliest stages at the inner end of the tubule to those that are ready to pass into the oviduct. The paired *oviducts*, into which these ovarian tubules open on either side, unite in a median ventral portion, the *vagina* (Fig. 180 A). There is also a tubular structure, the *seminal receptacle*, which opens within the space enclosed by the ovipositor, and which may be compared with the accessory gland of the male. The spermatozoa received by the female at the time of sexual union are stored within this seminal receptacle until used for fertilization at the time of egg laying (Fig. 186).

Nervous System. — The nervous system of the grasshopper, (Figs. 176 and 181), like that of the crayfish and other arthropods (cf. Fig. 164, p. 337) consists of a dorsal ganglionic mass called the *brain*, a pair of *circum-esophageal connectives*, and a *ventral nerve cord* composed of paired ganglia and their connectives. The resemblance to the type of nervous system found in the Annulata (cf. p. 297) is obvious. It will be recalled that "connectives" are the antero-posterior connections between the ganglia of such a system, and "commissures" the transverse unions; and that one expects to find a pair of ganglia for each segment of the body. When such a pair of ganglia are completely fused they may be spoken of in the singular as a ganglion. In the Carolina locust, the brain lies dorsal to the anterior end of the digestive tract between the compound eyes (Fig. 181 A). It consists of a median mass and large lateral lobes, the *optic ganglia*, which are closely applied to the bases of the compound eyes. The

median portion, which is the brain proper, consists of three parts that are indicative of its origin in the embryo from three pairs of ganglia that have become intimately associated. Posteriorly, the brain is continued into the circum-esophageal connectives which extend on either side of the esophagus to the *sub-esophageal ganglion*. These connectives give rise to the nerves of the labrum, to a pair of nerves that unite posterior to the esophagus, and to a pair that unite on the anterior face of the esophagus in the *frontal ganglion*. From this ganglion there arises a *sympathetic system* of ganglia and connectives that innervates the digestive system.

The *sub-esophageal ganglion* is a compact globular mass without indications in the adult of its multiple origin, but its three pairs of nerves to the mandibles, the maxillæ, and the labium are indicative of its origin from three pairs of ganglia that have become intimately associated. In the thorax are three pairs of ganglia, corresponding to the three pairs of appendages and joined by connectives (Fig. 181 B). The larger size of the third thoracic

FIG. 181.—Nervous system of locust, *Dissosteira carolina*.

A, brain and circum-esophageal connectives from posterior-dorsal aspect (cf. Fig. 176), drawn on a larger scale than the ventral nerve cord shown in B. B, ventral nerve cord from dorsal view. *a.n.*, antennary nerve; *ab. 1*, *ab. 3*, and *ab. 8*, abdominal segments; *br.*, brain; *cec.*, circum-esophageal connective; *e.*, esophagus; *fg.*, frontal ganglion; *h.*, head; *ln.*, labral nerve; *oc.*, ocellar nerves; *op.g.*, optic ganglion; *te.*, tentorium, an internal portion of the skeleton; *th. 1*, *th. 2*, and *th. 3*, thoracic segments. (After Snodgrass, *loc. cit.*)

ganglion is to be correlated with its innervation of the metathoracic legs. Since it also sends nerves to the auditory organs, which are located in the first abdominal segment, and since there is no pair of ganglia corresponding to this segment in the abdomen, it is probable that this third ganglion of the thorax is actually the third thoracic and the first abdominal pair of ganglia of the embryo, fused to form a single large ganglionic mass with many nerves.

In the abdomen of the adult there are five ganglia. These, however, represent fusions of paired embryonic ganglia, particularly at the posterior end. The primitive arrangement, in which there is a pair of ganglia in each segment of the body is, therefore, indicated in this region as in the head and thorax. The nervous system of the grasshopper is composed in the fashion typical for arthropods and annulates, and the correspondence between the number of ganglia and the number of segments in thorax and abdomen is tolerably certain. In some adult insects and in many insect larvæ the antero-posterior fusions of ganglia are less developed than in the locust. In others there is a more specialized relationship, but even in such instances the system can usually be traced to paired ganglia corresponding to the somites in the embryo. The nervous system and the appendages are thus the two most important systems of organs through which light is thrown upon obscurities in the metamerism.

Sense-organs and Behavior. — The locust, like the majority of insects, is well equipped with sense-organs. The sense of *touch* is distributed over the entire surface of the body, although the antennæ, mouth parts, cerci at the posterior end of the abdomen and the distal segments of legs are particularly sensitive (*cf.* Fig. 182 Left). The seat of the sense of *taste* (*cf.* Fig. 182 Center), which is a median area on the anterior face of the labium or second, pair of antennæ, has been mentioned in the description of these appendages. Although the antennæ are primarily tactile organs, the sense of *smell* appears to be located in their basal region, as may be demonstrated by testing the reactions to odors and then coating the antennæ with paraffin (*cf.* Fig. 182 Right). In some insects, such as the moths, this sense must be highly developed, since the males will "come up against the wind" for long distances in search of the females. The greater development of the antennary hairs of the male moth and the fact that the males are unable to find the females when deprived of their antennæ

point to the seat of smell in these organs in the moths as in many other insects.

Like the majority of insects, the locust possesses a sense of sight (cf. Fig. 183). It sees not only by means of the *compound eyes*, which are homologous with the structures of this name in the Crustacea, but also by means of another type of eye, the *ocellus*.

FIG. 182.—Sense-organs of insects.

Left, longitudinal section of portion of caudal cercus of a cricket, *Gryllus domesticus*, showing type of hair (*sh*) supposedly tactile in function, with its innervation, and another type of hair that is bladder-like (*b*). Center, section through an organ of taste of an insect. Right, olfactory sense-organ from antenna of the grasshopper, *Coloptenus*, with innervation.

b, bladder-like sensory hair; *c*, cuticle or exoskeleton; *h*, hypodermis or epidermis; *m*, membrane, or thin portion of cuticle; *n* (left), nerve; *n* (right), nucleus of sensory cell; *ns*, non-sensory setæ; *nv*, nerve; *p*, olfactory pit with peg-like sensory process; *pg*, pigment; *sc*, sense cell; *sh*, tactile hair; *tc*, taste cup. (Left, after Vom Rath; center after Will, right, after Hauser. From Folsom, "Entomology," copyright, 1906, by P. Blakiston's Son and Co., reprinted by permission.)

The ocelli are relatively simple in structure, consisting of a thickened portion of the skeleton, which is transparent and functions as a lens in condensing the light, and beneath this a modified portion of the epidermis with which are connected the fibers of the ocellar nerve. In some instances, however, their structure is more complicated, as in the ocellus of a honey bee, shown in Fig. 183 C. In this instance the pigmented epidermis not only forms a cup beneath the lens, but is bent inward for a short distance, at the rim of the cup, in the manner of an iris. The capacity of such an eye for forming images must be limited, although it is constructed on a

plan similar to that of a vertebrate. The form of the lens is unchangeable, as is also the distance between the lens and the retina. There is, therefore, no possibility of adjusting the focal

FIG. 183.—Eyes of arthropods.

A, compound eye of crayfish in longitudinal section showing the numerous ommatidia. B, two ommatidia of crayfish showing details of structure. C, ocellus or simple eye of honey-bee in longitudinal section. *c*, corneal facet or external surface of ommatidium; *c.h.*, hypodermis cells of facet; *c.i.*, crystalline cone, proximal part; *c.o.*, crystalline cone, distal part; *f.o.*, fibers of optic nerve; *h*, hypodermis; *m*, muscle; *m.b.*, basal membrane; *n.c.*, nucleus of cornea cell; *n.d.* and *n.p.*, nuclei of retinal cells; *om*, ommatidium; *p.i.*, pigment of iris; *pg.b.*, and *pg.p.*, pigment; *r*, retinal cells; *rh*, rhabdome; *s*, skeleton; *v*, vitreous body. (A and B redrawn from Howes, "Atlas of Zootomy," copyright, 1902, Macmillan & Co., Ltd., printed by permission; C, redrawn from Folsom, "Entomology," copyright, 1906, by P. Blakiston's Son & Co., printed by permission.)

plane, and hence an object to be "seen" must be at a fixed distance. As the lens is usually very convex, the focal distance must be short and the vision by ocelli correspondingly near-sighted.

Moreover, the image that is formed upon the retina of an ocellus must be coarse, because of the very small number of the retinal cells. In the grasshopper, the ocelli are probably no more than organs of light perception with lenses that merely condense the rays of light. Thus, when the compound eyes are coated with black paint the animal will find its way out of a box in which there is only one small opening. After the ocelli, as well as the eyes, have been painted, it does not find the opening except by chance.

The structure of the compound eye is remarkable for its complexity, although such an eye is composed of many units, the *ommatidia*, which are similar in structure (*cf.* Fig. 183 A and B). As the diameter of each of these units is slightly less at its inner end, each ommatidium is perpendicular to the curved outer surface. The functioning of such an eye must be very different from that of the eye of a vertebrate. After much investigation and discussion of this subject, the "mosaic theory," which was proposed almost a century ago, is still generally accepted.

It is thought that an image is formed by thousands of separate points of light, each of which corresponds to a distinct field of vision in the external world. Each ommatidium is adapted to transmit light along its axis only, as oblique rays are lost by absorption in the black pigment which surrounds the crystalline cone and the axial rhabdom. Along the rhabdom, then, light can reach and affect the terminations of the optic nerve. Each ommatidium does not itself form a picture; it simply preserves the intensity and color of the light from one particular portion of the field of vision; and when this is done by hundreds or thousands of contiguous ommatidia, an image results. All that the painter does, who copies an object, is to put together patches of light in the same relations of quality and position that he finds in the object itself — and this is essentially what the compound eye does, so far as can be inferred from its structure.²

It appears that such compound eyes are especially fitted to perceive moving objects. It is a familiar observation that insects like grasshoppers are sensitive even to slight movements in their vicinity; yet they may be picked up with the fingers if the approach is made slowly until the animal is within the grasp. This may be explained on the assumption that the moving object stimulates different ommatidia in succession without the necessity of turning eyes or head as in the vertebrate, and that this successive stimula-

² Folsom, "Entomology," pp. 111-112.

tion must be at a certain rate to cause a response. A flying insect moving rapidly at some distance from the ground, as does the honey-bee in its homeward journey, would find such a form of vision well adapted to the recognition of the landmarks by which it is assumed the animal directs its course. In view of their structural relationships, it has sometimes been maintained that the compound eyes of arthropods have arisen as collections of specialized ocelli. This theory is now regarded as untenable by most students of the Arthropoda. It seems more probable that ocelli and compound eyes are both derivatives of primitive visual organs that existed in the common ancestors of insects and crustaceans.

That insects have a *color sense* in some instances can be shown by simple observations and experiments, but the range may differ from our own. Ants, for example, will avoid violet light as they will sunlight, and they seem not to distinguish red or orange light from darkness. Again, they are very sensitive to ultra-violet light, to which man gives no conscious responses. It also appears, although the odor may be presumed to be an additional factor, that bees and moths may be somewhat influenced by color in their choice of flowers.

Before considering the sense of hearing in the grasshopper and other insects, something may be said regarding the power of *sound production* which exists in almost every insect possessing structures that can be anatomically regarded as auditory organs. The sounds produced by the rapid vibrations of the wings, as in a mosquito, need not be considered, since they are incidental to other activities and are not caused by special sound-producing organs. An example of the latter, in an insect closely related to the grasshopper, is the *stridulating organ* of the katydid, *Microcentrum laurifolium* (Fig. 184). In the male, the left mesothoracic wing, which is developed as a wing-cover, bears an elongated ridge with many transverse elevations, the "file," and the right wing, a ridge-like "scraper." In sound production the wings are slightly separated, and as they are drawn lightly together the scraper is rubbed across the file, giving a series of sharp "tics" in rapid succession. The sound thus produced is a sex call by which the female is guided to the male. There is also a short "chirp" which may be made by opening the wing-covers. The chirp of a cricket is produced in a similar manner. There are many forms of stridulating organs in insects. In the common

locusts there are two methods of stridulation. When at rest, certain species draw the hind legs across the wing-covers in such a manner that the ridges on the femoral joint of the legs are rasped

FIG. 184.—Stridulating or chirping organs of katydid, *Microcentrum laurifolium*.

A, dorsal aspect of file (*st*) when the wing-covers are closed. B, ventral aspect of left wing-cover to show file. C, dorsal aspect of right wing-cover to show scraper (*s*). In the male the left wing-cover, which overlaps the right, bears a file-like ridge (*st*) while the opposite wing-cover bears a scraper (*s*) at right angles to the file. The wing-covers are first spread a little; then as they close gradually the scraper clicks across the teeth, making from twenty to thirty sharp "tic"-like sounds in rapid succession. This call guides the female to the male and when they are a few inches apart she makes now and then a short, soft chirp, to which he responds with a similar chirp, which is quite unlike the first call and, moreover, is made by the opening of the wing-covers. These and other details of the courtship may readily be observed in twilight and even under artificial light, as the latter, if not too strong, does not disturb the pair. (From Folsom, "Entomology," copyright, 1906, by P. Blakiston's Son & Co., reprinted by permission.)

against a specialized vein of the wing-cover. Or, during flight, they may rub the wings and wing-covers together, producing the characteristic "clacking" sounds. A familiar example of another

type of sound production is the "shrilling" of the cicada, or "seventeen-year locust," which is produced by the vibration of

membranes on either side of the most anterior segment of the abdomen and operated by special muscles.

The sense of *hearing* may be regarded as developed in correlation with the foregoing power of sound production. Indeed, the very presence of special sound-producing organs would be presumptive evidence that insects could hear even if one could not locate the special auditory organs (cf. Fig. 185). In contrast with vertebrate animals,

in which the ears are homologous structures and always located in the same region, the "ears" of insects are of several types and located in different places. They may occur, according to the species, upon the abdomen, the legs, the antennæ, and other portions of the body. In the grasshopper the tympanic membranes and associated internal parts are assumed to be auditory organs, more on account of their structure than from any direct experimental evidence, since they consist of a membrane against the inner surface of which are processes that are connected

FIG. 185. — Diagrammatic transverse section through anterior thoracic appendage of katydid, *Microcentrum rhombifolium* (cf. Fig. 191, p. 373), showing structure of the organ of hearing.

Outer chambers (OTC) communicate externally by the openings CS. A tympanum or drum (TYM) separates these two outer cavities from the single inner tympanic cavity (ITC). AC and PC with which sensory cells (SC) are connected. Vibrations in the air are transferred to the sensory cells shown by the arrows. AC, anterior portion of inner tympanic chamber; BL, blood vessel; BP, tracheal tube; CS, opening of cell; GC, secondary ganglion cells which relay impulse to central nervous system; ITC, inner tympanic chamber; MU, cross-sections of muscle; N, nerve; NU, nucleus of sensory cell; OTC, outer tympanic chamber; PC, posterior portion of inner tympanic chamber; SC, sensory cell; SH, shield that protects tympanum; STR, prop-like support of sensory cell; STY, sensory process of cell; TYM, tympanum; V, membrane between inner cavities. (After Dahlgren, *Natural History*, Vol. XXV, No. 3, courtesy of American Museum of Natural History.)

with nerves at their inner ends. The mechanism resembles the

eardrum of a vertebrate with its chain of bones and nervous connections (*cf.* Fig. 68, p. 125). In contrast with this condition

FIG. 186.—Egg-laying of locust.

A. locust laying eggs B. egg-mass in ground (After Webster, from *Farmers' Bulletin* No. 747, U. S. Dept. Agr.)

in the locust, or short-horned grasshopper, the auditory organs of the long-horned grasshoppers, like those of the katydids, are

FIG. 187.—Stages in hatching of a locust.

(From *Bulletin* No. 172, South Dakota Agr. Exp. Sta.)

usually located on the anterior pair of legs (*cf.* Fig. 191, p. 373). It is as though one vertebrate should have its ears on the abdomen and another closely related type should have a different kind of

FIG. 188.—Development of locust after hatching.

The animal hatches from the egg (*cf.* Figs. 187 and 189) in an immature condition and grows to adult size by a series of molts (*cf.* Fig. 169) as shown by A to F of this figure. (After Packard, from Linville and Kelly, "Textbook of General Zoology," copyright, 1906, by Ginn & Co., reprinted by permission.)

auditory organ on the fore limbs. Again, in mosquitos, certain hairs on the antennæ of the male are regarded as auditory, because they may be caused to vibrate sympathetically to the note of a tuning fork that is approximately the same as that of the hum produced by the wings of the female. In nature, it is probable that the male adjusts its flight so that the two antennæ are stimulated alike, and thus by flying straight ahead is able to locate his mate with precision.

In addition to the organs enumerated, there are many structures in insects that are presumed to be sense-organs because of their structure and nervous connections. This raises the question whether some insects may not possess sensory mechanisms that enable them to receive stimuli to which human beings give no response. Ants, for example, respond to ultra-violet rays, to which man is insensible. Perhaps there are stimuli in the universe "undreamed of in our phi-

losophy," to which insects respond by virtue of appropriate sense-organs.

Reproduction and Life Cycle.—The structure of the reproductive organs has been described, and mention has been made of the breeding habits in the paragraphs on general activities. The spermatozoa of the male locust are transferred to the female by

FIG. 189.—Young locusts feeding on clover.
(From Farmers' Bulletin No. 748, U. S. Dept. Agr.)

sexual union and stored in the seminal receptacle (Fig. 180 A). As the eggs lie in the vagina, preparatory to laying, the spermatozoa enter the minute opening at one end of the egg membrane, and the sperm nucleus unites with the egg nucleus in fertilization. In egg laying, the ovipositor of the female is thrust deeply into the ground (Fig. 186) and expanded to form a cavity in which are laid the masses of eggs, fastened together by a sticky secretion. With the withdrawal of the ovipositor and the collapse of the edges of the excavation, this egg mass is left just below the surface. When the young grasshoppers hatch in the spring they are thus near the

surface. Plowing a field destroys most of the grasshoppers, because the surface is turned under so deeply that the eggs are destroyed or the young cannot escape after hatching. The period of development within the egg membrane is termed the *embryonic period*. At the time of hatching (*cf.* Figs. 187 and 188), the young locust resembles the adult, although the head is relatively larger and the wings have not yet appeared. The individual develops by a series of molts until it reaches adult proportions. Such a mode of development may be termed *direct*, since there are no larval stages markedly different from the adult which must change or metamorphose to reach the final condition. In contrast with this, the development of the frog, with its tadpole stage (Fig. 11, p. 23), or that of the butterfly, with its caterpillar stage (Fig. 195, p. 380), is termed *indirect* development, or metamorphosis. The grasshopper is sometimes referred to as an insect with incomplete metamorphosis, but this is no more justifiable than to say a chick develops by incomplete metamorphosis, because at birth it is not exactly like the parents. It is true, however, that, taking the insects as a whole, one finds all gradations between direct development, like that of the locusts, and a most complete metamorphosis, such as is shown by the moths and butterflies.

CHAPTER 16

SOME REPRESENTATIVE INSECTS

The importance of the Insecta in the Animal Kingdom and their interest to man, whether as pests or as objects of beauty, warrant a more extended discussion than has been accorded to any of the classes in other phyla. The bewildering diversity of insect life makes it impossible to attempt more than a survey of the classification and structural modifications, with brief mention of habits and life cycles in a few representative examples. The description of any one of these types might be profitably extended, even in an elementary discussion. While the internal anatomy of insects presents many points of interest to the comparative anatomist, the more important feature of insect morphology is the modification of external structures in adaptation to diversified modes of existence and in correlation with the habits of the species. Again, insect life cycles cover a wide range of possible combinations in food and environment. As a culmination, the intelligence of some insects, such as the solitary wasps, and the social life that is so highly developed in the "white ants" and in some of the bees and true ants present the opportunity for much more discussion than is possible within the present limits. The account that follows deals rather concretely with special cases. Upon such a foundation it is believed that the student can best build a more extensive knowledge of this great group of animals and of the biological phenomena they are particularly suited to illustrate. There is, for example, no better basis for a general consideration of Ecology, or the relation of organisms to their environment, than such a knowledge of insects.

Classification and General Organization

Classification. — Opinion differs among students of the Insecta as to the exact number of orders into which this class of the Phylum

Arthropoda should be divided. The seventeen that follow represent one of the widely recognized classifications. Such a grouping is not absolute, however, since it expresses only the opinion of some investigators as to what differences are sufficient to justify

a separation of types. Certain students of the *Insecta* think otherwise, and hence may place in a single order some of the types that are here separated. Others recognize even a greater number of orders. As the list of orders is a long one, we may use a more formal arrangement than would otherwise be chosen. It will be noted that the character of the wings is the feature most commonly used in the names of the orders.

A

B

FIG. 190.—Wingless insects.

A, a silverfish, *Lepisma saccharina*, one of the Order *Thysanura*. B, *Achorutes armatum*, one of the Order *Collembola*. (A, from Farmers' Bulletin, No. 681; B, from same, No. 789, U. S. Dept. Agr.)

ORDERS OF THE CLASS INSECTA

Order 1, *Thysanura*. — These may be regarded as the simplest of existing insects, because of the absence of wings in embryo and adult together with other primitive features. Common examples are the household pests known as “fish-moths” or “silverfish,” *Lepisma* (Fig. 190 A). Mouth parts mandibulate. Development direct. Species 175.

Order 2, *Collembola*. — These are sometimes united with the *Thysanura* in a single order, the *Aptera*, since they are likewise wingless. They are known as “springtails” because of a tail-like projection on the ventral side of the abdomen by means of which they can spring into the air. A common representative is the “snow flea,” *Achorutes nivicola* (cf. Fig. 190 B), which appears on the snow in spring and is sometimes a pest to the maple-sugar makers. Mouth parts mandibulate. Development direct. Species 700.

Order 3, *Orthoptera*. — The locusts and related forms such as the long-horned grasshoppers, katydids (Fig. 191), crickets, cockroaches, and walking sticks are here included. Mouth parts mandibulate. Two pairs of wings, with the anterior pair usually modified by thickening. Development so direct that the term metamorphosis is hardly applicable, although it is sometimes referred to as “incomplete metamorphosis.” Species 10,000.

FIG. 191.—A katydid, *Microcentrum rhombifolium*, one of the Order *Orthoptera*.

The openings of the auditory organs are seen on the second segment of each anterior thoracic appendage (cf. Fig. 185, p. 366). (From a sketch by Bruce Horsfall, in *Natural History*, Vol. XXV, courtesy American Museum of Natural History and Ulric Dahlgren.)

Order 4, *Platyptera*. — The so-called “white ants,” or termites, which are not true ants, are the most familiar examples. Mouth parts mandibulate and relatively simple. Wings, if present, two pairs and membranous. Development direct. Species 225.

Order 5, *Plecoptera*. — The stone-flies. Mouth parts mandibulate. Wings, two pairs, membranous and coarsely veined. Development is direct; the eggs are laid in water and the larvæ develop there until the last molt, when the wings are fully formed and the adult insect takes to the air. Species 200.

Order 6, *Ephemera*. — The may-flies (Fig. 193), like the *Plecoptera*, lay their eggs in water, but the larval life is so prolonged that the adult flies may live but a day, hence the name *Ephemera*. Mouth parts mandibulate in larva but degenerate

in adults. Wings membranous, posterior pair smaller and rarely absent. Direct development in water. Species 300.

Order 7, *Odonata*. — The dragon-flies and the damsel-flies. Mouth parts mandibulate. Wings four, membranous, and minutely reticulate. Direct development in water. Species 2000.

Order 8, *Thysanoptera* (Physopoda). — This includes the insects known as thrips and related forms. Mouth parts suctorial. Wings

FIG. 192.—The periodic cicada, *Tibicen septendecim*, one of the Order Hemiptera.

The eggs are laid under the bark of twigs which are slit by the ovipositor of the female. After about six weeks the larvæ hatch, and drop to the ground into which they burrow. For seventeen years they live underground, feeding upon decaying material and juices from roots. Growth is very slow, and the larvæ probably molt only four to six times. They come to the surface of the ground, and crawl up on trees where the last molt occurs after the longest larval period known among insects.

Left: *a* and *b*, the adult; *c*, the molted skin of the last larval stage as it appears after the winged adult has emerged. Right: galleries made by larvæ when they come to the surface; *a*, front view with opening, *c*; and *b*, section showing larvæ, at *c* and *d*, within. (Left, from Circular No. 132, U. S. Bur. Entomology; right, from Bull. No. 71, U. S. Bur. Entomology.)

present, rudimentary, even absent in some species. Development direct. Species 150.

Order 9, *Hemiptera*. — These are the true “bugs,” such as the cabbage-bug (Fig. 194), the cicadas (Fig. 192), the aphids or plant lice (Fig. 200), the scale-insects (Fig. 306, p. 551), and water boatmen. Mouth parts suctorial. Wings usually present. Development direct with few exceptions. Species 18,000.

Order 10, *Neuroptera*. — The ant-lion, the dobson-fly or hellgrammite, and related forms are included in this order. Mouth parts mandibulate. Wings almost always four, completely reticulate. Development indirect, that is, with metamorphosis during a pupal stage. Species 600.

Order 11, *Mecoptera*. — This is an order comprising but few known species and none with common names. Mouth parts mandibulate. Wings four, membranous, coarsely veined. Development with metamorphosis.

Order 12, *Tricoptera*. — This order includes the caddis-flies and their relatives. Mouth parts of adult rudimentary, mandibulate in larva. Wings four, membranous, hairy, posterior pair usually the larger. Development with metamorphosis. Species 550.

Order 13, *Lepidoptera*. — The butterflies and moths (Fig. 195). Mouth parts suctorial in adult, but mandibulate in the larvæ, or caterpillars, which feed upon vegetation almost without exception. Wings four, similar, membranous, but covered with scales. Development with highly specialized metamorphosis in the pupal stage. Species 50,000.

Order 14, *Coleoptera*. — The beetles (Fig. 197 and Fig. 306, p. 551). Mouth parts mandibulate. Wings four, but anterior pair modified as wing-covers. Development with metamorphosis. Species 15,000.

Order 15, *Diptera*. — The true "flies." Mouth parts suctorial though modified in various ways, as in the house-fly (Fig. 198) and mosquito (Fig. 199). Wings two, representing the anterior pair; posterior pair rudimentary. Development with metamorphosis. Species 40,000.

Order 16, *Siphonaptera* (Aphaniptera). — The fleas and related insects, all of which are parasitic. Mouth parts suctorial in adult, mandibulate in larva. Wings absent or rudimentary. Development with metamorphosis. Species 150.

Order 17, *Hymenoptera*. — The ants, bees, and wasps (Figs. 200 to 207). Mouth parts both mandibulate and suctorial in same adult individual. Wings four, similar, membranous, and transparent. Development with metamorphosis. Species 30,000.

In the foregoing brief descriptions it will be noted that the mouth parts, the wings, and the mode of development have been chosen as the most important diagnostic features of the seventeen orders of the Insecta. A general comparison of the various orders indicates that the more generalized types of insects possess mandibulate mouth parts, and that even those orders in which the mouth parts are modified in other ways possess mandibles in their larval stages. In the simplest orders of Insecta (Thysanura and

Collembola) wings are absent even in the larval stages. In other insects that are wingless as adults, there are indications, as shown by the presence of wing rudiments in larvæ or adults, that two pairs of wings existed in the ancestors but have degenerated in the course of evolution. Thus there are typically two pairs of wings in the majority of insects. The specialization of the anterior pair of wings into wing-covers, as in the Coleoptera and to a lesser extent in the Orthoptera, and the reduction of the posterior pair of wings in Diptera are to be regarded as evolutionary modifications of the more typical four-winged state. Likewise, the simpler insects exhibit direct development. Hence, the extreme metamorphosis that appears in the Lepidoptera and some of the other more specialized orders has probably been evolved from the more direct, and therefore simpler, type of development. It should be said, however, that the worm-like body which appears in caterpillars and in the larvæ of other insects that exhibit considerable metamorphosis may represent the ancestral type suggested by *Peripatus* (*cf.* p. 339) and hence may be the survival of a primitive feature in these more specialized modes of development.

Body Plan and Characteristics of the Insecta. — The body plan of insects agrees in general with that of other arthropods (Fig. 164, p. 337) as illustrated by the crayfish, and *Peripatus* (Fig. 165, p. 339). The locust, like the crayfish, is a sufficiently generalized type to be representative not only of its own class but of the phylum as a whole. Like the Annulata, the Arthropoda are bilaterally symmetrical and metameric animals. The mouth and the anus open ventrally near the two ends of the body, which is usually elongated. The nervous system consists of the dorsal brain, circum-esophageal connectives, and a ventral nerve cord of paired ganglia with their commissures and connectives. The appendages of the arthropod are, however, more complex than the simple parapodia of annulates like *Nereis*, with which they are sometimes compared, since they may be highly developed and are so typically jointed as to have suggested the name "arthropod" for these joint-footed animals. The characteristic exoskeleton of chitin, sometimes thickened by additions of carbonate of lime, is formed as a secretion from the underlying epidermis and is molted in a characteristic manner. The cuticle secreted by the epidermal cells of most annulates (Fig. 145, p. 302) resembles the skeleton of the arthropod in its mode of origin. In

these features the arthropods clearly resemble annulates. On the other hand, the existence in arthropods of a hæmocœle instead of a clearly recognizable cœlome is in marked contrast with the condition that is so typical of the annulates. In correlation with this condition is the free communication between the blood vessels and the cavities of the hæmocœle, but the ostia of the arthropod heart are a unique feature of the phylum.

Some Representative Insects

Orthoptera. — Among Orthoptera, the *crickets* and *katydids* (Fig. 191) resemble the grasshoppers sufficiently in their general external features to be recognized as allied forms. The crickets that are most familiar are the house and field crickets of the genus *Gryllus*. The antennæ are long and slender in correlation with the nocturnal habits of these insects, and the hind legs are elongated for leaping as in the grasshopper. The posterior pair of wings is well developed, and the anterior pair specialized as wing-covers, but in many species the wings are reduced in size, and some crickets are wingless. In the males, certain veins of the wings are modified as the sound-producing organs (Fig. 184, p. 365). The “mole” cricket is a type having its anterior legs adapted for burrowing, like those of a mole. The katydids are like green grasshoppers with long antennæ. Their “Katy did, Katy did, she did, she didn’t” is a familiar sound in the evenings of late summer, for, like the crickets, the katydids are nocturnal in their habits. The life cycles of the crickets and katydids are similar to those of the grasshoppers. Most species have sword-like ovipositors by which they slit the stems of plants in which their eggs are laid.

Ephemera, Plecoptera, Odonata and Tricoptera.—The may-flies, stone-flies, dragon-flies, and caddis-flies, which are representative of their respective orders, may be mentioned together because of the similarity in their life cycles. With a few exceptions, the eggs are laid and the larval stages occur in water. At the final molting the insect comes to the surface and casts its skin for the last time, emerging as the fully developed adult insect. In the may-flies (Fig. 193) the larva can be recognized by the three long caudal appendages and gills upon the abdomen. After many molts and at least a full year of larval life, the adult stage is reached. This lasts but a few hours in

FIG. 193.—May-fly, *Polymitarcys albus*, one of the Order *Ephemera*.

Above, the female hovering with egg-packets extruding. Below, larval stage on a larger scale. (After Needham, from Bull. U. S. Bur. Fisheries, Vol. XXXVI.)

most species. During this brief existence sexual union occurs and the eggs are laid in packets which separate as they sink in the water. The name *Ephemera*, which refers to the ephemeral life of the members of this order, is therefore well chosen. The larvæ of *stone-flies* (Plecoptera) somewhat resemble those of the may-flies, but they are commonly found in streams, attached to the under sides of stones. The adult life is of much longer duration than that of the may-flies.

The adult *dragon-flies* (Odonata), or devil's darning needles and snake-doctors, are more familiar. Wonderfully efficient in their powers of flight, they skim the surface of the ponds in the heat of the day. Although they are often supposed by the ignorant to be dangerous, they are in fact very beneficial to man, since they destroy innumerable small flies and mosquitoes which they catch by darting at them in full flight. Hence the name "mosquito-hawk," which is sometimes applied to these insects, is more appropriate than the terms mentioned. The larvæ of dragon-flies, which are more clumsy than those of the may-flies and stone-flies, are found in ponds and streams, crawling awkwardly about upon the bottom. At the final molting they climb along the stem of a water plant into the air, and after the adult emerges the cast skin of the larva remains clinging to this support as evidence that its possessor has left the water and assumed the adult form. The damselflies, which are classified with the dragon-flies in the Odonata, are smaller and more delicate of body and wing.

The larvæ of *caddis-flies* (Tricoptera) are of interest because of the tubes that they construct by fastening together bits of débris with silken threads which the larva spins. In locomotion the head and thoracic segments, with their legs, are extended and the animal crawls along the bottom of the stream, dragging its tube. When disturbed it withdraws and lies motionless.

FIG. 134.—Life cycle of the Harlequin cabbage bug, *Murgantia histrionica*, one of the Order Hemiptera.

a, adult; b, egg mass; c to g, larval stages. (From Farmers' Bulletin, No. 1061, U. S. Dept. Agr.)

Hemiptera.—The squash-bug, *Anasa tristis* (cf. Fig. 194), which is a pest upon squash and pumpkin vines the country over, is perhaps known best by its disagreeable odor. It is representative of the true "bugs" with its sucking mouth parts and the wings showing the X-shaped pattern that is characteristic of so many Hemiptera. The adults hibernate over the winter, dying in the spring soon after the eggs are laid upon the tender sprouts of the vines where the young are destined to feed. The development,

like that of other Hemiptera, is direct. The young hatch as wingless individuals and undergo a series of molts (cf. Fig. 169, p. 345). They are often to be found in all stages from the newly hatched young to the adult with its fully developed wings.

FIG. 195.—Life cycle of the Monarch butterfly, *Anosia plexippus*, one of the Order Lepidoptera.

a, egg; b, larva or caterpillar; c, pupa; d, adult. (From Jordan and Kellogg, "Evolution and Animal Life," copyright, 1907, by D. Appleton and Co., reprinted by permission)

They feed upon the plant by piercing leaves and stems with their beak-like mouth parts and sucking the juices.

Lepidoptera.—Among the butterflies the monarch or milkweed butterfly, *Anosia plexippus* (Fig. 195), is one of our commonest native species. It ranges over all of North and South America and has begun the invasion of other lands, particularly Western

Europe, Australia, and the Pacific Islands. Correlated with this wide distribution are its great powers of sustained flight, its hardiness, and the wide distribution of the species of the plant upon which it feeds. It is also claimed that the monarch butterfly is not eaten by birds because it has a disagreeable taste, but this has been questioned. The eggs are laid singly upon the leaves of various milkweeds, and in a few days at summer temperature, hatch as minute larvæ. These feed voraciously and reach their full size in two or three weeks as handsome caterpillars with light-green bodies conspicuously banded with black and yellow stripes and with pairs of antenna-like filaments toward either end. The molt that closes this larval period produces the so-called chrysalis or pupal stage in which the distinctive adult features, such as wings and antennæ, are recognizable in a rudimentary state. The chrysalid is attached to the food plant by its posterior end. Although this stage is quiescent to all external appearance, profound changes are occurring internally, with the result that after ten or fifteen days the individual molts for the last time and emerges as the adult. The wings are soft and crumpled at first, but they expand and stiffen within a few hours as the butterfly clings to some neighboring object, and soon the monarch is ready to take its flight. There is one generation a year in the north and two in the south. In the fall the adults are either killed by the cold or wing their way southward to pass the winter as adult butterflies in sub-tropical regions, passing northward again in the spring. Other butterflies have different seasonal relationships. For example, some spend the winter in the pupal state, others as eggs that hatch in early spring.

The *moths* (Fig. 196), of which there are many species, differ from the butterflies in that they fold the wings horizontally and not vertically above the back when at rest, and fly by night instead of by day as do the butterflies. They also differ in the character of their antennæ. Again, the pupal stage of a butterfly is typically a naked chrysalid attached to some object, while that of a moth is surrounded by a cocoon of silk which is spun in the last larval stage before the molting into the pupa. When the pupal skin is molted within the cocoon of the moth, the adult individual emerges by forcing its way out of the cocoon and, like the butterfly, is ready for flight after the expansion and drying of the wings.

FIG. 196.—A study in ecology: the life cycle and relationships to other species of the true army-worm, *Cirphis unipuncta*, one of the Order *Lepidoptera* (cf. Fig. 305, p. 550).

a, parent or adult moth; *b*, full-grown larva; *c*, eggs; *d*, pupa in soil; *e*, parasitic fly, *Winthemia quadripustulata*, laying its eggs on an army-worm; *f*, a ground beetle, *Calosoma calidum*, preying upon an army-worm, and, at right, *Calosoma* larva emerging from burrow; *g*, a digger wasp, *Spheg* sp., carrying an army-worm to its burrow; *h*, *Encospilus purgatus*, a wasp-like parasite of the army-worm. All about natural size. (From Farmers' Bulletin, No. 731, U. S. Dept. Agr.)

Coleoptera. — The Colorado potato beetle, *Leptinotarsa decemlineata* (cf. Fig. 197 and Fig. 306, p. 551), is representative. Like other beetles, it has the anterior pair of wings specialized into heavy wing-covers, the *elytra*, which meet on the median line and fit so tightly together that they seem upon first examination to constitute the dorsal side of a wingless body. When, however, they are pried apart, the functional wings are found folded neatly beneath. In flight the wing-covers are widely spread and the wings unfolded to their full length, which is somewhat greater than that of the

FIG. 197.—Life cycle of a blister beetle, one of the Order *Coleoptera*.

The larvæ of blister beetles are among the most important enemies of grasshoppers (cf. Fig. 173, p. 351). (From Bulletin No. 172, South Dakota Agr. Exp. Sta.)

covers. This species was originally native to Colorado, feeding upon the sand-bur. With the coming of the early settlers, about 1850, it began to attack the potato and gradually spread eastward, causing consternation until Paris green and other insecticides brought it under control. By 1874 it had reached the Atlantic Coast and is now distributed throughout North America wherever there is extensive potato culture. In laying, the eggs are fastened to the leaves of the food plant. The larvæ hatch as hump backed grubs that feed voraciously and are very destructive to potato vines. When they have reached the end of their

larval stage they crawl down the plants and burrow in the ground before undergoing the molts that produce the pupæ. In a week or ten days this pupa molts into the adult which emerges from the ground to renew its depredations. In the latitude of Missouri, there are three such broods each year, the larvæ of the last one crawling underground to pass the winter. Taken as a group, the beetles, like the butterflies and moths, present a bewildering array of species adapted for many diverse conditions. Predacious beetles haunt the ponds and streams in larval and adult stages; others bore into wood, particularly in their larval stages. The June-beetles live in the ground as fat, white grubs, pupating in the spring and emerging as the adults which blunder against our lamps.

Diptera. — The house-fly, *Musca domestica* (Fig. 198), is perhaps the most familiar of all insects, and now that it has been recognized as a carrier of the germs of disease its life cycle is becoming widely known. Like other Diptera, it has only the anterior pair of wings, but the posterior pair are represented by the "balancers," which are believed to function in maintaining the equilibrium of the body. The ubiquitous habits of this species are well known. The mouth parts are adapted for biting and lapping, and the fly feeds upon almost any kind of organic matter that may be exposed in the household. As it may easily frequent exposed closets, drains, cuspidors, and similar places, a house-fly may carry on its feet and mouth parts the germs of typhoid fever or other diseases that have recently passed from a human patient. If it feeds at our tables a few hours later, there is great danger of infection; for it can be shown by letting a fly walk across a sterile plate of gelatin, such as is prepared for bacteriological studies, that almost every footprint is later marked by colonies of bacteria that spring up along its trail. House-flies lay their eggs in various forms of decomposing organic matter, but most readily in stable manure. The larvæ, or maggots, which hatch from these eggs in about six hours grow for five or six days before the pupation. The skeleton of the pupa is a tough membrane from which the adult fly emerges in about five days. In this manner a generation may be developed every twelve days under favorable conditions, and since each female lays about one hundred eggs the potential multiplication in a single season is appalling. House-flies hibernate over the winter in the adult stage by crawling into protected places. The slogan

"swat the fly" is a good one, but if we "swat" the first flies of the spring the results are all the more effective.

FIG. 198.—Representatives of the Order Diptera.

Above, *Sarcophaga kellyi*, larvæ of which are parasitic on grasshoppers (cf. Fig. 174, p. 351). Below, the house-fly, *Musca domestica*, showing adult, pupa (left) and larva or maggot (right). (From Farmers' Bulletin No. 459, U. S. Dept. Agr.)

Mosquitos have assumed great importance since it was discovered about 1895 that the parasite which is the cause of malaria passes a part of its life cycle in the body of certain species of

mosquito (*cf.* p. 207). Since then the structure and life histories of mosquitos the world over have been exhaustively studied. The mouth parts of the adult female are adapted for piercing the human skin and sucking blood, which is prevented from coagulating by the saliva. The mouth parts of the male cannot thus pierce the skin, and the males feed, if at all, upon the nectar of plants and other available fluids. As females may be fed upon bits of banana in the laboratory, it is supposed that they sometimes feed as do the males. But in addition to such food the female must attack some warm-blooded animal, since it is impossible for her to mature the eggs without such a meal of blood.

FIG. 199.—Life cycle of the mosquito, *Culex*, one of the Order *Diptera*.

1, egg; 2 and 3, larval stages; 4, pupa; 5, emergence of adult from pupal skin; 6, adult.
(From Bulletin No. 348, New Jersey Agr. Exp. Sta.)

It has been found that the malaria parasite is seemingly restricted to mosquitos of the genus *Anopheles* and that the genus *Stegomyia* harbors the parasite of yellow fever. The most common genus of temperate latitudes is *Culex*, which does not serve as a host to either of these parasites. The species of the genus *Culex* (Fig. 199) lay their eggs fastened together in little rafts that float upon the surface of the water. The larvæ that hatch from these eggs are the "wrigglers" commonly seen in rain barrels and small bodies of water where they hang suspended from the surface film by the tube at the posterior end of the body through which air is admitted to the tracheal system. If disturbed they wriggle downward and fasten themselves upon the bottom or some submerged object, but soon they float upward and again hang from the sur-

face. The larval stage of *Culex* lasts from one to four weeks, according to the species and to some extent the temperature and food supply. The food during this period consists of minute organisms that are captured by the mandibulate mouth parts. With their third molt these larvæ change into active but non-feeding pupæ in which the head and thoracic regions are enlarged and the wings and antennæ of the adult are foreshadowed as in the chrysalid of a butterfly (cf. Fig. 195). The pupæ must secure air from the surface as do the larvæ, but their air tubes are located on the dorsal side of the thorax. They rest at the surface, and when disturbed swim downward by movements of the abdomen, rising to the surface again by virtue of the air contained in the tracheal system, as do the larvæ. It is the necessity of obtaining oxygen by this means that enables one to kill mosquito larvæ and also the pupæ by covering the surface of the water with a thin film of oil which the respiratory tubes are unable to penetrate. After two to five days the pupal skin is cast and the adult emerges. While drying and hardening the wings, it rests upon the surface, often supported by the pupal skin. Other genera of mosquitos differ in their habits and in the details of the life cycle, but all undergo the same general structural changes as *Culex*.

Hymenoptera. — Like the Coleoptera and the Lepidoptera, the Hymenoptera present a vast array of types, ranging from those of relatively simple habits to species with a highly developed social organization like the honey-bee. The examples that follow illustrate this diversity. A type of hymenopteran that is familiar by its effects upon vegetation, although the adults are not popularly known, includes the *gall-flies*, or gall-producing insects. Familiar examples are oak-apples, or galls of oak trees, which result from the peculiar habits of these species. The adult female lays her eggs within an oak leaf by means of an ovipositor, which is adapted for piercing such tissues. The larva that hatches from this egg sets up an irritation which causes the abnormal growth of the plant that constitutes the gall. Within this protecting mass the larva develops, feeding upon the plant juices. After pupation and metamorphosis, which usually occur in the fall and winter, the fully formed insect gnaws its way out to liberty. Thus dead oak leaves are often found on the tree or ground, showing the opening from which the gall-fly has escaped.

The *ichneumon flies* (cf. Fig. 196 h and Fig. 200) somewhat resemble the gall-flies save that their larvæ are parasites in insects instead of living in plants. The reader has perhaps seen cater-

FIG. 200.—A study in ecology: an ichneumon, one of the Order *Hymenoptera*, laying its egg upon an aphid, Order *Hemiptera*, and the emergence of the adult parasite after completing its development within the aphid.

(After Webster, from Circular No. 107, New Jersey Agr. Exp. Sta.)

pillars that were covered with minute cocoons and evidently dying. In such instances the caterpillar has been attacked by an ichneumon which, in laying its eggs, has attached them to the surface of its host or, more rarely, has placed them within the body. When the ichneumon larva hatches it burrows within the body of the host and lives as a parasite until its time of metamorphosis, when it comes to the surface and spins the cocoon that is seen externally. From this the adult fly emerges, while the host dies, if it has been heavily parasitized. There are many variants in this cycle in different species, but the essential features are the same. We think of the ants, bees, and wasps as constituting a majority of the Hymenoptera, although it is a fact that the parasitic species far outnumber these better-known forms.

FIG. 201.—Solitary wasp, *Sphecius*, flying with a cicada which it has paralyzed and is carrying to its nest (cf. Fig. 202).

(After Riley, Bulletin No. 71, U. S. Bur. Entomology.)

The *wasps* may be subdivided into the solitary species, in which

there is no colonial organization, and the social wasps, which live in colonies like those of bees and ants. As an example of the solitary type, the *mud-daubers* of the genus *Pelopæus* are frequently seen collecting the mud beside some nearby puddle and patiently making their trips to the protected spot, within the house or porch, that has been selected as the site of their building operations. The nest is usually in the form of several tubes, about an inch in length and placed side by side. When one of these tubes is completed

FIG. 202.—Solitary wasp, *Ammophila*, provisioning its burrow.

Left above, dragging to the burrow a caterpillar that it has paralyzed. Right above, burrows with same species of caterpillar shown on a smaller scale. Below, excavation of the burrow. (From Hartman, Bulletin No. 65, University of Texas.)

the wasp collects small spiders, which it paralyzes by its sting and brings to the nest (*cf.* Fig. 201). Having filled the tube with prey, she lays a single egg, which is attached to the topmost spider, before each tube is sealed. When the larva hatches, it utilizes the spiders as food, and after pupation gnaws its way out as the adult insect. Only the females are active in this nest-building operation, the males apparently dying soon after the mating by which the females receive the spermatozoa that are used in the fertilization of the eggs as laid. The digger wasps that excavate burrows, which they provision with insects (Fig. 202), and those that excavate tunnels

in the pithy stems of plants present further examples of this interesting habit.

Among *social wasps*, the species of the genus *Polistes* (Fig. 203) represent a simple type of organization. These build nests of "paper," obtained by the reduction of woody material to a pulpy mass somewhat after the manner of human paper-making, although the paper mill of the wasp is its mouth parts. The

FIG. 203.—Social wasp, *Polistes bellicosus*, and nest.

(After Harman, *loc. cit.*)

female, after hibernating through the winter, begins in spring or early summer to construct the nest, which is suspended by a short stem and arranged as a single layer of "cells" placed side by side in a "comb" with additions at the margin. By the end of the season, this nest may reach a diameter of ten or twelve inches. The single female, or queen, which begins this construction, is soon aided in tending the young and adding to the comb by other individuals, the "workers," which hatch from her eggs. When the larvæ are full-grown and ready to pupate, the top of the cell is sealed with paper through which the larva breaks upon

emerging. The males are drones which do not work and die soon after mating. In the fall, only functional females survive. These may be seen in large numbers in attics and similar places which they seek for the winter hibernation. *Polistes* thus presents a simple form of social organization. The nests of yellow-jackets and the nests of hornets that hang from the limbs of trees are composed of a series of combs resembling those of *Polistes* but enclosed in a common covering.

Among the *bees*, there are solitary and social species and others that present transitional stages. Hence, it is possible to picture the steps by which the highly organized communal life of a

honey-bee colony may have arisen in the course of evolution. In the solitary species each female constructs her own separate nest in which an egg is laid and which is stored with food. In other cases food is brought to the larva during this period of the devel-

FIG. 204.—The honey-bee. *Apis mellifica*.

Above, a, worker or sexually immature female; b, queen or sexually mature female; c, drone or male. Below, left, egg (a), larval stages (b and c), pupa (d); middle, comb showing some larger queen cells; right, side view of late larval stage within cell. (From various publications of U. S. Dept. Agr.)

opment. Some of these solitary species, however, show a tendency toward gregariousness that suggests the beginnings of social life. They build many nests close together, although each is the property of a single individual. In others the nests are separate, but the "neighbors" coöperate in the construction of a common entrance. The *bumble-bees* represent a more specialized

organization in which the females have become differentiated as queens and workers, and the males as drones, as is almost invariably the case in social insects. Thus, in the bumble-bees the females that have mated with the males in the fall survive the winter by hibernation as do the females of *Polistes*. In the

FIG. 205.—A swarm of bees clustered on a branch.

(From Farmers' Bulletin No. 1198, U. S. Dept. Agr.)

spring each of these queen bees finds a deserted burrow of some field mouse or similar animal, or excavates one for herself. She then deposits her eggs upon a pasty food mass made of pollen and honey that she has gathered from flowers. She tends the larvæ as they grow in the waxen cells she has made, collects more food, and lays more eggs. The larvæ pupate in silken cocoons from which they emerge as the modified females that are the workers. These are incapable of egg production, but they carry on all the other activities of the females. The males are drones, and are useless in the economy of the hive except in mating with

the functional females. In the fall the workers and the drones die and a few young queens that have mated, and therefore contain in their seminal receptacles the spermatozoa with which to fertilize their eggs the following season, survive the winter by hibernation and thus continue the species. The bumble-bee's nest may reach six inches in diameter and consists of irregularly arranged cells of wax, some of which contain pollen and a few, honey.

A colony of *honey-bees* (Figs. 204 to 206), with its combs filled with honey collected by the workers and stored as food, the

single fertile female or queen that lays eggs and is tended by the workers, and with many drones, may be regarded as a further specialization of such a state as that seen in the bumble-bee. The specialized structures and habits of the workers of a honey-bee colony are remarkable, as are also the activities of the queen. Food is collected and stored, the young are tended and fed, the integrity of the colony with its single queen is maintained by the killing of supernumerary queens or by the swarming of many workers with the old queen to found a new colony, leaving part of the old colony to rear a new queen. The honey-bee has been extensively studied because of its importance to man. Instead of undertaking a specific account of its habits and life cycle, we have here presented the stages through which such bees have probably passed in the evolution of their colonial life. Among the many fascinating problems that are presented by the honey-bees are the behavior of the individuals, which is

FIG. 206.—A collector of honey in ancient times.

(From a pre-historic rock painting in Valencia, Spain. After Obermaier, courtesy of the Hispanic Society of America.)

a marvel of precision and seeming adaptation of means to ends, but in reality consists of stereotyped processes based upon inherited reflexes that are modifiable only within the narrowest limits; the problem of how the characteristics of workers can have arisen and become inherited, since the workers leave no descendants; and the problem of the evolutionary origin of such a society through stages like those indicated.

The *ants* (Figs. 207 and 208) are even more specialized in their communal life, since there are no existing examples of solitary ants, and since the workers of most ant colonies are specialized into two or more "castes" adapted for special activities. Ant

colonies, particularly in some of the tropical species, may assume huge dimensions, both in the size of the domicile and in the number of individuals, but the essential features of the social organization are illustrated by many of our native forms. In a typical example, the males, which are winged throughout their brief existence, participate in the mating flight with the females and then die. These females then pull off their wings and establish nests of their own

FIG. 207.—The little black ant, *Monomorium minimum*.

a, male; b, pupa; c, wingless female; d, winged female; e, worker or sexually immature female; f, larva; g, eggs; group of workers in line of march below. (From Farmers' Bulletin No. 740, U. S. Dept. Agr.)

by laying eggs and tending the young until workers that can carry on these labors develop. When the mating season approaches, the winged males and females, the latter being the queens, are produced and leave the nests in the swarms that are seen at certain seasons of the year.

The ants, bees, and wasps are therefore of particular interest because of the development of their social life and their seeming intelligence. From the standpoint of social organization, the

insects represent the one other part of the Animal Kingdom in which anything approaching the complexity of human society exists.¹ From the standpoint of animal intelligence, the social insects are interesting for the extreme development of their "instinctive" forms of behavior, which are interpreted as inherited reflexes so definitely fixed in their nature that they are automatic and hardly modifiable. Intelligence, in the sense of indi-

FIG. 20S.—A study in ecology: showing how ants foster the corn root aphid.

These aphids, which are cared for by the ants in their nests during the winter, are carried through tunnels to the corn plants and placed on the roots in the spring. Hence, anything that will disturb or destroy the ant colonies of a field will reduce the number of aphids and promote the growth of corn (cf. Fig. 305, p. 550). (From Farmers' Bulletin No. 891, U. S. Dept. Agr.)

viduality and modifiability of responses, is better represented by forms like the solitary wasps and the ichneumons, although even here the individuality that has been claimed by some students of their activities is perhaps exaggerated.

In concluding this account of the Insecta as members of the Phylum *Arthropoda*, we may recall the points of resemblance

¹ Elaborate societies are also found among the "white ants," or *termites*. As these are not Hymenoptera but members of the Order *Platyptera*, their social organization must represent an independent evolution.

between the body plan of the Crustacea and that of the Annulata (*cf.* p. 336); and the structure of the Onychophora (Fig. 165, p. 339), which on the one hand resembles that of the Annulata, and on the other the organization that may have existed in the ancestors of the Insecta (Fig. 164, p. 337). This resemblance between Annulata and Arthropoda may not be thus significant, but it is suggestive of a relationship that may have existed in the remote past when the Arthropoda began to be differentiated into the great classes that have since grown and flourished in the ocean, in fresh water, and upon the land surface. As with other phyla, the evidence points to the ocean as the primitive habitat. There are many parallels between Insecta and Chordata in this apparent evolution from marine to terrestrial environment. Having become adapted to life upon the land surface, many insects, like the water beetles, have returned to the water for a part or the whole of their life cycles, as have the seals and whales among the Chordata; but their mode of respiration and other features tell the story of their ancestry. Since they have become so well established upon the land, it is not surprising that a high degree of social organization has been evolved in some types of insects and that there has been a marked increase in intelligence in insects and spiders over anything exhibited by the Crustacea, which are predominantly aquatic. The small bulk of the individual body among Insecta is a factor limiting their evolutionary advancement as compared with the terrestrial vertebrates, but the advantages in rapid reproduction and the innumerable ways in which animals of smaller size can become adapted to the conditions of environment are partial compensations. Alone of all the animal types, the insects among the Arthropoda compete with the terrestrial vertebrates for possession of the land surface, and they may even yet become the dominant forms of terrestrial life when man and his mammalian relatives have run their course.

CHAPTER 17

DEVELOPMENT OF THE FROG AND OTHER VERTEBRATA

The distinction was made in earlier chapters between reproduction, or the origin of a new individual, and development, or the process by which a fertilized egg undergoes cell division and differentiation to form a many-celled animal. Examples of development have been seen in the representative animal types that have been described. We shall now undertake a more intensive study of this important biological process, as specifically illustrated by vertebrates, and of some of the more general problems involved. The frog is selected for special study because we have become familiar with its adult organization and because its developmental stages have long been favorite objects of study for the zoologist. Moreover, the development of the frog is representative of what occurs in vertebrates, since the early stages are less modified by the presence of yolk than are the eggs of fishes, and the later stages are not complicated by the special conditions that exist in reptiles, birds, and mammals. It might be supposed that fishes would represent the simplest mode of development in the backboneed animals; but the egg of the fish has a relatively large amount of yolk and is quite specialized, although it develops into an adult which is the simplest type of vertebrate animal. To find a mode of development that is simpler than the frog's, it is necessary to disregard the fishes and examine the protochordate type, *Amphioxus*. As this animal presents interesting points of comparison, its development will be briefly described before the account of the amphibian is begun. Briefer accounts of development in the fishes and in reptiles, birds, and mammals are included, and a discussion of general problems in development is undertaken in the chapter that follows. Throughout all this discussion the importance of the cell will be apparent, since development is a process of cell division and differentiation.

Development of Amphioxus (*Branchiostoma lanceolatum*)

Reference to the table of classification on page 36 will show the position of amphioxus as a member of the Phylum *Chordata*. The adult animal (Fig. 4 B, p. 13) does not exceed two and one-half inches in length. It lives in shallow water, burrowing in the sand or swimming for short distances by fish-like movements of the fins and body. The *mouth* is located at the anterior end, surrounded by a fringe of *oral cirri*, while the *atrial pore*, or opening by which the excurrent respiratory water leaves the body, is located at about the position of the anus in most fishes. The true *anus* opens internally into the atrial cavity. The tubular *central nervous system*, with its dorsal position, the *notochord*, *gill slits*, and other structures mark the animal as unquestionably a chordate. It is particularly interesting because its structure is suggestive of an organization antecedent to that of the vertebrates.

The sexes are separate in amphioxus, and the ova and spermatozoa are discharged through the atriopore into the water where fertilization occurs. Cleavage (Fig. 209 and cf. Fig. 213) produces a symmetrical blastula, with the animal hemisphere composed of small cells and with somewhat larger cells toward the vegetative pole. Gastrulation occurs by a simple invagination, as in other cases where the egg has only a small amount of yolk distributed throughout the cytoplasm (homolecithal). The two-layered sac that is thus formed elongates as the blastopore becomes reduced in size, while a differentiation of the ectoderm cells marks the future nervous system on the dorsal surface of the body. Transverse sections of this stage show that the ectoderm and endoderm are being further differentiated into the beginnings of the *nervous system*, the *notochord* and the *cælome*, while the *archenteron* is becoming converted into the digestive tract. In longitudinal and transverse sections at a later stage, the typical chordate organization is apparent. Amphioxus, therefore, develops by cell division and differentiation from a single cell to a many-celled organism, like all other metazoa. The sequence of events in this development are well known, but the causes of the many steps, as, for example, the conditions that bring about gastrulation, notochord formation or the differentiation of the neural plate at a particular stage of the development, remain for the most part unsolved problems for the experimental embryologist.

FIG. 209.—Development of amphioxus, *Branchiostoma lanceolatum*.

A, zygote. B, cleavage stage. C, blastula in section. D to I, transverse sections showing origin of neural tube or central nervous system, notochord, and mesoderm. J, section in median plane of future adult (cf. E, F, and L). K, transverse section of a stage (cf. G, H, and I) in which the coelome has appeared. L, section in median plane and with the segmental arrangement of the mesoderm shown (cf. K). bp, blastopore; c, notochord; coe, coelome; e, archenteron; ec, ectoderm; en, endoderm; m, mesoderm; m.s., mesodermal segment; n, neural canal; ne.c., neurenteric canal; np, neuropore; n.t., neural tube; p.b., polar body; sc, segmentation cavity; s.t., tail of spermatozoön. (After Hatschek, with modifications from Cerfontaine.)

Development of the Leopard Frog (*Rana pipiens*)

Breeding Habits. — The eggs of the leopard frog are laid in the spring soon after the animals emerge from hibernation. Temperature seems to be an influential factor, since an early spring or one that is cold and late correspondingly advances or retards the date of spawning. Similar differences are observed in the period of egg laying in shallow ponds that are easily warmed by the sun, as compared with ponds and streams that are fed by springs and hence are lower in temperature. Previous to the egg laying, the male clasps the female tightly with his fore limbs, partially encircling the anterior end of her body and using the hind limbs only to help maintain the position on the dorsal surface of his mate. Such a process of sexual union is known as *amplexus*. The individuals remain in this position throughout a period of many hours, during which the eggs are extruded from the female and fertilized in the water by spermatozoa emitted by the male.

Reproductive Organs and Germ Cells. — It will be recalled (Fig. 30, p. 52) that the *ovaries* of the frog are paired organs attached by a mesentery to the dorsal face of the coelomic cavity, and that the *oviducts* are convoluted tubes opening anteriorly to the coelome and posteriorly to the cloaca. Internally, the ovaries are divided into compartments (Fig. 210) from the walls of which protrude the *ova*, surrounded by a single layer of *follicle cells* and the thin layer of cells by which the ovum is attached to the wall of the compartment. In their early stages within the ovaries, the ova are small cells with a centrally placed nucleus. As growth proceeds, yolk granules are deposited in the cytoplasm, particularly on the side that will be the lighter-colored or vegetative portion of the mature egg, and the nucleus becomes shifted to an eccentric position in the animal portion. While these changes are taking place the surface of the animal hemisphere becomes darkened by the deposition of pigment in the outermost region of its cytoplasm. In this manner the egg acquires, while still within the ovary, a "polarity" along an axis connecting the centers of its two hemispheres, so that one speaks of the animal and vegetative "poles" and their respective "hemispheres." This polarity acquired by the ovum within the ovary is believed to be definitely related to the body axes of the future animal (*cf.* Fig. 213).

At the time of *ovulation*, or discharge of eggs from the ovary,

the ova that have been matured for a given season burst through their coverings of cells (*cf.* Fig. 210) and through the outer wall of the ovary, to become free in the cœlomic cavity. In the cœlome they are carried by the cilia of the peritoneum to the funnel-like openings of the oviducts. The epithelium of the oviducts is also ciliated, and thus the eggs are conveyed to the *ovisacs* (*cf.* Fig. 30, p. 52) at the posterior end of either oviduct, where they accumulate before the act of laying. It is during their passage along the thicker-walled and convoluted region, composing the greater portion of the

FIG. 210.—Section through a lobe of the ovary of the frog.

b.v., blood vessel; *c.o.*, cavity of ovary; *f.c.*, nucleus of follicle cell; *o.1*, *o.2*, *o.3*, *o.4*, and *o.5*, stages in development of ova; *p*, pigment of animal hemisphere; *v.p.*, visceral peritoneum; *w.o.*, wall of ovary.

female duct, that they become coated with the gelatinous secretion which is so conspicuous a feature of the eggs of frogs and other Amphibia as they are usually found in the water. When first secreted by the oviducts, this jelly is merely a sticky fluid surrounding each individual ovum, but within a few hours after the eggs enter the external water it becomes swollen and assumes the character of a thick gelatinous covering which persists until it disintegrates after the hatching stages of the tadpoles (*cf.* Fig. 11, p. 23). When the jelly has thus swollen to its full dimensions (Fig. 211) it is seen to consist of two outer layers, of about equal thickness, and a thin inner layer that is closely applied to the *vitelline membrane*. The latter has by this time become completely sepa-

rated from the surface of the ovum, forming a perivitelline space.

FIG. 211.—The frog's egg with its layers of jelly.

1, 2, and 3, the three layers of jelly; *m*, vitelline membrane; *p.b.*, polar bodies; *s.t.*, pigmented track left by nucleus of spermatozoön as it moved toward the nucleus of ovum (cf. Fig. 213 A to C).

to the layer of pigment that lies just of the animal hemisphere (Fig. 212 B). The sun's rays may also be somewhat focused by passing through the curved surfaces of the jelly layers.

The *testes* of the male reproductive system, as described in Chapter 3 (Fig. 30, p. 52), are a pair of small bodies attached by a mesentery near the anterior end of the kidneys. The *spermatozoa*, which are produced within the testes (Fig. 212 A), arise from primordial germ cells by a process similar to that described

The egg is therefore encased by the jelly, but free to rotate within a central cavity; and since the vegetative pole is the heavier, the developing egg normally remains with the darker-colored animal pole uppermost. Although the function of the jelly is obviously protective, there is evidence that it also tends to raise the temperature of the egg by allowing free entrance of the sun's rays and checking the heat radiation, after the manner of the glass covering of a hot-bed. A similar function has been ascribed

FIG. 212.—Gametes of the frog. A, two spermatozoa. B, an ovum in section showing pigment of animal hemisphere, nucleus, and yolk granules in cytoplasm. The magnification of A is much greater than that of B.

in general terms in a preceding chapter (*cf.* p. 224). From the testes the sperm are conveyed by the *vasa deferentia* to the kidneys, whence they pass to the *ureters*, which function as ducts for both excretory and reproductive products. Thus the spermatozoa, like the ova, accumulate in terminal portions of the reproductive ducts before their actual discharge during the spawning. In the act of spawning the eggs pass slowly from the anal opening of the female while sperm are emitted into the neighboring water by the male. The union of ovum and spermatozoön, therefore, occurs in the open water between the germ cells of individuals that are paired in sexual union. Males that are unattached to females will sometimes emit spermatozoa upon egg masses that have been laid some hours previously, but the swelling that has taken place in the jelly usually prevents the entrance of such spermatozoa into any eggs that have not been fertilized at the time of laying.

Maturation, Fertilization, and Organization of the Zygote. — At the time of ovulation, the egg cell is naked save for the thin vitelline membrane produced while it is still within the ovary by the cells of its follicle. The jelly, as we have seen, is a secretion from the oviduct. The *first maturation division* (*cf.* Fig. 114, p. 228) begins about the time the egg enters the coelome and is completed before it reaches the ovisac. As a result, the *first polar body* appears during the passage through the oviduct as a small cell at the animal pole of the egg (*cf.* Fig. 211). In the frog, this first polar body does not divide into two cells, as shown in the schematic representation of maturation (Fig. 114, p. 228). The *second maturation division*, by which the *second polar body* is formed, does not occur until after the spermatozoön has entered the egg at the time of fertilization. By means of these two nuclear divisions, which form the first and second polar bodies, the number of chromosomes of the frog's egg is reduced one-half, in the manner described in the general account of maturation. The maturation of the spermatozoön occurs within the testis, as indicated in general by Fig. 113, p. 226. Thus, the nucleus of the ovum and that of the spermatozoön come to possess the haploid number of chromosomes, and by the union of these two haploid groups at the time of fertilization, the diploid number is restored.

In fertilization as it occurs in the frog, a spermatozoön enters the egg in the animal hemisphere somewhere in a zone from forty-five to ninety degrees from the animal pole. The nucleus of the

spermatozoön then moves toward the nucleus of the egg (Fig. 213). Before the entrance of the spermatozoön the egg is radially symmetrical around its polar axis, but during the fertilization a bilateral symmetry is established. There are further changes in the egg as the male and female nuclei approach one another. As seen in the plane of section shown by the figure, the cytoplasm becomes differentiated by segregation of its material into several regions, with the result that, even before the division of the zygote begins, it is possible to recognize the portions of the egg from which the ectoderm, endoderm, mesoderm, nervous system, and notochord will arise in the subsequent development. Although this point is difficult of determination, it also appears that the plane of bilateral symmetry in the adult animal coincides approximately with the bilaterality that is established by the entrance point of the spermatozoön and by the areas into which the cytoplasm comes to be differentiated. The anterior and posterior, dorsal and ventral regions, and other parts of the adult body may be traced through the subsequent stages. In this manner an organization, which foreshadows that of the adult animal, is developed within the cytoplasm of the zygote in advance of any cell division.

Cleavage.—The cell division, or cleavage, by which the zygote is transformed into a many-celled individual, begins soon after the union of the male and female nuclei, by a division of the cell into equal halves, in a plane that passes through the polar axis (Fig. 213 D). The external furrow of this *two-cell stage*, which begins at the animal pole and extends downward on either side until it encircles the egg, is the final stage by which the cytoplasm of the cell is divided following the division of the nucleus. In most instances the plane of this first cleavage seems to coincide with the plane of symmetry already established by the areas of cytoplasmic differentiation that have been described. Hence the right and left halves of the future embryo are usually represented by right and left cells in the two-cell stage.

The second cleavage, by which the *four-cell stage* is produced, is at right angles to the first along the polar axis (Fig. 214). The third cleavage, which forms the *eight-cell stage*, is at right angles to the previous ones in a plane parallel to, but somewhat above the equator. It thus separates four smaller, darkly pigmented cells toward the animal pole from four larger, lighter-colored cells in the vegetative hemisphere. From this time onward, the

FIG. 213.—Development of the frog, showing orientation of the zygote in relation to that of the tadpole as it appears in the median plane.

The polar axis of the egg is shown by the arrow. It will be noted that this shifts almost 180 degrees in the development from *A* to *I*. *A* and *B*, entrance of spermatozoön and beginning of differentiation of cytoplasm into areas that foreshadow certain adult structures. *C*, approach of egg and sperm nuclei and further differentiation of the cytoplasm. *D*, two-cell stage. *E*, eight-cell stage. *F*, early blastula. *G*, gastrula. *H*, transition from late neural-fold stage to early embryo. *I*, early embryo.

A and *P*, *D* and *V*, anterior-posterior and dorso-ventral axes; *bp*, blastopore; *c*, notochord; *e*, archenteron; *ec*, ectoderm; *en*, endoderm; *m*, mesoderm; *mo*, mouth; *n*, nerve chord; ♀ *n*, nucleus of ovum; ♂ *n*, nucleus of spermatozoön; *p.b.*, polar bodies; *s*, spermatozoön; *sc*, segmentation cavity or blastocoele; *y.c.*, yolk-laden cells. (Modified from Conklin, "Heredity and Environment," copyright, 1916, by Princeton University Press. printed by permission.)

cleavage becomes increasingly irregular, but there is a tendency, as long as the relationships can be determined, for each cleavage plane to appear at right angles to that which has preceded it, as in many other cases of cell division. The principal factor that modifies this ideal relationship is the mutual pressure which tends to

FIG. 214.—Early cleavage, blastula, and gastrula stages of the frog. *A*, the zygote or one-cell stage. *B*, two-cell stage with second cleavage furrow in process of development. *C*, eight-cell stage. *D*, late blastula in section, nuclei not shown. *E*, early gastrula in section corresponding with future median plane of body; direction of more active growth marked by arrows. *F*, late gastrula showing further development of archenteron; direction of more active growth indicated by arrows as in *E*.

bp, blastopore; *e*, archenteron; *p.b.*, polar bodies; *sc*, segmentation cavity or blastocoele. (*E* and *F*, redrawn from McEwen, "Textbook of Vertebrate Embryology," copyright, 1923, by Henry Holt and Co., printed by permission.)

make the cells assume particular outlines as do the units in a mass of soap bubbles. Thus, the two fourth cleavage planes by which the twelve- to sixteen-cell stage is formed, are in the polar axis, and therefore lie at right angles to the third (*cf.* Fig. 214 *C*). They consist of two planes, which may cut through the poles at right angles to each other or form a more irregular pattern, and which

separate each cell of the eight-cell stage into halves. Since these planes of the fourth cleavage begin at the animal pole and cut through the four smaller cells before they extend to those of the vegetative area, a *twelve-cell stage* is produced before the *sixteen-cell stage* is formed. Two fifth cleavage planes next appear, one above and one below the third furrow, dividing each cell of the sixteen-cell stage and forming a *thirty-two-cell stage*. In theory, at least, these are parallel to the equator and therefore at right angles to those that preceded them, but in fact the pattern of the mass of cells has by this time become so irregular that cleavage planes are followed with difficulty.

The feature which is apparent throughout is that the cell activities progress more rapidly at the animal pole, as shown by the way the first and second cleavage planes begin to appear in the animal hemisphere and extend to the vegetative pole, and by the more rapid division of all the cells of the animal hemisphere during the later cleavage stages. As a result, the cell outlines at the vegetative pole remain visible long after those of the animal pole have become indistinguishable to the eye. This difference in the rate of activity in the two hemispheres is an expression of the internal relationships, whereby the nucleus of the egg becomes eccentric and yolk accumulates in the vegetative hemisphere before the egg leaves the ovary (*cf.* Fig. 210). Since it contains relatively little active protoplasm, the vegetative half of the egg does not develop so rapidly as the animal region. The appearance of the third cleavage furrow somewhat above the equator is a part of this relationship, although its immediate cause is the position of the original cleavage nucleus, and thus of the nuclei of the four-cell stage, in the upper hemisphere. From the thirty-two-cell stage onward the cleavage proceeds rapidly by further cell divisions, some of which are vertical while others are at right angles to the surface, while the internal cavity, which begins to appear even in the eight-cell stage, enlarges rapidly. The stage thus developed is called the blastula.

The Blastula. — The *blastula stage*, which occurs in the development of many animals (*cf.* Fig. 148 E, p. 307, and Fig. 209 C), is a spherical mass of cells enclosing an internal segmentation cavity, or *blastocœle*. In the frog, the thirty-two-cell stage (Fig. 213 F) may be called an early blastula, since the blastocœle has already made its appearance by a separation of the cells at their inner ends,

which begins as early as the eight-cell stage. Sections of later stages (Fig. 214 D) show the development as cell division proceeds. The fully developed blastula is composed of many small darkly pigmented cells in the animal hemisphere and larger yolk-laden cells in the vegetative region. The roof of the blastocœle is several cells in thickness while the entire vegetative hemisphere is occupied by the larger cells. Such a blastula may be compared with the simpler types found in an animal like amphioxus, if we imagine an increase in the amount of yolk with a resulting enlargement of the cells in the vegetative hemisphere and consequent restriction of the blastocœle to the animal half of the egg.

The Gastrula. — The *gastrula* that arises from the blastula of the frog by the process of *gastrulation* can be better understood by reference to what occurs in an animal like amphioxus (Fig. 209) or the sea urchin, in which the blastula is more nearly a hollow sphere with the cells of the vegetative hemisphere only slightly larger than those of the animal region. According to the time-honored illustration, such a blastula becomes a gastrula by invagination of the cells of the vegetative portion, as one might push in the side of a hollow rubber ball to form a hemispherical two-layered structure. By a narrowing of its margin, the cup-shaped cavity thus formed becomes connected with the outside by a smaller opening, the *blastopore*, and the gastrula is produced, with an outer layer of *ectoderm* cells and larger *endoderm* cells lining the primitive enteric cavity, or *archenteron*. Referring again to the comparison between the blastula of the frog and that of amphioxus, it will be seen that such an invagination as occurs in the latter would be mechanically impossible for a blastula, in which the entire vegetative hemisphere is occupied by yolk-laden cells, although some modification of the process might take place. What actually happens in the frog may be characterized as an *invagination around one side of the yolk-laden cells*, whereby they are enclosed, along with the cavity of the archenteron, by an overgrowth of cells of the animal hemisphere. The process is rather complicated, but its essential features are as follows: There appears, upon the side of the late blastula stage that is destined to form the nervous system (*cf.* Figs. 213 G and 214 E), a crescentic groove, which may be called the blastopore, since it is the external opening of a cavity that originates by an infolding of the surface and grows inward as the archenteron. As gastrulation proceeds,

this blastopore extends laterally and becomes, within a few hours, a complete circle enclosing a "plug" of lighter-colored cells (*cf.* Fig. 213 G and 214 F). In this manner the developing embryo becomes entirely covered with darker-colored cells except within the circle of the blastopore, and the late gastrula or *yolk-plug* stage, as it is sometimes called, is produced. Further constriction at the edges of the blastopore continues this overgrowth, until the yolk-plug disappears and the blastopore becomes a small slit in the median plane at the posterior end of the embryo.

During these external changes the invagination of the archenteron has extended (*cf.* Figs. 213 H and 214 F), both by a folding over of the dark-colored cells at the lip of the blastopore and by an ingrowth at the inner end of the cavity. The blastula cavity disappears as the archenteron is thus extended into the mass of the developing embryo. The process, of course, occurs laterally as well as in the median plane shown in the figures, but the lateral extension of the archenteron may be disregarded in the present description. While these changes are in progress, *mesoderm cells* (Fig. 213 G and H) become differentiated, between ectoderm and endoderm, beginning in the region of the blastopore.

Finally, the yolk-plug disappears within the blastopore, and the external surface is completely covered with darkly pigmented cells. The archenteron, or *enteron* as it may now be called, is an extensive cavity in what will be the dorsal, and also in the lateral, regions of the future animal. The blastula cavity has almost disappeared. The mass of yolk-laden cells lies in a position that is ventral to the enteron. The *notochord*, or primitive skeletal axis, which was foreshadowed in the cytoplasmic differentiation of the zygote (*cf.* Fig. 213 B to I), is recognizable as the cells of the median dorsal lining of the enteron. The *ectoderm* is represented by the several layers of cells covering the outer surface; the *endoderm*, by the single layer of cells lining the enteron and the yolk-laden cells which are being gradually incorporated into the growing embryo; the *mesoderm* is extending between the ectodermal and endodermal layers. Thus the *three germ layers*, ectoderm, endoderm, and mesoderm, from which the various parts of the body are later differentiated, are formed during gastrulation.

In conclusion may be mentioned the changes by which the blastopore, and, hence, the vegetative pole, assume the positions which they occupy at the close of gastrulation. The dorsal lip of the

blastopore originally occupies a place near the equator of the spherical mass as it is oriented with reference to gravity. The extension of the crescentic blastopore and the encircling of the yolk-laden cells carries this dorsal lip downward through an angle of about ninety degrees (*cf.* Fig. 213 G to I), until its position about coincides with the vegetative pole. By this time, however, the development of the enteron and the reduction of the yolk-laden cells produce a change in the center of gravity, such that the embryo gradually rotates within its gelatinous capsule, bringing the blastopore and vegetative pole to a position at the posterior end of the embryo (Fig. 213 I). By growth of the dorsal region, the area representing the animal pole is gradually shifted to the antero-ventral surface of the tadpole.

The Neural-fold and Early-embryo Stages. — During the later stages of gastrulation other changes are in progress that have been omitted from the foregoing account for the sake of simplification. The outermost layer of ectoderm cells becomes thickened in a broad region, the *neural plate* (*cf.* Figs. 215 and 216), extending anteriorly from the blastopore along the future dorsal side of the embryo and terminating in a broadly rounded outline. As the gastrula develops into the *neural-fold stage*, which succeeds it, this thickening becomes more pronounced at the edges and forms lateral elevations which later rise above the surface as the *neural folds* or ridges. These become continuous at the anterior end of the neural plate and extend posteriorly to either side of the blastopore. Since the neural plate eventually becomes the central nervous system, the dorsal, ventral, anterior, and posterior regions of the future adult become increasingly evident from this point onward. Slightly elevated areas, known as the *sensory plate* and the *gill plate*, may also be recognized in such an embryo.

In subsequent stages the neural folds increase in height, and a furrow, the *neural groove* (*cf.* Figs. 215 and 216) appears in the median region of the neural plate. As this neural groove becomes deeper, the neural folds rise up laterally as ridges that increase rapidly in height and grow toward one another on the mid-line until they meet and fuse to form the *neural tube*, which is the rudiment of the brain and spinal cord. The manner in which this infolding is accomplished is clearly seen in transverse sections. As this fusion of the neural folds occurs first in the middle region, the neural tube remains open for a time at its broad

anterior end, where the brain is to form, and also posteriorly. Since the neural folds extend on either side and finally fuse posteriorly in such a way as to include the anterior part of the blastopore, a *neurenteric canal* (Fig. 215 E) is formed and persists for a time as a communication between the neural canal and the enteron. The anal opening arises as an invagination, the *proctodæum*, at the ventral side of the blastopore and outside the area

FIG. 215.—Neural-fold stages and transition to tadpole stage in frog. A, neural-fold stage, from the left, turned slightly to show folds at anterior end (cf. Fig. 216 A). B, later stage when neural folds have closed to form neural tube. C and D, transition to tadpole. E, an early tadpole stage in median section.

a, anus or proctodæum; br, brain; c, notochord; e, archenteron; ec, ectoderm; en, endoderm; ep, epiphysis; ey, eye or optic vesicle; g.p., gill plate; h, heart; hy, hypophysis; l, liver; m.g., mucous gland or sucker; m, mesoderm; m.s., mesodermal segment; ne.c., neurenteric canal; n.f., neural fold; s.p., sensory plate; sp.c., spinal cord; y.c., yolk-laden cells.

included by the neural folds in the formation of the neurenteric canal. With the growth of the tail in later stages (cf. Figs. 215 E and 217), the neurenteric canal extends posteriorly as a hairpin-shaped tube, which gradually degenerates. These details might have been omitted for the purposes of the present description, but an understanding of the origin and fate of the neurenteric canal is necessary for an understanding of the more important changes in this region of the embryo.

Comparison of longitudinal and transverse sections (Figs. 215 E and 216 B) at a stage when the neural folds have just completed their fusion shows that the general topography of the vertebrate animal is being rapidly established. At a slightly later stage (Figs. 216 C and 217), when the coelome has developed as a cleft in the mass of mesoderm cells on either side of the enteron and yolk-laden cells, the *muscle segments* have been differentiated from the mesoderm on either side of the *notochord*, and the resemblance to a trans-

FIG. 216.—Successive stages in the development of the general body plan of the frog as shown by transverse sections. A, early neural-fold stage (cf. Fig. 215 A). B, stage in which neural folds have recently closed to form the neural tube (cf. Fig. 215 C). C, stage in which the coelome and other features of the body plan are apparent (cf. Figs. 215 E and 217).

c, notochord; co., coelome; e, archenteron; ec, ectoderm; en, endoderm; l, liver; m, mesoderm; m.s., mesodermal segment; n, neural canal; n.c., neural crest; ng., neural groove; n.p., neural plate; n.t., neural tube; prn, pronephros; y.c., yolk-laden cells.

verse section of the adult frog (Fig. 19, p. 40) becomes apparent. The dorsal tubular nervous system, the axial skeleton now represented by the notochord and later by the vertebral column, the digestive cavity lined with endoderm, the visceral and parietal regions of the mesoderm with the coelome between them, and the ectodermal covering of the body indicate the fundamental chordate organization in a manner that is unmistakable. As shown by the outlines of these stages (Fig. 215), the antero-posterior elongation of the embryo begins during the neural-fold stage and thus the head and tail regions of the tadpole make their appearance.

The Tadpole Stages.—The elongation of the embryo during the neural-fold stage is coincident with the internal development of the general chordate organization. The conversion of the late

neural-fold stage into the tadpole involves a further elongation of the embryo (Fig. 215) and a change in curvature of its dorsal surface, which first becomes straight and then assumes an outline that is slightly concave, while parts of the head become recognizable anteriorly and the beginning of the tail is observed at the postero-dorsal region. Although it is now covered by the ectoderm, the neural tube is still recognizable as a dorsal median swelling that expands anteriorly where the brain is beginning to be

FIG. 217.—Median section of an early tadpole of the frog (*cf.* Figs. 213 *I* and 215 *E*).

a, anus; *br*, brain; *c*, notochord; *ep*, epiphysis; *h*, heart; *hy*, hypophysis; *in*, infundibulum; *l*, liver; *m*, mouth or stomodaeum; *sp.c.*, spinal cord; *u.d.*, urinary duct. (After Marshall from Ziegler.)

formed. In the head region, various structures gradually make their appearance.

It will be recalled that in a stage when the neural folds were well developed (Fig. 215 *A*) there was found anteriorly and ventrally a thickened area of the ectoderm known as the *sensory plate*, and posterior to this on either side another thickening, the *gill plate*. As these plates become more clearly recognizable, there appears on either side, in the dorsal part of the sensory plate, a slight swelling, the *optic vesicle* (Fig. 215 *C*), marking the rudiment of the eye, which is an outgrowth from the neural tube. Likewise, the *stomodaeum*, which is the ectodermal invagination forming the mouth, appears as a median depression in the antero-ventro portion of the sensory plate; and the *suckers*, which are really glands secreting a sticky mucus, as a pair of pits which eventually unite as a V-shaped structure lying ventral and lateral to the mouth.

At a later period, the *nasal pits* arise from the sensory plate as ectodermal invaginations antero-ventral to each optic vesicle. The beginnings of the *gill clefts* may now be seen upon the gill plate (Fig. 215 D) as vertical grooves separating the *branchial arches*, or gill bars; while the *muscle segments* become evident externally as a series of < shaped markings. At the posterior end is the *proctodæum*, or invagination of ectoderm that forms the anus (cf. Fig. 215 E). It will be recalled that this lies at a point that was once the ventral lip of the blastopore (cf. Fig. 213 I). The outer surface of the embryo has ciliated areas at this stage, and it rotates within its capsule.

In later stages the external shape of the tadpole becomes increasingly apparent by rapid outgrowth of the tail and development of the caudal *fin*, until a length of six to seven millimeters is reached at an age of one or two weeks, depending upon the temperature. Rudiments of what are called the *external gills* appear shortly before hatching as outgrowths upon the gill plates (cf. Fig. 219). Up to this point the developing individual may be referred to as an "embryo," because it is enclosed within the jelly in the way that many other animals are enclosed in egg shells or other protecting membranes. It may, however, be called a "tadpole" as soon as it has assumed these characteristic features. By the same terminology, the tadpole is a "larva," and the "larval period" begins when the "embryonic period" ends, at the time of hatching. In hatching, the tadpole of the leopard frog penetrates the jelly head foremost, and squeezes through a small opening to become free even before it is able to wriggle about actively as in later stages. The cilia are probably effective in this process. It is then seen clinging by its suckers (cf. Fig. 11 F, p. 23) to the remains of the jelly or to other objects, moving when disturbed, but for the most part quiescent until it becomes more tadpole-like in appearance. During this period the external gills develop rapidly as branched structures and the stomodæum breaks through into the anterior end of the enteron. The yolk persists for a considerable period after the tadpole has begun to feed upon the organic ooze covering submerged objects and the active life has commenced.

The external gills function as temporary respiratory organs, before the *internal gills*, which are comparable with those of a fish, develop. A fold that arises anterior to the gill region and

grows posteriorly on either side is obviously homologous with the *operculum*, or lateral covering of the gills, in teleost fishes. The external gills disappear as this operculum develops and the internal gills become functional. In its subsequent development the posterior margin of the operculum fuses with the body surface, leaving a small tubular opening on either side. Later, the opening on the right side closes, leaving the one on the left to function for both sides, since the right and left opercular cavities are in communication ventrally, until the gills disappear at the time of metamorphosis. The tadpole "breathes" like a fish, by taking water into the mouth, passing it through the gill slits, and discharging it through the opercular opening; but with the development of lungs in later stages (Fig. 11 G, p. 23) the animal comes to the surface to take in and discharge air by the mouth, and thus the branchial respiration becomes less important.

After reaching the condition described in the first two or three weeks of larval life, the tadpole develops more slowly until the time of metamorphosis, and increases considerably in size. The legs begin to appear at about the end of the first month. The fore legs develop first, although they are not seen externally because covered by the operculum until the time of metamorphosis; the hind legs develop a little later on either side of the anal opening at the posterior end of the globular body. In the leopard frog the tadpole stage lasts for a period of two or three months, depending upon food and temperature, and may be continued through the following winter under exceptional conditions. In the bullfrog, *Rana catesbiana*, which lays its eggs later in the season than the leopard frog, the first winter is normally passed in the tadpole stages.

Since all the more important organs of the body are present, at least as rudiments, in the later tadpole stages, this general description and discussion of the developmental processes may be concluded before describing the metamorphosis by which the tadpole becomes a miniature frog. To continue the account of internal development from the stage shown in Fig. 215 E, the central nervous system is formed from the neural tube by a thickening of the walls, and a consequent reduction in the relative size of the internal cavity until it remains only as a microscopic canal in the cord of the adult (*cf.* Fig. 61 A, p. 109). The brain region of the neural tube becomes differentiated first into three

vesicles known respectively as the *fore*, *mid*, and *hind-brain*. From the fore-brain arise the *cerebral hemispheres* (cf. Fig. 38, p. 65), with the *olfactory lobes* at their anterior ends, and the *diencephalon*; from the mid-brain, the *optic lobes*; and from the hind-brain, the *cerebellum* and the *medulla*. The *ventricles* of the brain and their connections represent a survival of the cavity of the neural tube, which thus extends as a closed canal from end to end of the adult nervous system.

The spinal nerves arise as outgrowths from the region of the central system, the nerve fibers in the ventral roots growing from cells in the neural tube, the dorsal roots from the dorsal-root ganglia that are formed from the *neural crests* (Fig. 216 B). The development of the cranial nerves is more complex, but in all cases the nerve fibers that make up the nerves grow outward from nervous cells at some point in the nervous system. The notochord is replaced by the vertebral column, which forms around the notochord as the latter ceases to develop and becomes resorbed. Reference has been made to the fate of the neurenteric canal and the formation of the *digestive tract* by union of the stomodæal and procotodæal invaginations with the enteron. The *lungs* and *larynx* originate as a median outgrowth on the ventral wall of the enteric cavity, which is at first single and becomes double as the lungs develop. The *liver* and *pancreas* (cf. Figs. 215 E and 217) likewise originate as evaginations of the enteron, at first separate and later united by their common duct. The *urinary bladder*, which also arises as an evagination from the ventral floor of the enteron, is a rudiment in the tadpole, developing further at the time of metamorphosis. Thus, the development of lungs, liver, pancreas, and urinary bladder is such that each of these organs is lined by cells of endodermal origin, which are covered externally by tissues of mesodermal origin, such as connective tissue, muscle fibers, and peritoneum. With the diminution of the yolk-laden cells (cf. Fig. 216 C), the cleft in the mesoderm that forms the *calome* becomes extended ventrally as a spacious cœlomic cavity. The *heart* appears as a tubular structure (Fig. 217), which begins to pulsate before the circulation is established; *blood vessels*, which are differentiated in their definitive positions, gradually become associated with the heart as a circulatory system, which resembles that of a fish in the tadpole stages, and assumes the adult form only at the time of metamorphosis. The *kidneys* and *reproductive organs*

differentiate in place within the mesoderm, and likewise the *skeleton* and *muscles*.

If one considers the histological structure of the adult, the *epidermis* that covers the entire body arises from the ectoderm of the embryo, the *mucous membrane* of the digestive tract from the endoderm. Everything between these two thin layers of cells is mesodermal in origin, with a few exceptions such as the cells lining the glands of the skin (*cf.* Fig. 52, p. 95) or the lungs and other organs formed by evagination. The *dermis* of the skin, the *muscles* and the *connective tissue* of the body wall, and the *parietal peritoneum* originate from the outer layer of the mesoderm in the embryo (*cf.* Fig. 216 C); the *visceral peritoneum*, *muscle layers* and *submucosa* of the digestive tract, from the inner layer of the mesoderm.

Thus there are differentiated, at the time of gastrulation, three layers of cells, the ectoderm, endoderm, and mesoderm. These were called *germ layers* by the embryologists of the early nineteenth century because of their layer-like arrangement in the embryo. From these germ-layers the organs and tissues of the body originate in the manner described, as summarized in the accompanying table (Fig. 218).

ORIGIN OF ADULT STRUCTURES FROM GERM LAYERS IN FROG

Ectoderm	Epidermis Lining of Skin Glands Stomodæum and Proctodæum Nervous System and Sense-organs
Mesoderm	Muscles Connective Tissue Peritoneum Circulatory System Reproductive Organs Urinogenital Organs Skeletal System
Endoderm	Mucous Membrane of Digestive Tract, except Stomodæum and Proctodæum Lining of Lungs Lining of Liver and Pancreas Lining of Urinary Bladder

FIG. 218.—Germ layers of frog and their derivatives (*cf.* Fig. 149 p, 309).

When less was known of the details of embryology, it was thought that development consisted in the appearance of the germ layers as the earliest recognizable differentiation of the embryo, and in the subsequent formation of adult parts from one or another of these three types of cells. It was then believed that the differentiation into ectoderm, endoderm, and mesoderm was irrevocable; and any case in which one germ layer gave rise to cells of another was held to be very exceptional. In its general features, this "germ-layer theory" can still be accepted as a description of such steps in differentiation as are indicated by the foregoing table. But there are many exceptions, as where certain cells of a regenerating animal form tissues that originate from all three of the germ layers during embryonic development. Moreover, the germ layers have themselves been traced to an earlier origin in the studies of *cell lineage* by which they have been followed back through all the preceding cell divisions to the zygote. In some animals it is also found that the principal regions of the adult body may be recognized in the cytoplasm of the zygote after the manner described for the frog, and hence there is a *promorphology* in the one-cell stage which is a first step in differentiation, even before cell division has begun.

Remarkable as it may seem, the development of some animals is, therefore, traceable not only to single cells or groups of cells that form germ layers and later organs, but even to the cytoplasm of the zygote. The germ cells, however, reveal no such organization and hence must be regarded as having the capacity to produce the organization seen in a zygote, which then proceeds with cell-division and differentiation, constituting a process of *epigenesis*, or the formation, step by step, of parts that gradually assume their resemblance to adult structures. This process should be distinguished from the *preformation*, which was supposed to exist by some eighteenth century embryologists, who represented the human spermatozoön as containing a miniature human being, the *homunculus*, which developed to an adult by a mere process of growth. It is now known that development, in its general features, is by epigenesis from germ cells with no exact resemblance to the adult, and not by the unfolding of a miniature organism that is preformed within the ovum or spermatozoön. The significance of the statement that *development is a process of cell division and differentiation* is thus concretely illustrated. The cell division is

by mitosis. Many of the steps in differentiation have been determined, and some of the underlying causes are known, but the problem of why some cells develop in a certain manner at a given period, and thus form a particular part in such definite correlation with other parts of the embryo, is still the central and for the most part unsolved problem of Embryology.

Metamorphosis and Juvenile Stages. — The changes by which the tadpole larva is converted into a young frog are termed the *metamorphosis*, as in other cases where a larva becomes metamorphosed into an adult (cf. Fig. 11 H to K, p. 23). Externally, the globular body assumes the color and shape of the frog; the skin is cast, and with it the horny lips; the small round mouth changes into the large wide mouth of the frog, with concomitant changes in the shape of the head; the eyes become prominent; the tympanic membranes appear; the fore legs break through the operculum; the hind legs grow rapidly to their adult proportions; while the tail dwindles to a mere stump in the final stages when the individual begins to hop about as a miniature frog. The internal changes are even more profound. The gills and gill slits disappear, and other parts of the gill apparatus either degenerate or become incorporated in modified form into other organs; the tongue enlarges; the circulatory system becomes adapted to pulmonary respiration; the lungs are completely developed; the digestive tract, which has a very long and coiled intestine adapted for the food of the tadpole, becomes changed by the enlargement of stomach and liver and by actual shortening of the intestine; and the sex glands become further differentiated. The young frog which is thus produced from the tadpole within a few days, is called a *juvenile* or youthful stage, according to the terminology used for developmental stages throughout the Animal Kingdom. If the eggs of the leopard frog have been laid in March, the individual is likely to reach such a stage by the early part of July. It then grows rapidly during the summer and again the next year, usually becoming sexually mature at two years of age. The age that may be attained by frogs is not definitely known, but it seems unlikely that they live many years. Bull frogs nine years of age are reported by the New York Zoological Park. Toads probably live for a much longer period.

Development of Other Vertebrates

The development of other vertebrate animals may now be examined in its general features. The Amphibia lay their eggs in water, with but few exceptions, and develop through tadpole stages to salamanders, or, by a more pronounced metamorphosis, attain to the tailless condition of frogs and toads. The development of the frog has been described in detail as an example of the fundamental features of vertebrate embryology. Although the fishes represent a lower type of vertebrate organization, their development is more specialized because of the presence of a greater amount of yolk in their eggs. For this reason the brief account of the protochordate type, *Amphioxus*, was inserted by way of introduction. The eggs of reptiles and birds are even more highly modified than those of fishes by the presence of yolk, but their mode of development holds additional interest because of its adaptation to terrestrial life. Fishes and amphibians are both aquatic animals insofar as their developmental stages are concerned. Reptiles and birds are completely adapted for terrestrial life, since their developmental stages, as well as their adult lives, can be passed on land surrounded by the atmosphere. It is true, however, that the embryo within the egg of a bird or reptile develops in a fluid medium which is kept from evaporating by the enclosing egg shell. Thus, the leathery shell of a snake's egg and the calcareous shell of a bird's egg are devices that make possible a thorough-going terrestrial existence such as is impossible for an amphibian. The development of mammals in turn presents interesting points for comparison with that of birds and reptiles. In all the classes of vertebrates the formation of the principal parts of the embryo is substantially the same in the early stages, being modified only by the conditions of development and the nature of the adult animal. The comparative study that is undertaken in the following sections shows not only the mode of life of the embryo in each of the classes, but also the changes in the mode of development that have probably occurred in the evolution of vertebrates from an aquatic habitat to the present terrestrial life of reptiles, birds, and mammals.

Development of Fishes.—Although the majority of fishes lay their eggs in the open water, where fertilization and development occur, there are many exceptions (*cf.* Fig. 219). The skates

lay eggs with a large amount of yolk and encased in tough egg capsules in which development to the juvenile stage occurs. In sharks the large yolk-laden eggs are retained in the oviduct of the parent, where they develop, and the young are "born" in the juvenile stage, in which they are known as "pups." Such a mode of development is called *ovoviviparous* in contrast with the *viviparous*

FIG. 219. — Embryonic and larval stages in fishes. Above, embryo of an elasmobranch, the torpedo, at a stage when the gill slits have reached a condition similar to that seen only in the embryos of higher vertebrates (cf. Fig. 287, p. 531). Below, larva of a lung fish, *Lepidosiren paradoxa*, at a stage when the external gills and general outline have a marked resemblance to the early tadpole stage of an amphibian like the frog.

a, position of proctodeal invagination that forms the anus; df, rudiment of dorsal fin; dt, yolk stalk by which embryo is attached to the yolk; h, heart; k, anterior gill slit; md, posterior end of neural tube; n, nasal pit; nt, blastoderm (cf. Fig. 224 E); ob, ear; oc, eye; sch, tail; v, protuberance due to developing kidney (pronephros). (After Ziegler.)

development in the Mammalia. Many fishes, including the stickle-back, build nests in which the eggs are laid; and in some species the eggs and young are cared for by the female or by the male, or by both parents, as in some species of catfish. Other fishes carry the eggs in a brood pouch or attached to some part of the body. There are thus a great variety of ways in which the young

of fishes may receive a favorable start in life, either by additional food in the yolk of the egg or by greater protection during the developmental stages. From the standpoint of Comparative Embryology, however, the development of amphioxus (*cf.* Fig. 209) is a better introduction to Vertebrate Embryology, since the development of fishes is so greatly modified by the presence of yolk (Fig. 219). The fish embryo develops on the top of this yolk, as a disc-like structure, or *blastoderm*, in which the parts of the body gradually become apparent along the median axis while the edges of the blastoderm are extending over the surface of the yolk. As the circulatory system is formed, blood vessels extend outward from the body to the yolk mass, which is thus consumed by the embryo. In later stages the connection between embryo and yolk becomes constricted, and the dwindling supply of nutrient material appears in the *yolk sac*, attached by the *yolk stalk* to the ventral side of the embryo. Although the exact relationships between embryo and yolk cannot be here described, it may be said that the development of the bodily parts of the fish resembles what occurs in Amphibia, being modified, of course, by the presence of a greater amount of yolk and by differences in adult structures.

Development of Reptiles.—The development of a reptile is fairly represented by that of the turtle or the American alligator (Figs. 220 and 221). The familiar turtles of fresh water, like the genus *Chrysemys*, produce eggs resembling those of a bird, except that they are encased in a leathery covering instead of a shell of carbonate of lime. Spermatozoa are introduced into the anal opening of the female during sexual union and thence find their way to the anterior end of the oviduct where fertilization occurs. In the oviduct the “white” and “shell” are secreted about the “yolk,” which is the part arising from the ovary and is therefore comparable with the ovum of the frog. At the time of laying, the female comes out upon the land and excavates a cavity, sometimes in hard ground at a considerable distance from the shore. Here a dozen or more eggs are laid, several inches below the surface, and, after being covered loosely with soil, are left to be incubated by the heat of the sun. The young emerge as miniature adults as do chicks from the eggs of a hen (Fig. 220 G), and immediately make for the water, where they may sometimes be seen in large numbers. The Florida alligator lays its eggs upon the land, in a rough nest constructed of flags and other

débris (Fig. 221), and the female apparently remains in the vicinity until the young hatch as juvenile alligators some five or six inches in length.

Most snakes and lizards lay eggs in a similar manner, concealing them in various ways (Fig. 222). Some snakes and lizards are ovoviviparous, however, since the embryo develops from a large yolk-laden egg which is retained within the body of the

FIG. 220.—Development of turtle. A, embryo drawn on a large scale showing gill slits. B, stage comparable with F, but showing yolk sac. C, later embryo drawn on same scale as A. D to F, stages within egg. G, hatching. H, just after hatching.

(After Agassiz, redrawn by George T. Kline.)

female. Neither of these cases resembles the mode of development in mammals, which will be described in a later section of the present chapter, since the embryo is nourished primarily by the yolk and not by a diffusion of food from the blood of the parent to that of the embryo. The body of the parent merely functions as an incubator for the eggs of such a fish or reptile, whereas the relationship between the mammal and its offspring is more like that of host and parasite.

The exact structure of the eggs of reptiles and the general stages of reptilian development need not be considered, since both resemble so closely the conditions found in birds as described in the following section. The embryonic development of birds, as well as their adult anatomy and fossil record, shows their close rela-

FIG. 221.—Alligator nest and eggs. Above, the nest, chiefly composed of flags, opened to show eggs. Below, external view of egg and same with shell opened (*cf.* Fig. 224 B).

(Nest after photo. by A. M. Reese; eggs, after S. F. Clarke.)

tionship to the reptiles. In the earlier stages, at least, it would be hard for anyone not an embryologist to distinguish the embryo of a bird from that of a reptile, and reptilian eggs are essentially like the eggs of birds save in the structure of their shells. In this connection it may be mentioned that in one group of birds, the Megalopodes, of which the Australian brush turkey is an example, the

eggs are laid in a mass of leaves and other dead vegetation, which is heaped upon them by the parents and incubates the eggs by the heat generated in its decomposition.

Development of Birds. — As explained in the preceding paragraph, a study of development in the birds is essentially an extension of one's knowledge of development in the reptiles, so close are the resemblances in the embryology of these two classes of vertebrates. Moreover, the presence of a large amount of yolk

FIG. 222.—A lizard, the blue-tailed skink, *Eumeces quinquefasciatus*, and its nest.

A, adult male catching insect. B, young. C, female with eggs in a cavity of a rotten log. (From Pearse, "General Zoology," copyright, 1917, by Henry Holt and Co., reprinted by permission.)

in birds and reptiles is important in the present summary of Vertebrate Embryology, since it may be compared on the one hand with the condition found in amphibians, and on the other with that existing in mammals, in which the embryo is nourished by diffusion from the blood of the parent. The development of the domestic fowl has been chosen as representative of the birds, because it has long been a favorite subject of investigation and is perhaps better known than the development of any other animal.

The *spermatozoa* are formed in the *testes* (cf. Fig. 223) and pass through the *vasa deferentia* to be stored in the *seminal vesicles*. In the female, the organs on the right side, although present in

the early stages, are almost completely degenerate in the adult animal, leaving the left *ovary* and *oviduct* as the functional parts. The spermatozoa that pass to the cloaca of the female during sexual union enter the oviduct and make their way to its anterior end, where they may be found when the egg leaves the ovary.

FIG. 223.—Urinogenital organs of the pigeon, *Columba livia*. Left, the male system. Right, the female system.

adr, adrenal body; *cl.*², urodaeum, or ventral portion of cloaca; *cl.*³, proctodaeum, or dorsal portion of cloaca; *k*, kidney; *lod*, left oviduct; *lod'*, opening of left oviduct into cloaca; *lod''*, left mesovarium, or mesentery of ovary; *lod'''*, left Fallopian tube; *od*, right oviduct; *ov*, ovary; *rod'*, opening of right oviduct into cloaca; *ts*, testis; *ur*, ureter; *ur'*, opening of ureter into cloaca; *v.d.*, vas deferens; *v.d.'*, opening of vas deferens into cloaca; *v.s.*, seminal vesicle. (From Parker and Haswell, "Textbook of Zoology," copyright, 1921, by Macmillan and Co., Ltd., reprinted by permission.)

The ovary of a laying hen (Fig. 224 A) contains ova in all stages, from very small ones, no larger than those in the ovary of a frog, to others that are about ready to be laid and are, therefore, the full size of the "yolk" of the hen's egg. The ovum of the fowl (Fig. 224 B) may, therefore, be compared with a frog's egg so greatly enlarged by additions of yolk that the active protoplasm has become restricted to a small area at the animal pole, composed of a disc-shaped mass of cytoplasm containing the egg nucleus and called the *germinal disc* or *blastodisc*. As a matter of fact, the eggs of the fowl arise by growth from the smaller ova, as may be seen even by superficial examination. At the time of ovula-

tion, the ovum breaks from the surface of the ovary, as does the ovum of the frog, and is, therefore, free in the coelome, although the ovary is so closely enfolded by the funnel-shaped mouth of the oviduct that the ovum has little chance of not reaching its proper destination. The two maturation divisions (*cf.* Fig. 114, p. 228) occur after the egg has reached the oviduct and do not begin until the entrance of a spermatozoön. The fertilized egg, or zygote, therefore, consists of the germinal disc resting upon a spherical mass of nutrient material which is the "yolk" of the future "egg." This "yolk" now passes along the oviduct, which secretes first the "white" or *albumen* with the buffer-like *chalazæ* that are attached at opposite sides of the yolk, then the *shell membranes*, and finally the *shell*. In this manner the hen's egg with its familiar structure is produced. One may, therefore, compare the "yolk" with a greatly enlarged ovum, and its several coverings with the jelly of the frog's egg.

The cleavage and initial development of the hen's egg consist of cell divisions and differentiation in the blastodisc (Fig. 224 C), beginning while the egg is in the upper part of the oviduct and continuing until it is laid, when the development is checked by the lower temperature of the outer world. As these changes progress, a shallow cavity, comparable with the *blastocæle* of a frog's egg, is formed beneath the blastodisc, or *blastoderm*, as it may be called from this time onward. The blastoderm then becomes a two-layered structure, by a process that may be called *gastrulation*, since the outer cells can be subsequently identified as the *ectoderm* and the inner ones as the *endoderm* of the developing embryo. When this initial development ceases the embryo consists of a mass of cells which is thinner and more transparent in its central portion, called the *area pellucida*, and thicker around the margin in the *area opaca*, as may be seen in the fertile egg when viewed with the unaided eye (Fig. 224 B). Unfertilized eggs have a spot at the animal pole that is quite different in appearance. In this stage the development ceases unless the egg is kept at a suitable temperature in an incubator or under a hen. If such an egg is placed under incubation, the blastoderm develops rapidly, extending over the surface of the yolk and producing an embryo in the center of the disc-like blastoderm in the manner shown in Fig. 224 D to F.

The more important internal changes by which the body of the

FIG. 224.—Development of the chick.

A, part of the ovary showing ova in different stages. *B*, the fertilized egg at time of laying, with shell removed, showing "yolk" suspended by cords of "white," the chalazae, and the blastoderm in center. *C*, early cleavage of the blastodisc. *D*, egg opened to show late neural-fold stage and extension of blastoderm over yolk. *E* and *F*, stages during which the circulation is becoming established as the blastoderm extends further over the yolk. The allantois appears as a bladder-like outgrowth at the posterior end of the embryo in *F*. *G*, stage in which the allantois has enlarged and the yolk surrounded by the yolk sac has become reduced by the progressive utilization of its nutrient material by the growing embryo. In *F* and *G* the amnion is shown closely surrounding the embryo. *H*, later stage, showing yolk stalk. *I*, front view of head showing eyes, nasal openings, mouth, and ears. *J*, a stage shortly before hatching showing yolk stalk and remains of yolk. (Redrawn from Duval.)

embryo develops and assumes the organization of the adult may be compared with those occurring in the frog, if due allowance is made for the modifying influence of the yolk. When the neural plate is developing into the neural tube (Fig. 224 D), the embryo is a flattened mass of cells resting upon the yolk, as though in a frog embryo, at a corresponding stage (Fig. 216), the yolk were so increased that the embryo became a disc upon a sphere as large as the yolk of the chick's egg. The flattened body of such a chick embryo (Fig. 225) is covered by *ectoderm*. The *endoderm* is in contact with the yolk laterally, while toward the center there is a

FIG. 225.—Transverse section of chick embryo at a stage when the body plan of the chordate is being established (cf. Fig. 216).

a, aorta; c, notochord; coe, coelome; ec, ectoderm; en, endoderm; m, mesoderm; m.s., muscle segment or mesoblastic somite; n, nerve cord; n.c., neural crest; nt., neural tube; v.v., vitelline vein; y, yolk.

space, between the endoderm and the yolk, that may be called an *archenteron*. The *mesoderm* is becoming differentiated into the muscle segments, or *mesoblastic somites*, and is beginning its separation into inner and outer layers to form the coelome. The *neural folds* arise and fuse to form the neural tube, and the *notochord* is formed in a similar position in both frog and chick. In a later stage these structures are further developed; but as long as a considerable portion of the yolk remains, the lateral parts of the embryo are spread widely as a thin plate. The margin of the body, therefore, extends over the mass of yolk material, which is gradually absorbed by the endoderm cells of the embryo and transferred by the peripheral blood vessels to the developing body. By means of this abundant food supply, the embryo grows rapidly and the yolk is correspondingly reduced (Fig. 224 F to G).

In brief, it may be said that the development of birds is fundamentally like that of the frog, as shown by such details as the origin and development of the mesoderm; the neurenteric canal, which occurs in reptiles and in some of the birds; the notochord, which is later surrounded by the vertebral column; the stomodæum and proctodæum; and by such larger features as the origin of the various organs from the germ layers and the manner in which the circulatory system is formed. This system is at first fish-like, with its two-chambered heart (Fig. 226) and arteries passing in the gill bars between gill slits, but is later modified by the appearance of the four-chambered heart of the adult bird and other parts adapted

FIG. 226.—Three stages in development of heart in chick, showing transition from two-chambered to four-chambered condition.

a, auricle; l.a., left auricle; l.v., left ventricle; r.a., right auricle; r.v., right ventricle; t, truncus arteriosus; v, ventricle. (Drawn by Wiley Crawford.)

for respiration by means of lungs. Features of the development of birds and reptiles that are entirely different from anything found in the Amphibia are the *embryonic membranes*. It will be necessary to explain these structures in a general way in order that we may understand the similar features of mammalian development.

Although these embryonic membranes of birds and reptiles present complexities of structure that cannot be described here, it will be possible to explain their schematic arrangement as they appear in one plane of section. In Fig. 227 A is shown a longitudinal section of a chick embryo in its relation to the yolk and shell, at a stage when the neural tube is beginning to be differentiated into the spinal cord and brain, while the head and tail regions of the animal are becoming apparent. The embryo is, of course,

covered by ectoderm, and the endoderm forms the roof of an enteric cavity which is ventral to the embryo, while laterally it is in contact with the yolk. Between the ectoderm and endoderm is the mesoderm. Shortly before the stage of development shown by this figure is reached, the so-called *amniotic folds* have arisen anteriorly and posteriorly, as the figure shows, and also on either side of the embryo. Since this folding involves the ectoderm and also the somatic or outer layer of the mesoderm, its cavity is an extension of the coelome and is lined with mesoderm. As development continues, the anterior and posterior amniotic folds approach and fuse (Fig. 227 B) and thus the embryo becomes enclosed in an inner membrane, the *amnion*, and an outer membrane, the *chorion*, each composed of ectoderm and somatic mesoderm. The cavity between the embryo and the amnion is lined with ectoderm and is called the *amniotic cavity*; the one enclosed by the chorion is called the *extra-embryonic coelome*. By the time the amniotic folds have thus fused, there has developed from the posterior end of the enteric cavity an evagination known as the *allantois*, which extends into the extra-embryonic coelome. The allantois is, therefore, lined with endoderm and covered externally by the splanchnic layer of the mesoderm. It is homologous with the urinary bladder of the frog, although this organ is not present in the adult bird. As the embryo increases in size (*cf.* Figs. 224 G and 227 C), the allantois extends farther and farther into the extra-embryonic coelome, and its outer face comes into close contact with the inner surface of the chorion. As the white of the egg becomes reduced, the allantois is closely applied to the inner surface of the chorion, which in turn lies against the shell membrane and shell, and thus becomes a respiratory and excretory organ by means of which oxygen and carbon dioxide are received and discharged. At the time of hatching, the remains of these membranes are still seen in contact with the shell membrane.

By continued growth of the embryo and corresponding reduction in the amount of yolk, the chick embryo gradually assumes its final dimensions (Fig. 224 H and J). The last remnant of the yolk disappears from view within the ventral side of its body shortly before the hatching. In these final stages, the name *yolk sac* is given to the endoderm and splanchnic mesoderm surrounding the yolk, and the constricted stem by which this is connected with the embryo is called the *yolk stalk*.

FIG. 227.—Development of the chick, as seen in median sections, showing relation of embryo to shell, yolk, and embryonic membranes (cf. Figs. 224 and 225).

A, 2 days' incubation. B, 3 days. C, 10–14 days. *al.*, allantois; *al.c.*, allantoic cavity; *al.st.*, allantoic stalk; *am*, amnion; *am.f.*, head and tail folds of amnion; *ec-so.*, ectoderm and somatic mesoderm; *e.m.*, egg membrane; *emb*, embryo; *en-sp*, endoderm and splanchnic mesoderm; *e.s.*, egg-shell; *se*, serosa or chorion; *y*, yolk. (Redrawn with modifications from Parker and Haswell, "Textbook of Zoology," copyright, 1921, by Macmillan and Co., Ltd., reprinted by permission.)

Birds and reptiles, therefore, produce eggs in which such a large amount of yolk is deposited on one side of the ovum that the active protoplasm, at the time of fertilization, becomes restricted to a small disc at what was the animal pole of the egg cell at an earlier stage of its formation. The great mass of yolk that is thus formed is surrounded by an albuminous fluid which serves as a cushion, and also as additional nutriment for the developing embryo, and by a shell which is sufficiently impervious to the evaporation of water to enable the development to take place in the atmosphere. It will be noted, however, that the embryo actually develops in contact with fluids of the amniotic cavity and of the other cavities enclosed within the egg shell. Terrestrial development is possible because of these conditions, but at the same time the immediate environment of the embryo is aquatic.

Development of Mammals. — It is a well-known fact that the more familiar mammals develop within the body of the female until they have reached the condition of miniature adults. Some mammals, however, are born in a less developed state as, for instance, the hairless young of rats and mice. More extreme examples are the young of opossums and kangaroos (Fig. 228), which are born at a very early stage and complete their development in the marsupial pouch of the mother, with their mouths holding fast to the nipples of the mammary glands. It is not so commonly known that the most primitive order of mammals, now represented only by the duckbill or platypus, *Ornithorhynchus anatinus* (Fig. 15, p. 29), and the spiny ant-eater, *Echidna aculeata*, develop within eggs, which are encased in a shell and laid like those of a bird or reptile. The embryonic membranes in these mammals are also like those of birds and reptiles. There is, therefore, no stage in their development comparable with the period of foetal life within the mother that occurs in higher mammals.

All other mammals develop within a part of the female genital duct called the *uterus*, to the wall of which they are attached by a structure known as the *placenta* (cf. Fig. 234, p. 450). The mammal, of course, develops from an *ovum*, which is detached from the ovary and enters the oviduct in the same general manner as the eggs of birds and reptiles; but this egg has no large accumulation of yolk, except in the two egg-laying mammals, the duckbill and the spiny ant-eater. The ova are fertilized by spermatozoa which are introduced during sexual union and make their way to the

upper ends of the oviducts. Development begins as the fertilized ovum passes down the oviduct to the uterus, where it becomes attached by the placenta, through which it receives its nutrition from the blood of the mother. Hence, although the development of the mammalian embryo itself resembles that of a bird or reptile, the method of nutrition is wholly different. The blood vessels of the embryo extend out to a system of capillaries in the part of the placenta originating from the embryo, where they parallel capil-

FIG. 228.—Development of opossum. Left, embryo a few hours before birth, showing rudimentary development of head and other parts of body as compared with fore limbs which are used for climbing to marsupium or brood pouch of mother. Right, an opossum and a few of her young at a stage after they have left the marsupial pouch.

(Embryo after Hensen, *Journal of Anatomy*, Vol. 28; Mother and young, photo. by courtesy American Museum of Natural History.)

laries within the maternal portion of the placenta (Fig. 237, p. 453). There is no actual confluence of the blood of the *fœtus*, as such an embryo is called, and the blood of the mother, although it is often supposed that this is the case. Nutrient materials merely diffuse from the mother's blood into that of the *fœtus*, and waste products pass in the opposite direction. The embryo appears to be as independent of the mother as though it were a parasite living at the expense of her body. Its circulatory system is its own, and all the other parts are clearly those of a separate organism.

As a matter of Comparative Embryology, the exact correspondence between the amnion that surrounds the *fœtal* mammal and that surrounding the embryonic bird or reptile may be noted (*cf.* Figs. 227 and 234). The chorion and the allantois

are also present in the mammal, but they are modified as the embryonic portion of the placenta. The presence of a yolk stalk and a greatly reduced yolk sac, containing no yolk, completes the resemblance. It therefore appears that the higher mammals possess the embryonic membranes and yolk sac of birds and reptiles, although these structures are modified to suit the peculiar conditions of mammalian development. These facts, along with the actual existence of mammals that lay eggs, lead zoologists to believe that the ancestors of the higher mammals once laid eggs like those of birds and reptiles, and that their earlier mode of development has become modified in the course of their evolution. If this be true it shows that the embryonic stages of animals, no less than their adult structures, may undergo profound evolutionary changes.

If we attempt, in conclusion, to picture the probable evolution of the mode of development in reptiles, birds, and mammals, it appears that the aquatic ancestors of these animals laid eggs, somewhat in the manner of the Amphibia of the present day. With the specialization of the adult for terrestrial conditions, there was developed an egg protected against evaporation by a shell, and the embryo came to be surrounded by membranes which served as adaptations to this new mode of development. In the evolution of higher mammals, the yolk disappeared in favor of another method of nutrition, which insured a greater degree of protection, since the embryo could develop within the body of the parent. Just as the bird cares for its young after hatching, so in the Mammalia there is a period of *infancy* during which the young are fed and tended by the parent until better able to care for themselves. The culmination of such an evolution in the mode of development is seen in species like the elephant, with its long period of association between parent and young, and finally in the human family.

CHAPTER 18

SOME GENERAL PROBLEMS OF DEVELOPMENT

We are now in a position to discuss certain general problems of development. All metazoa arise from eggs and not by processes of spontaneous generation, as was believed when frogs and mice were supposed to arise from the mud of the fields, or the human embryo to be generated spontaneously in the mother's womb through some mysterious influence exercised by the fluid from the male. General acceptance of the Cell Doctrine and the knowledge that the organism begins its life as an individual when the male and female germ cells unite in fertilization established the mode of origin for man as well as for other many-celled animals. Development was seen to consist of the cell divisions and the cell differentiations by which the diversified structures of the adult are produced. Although the topics of the following discussion are somewhat heterogeneous, each represents a problem that is appropriate for consideration at the conclusion of such an account of development as has been given in the preceding chapter.

Preformation and Epigenesis. — One of the most famous disputes among the earlier embryologists was that concerning preformation *versus* epigenesis. Is the organism already formed within the zygote, as in the bud of a plant, and does development consist merely in an unfolding of what is already existent; or is development the coming into being of one feature after another from a beginning that is *without form and void*, insofar as any resemblance to the completed organism is concerned? The preformationists of the eighteenth century went so far as to develop an elaborate theory of *encasement*, by which the egg was supposed to contain all of the adult structures in miniature, including the germs of all future generations, enclosed one after another in decreasing magnitude, like toy eggs within eggs carried inward to infinity. Thus, the ovary of Eve was supposed to have contained

the encapsuled representatives of all future generations of the human race.

Of course, no very extensive knowledge of embryonic stages was needed to demonstrate that the general course of development in all animals is by epigenesis and not by preformation. The fertilized egg possesses at the outset no obvious resemblance to the fully developed individual. The adult organization is attained through growth, by cell division and gradual differentiation (*cf.* Fig. 213, p. 405). Seemingly, nothing could be farther from an *unfolding* of what has already been *preformed*. But the fact that of two eggs, placed side by side in a dish of water, one develops into a frog and the other into a toad, or one into a starfish and the other into a sea urchin, is evidence that some sort of preformation does exist, unless one regards development as a supernatural process which cannot be subjected to scientific analysis. Hence, the question of epigenesis as opposed to preformation remains, in a modified form, as a problem for the embryologist of the present day. This problem has been attacked experimentally in animals like the frog, sea urchin, and starfish, the eggs of which are fertilized and develop in the external water. In such instances one is able to make experiments that cannot be made upon eggs developing within a brood pouch or other internal cavity of the parent, and it is possible to determine whether the protoplasm of the egg is preformed, to such an extent that certain of its parts can only give rise to certain parts of the adult, or whether there is more latitude in the developmental processes. For example, pieces may be cut from different regions of the fertilized or unfertilized egg of the sea urchin, and the four, eight, and even sixteen-cell stages may be separated into their component cells. These and many other experiments can be performed for the purpose of demonstrating the nature of the *organization* that the egg may possess, since it is obviously something within the egg that determines the major features of development.

So many and so diversified have been these experiments that only the general results can be mentioned. The eggs of many animals exhibit within their cytoplasm (*cf.* Fig. 112, p. 224) substances, unlike the adult parts but marking the places from which these parts originate. Such eggs are *organized* or *preformed*, to the extent that certain regions of the egg become definite regions of the adult. The eggs of other animals exhibit little

differentiation that can be recognized at present. This is true of the frog's egg before the entrance of the spermatozoön. In eggs of the latter sort, the values of the various areas are more nearly equal, and recognizable differentiation appears only at a subsequent stage of development. The truth seems to be that the eggs of different animals are not alike with respect to their visible differentiation at the one-cell stage; that the first signs of differentiation, while visible in some animals at the one-cell stage, are not apparent in others until a later stage of development; while in those forms that have, as adults, great capacity for the regeneration of lost parts, the organism is never so completely differentiated as to be unable to reform an entire body from a portion of the whole. Some kind of organization, or "preformation" in the modern sense, must be present in every egg, whether it is visible or not. Otherwise there can be no explanation of the phenomena of heredity that can satisfy the demands of science. The embryologist is of necessity a preformationist, although not in the older sense of the word. The situation is analogous to that found in Physics and Chemistry, in which the existence of invisible molecules and atoms is postulated as a basis for the visible phenomena. In problems of this nature, satisfactory analysis can only be based upon experiments which subject the organism to new and controlled conditions. No observation of normal development, however extensive, will go so far toward determining whether at the two-cell stage the right and left portions of the animal are irrevocably distributed to right and left cells, as will the simple experiment of separating these two cells and seeing what happens.

In addition to this study of embryonic stages, there is another method of attacking the problem of preformation, which may be illustrated as follows: If, in a game of cards, the hands are dealt out and the cards in each hand then examined, it is possible, if the nature of the dealing is known, to *infer* the manner in which the cards were arranged in the pack before the dealing began. One must either recognize a causal relation between the arrangement within the pack and the arrangement that appears as a result of the deal, or must assume the miraculous origin of the latter. Studying the inheritance of the qualities that appear in an adult animal is like examining the cards in a hand, while knowing something of the dealing, without knowing the organization of the pack.

If it is found that adult characteristics appear in a certain manner, the probable arrangement of whatever it is in the zygote that represents these characteristics can be inferred.

An amazing result of the recent experimental work upon the heredity of adult characteristics is that the knowledge thus gained enables us to picture, without seeing, certain characteristics of the organization of the germ cells, much as the chemist pictures the organization of molecules. There is, however, one respect in which the biologist, who seeks to understand the organization of the germ cells, has an advantage over the chemist, who postulates the structure of invisible molecules. There exists within the nucleus of ovum and spermatozoön, as in all other cells, a visible substance, *chromatin*, that appears at the time of cell division in the form of *chromosomes* (*cf.* Fig. 76, p. 138), which are constant, in number and appearance, for any given species. The behavior of these chromosomes, as seen by the microscope, is so specifically related to the end results of heredity as virtually to identify them with the mechanism of inheritance for certain adult qualities, and hence to suggest the probable organization of the germinal substance. It is thus possible to attack this aspect of the problem of development at its two extremes and to correlate the attacks so that each supplements the other.

Heredity and Environment in Development. — Although the discussion of heredity is reserved for a later chapter, we may here consider the relative importance of hereditary and environmental factors in the development of the individual (*cf.* p. 484). The physical basis of heredity is found in the germ cells and in the processes of development which have been described in the foregoing chapters. We have, therefore, become somewhat acquainted with the mechanism of heredity as it operates during development, if not with the organization of the germ cells and inheritance as described in the chapter on Genetics. The development of an individual from the germ cells is a result of the internal factor of heredity and the external factor of environment, or of "nature" and "nurture" as they are often called. On the one hand, the zygote that is formed by the union of ovum and spermatozoön possesses certain potentialities; on the other, it is subjected to environmental influences at every stage of its development. The famous experiment by Castle (Fig. 229) in which the ovary of a black guinea pig was transplanted into a white female, which was

FIG. 229.—A famous experiment showing that germ cells are relatively independent of the body in which they are found.

The ovaries of a young female guinea pig (A) were transplanted into a white guinea pig (B) whose ovaries had been removed. This white guinea pig (B) with the "black" ovaries from A was then bred with a white male (C). Since white is recessive, only white offspring would be expected from such a cross between two white guinea pigs (*cf.* p. 466). Instead of this *all the offspring produced were black* like D. The results thus conform to the Mendelian expectation in a cross between black (dominant) and white (recessive) individuals as would be the case here if the eggs of the "black" ovary transplanted into B were unmodified by the white body. (After Castle.)

then bred to a white male and produced only black offspring, presents conclusive evidence of the importance of heredity. Yet much is due to environment. The interaction between these two factors is so complex that it is impossible to say, for any characteristic of the adult, how much is due to heredity and how much to environment, although it is often possible to assign a preponderant influence to one or the other. The greatest problem of Embryology might even be said to be the determination of the relative importance of heredity and environment at each step in development. This is not a new question, since it has been discussed for centuries; and to-day the extent to which the environmental factor called education can make amends for a defective heredity is of vital importance to mankind.

The possibilities of environmental influences are so readily appreciable that men have often ascribed to them a major rôle and have overlooked the more subtle factor of heredity in the development of the individual. Scientists like Lamarek and his modern followers have believed that the environment, acting directly upon the organism, can be the cause of evolution. To cite other examples, it has been supposed that such differences as those between the sexes of higher animals may be the result of environmental conditions, like food and temperature, and that skin color in the various races of mankind may have been produced by the intensity of the sunlight to which the individuals were subjected generation after generation. Our democratic social institutions are based largely upon the doctrine that "all men are created equal," by which the importance of heredity is virtually denied while that of environment is magnified. The advance of biological knowledge has shown the importance of heredity in the production of the individual, and modern theories of the causes of evolution incline toward factors that originate in the hereditary constitution rather than in the environment. Yet it cannot be too strongly insisted that the individual that develops from a fertilized egg is a product of both of these factors.

The environmental conditions that affect development may be classified as the *physical factors* of mechanical relationships, heat, light, gravity, density of medium, etc.; and the *chemical factors*, such as the oxygen, carbon dioxide, water, food, and such elements or compounds as may be necessary for normal development. In the study of development, physical or chemical factors that

are not normal may be introduced for experimental purposes. For example, the exact pattern of the cells on the outer surface of the sixteen or thirty-two cell stage of a frog's egg is fundamentally dependent upon the internal factors of cell division and organization, but is influenced to some extent by the mechanical pressure that is exerted by the cells upon one another. Each cell tends, when isolated, to become a sphere, as does a single soap bubble, but in the mass the outline of any particular cell is the result of its relationships with neighboring cells, that is, with its environment. Under normal conditions the egg of a frog or a starfish develops as a spherical mass, but under the pressure of a cover slip it may be caused to develop into a plate of cells. If the pressure is too long continued a hopelessly abnormal embryo is produced, but if the slip is removed in time the mass will gradually become adjusted and a normal embryo may be formed. Again, it was thought from earlier experiments, in which one of the cells in the two-cell stage of the frog was killed by destroying the nucleus with a needle, that the remaining cell could produce only one-half of the adult, as it appears to do under normal conditions. When, however, a method of separating the two cells was devised, it was found that each might become spherical and develop into an embryo of half the normal size, as do the cells in the two-cell stage of the starfish, which may be easily separated by shaking. It therefore appears that one of the cells of the two-cell stage in the frog produces the right side of the adult organism, and the other the left side, because these cells have the inherent capacity to produce a frog and not a toad, and also because each cell develops in contact with the other. The resulting embryo is, therefore, the product of a combination of hereditary and environmental factors, if we consider contact with the other half as part of the environment for each half of the embryo.

The influence of temperature upon the rate of development of organisms is a familiar fact, as with the frog, where development proceeds very slowly if the weather is cold, and more rapidly in warmer weather or when the eggs are brought to the laboratory. Extremes of temperature produce abnormalities, but there are wide limits. Ordinarily the temperature influences only the rate and not the nature of the development and may thus be interpreted as acting through its effect upon the rate of chemical changes in the embryo. Another effect of an alteration of temperature is

seen in some invertebrates, where the endoderm may be caused to evaginate instead of invaginating at the time of gastrulation (Fig. 230).

An extreme example of the effects of chemical changes in the environment is the production of one-eyed or cyclopean monsters in the embryos of fishes through alteration of the chemical constituents of the water (Fig. 231). By adding magnesium or other salts it is possible to produce embryos in which the two optic vesicles have fused together at the ventral anterior end of the body as a single cyclopean eye. Although such monstrosities are not longlived, their production demonstrates that the organism develops normally only under a given set of conditions. If the sea water were not what it happens to be, fishes might be quite different from what they are now and would be called normal. The influence of the environmental factor of light upon the formation of chlorophyll in plants is seen when a board is left upon the lawn for a few days and the grass beneath it becomes colorless. The influence of gravity is seen when a seed is allowed to begin its growth of "root" and "stem" and is then inverted. Many other examples might be cited, all showing how changes in environmental conditions bring about differences in the development, sometimes within wide limits. The corollary of this is that the "normal" organism becomes

what it does because of a certain normal or "average" set of conditions which are fairly constant and hence productive of the kinds of individuals that occur in nature. The adult is what it is because its hereditary organization, which is embodied in some manner in the germ cells, develops under a particular environment. As will be explained in discussing the possible causes of racial development or Evolution in Chapter 21, the

FIG. 230.—Effect of environmental conditions upon gastrulation in the mollusc *Crepidula*.

If the temperature or density of the surrounding water is altered in certain ways during gastrulation, the endoderm is caused to turn out instead of in, producing the abnormal condition known as an "exogastrula" (cf. Fig. 209 E). In the figure the ectoderm is above and the endoderm below. (From Conklin, "Heredity and Environment," copyright, 1916, by Princeton University Press, reprinted by permission.)

Lamarckian Theory of the inheritance of acquired characteristics maintains that differences acquired by the individual as a result of changes in the environment may become a part of its inheritance and thus be transmitted to future generations. The majority of biologists, however, do not believe that the evidence justifies such a conclusion.

In the higher organisms, where the effects of habit formation are much in evidence, the influences referred to in the preceding para-

FIG. 231.—Effect of environmental conditions upon development of a fish *Fundulus*.

Above, a normal free-swimming embryo from dorsal view. Below, cyclopean monster, with the two eyes grown together ventrally and anterior to the mouth (*m*), as developed in sea water to which magnesium salts had been added. (After Stockard, *Anatomical Record*, Vol. III.)

graph as factors of environment are further complicated by the effects of training, as when a horse is trained to trot, a dog to fetch and carry, or a child to read and write. The relationships of the factors involved, including that of heredity, are often represented by a triangle (Fig. 232) in which the base represents the factor of heredity, or what the organism *is* potentially, and the sides the environmental factors, which may be conveniently divided into the influence of the *surroundings*, or what the organism *has* during its lifetime, and its *training*, or what it *does*. The shape and size of such a triangle, therefore, shows what the individual *becomes* in its final adult stages. Modifications of the sides and base show what can be done by various combinations of the fundamental hereditary factor and the two environmental factors in the production of an individual.

For the human species, the interaction of these three factors may be expressed in tabular form by saying, as one American zoologist has done, that there are twenty-seven different kinds of men (Fig. 233). The case is more complex, because *good*, *medium*, and *poor* do not represent all the innumerable gradations that may occur in the three factors represented by the triangle. Nevertheless, the table indicates how environment and heredity make

FIG. 232.—Diagram to illustrate the influence of heredity, environment and training in the development of an individual (cf. Fig. 233).

The heredity is assumed to be a constant in the particular individual, but heredity is expressed in different ways according to the environment and training. Thus various types of individuals, as represented by the several triangles, may be produced from zygotes having the same hereditary potentialities. (After Conklin, "Heredity and Environment," copyright, 1916, by Princeton University Press, reprinted by permission.)

an individual what he finally becomes. Environmental factors are important at every step in development, whether of men or sponges; yet the biologist can hardly escape the conviction that the ultimate possibilities of the individual are limited by its heredity even though certain environmental conditions are necessary if a given hereditary constitution is to reach its fullest development. The manner of sex determination, as described in the section that follows, is an example of such interaction with a preponderance of hereditary over environmental factors in development.

<i>Inheritance</i>	<i>Environment</i>	<i>Training</i>
1. Good	Good	Good
2. Good	Good	Medium
3. Good	Good	Poor
4. Good	Medium	Good
5. Good	Medium	Medium
6. Good	Medium	Poor
7. Good	Poor	Good
8. Good	Poor	Medium
9. Good	Poor	Poor
10. Medium	Good	Good
11. Medium	Good	Medium
12. Medium	Good	Poor
13. Medium	Medium	Good
14. Medium	Medium	Medium
15. Medium	Medium	Poor
16. Medium	Poor	Good
17. Medium	Poor	Medium
18. Medium	Poor	Poor
19. Poor	Good	Good
20. Poor	Good	Medium
21. Poor	Good	Poor
22. Poor	Medium	Good
23. Poor	Medium	Medium
24. Poor	Medium	Poor
25. Poor	Poor	Good
26. Poor	Poor	Medium
27. Poor	Poor	Poor

FIG. 233.—Twenty-seven different kinds of men.

Human beings cannot be arbitrarily classified as good, medium, and poor, but such distinctions may be made for purposes of this illustration and the possible combinations tabulated in the manner shown (*cf.* Fig. 232). (From Walter, *Science*, June 22, 1923.)

The Determination of Sex. — The factors that determine sex in man and the familiar animals have been the subject of innumerable theories since ancient times, all of which now appear to be groundless. Toward the close of the nineteenth century, the hypothesis most widely accepted was that the sex was dependent upon the amount or kind of food the individual happened to receive during development. Experiments in over-feeding and under-feeding of the early stages of vertebrates, such as frog tadpoles, and of insects, such as the caterpillars of moths, gave what appeared to be conclusive evidence. But the repetition of these experiments and other discoveries in recent years have failed to confirm the earlier conclusions. It seems that the great proportion of males obtained upon a scanty diet was merely due to the fact that the death rate was higher for the females under this condition, and,

conversely, that more males were killed by a rich diet while the females survived. The investigators were therefore misled by not taking into account the sex of the individuals that died. In addition to such destructive criticism of the older theory, it has been found that the sex of many animals appears to be determined as early as the one-cell stage by the combination of chromosomes that the individual happens to receive at the time of fertilization.

When this chromosome theory was first promulgated about 1905, it was supposed that the sex determination was irrevocably settled at the outset and could not be changed by anything that might happen in the subsequent history of the individual. Later investigation has shown that modifications may occur in some exceptional cases, but the essential fact that sex is related to the number of chromosomes now seems thoroughly established. The account that follows will begin with an explanation of the fundamental relationship, and will conclude with a statement of the modifications of the theory that have been necessitated by recent investigations.

It will be recalled (*cf.* Fig. 113, p. 226, and Fig. 114, p. 228) that in the *diploid* grouping the chromosomes occur in pairs and that one member of each of these has descended from the chromosomes of the ovum and the other member from those of the spermatozoön. In maturation the members of these chromosomal pairs are separated, so that each gamete receives one member of each pair and therefore one-half the number otherwise found in body and germ cells, thus producing the *haploid* number. Hence, before the "sex" chromosomes were recognized it was supposed that the diploid number was always even, and the haploid number necessarily one-half of the diploid number. The chromosome theory of sex was first suggested when it was observed that not all the cells of a given species possess an even number of chromosomes in the diploid phase of the cell cycle. For example, in some insects, it was found that the cells of the male, as seen in the spermatogonia (Fig. 113), possessed one chromosome less than the oögonia (Fig. 114). This odd chromosome was first called the "X-chromosome," because its significance was unknown, and later the *sex chromosome* when it came to be identified with the mechanism of sex determination. In contrast with the sex chromosomes, the other chromosomes are known as *autosomes*. Fig. 113 shows how the unpaired sex chromosome of the male divides at every

mitosis and maintains its original condition as it descends to all the body cells and to all the germ cells until the time of maturation. When synapsis occurs the autosomes unite in pairs, while the sex chromosome has no synaptic mate. At the first maturation division the synaptic pairs of autosomes divide, and also the sex chromosome, and there is no change in the relationship; but in the second maturation, when the synaptic pairs separate instead of dividing lengthwise as in all other mitotic divisions of body and germ cells, the sex chromosome passes undivided to one member of each of the two pairs of cells shown in the figure. There are, therefore, two kinds of spermatozoa produced in equal numbers, one with and one without the sex or X-chromosome.

In the female, on the other hand, there are two sex chromosomes in the original zygote and in all of its descendants, both body and germ cells (Fig. 114, p. 228). In contrast with the spermatozoa, the mature ova are all alike, since every one contains a single sex chromosome and the haploid number of autosomes.

As shown in Fig. 114, the male combination is produced when an egg is fertilized by a spermatozoön without an X-chromosome; the female, when the spermatozoön possesses an X-chromosome. The chromosome combination that happens to be present at the time of fertilization is supposed to descend from the zygote, by mitosis, to all the cells of the individual, both body and germ cells. The sex chromosome would, therefore, function by chance combination at every period of maturation and fertilization as the determiner, or at least the indicator, of sex. According to the laws of chance, the number of males and that of females would be approximately equal wherever large numbers of individuals were involved. This seems to be the fact in most instances where large counts have been made to determine the sex ratio, although there are some exceptional cases.

Such combinations of chromosomes in relation to sex have been discovered in many insects and in other animals. A modification of the relationship described is seen in some insects and in other species, where the male has an X-chromosome and another smaller one, the Y-chromosome, which is its mate, while the female has two X-chromosomes. The diploid number of the male in such cases is, therefore, $2n + xy$, and that of the female $2n + xx$. These appear as $1n + x$ and $1n + y$, respectively, in the two types of spermatozoa, and as $1n + x$ in all the ova. The substitution of

such a scheme in Figs. 113 and 114 will give a mechanism of sex determination which might be called the exception that proves the rule. In a more exceptional type which is found in some moths, and perhaps in birds, the female possesses the single sex chromosome and the male the paired condition, so that there are two kinds of ova, one with and the other without an X-chromosome, while all spermatozoa have this chromosome.

As the investigations have been continued, they have revealed many lesser exceptions to the general scheme, which complicate, but do not overthrow, the fundamental relationship between sex and the number of chromosomes. A more important modification of the original concept is necessitated by the recent evidence that sex-determining factors are also contained in some of the autosomes. It has also been shown, in some rare instances, that the sex of an individual may be reversed, as in poultry, where an apparently functional female is said to have become a male, and in some of the fishes and Amphibia where the sex may be normally reversed as the individual grows older. In a few instances it has even been shown that the sex may be reversed experimentally by changes in environmental conditions. These complications of the fundamental theory cannot be detailed in so brief a discussion. In a modified form, the chromosome theory of sex determination now seems well established, although it is not so simple as was once supposed or as might seem from the examples that have been chosen to illustrate the principle. According to this theory, the maleness or femaleness of an adult animal is determined primarily by hereditary factors transmitted in the germ cells and not by environmental influences during development. The discovery of this relationship, and the consequent overthrow of the earlier theory that the food of the embryo was the fundamental cause of sex differentiation, further illustrates the difficulty of disentangling hereditary and environmental influences, as explained in a preceding section. The hereditary factor is often difficult to recognize, but, once discovered, it may be shown to exercise the greater influence.

Problems of Mammalian Development. — *Prenatal Influences.*

— The retention of the mammalian embryo within the body of the female parent (Figs. 234 and 235), during the stages of development corresponding to those of a bird or a reptile within the egg (*cf.* Fig. 220, p. 423, and Fig. 224, p. 428), raises questions regard-

FIG. 234.—Diagrammatic section through human uterus and embryo at the seventh or eighth week of pregnancy. The blood vessels of the embryo extend out to the placenta, but the circulation of the embryo and that of the mother are distinct (cf. Fig. 237). The technical designations of parts by the author of the figure, as given below, are not explained, but the student can see from the figure how the embryo is placed in the uterus and how its blood vessels extend out to the placenta where they form a capillary system that is independent of, although closely associated with, that of the mother.

al, allantois; *am*, amnion; *c*, openings of the oviducts (Fallopian tubes) into the uterine cavity; *c'*, cervix or outer opening of uterus filled with mucous plug (the reference letters *c*, *c'* are placed in the cavity of the uterus); *ch*, chorion with vascular villi growing into the maternal tissue, decidua capsularis and decidua basalis; *dr*, decidua capsularis; *ds*, decidua basalis or basal plate; *dv*, decidua vera; *i*, embryo; *u*, umbilical cord; *y*, yolk-sac; *y'*, yolk stalk. (From Kellicott, "Chordate Development," copyright, 1913, by Henry Holt and Co., reprinted by permission.)

ing the relationship between parent and offspring in such a type of development. There are many instances of brooding and similar modes of protected development in the Animal Kingdom (*cf.* Fig. 236); but the example to be considered is of interest because the Mammalia are the highest form of animal life. In a starfish or a frog, the eggs are laid in the external water and develop independently of parental influences, once the spawning is complete. Eggs and sperm may even be taken from the reproductive organs of the parents, which are killed by the operation, and when they are mixed together in water normal fertilization and development will follow. Under such a mode of development, no one would think of the female parent as exercising an influence upon the developing young other than what might affect the germ cells while still within the parental body. The same is true of the development of a bird. The parent incubates the egg, but any female can perform this function, and chicks may often be more effectively hatched in an incubator than by hens. In the mammal, however, where the young are retained within the parent, it is not unnatural to think that changes in the mother's body may influence the embryo, and this is commonly supposed to be the case, although there is no scientific foundation for the beliefs that are usually accepted.

For example, it is believed by many persons that the foetus of a human being or of any of the familiar domesticated mammals may be profoundly influenced by changes in the mother during pregnancy and that such influences may even be exercised by her mental states. Everyone has heard stories of how the deformities of certain individuals were caused by some injury to the mother or

FIG. 235.—Human embryo of the fourth month as it appears in uterus.

c, chorion and amnion; p, placenta; u, umbilical cord. (After Strahl, from Kelliecott, "Chordate Development," copyright, 1913, by Henry Holt and Co., reprinted by permission.)

even fright before the birth of her child. Often these cases are given with great explicitness and accepted as unquestionable evidence, without realization that the conclusion is no more than an "after-which-on-account-of-which" without scientific foundation. While it is true that general conditions of nutrition in the mother may affect the foetus and that certain poisons in her blood may diffuse into the blood of the embryo, it seems wholly untrue that her mental states can affect the offspring or that injury to a

FIG. 236.—Planarians, eggs, and young. Modes of development in which the young are encased in protective shells and provided with nutrient material occur even in some of the lower animals. For example, in the fresh water planarians (Class *Turbellaria*, Phylum *Platyhelminthes*, cf. Fig. 117, p. 240), eggs, consisting of tough capsules attached by a stalk and containing several zygotes and many yolk cells, are laid in protected places and the young hatch as miniature adults (cf. Fig. 220, p. 423).

A, adult planarians feeding on bit of meat. B, egg capsules attached to lower side of a stone and juvenile planarians escaping from a capsule. (Drawn by George T. Kline.)

particular part of her body can produce a similar change in the body of the foetus. The idea of *prenatal influence* as it is commonly held is a myth when judged by scientific standards, but there are certain conditions in the parent that may affect the embryo during its development within the uterus.

To understand the kind of prenatal influence that may be effective, it is necessary to understand the structural relationship between the parent and the foetus (cf. Figs. 234 and 237). The placenta by which the foetus is attached to the uterus consists of a maternal portion, containing capillaries of the mother's circulatory

system, and a foetal portion, containing capillaries of the embryonic circulation. In general, there seems to be no direct connection between these two blood systems, since the introduction of injection fluids into the capillaries shows their complete independence. Anything that passes between parent and offspring must, therefore, be in the form of a diffusible substance, and

FIG. 237.—Diagram of a section through the human placenta at the middle of the fifth month of pregnancy. The maternal blood system and tissues are intimately associated with those of the fetus, although the two circulations are distinct and material is interchanged between parent and offspring only by diffusion. The technical designations of parts by the author of the figure, as given below, are not explained, but the student can interpret the essential facts to be illustrated by understanding that the area with horizontal lines above represents tissue of the embryo; the black, maternal blood spaces; and the parts below the black other maternal tissue.

A, amnion; *bl*, afferent maternal arteries; *BP*, basal plate or decidua basalis; *Ch*, chorion; *Ff*, *f*, and *h*, chorionic vascular villi of embryo; *i*, intervillous blood spaces or lacunae (maternal blood); *m*, chorion; *M*, musculation of the uterine wall; *r*, marginal sinus; *sp*, spongy layer of decidua basalis; *Tr-tr*, line along which the placenta will separate at parturition; *Z*, Chorionic villi; *, closing plate. (After Hertwig, from Kellicott, "Chordate Development," copyright, 1913, by Henry Holt and Co., reprinted by permission.)

experiments show that not all diffusible substances can pass with equal readiness between the two systems. The embryo of a mammal is a separate organism developing within the mother in a relationship which resembles that of a parasite to its host. At no stage is there any relationship whatsoever between the nervous system of the fetus and that of the mother. The idea that her mental states can be impressed upon the offspring necessitates the absurd belief that nerve impulses can pass through the placenta,

which is a non-nervous tissue, and mysteriously affect the nervous system of the fœtus.

As a matter of fact, the female does not seem to exercise a preponderating influence even upon the normal phases of development, as might be supposed since the offspring are nourished within her body. If this were the case, one would expect to find children resembling their mothers to a greater degree than their fathers, whereas the resemblance is about equally divided, as in other forms of development. Moreover, there is no direct evidence for such prenatal influences as are popularly supposed to exist. Malformations are explained by causes other than the mental or physical states of the parent. It is true that conditions of malnutrition in the mother and specific poisons in her blood, such as lead poison or the toxins of certain diseases, may affect the embryo in the same way that a frog embryo might be affected by substances in the surrounding water, or a chick embryo by substances introduced into the albumen of the egg and by the atmosphere of an incubator. Insofar as belief in prenatal impressions leads to a state of fear in pregnant women, it is a cruel superstition no better than belief in witchcraft. The more pleasant belief that a mother can make the eyes of her child a desired color by so wishing, or create a musician by listening to music, rests upon no better foundation. What is probably true is that the body of a nervous and overwrought mother is less able to carry on the processes necessary for the proper nutrition of her child, whether in the foetal stages or during nursing; while contentment resulting from the belief that something is being accomplished, even though it rests upon a false foundation, makes for good digestion and hence for a metabolism that results in better nutrition of the fœtus.

Telegony. — Correlated with the belief in prenatal influences is that in telegony. It is widely believed among breeders that if a pure-bred female is mated with an inferior male her offspring by subsequent matings with pure-bred males will show the influence of the previous sire. This belief rests upon many alleged examples and was once supposed to possess some scientific foundation. Scientific study, however, gives no indication of any such influence, and on theoretical grounds there is no warrant for the belief. The inheritance from the male is in some manner carried in the spermatozoa. These are introduced by sexual union and, so far as the evidence goes, they do not remain alive in the female mammal for

any great length of time, certainly not so long as from one pregnancy to the next. To believe in telephony it is necessary to suppose either that the spermatozoa of a previous mating remain alive in the female and fertilize some of her eggs in subsequent pregnancies, or that the development of a foetus from a given male in some manner changes the hereditary complex that her germ cells will transmit to subsequent generations. In the absence of any scientific evidence that telephony exists, belief in its occurrence is ridiculous, since it is opposed to the well-established facts of heredity and reproduction. The alleged examples are to be explained as the result of impurities in the stock of the female or the male with which she is subsequently mated. The appearance of such defects in the offspring of supposedly pure stock is easily understood as the chance appearance of latent combinations according to the laws of heredity.

In concluding this general discussion of development, it may be remarked that the field of Embryology is still attractive to investigators because it includes so many unsolved problems. There is, indeed, no phenomenon of nature which seems so inexplicable as the development of a complex animal from a single cell, by cell divisions and differentiations. The sequence of stages in development has now been ascertained in a fairly complete manner for representative types in each phylum of the Metazoa, as illustrated by the accounts that have been given of individual animals. But why the differentiation occurs at particular stages and in particular parts of the embryo is the great problem of Embryology to which we are only beginning to find answers. The embryologist is also confronted with the philosophical problems involved in the origin of men from germ cells by a process of development.

CHAPTER 19

GENETICS

In the chapters on Development the student has become acquainted with the known facts concerning the processes of cell division and differentiation in the origin of a new individual. We may now consider the origin of new individuals with respect to their resemblance to their parents. It is often said that like reproduces like; and inheritance, in the biological sense, means that offspring are similar to their parents. Members of a new generation, however, always differ from the generation from which they arise; they also differ among themselves, except in the case of "identical twins." Even in such instances a careful observer will be able to detect a certain lack of exact resemblance. Such differences between individuals that are in general alike are known as "variations." We see, therefore, that in the reproduction of new generations the offspring resemble and yet are unlike the parents. The phenomena of inheritance and variation go hand in hand. Heredity is, in fact, sometimes defined as "correspondence of deviations from type," which might be expressed as a correspondence in variations from the general likeness between generations. Genetics is that part of biological science which deals with the facts and theories of heredity and variation in the origin of new individuals from generation to generation.

It has been pointed out in previous pages that new individuals arise from preëxisting individuals by the process of asexual or sexual reproduction. Sexual reproduction followed by an orderly course of development, consisting essentially of growth and differentiation, gives rise to a new individual which is like, as well as unlike, its parents. Whatever it is that determines the course of development must determine the heredity and variation of the individual. In other words, the offspring inherits a course of development which under normal environmental conditions will make it like the parents. A discussion of the theoretical concep-

tions of the factors that condition the course of development, and, therefore, the resemblance between generations, is reserved for later paragraphs. A great mass of evidence indicates that the mechanism of heredity and variation is carried in the so-called germplasm. While this is undoubtedly true in many of the cases to be mentioned, the facts of asexual reproduction by budding in multicellular animals, and of regeneration in forms like hydra, planaria, and the annulates, make it certain that the mechanism that controls the course of development is also distributed to the somatoplasm.

Several methods of studying the subject matter of Genetics are in use. It is possible to observe and analyze resemblances and variations from one generation to another in large groups of individuals as they are found under natural conditions. This is the *statistical method*, or the method of *Biometry*. In contrast with such mass analysis is the observation of inheritance and variation in animals bred under experimental conditions for generation after generation. This method of *Experimental Breeding*, under controlled conditions that give the best environment for the organisms, makes it possible to know in detail the character of heredity and variation in any particular individual, as well as to compare, specifically, individuals of successive generations. In order to interpret the results of experimental breeding it becomes necessary to study, by the method of *Cytology*, the germ cells from which new individuals arise. The greatest progress in the theory of Genetics has come from correlation of results obtained from experimental breeding and such study of germ cells. A fourth way of approaching the study of the mechanism of heredity and variation is by the method of *Experimental Embryology*, in which individuals of known ancestry are subjected to conditions that are not usual for their development. The comparison of results obtained from these several ways of approach has yielded considerable information concerning many facts of heredity and variation, and has led to the formulation of theories of the mechanism involved. Clarification and extension of problems in Genetics may be expected to continue in view of the great amount of interest in research in this field.

The Method of Biometry

Galton's Work. — The biometrical method is that of collecting a great amount of observational data upon organisms under nat-

ural conditions, analyzing these data by mathematical or statistical methods, and formulating generalizations concerning heredity and variation that will be true for the whole group but for no particular individual. Sir Francis Galton (1822–1911) did the first serious work of biometrical character, although Quetelet (1794–1874) had foreseen the value of such a method of attack.

FIG. 238.—Diagram illustrating Galton's law of Ancestral Inheritance. The large square represents the total of any individual's inheritance. The smaller areas indicate in what proportions the total is derived from the ancestors.

Galton studied the relation between height of parents and height of offspring in over a thousand cases in man. From these data he proposed his laws of "Ancestral Inheritance" and "Filial Regression." According to the law of Ancestral Inheritance, the parents of any individual contribute one-half of his inheritance while the grandparents contribute one-fourth, the great-grandparents, one-eighth, the great-great-grandparents, one-sixteenth, etc. (Fig. 238.) The individual is, therefore, like its parents, but varies

from them because of the influence of more remote ancestors. The law of Filial Regression is an expression of the fact that in any large group, in which considerable variation occurs, the offspring tend to be like the average and not like the extremes of the parent generation. In other words, the offspring of average parents are average; those of parents below the average are below the average; those of parents above the average are above the average; *but the*

FIG. 239.—Diagram illustrating Galton's law of Filial Regression. The circles represent the height class to which the parents belong, while the arrow points indicate the average height of their respective offspring. The children of parents that are either below or above the average are nearer the average than were the parents.

(From Walter, "Genetics," copyright, 1922, by The Macmillan Co., reprinted by permission.)

offspring of parents that are either below or above the average are nearer the average than were the parents (Fig. 239). The original study of Galton on human height has been supplemented by investigations of inheritance of eye-color, mental ability, length of life, and other characteristics by Karl Pearson, Raymond Pearl, and other biometricians of to-day.

Pure Lines and Selection. — Galton's observations were made on groups that were not subjected to experimental control. His

law of Regression furnished the stimulus for the experimental work of Johannsen, a Danish botanist. Johannsen conceived the idea that if offspring of parents who were above or below the average were also above or below the average, it might be possible to shift the average by continued selection of parents from among the unusual groups. Working with beans in which self-fertilization occurred, he chose the heaviest seeds from which to raise his next generation. The progeny seeds varied around an average of 35 cg. on some plants to an average of 60 cg. on others, all of the

FIG. 240.—Diagram illustrating the fact that selection of variations that result from environmental conditions does not shift the average. Above, the size variations of seeds from a single bean plant are shown. Below, the size variations in progeny from the largest and smallest of these seeds.

(After Baur in "Grundlagen der Pflanzenzüchtung.")

plants having been produced by seeds weighing 80 cg. He next tried similar experiments on the progeny of single plants that were propagated by self-fertilization so that biparental inheritance was not a factor. Such progeny constitute a "pure line." Within a pure line Johannsen found that he could not shift the average by selecting the heaviest and the lightest seeds for parents (Fig. 240 and cf. Fig. 308, p. 559).

In the work of practical breeders it is common to select the animals or plants that have the most favorable characteristics as the parents of the new generation. This selection must, however, be continued in each generation since it is not possible to

“fix” a new average. From any group of individuals many pure lines can be sorted out, and such a mixture of pure lines is known as a “population.”

Johannsen demonstrated the relationship of pure lines to population (Fig. 241). If one starts with a population one can, by selection, sort out pure lines having any characteristics that may be desirable. Such pure lines are stable only if mixing with other lines is prevented. Galton was, of course, dealing with populations in his work. Just as each pure line varies around its average, so the population varies around the average of its pure lines. Other workers have tested selection in pure lines. These experiments have been made on size variation in different organisms, chemical content of potatoes and sugar beets, egg-laying capacity in poultry, time of maturity of seeds, distribution of color in coats of mammals, and many other characteristics. In no case has selection been shown to have shifted the average about which a pure line varies. These variations, which are known as “fluctuations,” are the result of environmental effects during develop-

FIG. 241.—Diagram illustrating the variations in weight of five “pure lines” of beans, and in the “population” formed when all are put together. Beans of the same weight are shown in the test tubes of each vertical line (cf. Figs. 307 and 308).

(After Johannsen, from Walter, “Genetics,” copyright, 1922, by The Macmillan Co., reprinted by permission.)

ment and do not influence heredity in succeeding generations.

The Method of Experimental Breeding

Mendel's Contribution. — While the statistical or biometrical method gives a survey of the average course of heredity and variation in populations and pure lines consisting of numerous individuals, it is of no value in the analysis of individual cases. Experimental breeding, in a controlled environment, makes possible the accumulation of data on the process of heredity in all the individuals produced from generation to generation.

FIG. 242.—Gregor Mendel, 1866

Enlarged from a group of the brethren of the Königs-kloster. (From Bateson, "Mendel's Principles of Heredity," copyright, 1909, by Cambridge University Press, reprinted by permission.)

The first recorded experiment in breeding was that of Camerarius, in 1694. Not until Father Gregor Mendel (1822–1884) of the Augustinian Order, carried out his careful work on the breeding of peas in the monastery garden at Brunn in Austria, did this method yield results that made clearer the principles of heredity. Mendel's success resulted from the fact that he followed the inheritance of single specific characteristics in many individuals for many generations. One of his original experiments was that of cross fertilization between peas with tall stems and those with dwarf stems. The use of parents that differ with respect to one or more characteristics is known as "hybridization," and

the offspring of such a cross fertilization are "hybrids." If the parents differ with respect to one characteristic, such as length of stem in peas, a cross between them is called *mono-hybridization*. Mendel found that the offspring produced by hybridizing tall and dwarf peas were, without exception, tall (Fig. 243) whether the male parent was tall and the female dwarf, or *vice versa*. When these tall hybrid peas were crossed among themselves, three-fourths of the next generation were tall, while one-fourth were dwarf like their dwarf grandparents. Further breeding showed that the dwarf progeny of the tall hybrids gave only dwarf offspring when interbred. That is, the characteristic of the dwarf stem, which

was not revealed in the first filial generation, or F_1 generation, arising from a cross between tall and dwarf parents, or P_1 generation, emerges unchanged in the second filial, or F_2 generation. Dwarfness in such peas is as pure as was the dwarfness of their

FIG. 243.—Diagram to illustrate mono-hybridization of peas that differ with respect to length of the stem. Tall stem is dominant to dwarf stem.

grandparents, and they give rise only to dwarf peas so long as they are bred together.

Breeding of the tall peas that constitute three-fourths of the F_2 generation reveals the fact that, although these tall individuals

superficially resemble one another, they are dissimilar as parents. One-third of this tall group give rise in successive generations to tall offspring without exception. Such tall specimens, which constitute one-fourth of the total F_2 generation, correspond, in their resemblance to the pure tall pea of the P_1 generation, to that quarter of the group that are like the dwarf pea of the P_1 . The remaining two-thirds of the tall peas of the F_2 generation, or one-half of the offspring of the hybrid tall peas, are like their parents. When interbred, they give rise to offspring in the ratio of three tall to one dwarf. As shown in the diagram, this group again breaks up, when analyzed, into three types that occur in the ratio of 1 : 2 : 1; that is, one-fourth are pure tall peas, one-half hybrid tall peas, and one-fourth pure dwarf peas. In the case under discussion, tallness is said to be "dominant" to dwarfness. Conversely, dwarfness is "recessive" to tallness, and is obscured or suppressed by it when the two occur together in a hybrid individual. However, neither characteristic is altered in any way by association with the other, as is clearly shown by the "purity" of individuals of the second generation for these qualities. The essential contribution of Mendel's work to our knowledge of heredity is this demonstration of *the purity of germplasm with respect to determiners of characters that are inherited*. Some elements of the hereditary make-up of an individual may be temporarily obscured by others, but segregation and recombination will occur in new generations. The analogy to a deck of cards from which new hands can be dealt after shuffling is one that illustrates the possibilities of segregation and recombination: the separate cards of the deck remain the same.

It has been stated that the offspring of a cross between tall and dwarf peas are tall. Superficially, they cannot be distinguished from their tall parent. Yet these tall hybrids when bred together give some tall and some dwarf individuals. The tall peas of the F_2 generation are all similar in appearance; but experimental breeding proves that some reproduce only tall peas, while others are like their parents in giving rise to both tall and dwarf offspring. In such cases of inheritance with dominance it is impossible to distinguish, externally, a hybrid individual from an individual that will breed true for the dominant character. On the other hand, an individual that appears recessive will always breed true.

If any dominant characteristic be represented by D and any

with many plants and animals. For example, when a gray mouse is crossed with a white mouse all the offspring are gray, which shows that gray coat-color is dominant to white coat-color in mice (Fig. 245). In the F_2 generation gray and white mice occur in the ratio of 3 : 1. Of the gray mice, which constitute three-fourths of

FIG. 245.—Results of mono-hybridization of mice which differ with respect to color of coat. Gray coat-color is dominant to white coat-color (cf. Fig. 252).

this generation, some are found to breed true for grayness, while others reproduce both gray and white offspring. Complete analysis reveals that 25 per cent of the F_2 generation are gray and will breed true for gray coat-color, 50 per cent appear gray but will not breed true, and 25 per cent are white and reproduce only white individuals.

Up to this point the examples used have been cases of *inheritance with dominance*. Dominance and recessiveness are not, how-

ever, always present. If red and white four o'clocks (*Mirabilis jalapa*) are crossed, the hybrids of the F_1 generation are neither red

FIG. 246.—Results of mono-hybridization of fowls which differ with respect to color of feathers. This is an example of inheritance without dominance since black and white parents yield blue hybrids. In the F_2 generation three visibly distinct types are produced in a 1 : 2 : 1 ratio.

nor white, but pink. When these pink hybrids are interbred, offspring occur in the ratio of 1 red: 2 pink: 1 white. The red and white individuals breed true for these characteristic colors, while

the pink always give three kinds of offspring in the typical 1 : 2 : 1 ratio. Another case of *inheritance without dominance* is that of the blue Andalusian fowl (Fig. 246). Blue Andalusian fowls are produced by crossing a type of black fowl with a type of white fowl. They are, therefore, hybrids and, as would be anticipated, do not breed true. Blue Andalusian parents yield 25 per cent black

FIG. 247.—Results of di-hybridization in guinea pigs which differ with respect to color of hair and quality of coat. Black hair is dominant to white hair, and rough coat is dominant to smooth coat (cf. Fig. 256).

Rearrangement of figures from Castle, "Genetics and Eugenics," copyright, 1916, by Harvard University Press, printed by permission.)

chicks, 50 per cent blue chicks, and 25 per cent white chicks. The black and white offspring breed true, but the blue offspring, like all other blue Andalusians, will always yield 25 per cent black, 50 per cent blue, and 25 per cent white individuals. The course of inheritance is, therefore, in no way different for characteristics that do not exhibit dominance and recessiveness than it is for those in which dominance occurs. In inheritance without dominance,

the hybrid individuals, or those that will not breed true, can be distinguished superficially from those that will give rise to offspring like themselves. *Dominance is not an essential feature of Mendelian theory*, although almost universal in practical breeding. The purity of the germplasm is completely established whether or not dominance is involved.

FIG. 248.—Results of tri-hybridization in guinea pigs which differ with respect to color and length of hair and quality of coat. Black hair is dominant to white hair, short hair to long hair, and rough coat to smooth coat.

(Rearrangement of figures from Castle, "Genetics and Eugenics," copyright, 1916, by Harvard University Press, printed by permission.)

If individuals that differ with respect to two characteristics are crossed, the process is known as *di-hybridization*. In guinea pigs, black hair and rough coat are dominant to white hair and smooth coat. When a black-haired, smooth-coated guinea pig is bred with a white-haired, rough-coated one, the offspring are all black-haired and rough-coated (Fig. 247). Whether these characteristics have been contributed by the male or the female parent, the combination always gives individuals that exhibit both dominant char-

acters. When F_1 hybrids are crossed, four kinds of offspring result in the F_2 generation, in the following ratio: 9 black-haired, rough-coated: 3 white-haired, rough-coated: 3 black-haired, smooth-coated: 1 white-haired, smooth-coated. Mendel's original work on di-hybrids consisted in crossing wrinkled, green peas with smooth, yellow peas. The offspring of such a hybridization are smooth, yellow peas, which indicate the dominant characteristics. In the F_2 generation, smooth, yellow peas; smooth, green peas; wrinkled, yellow peas; and wrinkled, green peas occur, in the ratio of 9 : 3 : 3 : 1.

Tri-hybridization is the crossing of individuals with three differing characteristics. A third character that can be used in guinea pigs is length of hair, short hair being dominant to long hair. When a black, short-haired, smooth-coated guinea pig is crossed with a white, long-haired, rough-coated guinea pig, all the offspring of the F_1 generation are black, short-haired, and rough-coated (Fig. 248). Eight different kinds of individuals are produced in the F_2 generation, in the ratio indicated: 27 black, short-haired, rough-coated: 9 black, short-haired, smooth-coated: 9 white, short-haired, rough-coated: 9 black, long-haired, rough-coated: 3 white, short-haired, smooth-coated: 3 black, long-haired, smooth-coated: 3 white, long-haired, rough-coated: 1 white, long-haired, smooth-coated.

In the crosses previously considered, the question of the sex of the parent having a particular characteristic has been of no importance. There are, however, cases of *sex-linked inheritance* in which the sex of the parent that possesses a certain character modifies its distribution in the offspring. Much of the most important experimental breeding has been carried on by Professor Morgan (Fig. 249) and his students at Columbia University, with the fruit-fly, *Drosophila*. An example of sex-linked inheritance may be selected from the abundant data concerning heredity in this small insect. Red eye-color is dominant to white eye-color in *Drosophila* (Fig. 250). When a red-eyed female is crossed with a white-eyed male, the offspring, both male and female, of the F_1 generation are red-eyed. If such red-eyed individuals are intercrossed, all of the females and one-half of the males of the F_2 generation will have red eyes, while one-half of the males will have white eyes. The reciprocal cross between a white-eyed female and a red-eyed male gives very different results (Fig. 251). The males of the F_1 generation

are white-eyed and the females are red-eyed. In the F_2 generation red-eyed and white-eyed males and females occur in equal numbers. This does not seem to substantiate the Mendelian principles, but when the theoretical conceptions are considered in the following section it will be found to conform.

The method of experimental breeding, first carefully used by Gregor Mendel, has yielded a vast amount of detailed informa-

FIG. 249.—Edmund Beecher Wilson, 1922 (on the left). Thomas Hunt Morgan 1923 (on the right). (Photos. by courtesy of A. F. Huettnner.)

tion concerning the course of inheritance of specific characteristics by particular individuals through many successive generations. All of this work has verified the Mendelian Law of Heredity. The fundamental point that Mendel brought out was that hereditary determiners of characters are *not modified* by association with other hereditary determiners of characters. This is often spoken of as the “purity of the germplasm.” Because the character determiners are not altered but retain their unmodified independence, they *segregate* and *recombine* in successive generations, producing the characteristic ratios of mono-, di-, and tri-hybridization experiments. The hereditary units, or determiners, of the characters that are recognizable in the adult individuals are now

FIG. 250.—Results of crossing a red-eyed female *Drosophila* with a white-eyed male. The X-chromosomes are represented as carriers of the genes determining eye-color. *W* is the symbol used for a gene for red eye-color which is dominant to a gene, indicated by *w*, for white eye-color (cf. Fig. 257, p. 481). The hook-shaped chromosome which does not contain a symbol for a gene represents the Y-chromosome of the male (cf. p. 448). This cross is the reciprocal of that shown in Fig. 251.

(From Morgan, *et al.*, "The Mechanism of Mendelian Heredity," copyright, 1922, by Henry Holt and Co., reprinted by permission.)

FIG. 251.—Results of crossing a white-eyed female *Drosophila* with a red-eyed male (cf. Fig. 258, p. 482). The X-chromosomes and the symbols for the genes are explained in the legend of Fig. 250, which shows the reciprocal of this cross.

(From Morgan, *et al.*, "The Mechanism of Mendelian Heredity," copyright, 1922, by Henry Holt and Co., reprinted by permission.)

usually called *factors*, or *genes*. For each character of an individual, such as height, and color of hair or eyes, there are at least two factors present as determiners. These pairs of factors are known as *allelomorphs*. In many well-known experiments more than two factors are concerned in the production of a character, but for the purposes of this discussion the examples are selected from the simplest cases.

The Method of Cytology

Chromosomes as Carriers of the Genes. — When Mendel's work was brought to light in 1900, it was, of course, well known that, in sexually reproducing organisms, a new individual develops from a zygote formed by the union of an ovum and a spermatozoön. These gametes, or germ cells, carry half the number of chromosomes characteristic of the species, and the full number is restored in the zygote. As the zygote divides by mitosis the chromosomes are distributed equally, both as to quantity and quality, by the longitudinal halving, to the cells of the new individual. The primordial germ cells of any individual contain a number of chromosomes that can be grouped in pairs of similar size and shape. One member of each pair is of paternal and the other of maternal origin. When the reduction division of maturation occurs, the chromosomes are reduced to one-half the number present in the other cells of the body. This reduction does not involve the separation of the chromosomes that came originally from one parent from those that came from the other, and the placing of the two groups in separate gametes. On the contrary, the distribution is a random one, with the members of each pair of chromosomes separating independently of other pairs. The details of the behavior of the chromosomes during mitosis and maturation have been stated in previous chapters (*cf.* pp. 137, 227, and 229). These facts have been discovered by the microscopical examination of germ cells, or by the methods of Cytology. Sutton, in 1902, called attention to the behavior of the chromosomes as furnishing a cellular mechanism for the theoretical explanation of Mendelian results. Since that time the theory of the chromosomes as carriers of the genes has been greatly extended, and they may be regarded as the physical basis of heredity. The research of Professor Wilson (Fig. 249) was important in the analysis of the numbers and types

of chromosomes; while the work of Miss Carothers furnished evidence of their independent segregation during maturation.

If the example of mono-hybridism between a gray and white mouse be analyzed according to this theory, the assumption is that the zygote from which the gray mouse developed contained

FIG. 252.—Diagram illustrating independent segregation and possible recombinations of a single pair of chromosomes bearing a single pair of genes in a case of mono-hybridization between a homozygous gray mouse and a homozygous white mouse (cf. Fig. 245).

G, gene for gray coat-color; *W*, gene for white coat color.

two genes for grayness, one from each of its parents, while the zygote from which the white mouse developed contained two genes for whiteness, one from each of its parents (Fig. 252). Each gene is regarded as being carried in a separate chromosome, but the two genes of each animal are resident in similar chromosomes, forming a pair. At the time of reduction the members of a pair of chromosomes separate and pass into different gametes. All the gametes

of the gray parent possess a single gene for gray coat-color, and those of the white parent a single gene for white coat-color. When fertilization occurs only one type of offspring can result. This zygote contains two genes for coat-color, but one is for whiteness and one for grayness. A zygote of this kind is called a *heterozygote*, in contrast with zygotes like those from which the parents developed, which are known as *homozygotes*, because the genes of the pair are alike. The F_1 individuals are spoken of as *hetero-*

FIG. 253.—Diagram illustrating independent segregation and possible recombinations of chromosomes bearing genes when a heterozygous gray mouse is crossed with a homozygous white mouse.

G, gene for gray coat-color; W, gene for white coat-color.

zygous, while the parent generation, in this case, is *homozygous*. As can be seen from the diagram, two kinds of gametes are formed by individuals of the F_1 generation, and three recombinations are possible in the F_2 generation. According to the law of chance, one of these classes, the GW combination, will occur twice as frequently as either the GG or the WW . The effect of the dominance of the gene for grayness is such that both homozygous and heterozygous gray mice appear alike, and the apparent ratio in the F_2 generation is 3 gray : 1 white. It is, therefore, necessary to obtain offspring from particular cases in order to differentiate genetically

between individuals that exhibit a dominant characteristic. The theoretical explanation of the results obtained when a heterozygous gray mouse is crossed with a white mouse, which will always be homozygous since white is recessive, is presented in Fig. 253. It is the difference between the offspring obtained in this cross and those obtained by crossing a homozygous gray with a white (Fig. 252), that furnishes the type of breeding test used for differentiating homozygous from heterozygous dominant individuals. The dia-

FIG. 254.—Diagram illustrating independent segregation and possible recombinations of chromosomes bearing genes when a homozygous gray mouse is crossed with a heterozygous gray mouse.

G, gene for gray coat-color; *W*, gene for white coat-color.

gram in Fig. 254 shows why indiscriminate crossing between the gray mice would fail to yield information that would enable one to distinguish homozygous gray mice with certainty. The breeding results are adequately explained in these cases of mono-hybridism by the theory that the genes, or Mendelian units, are carried in the chromosomes and so distributed to gametes and zygote (Fig. 255).

The theory of the chromosomes as the physical basis of heredity can likewise be used to explain cases of di- and tri-hybridism. In

FIG. 255.—Results of mono-hybridization of *Drosophila* which differ with respect to type of wing. The chromosomes are shown as the carriers of the genes. *V* is the symbol used for the gene for long wing which is dominant to a gene, indicated by *v*, for vestigial wing (cf. Fig. 252).

(From Morgan, *et al.*, "The Mechanism of Mendelian Heredity," copyright, 1922, by Henry Holt and Co., reprinted by permission.)

Drosophila, long wings (V) are dominant to short or vestigial wings (v), and gray body-color (E) is dominant to ebony (e) or black body-color. A fly with vestigial wings and gray body ($vvEE$) is mated with a long-winged fly with ebony body ($VVee$) (Fig. 256). At the time of maturation the chromosomes of a pair separate and pass into different gametes. The gametes of the parent generation will be (vE) and (Ve), respectively. The zygotes of F_1 will be ($VvEe$) and will develop into long-winged, gray-bodied flies. Four different kinds of gametes can be formed by these F_1 individuals, since the different pairs of chromosomes pass independently into gametes at the time of reduction. The possible segregation of genes in any one individual is as follows: (VE), (Ve), (vE), and (ve). Recombination of such gametes to form the zygotes of F_2 , according to the laws of chance, is shown in the checkerboard at the bottom of Fig. 256.

Linkage. — The discussion of the chromosomes as the carriers of the genes, in the previous section, has been concerned with what could occur if each gene mentioned were carried in a separate chromosome. It was discovered by Bateson and Punnett, in 1906, that certain factors are coupled or linked in inheritance. They found, in crossing a sweet pea carrying genes for purple flowers and long pollen grains with a sweet pea in which the genes were for red flowers and round pollen grains, that the factors that came from each parent were inherited together instead of being segregated and recombined independently. The study of the inheritance of some 400 factors in *Drosophila* shows that they fall into four groups. The genes composing each of these groups are said to be "linked." Cytological investigation demonstrates the presence of four pairs of chromosomes in *Drosophila*, and linked genes are believed to be carried by the same chromosomal pair. Furthermore, there is evidence which can be interpreted to mean that genes in a chromosome are arranged like beads on a string. This linear arrangement of the genes makes the equal longitudinal splitting of chromosomes during mitosis significant as a *qualitative* division (cf. p. 139).

The example of sex-linked inheritance described as a breeding experiment (p. 470) can be explained if the chromosomes associated with sex determination are assumed to carry the factors concerned with eye-color. It will be recalled that in the cells of a female there are two so-called X-chromosomes, while in the male one

FIG. 256.—Diagram illustrating independent segregation and possible recombinations of two pairs of chromosomes and two pairs of genes in a case of dihybridization between a vestigial-winged, gray-bodied fly (*Drosophila*) and a long-winged, ebony-bodied fly (cf. Fig. 247).

E , gene for gray body; e , gene for ebony body; V , gene for long wing; v , gene for vestigial wing.

X-chromosome is found (*cf.* pp. 226, 228 and 447). The male sometimes possesses a Y-chromosome which seems to carry no genes. At the time of reduction during maturation the eggs formed contain one X-chromosome. Two types of sperm are produced in equal numbers. One kind of sperm has an X-chromosome; the other either has no chromosome homologous with the X, or contains a Y-chromosome. The male *Drosophila* contains both an X and a Y-chromosome. Since the Y carries no genes and never leaves the male line, it does not influence the course of heredity. In the cross between a homozygous red-eyed female *Drosophila* and a white-eyed male each egg will contain an X-chromosome carrying a gene for red eye-color, while half the sperm will have an X-chromosome bearing a gene for white eye-color and half will have a Y-chromosome (Fig. 257). Random unions of eggs and sperms will result in red-eyed females and red-eyed males in the F_1 generation. The females are red-eyed because the gene for red eye-color is dominant to the gene for white eye-color. They are, however, heterozygous for eye-color, and give rise to two kinds of eggs, in one of which the X-chromosome carries a gene for white eyes, while in the other the X-chromosome carries a gene for red eyes. Half of the sperm produced by the red-eyed males have an X-chromosome with a gene for red eyes, and half have the Y-chromosome. Combinations of the gametes in a cross between a male and a female of the F_1 generation result in red-eyed females, red-eyed males, and white-eyed males. In this kind of inheritance the white-eyed characteristic of the male parent is superficially lost in the F_1 generation only to reappear in one-half the males of the F_2 generation. The reciprocal cross, in which a white-eyed female is mated with a red-eyed male, is shown in Fig. 258. If the distribution of the X-chromosomes is followed, the reason for the difference between the offspring from these two crosses should be clear.

It is to be understood that cases of sex linkage are not exceptions to the Mendelian principles, but give great weight to the theory of the chromosomes as carriers of the genes. Cytology has furnished the knowledge of the behavior and transmission of chromosomes from one generation to the next. The experimental breeder has been able to explain adequately the results obtained in his breeding experiments, by the assumption that whatever it is that is present in the gametes and determines the appearance

of a character in an adult organism, it is carried by the chromosomes. These hypothetical determiners of inherited characters are known as Mendelian units, factors, or genes. It is believed that many genes are found in a single chromosome and that they are arranged in a row along the length of the chromosome. They are, there-

FIG. 257.—Diagram illustrating independent segregation and possible recombinations of X-chromosomes carrying genes determining eye-color, in a cross between a red-eyed female *Drosophila* and a white-eyed male. (Cf. Fig. 250, p. 472.) This is the reciprocal of the cross shown in Fig. 258.

X, X-chromosome carrying gene for red eye-color; XX, X-chromosome carrying gene for white eye-color; Y, Y-chromosome which is confined to males and does not carry genes.

fore, equally distributed to all cells that are derived from a zygote by mitosis. The mechanism of independent assortment of the members of chromosome pairs during maturation of the germ cells, together with the possibilities of recombination, furnishes a morphological basis, within the cell, upon which Mendelian ratios may be explained.

The Methods of Experimental Embryology

Experimental breeding is usually carried on under conditions that are most favorable for the organisms concerned. The results obtained are, therefore, comparable with what might be expected to occur in uncontrolled breeding in the natural habitat. This

FIG. 258.—Diagram illustrating independent segregation and possible recombinations of X-chromosomes carrying genes determining eye-color, in a cross between a white-eyed female *Drosophila* and a red-eyed male (cf. Fig. 251, p. 473). This is the reciprocal of the cross shown in Fig. 257, and the symbols are described there.

“normal” course of inheritance can be observed and interpreted. However, in this as in many fields of study, a knowledge of what happens under abnormal or unusual conditions may clarify our understanding of the normal situation.

In the examples cited to illustrate Mendelian principles, a

certain combination of genes always gives a certain type of individual. However, if the environment be changed and the genetic combination remain the same, the individuals may be different (cf. p. 439). For example, the red primrose has red flowers if kept at a temperature ranging from 15° to 20° C. A plant with the same genes but reared at a temperature of 30° to 35° C., with other environmental conditions unchanged, produces white flowers. If a plant with white flowers is brought into a room at 15° to 20° C., the flowers that develop later will be red. The effect of the genes for color of flower is limited by the temperature of the environment in which the flowers develop. That the gene is not altered is shown by the ability of the plant to cease producing white flowers and give rise to red ones at a different temperature.

The same type of effect has been demonstrated in *Drosophila*. A certain race of the fruit-fly is distinguished by the fact that there are almost no black bands on the abdomen in contrast to the regular bands of the normal race. When this race is reared in a rich supply of moist food, the abdominal bands are almost completely absent in all individuals. The same stock, raised on scant, dry food, appears normal as to banding of the abdomen. If a culture is started with abundant moist food which is not replenished but allowed to become dry, the individuals that develop first will show abnormal banding, while those that develop later will appear normal. These flies are genetically the same, but their appearance is determined by the environment in which they develop. In other words, the appearance of characters in an adult individual is dependent on the presence of genes in the zygote, acting in a particular environment during development.

The age of an individual sometimes affects the development of characters. Certain characters may not appear until the individual reaches a particular age. In other cases, a character may appear in early stages of development and be lacking in the adult. Age is, in this sense, a phase of the environment.

Another condition that shows the relationship between genes and environment is the fact that the genes that determine red color in eyes do not cause this color on legs or wings. The mechanism of mitosis makes it reasonable to suppose that all genes are equally distributed to all cells. Yet these genes are effective in determining an external character only in certain parts of the organism.

The influence of genes is likewise dependent upon their associa-

tion with certain other genes. The evidence for interaction of genes is clear-cut but very complicated, and will not be given here. Morgan states that at least twenty-five allelomorphs are concerned with eye-color. Conversely, a single pair of genes may influence more than one character. In *Drosophila* the genes for rudimentary wings affect characters of the legs and number of eggs laid, among others.

Genes are the hypothetical units that determine inheritance in organisms. For each character of the individual, at least two allelomorphic genes are responsible. There may be many allelomorphic pairs of genes that interact to produce a given character; a single pair of genes may also influence the appearance of more than one character. The characters, thus determined by genes, require, for their realization in the adult, certain conditions of the environment in which development occurs. The tentative hypothesis concerning the nature of genes proposes that they are chemical compounds, and experiments are being made to test this idea. More definite knowledge awaits additional information concerning the physico-chemical nature of the protoplasm, of which the genes must be a part. We return, therefore, to the generalization that the individual inherits a "course of development." The researches of geneticists have clarified the problems to the extent indicated in the previous detailed discussion.

Genetics in Relation to Evolution

Organic Evolution or the origin of present-day organisms from organisms of the past by a series of gradual changes, is dependent upon the inheritance of variations. Offspring must be different from their parents, and the differences must be hereditary, in order that evolution may occur. The Mendelian principles would seem to deal with units that are fixed and unchanged from generation to generation. Yet the variations that Galton studied in populations, and Johannsen in pure lines, can be explained in Mendelian terms.

The variety of recombinations possible in a cross involving three pairs of genes gives some indication of the range of genetic variation that occurs when heterozygous individuals interbreed. When one considers that many pairs of genes are necessary to produce certain characters, and that a single pair of genes may affect more

than one character, it is easy to see that great variation can occur in a heterozygous population. Recombinations of genes are not, however, changes in genes. Gradual progress or evolution could not continue by that method. The possibilities of gene combinations are limited by chance, and even if certain types were better suited to the environment, the sorting of genes would always give again those less well adapted.

In the case of a pure line, the individuals are homozygous and variation does not result from new assortments of genes. Differences between individuals in a pure line are the result of the environment in which the individuals develop. When the fact that the individuals of a pure line are homozygous is understood, the failure of selection becomes very clear. Environment does not change the genes when it limits or obscures their presence, as in this kind of variation. These variations that are not inherited are known as *fluctuations*.

More and more is becoming known about another kind of variation, which is called a *mutation*. A mutation is a variation that is apparently the result of a change in the genes, or Mendelian units, because it is inherited. Many cases of mutation have been carefully studied in *Drosophila* and other organisms. They are inherited according to the expected segregation and recombination of genes in the germplasm. While a variation of this kind may be particularly conspicuous with reference to a certain character, it is often found to affect other characters as well. Mutated genes may be dominant, recessive, or without dominance, as are other genes. It is obvious that mutations are the kind of variations by which evolution can occur.

The question of how genes become changed to produce mutations naturally arises. There is some evidence that mutations may result from changes in the position of a gene in the chromosomal group. Again, atypical distribution of chromosomes is often associated with mutations, as when an organism has one more chromosome or twice as many as the normal specimen. These facts make it appear as if the unusual appearance of inherited characters were closely bound up with a particular arrangement of the interacting set of genes. Any disturbance in location or amount upsets the end result. These disturbances are, however, of a permanent kind. Whatever produces them may duplicate the effect many times. That is, in a normal stock the same muta-

tion may appear time after time, with many generations between its recurrences, or in successive generations. Reversion of a mutant race to the normal type, which may again produce the mutant type, is also known.

Some races seem more unstable with respect to change in genes than others. Mutations are unknown in some experimental forms, and frequent enough to be carefully studied in others. It has been suggested that types of organisms may have cycles of mutability at which times the germplasm is more unstable than at others. Experiments on the induction of mutations by changes in the environment of the individuals have shown that, in the individual life cycle, some stages are more susceptible to abnormal environmental conditions than others. Such experimental methods as changes in temperature, moisture and food, and exposure to X-rays and radium rays have been used. Knowledge of mutations is rapidly increasing and their rôle in the evolution of organisms seems very significant.

Genetics in Relation to Human Affairs

In man's utilization of natural resources, knowledge of inheritance has been a useful tool. New varieties of plants and animals have been established by hybridization and continued selection. Early-bearing plants, or plants otherwise adapted for particular environments, have been isolated as pure lines from heterogeneous populations. The breeding of the types of cattle best suited for beef, milk, or butter-fat production, and of horses for speed or draft purposes are examples of the application of Mendelian principles (*cf.* Figs. 281-284). The preservation of mutations in establishing new races has been accomplished in the case of the short-legged Ancon sheep, polled Hereford cattle, and certain plants. Genetical information is of the utmost value in the betterment of the animals and plants domesticated by man, and in the establishment of new kinds of animals and plants for food or other purposes.

Man's characteristics are inherited from generation to generation as in the case of other living organisms. The course of heredity is well understood in many cases and much information has been accumulated. In human eye-color, the presence of a pigment on the back of the iris gives rise to all shades of blue eyes. In addi-

tion to the pigment on the back of the iris, there may be pigment on the front of it. This produces eye-colors from hazel to dark brown. The presence of pigment on both sides of the iris is dominant to the absence of pigment from the front of the iris, that is, to its presence on the back only. Therefore, brown eyes are dominant to blue eyes. In the rare condition known as albinism, pigment is absent from both sides of the iris, and the blood-vessels of the iris give the eye its pink color. Such a condition is recessive to blue eye-color. Curly hair is dominant to straight hair. In color-blindness, which is the result of an inherited defect of the retina, and in hæmophilia, a defect of the blood that prevents its clotting, the genes are sex-linked. Mental as well as physical characteristics appear to be inherited. The tracing of families like the Jukes, the Kallikaks, and the Edwards indicates that mental qualities leading to degeneracy, crime, and pauperism, as well as those yielding leadership in all social fields, may be inherited according to Mendelian principles.

The environment in which a particular gene-complex develops may limit and obscure its possibilities, as we have seen. Thus a given combination of genes in a human individual may produce a better adult in a favorable environment than it could in an unfavorable one. On the other hand, a good combination of genes will give rise to a better individual in a particular environment than will a poor set of genes. Training is another element that is very important in the unfolding of human potentialities. An inferior inheritance with superior training may result in an individual better fitted for society than a good inheritance with no training. But no amount of training can produce anything for which the inherited capacities are not present, nor can the best of environment implant qualities that are lacking in the germplasm. In other words, heredity limits very definitely the possibilities of training and environment (*cf.* Fig. 232, p. 445). Eugenics is that particular branch of Applied Genetics which deals with the improvement of the mental and physical characteristics of future generations of the human race. Its problems are: first, extension of our knowledge concerning the facts of human heredity; and, second, the education of the public for appreciation of the meaning and application of this knowledge. For the methods of eliminating inferior germplasm and perpetuating superior genetic factors, human society must turn to Genetics.

CHAPTER 20

THE THEORY OF EVOLUTION

Organic Evolution may be defined as *the historic process of change* by which existing animals have reached their present state. If living things have had such a history, it has been a process involving many millions of years. This doctrine is in marked contrast with the theory that animals and plants originated in their present form and within a comparatively recent period. Evolution involves more than the history of organisms, however. Astronomy tells us that our solar system probably originated through countless years, as other solar systems seem to be originating at the present day; and Geology that our planet has had a long history. The doctrine of Evolution therefore embraces Inorganic Evolution, which includes the Cosmic Evolution of which Astronomy teaches, and Geologic Evolution; and, also, Organic Evolution, or the evolution of living things.

As we are primarily concerned with Organic Evolution, the discussion cannot be extended to the inorganic field. It will be understood, however, that evolution is the scientist's answer to the question of how the world about us—sun and stars, mountains and oceans, animals and plants—has reached its present form. Evolution is, in fact, the entire process of *change* that is going on in the universe and that is believed to have been in operation for as long a period as the mind can picture. As a corollary, it may be supposed that this process, at least insofar as it affects inorganic bodies, will go on forever. Hence, the doctrine involves events that have no recognizable beginning or end in time or space, since they include the changes by which suns and planets as well as living beings have come to exist and will exist in the future.

The Origin of Life

Time of Origin.—The period at which protoplasm appeared upon the earth must have been remote, since the age of the fossil-

bearing rocks is to be reckoned in hundreds of millions of years, and since the original organisms must have antedated any fossil remains by a considerable period (Fig. 259). There must have been a time when the earth was too hot to support anything resembling protoplasm as we know it to-day. Protoplasm must have appeared during the period between this heated state and the time of the earliest fossils, after suitable environmental conditions had arisen. If the age of the Cambrian fossils is as great as 800,000,000 years, as some geologists now believe, organisms may have come into existence 1,500,000,000 years ago. In arriving at such a conclusion one must have due regard for the limitations of all attempts to estimate geologic time. What can be said with certainty is that protoplasm has existed upon our planet for a very long period, as shown by the record in the rocks, and that it was presumably in existence for a long time before the period of the earliest fossils. In this connection it will be noted that the time during which the higher animals, such as the vertebrates, have been in existence is a very small fraction of the entire history of life.

Manner of Origin. — Here again, one must have recourse to speculation, based upon facts that suggest possibilities. According to the *Cosmozoic Theory*, or, as it might be called, the "Infection Hypothesis," the original germs of protoplasm accidentally reached the earth from some other body in space. A simple form of protoplasm thus "infected" a waiting planet, much as germs infect a test-tube containing a sterile medium fit for their development. It might be supposed that the primeval organisms arose from such an original infection, and that by evolutionary development there were produced the vast array of plants and animals that have since existed. This theory is unsatisfactory because it does not explain how the protoplasm *originated*, which is the real question at issue. The problem is sufficiently remote from any possible solution, if the origin of life is traced to the early stages of our earth. It becomes hopeless if removed to some other body in time and space, since there still remains the question of how life could have come into existence in some other part of the universe. Moreover, it may be objected that the infecting germs could hardly have survived the low temperature of interstellar space; nor could they have survived the heat generated by bodies entering the atmosphere. The possibility that such a "cosmic rain" of germs

ROCKS GENERALLY METAMORPHOSED: IGNEOUS PREDOMINANT;
SEDIMENTARY SECONDARY. LIMESTONE, IRON ORE, AND GRAPHITE
INDIRECT EVIDENCE OF FORMER LIFE. FOSSILS SCARCE.

"PRECAMBRIAN," 30,000,000 TIME UNITS

FIG. 259.—Geologic time-scale, eras, and succession of animal life.

Time-units in geology can be stated relatively with a fair degree of certainty, but not absolutely. Thus it is possible to say that the Quaternary, or the Tertiary, or the Cambrian represents a certain fraction of the whole; but for the absolute length of time represented by the 60,000,000 units shown, it can only be said that the entire period represents a vast lapse of time, as long as 1,500,000,000 years according to some geologists. It will be noted that the time-units before the Cambrian are as great as those shown by the scale. The absence of many fossils in the pre-Cambrian rocks is probably due to the metamorphosis of sedimentary deposits that once had fossils, and perhaps to the restriction of abundant life to limited areas. (After Osborn, from the time-scale of Pirsson and Schuchert.)

became the source of living things upon our planet has, therefore, never appealed to biologists.

Another theory of the origin of organisms is that of *Miraculous Creation*. As a philosophical concept, one may suppose that the primeval protoplasm arose by some "creative" act which was "miraculous" in the sense that it was not a part of the established order of nature. Science can only say regarding this theory that there are no facts which are suggestive of such a process.

There remains what may be termed the *Naturalistic Theory*. Here again, we have only suggestive evidence, although it is possible that facts may some time be discovered that will lend more definite support. According to this hypothesis, when conditions became suitable a primitive substance arose, having the properties of life, though perhaps in a more elementary fashion than any living bodies that now exist. If such a substance were able to assimilate other matter, with consequent increase in bulk, and to eliminate the end products of its activities, and if portions accidentally detached possessed the properties of the original mass, metabolism and reproduction would occur. If the organization became sufficiently elaborate, such a primitive form of life might respond to stimulation in a more complex manner than anything not alive. From such a primeval substance, it is conceivable that protoplasm, organized in the form of the units termed cells, may have arisen. The division of labor between nucleus and cell body, as it appears in the cell, would then be regarded as the first great step in the evolutionary changes whereby this primeval protoplasm became differentiated into the living forms of the present day. According to this theory, the cell would not be the primitive form of organism, although it is the simplest vital unit now recognized. If this speculation is followed a step farther, it may be supposed that the unicellular organisms of the present day have descended from such early cells without evolving beyond the unicellular state, but with much specialization as single cells; while many-celled organisms have arisen by an advance beyond the single-celled condition.

It is not necessary to present at this point the detailed speculations regarding the manner in which such a union of organic materials, to form a physico-chemical system having the characteristics of protoplasm, might have occurred. These speculations are many and varied, but are obviously based solely upon what is

known of the physico-chemical properties of matter as it is now found. According to one such theory, protoplasm may have originated under conditions of great heat. The general hypothesis is of an origin in a *natural course of events*, and hence one that is open to scientific examination.

Certain facts of biological knowledge have a bearing in this connection. In the first place, living organisms are not now known to originate by any such "natural" or spontaneous process, but only from preëxisting protoplasm, by growth, or by the detachment of parts that occurs in reproduction. Up to the present day, all theories of "spontaneous generation" have failed to be substantiated (*cf.* p. 202). This does not support the idea that protoplasm could have been so produced in the past. It can be claimed that conditions in the past, although natural, were not like those of the present. This may seem to belie the scientific presumption of the constancy of Nature, but it is a possibility that may be given consideration. In this connection one may consider, for example, the geological indications that the earth's atmosphere was more suited to support certain forms of plant life during the Carboniferous Period (*cf.* Fig. 259), than at a later time. There is, however, one way in which evidence corroborative of the Naturalistic Theory of the origin of organisms might be obtained. If the biologist is ever able to produce protoplasm under the artificial conditions of laboratory experimentation, it will not be unreasonable to suppose that such a process might have occurred in the remote past, even though it does not occur naturally in the present. There is, however, small likelihood that an artificial production of the living substance will be realized in the near future, although it is not an impossibility.

Place of Origin. — As to the place or places in which organisms may have originated upon the earth, it has usually been assumed that they existed first in water, and hence in the primitive oceans. The seas were formed, according to the theories of Geology, when the atmosphere began to be differentiated from the hydrosphere, or watery covering of the globe. Presumably, the first oceans were boiling hot, and the land was, at the same time, the scene of great volcanic action. For a long time, therefore, protoplasm, as we know it, could not have existed. As cooling progressed and conditions became more favorable, the seas may have teemed with living beings before the land became ripe for habitation. There are

certain facts of marine ecology that are suggestive of this interpretation.

These suggestions regarding the time, the manner, and the place in which living beings had their origin on our planet are not solutions of the problem; but in science we must be content to face such unsolved problems in the hope that a solution may be eventually obtained. The question lies in the field of biological speculation. Such speculations are profitable if based upon facts and not too greatly extended. They appeal to the imagination and are worth discussion if one does not neglect other problems that are open to solution.

Organic Evolution

The History of Organisms. — We have seen that Inorganic Evolution is the historic process of change by which the world of lifeless objects has reached its existing state and by which it is changing at the present time. A similar definition applies to Organic Evolution, which is the process by which existing animals and plants have come to be what they are in the course of their descent from ancestral forms of a different nature. The word "development" has been used for the changes by which the many-celled organism arises from the egg. One may, however, speak of "evolutionary development" as well as the development of the individual. Organic Evolution, or Evolutionary Development, is, therefore, the history of living things as interpreted by the biologist. As with the facts and interpretations of Geologic Evolution, the conclusions regarding Organic Evolution are based upon evidence that is immediately before us, such as the structure and development of animals, their distribution over the earth, and the fossils in the rocks.

The Fact, Course, and Cause of Organic Evolution. — Much confusion arises regarding Organic Evolution through failure to distinguish between what may be termed the *fact*, the *course*, and the *cause* in such a progressive series of events. This may be illustrated by an analogy. Let us suppose that a ship leaves a European port and sails across the Atlantic to New York. One may distinguish between the *fact* that the ship crossed the ocean, instead of being created in New York Harbor; the *course* it pursued, whether a northern or a southern route; and the *causes* that made the ship go, whether internal forces like steam and elec-

tricity, or external ones like winds and currents, or even direction by wireless. Similarly, in the case of the doctrine of Evolution, there is the *Fact of Evolution* as the historic series of events; the *Course of Evolution*, for example, whether the land vertebrates arose from fish-like ancestors, or birds from reptiles; and the *Causes of Evolution*, or what made it take place. These three aspects of the evolutionary process are separate though related factors. They must be distinguished if there is to be any clear thinking in these matters.

To illustrate concretely, the fossil record shows that there were originally only fish-like vertebrates (*cf.* Fig. 259). These are connected by a series of fossils with the fishes of the present day. Later there were amphibians in addition to the fishes, then reptiles, followed by mammals, and birds. In each of these cases the original types are connected with those of the present by the fossils of subsequent strata. Such facts as these led the great paleontologist Cuvier (1769–1832) to acknowledge a fact that is evident throughout the geologic record, i.e., that *the animals of the past are different from the animals of the present, save in exceptional cases, and that the farther back one goes the greater are the differences*. In addition, there occur in the fossil record *synthetic types* which seem to be intermediate between the different lines, like the toothed birds (Fig. 279), which are “missing links” between birds and reptiles; and the forms that suggest transitions from fishes to amphibians, and from amphibians to reptiles.

Such fossil records, together with the vast body of evidence derived from the representatives of this group that are now living, constitute the evidence for evolution in vertebrate animals. If the vertebrates have had such a history, one may distinguish the *fact* that their ancestors were fish-like animals from which present-day forms have originated by evolution, from the *course* that this evolution has pursued in the origin of the various types, and from the *causes* by which such evolutionary changes have been effected. In general, it may be said that scientists regard the historic fact of Organic Evolution as the most reasonable interpretation of the evidence; that the course of this evolution is apparent in many of its broader aspects and in special cases, such as the horse and camel families (Figs. 276 and 280); but that the causes are not yet known, although various theories have been proposed. This does not mean that the causes of Organic Evolution cannot be discovered,

but rather that they are obscure and complex, and that they have not yet been demonstrated in the same convincing manner as the broad fact of evolution. Biologists are convinced that the ship crossed the ocean of time, and they know something of the course

FIG. 260.

FIG. 260.—Georges Cuvier (1769–1832), comparative anatomist and paleontologist.

(From Loey, "Biology and its Makers," copyright, 1908, by Henry Holt & Co., reprinted by permission.)

FIG. 261.

FIG. 261.—Sir Charles Lyell (1797–1875), author of the "Principles of Geology" (1830), a book that established the doctrine of evolution in geology.

(From Pirsson and Schuchert, "Textbook of Geology," John Wiley & Sons, copyright, 1924, reprinted by permission.)

pursued, although they do not yet understand the causes that made the ship go.

In the light of the foregoing explanation, one can understand certain popular misconceptions regarding the opinions of many scientific men upon evolution. The word "Darwinism" is unfortunately used as a synonym for evolution, because Charles Darwin in his "Origin of Species" (1859) was the first to convince the scientific world of the truth of evolution as a historic fact. Darwin's distinctive contribution, however, was the theory of "Nat-

ural Selection," or the "Survival of the Fittest," which he regarded as an adequate cause for evolution. When a biologist speaks of "Darwinism" he may, therefore, refer either to the general fact of evolution, or to Darwin's theory of the cause of evolution, Natural Selection. While this theory seemed adequate to most biologists during the decades immediately following 1859, it gradually came to be regarded as a less satisfactory explanation. Many criticized the theory of Natural Selection, although their convictions regarding the truth of evolution as the historic fact were progressively strengthened.

A great deal of discussion thus arose regarding "Darwinism," that is, Natural Selection, which was held to be inadequate as a cause of evolution by many competent scientific men who had no intention of questioning the fact of evolution. Hearing the rumblings of this controversy, many who were not scientists supposed that evolution as a historic fact was being rejected, since in their minds evolution and Darwinism were equivalent terms. The now famous address of Professor William Bateson at the Toronto meeting of the American Association for the Advancement of Science, in 1921, is a recent illustration of this misconception. Although he asserted that "our faith in evolution is unshaken" — meaning by "faith," of course, a *reasonable belief resting upon evidence*, his remarks were misconstrued as a criticism of the general fact of evolution. What he said was only that we do not yet know the causes of evolution. A similar position is taken by many biologists, who, nevertheless, do not regard these causes as past finding out. As knowledge advances, it is hoped that they may be discovered. With these preliminary explanations, we may proceed to a discussion of the evidence for organic evolution, its course, and its causation.

The Evidence for Organic Evolution

Outline of the Evidence. — The evidence which has led biologists to conclude that the innumerable species of animals and plants now living and all the species which lived in the past have arisen by an evolutionary process may now be presented. In so doing we shall be considering what has been called the *fact* of evolution, and the *course* which evolution has taken in particular instances. It has been explained that the fact and course of

FIG. 262.—Evidence for evolution from Comparative Anatomy and Embryology.

A to C, stages in development of the flounder, *Pleuronectes*, a fish that begins as a symmetrical type and changes during development to one with both eyes on the right side of the body and becomes otherwise adapted for life on the bottom where it rests upon its left side instead of ventrally. D, whalebone whale, showing bones in flipper like those of fore limbs in typical terrestrial mammals (cf. Fig. 18, p. 39), and degenerate pelvis and hind limbs shown embedded in flesh and on a larger scale above. Plates of whalebone are attached to the upper jaw. Both jaws are toothless in the adult, but there are rudimentary teeth in the embryo. The young are born in the water, but suckled like other mammals. E, seal, another type of mammal adapted for aquatic life although still able to come upon the land, showing skeleton of fore and hind limbs for comparison with same in terrestrial mammals. f, femur; isch, ischium; p, pubis. (A to C, from Ziegler after Agassiz; D and E from Romanes, "Darwin and after Darwin," copyright, 1896, by Open Court Publishing Co., reprinted by permission.)

evolutionary change can be ascertained apart from its causes. Although this evidence for organic evolution as the fact is subject to the limitations of all historic data, it has proved convincing to biologists, because so many special cases tell the same story. Perhaps no one of the principal lines of evidence would be sufficient in itself, but taken together they are overwhelming. The following outline indicates the relationship between these lines of evidence and the order in which they will be presented:

Evidence from Structure

- Comparative Anatomy
- Comparative Embryology
- Classification

Evidence from Distribution

- Paleontology
- Zoögeography

Evidence from Physiology

- General Physiological Resemblances
- Specific Physiological Resemblances

Evidence from Observation and Experimentation

- Unconscious Experiments upon Animals and Plants since their Domestication
- Conscious Experiments by Breeders and Scientific Investigators.

The first three groups include only indirect or circumstantial evidence; that is, *the facts are what one might expect if evolution has occurred*. The fourth may be called direct or observational evidence, since it shows the evolutionary process at work. The limitation of circumstantial evidence is that one does not observe the occurrence; but such evidence may be convincing if extensive and diversified. The limitation of observational and experimental evidence is that so little evolutionary change can be observed in a brief period of time.

EVIDENCE FROM STRUCTURE

Comparative Anatomy. — Whether one examines the broader features of Anatomy in the several phyla of animals or the lesser structures in a single group, one finds everywhere facts that are

most reasonably interpreted by evolution. In vertebrates, there are two pairs of limbs, a body, head, tail, and various internal organs, always laid down according to a similar general plan, but with endless modifications in relation to the mode of life. It is, therefore, possible to construct a generalized plan of a vertebrate (*cf.* Fig. 29, p. 50), representing not any particular vertebrate but vertebrates in general. The same may be done with other groups, as in the accounts of the general body plan in the several phyla, given in preceding chapters. Thus, the coelenterate plan, the annulate plan, the arthropod plan, and the vertebrate plan may be

constructed. More specific resemblances are seen in the corresponding parts of the body when comparisons are made among the animals of a single phylum. The flipper of a whale, the wing of a bird or a bat, the fore limb of a horse, and the arm of a man all show the same plan of structure despite differences (*cf.* Figs. 262 to 264). Similar resemblances between parts could be cited from every group of animals. This fact of resemblance in plan, whether of the body as a whole or of its special parts, is the great

FIG. 263.—Flipper of a whale compared with hand of man (*cf.* Fig. 18, p. 39).

(From Romanes, "Darwin and after Darwin," copyright, 1896, by Open Court Publishing Co., reprinted by permission.)

principle of *homology*, which appears in every phylum of the Animal Kingdom. It may even be extended to comparisons between the several phyla (*cf.* Fig. 117, p. 240). Such are the facts that any one can see for himself by the dissection and comparative study of existing animals, just as one might study the comparative anatomy of chairs or houses or automobiles. If there is any point in dispute one can look again and determine the exact relationships.

For the purposes of this discussion, the question is: What do these obvious facts indicate regarding the history of animal life? The preëvolutionary explanation was that each species of animal, though created separately, was nevertheless formed in accordance

FIG. 264.—Wing of pterodactyl, an extinct flying reptile; of a mammal, the bat; and of a bird, showing three modifications of the appendage (cf. Fig. 18, p. 39).

(From Romanes, "Darwin and after Darwin," copyright, 1896, by Open Court Publishing Co., reprinted by permission.)

with an ideal type, hence the homologies. This was the belief of Louis Agassiz (1807-1873), who was unable to adjust his thinking to the concept of evolution as set forth by Darwin in 1859. Such an idea is a theoretical possibility, provided there is evidence that animals originated in their present form and have not changed since their appearance on the earth. However, species do not seem to have originated in their present form and they do seem to

FIG. 265.—Representative fossil records.

Left, fossil tree trunks; right, section of Amythest Mountain, Yellowstone National Park, showing by fossil tree stumps that at least seventeen forests became established and were successively killed out by deposits of volcanic ash. Some two thousand feet of rock are shown, and the whole rests upon other strata that show unconformity due to erosion of earlier land surfaces (*cf.* Fig. 274). (Left, photo. by courtesy of the American Museum of Natural History; right, after W. H. Holmes, photo. by courtesy of H. F. Cleland.)

have changed during geologic time. The evolutionary explanation of these anatomical resemblances between animals is, of course, that the members of any group, as the vertebrates, for instance, are similar in structure because they have inherited a similar plan of organization from ancestors which all vertebrates had in common. Each subdivision and species has been modified in particular ways in relation to its habits of life. They are fundamentally alike, however, because they have never lost the underlying plan of body that existed in their ancestors. Because whales

and horses and all other mammals had a common ancestry at a remote period, their fore limbs and many other parts have certain similarities to-day. Mammals resemble other vertebrates for a similar reason. The facts of Anatomy are, therefore, what might be expected if evolution has occurred.

FIG. 266.—Representative fossils.

A, impressions of a leaf and an insect larva. B, a trilobite, *Phillipsia griffithides*, representative of a great class of Arthropoda that flourished in the Palæozoic era (cf. Fig. 259) and later became extinct. C, a rich deposit of shells, principally the marine mollusc *Astarte*. It was such remains as these (C) that led Leonardo da Vinci (1452–1519) to conclude that the rocks he observed even in the high mountains of Italy had originated on the ocean's floor and hence that profound evolutionary changes had occurred in the history of the earth. (Photos. by courtesy of the American Museum of Natural History.)

Comparative Embryology. — Almost everyone who knows anything of the evidence for organic evolution has heard the statement that the development of an individual is a repetition of the development of the race. This “Recapitulation Theory,” as it is called, maintains that certain developmental stages or structures are *palingenetic*, that is, related to ancestral conditions; while others

may be *cenogenetic*, or adaptations to the present manner of development.

To cite a familiar example, the embryo of a fish (*cf.* Fig. 219, p. 421) develops gill slits and gills with blood vessels and a two-chambered heart, which persist in the adult. The tadpole of a frog develops a similar organization, which is fish-like in the arrangement of gills and blood vessels and in the two-chambered condition of the heart. But this structure is completely reorganized at metamorphosis when the tadpole changes into an air-breathing animal with the lungs and three-chambered heart of the frog. In

FIG. 267.—An ancient member of the shad family, *Diplomystus*, from the fishbed at Green River, Wyo.

(From Lucas, "Animals of the Past," by courtesy American Museum of Natural History.)

reptiles, birds, and mammals, the embryo also develops gill slits (*cf.* Fig. 287, p. 531) and a circulatory system that is fish-like, along with a two-chambered heart (*cf.* Fig. 226, p. 430), only to have these structures reconstructed in later stages to form a different adult organization. These stages of development in vertebrate embryos are as well known as any facts in the anatomy of the adult animal, and may be seen by any student of Embryology.

Such stages might be expected in fishes, and perhaps in the amphibians, which develop in water; but it is surprising that they should occur in reptiles, birds, and mammals. In view of the effectiveness of adjustment in the structure and functions of animals, it seems a wasteful process for an organism to develop by such a round-about course. When, however, this course of

development is viewed in the light of an evolutionary interpretation, it becomes reasonable. In fact, anything else might be impossible. If the ancestors of vertebrates were originally fish-like animals, as the fossil record indicates (*cf.* Fig. 259), it is seen that the Amphibia represent a transition from aquatic to terrestrial life and that their development has been modified accordingly. The reptiles, birds and mammals are true terrestrial animals in their mode of development and in their adult condition. The later stages have been modified, but the early stages still resemble those of fishes. It is not correct to say that the embryo of a reptile,

FIG. 268.—An ancient reptile, *Ichthyosaurus*, adapted for aquatic life like the whales among mammals at the present time.

This is an unusual fossil since the outline of the body is shown by a darkening of the rock due to carbon from the flesh. (Courtesy, American Museum of Natural History.)

bird, or mammal is a "fish" at one stage of its development, but it can be said that such embryos resemble the embryos of fishes at corresponding stages. The statement that the animal "climbs the ancestral tree" in the course of its development is likewise unfortunate, although it can be said that an animal has certain structures in its development that were present in its ancestors, because it "has never lost them." Thus, the fish embryo becomes an adult that is not unlike the embryo, while the embryo of a terrestrial vertebrate develops the organization of the reptile, bird, or mammal. This is what might be expected if the ancestors of these higher forms were fish-like organisms. The gill-slit stages may, therefore, be regarded as occurring in reptiles, birds, and mammals, *because they were present in the ancestors and have never been completely obliterated despite evolutionary changes that have produced a very different organization in the adult animal.* Indi-

vidual development, or *ontogeny*, is not an exact repetition of ancestral development, or *phylogeny*, but certain structures that are reminiscent of ancestry may be found in embryos.

In addition to gill slits, many other features in the embryos of amphibians and higher vertebrates are evidently palingenetic; and similar reminiscences appear in the development of other types of animals. The difficulty is that palingenetic and ceno-

FIG. 269.—Reconstruction of one of the carnivorous dinosaurs, *Ceratosaurus*, shown feeding with background of vegetation based upon associated fossils of plants.

The dinosaurs were the dominant land animals in the Age of Reptiles (cf. Fig. 259), but became extinct as the mammals increased in numbers. (From Lucas, "Animals of the Past," courtesy, American Museum of Natural History.)

genetic features are so intermingled that it is often impossible to distinguish between them.

Classification. — *The Basis of Biological Classification.* — Animals and plants may be classified in a variety of ways. If one is interested in Ecology one may group them according to habitat, by separating fresh-water animals from land animals or the animals of forests from those of prairies. Again, they may be classified according to their food, or even according to their size, as one classifies books by putting them in a book-case to suit the shelf room. But just as there is one basis of classification that is the most fundamental for books, namely subject matter, so for living

beings there is a *natural classification*, the basis of which is *structure*. When one classifies animals on this basis, one does no more than recognize and apply the principles of Comparative Anatomy and Embryology. Such a classification merely expresses the degree of structural resemblance, as when a certain number of animals are placed together in the Phylum *Chordata*, the Class *Amphibia* (cf. p. 12), the Order *Anura*, the Family *Ranidæ*, or the Genus *Rana*. A complete classification of the animal kingdom would be a family tree of animal life after the manner explained in the chapter on Classification (cf. pp. 237-243). Indeed, classification summarizes all the evidence for evolution that is derived from structure. This summation need not be introduced into the present discussion, since it is only an extension of the principles of Comparative Anatomy and Embryology.

EVIDENCE FROM DISTRIBUTION

Geological Distribution. — *Paleontology.* — The study of fossils constitutes the science of Paleontology. This may be regarded either as a biological or as a geological subject, although it is more commonly associated with Geology. What is called *geological distribution* is a study of the distribution of fossils and is included in Paleontology. It may be contrasted with the distribution of animals over the earth at the present time, which is the subject matter of zoögeography, or *geographical distribution*. These two kinds of distribution cannot be separated, since geologic distribution represents only the geographic distribution that occurred in by-gone times. In like manner the structure of fossil animals cannot be separated from that of existing forms, if the animals now living are believed to have descended from those of the past. It is convenient, however, to discuss separately these two phases of distribution before explaining the correlations between them.

Fossils. — The remains or traces of animals and plants that occur in rocks of periods before the present are known as *fossils*. Shells and other hard parts are buried in the sands and muds of river flats, of lake beds, and ocean bottoms, by the deposit of sediments. In time they may become "petrified," or hardened into stony material, as water dissolves the original substances and replaces them with others. Shells usually become filled with mud during burying, and later the shell itself may be dissolved by

ground water after the mud has changed to rock. In this manner a *mold* of the shell may be formed, but shell-bearing animals usually leave only their shells and vertebrates usually no remains but bones and teeth. The soft parts of animals are never preserved in the rocks, although they may leave imprints as fine as a human

FIG. 270.—Tracks of dinosaurs (*cf.* Fig. 269).

Above, where a dinosaur sat down; below, photograph of a slab of Connecticut Valley brownstone from specimen in museum of Amherst College. (From Lucas, "Animals of the Past," courtesy, American Museum of Natural History.)

finger print (*cf.* Fig. 266 A). Even an animal like a jellyfish may leave an impress upon a mud flat and be preserved if soon covered with fine sediment, as has happened in at least one instance. In a similar manner, the tracks of small animals that have walked or crawled upon muddy beaches have become part of the fossil record; and the tracks of large animals, such as the great reptiles known as dinosaurs, may be found in places where no traces of their bones remain (Fig. 270). Leaves buried in mud have formed

the "leaf impressions" (Fig. 266 A) that are often seen in collections of fossils. Insects have sometimes been preserved in almost perfect condition after being caught in resins of trees, when this material became hardened into a more permanent substance, as with the insect-containing amber of the Baltic region. Animals of the Glacial Period were sometimes frozen in the ice and snow and preserved for many thousand years, as was the mammoth found in Siberia (Fig. 272). The peat bogs of the north and the tar pools of Southern California contain the skeletons of animals that ventured upon the edges of the treacherous surface and sank to their death. But these are exceptional cases as compared with the great majority of fossils, which are portions of the hard parts of animals embedded in solid rock (Fig. 266 C).

FIG. 271.—Eggs of a dinosaur, with matrix of stone partially removed, as found in the Gobi Desert, Mongolia.

Although there is a wealth of fossils, the incompleteness of the fossil record must be recognized. Not only are the great majority of fossils merely fragments, but the known species cannot include more

than the merest fraction of the animal and plant species that have lived, because the chances are very small that the remains of any organism will ever become fossilized. Sometimes, however, skeletons are found that are almost complete (Figs. 267 and 268) and the record as a whole seems to give a fairly representative picture of the life existing in the past. In a famous chapter of "The Origin of Species," entitled "The Imperfection of the Geological Record," Darwin compared this record with a book which had been mutilated by the removal of many whole pages and the injury of others, but in which one could still trace the later course of the story.

The Geologic Succession.—It is necessary to explain certain principles, used by geologists in their study of the rock layers, if one is to understand the evidence for a succession of animal types

These extinct reptiles (*cf.* Fig. 269) presumably laid eggs like existing reptiles. The discovery of such eggs by the Third Asiatic Expedition of the American Museum of Natural History proves this in the case of one species. In one instance the remains of a dinosaur embryo were discovered in an egg. (From Report Field Museum of Natural History, Vol. VII.)

appearing in the fossil-bearing rocks. In view of the manner in which sediments are deposited in water, it is a truism to say that the oldest layers or strata are at the bottom and the youngest at the top, when such deposits have been elevated above sea level and hardened into rock with no disturbance of their horizontal relationships. In many places this elevation has occurred without

FIG. 272.—Mammoth found frozen in a cliff in Siberia.

Above, the specimen partially uncovered showing skull and fore feet; below, the specimen as mounted in the Zoological Museum at Leningrad. The animal had slipped into a crevice from which it was unable to extricate itself and been covered with snow, which hardened into ice, before the flesh could decompose. (Adapted from Herz, Report Smithsonian Institution, 1903.)

such disturbance (*cf.* Figs. 273 and 274). In such cases it may be possible to recognize not only the fossils but traces of the ancient topography, as when there are signs of beaches, mud flats, or deep water. In other parts of the earth, particularly in great mountain ranges, strata that were originally horizontal have been folded or broken as *faults* during their elevation. Although the conditions presented are often perplexing after folds some thousands of feet in thickness have been worn away by erosion, the

relationships can usually be determined by sufficient study; even though strata that were originally beneath, and hence older, may lie above the later deposits. The oldest fossils are, therefore, in the lowest rocks, or in rocks that were the lowest in the undisturbed formation, for the same reason that the bottom layers of a cut through filled ground are older than the upper ones. By applying this simple principle to the rock outcrops in all parts of the world, and with the aid of fossils, geologists have pieced

FIG. 273.—Outcrop of sedimentary rock in horizontal strata, Bennett quarries, North Buffalo,* N. Y.

(At top is limestone, Onondaga, resting unconformably at *a a* upon an upper Silurian formation, Cobleskill, which lies conformably along the line *b b* upon the cement rock, Bertie, that reaches to the floor of the quarry. Photo. by courtesy of Professor Charles Schuchert.)

together a series of sedimentary formations resting upon the earlier igneous rocks and constituting the record of geologic history (*cf.* Fig. 259). The fossils in these strata indicate the order of appearance or succession of the various forms of life.

In the record as it appears, there is a succession from simpler to more specialized types, which is of the greatest significance for organic evolution. Not only are the animals of the past different from those of the present, but the record begins with forms that are vastly different. These are gradually succeeded by others that become more like existing species until they merge with

FIG. 274.—How the geologist interprets facts that tell of the evolution of the earth's surface.

A, section of an exposure similar to that shown as Fig. 273, in which the underlying solid rock has weathered into loose mantle rock and overlying soil. B, section showing a former land surface (*c-d*) upon which boulders, gravel, and sand have been deposited by flowing water, as indicated by the horizontal layers. C, section similar to B showing a former land surface (*c-d*) upon which are glacial deposits as indicated by the irregular distribution of boulders, gravel, and sand. D, section of a mountainous region, showing how the folding of the rock layers and the former land surface (*c-d*) can be reconstructed by study of the angles at which the rock outcrops occur on the existing land surface (*a-b*) which has resulted from the erosion. *a-b*, existing land surfaces; *c-d*, former land surfaces (cf. Fig. 265). (A to C, after Brauns, "Geology of Missouri," University of Missouri Bulletin, Vol. 19.)

those now living. There are many gaps, and many types have become extinct, but the geologic succession shows the "grand course of evolution" so far as it can be ascertained from the fossil record.

Special Examples of Geologic Succession.—*Invertebrates.*—There are many instances among invertebrate animals, particularly in molluscs and brachiopods (Fig. 275) where the succession of fossils shows the course of evolution. In the interpretation of such a series one must first ascertain the order in which the strata were originally laid down and thus the relative age of the fossils they contain. A striking example is found in the extinct forms called *ammonites*. These were cephalopod molluscs (*cf.* Fig. 117, p. 240) that flourished in Palæozoic times. Beginning with the so-called nautiloid type in the Ordovician, the fossils show a succession that culminated in greatly specialized shells and such a wealth of species that the ammonites were for a time the dominant forms of marine life. Later, the ammonites became extinct, while the ancient nautiloid type persisted as the genus *Nautilus*, which is still living in the Philippine region and the Indian Ocean.

Thus the *Nautilus* has preserved its general organization without substantial changes throughout a span of geologic time sufficient for the evolution of the entire series of vertebrate animals. This is a very exceptional case, since the vast majority of animals seem to have been modified with the passing ages, or to have become extinct.

The Horses.—The fossil record of horses is probably more complete than that of any other mammalian type. Hence, it is almost always cited in elementary accounts of the evidence for evolution (Fig. 276). The series shown occurs in the fossil beds of the Western United States, where horses flourished for a long period but became extinct during the Pleistocene. In more recent times the members of the horse family, including the horses, wild asses, and zebras, have been found only in Europe, Asia, and Africa. The "wild" horses of the Americas in recent centuries are the descendants of horses that escaped from the settlers.

In further explanation of the figure, it seems probable that the ancestors of the earliest American horses, like the "dawn horse" *Eohippus*, must have originated in another region and migrated to North America, since they appear suddenly in the fossil record without antecedent types. Central Asia is suspected as the place

FIG. 275.—The course of evolution in the brachiopod genus *Stropheodonta* as shown by rich fossil deposits in Eastern Missouri.

The species *Stropheodonta demissa* appears throughout the series. In the Mineola limestone it is connected by a complete series of intermediate stages with *S. mineolaensis*, a species that thus arose from *S. demissa* but became extinct. In the Snyder Creek shale six other species seem to have likewise arisen from *S. demissa*, as shown by the intermediate stages, only to become extinct while *S. demissa* continued. The record illustrates a period at which a species for some unknown reason produced several other species and also that the primitive types are sometimes the ones to survive. It shows on a smaller scale the same thing that occurred among cephalopods in which the primitive nautiloid type has survived while the more specialized ammonites have perished. (After original studies by J. S. Williams.)

FIG. 276.—Evolution of the horse (cf. Time-scale with Fig. 259).

(After Matthew, courtesy of American Museum of Natural History.)

of origin, although the ancestors of *Eohippus* have not yet been discovered. After the horse family had flourished for a considerable period in North America, some of its members migrated to South America, if we may judge from the fossils, and spread widely on that continent. This southern branch of the American family became extinct in the Pleistocene, as did the North American horses. As in the case of the disappearance of ammonites and many other types that have flourished and declined, the causes of this extinction have not been ascertained. A plausible theory is that all the horses of the New World may have been swept away by some disease-producing parasite, but this is wholly speculation. We only know that they disappeared in the Americas, while a few species survived on the continents of the Old World, probably migrating back to this region as the ancestors of the original American horse family (*cf.* Fig. 276) had migrated into the New World from an unknown locality.

The probable course of evolution by which forms like *Eohippus* became changed into horses of the modern genus *Equus* are indicated by the succession of fossils (Fig. 276). The series begins with an animal about the size of a fox, with relatively short neck and limbs. The feet are also short and there are four functional toes on the front foot and three on the hind; but the hind foot has splint-like remains of other digits, as though a man should have three toes functional and the little toe and great toe rudimentary. Since similar rudiments of a fifth toe occur on the fore feet, it appears that the ancestors of *Eohippus*, and therefore of modern horses, were five-toed (*cf.* Fig. 277). The principal evolutionary changes, as shown by the succession of types, are the loss of side toes until only one persists as the functional digit; consolidation of leg bones so that the radius and ulna and the tibia and fibula become fused; increasing complexity of the teeth in relation to the functions of grazing with incisors and grinding with molars; increase in size and complexity of the brain; and a great increase in size of the whole body with changes of shape and proportions, particularly in the head, neck, and back. In the modern horse there is only one fully developed digit, but there are splint bones on the fore limbs representing the rudiments of two others, and in the early embryo there are five digits upon both fore and hind limbs.

The Elephants.—The succession of types that is believed to be

ancestral to the elephants of the present day is another example of a relatively complete fossil record (Fig. 278).

The earliest known representative of the elephant family appears in the rocks of the late Eocene in the Libyan desert of Africa. Types that are believed to have descended from this one may be traced to all the other continents except Australia. In this progenitor, *Maritherium*, there is no proboscis, and the head has

FIG. 277.—Comparison of stages in evolution of forelimb of horse with human hand.

(Photo. by courtesy American Museum of Natural History.)

no obvious resemblance to that of a modern elephant. In passing through the series the snout becomes elongated to form the proboscis; the jaws become shortened, in the line of descent that gave rise to the present-day elephants; the teeth become modified; and there is a great increase in size of body and of the brain. Like the horses, the elephants became extinct at the close of the Pleistocene in Europe and North America, where the mammoths and mastodons, which are members of the elephant family, had ranged widely during epochs when the family was in its most

flourishing condition. The only survivors are the African elephants and the species native to Southern Asia.

FIG. 278.—Evolution of the elephant from the Eocene Period or early Tertiary (cf. Time-scales, Figs. 259 and 276).

(From Scott, "Land Mammals of the Western Hemisphere," copyright, 1913, by The Macmillan Co., reprinted by permission.)

Synthetic Types. — It is sometimes said by critics of evolution that the "missing links" which should exist are not forthcoming.

In the case of man, for example, one might ask "Where are the forms that link man with the apes?" The foregoing discussion of fossil records shows that missing links, or *synthetic types*, as they are called scientifically, are not to be looked for among existing animals, but among fossils, *since the connecting links are the common ancestors in the past*. Thus the links between modern horses, zebras, and wild asses are members of the horse family that were ancestral to these types. The connecting links between the Asiatic and Indian elephants, and between existing camels and guanacos (*cf.* Fig. 280) are likewise extinct. The connecting links between men and apes are the extinct pre-human races (*cf.* Figs. 289 to 292).

Connecting links between larger groups are not wanting, as in fossils showing structures that are transitional between amphibians and reptiles, or between reptiles and birds, or reptiles and mammals, although no one animal shows all the transitions in these instances. The most spectacular examples, perhaps, are the primitive birds that show reptilian features, notably *Archæopteryx* (Fig. 279). In this instance there are teeth, clawed digits on the fore limbs, and an elongated tail with feathers on either side, while various features of the skeleton are distinctly reptilian. We have seen in our study of development (*cf.* p. 424) that birds closely resemble reptiles. It is also true that their adult anatomy is far more like that of reptiles than would be supposed from casual examination. As Huxley put it, birds are "glorified reptiles." *Archæopteryx* is perhaps as nearly a "connecting link" as one could hope to find in view of the imperfections of the fossil record. Here, as elsewhere, the facts of Anatomy, Embryology, and Paleontology tell the same story of evolution.

Many other examples of the geologic succession of fossils could be cited. The most important feature of all this evidence from Paleontology, as of the evidence from Anatomy and Embryology, is its cumulative nature. The facts in many lines tell a consistent story when interpreted as evidences of evolution.

Geographical Distribution. — The study of geological distribution includes both the lateral distribution of fossils, which indicates past distribution over the surface of the earth, and their vertical distribution, which indicates relative age. For example, study of the horse and elephant families includes the distribution of species over the various continents and their order of appearance in

geologic epochs. Hence, the problems of Paleontology are inseparable from those of Zoögeography, or the geographical distribution of animals at the present day. The camel family illustrates this inter-relationship. Approaching the problem from the standpoint of present geographical distribution, this family consists of two types which are widely separated. The genus *Camelus*, which

FIG. 279.—*Archæopteryx*, the earliest bird.

Left, one of the fossils as preserved in fine-grained stone. Right, a reconstruction of this fossil. The feathers and general shape of the body are those of a bird, but the teeth, the tail, the claws on the wings, and other features are reptilian. (Left, from Lucas, "Animals of the Past," courtesy American Museum of Natural History; right, from Parker and Haswell, "Textbook of Zoology," copyright, 1921, by Macmillan & Co., Ltd., reprinted by permission.)

includes the animals popularly called "camels," consists of two species: the one-humped Arabian camel, or dromedary; and the two-humped Bactrian camel of Central Asia. On almost the opposite side of the world, in the Andes of South America, are the only other camel-like animals that are now in existence: the genus *Auchenia*, with its two species, the guanaco and the vicugna; and their domesticated descendants, the llama and the alpaca. The wide separation of these two genera of a single family is surprising,

but it becomes intelligible when we examine the geologic distribution (Fig. 280). As shown by the fossil record, camels originated as a family of hoofed animals in North America, where they flourished from the Eocene to the end of the Pliocene epoch. During the Pliocene they migrated, on the one hand to South America, and on the other to Asia by way of a former land con-

FIG. 280.—Evolution of the camel family from Eocene Period of early Tertiary (cf. Time-scales, Figs. 259 and 276).

(Figures from Scott, "Theory of Evolution," copyright, 1917, by The Macmillan Co., printed by permission.)

nection in the Bering Sea region. The extinction of the North American forms at the close of the Pliocene left representatives in South America and Asia from which existing species have descended. The seemingly inexplicable separation of the two branches of the family thus finds an explanation in terms of evolution and the past migrations of animals. Numerous examples

could be cited, all showing that the evolutionary theory gives meaning to the geographical distribution in special types of animals.

In many cases it is possible to explain the peculiarities of a whole *fauna*, which is the name applied to the animal population of any particular locality, by the extension of a similar line of reasoning. Island life is an illustration. There are, geologically speaking, two types of islands in the ocean: *continental islands*, like the British Isles and our own Long Island; and *oceanic islands*, like the Azores, Bermuda, and the Hawaiian Islands. The former are not far from continents, of which they seem to have been once a part; the latter are islands that have appeared in the ocean without previous connection with any continent, or surviving elevations of continents that have existed in the past but have never been united with the well-known continental areas. The faunas that are found upon these two types of islands bear out the theories of their geologic origin and of the origin of faunas by evolutionary processes. Without going into details, it may be said that the native fauna of the British Isles is like that of northwestern Europe, because these islands were recently part of the neighboring continent. The native fauna of the Hawaiian Islands, on the other hand, is an odd mixture and unlike that of any continent, because these islands have had no recent connection with any continent and were presumably populated by animals and plants brought to them by chance, on floating objects or otherwise. Only from some such parentage could such bizarre combinations be expected to originate as occur on oceanic islands. Again, the continent of Australia has a fauna very different from that of Asia, because the two have been so long separated. Eurasia, Africa, and North America have similar mammalian faunas, because of former connections across Bering Sea and Greenland. As elsewhere, the argument is that the facts find a more reasonable explanation in the theory of evolution than in any other theory.

EVIDENCE FROM PHYSIOLOGY

General Physiology. — The similarity of the great physiological functions of metabolism, irritability, and reproduction is additional evidence for evolution. Since all forms of animal life agree in these fundamental processes, one may reasonably suppose that all have descended from an ancestral protoplasm which functioned in this manner. Taken alone, this general uniformity of functions

is less impressive than the many special cases presented in the discussion of structure and distribution in the two preceding sections, but at least it corroborates the evidence from other fields.

Special Physiological Resemblances. — There is, however, one line of physiological evidence that is very specific. It has been ascertained, by methods which need not be here described, that the blood of various animals shows certain physico-chemical resemblances. Extensive tests have been made, particularly among vertebrates. In general, it is found that animals that are closely related, according to the classification based on structure, exhibit a parallel degree of relationship in the physico-chemical nature of their blood. The blood of man, for example, is very much like that of a gorilla or a chimpanzee, less like that of a monkey, and so

FIG. 281.—Male (A) and female (B) of the jungle-fowl, *Gallus bankiva*.

Domestic poultry have apparently all descended from the jungle-fowl, now found wild in southern Asia, with some admixture from the Aseel or wild Malayan fowl. (After Davenport, Carnegie Institution Pub. 121.)

on, showing degrees of relationship that agree closely with the classification of the Mammalia. The blood of any mammal is more like that of other mammals than it is like the blood of birds or reptiles. Bird blood is like bird blood, reptile like reptile; but there is a closer resemblance between the blood of birds and that of reptiles than between either one of these and the blood of Mammalia or Amphibia. This is to be correlated with the relationships inferred between birds and reptiles on other grounds (*cf.* p. 519). The numerous tests that have been made confirm to an amazing extent the degrees of resemblance previously inferred from Anatomy, Embryology, and Paleontology, and expressed in Classification. Thus the chemistry of blood presents remarkable corroborative evidence for the evolutionary theory.

OBSERVATIONAL AND EXPERIMENTAL EVIDENCE

The History of Domestic Animals. — Evidence from observation and experimentation is found in the history of animals and

plants under domestication, and in the experiments conducted by breeders and scientists. Domestic animals must have originated from wild ancestors that were gradually tamed by man, although in most instances there is no historic record of the original domestication. Some forms are still in the preliminary stages. The

FIG. 282.—Evolution of domestic swine.

Above, the wild boar *Sus scrofa* and its young; below, a prize-winning Duroc Jersey barrow on a somewhat smaller scale. The domestic pig of Europe and America has descended from the wild boar of Europe, *Sus scrofa*, with some admixture from the wild boar of Asia, *Sus vitatus*. (Above, from Flower and Lydekker, "Mammals Living and Extinct," copyright, 1891, by A. and C. Black, reprinted by permission; below, courtesy College of Agriculture, University of Missouri.)

Indian elephant, for example, is not reared in captivity, but caught when nearly full-grown and trained. The attempts to domesticate the few surviving bison of the North American continent and the rearing of certain furbearing animals in captivity illustrate possible beginnings of domestication in the present. In the great majority of cases, however, the original domestication occurred before the period of the earliest historic records.

In some instances, like those of the domestic fowl (Fig. 281) and the pig (Fig. 282), the original wild species, from which all the domestic breeds seem to have descended, can be determined with reasonable certainty. In other cases, like that of the dog, there is no single

wild species that can be so identified. The argument regarding evolution in all these cases is that many types, so different that they would be called species if found in nature, have actually originated under the eyes of man without his appreciating what was taking place. Thus, there has been an "origin of species" among domesticated animals. From this, one may argue,

as Darwin did in his famous volume, that if one species can come from another the process can continue indefinitely, and, given time,

FIG. 283.—Evolution in European and American cattle.

A, an early figure representing the principal ancestral species, the urus or German aurochs, abundant in Europe and Britain during Roman times, but now extinct, unless some of the herds preserved in English parks are survivors. B, an early type of the Jersey breed. C, modern Jersey. D, hornless breed of Egyptian cattle, not ancestral to modern hornless breeds, but showing that there were special breeds, and hence a long antecedent domestication of cattle even in ancient times. E, modern prize Hereford steer, showing contrast with type C that is bred for milk production. (A, after Cuvier, "Animal Kingdom," London, 1827; B, from the *Country Gentleman*, 1853; C and E, by courtesy College of Agriculture, University of Missouri; D, after Breasted from a tomb relief at Gizah, 29th century, B.C.)

any possible amount of evolutionary change can be produced. Certainly one could hardly expect greater changes in a few thou-

sand years than are seen in the "evolution" of domestic poultry from the jungle-fowl and the Malayan fowl or aseel; or of the many breeds of pigeons from the wild rock-pigeon which was one of their most important if not the sole ancestor. Other domestic animals tell the same story (*cf.* Figs. 283 and 284).

In one respect, however, these domestic species differ from wild species; they can usually be bred among themselves. Wild species seldom can be crossed. This is not such a serious objection as it might seem, in view of the physiological adjustments that must exist in domestic as compared with wild animals. It is also true that domestic animals are modified to suit the needs or fancies of man, and not necessarily their own needs as are species in nature. But they have been bred for this, as natural species are bred in nature to meet the necessities of their lives or perish. Instead of a defect in the evidence, this might be regarded as an element of strength, since it shows that under one set of conditions one kind of characters can arise by evolution, and, under other conditions, characters of a different sort.

Experimental Evolution.—The evolution that has occurred in domesticated forms, as described in the preceding paragraphs, has been brought about by the attempts of men to secure desired types of animals and plants. The early men, who caught jungle-fowls and penned them up, used the wilder ones as food or let them escape, and thus the tamer individuals survived to breed. In later times there was more conscious effort to improve the breeds by crossing and by selecting only the desired types for breeding. Thus, Darwin tells us that in Saxony during the early nineteenth century men followed the breeding of sheep as a trade. "The sheep," he says, "are placed on a table and are studied like a picture by a connoisseur; this is done three times at intervals of months, and the sheep are each time marked and classed, so that the very best may ultimately be selected for breeding."

In our own generation, breeders have effected great changes and established new breeds. A conspicuous example among plant breeders was Luther Burbank, who worked by crossing different types of plants in large numbers and selecting, out of many thousands, the ones that seemed most desirable. All such work tends to become increasingly scientific. Knowledge of the Mendelian laws of heredity and some of the fundamental facts concerning variation enables the scientific experimenter to excel any

FIG. 284.—Evolution in horses.

It appears that the domestic horse has come from at least two original wild stocks. One species, represented by the Sewalik horse, was tall and slender-limbed, with broad forehead and tapering face. The other, represented by the tarpan, was a shorter and stouter-limbed type. The Shetland pony and draft horse have arisen from the generalized domestic type existing in northwestern Europe in Roman times. Above, tarpan, a wild horse of Mongolia; middle, Shetland pony; below, draft horse. (Photo. of tarpan from Thomson, "Outline of Science," copyright, 1922, by George Newnes and Son, Ltd., reprinted by permission; others by courtesy of American Museum of Natural History.)

“practical” man who is ignorant of these principles. Illustrations of what can be accomplished by the application of scientific principles to the practical problems of breeding are seen in the production of desired varieties of wheat and corn, and of better cattle. Attempts to produce new breeds thus merge with the effort to determine how evolution occurs under the conditions of rigorous scientific experimentation that are described in the chapter on Genetics.

In conclusion and summary of this evidence for organic evolution, it may be said again that biologists accept evolution as the historic course of events in the development of animal life because of evidence from many fields of investigation. Animals resemble each other structurally in varying degrees that seem to indicate the degrees of evolutionary relationship. The structure of animals and their mode of development are as we might expect them to be if evolution has occurred. Likewise, the fossil record of animals and their present geographical distribution can be most reasonably interpreted according to the evolutionary theory. Thus far, the evidence is circumstantial, but it is so extensive as to be convincing. In addition, there is the evidence that evolution has occurred among domesticated animals and is still occurring under the direction of skilled breeders and scientific investigators, although its causes have not yet been fully ascertained. The whole body of evidence is, therefore, overwhelming. For this reason it is hardly possible to find a competent biologist of the present generation who is not convinced of the fact of evolution, no matter how uncertain he may be of its course and causes.

Human Evolution

Man's Place in Nature. — With the evolution of all other living beings thus attested, it is impossible to exclude man from this universal process of organic nature. Human Anatomy and Embryology; the classification of mankind in the Family *Hominidæ*, closely allied to the Family *Simiidæ* which includes the tailless apes; the fossil record; and the existing races of mankind all point to evolution as the one reasonable explanation of the facts. Paleontology shows that the Order *Primates*, which includes man, the apes, and monkeys, arose from the general mammalian stock (Fig. 285). In more recent geologic times, fossil remains of

J. H. MCGREGOR-MODIFIED FROM W. K. GREGORY ET AL.

FIG. 285.—Ancestral tree of the Anthropoid Apes and Mankind, showing also the bases of the branches leading to the tailed monkeys, to the primitive type, *Tarsius*, and to the lemurs.

Owing to the incompleteness of the known fossil record certain parts of the tree are necessarily tentative; for example, the separation of anthropoid and human families may have occurred as late as Miocene or as early as Oligocene time. In *Parapithecus*, *Propliopithecus*, and the Heidelberg Race, only the lower jaws have been found; in *Pithecanthropus* only the skull cap, some teeth, a jaw fragment, and a femur. The skull of *Australopithecus* is that of a juvenile type that would have had an adult state as shown, if we may judge from the development of the skull in other anthropoids. The words Taigai, Rhodesian, Boskop, and Brunn are names of other races of mankind, related to those figured in the manner shown.

(From a drawing by J. H. McGregor, based upon data modified from W. K. Gregory *et al.*, courtesy of J. H. McGregor.)

pre-human races indicate the line of human descent. On man's intellectual side, Psychology is showing the animal nature of human intelligence, and the foundations of morality are believed by some to exist in the higher Mammalia. By another fifty years it is safe to assert that many other facts bearing upon human origins will have been discovered.

Anatomical Evidence. — The anatomical details of the human body are fundamentally like those of other Mammalia, particularly the Family *Simiidae*, which includes the four species of tailless apes: the gibbon, orang, gorilla, and chimpanzee. There is no essential detail of structure in human anatomy that is not repre-

FIG. 286.—Ears of apes and men.

A, Barbary ape. B, chimpanzee, one of the anthropoid apes. C, hairy human ear. D, human ear with point (a), supposedly comparable with the point in A folded inward. (From Romanes, "Darwin and after Darwin," copyright, 1896, by Open Court Publishing Co., reprinted by permission.)

sented in these apes; although the more erect posture of man has resulted in characteristic specializations of the pelvis and viscera, the fore limbs, and the foot. The brain, of course, is the most distinctive feature of man. It exceeds in relative bulk that of any other animal except some very small vertebrates like the humming bird (cf. Fig. 288). In specialization of function it exceeds the brain of any other mammal, but here again the structural and functional relationships are all paralleled in the higher apes. The psychology of these apes likewise resembles that of man in the earlier states, but later undergoes a retrogression. It is reasonable to believe that the ancestors of man went on to articulate speech and the development of hand and brain, while another line of descent, which produced the tailless apes, failed to progress and perhaps underwent regression.

What are called *vestigial organs* are often cited as evidences

of man's kinship with lower animals. The direction of growth of the hair on the arms and hands resembles that of the tailless apes, in which it is related to the shedding of water when the arms are clasped above the head with the elbows pointing downward. The vermiform appendix is a structure that is vestigial in man. It is larger in the apes and functional in some mammals. The Darwin's point (Fig. 286) that occurs in some human ears is interpreted as a reversion to a condition showing the inturned point of an ape-like ear. Rudimentary muscles that move ears and scalp in man, the rudiment of a nictitating membrane at the inner

FIG. 287.—Human embryo in three stages, showing rudimentary gill-slits, tail, and limbs, and development in later stages.

(Adapted from Mall, and drawn by Wiley Crawford.)

corner of the eye, and the pineal body of the brain, which is homologous with the median eye of some reptiles, notably the lizard *Hatteria*, are further examples. Many other instances of less familiar structures could be given. The argument here is the same as elsewhere. The rudimentary digits on the fore limb of a horse can be explained if we suppose that horses descended from ancestors with more than one digit. The complete set of bones of a fore limb in the flipper of a whale or seal are reasonably there, if it is supposed that seals and whales came from ancestors in which these parts functioned like the fore limbs of land vertebrates. So the argument runs with man. It is said by competent anatomists that there are no less than seventy vestigial relics of ancestry that can be easily recognized in the adult human body.

What may be called *embryonic vestiges* are even more numerous. Rudimentary gill slits and a fish-like blood system are formed

FIG. 288.—Evolution of the brain in vertebrates as suggested by comparative anatomy of adult structure (cf. Fig. 39, p. 67).

in human embryos as in other vertebrates (Fig. 287). The tail is noticeably developed in the embryo but becomes rudimentary in the adult. The entire body is covered with a well-developed coating of hair at one stage of the foetal life. The grip in the hands of a young infant is believed to be a survival of the muscular functions present in our ancestors at birth and necessary for holding to the body of the parent, just as it happens that a young colt must have a muscular system that enables it to run with its mother a few hours after it is born. The great anatomist, Wiedersheim, said that there are at least one hundred and eighty vestigial structures of this kind in the human embryo. These facts of structural resemblance are summarized by the classification of man in a family *Hominidæ* which is placed next to the *Simiidæ*, or tailless apes, among the Primates.

Physiological Evidences.—Functional resemblances have

In their early embryonic stages the brains of reptiles, birds and mammals show relatively less development of the cerebrum, and thus resemble the adult brain in a fish or an amphibian. *CBL.*, cerebellum; *CBM.*, cerebrum; *DIEN.*, diencephalon; *MD.*, medulla; *OL.L.*, olfactory lobe; *OP.L.*, optic lobe.

FIG. 289.—Skulls of anthropoids and pre-human races.

A, adult chimpanzee. B, reconstruction of adult skull of *Australopithecus africanus* (cf. Figs. 285 and 290), the newly discovered ape of Taungs, South Africa. C, restoration of *Pithecanthropus erectus*, the ape-man of Trinil, Java. D, restoration of *Eoanthropus dawsoni*, the dawn-man of riltown, England. (Redrawn from Broom, *Natural History*, Vol. XXV, courtesy American [Museum of Natural History and author].)

been indicated in connection with the structures mentioned in the foregoing descriptions. These are further illustrated by *blood tests* (cf. p. 523) which show a closer resemblance between man and the higher apes than between man and any other animals; and by the reactions to certain diseases, as well as all the more general functions. It is impossible to discover any essential physiological reaction in man that is not paralleled in the higher apes and even in the monkeys. These physiological resemblances would not be so important of themselves, but they are significant as corroborative of all the other evidence.

FIG. 290.—The most recent discovery of pre-human remains, *Australopithecus africanus*, found at Taungs, South Africa (cf. Fig. 289 B).

The shape and size of the brain is shown by material that filtered into the skull cavity and hardened into stone. The remainder of the skull was destroyed in the quarrying operations that unearthed the specimen. The low forehead, angle of chin, teeth, and brain capacity make this species a very important find. (After Dart from Broom, *Natural History*, Vol. XXV, courtesy American Museum of Natural History and author.)

FIG. 291.—How a reconstruction of the flesh over a skull can be made (cf. Figs. 285 and 292).

A, skull of a member of the Neanderthal race found at La Chapelle aux-Saints, France (from Boule). B, reconstruction of this skull with aid of other specimens showing the missing parts. C and D, addition of flesh after careful comparison of size of muscles, thickness of flesh, etc., in apes and man. E, the completed reconstruction of A. F, similar reconstruction of a man of Cro-Magnon, one of the prehistoric races of *Homo sapiens* with a brain capacity equal if not greater than that of the modern European. (Copyright by J. H. McGregor, reprinted by permission.)

Evidence from Fossils and Artifacts.—Further evidence of man's descent appears in the remains of pre-human beings discovered in Java and in Africa, and especially those of the Pleistocene in Europe (*cf.* Fig. 285 and Figs. 289 to 292). The record is becoming more extensive year by year, although it can never be so complete as that of animals whose habits render them more likely to become fossilized. Fortunately, the fossil record of man is supplemented by *artifacts*, weapons and implements of stone or other enduring material (Figs. 293 and 294), by rock carvings (Fig. 295), and by signs of his activities like the making of fire. In Europe, great camp sites have been discovered, as shown by the numerous implements, roasted bones, and other debris, although there may not be even a skeletal fragment of the man-like beings that must have frequented these localities for innumerable generations.

FIG. 292.—Neanderthal man, *Homo neanderthalensis*, restored by J. H. McGregor from the skull of La Chapelle-aux-Saints (*cf.* Figs. 285 and 291).

The most extensive series of human and pre-human remains have been found in the European region, although it is not probable that Europe was the original home of man. The discovery of the ape-man of Java (Fig. 289 C), and of an even earlier type in Africa (Fig. 290), point to Asia, or perhaps the African continent, as the place of origin for early types whose descendants migrated into Europe. It is not strange that more of these fossils should have

This is the same as Fig. 291E with addition of hair and eyebrows, and suggestion of beard not sufficient to obscure form of chin. A few wrinkles were added and the iris and pupil incised so that their shadows might lend life to the eyes. (Photo. by A. F. Huettnner, copyright by J. H. McGregor, reprinted by permission.)

been reported from Europe than from any other part of the world, since the finds in this region have led to extensive exploration and popular interest; and where these conditions exist, the attention of competent authorities is often called to remains discovered in excavations made for other purposes. When Africa and Asia are fully explored, many additions will no doubt be made to the present list.

On the American continent there were great apes in Pliocene times, but later these became extinct. The American Indians are

FIG. 293.—Cliff and beach at Cromer, England, showing the deposit called the “crag” in which primitive flint implements (cf. Fig. 294 B) are found.

The age of the crag deposit is regarded by some geologists as Pliocene or late Tertiary (cf. Fig. 285). No skeletal remains of the man-like beings who made the implements have yet been found in this deposit. (After Moir, *Natural History*, Vol. XXIV, courtesy American Museum of Natural History.)

usually believed to have reached this continent perhaps 10,000 years ago, by migration across Bering Strait from Asia. There is,

FIG. 294.—Primitive types of flint implements.

A, an eolith or dawn-stone from Kent, England; B, an early paleolith or old-stone-age implement of Chellean type from the crag deposit (cf. Fig. 293). (After Moir, *loc. cit.*)

however, one instance, at Attica, New York, of pottery fragments in undisturbed clay beneath the skeleton of a long-extinct mastodon (*Mastodon americanus*). In Logan County, Kansas, an arrow-head was found beneath the shoulder of an extinct bison (*Bison antiquus*), as though it had been embedded in the flesh when the animal died. In like manner,

near the town of Colorado, Texas, three large arrow-heads of markedly different type from those of recent origin

were found beneath the fossilized skeleton of a bison that was embedded in deposits of unquestionable Pleistocene age. Associated fossil fragments in this Texas deposit show a fauna including mammoths, camels, and extinct horses. Remains of human skeletons found in Florida have been said to be of Pliocene age, but this is not generally accepted. These Florida remains are probably post-Pleistocene, although they may be at least

FIG. 295.—Rock carvings from walls of cavern of Les Combanelles, France (cf. Fig. 206, p. 393).

A, group of horses. B, grotesque human heads or masks. C, mammoth. D, tectiform figure, perhaps representing a tent. E, group of animals. (After Breuil.)

20,000 years old, by a conservative estimate. Despite the opinion of many anthropologists that man was a comparatively recent arrival upon this continent, it is, therefore, expected by others that new finds will confirm the above evidence of his existence in America during the Pleistocene or Glacial Epoch when more than one race flourished in Europe. Even though the American Indians of North and South America did enter by way of Bering Straits in comparatively recent times, they may have been preceded by earlier races.

On the European continent, man came upon the scene during the Pleistocene, one of the most dramatic periods in the geologic history of the northern hemisphere. Great glaciers slowly spread southward in Europe, as they did in America, covering a large part of the continent, not once but four separate times, during a period variously estimated as lasting from 500,000 to 1,500,000 years. At times during the inter-glacial periods the European climate was even more equable than now. There were extensive forests, and gigantic mammalian types, like the mastodon and mammoth, the woolly rhinoceros, and the saber-toothed tiger, still walked the earth. Man entered Europe as a puny competitor of this mighty fauna, but spread and flourished, if one may judge from the flint implements and the occasional skeletal remains that enable us to picture the lives of these early human beings. Before the dawn of the historic period, other races, from which descended the modern Europeans, had entered and displaced the earlier ones.

NOTE.—More recent discoveries of human artifacts confirm the previous evidence for the existence of man upon the North American continent during the Pleistocene or Glacial Epoch. Near Folsom, New Mexico, two arrow heads were found (1925) by a field party collecting for the Colorado Museum of Natural History. Both of these artifacts were associated with skeletons of an extinct species of bison and in one instance the arrow or spear point was beside a rib in such a position that the animal must have died with the point embedded in its flesh. In this deposit the bison seem to have died at the edge of a lake or stream. The bones and matrix in which they are embedded show the marks of trampling by other bison, as though their possessors had died at some drinking place and later been stamped deep into the soft mud, which now appears as a tough clay silt cemented by lime. The age of these deposits has been tentatively placed by H. J. Cook of the Colorado Museum in the late Pleistocene or Glacial Epoch. Even more important finds have been recently brought to the attention of scientists (1926) in a gravel pit near Frederick, Okla., through the interest of Dr. F. G. Priestly, a local physician, and the owner of the pit, Mr. A. H. Holloman. In this instance the artifacts, which include flat grinding stones or metates and pesiles, as well as arrowheads, were embedded in old river gravels at two distinct levels. The associated fossils include scattered bones of extinct animals, like the mammoth, *Elephas columbi*, and at the lower levels the more primitive mammoth, *Trilophodon*; the giant ground sloths, *Megatherium*, *Myiodon*, and *Glyptodon*; and three species of horses of the genus *Equus*. These deposits, which have also been studied by the Colorado Museum, are regarded as early Pleistocene, because of their contained fossils and because they were laid down so long ago that erosion by the present drainage system of the Red River has since cut to a level more than 250 feet below the Holloman gravel deposits. Whatever may be the final verdict of geologists upon the age of these deposits, they place the existence of implement-making beings far earlier than any of the known skeletal remains or artifacts of the American Indians. The discovery of skeletal remains of these early North Americans would be of great interest for comparison with those of the early human races found in Europe and Asia.

CHAPTER 21

THE CAUSES OF EVOLUTION

Evolution as the historic fact is attested by the evidence outlined in the preceding chapter. It is impossible to present this evidence of the fact without indicating what is known of the course of evolution, since fact and course are so intimately related. It is, however, possible to know much concerning the fact and course of organic evolution without understanding its causes. Such is the position of biological science at the present day. Evolution is by far the most reasonable explanation of the history of animal life, but the course of evolution is known only in a general way and its causes are still uncertain. Attempts to discover and formulate these causes are represented by the Lamarckian Theory of the Inheritance of Acquired Characteristics, the Darwinian Theory of Natural Selection, the Mutation Theory of de Vries, various theories of Orthogenesis, and the Theory of Evolution by Hybridization which has been suggested by the Mendelian laws of heredity; together with lesser theories, like Darwin's Theory of Sexual Selection and the Theory of Isolation, which may be classified under those enumerated. These theories of evolutionary causation are the subject matter of the present chapter. Evolution depends primarily upon variations by which new characters make their appearance, and upon heredity, by which variations are passed on to subsequent generations. Any theory of evolutionary causation that is complete must deal with these two phenomena.

The Lamarckian Theory of the Inheritance of Acquired Characteristics

Historical.— A theory of the evolutionary process as a whole and of the inheritance of acquired characteristics as the cause of evolution was formulated in the works of Lamarck (1744–1829), written principally during the first quarter of the nineteenth century. Another Frenchman, Buffon (1707–1788), had previously formu-

lated the concept of evolution as opposed to creation, and Lamarck built upon this foundation. Many of Lamarck's original ideas and statements were crude and have since been ridiculed; but his essential claim, that *characteristics acquired by an individual in its lifetime are inherited by its offspring and thus produce evolutionary changes*, is the basis of the Lamarckian Theory of to-day. This theory is maintained by certain biologists, who are sometimes

called Neo-Lamarckians, since they maintain the old theory in a "new" guise.

Neo-Lamarckism.—In this modern form, the Lamarckian Theory includes, as causes of evolution, acquired characteristics resulting from the effects of use and disuse and also from environment. It is a familiar fact that the use of muscles tends to their development. The old adage "practice makes perfect" finds many illustrations in the neuromuscular coördinations that are perfected by use. Conversely, disuse leads to deficiency or even complete loss of function, as in the fanatics of India who hold a

FIG. 296. — Georges Buffon (1707–1788) scientist and popular writer who has not received due credit for his early advocacy of organic evolution.

(From Loey, "Biology and its Makers," copyright, 1908, by Henry Holt & Co., reprinted by permission.)

limb in one position until it cannot be moved. A white man who lives for years in the tropics may acquire a coloration that is recognizable long after his return to a temperate climate. Horses that are kept in mines, and men in dungeons, have their eyes so impaired that they can be restored to sight only by gradual exposure to light, if at all. Such examples of the effects of use and disuse and of environment, which are known as "acquired characteristics," could be cited without number among animals. We have considered in an earlier chapter (*cf.* p. 439) the importance of environmental factors in development. To this extent the conclusions of Lamarck may be modernized to express a fact that is everywhere recognized.

The Lamarckian must, however, go farther than this to prove his case, by showing that these effects upon individuals are inherited by their offspring. The process of such evolutionary causation may be illustrated concretely by citing some of Lamarck's own examples in modern terms. If swift-footed animals, like deer, have acquired their fleetness by running from their enemies, it follows that each generation has been forced to exert itself to the

utmost, like an athlete always in training for a race, and that the effects of this training in each generation have been passed on to the next. Thus, fleetness has gradually increased up to limits determined by the nature of the organism. In like manner, the fleetness of the pursuing wolves may have been increased generation after generation. If cunning were practiced, the more effective use of the brain would be passed on to the descendants. Animals living in caves cease

to use their eyes, and the degeneration that follows is supposed to be cumulatively inherited until blind species are produced. Animals living in cold climates, where the environment stimulates a

heavier growth of hair or the formation of more fat beneath the skin, are believed to transmit these characters by heredity and thus to reach the state seen in Arctic forms. An animal like the giraffe (Fig. 298) is assumed to have developed its neck by reaching up to browse upon the higher vegetation and to have inherited the slightly greater length of neck acquired by each generation.

Objections to the Theory.—There would be no objection to the Lamarckian Theory, if it could be shown that the effects

FIG. 297.—Jean Baptiste de Lamarck (1744–1829), first to propose a theory of the causes of organic evolution that received serious consideration.

(From Pirsson and Schuchert, "Textbook of Geology," John Wiley & Sons, copyright, 1924, reprinted by permission.)

of use and disuse and of environment are actually inherited. If such inheritance does not occur, there is no real evolution, since each generation starts as did the parents (*cf.* Fig. 299). Herein lies the weakness of the entire scheme. No one has yet presented evidence that is generally accepted, for the inheritance of such acquired characteristics. It would seem possible to obtain such evidence if the theory holds. Lamarekians no longer believe that the disuse following mutilation causes hereditary degeneration. As one writer puts it, "wooden legs do not run in families, although wooden heads may." Experiments in the destruction of parts,

FIG. 298.—Modification of neck in giraffes.

Left, the familiar long-necked species that lives upon the savannas and browses upon the higher branches of trees; center, the okapi or forest giraffe, a species that feeds upon lower branches; right, head and neck of long-necked giraffe for comparison with okapi. (Photos. by courtesy of the American Museum of Natural History.)

such as the amputation of tails in mice during many generations, as well as the special functional stimulation of parts, and in the effects of changed environment have given results that are considered negative by most investigators. The organism may develop new characteristics, but when it is returned to the original environment these effects are not lasting. Hence, the results of actual experimentation seem to indicate that the Lamarekian Theory is unsatisfactory as an explanation of the cause of evolution, because the characteristics thus acquired by individuals are not inherited.

A theoretical objection that arises is the mechanism of such inheritance, if it be assumed to occur. An individual develops not from its parent's body, but from germ cells (*cf.* Fig. 111, p. 222),

which seem in many instances to be set apart from the body cells at an early period and to be relatively uninfluenced by them. If the Lamarckian scheme holds, one must suppose that a change in a given part of an animal is transferred to the germ cells in such a way as to affect whatever it is in the germinal material that causes the development of this part. A blacksmith's son inherits his arms not from his father's arms but through his father's germ cells,

FIG. 299.—Cypress trees in the Dismal Swamp, Va.

The "knees" or pointed growths from the roots that project upward and are supposed to aid in aëration are not produced when the same species of tree grows on dry land. They are evidently a modification due to environment and not inherited. (After Russell, U. S. Geol. Survey, reprinted by permission from Pirsson and Schuchert, "Textbook of Geology," John Wiley & Sons, copyright, 1924.)

and so the germ cells of the father must have been changed if any modification has been inherited. The facts of animal structure and function make it difficult to understand how such influences can be transferred, but it is not necessary to picture such a process so long as there is no satisfactory evidence of its occurrence. This theoretical objection merely confirms the conclusions drawn from the failure of experimental evidence, although it would not be

convincing by itself. In conclusion, it should be said that there are certain biologists who find some of the modern experimental evidence more satisfactory than is indicated by the foregoing criticisms. The problem is a complex one, and evidence of the inheritance of characteristics acquired by use or disuse and under the influence of environment may be discovered at any time. The old Scotch verdict of "not proven" is a good one in such a case; yet the long-continued failure to secure evidence for the inheritance of acquired characteristics counts heavily against the theory.

The Darwinian Theory of Natural Selection or the Survival of the Fittest

Historical. — The ideas of Lamarck regarding the fact of evolution and its causes attained considerable vogue during the early nineteenth century, but were apparently overthrown by Cuvier (1769–1832, *cf.* Fig. 260, p. 496), the greatest zoologist of his day, who opposed the idea of evolution. In 1830, the year following Lamarck's death, a debate was held before the French Academy, in which St. Hilaire (1772–1844) upheld the Lamarckian doctrines against Cuvier and in which the latter was victorious. Although Cuvier was not an evolutionist he was forced to admit the difference between the animals of the past and those of the present, a difference which could not exist if animals were originally created as they are now and had not changed. Accordingly, he espoused the Doctrine of Cataclysms, which assumes not one but a series of creations, each followed by a "cataclysm" which destroyed all life. By supposing that each creation was on a higher level than the preceding one, it was possible to explain the succession of types appearing in the fossil record. This theory was exploded by the geologists, principally Lyell (1797–1875, *cf.* Fig. 261, p. 496), who showed that there had been no cataclysms. The date of publication of Lyell's famous "Principles of Geology" coincides with the debate in which Cuvier was supposed to have overthrown Evolution. The period from 1830 to 1859, during which Darwin was engaged in the work that was summarized in his famous volume, "The Origin of Species," was one of quiescence for the evolutionary theory. There was much popular and scientific interest, however, as shown by the large sales of a popular work by Robert

Chambers, entitled the "Vestiges of Creation" (1844), to which due credit has not been given by historians of Evolution.

Charles Darwin (1809–1882) thus began his work twenty years before the publication of his "Origin of Species." The fact that he was interested in determining whether species originated by creation or by transmutation, that is, by evolution, shows that the question was then under discussion. The idea of evolution seemed new in 1859 only because the evidence was so ably presented by Darwin and so rapidly accepted by scientists and by others who had previously known nothing of such a doctrine. It is rather discreditable to biologists that they failed to recognize at an earlier date evidence which had been steadily accumulating since the work of Buffon (1749), and which was quite adequate for acceptance of evolution, aside from its causes, as early as 1840. Nevertheless, Darwin deserves the place he occupies, because he brought about the acceptance of evolution by his masterful summary and extension of the evidence.

The publication of "The Origin of Species" was the beginning of a new epoch, both in biological science and in human thought. In 1900 the "Origin" ranked as one of the half-dozen most important books of the century in the number printed. What is less well understood, even at the present day, is the ramifications of evolution, as thus established by Darwin, in other fields of thought and investigation.

FIG. 300.—Charles Darwin (1809–1882), first to establish the doctrine of organic evolution upon a secure foundation, and to propose Natural Selection as a cause of such evolution.

(From Pirsson and Schuchert, "Textbook of Geology," John Wiley & Sons, copyright, 1924, reprinted by permission.)

The Origin of Species by Natural Selection.—The Darwin-

FIG. 301.—Alfred Russel Wallace (1823–1913), who also proposed Natural Selection as a cause of organic evolution and who was a lifelong friend of Darwin and supporter of his views.

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ian Theory of Natural Selection is outlined in Wallace's Chart (Fig. 302). This was originally published in one of the volumes by Alfred Russel Wallace (1823–1913), who was the co-discoverer with Darwin of the selective principle.

Rapid Increase.—If we elaborate the theory as outlined by Wallace, there is in all forms of life an ever-present tendency to *Rapid Increase in Numbers*. This is shown by theoretical calculations of the potential rate of increase and by the increase that actually occurs when species invade new territory that is especially suited to their needs. According to theoretical calculations, a plant

WALLACE'S CHART OF NATURAL SELECTION

Proved Facts	Consequences
A. Rapid Increase of Numbers B. Total Numbers Stationary	Struggle for Existence
C. Struggle for Existence D. Variation and Heredity	Survival of the Fittest (Natural Selection)
E. Survival of the Fittest F. Change of Environment	Structural Modifications

FIG. 302.—The evidence and argument for Natural Selection as outlined by Alfred Russel Wallace.

producing only two seeds a year would give rise to sixty-four plants in seven years, and to 1,048,576 in twenty-one years, if all lived to maturity. If an animal produced ten pairs of young annually and each individual lived ten years, there would be 25,937,424,600 in ten years and over 700,000,000,000,000,000 in twenty years. In the elephant, one of the examples cited by Darwin as a slow breeder, there would be alive at the end of 750 years nearly 19,000,000 elephants as descendants of a single pair, if all the individuals lived ninety years and each female brought forth six young. Examples of forms that would increase much more rapidly are: the conger eel, which has been estimated to produce 15,000,000 eggs annually; and the herring, which may produce 20,000,000. For the American oyster, which may produce as many as 60,000,000 eggs, Marshall gives the following calculation. If one should start with a single oyster and let it produce 16,000,000 eggs, all of which are fertilized and come to maturity, and if half of these should become females and go on increasing at the same rate, there would be in the third generation sixty-four millions of millions of females and in the fifth generation thirty-three thousand millions of millions of millions of millions of females. If to these be added an equal number of males, the bulk of the shells would then be equal to more than eight times that of the earth. Again, in the pedigreed cultures of the protozoan paramœcium, Woodruff calculated that 3029 generations might

FIG. 303.—Thomas Henry Huxley (1825–1895), comparative anatomist and paleontologist, and effective popular advocate of organic evolution in the decades following the publication of Darwin's "Origin of Species."

From Pirsson and Schuchert, "Textbook of Geology," John Wiley and Sons, copyright, 1924, reprinted by permission.)

have produced cells, similar to the original organism, to the number represented by 2 raised to the 3029th power, or a volume of protoplasm not less than 10^{1000} times the volume of the earth. These 3029 generations were produced in a period of five years. Such rates of increase are never realized, but they exist potentially in all animals and plants.

Evidence that some such increase can actually occur is seen where animals and plants

FIG. 304.—Louis Agassiz (1807–1873), pupil of Cuvier and distinguished Swiss zoologist, later professor at Harvard University.

Unlike Huxley and Wallace, Agassiz was unable to appreciate the evidence for organic evolution, although his own studies often present this evidence in a striking manner (*cf.* Fig. 262, A to C).

spread rapidly over new territory. The English sparrow was first imported into the United States about 1850, and a few were introduced later. Within twenty-five years it had spread and become a pest. It is now our most abundant and widely distributed bird. The German carp was introduced from China to Europe, and thence to the United States, by importation of small numbers. In the Mississippi Valley alone it has now spread into almost every stream, to the limits of colder water and other unsuitable conditions. The rabbits that have over-run Australia were introduced, likewise the herds of wild

horses that were abundant in North and South America in the early nineteenth century. There are so many instances of pests which have been introduced and spread widely, that governments have established quarantines against the importation of plants that might be infested with insects, and there is a law in the United States against the commercial importation of animals without inspection by the Department of Agriculture. Other examples of actual in-

crease that approximate the theoretical possibilities are seen in the "plagues" of insects and other small animals that occur in years when the conditions are favorable and an unusual percentage of the eggs develop. We may, therefore, conclude that the possibilities of great increase are always present, although never fully realized.

Total Numbers Stationary. — Despite the potentialities of increase, as stated in the foregoing paragraphs, it is evident that the total number of any species in nature must remain about stationary save for the annual fluctuations due to varying conditions and the occasional expansions that occur when new territory is invaded. Only a certain number of trees can find standing room in a forest; only so many fish can obtain food in a stream; and the number of insects and large herbivorous animals is determined by the supply of food and by the number of enemies. Thus, numbers are held stationary by what Darwin called the *checks upon increase*. These are often very complex, involving interrelationships between different species, as in the case of mice and clover (*cf.* p. 34). As Darwin says, "We know not exactly what the checks are, even in a single instance." Food and standing room are the ultimate checks, but in most cases it is probable that others intervene before these become operative. There is usually plenty of food for herbivorous animals, for their numbers are held well below the food limits by carnivorous enemies, as where rabbits are kept down by coyotes. Parasites play a rôle similar to that of enemies. The young of plants and animals are destroyed in great numbers; many seedling trees in a forest fail to find a foothold, and countless young birds fall an easy prey to enemies just after leaving the nest. Again, climatic and seasonal conditions may act as checks. So effective are these checks that the abundance of adult individuals in any species is not so much a matter of the eggs or young produced as of the chances of destruction. Darwin says, "The condor lays a couple of eggs, the ostrich a score, and yet in the same country the condor may be the more numerous of the two; the fulmar petrel lays but one egg, yet it is believed to be the most numerous bird in the world." Again, "one fly deposits hundreds of eggs, and another, like the hippobosca, a single one; but this difference does not determine how many individuals of the two species can be supported in a district. It would suffice to keep up the full numbers of a tree,

which lived a thousand years, if a single seed were produced once in a thousand years, supposing that the seed were produced and never destroyed and could be ensured to grow and germinate. Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount."

FIG. 305.—Representation of the equilibrium in the food relations of a community of organisms in a pond.

Algae are simple green plants; mussels, Sphaeriidae, Physae, and Limnae are mollusks; and amphipods, entomostraca and crayfishes are crustaceans. The arrows point from the food organisms to the feeding organisms.

Modern studies in ecology have further emphasized the intricacy of the inter-relationships between organisms that was discussed by Darwin in connection with his formulation of natural selection. Professor Shelford writes as follows in explanation of this diagram:

"Any marked fluctuation of conditions is sufficient to disturb the balance of an animal community. Let us assume that because of some unfavorable conditions in a pond during their breeding period the black bass decreased markedly. The pickerel, which devours young bass, must feed more exclusively upon insects. The decreased number of black bass would relieve the drain upon the crayfishes, which are eaten by bass; crayfishes would accordingly increase and prey more heavily upon the aquatic insects. This combined attack of pickerel and crayfishes would cause insects to decrease and the number of pickerel would fall away because of the decreased food supply. Meanwhile the bullheads, which are general feeders and which devour aquatic insects, might feed more extensively upon mollusks because of the decrease of the former, but would probably decrease also because of the falling-off of their main article of diet. We may thus reasonably assume that the black bass would recover its numbers because of the decrease of pickerel and bullheads, the enemies of its young. A further study of the diagram shows that a balance between the numbers of the various groups of the community would soon result. Under other circumstances, such as the extinction of the black bass, the resulting condition would be entirely different from the original one, but a balance between supply and demand would nevertheless finally be established."

(From Shelford, "Animal Communities in Temperate America," copyright, 1913, by Geographic Society of Chicago, reprinted by permission.)

The Struggle for Existence. — As a result of these conditions of overproduction and stability, many more individuals come into existence and struggle to live than can possibly survive. Hence, the conclusion is drawn that there is a “struggle for existence” in all life. This phrase was used by Darwin in a general and metaphorical sense, for the struggle is seldom an actual conflict; al-

FIG. 306.—The lady beetle, *Pentilia misella*, and its larvæ feeding upon another insect, the San José scale, a dangerous enemy of fruit trees.

Various species of lady beetles have proved efficient checks upon the multiplication of scale insects. *a*, adult; *b*, larva; *c*, pupa; *d*, the beetles and larvæ feeding upon the scale insects, the scale-like bodies of which are shown upon a twig of a pear tree. (From Bulletin No. 3, N. S., U. S. Dept. Agr. Div. Entomology.)

though it may be so, as when carnivorous animals fight with one another for food or mates. In general, it is most acute between individuals of the same species, since these compete for the same conditions of life. A similar competition may occur between widely different species, if they use the same food, as when insects devour the food of grazing animals. Another example of struggle between individuals of different species is that of carnivorous forms

like wolves hunting herbivora like deer. In certain species, like the fur seal, there may be a literal struggle among the males at the breeding season for possession of the females. Finally, there is the struggle with the physical factors of environment, like heat and cold, moisture and dryness, changing climate, and changing conditions upon the land surface or an ocean bottom swept by varying currents. Hence, J. Arthur Thomson has characterized the struggle as one that is three-fold, for food, for mates, and against fate. Such a struggle, in one or more of its aspects, is ever-recurring for all life, although it is intermittent and may not act for considerable periods in the life of any individual. Because it thus seems to be a necessary consequence of the limitation of numbers in the face of great overproduction, the struggle for existence may be placed in the column of proved facts as the chart indicates.

Variation and Heredity. — The modern concept of variation and heredity was discussed in the chapter on Genetics. It is sufficient to repeat that variations are the differences between individuals of a species, and that heredity is the resemblance in these characters as they occur from generation to generation. Some variations are inherited, others are not. The theory of selection, of course, deals only with such variations as may be inherited, since only these can play a part in evolutionary changes. It is important for us, therefore, to discover the way in which the struggle for existence acts upon variations that are inherited.

Survival of the Fittest. — Given inherited variations of many sorts, some will be of value to the individual in its struggle for life. If the members of a species of plants differ in their ability to resist frost, those that are most resistant will survive low temperatures. If this variation is inherited, the next generation will be composed of more resistant individuals. If such a process of natural selection is repeated generation after generation, sufficient resistance to meet the exigencies of life will become a part of the permanent inheritance of the species. Thus, evolution might occur by change of this particular feature of the organism, in such a manner as to suit a changing climate or to enable the species to extend its range northward. If rabbits differ in quickness of start and in sustained speed, and if these differences are important, the quickest and speediest in each generation will tend to survive. If these variations are inherited, a race having greater speed will gradually come

FIG. 307.—Variation in scallop shells.

Specimens taken at random from a species and measured for any feature usually show a curve of variation of this general type, although a study of the descendants of single individuals may resolve the group into a number of pure lines, each with its curve of fluctuating variations (*cf.* Figs. 241 and 308). If there appeared in a population, such as is represented by this figure, individuals whose shell rays fluctuated between limits below fifteen or above nineteen, and if such individuals bred true, this would be a clearly recognizable case of mutation. (Photo. by courtesy American Museum of Natural History.)

into existence. If animals have heritable differences in their resistance to a disease which is an important factor in their lives, a more resistant race may be evolved by a selective process. If wits are more important than strength in the struggle for life, selection may develop a more intelligent type. If concealment is of life-and-death value, coloration and other features that tend to make the individual resemble its surroundings will be at a premium and therefore will be selected. So goes the theory, but all such variations must be heritable, and therefore mutations rather than fluctuations are the variations selected (*cf.* p. 486).

Darwin called this process "Natural Selection," because of its resemblance to the "Artificial Selection" by which breeders of animals and plants select the individuals that please the fancies or the necessities of man and thus bring about changes that have been described as evolutionary in the preceding chapter. Herbert Spencer called the same process "Survival of the Fittest," since the individuals best fitted to the conditions of life are the ones that survive. There must, of course, be a limit to the fitness that can be built up, just as there is a limit to the efficiency that can be secured by gradual improvement of a piece of machinery. The speed of a deer or a wolf would be limited by the nature of the bodily mechanism, intelligence by the brain cells, resistance to disease by the chemico-physical reactions of which a given organism might be capable. But there are possibilities of further evolution, as appears in the final item of the chart.

Change of Environment. — We have spoken of the environment as though it were constant. Yet great changes take place over long periods of time, as when continents are made and unmade by the processes of geologic evolution, or profound climatic changes occur, such as the advent of an Ice Age or the change from forest to desert conditions. These are probably less important than changes of environment that may seem to us insignificant. The introduction or destruction of a plant upon which various animals feed may produce far-reaching changes in the environmental conditions of a given species. New enemies entering a district may bring new standards of selection; new parasites or disease-producing organisms may put a premium upon qualities that have not been hitherto selected. In the complex interplay of forces there is the possibility that conditions, and therefore selection, may remain stable for long periods, or that selection may sud-

denly take new directions. Hence, there is the possibility of changes of all sorts, some progressive, others degenerative as in organisms that have been selected as parasites. Under natural selection the environment has been compared to a sieve that selects a certain type of individual. This sieve may change and produce new lines of evolution. It was such a mechanism in nature that Darwin conceived to be most important in directing the course of evolution.

Present Status of Natural Selection. — It is almost self-evident that the process of Natural Selection is one of the major causes of evolution; although the selective process has obvious limitations. It has sometimes been urged that natural selection is inadequate because it does not explain variation and heredity, which are the fundamental causes of evolution. Thus it is said that the "origin" of species is to be sought in the origin of variations that are inherited, and that selection merely determines what variations, and hence what incipient species, shall survive after they have originated from other causes. This is perhaps a fair criticism of the title of Darwin's great book, "The Origin of Species by Natural Selection or the Preservation of Favored Races in the Struggle for Life"; but it fails to recognize that the argument for selection is: *given heredity and variation, certain things will follow*. Heritable variations are known to exist, just as reproduction in excessive numbers is known to exist, and it is as unfair to criticize the selection theory because it does not explain heredity and variation as it would be to criticize it because it does not explain reproduction. Heredity and variation demand investigation by reason of their intrinsic interest as well as their importance in evolution, but we do not need to know how heritable variations arise and are perpetuated in order to be convinced that selection exercises a directive influence upon the course of evolution.

Another criticism of selection is that it explains only the existence of useful or adaptive characters, while organisms seem to have many characters which must have arisen during evolution and which are non-useful without being particularly injurious. This limitation is recognized by all who understand the theory, since the nature of the process is such that only useful characters can be selected. Conversely, injurious characters are eliminated by selection whenever they are sufficiently important. Selection involves the elimination of the unfit as well as the preservation of

the fittest. As it now stands, selection is the most satisfactory explanation that can be given of the adaptations that are present in organisms (*cf.* p. 24). The alternative Lamarckian Theory has scant foundation. In this connection it is also said that selection can act only upon differences that are of marked importance, and most characteristics of animals are not on this level. How such non-selective characters may become established in a race is shown in the sections upon Mutation and Isolation.

Again, it is said that no one has seen selection at work in nature, and that we merely argue, because of the facts, that it must work (*cf.* Figs. 305 and 306). This only means that nature is too complex to show all that happens. We see dimly and incompletely, but none the less certainly, the existence of a selective process which is always in the background even though it may be temporarily in abeyance. This is all that one can expect to see in so complex a situation, although special cases of selection may be demonstrated experimentally, as when chicks of different colors are let run in a large enclosure and it is found at the end of the season that the white ones have been picked off by hawks.

It is true that many examples of variation that Darwin cited in his argument for Natural Selection are now believed to be fluctuations rather than mutations and therefore not heritable. In Darwin's day, extreme examples of mutation, or "sports" as they were called by breeders, had been recognized; but Darwin regarded such variations as too infrequent to be important. At the present time we know mutations to be of frequent occurrence and to include all sorts of differences. The argument for selection is sound so long as there are such heritable variations, that is, mutations, even though Darwin had in mind principally variations that are now known to be fluctuations and therefore not inherited.

Perhaps the strongest argument for Natural Selection is based upon the results obtained by Artificial Selection. Varieties of domesticated animals and plants have been developed by the artificial selection of individuals having variations that pleased the fancies or the necessities of breeders. Insofar as these variations are inherited, they may thus be perpetuated and the breed modified. The breeder does not even need to know the special laws of heredity and variation in order to accomplish notable results, although such knowledge enables him to select much more effectively. Arti-

ficial selection may differ from natural selection in the characters that are perpetuated, but the method is the same. In nature only those characters can be selected that are useful to the species itself. It would, therefore, be impossible for natural selection to modify a species to its own disadvantage or to the advantage of another species, save as this might be an incidental result. Under artificial selection, however, animals are often modified in ways that would be injurious were it not for the protection afforded them by man. While this difference between artificial and natural selection must be recognized, it is perhaps the more significant that the selective process can be made to work in another way than it does in nature. If man chose to select for the good of the organism rather than for his own, he could no doubt produce results parallel to those of nature.

A selective process, or survival of the fittest, undoubtedly functioned in the human species in the past. At times it requires a good deal of optimism to believe that it has ceased to function. The declaration that it *should* apply in civilized life is perhaps one of the chief causes for the offense that has been given by some biologists and others to individuals who are laboring for an increase of human sympathy. Although the problem is a complex one, it is perhaps a sane view that mankind, having arisen by evolution, was subject in the past to the law of tooth and claw, and that discouraging evidences of this condition survive. The finer human relationships, however, rest upon a basis of coöperation rather than of conflict. Perhaps the evolutionary beginnings of these relationships may be seen in parental care and in the relationships of mutual helpfulness that exist in family life.

The Mutation Theory

Historical. — During the decades immediately following the publication of "The Origin of Species" (1859), biological investigation consisted principally in extensions of the Doctrine of Evolution and of Natural Selection. It was hoped that unquestionable phylogenetic relationships could be established for the Animal Kingdom (*cf.* Fig. 117, p. 240); and natural selection was accepted as the all-sufficient cause of evolution. In the last decade of the century, however, it became apparent that mere confirmations of the general process of evolution were no longer profitable,

and more critical investigations were undertaken. As a result of these investigations, the general fact of evolution has been amply confirmed, while the selective process has been assigned to its appropriate place among the causes of evolution. The Mutation Theory of the Dutch botanist, Hugo de Vries, is an example of this post-Darwinian study of evolutionary problems.

The Work of de Vries. — The author of the Mutation Theory conducted his investigations upon the evening primrose, *Enothera lamarckiana*, which he obtained from stock found growing wild near Amsterdam, Holland. Although *Enothera* has since been shown to be less favorable for such studies than some other species, and although the mutations studied by de Vries are now thought to be rare combinations of genes rather than true mutations, the existence of mutations and the correctness of de Vries' views regarding their importance have since been established in other plants and animals, notably the fruit-fly, *Drosophila*. Since the work of de Vries was thus the clew to these important discoveries, something may be said regarding the original results that led to the Mutation Theory.

The distinction between the two types of variations known respectively as fluctuations and mutations has already been explained (p. 486 and *cf.* Figs. 307 and 308). In studying the evening primrose, de Vries found several aberrant types growing wild with the typical form, *E. lamarckiana*. When the typical form was self-fertilized and the seeds planted in his garden, these new types reappeared in small numbers, year after year and generation after generation. Moreover, the new types bred true, except that they gave occasional aberrant types, as did the parent type, *E. lamarckiana*. This led de Vries to believe that new types, comparable in some instances with the varieties or sub-species of plants and animals that are frequently recognizable in nature, were appearing in the evening primrose, and that he was actually observing evolution at work. But the changes observed were the result of mutations, and not, as Darwin had supposed, of fluctuations extending over many generations and producing a cumulative effect in a certain direction. This agrees with the conclusion that, since fluctuations are not inherited, they can have no part in evolutionary changes, and that, since mutations are inherited, they must constitute the type of variation that is important in evolution. It remains to be shown that mutations are sufficiently common to

furnish the material for evolutionary changes. De Vries believed this to be the case in *E. lamarckiana* and in other species, at least at certain times in the history of the race. If his supposition were correct the problem would be to discover the causes of the muta-

FIG. 308.—Fluctuations in pure lines of paramecium.

By rearing pure lines, or the descendants of single individuals in paramecium, it was found that each pure line fluctuated between certain limits. If all the individuals of this figure were plotted in a single curve the result would be a curve of variation similar to that shown in Fig. 307 (cf. Fig. 241). In the present figure, each row represents a single pure line, showing the maximum, minimum, and intermediate sizes of the individuals. The differences in size within the pure line are fluctuations due to differences in growth and environment. The differences in average size between the several lines are hereditary and comparable with mutations.

The numbers show the length in microns. The average length for all the lines taken together is given by the perpendicular line *xx* at 155 microns. The average size for each pure line is that of the individual above which is placed a + sign. Other letters represent investigator's special designations. (After Jennings, *American Naturalist*, 1909.)

tions and the manner of their inheritance, together with any factors, such as natural selection, that might determine the survival of mutations once they had appeared.

Mutations and Selection.—The relation of the Mutation Theory to the Theory of Natural Selection will now be clear. If

fluctuations are not inherited, they may be weeded out by natural selection and thus produce no results. Selection of mutations, on the other hand, will result in the establishment of new types. The matter is more difficult to study where the sexes are in separate individuals and cross fertilization must occur, as in most animals, although many cases of this sort have been investigated in the fruit-fly. Analysis can be more easily accomplished in a self-fertilizing species, like the bean plants studied by the Danish botanist, Johanssen, or in a protozoan that reproduces asexually, like the paramœcia, studied by Jennings (Fig. 308).

Present Status of the Mutation Theory.—The Mutation Theory, therefore, does not supplant the Theory of Natural Selection. It shows the material upon which selection must work. It is a study of the variation and heredity which are taken for granted in the scheme of natural selection. In a concrete instance, one might suppose selection to weed out, in each succeeding generation, the fluctuations that rendered individuals less fit to survive. Under these circumstances no evolutionary change would be effected, because such variations would not be inherited and the individuals exhibiting them would give a similar population in each generation, no matter how rigorous the selection. When, however, a mutation occurred that was sufficiently advantageous, selection would act upon the individuals exhibiting it, and upon their descendants, and might establish a new type. The older type might be obliterated if it were at sufficient disadvantage in competition with the new one; or the old and new types might persist side by side, as often seems to be the case. In this manner the appearance of mutations and their selection might bring about evolution by a series of steps which Darwin would have considered too large to be possible. We have seen that Darwin recognized the existence of the extreme variations which, even in his day, were known as mutations and called "sports" by breeders, but he did not suppose them to be sufficiently frequent to be important for evolution.

In further support of this relationship between mutations and selection, it may be said that many domesticated breeds seem to have arisen from mutations that appeared fully formed, and the descendants of which were selected with considerable inbreeding until the type was established. The origin of the Ancon sheep, a short-legged breed descended from a single ram that appeared

in 1791; of the hornless or polled Hereford cattle from a single calf born at Atchinson, Kansas, in 1889; of tailless cats and dogs; and of hairless cattle, dogs, mice, and horses are further examples of Evolution by Mutation. Such an evolutionary process supplements rather than supplants Evolution by Natural Selection in the scheme of evolutionary causation, and such was de Vries' concept of its relationship. It is more fundamental than the Theory of Selection, since it deals with the underlying phenomena of variation and heredity. Natural Selection appears in a more limited rôle, but, on the other hand, it is relieved of the criticism that the fluctuating variations emphasized by Darwin can not be the means of evolutionary change, because not inherited.

Objection to the Mutation Theory has been raised on the ground that mutations are not of sufficient frequency in nature to be the material of evolution, and again that the limited number of individuals exhibiting a particular mutation would have small chance of leaving enough descendants to establish a population. The answer to this criticism is that any mutation seems likely to appear not once but a number of times in any generation, and in successive generations. Again, it was believed by de Vries that species have mutating periods, lasting, perhaps, thousands of generations, during which numerous mutations appear and hence evolution proceeds rapidly. A similar idea has been expressed by paleontologists. It may also be supposed that mutations, which are due to certain changes in the germplasm, are caused by environmental influences and that similar influences may produce similar results again and again, thus offering repeated opportunities for selection. It has already been explained that the cases actually studied by de Vries now seem to be examples of unusual combinations occurring according to the Mendelian laws of heredity and not true mutations. The work of de Vries, therefore, occupies a curious position in that it brought to light principles that seem to apply elsewhere but not in the cases in which they were "discovered."

Orthogenetic Theories

The Origin of Variations by Orthogenesis. — Throughout the preceding sections the origin of variations that are inherited has been emphasized as the basic phenomenon to be explained in any

theory of evolutionary causation. The Lamarckian Theory supposes such variations to be induced by use, disuse, and environment. The Theory of Natural Selection assumes the appearance of such heritable variations without attempting to explain their causation. The Mutation Theory distinguishes between fluctuations, which are not inherited, and mutations, which are inherited and may furnish material for evolution. It does not necessarily explain the causes of mutations. It is true that de Vries put forth the theory that species have mutating periods extending over many generations, but he offered no adequate explanation of the occurrence of such periods. Orthogenetic theories attempt to explain why heritable variations occur; but, more than this, they postulate that certain kinds of variations are destined to arise and hence to determine the course of evolution.

Mechanistic Orthogenesis. — Orthogenetic theories that are mechanistic suppose variations to be restricted, and evolution thus directed, to certain lines, by the chemico-physical nature of the organism and its environment. Cases are believed to exist in which the fossil record suggests a determinate course of evolution (*cf.* Fig. 275, p. 514). Examples are found among the dinosaurs (*cf.* Fig. 269, p. 506), in which horns first appear as protuberances that are hardly distinguishable, and certainly not useful, and increase as though destined to a certain course. Again, many fossil series suggest that types begin simply, and evolve complexities, such as over-developed spines and plates, which foreshadow extinction. Isolated examples of this would not be significant, but some paleontologists claim that changes of this general sort have occurred so often in wholly different types of animals that they can only be explained as the result of forces inherent in the race and carrying it along a "straight" or orthogenetic line of evolution. Other evidence of orthogenetic evolution is found, by advocates of this theory, in living animals; as in the studies of Professor Eimer upon color markings of lizards, beetles, butterflies, molluscs, etc. According to the mechanistic concept, all such evolution is due to unknown but determinate physico-chemical factors.

Vitalistic Orthogenesis. — On the other hand, orthogenesis may be conceived as due to a *vital force* inherent in protoplasm and determining alike its immediate responses and the course of its evolution. In criticism of all theories of orthogenesis, it can be said that they are more philosophical than scientific. For all we

know there may be directive forces inherent in the protoplasm, but it is impossible to say that evolution might not have taken a different path, however determinate a given course may seem. As for the paleontological evidence, the incompleteness of the fossil record and our limited knowledge of environmental conditions in the past make it unsafe to generalize.

Isolation as a Cause of Evolution

Isolation seems well established as a factor of some importance in evolutionary causation. The classic example is the work of Gulick upon snails of the family *Achatinellidae*, which occur in the Hawaiian Islands. These snails live upon trees. Since they do not easily move upon the ground and never travel any distance over a land surface devoid of shade or moisture, their distribution is restricted. In the island of Oahu there are, along the sides of the principal mountains, small valleys in which these snails find suitable habitations, but they can not cross the ridges between neighboring valleys nor the crest of a mountain. Neither can they move out upon the plain below. Thus the population of snails that might happen to be established in any valley would tend to remain isolated as long as similar climatic and topographical conditions prevailed. In this instance almost every little valley has its particular variety or varieties, differing in size, color, and shape of the shell. These differences can hardly be accounted for by anything in the environment, since conditions in the different valleys must be almost identical.

The most reasonable explanation of the facts is that when a population is thus isolated the individuals become differentiated because some types happen to be present originally and to survive in one locality, and others in another. There can hardly be any selective action of features like those mentioned under such uniform conditions. Some of the more recent collectors of these shells even report one variety which seems to have been restricted to a single tree that happened to be sufficiently isolated to prevent transfer. It appears, therefore, that evolution of non-useful characters may occur merely as a result of isolation. Having become established, such characters might later become subject to selection if the environment changed and rendered them important in the struggle for life. A similar case has been observed by Kincaid

in marine snails of the genus *Thais* in Puget Sound. These live on rocky shores and cannot cross sand or go into deep water. Since their young are hatched as miniature snails there is no chance for dispersal as free-swimming larvæ. Each rocky point or other area that is isolated from other suitable places has its particular variety. Another example is seen in the snails of the genus *Partula*, studied by Crampton in Tahiti. In such cases evolution proceeds in a manner which is not so different from the Darwinian scheme, since the isolation of certain individuals might be called a form of selection, although the characters evolved cannot be regarded as necessarily useful.

Evolution by Hybridization

From the account of complex Mendelian hybrids that was given in the chapter on Genetics, it is possible to understand how evolution might occur by the appearance of characteristics that are new only in the sense that they are new combinations. Thus, if a black, short-haired guinea-pig is bred with a white, long-haired individual, there will be in the second filial generation (Fig. 247, p. 469) a theoretical ratio of one white, short-haired individual to fifteen of other types. Neither the short hair nor the white hair is new, but the combination of short and white hair might be something that had never occurred before. If such a new type of guinea-pig were thus produced under domestication, or if a new combination thus appeared in nature and was perpetuated, this might be called evolutionary modification. Although there would seem to be a limit to the amount of change that could arise in this manner, the Dutch botanist, Lotsy, has argued for the importance of such hybridization in evolution. The English geneticist, Bateson, even went so far as to maintain, whether seriously or as a stimulus to a more critical attack upon the problem, that recombination and loss of characters might account for all evolution.

Organic evolution is, therefore, but one aspect of the historic process of change which has occurred throughout nature in the past, which is happening in the present, and which it is presumed will go on happening in the future. The universe is not static but dynamic, that is, it is a "going concern," if we wish to put the idea in the language of the street. In the physical sciences of

Astronomy and Geology this idea of a dynamic universe finds little opposition. In the biological sciences the conclusions are more recent and less widely acknowledged. Organic evolution is regarded by biologists as established, because it explains, in a reasonable manner, innumerable facts that have no other scientific explanation. The course and causes of organic evolution are less certain than those of the inorganic evolution described in Geology, but organic evolution as the historic fact seems attested by overwhelming evidence.

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