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PRINCIPLES OF ANIMAL BIOLOGY

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FRONTISPIECE.—Three-toed sloth Bradypus, from South America, an example of an animal adapted to arboreal life. The sloth lives in trees, usually suspended from a limb. It cannot support itself on its legs and hence cannot walk on the ground. (*Photograph by A. G. Ruthven.*)

PRINCIPLES OF ANIMAL BIOLOGY

BY

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To the Teachers of

ZOOLOGY

WHO HAVE BEHELD THEIR SUBJECT
OUTGROW A PEDAGOGICAL METHOD

PREFACE

The changes introduced in this sixth edition are more than usually varied. While none can be regarded as radical, they affect in important ways nearly every part of the general plan. The book is still devoted to principles; indeed, the changes appear even to emphasize its devotion to fundamental concepts.

If any one statement can be made which would characterize much of the alteration now made, it is that the treatment of function has been increased or clarified or thrown into relief by emphasis. Such changes relate, among others, to enzymes, photosynthesis, oxidation, muscle action (including cardiac), breathing movements, transfer of respiratory gases, blood composition, the clotting process, kidney function, vitamins, endocrines, the placenta, and reflex arcs. The authors have not hesitated to give chemical formulas and reactions that beginning students need not be expected to remember or reproduce, because these exact forms of expression carry conviction concerning the precision of present knowledge which no more general statement can produce.

Greater clarity of exposition has been sought at many places by illustrations and slight changes of language or inclusion of features not heretofore expressly described. Comparisons that were formerly illustrated by figures borrowed from research contributions are now in several instances portrayed by simplified diagrams placed side by side with the contrasts indicated. Among the phenomena thus treated are symmetry, centralization and cephalization of the nervous system, endocrine secretions, the hydroid metagenetic cycle, and the evolution of living things in geological time. More explicit description is the method adopted for the types of circulatory and excretory systems, for the operations of the kidney, for the biogenetic law, and others.

Order and emphasis have occasionally been changed at the suggestion of teachers elsewhere, even when the authors were not quite convinced that the new method was an improvement but could see no objection to it. Molecules and atoms have been introduced before protons, neutrons, and electrons. The names of the phases of mitosis have been restored in the belief that under the guidance of a good teacher cell division will still be conceived as a continuous process. Biological terms have been introduced in a number of places with the conviction that names sometimes clarify ideas, simply because terms must have definitions. Yet the glossary is today shorter than in the early editions.

In the treatment of genetics the simple phenomena have been described in less space than formerly but, it is believed, with greater clarity. Description of the mechanism in advance of its operation, a method used with success in genetics courses, should contribute to this result. The two linkages have been restored to the general text—at the request of teachers and in conformity with the authors' preference. If the work in genetics is to be shortened in any institution, this can still be done by omitting the later parts of the chapter, for the topics are treated in the order of their importance and desirability for beginning students. The problems in genetics have been modified to call for precise (usually numerical) answers, not for charts or discussions. There is no reduction in the thought or organization required of the student in solving them; he merely gives one specific part of his conclusion instead of all of it, which should facilitate checking his accuracy.

Among the more general of the other changes should be mentioned the addition of marine habitats to the chapter on ecology, a considerable extension of the historical treatment in zoogeography, and an enlargement of the account of prehistoric man.

To compensate in part for the increase of space that many of the foregoing revisions entail, omissions and condensation have been effected elsewhere. The authors will be interested to learn whether the omissions are missed.

One incidental consequence of these extensive revisions is the removal of some distinct contrasts of literary style, which are seemingly unavoidable results of joint authorship. While the present style may not be better, uniformity of style is surely to be desired.

As usual, the authors' colleagues who use this book in an elementary course have been generous with suggestions for improvement. Among teachers in other institutions who have furnished ideas, special mention should be made of Prof. Roy D. Shenefelt, whose recommendations could have come only from a well-considered philosophy of teaching.

A. Franklin Shull.

Ann Arbor, Mich.
May, 1946.

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PRINCIPLES OF ANIMAL BIOLOGY

CHAPTER 1

THE GROWTH AND SCOPE OF BIOLOGY

When knowledge can be classified and organized on some basis which exists in nature, not just in the minds of men, the body of knowledge so arranged is science, or a science if the field is limited. The devotees of science seek to discover the natural principles which control the phenomena they observe. The more fundamental the ascertained principles are, the more significant the science is. The first step in discovering principles is usually observation of the facts or phenomena which require explanation. Very often the second step is experiment, or interference with natural events, with possible alternative outcomes in mind. Finally, there is the logical consideration of all facts to see what relation exists among them.

When the phenomena studied are those of living things, the organized knowledge is called biology. It is not distinct and separate from other sciences, for all life processes are fundamentally physical and chemical. Indeed, no science is a province unto itself, for the constitution of matter and energy, with which they all deal, is everywhere the same. Each division of the field of science emphasizes certain types of phenomena, but the more the various fields can be intertwined the more fruitful scientific work becomes.

The several sciences have also been interrelated as they developed over the centuries. Let us see how biology has shared in the early stages of this growth and what it has come to be in later times.

Ancient Civilizations.—Among primitive peoples knowledge and superstition regarding life came chiefly from three sources: from their wonder and awe at the phenomenon of death and customs relating to the preservation of the bodies of the dead, from their fear of the great wild beasts, and from their attempts to cure disease and heal injury. The earliest known civilization is that of Babylon. Medical science, which is the form that early biology most often took, made some progress there. Clay models of various organs of the human body have been preserved, and Babylonian writings show that two kinds of blood, light and dark, were recognized. The heart, however, was regarded as the seat of intelligence. In Egypt, another very old civilized country, embalming of the dead led to a knowledge of anatomy, and an art of healing based not upon superstition but upon observation was developed. The Israelitic tribes borrowed their scientific knowledge from other peoples and clothed it with a religious significance but added nothing to the store of biological information. The other great peoples who might have contributed to early biological knowledge were interested in other branches of culture—the Hindus in mathematics, the Chinese in ethical and social problems.

Early Greeks.—It was among the Greeks, therefore, that biology received its first great impetus. The passion of these people for intellectual inquiry was due partly to their innate qualities but in part to the practical absence of powerful restrictive governmental and religious organizations. The Ionic tribes, coming into contact with the cultivated peoples of the East, through their colonies in Asia Minor, developed the earliest natural philosophers. One of these was Thales (about 650–580 B.C.), who, though he left no writings, is reputed to have regarded water as the source of all things, including life. Anaximander (about 611–546 B.C.) entertained a theory of the origin of the universe from a vague something which he called "apeiron," but his chief concern with biology was his supposition that living things arose from mud. First, he thought, came the lower animals and plants, and then human beings; but the latter were in the form of fish and lived in water. Later these human beings cast off their fish form and lived on land. This view of the origin of living things was adopted by Diogenes of Apollonia (not the famous cynic Diogenes), who conceived that the agent which brought forth living things out of the earth was solar heat. Diogenes was the author of the earliest known work on anatomy, fragments of which are still preserved, and his ideas of human embryonic development give evidence of being based on dissection.

Some of the more important of the remaining Greek natural philosophers came from the colonies of the west. Xenophanes, who had wandered to southern Italy, is chiefly noted for his discovery of fossils, his recognition that they were animal remains, and his conclusion therefrom that in some cases what are now mountains were once under the sea. He died about 490 B.C. Another western Greek was the braggart Empedocles, in Sicily, who lived about the middle of the fifth century before Christ. Among the many things which he boasted of doing, he appears actually to have rid a neighboring town of malaria by draining the district. On the theoretical side of his biology, he conceived living things to have arisen out of the earth, plants having come first. Animals arose in the same way, but in pieces. Separate limbs, trunks, etc., arose, kept apart by the force of hate. When love triumphed, these members joined in accidental manner. Some such combinations were malformed monsters incapable of life; others, more fortunately constructed, survived and gave rise to the animals of today. The blood he regarded as the seat of intelligence, the eye he likened to a lamp, and respiration he thought to occur partly through the skin.

Democritus.—More important for natural science than any of his predecessors was Democritus (Fig. 1) who was born about 460 B.C. Chaste in morals and temperate in habits, he lived to the ripe age of a century. Curious about the world, Democritus spent his patrimony in travel, then lectured for pay to avoid the serious Greek charge that he had wasted it. His interests were exceedingly inclusive, and he is best known for a materialistic ("atomic") theory of the universe, some features of which have a distinctly modern flavor. While it was through his general philosophy that he most influenced subsequent thought, not a few strictly biological concepts are found in his writings. He distinguished types of animals differing in the quality of their blood, a basis of classification later adopted by Aristotle. In embryonic development, he supposed the external organs arose first, the internal structures later. He knew that mules are sterile and conceived an anatomical reason for it. He regarded the brain as the organ of thought, the first of the natural philosophers to do so. In his more subtle theoretical ideas, Democritus was strictly materialistic; even the soul was regarded as a material thing, consisting of globules of fire which impart movement to the body. He represents the climax and close of the first scientific period of Greek philosophy, which was an era of search for purely natural causes.

Fig. 1.—Democritus.

Hippocrates.—A contemporary of Democritus was Hippocrates, the Father of Medicine. What Hippocrates actually wrote is not certainly known. A collection of about a hundred works has been attributed to him, but many of these were probably not his. His interest was scarcely scientific, but rather in the healing of men; yet in one of the works on diet in the collection is a reference to an attempt to classify animals. While the study of medicine is biology, Hippocrates treated it as an art; his descriptions of operations are models of clarity. The social and moral responsibilities of physicians engaged his attention, and a famous oath administered to medical graduates was based on his teaching.

Aristotle.—A reaction set in against the materialistic conceptions of Democritus and others. Philosophy came to be dominated by Socrates, who was interested in ethics, and by Plato, who found true reality in the world of abstract thought. The latter says expressly that no true knowledge is to be attained through observations of the senses. One leading philosopher who came under Plato's influence was Aristotle (384–322 B.C.) (Fig. 2), the greatest of the early biologists, to whom the essence of living things was their form. Everything that happens, he taught, is due to a supreme intelligence, everything is done

FIG. 2.—Aristotle, 384–322 B.C. (*From Hekler, "Greek and Roman Portraits," G. P. Putnam's Sons.*)

for a purpose, and the primary purpose in nature is the development of a higher form. As a result of this continuing purpose, there has been an evolution from lower types to higher ones.

Despite his leaning to supernatural causes, Aristotle made some excellent observations in biology and sought to organize them wherever possible. He classified animals according to their mode of life and their structure and knew over five hundred kinds, all Greek; those from other countries he knew only from descriptions. He insisted that the study of anatomy should be comparative, which is a fruitful procedure at the present time. The heart was regarded as the organ of the soul and intelligence; here Aristotle drops behind his predecessor Democritus. Digestion was to him a process of "cooking." Nerves were confused with tendons; the brain was thought to be cold and the spinal cord hot. Fleas and mosquitoes were held to arise by spontaneous generation out of putrefying substances, while other insects originated through sexual reproduction. His descriptions of the embryonic development of animals, mostly the chick and certain marine forms, are rather accurate. He devised an ingenious scheme of heredity and regarded temperature as a sex-determining agent. He believed that the future of a man could be read from the lines of his palms and that flat-footed people have treacherous dispositions. Indeed, a curious mixture of truth, error, and superstition!

Aristotle's greatness in biology lay not so much in his discoveries as in the fact that he devised a system of thought that dealt with the entire realm of living things. He has long been credited with insisting upon the inductive method, in accordance with which one first collects facts and then draws conclusions based upon them. Other philosophers had been prone to reach a conclusion first and then to decide what the facts must be to accord with the adopted principle. Aristotle did more than urge the inductive method, he used it—part of the time. In general, his work in natural history followed this method. For his scheme of the universe, however, he had not enough facts at his disposal, and here he drew upon fancy. As a consequence, his concept of the cosmic system had what modern biologists consider a serious fault in that it called for the guidance of nature by an outside intelligence. Democritus had come nearer than he to the modern scientific view in that he postulated a natural necessity which determined the course of events; but Democritus had no inclusive theory relating to living things in particular.

Pliny.—At the time of Aristotle's death, Greek culture was already declining, so that the accomplishments of this naturalist-philosopher represent the highest attainment of antiquity in most fields of science. His successors and followers include Theophrastus, generally regarded as the founder of botany, and a number of others by none of whom was any notable advance made. Specilized phases of biology fared a little better, particularly anatomical studies at Alexandria.

Rome did not advance far until a much later time. Her chief biologist of this period was Pliny (A.D. 23–79), who is best known through his "Natural History" of 37 volumes. This work was a curious compilation of all the stories of nature which the author was able to gather. Nothing appears to have been rejected, so that fantastic fables abound, along with reliable accounts of the habits of animals, their utility, the particulars of cattle husbandry, etc. Pliny had recourse to two thousand books in the preparation of his "Natural History," and for fifteen centuries thereafter this work supplanted all of them in the popular mind as the source of information regarding natural objects. The author did not, however, add anything of importance to the store of knowledge by his own observations.

Galen.—Rome, though succeeding to a dominant position in world affairs, did not foster learning in scientific fields. Instead of an intellectual revival during her period of prosperity, there was a notable decline. Pliny lived in the midst of this decline. The last great biologist of antiquity was Galen (131–210?), a physician living in Rome but of Greek parentage. He dealt mostly with human anatomy and reveals a profound admiration for the creator of so marvelous a mechanism. Every organ had its use and was constructed on the plan best calculated to serve that end. He was obliged to study these organs mostly in other animals, for dissection of human bodies, once permissible, was in Galen's time forbidden. When he describes the human hand, it is obvious that the object before him is the hand of an ape. His errors are mostly traceable to this necessity of using other animals.

His accomplishments are numerous, such as his proof that the arteries and the left side of the heart contain blood, instead of air as others supposed, and his inference that the arteries and veins must be connected. He seems not to have been fully appreciated in his own time, yet Galen's books were for many centuries thereafter the standard of reference. They were used in the medical schools, where anatomy was taught from the desk with little or no demonstration, and modern criticism has given to him a high measure of praise.

The Dark Ages.—The thousand years and more following Galen's time constitute the dark ages for biology as for other fields of learning. Among the Arabs, who were dominant in the East, mathematics, astronomy, and chemistry made some advance, but writings in the field of biology were mostly commentaries on the works of Aristotle and of Galen. The division of the Roman Empire and the ravages of migratory peoples in the West were not conducive to learning. Universities arose beginning about the eleventh century, but these came to be controlled by religious orders. The churchmen, finding a powerful ally in Aristotle's conception of the earth as the center of the universe and his belief in a dominating intelligence directing natural phenomena, turned the reverence in which ancient philosophy was held to their own advantage. It took little guidance from them to ensure that biological inquiry should consist merely of commentaries on the writings of Aristotle, with no effort to ascertain facts afresh. The views of the Greek natural philosopher were accepted as correct even where simple observations could easily have proved them wrong. The few books about animals which appeared in this era, aside from the commentaries mentioned, contained only entertaining stories and notes on the usefulness of animals to man.

To deliver biology from the dominance of Aristotle, it was necessary to destroy his system of thought. Aristotle, as was pointed out earlier, based his theory of a universal order on an outside intelligence which directed the transformations of matter. This outside intelligence was naturally not subject to inquiry, and it was this feature of the Aristotelian doctrine which won to him the support of the conservatives of the Middle Ages. The uprooting of this system of thought required time, and it was not until the seventeenth century that other well-defined systems of philosophy replaced it. In the meantime biology was struggling up out of the inaction of the Middle Ages, through the period of the Renaissance.

The Revival.—In the early part of the period of renewed interest in learning, several works on natural history appeared, which showed they

FIG. 3.—Andreas Vesalius, 1514–1564. (*From Garrison, "History of Medicine," W.B. Saunders Company.*)

were based in part upon observations made by their authors. The leadership in the revival, as far as it concerned biology, was taken by Andreas Vesalius (1514–1564) (Fig. 3), an anatomist. Born at Brussels, he went to Paris at the age of eighteen to study medicine and there showed great independence and force of will. After several years of practice he was called to the University of Padua, in Italy, where everything was favorable to his work. In his teaching he first followed Galen but soon found the latter incomplete and in places self-contradictory. He then realized that he must teach from his own observation and, to make this possible, published two anatomical works which were masterpieces. His overthrow of Galen infuriated conservative anatomists, including Vesalius's revered teacher Sylvius, himself an anatomist of high reputation. Vesalius was charged with all sorts of crimes, from being godless and sordid to dissecting men alive. This persecution finally drove him to resign his professorship, after which he was physician to Emperor Charles V. Upon the succession of the less liberal Philip II, Vesalius found small opportunity for creative work. He left the court and tried to regain his old post at the university but died on a journey to Jerusalem before the appointment was made. His ideas of anatomy, and particularly of the functions of the organs, were not wholly correct. Some of them were borrowed from Galen, whom he still admired, and now seem absurd. His great contribution was his overthrow of authority and his return to firsthand observation as the basis of knowledge.

FIG. 4.—William Harvey, 1578–1657. (*From Garrison, "History of Medicine."*)

Harvey and the Circulation of the Blood.—One of the sharpest reactions against the authority of antiquity, and one of the most hotly contested, was the recognition of the circulation of the blood. Against the prevailing early view that the arteries conveyed air, Galen had held that they carried blood; but he was never clear how the arterial blood became converted into venous blood, and in the veins he definitely supposed the blood to flow in both directions alternately. His views on this question were still accepted in the sixteenth century.

The first recognition that the entire course of the blood is a circulation is found in the works of William Harvey (1578–1657) (Fig. 4), of England. He proved that the wall of the heart is muscular and that its contraction drives the blood forward into the arteries; in the old theory the heart was regarded as passive. By a simple calculation he demonstrated that the quantity of blood passing through the heart in a very short time exceeded the weight of the whole body and reasoned that new blood could not be produced at such a rate. He showed by the swelling of the veins below a ligature, and by the point of exit of blood at a wound, that blood flows toward the heart in veins and away from it in arteries. He concluded as a logical necessity that there must be a connection between arteries and veins, but without a microscope he could never visually demonstrate the capillaries.

Besides correcting an ancient mistake, Harvey performed a service to biology in making it an experimental science. While others before Harvey had occasionally used experiments, he gave the method a strong impetus. But while Harvey was modern in his method of solving problems, at the same time his concept of life and its manifestations in general was no more advanced than was that of Aristotle.

The Seventeenth and Eighteenth Centuries.—The two centuries following Harvey mark a distinct phase in the development of biology. The lethargy of the Middle Ages had been definitely cast off, and the spirit of inquiry was again prevalent among intelligent people. Two

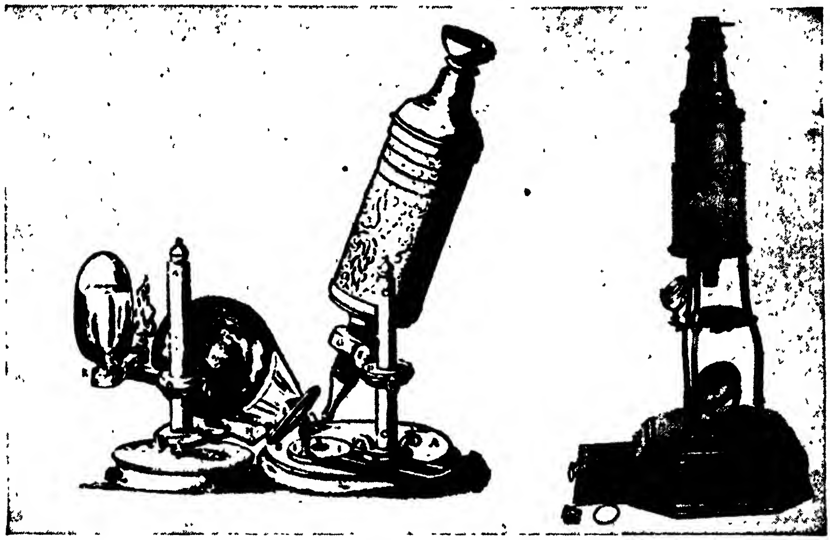

Fig. 5.—Two early microscopes. Left, that used by Robert Hooke; right, from eighteenth century. (*From "Educational Focus," Bausch & Lomb Optical Co., and American Museum of Natural History.*)

general concepts of natural phenomena arose, one of them mechanistic, the other mystical; and the history of biology ever since has been in part a conflict between these two systems of thought, with the former steadily gaining ground. The science of chemistry was coming to the aid of biology by enabling physiology to seek for purely mechanistic explanations of life processes. Following Harvey's proof of the circulation came the dicovery of the lymphatic system of vessels carrying digested food from the intestines to one of the larger veins. The nervous system was more thoroughly studied, and the functions of the divisions of the brain began to be understood. The contraction of muscles was explained by fermentation—incorrectly, but it is significant that the role of chemistry in living matter was recognized. However, the early advances were mostly in the field of morphology, the science of structure.

The Microscope.—One important aid to the mechanistic theory of living matter was the invention of the compound microscope. The refractive power of glass had long been known, and simple lenses had come to be used in the sixteenth century for spectacles and as scientific toys. The combination of two or more lenses in a tube to form a compound microscope is generally attributed to Zacharias Jensen and is said to have been first used about the year 1591. During the following century considerable improvement of these instruments was effected. An early microscopist, Robert Hooke (page 15), described the one at the

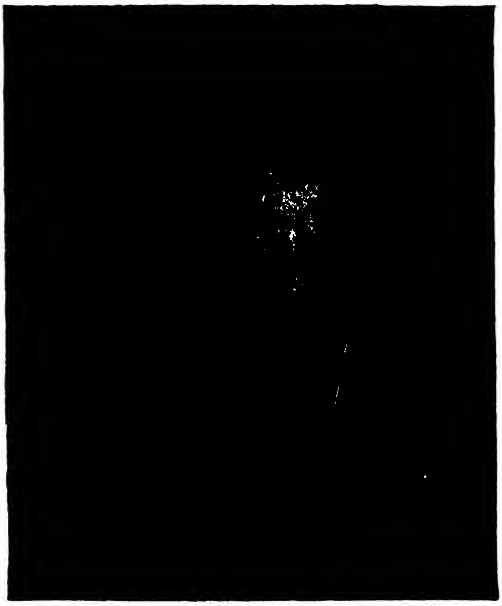

FIG. 6.—Marcello Malpighi, 1628–1694. (*From Garrison, "History of Medicine," after the painting by Tabor, Royal Society.*)

left in Fig. 5, while a moderately improved one is on the right. Almost no further improvement was made thereafter for a century and a half.

The founder of microscopic anatomy was Marcello Malpighi (1628–1694), of Italy (Fig. 6). He studied the lungs and observed the capillaries, thus confirming the theory that blood circulates through them. He also examined various glands, the embryo of the chick, the structure of the silkworm, and the tissues of plants. His work on plants was extensive, and, with Nehemiah Grew (1628–1712) of England, he became the founder of plant anatomy. Anton van Leeuwenhoek (1632–1723) (Fig. 7), of Holland, stepped out from behind his dry goods and notion counter often enough to become one of the most skillful of the makers of lenses; one of his lenses, still in existence, magnifies two hundred and seventy times. He made these for his own use, never sold one, and never loaned one. Everything that could be observed with a microscope became an object of his study. The biological objects included were the blood capillaries, red blood cells, spermatozoa (male germ cells), striated muscle, the crystalline lens of the eye, the eggs of insects, and minute organisms in pond water. Another Dutchman, Jan Swammerdam (1637–1680), besides some work on gross anatomy, studied the minute anatomy of insects and snails and the development of the eggs of various animals. Microscopes existed in America in the seventeenth century, but no important use of them in biology appears to have been recorded.

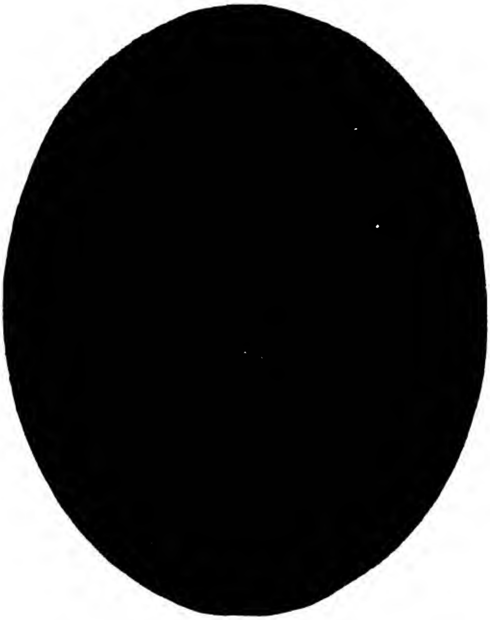

Fig. 7.—Anton van Leeuwenhoek, 1632–1723. (*From Garrison, "History of Medicine."*)

Classification of Animals and Plants.—One of the early trends away from structure was the series of attempts to classify living things. Efforts to systematize the listing and arrangement were made in very early times by Plato and Aristotle. These were very simple; Aristotle mentions by name only two ranks, which correspond roughly to the species and family of our present classification. When the great geographic discoveries of the sixteenth and seventeenth centuries were made, and many new animals became known, such simple groupings were of little use. The first classification worthy of note was that of John Ray (1627–1705), in England. Ray's idea of the species was very similar to that of the present time. He grouped similar species into a genus, but his genera were much more inclusive than at present. Anatomical likeness was the basis on which species were grouped together, though he allowed old prejudice to prevail in some cases, as when he included the whales with the fishes despite his knowledge that they more closely resemble the mammals.

It was Carolus Linnaeus (1707–1778) (Fig. 8), however, who made the greatest advance in classification. Of a Swedish family and trained to be a physician, he yielded to his interest in natural history and was eventually named professor of botany in the University of Uppsala. He had a passion for arranging all sorts of natural objects into groups on the basis of like qualities. The choice of qualities to form the basis of this classification was sometimes arbitrary, especially in his earlier years, as

FIG. 8.—Carolus Linnaeus, 1707–1778, in Lapland dress at the age of thirty. (*Courtesy of New York Botanical Garden.*)

when he classified plants according to the number of stamens and pistils in their flowers. In later life he recognized that likeness in a single character, in the absence of other similarities, was not a safe ground on which to group organisms. He followed Ray at first in assuming that species have now the characters with which they were created, and in general he held to the "fixity" of species. Yet in his later writings he questions whether the several species belonging to one genus may not have evolved, by change, from a single origin in creation. One of Linnaeus's greatest services was the introduction of two terms in the name of a species—the first the name of the genus, the second that of the species—a method which is used at the present time. It was fully developed in his great work, the "Systema Naturae," in which all the animals and plants which Linnaeus knew are described and named. So accurate are the descriptions that many of his species are recognizable today, and his names for them are still applied.

Foundations of Modern Biology.—Naturalists of a certain stamp have always found the classification of objects a fascinating occupation, and Linnaeus had many followers. For the most part they were less able than he, and their labors often degenerated into an attempt to discover and name as many species as possible. Because of this tendency, classification suffered a degree of disrepute. Moreover, there were many other features of living things to engage attention. Discoveries were made and theories formulated in nearly all the fields of biology. The physiology of sense organs and the nervous system was studied. Embryology, the science of development of the individual, was greatly advanced. The process of fertilization of eggs by spermatozoa came gradually to be understood, and it was found that some eggs could develop without the intervention of the male cells. The existence of sex in plants was recognized, and some crosses were made to ascertain the course of heredity. Mutilated animals were observed to regenerate their missing parts. Comparisons of the structure of various animals foreshadowed the comparative anatomy of the next century. The behavior of the castes of social insects was studied, marking the beginning of animal psychology. In the sister science of chemistry, the nature of oxygen and carbon dioxide was discovered, and naturalists began to see their relation to the respiration of animals. Vague ideas of change of species, implying concepts of evolution, began to be put forth.

With this increase in the factual phase of biology, philosophy declined; and with the rising tendency to limit theory to what could be reasonably supported by the ascertained facts, biology entered upon what may be regarded as its modern period. This period corresponds roughly to the nineteenth and twentieth centuries. It witnessed the rise of comparative anatomy, the discovery of cells, the development of embryology and cytology, the general acceptance of the evolution doctrine, the rapid increase in the use of the experimental method, research in heredity, the study of the general physiology of protoplasm, and specialization in several of the narrower fields of biology.

Comparative Anatomy.—The earliest well-defined modern trend was in the field of comparative anatomy. The founder of this branch of biology was Georges Cuvier (1769–1832) (Fig. 9). Cuvier possessed a natural interest in living things and, being a clever draughtsman, had made pictures of many of the animals he studied. Some of these pictures, exhibited in Paris, won him a professorship of comparative anatomy there. His rise was rapid, and numerous honors were bestowed upon him. Cuvier's comparative anatomy differed from all previous brands in that the standard of comparison was not man but the lower animals. He had begun his biological career by studying marine animals; and, while he later went over almost wholly to the vertebrates, he never, as did the medically trained anatomists before him, adopted man as the starting point for comparison. Paleontology also traces its origin to Cuvier, since his comparative studies were extended to fossils, especially to the elephantlike forms, the mastodons.

It is curious that Cuvier, who was forcibly brought face to face with the evolution theory, never saw fit to embrace it. His discoveries in comparative anatomy are now regarded as indicating kinship of various

FIG. 9.—Georges Cuvier, 1769–1832. (*From Locy, "Biology and Its Makers."*)

animals, and the fossils he studied clearly demonstrate that living things of successive ages were of very unlike kinds. Cuvier chose to explain these successive types of beings by catastrophes, which destroyed all life, and subsequent recreation of new kinds of beings. He was not merely passive in rejecting the evolution doctrine but actively opposed it. In a series of discussions participated in by him and Geoffroy St. Hilaire before the French Academy of Sciences in 1830, his opposition was repeatedly stated. Cuvier, who was an excellent debater and very influential, was then generally held to have won this debate.

The Cell Theory.—The comparative method of study was applied to smaller and smaller objects as rapidly as means of doing so were available. Further progress in the improvement of the microscope (such as the first production of achromatic lenses about 1827), after a period of nearly a century and a half in which little change took place in these instruments, led to the discovery of the universal occurrence of cells. The credit for this discovery belongs to no one person. Hooke had seen the boxlike cavities in cork in 1665, and Malpighi observed those of other plant tissues in 1670. Lamarck and Mirbel taught, early in the nineteenth century, that plants and animals are composed of "cellular tissue." The nucleus was sporadically seen and in 1833 recognized by Brown as of regular occurrence in plants. His observation was verified by Schleiden, and Schwann (Fig. 10) extended it to animals. The universal occurrence of cells in living things was recognized by Dutrochet and Purkinje (Fig. 11),

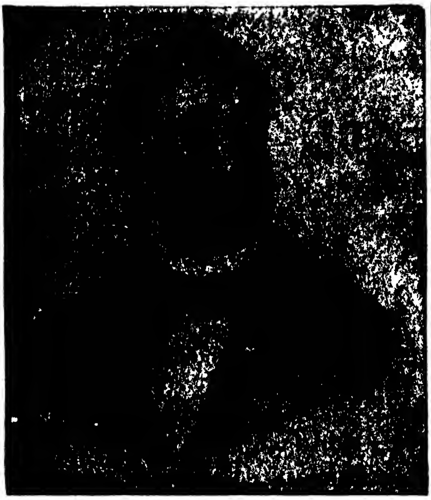

FIG. 10. FIG. 11.

FIG. 10.—Theodor Schwann, 1810–1882. FIG. 11.—Johannes Evangelista Purkinje, 1787–1869. (*Both from Garrison, "History of Medicine."*)

and a formal statement of that universality was published by Schwann in 1839. Knowledge of the nature of cells was gradually accumulated through the work of various biologists, culminating in the convincing proof by Max Schultze, about 1861, that the essential feature of living things is the jellylike substance called protoplasm, which was at first regarded as merely incidental.

This knowledge of cells had a profound influence upon further advances in morphological biology. The study of tissues, begun several decades before, now became a study of like cells grouped together. Embryology was pushed back to the very beginning of development, to the egg cell, and the so-called germ layers (of cells) in the embryo of the chick were discovered. Unfortunately, knowledge of the minute structure of cells was not sufficient until much later to influence physiological work appreciably. The theoretical and natural history phases of biology also went on quite unaffected, for the time, by cell discoveries.

Modern Physiology.—*Physiological investigations* were much more dependent upon the advances being made in animal chemistry than upon cell studies. Knowledge of the composition of all sorts of animal structures was strengthening the belief that life is a group of chemical phenomena. Studies of function necessarily made use of the experimental method, which once more became one of the most valuable tools of biology. One of the leaders of this period in physiology studied the

FIG. 12.—Jean Baptiste Lamarck, 1744–1829. (*From Locy,* "*Biology and Its Makers*" *and Thornton,* "*British Plants.*")

processes of nutrition (particularly the role of the liver), the production of sugar in animal bodies and the influence of the central nervous system upon this process, the secretion of the pancreas, and the effects of poisons. Another studied sense perception and the function of different kinds of nerve cells, while a third worked on reflex actions. But all this was done without particular reference to cells. It was only much later that the physiology of the cell was recognized as lying at the foundation of all physiology.

Evolution.—Another of the great developments of the nineteenth century which occurred quite without reference to the knowledge of cells was the growth of the evolution doctrine. The idea of evolution, or change of species, was briefly and crudely stated or suggested in the writings of the early Greeks, Empedocles in particular. Linnaeus, in the eighteenth century, betrayed a slight leaning to the possibility of evolution in his later writings when he conceived that the species belonging to the same genus might have had a common origin. His contemporary, Buffon, speculated more openly upon the origin of the various life forms and was unwilling to accept the notion of independent creations. It was not until the time of Lamarck (Fig. 12), however, that any general theory of evolution was proposed. Lamarck observed the great variation exhibited by animals and conceived that it was due to the effects of use or disuse of the various organs by the animals. He supposed that the changes thus induced were inherited, thus becoming permanent—a view that has been

FIG. 13.—Charles Darwin, 1809–1882. (*From University Magazine. Photograph by Leonard Darwin.*)

abandoned by most biologists since then. These views of Lamarck were expressed most fully about 1809, at the beginning of what may be regarded as the modern period in biology. As has been pointed out in an earlier section, Cuvier opposed the evolution doctrine, notably in the series of discussions in the French Academy of Science in 1830, and his great personal influence determined the attitude of French biologists toward the new doctrine.

It was in another land, therefore, that the chief modern development of the evolution idea had its origin. To Charles Darwin (1809–1882) (Fig. 13), of England, is due the credit of convincing the thinking world that change of species has taken place throughout the whole history of living things. This he did partly by marshalling such a mass of evidence in favor of evolution that there was no rejecting it, partly by devising a theory—natural selection—to account for it, so plausible that acceptance of the fact of evolution was rendered easy. Within a few years of the publication of Darwin's "Origin of Species" in 1859, the supporters of the evolution idea far outnumbered its opponents in intellectual circles. Naturalists everywhere were busy finding examples of apparent evolution and striving to fit the observed facts into the natural selection theory. The whole course of development of biology was modified by this prevalence of evolutionary speculation during the two or three decades after 1859.

Not all discussions of evolution were wholly speculative; some were founded on detailed facts which were gained by hard labor. An example is the expansion of work in comparative morphology in Germany. This science became distinctly evolutionary; the comparisons were made with an eye to kinship and became some of the most important of the evidences of evolution. Embryology, too, profited by the idea of kinship of animal forms and in turn furnished much of the evidence on which the evolution theory is based. Only among the French, of the great intellectual peoples, was the acceptance of the evolution doctrine long delayed; and when the idea finally triumphed there, it was rather in the form proposed by their countryman Lamarck (as a consequence of use and disuse) than in the Darwinian form (as guided by natural selection).

Genetics.—In one respect in particular did enthusiasm for the evolution theory overreach itself. Since evolution can consist only of *hereditary* variations, it would be supposed that any information regarding the phenomena of heredity would be promptly seized upon as of importance to evolution. Darwin himself did strive to learn from practical breeders and others what was known of these phenomena. His feeling of their importance was not shared sufficiently by biologists in general, so that when in 1866 Gregor Mendel (Fig. 14), an Austrian monk, published some experiments dealing with inheritance in garden peas, they attracted no attention. Mendel's work lay unnoticed until 1900. By that time the ardor of the natural selectionists had cooled enough that the futility of attempting to discover the course of evolution by speculation alone was duly recognized. Realizing that in a knowledge of heredity lay the best hope of explaining evolution, various biologists had resumed the study of inheritance by means of experiments. Plants, being simplest, yielded the first results, and in 1900 three European botanists, working independently, published at about the same time accounts of their crosses, from which they derived the same conclusion as Mendel had derived before them. Fortunately they also discovered Mendel's old paper. These experiments were capable of being explained in so simple a manner that a great impetus was given to the experimental study of heredity. Hundreds of plants and animals have been shown to follow the fundamental rule laid down by Mendel. His principles have undergone some modification, as a result of the investigations of T. H. Morgan and others, so that the known operations of heredity are no longer so simple as Mendel's statement. Further complexities are still being discovered, but with few exceptions they form a harmonious whole, and genetics at the present time approaches more nearly the condition of an exact science than any other division of biology.

Fig. 14.—Gregor Johann Mendel, 1822–1884. (*From a photograph taken about* 1880. *Reproduced from the report of the Royal Horticultural Society Conference on Genetics*, 1906, *by permission of the President and Council.*)

Cytology.—The handmaiden of genetics in all this advance has been the science of cytology, which deals with the very small structures of the cell. Advance in this field beyond the stage to which Max Schultze brought it has depended upon further improvement of the microscope, the discovery of dyes or stains by which these minute objects could be made more readily visible, and the invention of mechanical devices for cutting cells into very thin sections. These improvements in technique led early to an understanding of cell division (in the eighteen seventies) and later of the ripening of the germ cells. While cytology has been concerned with all sorts of cell structures, the chromosomes, minute objects in the cell nucleus, have long been regarded as of chief importance. It is the chromosomes that have allied cytology so closely with genetics, for the machinery of heredity is found in the chromosomes. At first, in this alliance of genetics and cytology, the latter took the lead. Chromosomes were observed (1880–1910) to behave in certain ways before their genetic significance was understood. Later the order of discovery was reversed; the demonstrated workings of heredity required that the chromosomes should operate in a certain manner, and in many cases their behavior has been subsequently found to coincide with the theoretical expectation.

General Physiology.—While stains, smears, section-cutting apparatus, and improved microscopes have been the traditional tools of the cytologists, recent work in that field has dealt with living cells and has included minute dissection of cells by means of ingenious devices which can be operated under the microscope. This phase of cytology borders closely upon general physiology, which deals with fundamental activities of protoplasm. General physiology is concerned with chemical composition and reactions of living matter, permeability, viscosity, colloid structure, electrical charges, transformations of energy, etc., in an attempt to relate these conditions or processes to the phenomena of life. The material used in such studies is partly a host of one-celled organisms, partly the eggs of various aquatic forms, and partly the specialized masses of cells, or tissues, of higher animals. Although these cells differ much in appearance and in their ultimate fate, they must do certain fundamental things in common. It is in the province of general physiology to discover these common processes. This development is comparatively recent, and a large number of biologists at the present time are engaged in this type of work.

Change in Content of Biology.—It will have been observed that throughout the development of biology, from the early Greeks to the present time, the bulk of what was known regarding living things concerned their structure. This branch of biology is known as *morphology*. At first little else was known, and in the Middle Ages the continuity of biology hung on the one thread of anatomy. Only gradually did the functions of organs come to be of much interest, and William Harvey, in the seventeenth century, is often regarded as the founder of *physiology*. At first a study of mechanics, physiology later became concerned with the principles of organic chemistry. Attempts were made to apply these principles not only to the workings of the organs of the adult but to the processes of embryonic development. Embryology thus became physiological as well as morphological, and modern work in embryology is chiefly of the former kind.

Simultaneously with physiology there grew up the science of classification, or *taxonomy*. At first, as developed by Linnaeus, classification was arbitrary. Though similar animals were grouped together, their similarity was not held to have any significance. A century later, when evolution was generally accepted, the basis of taxonomy came to be kinship.

Similar animals were grouped together because they were believed to be related through common descent. Concepts of evolution and hence of taxonomy were altered in quite recent times by increasing knowledge of *genetics* which lies at the foundation of both of the sciences just named.

These five sciences, morphology, physiology, taxonomy, evolution, and genetics, are the main fundamental divisions of pure biology. Because they are all concerned with living things, they necessarily overlap. Evolution and genetics have much in common, as have both with taxonomy. Physiology and morphology are not wholly separable, since function cannot exist apart from structure. Yet there is considerable independence among them. It is possible to study morphology without being concerned with the function of the structures involved. One may study genetics without knowing or caring what bearing the discovered facts have on evolution. Taxonomy may—and did for a century—proceed without any relation to evolution, even though that kind of taxonomy would be regarded now as without significance.

Composite Biological Sciences.—There are several divisions of biology, however, which do not possess this degree of independence, but which are only special phases or combinations of the five named above. One of these is *paleontology*, the science of extinct animals. Paleontology is only a specialized form of zoology, limited in its scope because it is concerned only with fossil types, not with living animals. It deals largely with morphology, chiefly of external features, though internal anatomy is sometimes preserved in fossils. Taxonomy is quite feasible in paleontology, since external form of fossils, taken in connection with similar kinds of living animals, is sufficient to indicate probable kinship. Evolution is clearly shown by the differences between fossils of successive geological periods. However, the physiological processes of extinct animals can only be inferred from their structure, and knowledge of genetics is impossible in the absence of detailed comparisons of parents and offspring. Paleontology is thus a limited sort of zoology.

Ecology, which is a study of the relation of living things to the environment, is likewise a composite of the fundamental biological sciences. The ecologist strives to discover in what ways organisms meet the conditions imposed by the world around them. He learns in what situations animals live, and why they are there. He studies the interplay of processes within organisms and processes occurring outside. To some extent this relation to the environment is purely structural; very largely it concerns function. So far as ecology concerns the organisms themselves, therefore, it is but a combination of morphology and physiology. The other things with which ecology has chiefly to deal concern the organization of the environment. This latter phase of ecology is not really biology at all, except as the environment of one animal is made up of other living things; but it is as essential to ecology as is a knowledge of physics and chemistry in general physiology.

Somewhat related to ecology is the geographic distribution of animals, or *zoogeography*. Ecology relates partly to local distribution of organisms, as determined by environmental conditions. Zoogeography also involves these questions of local distribution, since no species can live where the conditions are not suitable, and wrong conditions constitute barriers to distribution. However, no kind of animal is found in all the places on the earth where conditions suitable for it exist. The absence of a species from some regions entirely capable of supporting it is accounted for by such things as the place where the group originated and the time of its origin. These things are historical; ecology has nothing to do with them, but they are an important part of zoogeography. The latter science is therefore morphology and physiology, as far as the fitness of species to occupy certain regions is concerned; and it is evolution and geology whenever absence from a given region is explained by the time or place of origin of the species.

Too much emphasis should not, however, be placed upon the clearly composite nature of these several biological sciences. All the divisions of biology overlap to some extent; indeed, the unity of them all, which makes them biology, would not exist but for such overlapping. Plants share this unity with animals. There is a morphology, a physiology, a taxonomy of plants. These sciences differ from the corresponding ones for animals in the objects with which they deal, but not greatly in the principles involved. Each of the other divisions of biology discussed above relates to plants as well as to animals. It is traditional to separate botany from zoology, but there is scarcely more difference between plants and animals as they relate to one of these sciences than there is between some of the more extreme animals.

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CHAPTER 2

PRIMARY ORGANIZATION OF LIVING MATTER

No feature of organisms has so many and such varied consequences as the fact that they are composed of protoplasm which is usually arranged in the form of cells. If a bit of animal tissue, cut thin, be it from muscle, gland, skin, brain, or sense organ, is examined under a microscope, it is found to be blocked off in small areas, all of which resemble one another in certain respects and some of which are alike in a great many ways. These are the cells. We have seen (pages 14, 15) how the existence of cells gradually became known, and how much this discovery influenced work in different fields of biology. The authors of the cell theory, as it was first formulated, were content to claim that all things are composed of these units. Its immediate effect was therefore only on the structural side of biology, as has already been related. Had the theory developed no further, it would have continued to affect only morphology. When, however, the chemical and physical composition of the protoplasm was studied, and when the minute structure of the parts of the cells began to yield to the microscope, it became apparent that the existence of cells was highly important in physiology, heredity, and evolution. A knowledge of cells therefore lays a foundation for much of the rest of biology.

The Size of Cells.—It is surprising to find how much difference there is among cells with respect to size. The radius within which the various activities of cells must occur should be of some significance. Each cell consists typically of a *nucleus* lying within a bit of protoplasm which is the cell body or *cytosome.* Important reactions take place between the different parts of the cell. Since the nearness of these parts to one another must influence the ease with which they work together, the size of the cell should be of some importance. Yet cells show very great differences in this respect. Some bacteria are so small as to be almost invisible even with a good microscope; somewhat larger are most tissue cells, which are quite easily seen when thus magnified but cannot be seen without such aid; but all these are topped by the egg yolks of the larger birds, which are 2 or 3 inches in diameter. Nerve cells often have great length, particularly those which extend from the spinal cord to the ends of the extremities in man or the other large mammals, but are quite slender. Sometimes these great differences in size fit the cells for their particular functions, but in most cases no such explanation is known. When cells that are presumably alike in their origin and function show great differences in volume, as when one unicellular animal (Paramecium, for example) is several hundred times as large as another of the same species (Fig. 15), it is probable that differences in the environment have caused part, though not all, of the contrast.

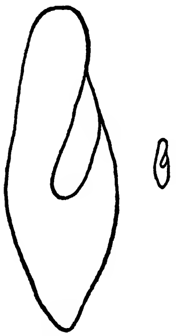


Fig. 15.—Extreme difference of size in otherwise similar cells; two members of same species of Paramecium, one 300 times as large as the other.

The size of cells bears no constant relation to the size of the animals or plants in which they are found. In very many kinds of animals, large individuals have more, but not larger, cells than do small ones. In others, the number of cells in each individual is always the same, and in them large size is attained only by the growth of each cell. In salamanders in which, through some abnormal step in cell division, the cells have extra chromosomes, the cells are larger but the body is not: such animals simply have fewer cells. Sluggish animals like frogs generally have larger cells than active ones such as birds, and there is presumably some important connection between these facts.

Gross Shape.—The shape of cells is also very variable. Some cells, owing to surface tension, are typically spherical; but that shape is attained, even approximately, only in free cells, such as eggs and a few of the one-celled organisms. Cells take on other forms for various reasons. Amoeba and other related protozoa may actively change their

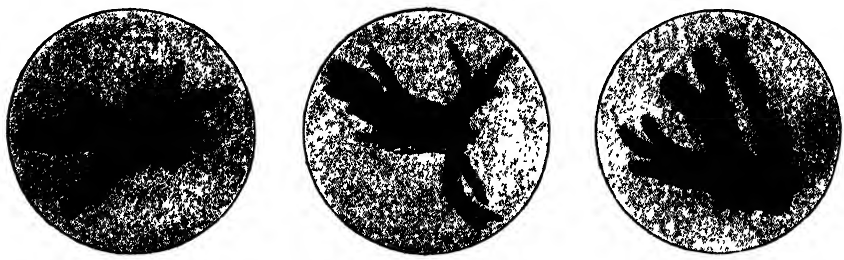
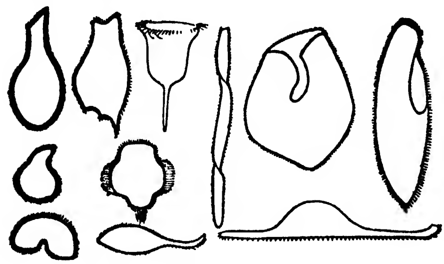


Fig. 16.—Change of shape in amoeba. Half-minute interval between first and second, five minutes between second and third. (*Courtesy of General Biological Supply House.*)

shape by thrusting out portions of the body into fingerlike pseudopodia. Such an animal is seldom of the same shape for any considerable time (unless it goes into a "resting" state, in which it is apt to be nearly spherical), and it may even be changing every instant (Fig. 16). Other free-living cells, of more or less constant form, are kept constant by a wall or pellicle that the cells themselves have secreted (Fig. 17). These pellicles may be flexible but firm, so that while the shape of the body may become temporarily distorted it is characteristic of the species.

Cells that exist in groups usually have their form altered by the mechanical pressure of the cells around them. When this pressure is the only factor altering their shapes, the cells are irregular polyhedrons. Other factors, such as unequal growth in different directions and perhaps inequalities of surface tension, combine to produce cells of a great variety of shapes. They may be box-shaped, as in plants; long cylinders, as in voluntary muscle; greatly flattened cells with their largest sides polygons, as in the outer layer of frog skin; somewhat flattened elliptical cells, as in the blood of many animals; circular and flattened, as in human blood; narrow and spindle-shaped, as in involuntary muscle; or finely branched,



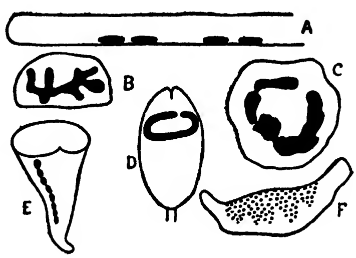


Fig. 17. Fig. 18.

Fig 17.—Various forms of ciliated protozoa whose body shape is kept fairly constant by a surrounding pellicle. Though this shape may be altered by pressure, it is restored when the pressure is removed. Cilia project from the surface.

Fig. 18.—Various forms of nuclei in cells. *A*, part of muscle cell with multiple ellipsoidal nuclei; *B*, gland cell of butterfly with branching nucleus; *C*, marrow cell of rabbit with ring nucleus; *D*, Epistylis with curved rodlike nucleus; *E*, Stentor with beaded nucleus; *F*, Trachelocerca with distributed nucleus. (*B, C, and F after Wilson, courtesy of The MacMillan Company.*)

as in pigment cells of the skin of frogs and salamanders, or bone and nerve cells.

The Nucleus.—The most important part of a cell is its nucleus. This body is ordinarily located somewhere near the middle of the cytosome but may be crowded to one side by other structures and may move from one place to another. It is most often spherical, owing to the tension of the very thin film, or *nuclear membrane*, which surrounds it, but other shapes may be impressed upon it or it may actively take other forms. In long narrow cells the nucleus is generally elongated (Fig. 18*A*), and in flat cells it is disk-shaped. Physiologically very active cells often have branched or lobed nuclei (*B*, *C*); and in certain unicellular organisms the nuclei may be of odd shapes—ropelike, beaded, or broken up into many small bits (*D–F*)—characteristic of the species but without any known significance. The red cells of human blood are devoid of nuclei, a condition generally held to be due to degeneration of the nuclei which they possessed in young stages.

The importance of the nucleus derives from a substance known as *chromatin* which it contains. This substance, as will appear in later chapters, exercises some control over physiological processes, development, and heredity. It owes its name to the fact that it colors deeply in most ordinary dyes such as are used by cytologists to make it conspicuous enough for study. The chromatin is collected into a number of distinct masses, the *chromosomes*, but these bodies are so diffuse in their structure that they cannot usually be recognized as separate objects except at the time of cell division. During the periods between cell divisions one common form in which chromosomes exist is that of distended bags, the walls of which contain the chromatin itself, while the interior is filled with a

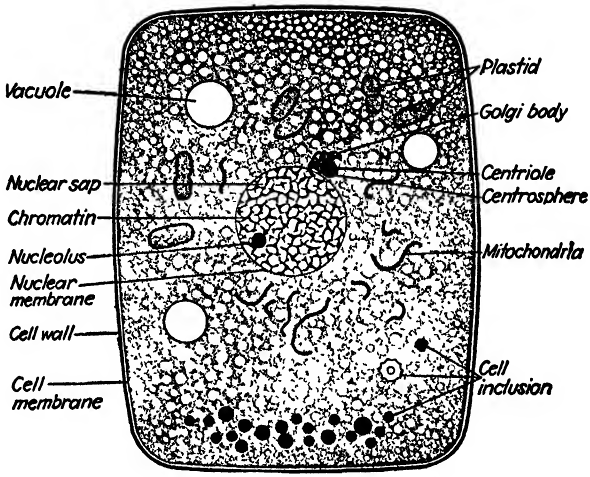


Fig. 19.—Generalized cell.

semiliquid substance called the *nuclear sap*. The chromatin is thus greatly thinned out, though quite irregularly so, for there are little knots and branching strands of it thick enough to be seen when stained. Some chromosomes are shown in Fig. 38 (page 59), gradually experiencing this expansion at the end of cell division. When the chromosomes in this distended form are packed closely together in a nucleus, it is usually quite impossible to see the outlines of the chromosomes, but the knots and strands of thicker chromatin are visible, together giving the appearance of a network (Fig. 19). In other cells the chromosomes appear to be in the form of branched threads rather than bags, but the resulting appearance of the nucleus is still that of a chromatin network whose spaces are filled with nuclear sap.

Some nuclei contain, in addition to the sap and the network of chromatin, a *nucleolus*. Two or more nucleoli may be present. They are rounded bodies that stain readily, but in a manner different from the chromatin. Nucleoli are therefore not to be confused with bunches of chromatin, which have sometimes been called nucleoli. The nature and function of the nucleolus, when it is present, are not understood. Some biologists have regarded it as a waste product; others have held it to be a reserve supply of materials used in cell division, since it disappears during that process; and it has been regarded as a reserve food supply for the nucleus.

The Cytosome.—The body of a cell is seldom uniform in composition but includes a number of different structures. The more common ones are here described, though very few cells have all of them. At the surface there may be a definite *cell wall* which is lifeless, not composed of protoplasm but secreted by the cell. It is very common in plants, where it is composed mostly of cellulose, one of the principal components of wood. Some animal cells have such a lifeless covering, but in them it is often made of other materials. Sometimes the cell is covered by a much thinner and more flexible coat, the *pellicle*, as are the cells of Fig. 17. Beneath the cell wall, or at the surface of the cell if there is no other cover, a somewhat firmer layer which may be called the *cell membrane* is formed out of the protoplasm itself in about the same way that water forms a film at its surface.

Within the cytosome, *plastids* are common. In the higher plants they are universal and are usually green. Some are of other colors, as in fruits and flowers, and some are colorless. In animals, plastids are found chiefly in certain classes of protozoa (one-celled animals) where they are mostly colored.

Vacuoles are vesicles of liquid enclosed in the protoplasm. They may be permanent or temporary. In the protozoa, temporary vacuoles are common. They usually either enclose bodies of food in process of digestion, in which case they are called *food vacuoles*, or disappear at intervals by ejecting their liquid contents through the surface layer of protoplasm into the surrounding medium. The latter kind is called a *pulsating* or *contractile vacuole*. In some cells a *centrosphere* is found, usually near the nucleus. It is a mass of somewhat differentiated protoplasm, containing a minute body that stains deeply, the *centrosome* or *centriole*. When present, the centrosphere takes a conspicuous though probably unimportant part in cell division, as described in another chapter.

Structures known as *mitochondria* (Fig. 19) are found in many kinds of cells, perhaps in all cells. They are of various shapes—rods, threads, granules—and occur almost anywhere in the cytosome. Many conjectures regarding their function have been made, but little is definitely known regarding it. An object known as the *Golgi apparatus*, of various forms, often a conspicuous network, occupies various positions, usually near the nucleus and in some cases characteristically near the centrosphere. The function of the Golgi apparatus is still unknown, though there is some indication that it takes part in the process of secretion by gland cells.

Besides all the above structures which serve, or may serve, some function in the cell, and which may therefore be regarded as cell organs, there are often lifeless matters enclosed in the protoplasm. These may be grains of starch, or oil or fat globules, which the cell has produced and which are stored as future food. Or the lifeless objects may be undigested remains of organisms taken as food, or even objects picked up incidentally along with food or otherwise. These nonliving objects may be spoken of as *cell inclusions*.

Polarity.—Beside the differentiations described above, cells may possess another type of organization which is termed *polarity*. One portion is destined to perform certain functions, another portion other functions, even when these portions are visibly alike. In a developing egg one part will become the nervous system and associated sense organs, another part the digestive tract. In the ordinary course of development these parts are not interchangeable. This evident arrangement of parts, as shown by their future activities, is the phenomenon which is called polarity. Examples of polarity are found in the eggs of insects, in which one end of the egg, in some way different from the other end, always becomes the head. Other cells than eggs are commonly polarized. Thus, cells bearing cilia (hairlike projections) on one end are polarized. So also is the connection (synapse) between nerve cells, since nerve impulses travel over it in only one direction. Many gland cells receive materials from the blood on one side and after working them over extrude the product into a chamber on the opposite side. When long slender cells standing on end are crowded together to form a layer covering the surface of some organ, the nuclei of the cells are usually near the lower end. These are all polarized cells. In some cases the polarity is visible; but, before the structures indicating the polarity were developed, there was presumably an invisible difference in the protoplasm. The nature of this organization is not known, and there is much disagreement as to whether it is inherent in the cells or is impressed on them by external circumstances.

Structural Relation to Other Cells.—When cells are free-living and independent, as in the protozoa, they may have little or no influence upon one another. When they are aggregated into masses, as in the multicellular animals, there is always the possibility that each cell may be modified, and its activities guided, by the cells around it. Often such interdependence must follow merely from the diffusion of fluids from cell to cell, or from electric phenomena. In some cases, however, protoplasmic connections extend from one cell to another. These have been demonstrated in the skin of the salamander, are conspicuous in Volvox, and have been described for many kinds of animal cells (Fig. 20). In plants, cell bridges are usually present, the fine protoplasmic filaments passing through minute pores in the cell walls. Presumably these bridges are lines of communication between cells, but they are not

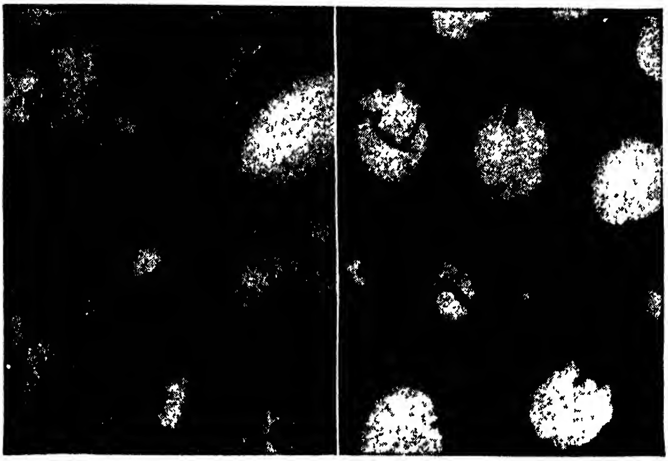


FIG. 20.—Intercellular bridges; left, highly thickened human epithelium; right, persimmon. (*Courtesy of General Biological Supply House.*)

essential, since cells in contact with one another are capable of passing liquids or electric currents from one to another without such connections.

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CHAPTER 3

SOME FUNDAMENTAL PHYSICS AND CHEMISTRY

In the activities of cells, great importance is to be attached to that very fine, mostly invisible, structure which inheres in the chemical composition and minute physical constitution of the protoplasm itself. These features of protoplasm are appropriately discussed along with the physiological processes which depend on them. Such processes should next engage our attention. Since, however, an understanding of this minute structure presupposes a knowledge of elementary chemistry and physics, it is advisable to pause a moment to acquire some of the more important ideas in that field.

Composition of Matter.—The physical substance of which objects are composed is called *matter.* Matter exists in a number of different forms called *elements.* An element is a substance possessing a characteristic structure which is different from that of every other element and which cannot be broken down into substances different from itself (that is, into other elements) by ordinary chemical means. The stipulation "ordinary chemical means" is intended to exclude radioactivity and powerful electronic machines. Among the more common elements entering into the composition of living things are carbon, nitrogen, oxygen, and hydrogen.

The elements may exist by themselves, chemically separate from other elements, as do oxygen and nitrogen in the air. More often they exist in *compounds;* these are distinct substances, made up of two or more elements, joined in definite proportions and with characteristic internal structure. Carbon dioxide is a very stable compound, made of carbon and oxygen, which is eliminated as a waste product by all living things. Calcium carbonate, of which bones are largely built, is a compound composed of three elements: calcium, carbon, and oxygen.

Both elements and compounds are divisible into *molecules.* These are the smallest units of a substance in which its characteristic chemical structure is maintained. The molecules are likewise the smallest units which exhibit the chemical properties of that substance. If a molecule is divided or broken up, its parts no longer have those properties. The elements which enter into a compound are present in each molecule in the same proportion as in large masses of the substance. Each molecule is exactly like every other molecule of the same substance, not only in the quantity of its elements but also in their structural arrangement. The molecules are completely separable from one another; in a solution of sugar in water, the molecules of sugar float singly, and in air the molecules of oxygen or of nitrogen are free from other molecules.

The molecules of many substances are in turn composed of *atoms*. These are defined as the smallest divisions of matter that may exist, either singly or in combination. Some molecules consist of only one atom, as in the gas helium. In such substances there is no distinction between molecule and atom. In oxygen, however, the molecule is composed of two atoms. Here the atoms have properties very different from those of the molecules; the atoms enter into chemical reactions much more readily than do the molecules.

Protons, Neutrons, and Electrons.—Even the atoms are not the ultimate units in the structure of matter, for they are made up of protons, neutrons, and electrons. These entities may be spoken of as particles, though they may be such only in a very special sense. The astounding feature of these units is that they are the same in all kinds of matter. The protons of an atom or molecule of oxygen are exactly like the protons of chlorine. Similarly the neutrons are everywhere the same, in all elements, and the electrons are the same in all.

The protons have mass, and each of them bears a positive electric charge. This positive charge is a unit which is the same in all protons. Neutrons have mass, practically identical with that of the protons, but they carry no electric charge. Electrons are units of negative electric charge; their mass is negligible. Atoms and molecules of all substances are made up of these units. The mass (weight) of an atom is dependent almost entirely on the protons and neutrons it contains, while its volume is determined mostly by the electrons. These relations will be made clear by an examination of the structure of the atom in several elements.

Structure of the Atom.—An atom of any substance consists of a central nucleus, around which one or more electrons are distributed. The nucleus of an atom contains one or more protons, and usually one or more neutrons. Since the protons bear positive electric charges, the nucleus of an atom is always positively charged. How great a charge it carries depends on how many protons it contains. Both protons and neutrons contribute to the mass of the nucleus, but only the protons furnish the charge. This positive charge of the nucleus is balanced by the negative charges of the surrounding electrons. There are as many electrons around the nucleus as there are protons in it, so that the atom is neutral.

Structure of the Elements.—With this knowledge of the fundamental similarity of all matter let us return to the elements. The number of protons and neutrons in the nucleus varies considerably, as does also the number of electrons surrounding it. In hydrogen (H), which is the simplest and lightest of the elements, the nucleus consists of just 1 proton, no neutron, and the atom has just 1 electron (Fig. 21, left). The single unit of positive charge furnished by the proton is neutralized by the negative charge of the electron. Helium (He), has 2 protons and 2 neutrons in the nucleus, which is therefore four times as heavy as the hydrogen nucleus, but it bears only twice as great a positive charge. To balance this positive charge, there are 2 electrons in the atom (Fig. 21, right). Carbon (C) has 6 protons and 6 neutrons (in the nucleus) and 6 associated electrons; oxygen (O) has 8 protons and 8 neutrons in the nucleus, with 8 electrons; while chlorine (Cl) exists in two forms, one of which has 17 protons and 18 neutrons, the other 17 protons and 20 neutrons in the nucleus, with 17 surrounding electrons.

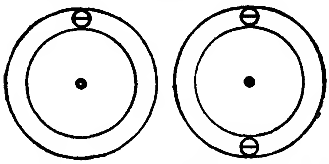

FIG. 21.—Diagrams of atoms of hydrogen (left) and helium (right). The central black spot is the nucleus; the concentric circles mark off the shell of negatively charged electrons.

The details of these particular elements are not important to the biologist, but the fact that they are composed of identical kinds of units and that they differ only in the number and arrangement of these units should be understood. Every element has a different number of protons and electrons from every other element. From the lightest element, hydrogen, which has 1 proton and 1 electron, to the one long believed heaviest, uranium (U), which has 92 protons and 92 electrons, there should be 92 elements. All but two or three of these have been obtained in chemical laboratories. Newspapers occasionally report the discovery of one or more of the missing elements, which await confirmation by other investigators. In the construction of the atomic bomb two elements with 93 and 94 protons, respectively, were produced.

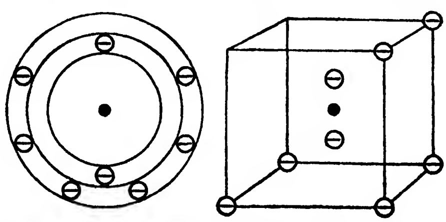

FIG. 22.—Atom of oxygen; two ways of representing its two shells of electrons.

The chemical properties of an element, the ways in which it reacts with other elements, are determined by the electrons surrounding the nucleus. When these electrons are numerous, they are arranged in shells, some near the nucleus, others farther away. The 2 electrons of helium (Fig. 21) constitute such a shell, and a similar inner shell of 2 is in all elements heavier than helium. Outside this is a shell which may contain from 1 to 8 electrons. Oxygen has 6 electrons in this outer shell, as diagrammatically indicated in Fig. 22. When the number of electrons is greater than 10, the additional ones are in a shell outside of a first shell of 2 and a second shell of 8.

It is only the electrons of the outermost shell which enter into ordinary chemical reactions. Different elements having the same number of electrons, similarly placed, in this outermost shell tend to possess similar properties and enter into similar reactions. A number of families of elements are thus recognized whose properties are much alike, such as the halogen family which includes fluorine (F), chlorine (Cl), bromine (Br), and iodine (I), in which there are 7 electrons in the outer shell—but a different shell in each of these elements.

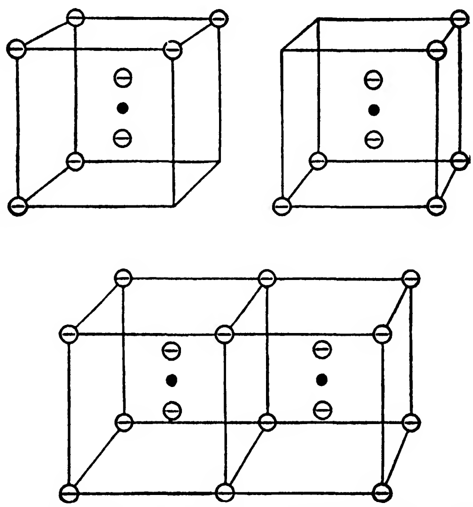

FIG. 23.—Two atoms of oxygen combined to complete their outer shells of electrons.

Chemical Reactions.—Some elements react more easily than others. The difference between them in this respect lies in their outermost shells of electrons. In each shell of an atom there is a maximum possible number of electrons. An element which has this maximum number of electrons in its outer shell does not react readily; the inert gases, such as helium used in balloons and neon in electric signs, are in this state. Most elements, however, have less than the maximum number of electrons in the outer shell, and it is easy for such elements either to complete that shell or to lose the electrons which are already in it. Because of this ease of reaction, two atoms of the same element sometimes join to complete their outer shells. Oxygen, as already stated, has six out of a possible eight in its second (outer) shell. If one atom shares two of its electrons with the other atom, and in turn accepts two electrons from the latter, each has a complete shell of eight electrons (four of them in common) and the two atoms are combined (Fig. 23). A molecule of oxygen is thus formed. In chlorine, which has seven of the possible eight electrons in its outer shell, two atoms combine by sharing two electrons (one furnished by each atom, Fig. 24), thus making a molecule of chlorine.

Two atoms of different elements may combine, for the same reason, and thus a compound is produced. Sodium (Na), for example, has just one electron in its outer (third) shell, which it readily gives up to any other atom capable of accepting it. Chlorine, as just explained, has seven in its outer shell and readily accepts an electron from an outside source. The two atoms perform these easy reactions by combining; they form a new substance, sodium chloride (NaCl).

Valence.—The number of electrons which an atom readily gives up or acquires constitutes its *valence.* Sodium has a valence of one, since

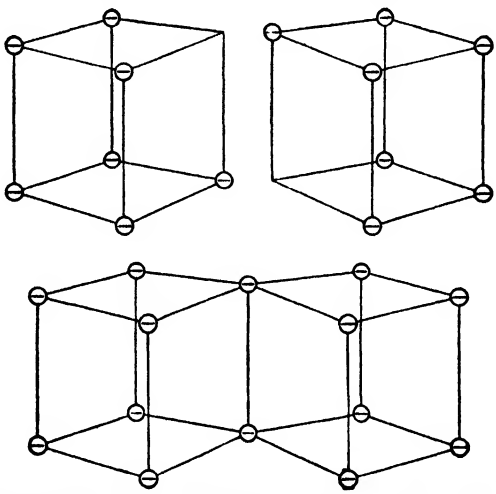

Fig. 24.—Two atoms of chlorine combined to complete their outer shells of electrons.

it easily loses but one electron. Magnesium easily loses two electrons, because that is the number in its outer shell, and its valence is two. These valences must be matched when compounds are formed. Thus, while one atom of chlorine (whose valence is one) matches one of sodium, it requires two atoms of chlorine to take up the two extra electrons of magnesium and form magnesium chloride ($MgCl_2$).

Ions.—When a sodium atom gives up its one outermost electron to some other atom, its electric balance is disturbed. It has lost one unit of negative electric charge; hence the net charge of the remainder is positive. Such a positively charged body is no longer the element sodium, it is not even an atom; it is instead an *ion* (Na^+). Similarly, when a chlorine atom acquires one extra electron (which is, of course, negative), its electric balance is disturbed and it becomes negative. It is no longer chlorine, no longer an atom, but a chloride ion (Cl^-). An ion may be defined as part of a molecule, consisting of one or more atoms with an electric charge. Ions are either positive or negative, depending on whether the atom has lost or gained electrons in producing them.

When sodium and chlorine combine to form sodium chloride, which is common table salt, a crystal of the salt is supposed to have the lattice structure shown in Fig. 25. There is no sodium in the crystal, no chlorine, but only sodium ions and chloride ions. There are not really any sodium chloride molecules, since each chloride ion (observe the central white one in the figure) is surrounded by six sodium ions at equal distances, and each sodium ion is surrounded by six chloride ions at equal distances. One cannot say which negative ion neutralizes a given positive one, so that no specific pair of ions can be said to form a molecule. A molecule can hardly be said to exist in a sodium chloride crystal, but only positive and negative ions.

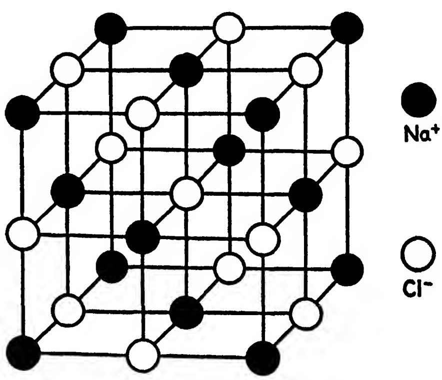

FIG. 25.—Crystal of sodium chloride, showing lattice arrangement of sodium ions and chloride ions.

Radicals.—In all the above examples, the units of chemical reactions have been atoms of elements or ions derived from them by transfer of electrons. Very often such reaction units are formed of two or more different elements. Sulfur (S) and oxygen, for example, may unite in the proportion of one of the former to four of the latter. In this proportion, however, their electric charges are not balanced, and the group bears two units of negative electric charge—that is, two extra electrons. They constitute a negative ion. In this form they act as a unit in combining with atoms which have lost electrons (positive ions). Potassium (K) may unite with them, but it takes two potassium ions to balance them, and K_2SO_4 (potassium sulfate) is formed. A group of atoms acting as a unit, as do the sulfur and oxygen ($SO_4^{=}$) in this example, is called a *radical.* Other groups of atoms (radicals) are positively charged (as NH_4^+), forming positive ions.

Acids, Bases, and Salts.—When a hydrogen atom (see Fig. 21) gives up its electron, only its nucleus remains. This nucleus is a proton and is positively charged: it may also be called a hydrogen ion (H^+). Certain substances in water readily yield up these protons to other substances, and they possess certain properties as a consequence. They have a sour taste, color litmus paper red, and do a number of other characteristic things. Suustances which readily donate hydrogen ions (protons) are called *acids.* Other substances which easily accept protons are called *bases.* They do so through the formation of negative ions consisting of oxygen and hydrogen (OH^-), known as hydroxyl ions. Bases in solution have the properties of lye, are said to be alkaline, and are recognized by the blue color they confer on litmus.

It will be observed that the characteristic positive ions (H^+) of acids and the characteristic negative ions (OH^-) of bases together contain the components of ordinary water (H_2O). Now water is an exceedingly stable compound. It is to be expected, therefore, that when an acid and a base are brought together in a solution the above ions will promptly unite to form water. This they do. But what becomes of the other radicals that belong to the acid and the base? They also combine in the sense that sodium ions (Na^+) and chloride ions (Cl^-) combine to produce sodium chloride. What they produce depends on what the other radicals of the acid and base were, but in any case the product is called a *salt.* A salt is defined as a substance which produces, or is a combination of, positive and negative ions other than H^+ and OH^-.

If the acid used was hydrochloric (HCl) and the base was sodium hydroxide ($NaOH$), the solution containing the former would contain hydrogen ions (H^+) and chloride ions (Cl^-), while the latter in solution would consist of sodium ions (Na^+) and hydroxyl ions (OH^-). When these two solutions are mixed, the hydrogen ions (H^+) and hydroxyl ions (OH^-) promptly unite to form water. The ions of the other two kinds, Na^+ and Cl^-, do not actually unite, but they form a solution of sodium chloride. If such a solution is dried up, crystals of sodium chloride having the lattice structure shown in Fig. 25 are formed. The sodium chloride is a salt.

If sulfuric acid (H_2SO_4), in which there are hydrogen ions (H^+) and sulfate ions ($SO_4^{=}$), is mixed with potassium hydroxide (KOH), in which there are potassium ions (K^+) and hydroxyl ions (OH^-), water is again formed by the H^+ and OH^- ions. This leaves the potassium ions (K^+) and sulfate ions ($SO_4^{=}$) to form potassium sulfate (K_2SO_4). The potassium sulfate is likewise a salt.

Salts may be obtained in other ways than by mixing acids and bases. Mixing two salts gives rise to two other different salts. Thus, if a solution of sodium chloride is mixed with a solution of potassium sulfate, the combined solution contains two kinds of positive ions (Na^+ and K^+) and two kinds of negative ions (Cl^- and $SO_4^{=}$). While the ions do not join in solution, it is just as correct to regard the solution as containing potassium chloride (KCl) and sodium sulfate (Na_2SO_4) as the original two.

Electrolytes.—Ions, because of their charges, are able to carry an electric current when they are free to move. The sodium and chloride ions in a crystal of common salt are too rigidly held to move, but if the crystal is dissolved in water they are free. If into different parts of such a solution wires from the two poles of a battery are placed, a current of electricity is carried through the solution from one pole of the battery to the other (Fig. 26). The positive ions (Na^+) go toward the negative pole and, by taking up electrons from it, becomes ordinary neutral sodium (Na). Removal of electrons from the negative pole reduces the negative charge conferred upon it by the battery and sets up a current in the wire. The negative ions (Cl^-) pass in like manner to the positive pole, where they deposit their surplus electrons on that pole, forming neutral chlorine (Cl). Sodium is thus collected about one pole of the battery, where it reacts with the water; chlorine collects about the other pole and escapes as a gas. Decomposition of a substance in this manner is known as *electrolysis*. In the metal industries this process is used to separate certain metals from their ores. Substances which, like sodium chloride, form ions in solution and are thus capable of carrying a current are called *electrolytes*. Most of the salts are good electrolytes.

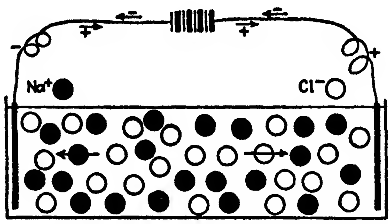

FIG. 26.—Diagram of electrolysis of sodium chloride in solution. Chloride ions move to the right, sodium ions to the left.

Energy.—Energy is the capacity to do work, that is, to produce change. The arrangement of the electrons and protons in an atom involves energy. Changing that arrangement either requires that energy be expended upon the change or releases energy no longer needed in the new arrangement. Both types of change are exceedingly common. Of the common elements about us near the earth's surface, oxygen is by far the most abundant, making up nearly half of the total. It is also very common in living things. Since oxygen is a fairly active element, some of the most frequent chemical reactions are the combinations of oxygen with other substances. These changes are called *oxidation*. The rusting of iron and the burning of wood or coal are examples. An important feature of oxidation is that it releases energy. Use is made of this fact in industry, when the energy of steam engines or electric current is furnished by burning coal, and in plants and animals whose activities depend on energy obtained by oxidizing food. The energy which is tied up in the composition of chemical substances, whether foods or any other, is called *potential* energy. When converted by a chemical reaction into the energy of heat or of movement, it becomes *kinetic* energy.

Applications to Biology.—The examples used in this chapter to illustrate chemical principles have been taken mostly from inorganic chemistry because of their simplicity. The examples therefore need hardly be remembered if the ideas they represent are mastered. The principles have been kept at a minimum but should suffice for a fair understanding of the simpler operations of protoplasm. Living things are essentially chemical and physical laboratories, with this distinction, that the chemical substances are not limited to a few reagent bottles on the shelves nor the physical apparatus to a few resistance boxes and potentiometers in the cabinets; instead these things constitute most of the building itself. Changes are going on in them everywhere and all the time. It is of these chemical and physical processes that life consists. As explained in other parts of this book, the common physiological processes of digestion and respiration are chemical reactions and physical phenomena that are fairly well understood. Not so well known but assuredly chemical and physical are muscular contraction and elimination of wastes. Even growth, the development of the embryo or young stages, and the conduction of impulses by nerves must be largely physicochemical.

It is important to know, in connection with all these life processes, that substances react as they do because of their electronic structure. This structure is, in most protoplasmic substances, enormously complicated by radicals of complex design. Their reactions and structure are for this reason not easy to discover, but there is every reason to assume that their physiological behavior is quite as dependent upon their architecture as are the reactions of the simplest inorganic compound. Valence determines the proportions of different substances which will unite in protoplasm as certainly as in the salts. Electric phenomena result from electronic reactions in living things just as in batteries. Energy, one of the most important requirements of animals and plants, flows from chemical combination as abundantly and as certainly in protoplasm as in a test tube or an engine. It seems likely that life consists entirely of physical and chemical changes.

With this equipment of elementary knowledge in a pair of sister sciences, and an understanding of the extent to which these sciences underlie all knowledge of biology, we may now return to the operations of cells.

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CHAPTER 4

THE FUNCTIONS OF PROTOPLASM AND CELLS

The living substance whose functions we are to study differs from nonliving matter in certain characteristic ways. It has certain types of chemical structure, not easily defined, but not duplicated in inorganic bodies. It is arranged in unit masses, the cells, which are usually recognizable by their form and such nearly universal features as the nucleus. This living matter moves spontaneously, that is, from causes arising within itself. It grows by taking up new material throughout its interior, not just by additions on the outside. It is irritable; that is it responds in some way to changes in the environment, or changes within itself, which are great enough to act as stimuli. And finally, individual living things are capable of producing other individuals of their own particular kind; that is, they reproduce.

These statements are not intended as a definition of life, or of living things, because there are exceptions to them, or situations in which the criteria could not be practically applied. They are meant merely to indicate the general types of functions which must be examined in a survey of life activities.

Protoplasm is not a chemical compound, the structure of which may be expressed by a chemical formula, but is an elaborate mixture of chemical compounds in water. A bit of protoplasm large enough to analyze, from any source, always yields carbon, hydrogen, nitrogen, oxygen, phosphorus, sulfur, sodium, potassium, magnesium, calcium, iron, and chlorine. Additional elements that frequently occur in such analyses are aluminum, silicon, manganese, copper, fluorine, bromine, and iodine. Naming these elements tells very little, however, concerning protoplasm, since it does not suggest the manner in which the elements are combined, and it is the compounds, not the elements, that are of real importance. These compounds in protoplasm are of a variety of kinds, which are partly organic (produced in living things) and partly inorganic. The latter are described first; they are water and the various salts.

Water and Salts.—Water is the most abundant constituent of protoplasm, making on the average about 80 per cent of the total mass. The properties and activities of protoplasm are quite as dependent upon the remarkable properties of water as upon the properties of its other constituents. Some of these properties of water are its power to absorb or give off great quantities of heat without changing much in temperature, its capacity to dissolve many different substances, and the free movement which it permits in the ions of salts dissolved in it. These features of water enter into so many of the living processes that life without water, if it could exist at all, would have to be of a very different sort from any that is known.

Dissolved in this water of protoplasm are the salts. The commonest ones have sodium and calcium as their positive ions, but potassium, magnesium, iron, and manganese are also present in this positively charged state. The negative ions are the chloride ion and the radicals known as carbonate, nitrate, sulfate, and phosphate. These ions of salts dissolved in water give protoplasm certain electrical properties. Inorganic salts make up about 1 per cent of average protoplasm.

The Organic Compounds.—There are three principal classes of organic compounds, the *carbohydrates, lipids,* and *proteins.* The carbohydrates are the sugars, starches, celluloses of plant walls, glycogens or animal starches, and some others. They constitute less than 1 per cent of most protoplasm but are important out of proportion to their quantity. They are composed of only three elements: carbon, hydrogen, and oxygen. The hydrogen and oxygen are always in the ratio of 2:1; that is, there are twice as many atoms of the former as of the latter, just as in water. In most carbohydrates the carbon atoms are in multiples of six. A simple sugar has only six carbon atoms and is known as a *monosaccharide.* Glucose, one of the most common of them, is present in nearly all cells. Other simple sugars are fructose (fruit sugar) and galactose. The formula of all these simple sugars is $C_6H_{12}O_6$, but there are differences between them in internal arrangement. When two molecules of a monosaccharide are combined into one (with loss of water) the combination is a *disaccharide.* Sucrose ($C_{12}H_{22}O_{11}$), the ordinary cane or beet sugar of table use, maltose (malt sugar), and lactose (milk sugar) are of this type. When many molecules of simple sugar are combined (with more loss of water), a *polysaccharide* is produced. The starches (of plants), glycogens (animal starches), and celluloses (of cell walls) are of this kind. The polysaccharides are practically insoluble in water, so that the starches and glycogens are excellent food-storage forms. None of the carbohydrates forms ions when dissolved; hence they play no role in electrical phenomena. They contain a great deal of potential energy, which may be released by oxidation.

Other reservoirs of stored energy are the lipids. The physical properties of these substances are very characteristic, including the nonevaporating grease spots which they make and their insolubility in water. This insolubility is what makes them good storage products. The lipids constitute about 3 per cent of ordinary protoplasm, though stored lipids may be many times that fraction of an animal's body.

Among the lipids are the *true fats,* such as butter fat, olive oil, and the fat of beef or pork. True fats are composed entirely of carbon, hydrogen, and oxygen, with the proportion of oxygen much lower than in carbohydrates. The natural fats have large molecules—around 50 atoms of carbon, double as many of hydrogen—but only 6 atoms of oxygen. They are a combination of 1 molecule of glycerol (commonly called glycerin) with 3 molecules of fatty acid. There are a number of different fatty acids characteristic of different fats, some of them used commercially in water emulsions to produce the brushless kinds of shaving cream.

In other types of lipids there may be more than the three elements which true fats contain. Lecithin, which includes phosphoric acid and another substance in place of one of the fatty acid molecules, is abundant in egg yolk and is probably present in all cells as part of the protoplasmic structure. Cholesterol, which is found in bile and is a source of gallstones, consists only of carbon, hydrogen, and oxygen, but the carbon in it forms a "skeleton" in rings instead of straight chains as in the fats.

Most significant of the organic compounds are the proteins, because it is they that make one kind of living thing so sharply and definitely different from others. Aside from water, they are the most abundant substances in protoplasm—about 15 per cent of the total mass. Proteins are especially characteristic of lean meat (muscle) but are distributed through all cells. They do not diffuse readily through other substances but allow some, though not all, other substances to diffuse readily through them. Chemically they are compounds of the *amino acids,* a group of 25 different organic acids. A generalized formula of amino acids is $R—CH(NH_2)·COOH$, in which R stands for the "body" of the molecule, different in each of the 25 acids. The rest of the formula applies to all of them. The COOH makes them organic acids, the NH_2 makes them amino acids. In the simplest amino acid, glycine, R is simply an atom of hydrogen, H; in the next simplest, alanine, R is the radical CH_3. These amino acid molecules may be joined with one another, as carbohydrate molecules are joined, with the loss of a molecule of water at each junction. The more complex of these combinations are the proteins. The molecules of proteins are relatively huge, containing hundreds or even thousands of atoms. With such large molecules, which may include varying proportions of most of the amino acids, and frequently carbohydrates or lipids, there may be an enormous number of kinds of proteins.

Enzymes.—Many chemical reactions are greatly hastened by the presence of certain chemical substances which do not enter into the reaction in a definitive way. Hydrogen peroxide (H_2O_2) is stable enough to last for months in a bottle; but if a pinch of manganese dioxide (MnO_2) is added, the extra oxygen of the peroxide comes away so rapidly as to produce a froth. The manganese dioxide acts as a *catalyst*, which is the name applied to inorganic accelerating agents. Now, many living tissues are constantly producing hydrogen peroxide, but it is promptly decomposed. Something in the cells does what manganese dioxide does in the bottle. That something is called *catalase*. It is one of many organic accelerators called *enzymes*.

For the first time in 1926 an enzyme was isolated, and now some 30 of them have been purified. All of these are apparently proteins or protein compounds. Some of them work in the cells; others, as the digestive enzymes, are extruded from the cells and do their work outside. They work best at temperatures of 30 to 40°C., are inhibited by temperatures around 50°, and destroyed by prolonged exposure to this temperature. Each enzyme accelerates some particular reaction, and all cells possess a wide variety of these agents. Theoretically an enzyme may accelerate a reversible reaction in either direction, and the direction is dependent on other conditions. Actually, however, the other conditions in living things are usually such that the enzyme works only one way. Some enzymes ordinarily break down substances (for example, the digestive enzymes); others build up materials into more complex substances. The destructive type may be extracted and work in about the same way under artificial conditions. Those of the constructive class, however, seldom work outside of cells. Perhaps protoplasm could be manufactured in the laboratory if constructive enzymes worked as well in test tubes as the analytical or destructive ones do.

Physical Structure of Protoplasm.—No matter how smooth and structureless protoplasm may look to be in a microscope, it is far from homogeneous. In general, it consists of particles of various sizes, mostly very minute, distributed through a supporting liquid substance. In the terms of physical chemistry, protoplasm is a "system" consisting of two "phases," of which the particles are the "dispersed" phase and the supporting liquid is the "continuous" phase. In so far as the dispersed particles are liquid and large enough to be visible in a microscope, such a mixture is an emulsion (Fig. 27). If the particles are submicroscopic in size and liquid, as they usually are, the mixture is an emulsoid. Material in such a finely divided state is also said to be colloidal, or,

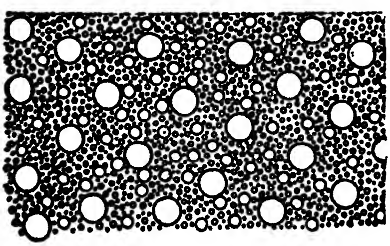

FIG. 27.—Diagram of an emulsion, illustrating the physical structure of a very common kind of protoplasm.

though somewhat improperly, such substances are called colloids. The existence of invisible particles may be detected and they may be counted with the ultramicroscope against a dark background. Some of them may be photographed by means of the electron microscope. Even the fine particles are mostly larger than molecules and so may be composed of more than one substance. Their composition cannot be precisely known, but they must be relatively insoluble in water in order to maintain themselves as particles. There are indications that the particles are surrounded by a lipoid film, which may have something to do with their insolubility in water.

This whole structure is, of course, permeated with water, and there are always salts, and usually sugars, in solution. The particles of these dissolved substances, being either ions or single molecules, are much smaller than the dispersed emulsoid particles and confer very different properties on the protoplasm.

Diffusion and Osmosis.—The molecules and ions of a substance in solution engage in continual spontaneous movement. So do the molecules of the water or other liquid in which the substance is dissolved. The particles bombard one another and the walls of the containing vessel if there is one. The direction of movement of individual particles is entirely unpredictable. Yet if a substance is more concentrated in one part of a solution than in another, the particles spread more from the place of high to the place of low concentration than in the opposite direction. The spontaneous random movement of the particles in a solution is known as *diffusion,* and it tends to equalize the concentration in all parts. Protoplasm is the scene of constant shifts of this kind. The elimination of the waste product carbon dioxide is effected by diffusion from a place of high concentration in a cell or tissue to a place of low concentration in the surrounding air or water. The entrance of oxygen into the cell is dependent on the same principle. Rapid entrance of water into single-celled animals, requiring its elimination by pulsating vacuoles, is practically simple diffusion. There are many situations where an important physiological process is merely diffusion.

There are places, however, in which the diffusion of different substances is quite unequal. The membrane of a cell—not the dead wall or the secreted pellicle, but the outer film of protoplasm itself—exercises a selective influence on the passage of substances through it. Some substances pass through it readily, others slowly, still others practically not at all. The membrane is said to be *semipermeable.* The exchange of particles between two solutions on opposite sides of a semipermeable membrane is known as *osmosis.* In general, the gases (carbon dioxide and oxygen) and water pass through a cell membrane rapidly. Simple sugars (glucose), the amino acids (components of proteins), and glycerol and fatty acids (components of fats) pass through slowly. The ions of inorganic salts, and the disaccharides (sucrose, etc., page 40) penetrate the membrane very slowly, and the proteins, polysaccharides, and fats practically not at all. For some of these substances the inability to traverse the membrane is explained by the large size of their particles. For the ions of salts it is probably their electric charges which keep them out. The cell membrane itself has a charge, usually negative, which repels ions of like charge; and since the oppositely charged ions cannot part company, both are excluded. There are probably other reasons, not yet understood, for the retardation of passage of particles through membranes.

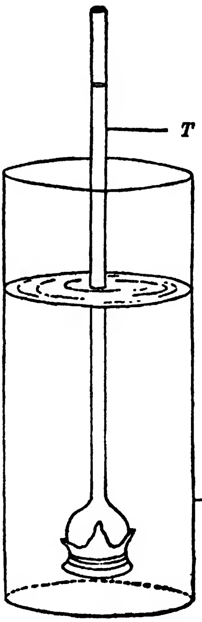

FIG. 28.—Diagram of apparatus used to illustrate osmosis. *T*, inverted thistle tube covered with animal membrane and containing a solution of sugar in water; *V*, vessel of water.

The result of osmosis is easily illustrated by tying a piece of bladder tightly over a thistle tube, filling the tube with sugar solution, and immersing the expanded end in a dish of pure water (Fig. 28). After a short time it is found that the sugar solution in the tube has risen to a higher level, but that it is not so concentrated as at first. Water has obviously passed through the bladder into the sugar solution. A little, but not much, of the sugar has also found its way through the membrane into the water. The molecules of water are in constant motion, striking the walls of the dish, the membrane, and other molecules of water. Their impacts against the membrane drive some of them through. Now the water inside the thistle tube is also in motion, and some of its molecules pass out into the water of the larger vessel. But there are fewer molecules in a given volume of the sugar solution because the sugar molecules take some of the space, and their movement is less vigorous owing to hindrance by the sugar. Hence fewer molecules of water get out of the thistle tube than would do so if the sugar were not there. Water is thus passing through the membrane in both directions, but more of it goes toward the sugar solution than away from it. The sugar solution thus rises in the tube but becomes more dilute.

Surface Phenomena.—An important consequence of the colloidal structure of protoplasm is the enormous surface exposed by the dispersed particles. Extremely finely divided particles present a greater surface relative to their volume than do larger particles. This great surface increases the rate of chemical and physical activity at every face of contact between the two phases of the system. These activities have been called *surface phenomena.* Some surface phenomena are surface tension, adsorption, and various electrical phenomena.

Surface tension is exemplified by the film at the surface of water, the external membranes of cells, the membrane of the nucleus, and the films that surround vacuoles. A considerable pull is exerted by these films.

Extremely finely divided solids or those with extremely fine pores tend to condense on their surfaces any gases or vapors or other substances with which they are in contact. Such substances are said to be *adsorbed.* The thin films of these adsorbed substances are held so tenaciously that great pressures are required for their removal. A gas mask removes gases from the air because of the great adsorptive power of charcoal, and the clarification of sirups and sugars is accomplished by making use of the adsorption of coloring matter by bone black. Certain properties of living matter are best explained on the basis of adsorption.

Electrical properties are conferred on protoplasm by its ionized salts. Ions are capable, as explained in Chap. 3, of conducting electricity but in protoplasm are more important because they are probably adsorbed upon the surfaces of the colloidal particles. These particles thereby acquire an electric charge. Through the interior of the cytosome the particles appear to carry positive charges, but in the nuclear sap they are negative. The surface of a cell as a whole seems, as stated before, to be negatively charged. The occurrence of like charges on the interior particles causes mutual repulsion and is probably the chief reason why these particles do not adhere to one another. If they did adhere, the protoplasm would coagulate or harden.

Changes in Viscosity.—Viscosity is the resistance which the particles of a substance offer to movement upon one another. The viscosity of light liquids like water or gasoline is low, while that of thick sirup—or still more so of solids—is high. When a bit of fresh meat is subjected to pressure while still warm, even if it be from an organ which like the liver has no conspicuous fibers in it, it appears to be highly viscous. The resistance is offered mostly, however, by the cell membranes. These are firm enough, like well-filled bags of wheat, to tend to preserve the shape of the cells. The interior protoplasm of a cell, at least of those which have been studied in this respect, turns out to be quite liquid. In one kind of cell the protoplasm is only about ten times as viscous as water and only about one one-hundredth as viscous as ordinary glycerin.

This fluid state is probably maintained, as indicated in the preceding section, by the like electric charges on the colloidal particles in the protoplasm, causing these particles to repel one another. The viscosity changes frequently, however, for reasons not yet understood. Such changes occur regularly during cell division, the protoplasm being firmer at the beginning of division, more liquid (less viscous) later on.

Metabolism.—The protoplasm of a cell carries on all the general processes of any living body. Within it occurs a multitude of complex chemical reactions by which the protoplasm maintains and renews itself and produces more protoplasm. Protoplasm digests food and for this process secretes various chemical substances. When food is broken down into simpler substances during digestion, it is absorbed and built up into the living substances itself or perhaps is combined with oxygen for the production of heat and motion. Protoplasm also respires, gets rid of waste materials by the process of excretion, grows, is capable of movement, and responds to changes in external conditions, or exhibits irritability. The chemical processes involved in all these activities of protoplasm are included under the term *metabolism.*

Metabolism may be defined as the sum of all the chemical and physical processes carried on within the protoplasm. It consists of two phases, namely, the constructive phase or *anabolism* and the destructive phase or *catabolism.* Anabolism includes all the processes concerned in the growth and repair, or upbuilding, of protoplasm. It includes all processes by which substances are transformed into reserves of food. Catabolism includes all those processes opposed to anabolism. These are the processes by which protoplasm is broken down and the waste products eliminated. Both anabolism and catabolism are continous processes. As long as anabolic processes are in excess of catabolic processes, growth occurs; but when catabolic processes are in excess a diminution in size takes place.

So far as metabolism of animals relates to food, it pursues the following cycle in the economy of living things collectively. Organic food is first made out of inorganic matter through the process of *photosynthesis* in plants. These organic substances become the food of animals which are unable to subsist on inorganic food. The animals digest these foods, and from the simpler digestive products build up their protoplasm through the process of *assimilation.* To supply the energy required for all this work the animal must secure oxygen by *respiration.* Waste materials produced along the way are eliminated by *excretion,* and useful products accessory to the general processes are elaborated by *secretion.* One of the products of the food cycle is commonly *growth.* All these processes are part of metabolism; they are described in the next seven sections.

Photosynthesis.—The things which plants may take in are water and salts from the soil, and oxygen and carbon dioxide (CO_2) from the air (or water, in the case of aquatic plants). The first three of these are utilized in about the same way in plants as in animals. The carbon dioxide and some of the water, however, are put to a totally different use. Carbon dioxide is a by-product of the burning of coal or wood or the decay of dead animals and plants or of anything else composed partly of carbon. It is constantly being thrown off as a waste product by animals and by plants, except as they use it in the process about to be described. Plants absorb the carbon dioxide into their leaves or other green parts and there combine it with water to form one of the simple sugars, glucose.

The final results of this reaction are indicated by the equation

$$6CO_2 + 6H_2O + \text{energy} \rightarrow C_6H_{12}O_6 + 6O_2$$

In words this means that six molecules of carbon dioxide and six of water are decomposed and their parts recombined to form one molecule of glucose and six molecules of oxygen. The energy expended in bringing about this change comes from sunlight, hence the process is called photosynthesis, literally construction by light. In most plants production of glucose can occur only in the presence of *chlorophyll*, the green substance in their plastids, and certain enzymes. The energy of the sun in this reaction appears not to affect the carbon dioxide directly, but to decompose the water. The hydrogen set free from the water is picked up by other substances which then, without any aid from light, proceed to attack the carbon dioxide. The oxygen that is liberated is not produced directly by the decomposition of the original raw materials; it comes from a peroxide which is an intermediate product. That oxygen is liberated may be demonstrated by an experiment with water plants. In such an experiment the cut ends of a water plant, as Elodea, are inserted in a test tube filled with water, the plant and tube are immersed in water, and the tube is inverted (Fig. 29). When the plants are placed in sunlight, bubbles of gas escape from their cut ends and collect in the tube. Suitable tests show the gas to be oxygen.

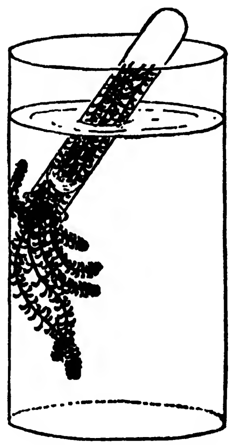

Fig. 29.—Method of collecting oxygen produced by the aquatic plant Elodea during photosynthesis. The oxygen rises from the plant into the closed end of the test tube.

Photosynthesis is not absolutely limited to plants, for there are some simple animals which contain chlorophyll, and in these glucose is produced in the same way as in plants. Nor are chlorophyll and light always necessary for the production of glucose, since some colorless organisms are capable of doing this in darkness.

Plant Products as Food of Animal Cells.—Inasmuch as most animals are incapable of producing carbohydrates directly from inorganic compounds or the simple elements, they must get them from plants. Plants store any excess of carbohydrates above their immediate needs, in some insoluble form, usually starch or some similar substance. Animals, from the simplest one-celled ones up to the most complicated, use these stores of plant starch for food. Out of these plant carbohydrates the characteristic components of animal protoplasm are made. Glucose is to be had by merely breaking down the starch. Glucose can be converted, mostly by rearrangement, into glycerol and fatty acids; from these, fats may be formed.

For one of the essential parts of animal protoplasm, however, the plant starches will not suffice; that is the highly important class of proteins. Animals in general cannot make proteins out of inorganic substances. Only a few can make proteins out of carbohydrates. There is something lacking in the physiology of most animals which prevents them from making this particular synthesis. The missing thing is probably an enzyme or a set of enzymes. Animals must therefore get their proteins, as well as their carbohydrates, either directly or indirectly from plants. They may obtain these proteins from other animals, as the carnivorous animals almost exclusively do, but these other animals must get the proteins ultimately from plants.

Conversion of Food.—Very little of the food which animals take can be utilized at once for its ultimate object, unless water and oxygen be considered food. Most of the food has to be worked over in some way. Glucose and other equally simple sugars are ready to use, but these constitute only a very small fraction of the food of animals. One of the chief reasons why other foods cannot be used at once is that they are not soluble. The starches, lipids, and proteins must all be converted into some form that will diffuse through protoplasm. This conversion is effected in the process of *digestion.*

Digestion is essentially the same process everywhere but will be considered here chiefly as it occurs within cells rather than in the cavities of large organs like the stomach. Unicellular animals take in small organisms and surround them with a droplet of water containing one or more enzymes, thus forming a food vacuole. All such animals can produce enzymes that will digest proteins, many can digest starches, most of them can digest fats. Proteins are dismembered to yield their amino acids; fats are split up into glycerol and fatty acids; starches are converted into simple sugars. The final products named in each case are all soluble in water and can diffuse through protoplasm.

In this soluble form they pass to every part of the cell, or from cell to cell. Oxidation of them may occur if energy is needed. The derivation of energy from oxidation of glucose is represented by an equation which is just the reverse of that by which glucose is formed in photosynthesis, namely,

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6H_2O + 6CO_2 + \text{energy}$$

This equation says, in words, that one molecule of glucose and six molecules of oxygen are recombined (in combustion) to form six molecules of water and six molecules of carbon dioxide, with the release of energy. Even some of the transitory steps involved in this reaction are reversals of those occurring in photosynthesis.

If new protoplasmic structure is required, the soluble products of digestion are available for this purpose. If the digested foods are in excess of the requirements for these two purposes, they may be stored; but in this case they must be rendered insoluble again, for otherwise they could not be retained. If carbohydrates are to be stored in animals, the glucose is commonly converted into animal starch or glycogen. Glycerol and fatty acids are again converted into fats, although the fats are likely to be of different kinds from those which were taken as food. The production of these insoluble storage products is done by enzymes, and the same enzyme may work in both directions, that is, either break down substances (starches, for example) or build them up.

Little is known about the construction of new protoplasm out of digested foods. The name assimilation is given to the process, and it seems certain that enzymes are engaged in the work, but of its nature we are mostly ignorant.

Respiration.—To provide energy or new protoplasm, all living things require oxygen. Land animals and plants get it from the air, submerged aquatic ones from the oxygen which is dissolved in water. There are, however, some kinds of animals and plants that normally live in situations devoid of oxygen, and some of these organisms would die if brought into contact with free oxygen. Such organisms require oxygen in their metabolism, but they secure it from compounds in which it occurs.

The combination of oxygen with protoplasm and foods results finally in the formation of water and carbon dioxide, as indicated by the equation in the preceding section. The carbon dioxide must be eliminated. The absorption of oxygen and the elimination of carbon dioxide are together called respiration.

In simple animals and plants, dissolved oxygen diffuses directly through the surface of the organism into the protoplasm. Thence by diffusion and protoplasmic currents it is carried to all parts of the cell. In many small multicellular animals and plants with few layers of cells the oxygen may readily diffuse through the intervening cells to those which lie deeper. In larger organisms, however, a transport system is required, as discussed in Chap. 11.

Excretion.—Metabolism results in the formation of various gases, water, and other compounds, which are of no value in the body or would be harmful if allowed to accumulate. The process of their elimination is called excretion. Gases resulting from metabolism are eliminated along with carbon dioxide in respiration. Other waste substances pass through the cell membranes to the exterior, or in some of the protozoa they are collected by the contractile vacuoles, along with excess water, and voided through the outlets of these organs. In higher animals excretions are taken up by the blood and lymph, from which they are then separated by special organs.

Secretion.—All cells produce certain chemical compounds which may be used in the processes going on within the cell or in cavities adjoining the cells. Such products are called secretions. They differ from excretions in that they are used in performing some function. Many of the secretions which are discharged from the cells are first stored in the cells as granules, which finally break out of the cell and then become gaseous or liquid. Other secretions produced as liquids within the cell diffuse out and escape as rapidly as formed, are absorbed by other cells, or are carried in the blood stream. Such secretions may perform their functions at a considerable distance from the cells where they were elaborated. Secretions are very diverse in their uses. Some aid in digestion, others give protection because of their odor or because of poisonous properties, some serve as lubricating material, others oxidize readily with the production of light as in fireflies.

Growth.—Growth is caused by the conversion of foods into protoplasm at a more rapid rate than protoplasm is being broken down. Increase in the size of cells may not be wholly due to increase in the quantity of protoplasm. Fat cells increase in size because of the deposition of globules of fat, a process which may be continued until there is much more fat than protoplasm. In plant cells and certain animal cells volume may be increased by the imbibition of water which may be stored in vacuoles. In such extreme cases as those mentioned, the quantity of protoplasm may be actually decreased, although the cell may be larger.

Reproduction.—Reproduction, or the formation of new individuals, is likewise characteristic of living beings. In unicellular organisms, and only in these, reproduction is equivalent to cell division. In higher organisms, reproduction usually involves the formation of special cells, the germ cells, which by their division, with rearrangement of the resulting cells, give rise to new organisms. Here reproduction involves cell division too. Cell division is described in Chap. 5, reproduction in Chap. 14.

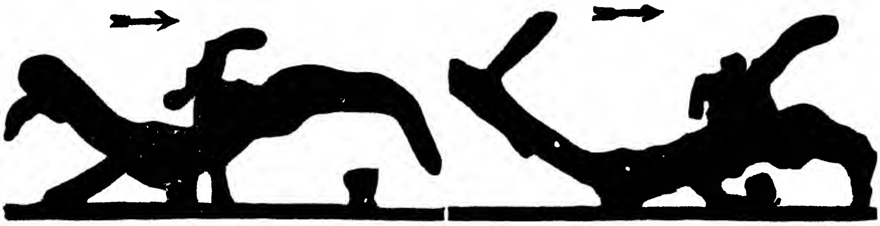

FIG. 30.—Locomotion in an amoeba with several pseudopodia, which rest on the substratum only at their tips. (*From Dellinger in Journal of Experimental Zoology.*)

Protoplasmic Movement.—One of the attributes of living organisms usually distinguishing them from nonliving matter, is the power of independent motion. Most animals at some stage in their existence, many plants of the lower orders, and the swarm spores of other low plants are motile. Higher plants are not capable of locomotion, but within their cells the protoplasm may undergo movement.

FIG. 31.—Fibrillar structure of cilium of Stylonychia. (*From Dellinger in Journal of Morphology.*)

In many cells the protoplasm frequently travels as if in channels, particle following particle, carrying plastids, food vacuoles, and cell inclusions along with it. When an amoeba (a one-celled animal) moves, it thrusts out one or more lobelike processes, called *pseudopodia.* Then the body is pulled forward or flows forward. Sometimes there is only one pseudopodium, and the amoeba just flows along. In other kinds of amoeba there are several pseudopodia at one time, and only their tips touch the substratum, in which case the animal may almost be said to walk (Fig. 30). A pseudopodium is extended apparently because of a local increase of viscosity in the outer layer of protoplasm at some part of the cell, carrying with it a slight contraction which forces the protoplasm elsewhere to protrude; but how the change in viscosity is effected is not clear.

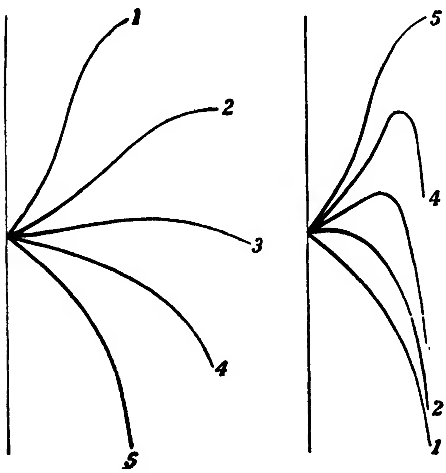

FIG. 32.—Form of cilium during strokes; forcible stroke at left, return stroke at right. Numbers show successive positions, indicate direction of movement.

Many of the simple unicellular animals and some of the multicellular ones perform movements by means of *cilia* or *flagella*. The cilia are minute hairlike projections capable of rapid vibration. Each cilium has an elastic outer layer containing one or more contractile threads within it, as in Fig. 31. Contraction of the threads on one side bends the cilium in that direction, and elasticity of the sheath causes it to return.

In the vigorous stroke of a cilium, it is extended and moderately stiff, so as to catch much liquid; on the return stroke it bends limply nearer the surface of the cell (Fig. 32). Neighboring cilia usually beat in unison or in waves.

Flagella differ from cilia chiefly in their greater length and are few in number (usually one to eight per cell). Sometimes the flagellum is surrounded by a vaselike collar (Fig. 33). Flagella may beat regularly in one plane, as do cilia, or they may have a rotary motion. The whole flagellum may move, or only the free end of it. The flagellum is composed of an elastic peripheral layer within which are several contractile threads (Fig. 34), and the movement is due to the contraction of these threads. Flagella give a motile cell a jerky erratic movement; cilia cause it to glide.

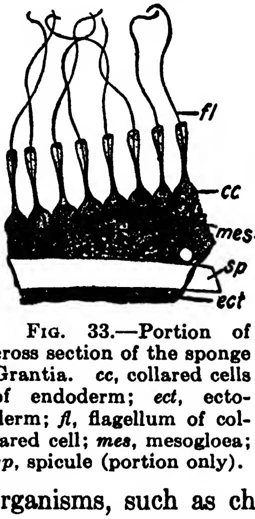

Fig. 33.—Portion of cross section of the sponge Grantia. *cc*, collared cells of endoderm; *ect*, ectoderm; *fl*, flagellum of collared cell; *mes*, mesogloea; *sp*, spicule (portion only).

Responses to Stimuli.—A characteristic property of living matter is its ability to respond to stimuli. A stimulus is any influence of sufficient magnitude to cause a change in protoplasm. The stimulating agent may be external to the organisms, such as changes in light, temperature, chemical substances, sound, pressure, or electric current; or it may originate within, through osmosis, electric charges, chemical substances, pressure, or nerve impulses. To be a stimulus, the modification must have a certain degree of suddenness. A very gradual change in the intensity of light may have no observable effect, while a sudden change of the same amount produces a marked reaction.

Responses are of very different sorts. Muscle cells and others contract; gland cells produce secretions. Pigment cells in the skin of a frog, which are highly branched and have their pigment distributed throughout all parts of the cell when at rest, contract their pigment into a small compact mass in response to light, thereby changing the animal's color. Streaming of protoplasm in plant cells stops in response to an electric current. A chemical substance in the retina of the eye of vertebrate animals is decomposed by light. The electric organs of certain fishes produce a series of discharges.

The nature of the response is determined by the nature of the responding protoplasm, not by the kind of stimulus. A muscle cell contracts, whether the stimulus be chemical or electrical. A gland cell secretes, and its product is always the same, regardless of what started its activity.

The extent of a response is, in general, rather definitely fixed for any given cell. If the cell responds at all, it does so to its full capacity. An organ made of many cells may respond in various degrees, depending on whether few or many of its component cells join in the response. How many cells respond depends on the intensity of the stimulus. Each individual cell, however, follows the all-or-none rule of acting either at its maximum capacity or not at all.

FIG. 34.—Flagellum (*fl*) of Euglena, showing (right) contractile threads within it. (*B after Dellinger in Journal of Morphology.*)

What Is Living Matter?—The characteristics of living matter enumerated in the opening paragraph of this chapter do not constitute a criterion which would enable even an expert to say in a specific instance whether a bit of matter were alive. Application of the rules would occasionally be futile. The chemical composition of recently killed protoplasm would, on analysis, be indistinguishable from that of living protoplasm; but something intangible would be gone from it. Spontaneous movement and change of shape may occur in a drop of liquid, under certain circumstances, because of changes in the surface film. Moreover, living things in the form of resting spores exhibit no detectable movements over long periods of time. A crystal may be made to convert part or all of itself into a flock of smaller crystals, in a way that would be hard to exclude in a definition of reproduction. Finally, metals respond to things in the environment, such as a magnet or electric potential.

A definition of life which lists the ordinary activities or conditions of living things is feasible; but it could not be used practically for a complete classification of all objects into two categories, living and nonliving.

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CHAPTER 5

CELL DIVISION

When cells were first discovered, and even after it became fairly certain that all organisms were composed of them, no one appreciated how fundamentally the cells were involved in the constitution of living things. They were thought, for example, to be of secondary origin; that is, animals and plants were believed to possess a formative or nutritive substance without any particular organization or structure, and out of this the cells were supposed to be formed. While all organisms were found to contain cells, it was not thought that these cells had any necessary function in the production of new cells out of the formative material. Gradually, however, the idea gained ground that the origin of new cells occurred by division of old cells, a doctrine which in 1855 was expressed by the famous pathologist Virchow in the words *omnis cellula e cellula*—all cells from cells. While the origin of cells from cells was thus early recognized, the mechanism by which cells originated from other cells was not known until twenty or thirty years later. It was not until 1873 that the common method of cell division—resolution of the chromatin into distinct separate bodies and the formation of a spindlelike mechanism manipulating these bodies—was discovered. The same method was soon witnessed in a variety of plants and animals and is now found to be nearly universal. To this method of cell division the names *mitosis* and *karyokinesis* are applied. The latter is the more descriptive, but the former is more often used.

Interphase.—A cell not in division is said to be in *interphase.* In such a cell the chromatin is so diffuse as to present the appearance of a network (Fig. 35*A*). Actually, in most cells, this chromatin exists in a number of distinct portions, the *chromosomes;* but the threadlike form which these chromosomes take in most animals makes it impossible to distinguish them. In a few organisms (some grasses among them) the chromosomes are more condensed and are separately visible even in the interphase. In some special tissues, such as the salivary glands of flies, the chromosomes are greatly enlarged and are more easily recognizable in interphase than in any cell division. The chromosomes of these glands also have a pattern by which they can be distinguished; and every nucleus has a set of chromosomes identical in pattern with those of any other nucleus. The individuality of the chromosomes which is so evident in these glands undoubtedly exists elsewhere. One indication of this is found in animals which have different shapes and sizes of chromosomes. At every division there is the same number of chromosomes of a given shape and size, which could hardly be true unless the chromosomes maintained their identity in the intervening interphase. Also, chromosomes may be broken up by X rays, and reconstituted in new sizes and shapes, and these new chromosome forms appear again after cell division and in later generations. Obviously chromosomes

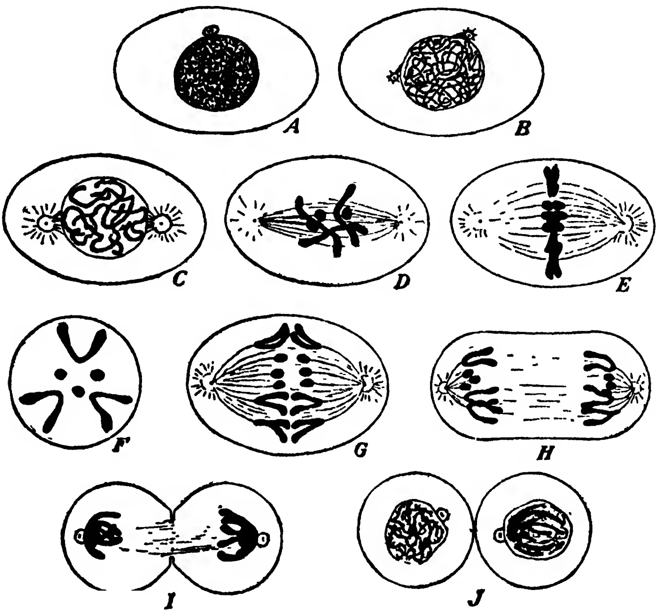

FIG. 35.—Mitotic cell division. *A*, cell not in division; *B*, centrioles move apart; *C*, distinct chromosomes formed; *D*, nuclear membrane dissolved, spindle completed; *E*, *F*, equatorial plate, side and end view, with chromosomes duplicated; *G*, *H*, chromosomes move apart; *I*, *J*, division of cytosome and construction of new nuclei. (*A*, interphase; *B-D*, prophase; *E*, *F*, metaphase; *G*, *H*, anaphase; *I*, *J*, telophase.)

maintain their individuality in the interphase, even though it cannot be observed.

Prophase.—Mitosis is nearly enough alike in most cells to make possible a general account of the process. Starting with a cell in interphase, in which the centriole is already divided into two parts, one of the early signs of division is the condensation of the chromatin into distinct threads tangled about in the nucleus (Fig. 35*B*). In whatever way the chromosomes (page 26) are spread out through the nucleus, they now contract into smaller compass, usually in the form of slender strings or ribbons. The parts of the centriole separate and move toward opposite sides of the nucleus. Sometimes between them a few threadlike lines are stretched, and around each one radiating lines may develop, giving the appearance of a star. The contraction of the chromatin continues, and before the process is more than well under way the chromosomes are distinguishable as separate bands or ropes (*C*). The entire scattered chromatin of the interphase nucleus is now collected into these conspicuous bodies. Though the chromosomes have been separate bodies all the time, it can now be seen for the first time that they are distinct. While this change in the chromatin has been taking place, the nucleolus, if one was present, has disappeared. The centrioles have moved around to opposite sides of the nucleus, and very distinct threads from them appear to be pushing against or even into the nucleus. The membrane of the nucleus then dissolves away, leaving the chromosomes free in the general protoplasm. Some of the threads from each centriole quickly pass through the space formerly occupied by the nucleus and connect with the other centriole, establishing a complete *spindle* between them. Other threads go only halfway and end at the chromosomes. The chromosomes shorten still further and thicken to form definite bodies, often of very different shapes and sizes within the same cell. The chromosomes are placed where the nucleus was, without any particular arrangement. The changes so far described, including stages *B* to *D* in the figure, are collectively called the *prophase*, though the plural form would be more accurate.

Metaphase.—The chromosomes then move, probably are drawn, into a flat group across the middle of the spindle. In this position they form what is called the *equatorial plate*. Seen from the side of the spindle they appear as in *E*, but viewed from one of the centrioles they are as in *F*. This stage of mitosis is called the *metaphase*. It is of very brief duration, so that it appears less often in preparations than the other stages do. Either in the metaphase or at some earlier time, the chromosomes become double structures. This doubling is usually described as a division, but it may equally well be conceived as a duplication, that is, the formation of a second chromosome just like the original. It is not important to decide at this point which of these methods is employed, since in either case two identical chromosomes exist where only one of that kind existed before. The chromosomes are shown thus duplicated in *E*, less clearly so in *F* because of the direction from which they are viewed.

An important feature of this division is that the two chromosomes produced from one are, in all significant features, identical with each other and with the original chromosome which produced them. To understand this fact one must know that the chromosomes have a longitudinal pattern. They contain different substances at different points in their length. A longitudinal division of the chromosome divides all the different components, so that the resulting two chromosomes have the same pattern as the original one.

Anaphase.—From their position in the equatorial plate the two chromosomes, formed from one, move or are drawn toward opposite ends of the spindle. This stage is known as the *anaphase.* The shapes of the chromosomes often indicate that they are being pulled. Thus, in Fig. 35*G*, the long chromosomes could be given their V shape by being pulled from their middle points toward the centrioles. Moreover, some of the so-called fibers extending out from the centrioles may often be seen to attach to the chromosomes at these points. Consequently, the fibers are often thought of as pulling the duplicated chromosomes apart. Whether they actually pull or not is uncertain. The fibers may be only lines of flow in the protoplasm, that is, courses along which the fluid protoplasm is moving. Whatever causes this flow could drag the chromosomes along. If the middle parts of the long chromosomes were caught in this current, the characteristic V form of such chromosomes would still result.

Whatever the cause of their movement, one chromosome of each pair of duplicates goes to each end of the spindle (*H*). Here they collect in two close groups (*I*), ready to form two new nuclei. In the meantime the cytosome narrows between the retreating groups of chromosomes (*H*, *I*) and finally constricts in a sharp furrow (*I*) which eventually cuts the cell completely in two (*J*). In many cells, about this time, the centriole divides in two, as if in preparation for the next division (*I*), so that during the whole ensuing interphase the centriole is double.

This separation of the daughter chromosomes has as important a consequence as does the longitudinal duplication of each one. The chromosomes are of different kinds; they contain different things. Each cell possesses a complete set of the different kinds of chromosomes. The accurate separation of the sister chromosomes, one going to each pole of the spindle in the anaphase, insures that the two daughter cells will likewise have a complete set of chromosomes. All the cells of a multicellular animal thus have identical chromosomes in them.

Telophase.—The remainder of the process of cell division consists of the restoration of the chromosomes to the diffuse state in which they existed before division began, and the disappearance of all remnants of the division apparatus from the cytosome. The chromosomes become diffuse either by becoming filled and distended with a fluid or by spinning out their chromatin into fine, perhaps branching, threads, as explained on page 26. Some particulars of this process are given later. By either method the chromatin comes to be scattered in irregular knots or strands, giving the appearance of a network. A membrane is formed about the whole group of chromosomes (*J*) and the reconstruction of the nuclei approaches completion. During these changes the new nucleus may rotate considerably in the cytosome, as it is shown to have done in the illustration. In the figure (*J*) the two cells are shown in different stages of the reconstruction process. This is done merely to illustrate the steps involved, for as a rule they transform at about the same speed and are at all times in about the same stage.

A *B* *C*

Fig. 36.—Chromosomes of various shapes and sizes shown just before they are arranged across the middle of the spindle. *A*, oögonium of the beetle Dytiscus (*from Debaisieux in La Cellule*); *B*, spermatogonium of arrow worm Sagitta (*from Bordas in La Cellule*); *C*, egg of hellbender (*from B. G. Smith in Journal of Morphology and Physiology*).

The principal other features of the reconstruction are the loss of the remaining spindle fibers in the cytosome and the formation of a nucleolus if there was one prior to division (*J*). When these steps have been taken, two new cells of smaller size, essentially identical with one another, have been produced from one older cell.

Variations Relating to Chromosomes.—While the foregoing account represents a fairly typical mitosis, there are many variations in the process. The number of chromosomes differs greatly in different species.

Fig. 37.

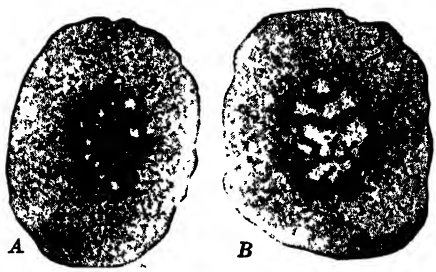

Fig. 38.

Fig. 37.—Splitting of the chromosomes before the equatorial plate stage; peritoneum of the salamander Ambystoma. (*From Parmenter in Journal of Morphology.*)

Fig. 38.—Reconstruction of nuclei through imbibition of liquid by the chromosomes to form vesicles. *A* and *B*, early and late stages of vesiculation in the egg of the sea urchin, in which the vesicles fuse. (*From Danchakoff in Journal of Morphology.*)

In the parasitic worm *Ascaris megalocephala* each cell has 4 chromosomes; in the vinegar fly *Drosophila melanogaster* the number is 8; and man has 48 chromosomes. Most of the numbers from 4 to 60 are found in one or more species, and there are some numbers above and below these limits. The number differs in the two sexes in some animals, being usually more numerous in the female when there is such a difference.

The chromosomes differ greatly in size in different organisms, and often in the same cells. Two sizes of chromosomes are shown in Fig. 35, and further differences are represented in Fig. 36.

The time of duplication or splitting of the chromosomes varies considerably. In some cells, as in Fig. 35, the chromosomes do not duplicate

FIG. 39.

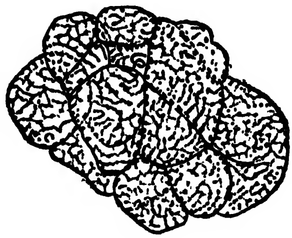

FIG. 40.

FIG. 39.—Vesiculation of chromosomes by formation of protoplasmic film around each chromosome; *A* early, *B* late stage. The vesicles do not fuse.

FIG. 40.—Interphase nucleus of the hellbender, showing the chromosomes distinct and separate as vesicles, in which, however, the chromatin is very diffuse. (*From B. G. Smith in Journal of Morphology and Physiology.*)

themselves until they are in the metaphase. In others they are doubled while still in the long ropelike stage before taking their places on the middle of the spindle (Fig. 37), that is, in the prophase.

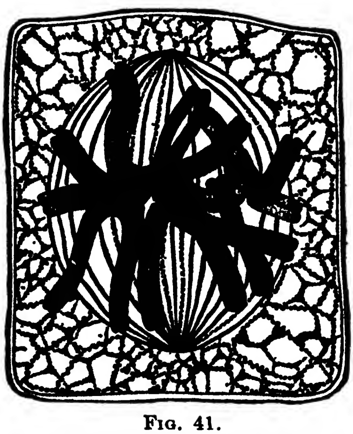

FIG. 41.

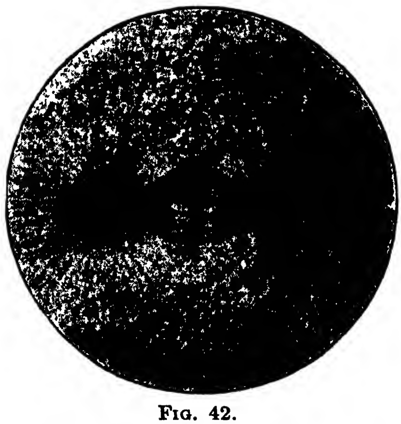

FIG. 42.

FIG. 41.—Mitosis without centrioles in a cell of the root tip of the hyacinth. (*From Dahlgren and Kepner, "Principles of Animal Histology."*)

FIG. 42.—Dividing cell with conspicuous spindle in whitefish embryo. (*Courtesy of General Biological Supply House.*)

The expansion of the chromosomes to form new nuclei at the close of division differs in different animals and plants. In some species there is a very plain formation of vesicles by the accumulation of liquid within each chromosome (Fig. 38*A*). Then the vesicles fuse to form one large vesicle (*B*), though it is still quite likely that the chromosomes maintain their individuality in and at the wall of this vesicle. In other organisms a film of protoplasm forms around each chromosome, and within the vacuole so created the chromatin spreads out in diffuse form (Fig. 39). In the example used in this figure these vacuoles do not fuse but remain separate. A third way of rendering the chromosomes indefinite in appearance, hinted at in the preceding account and earlier on page 26, is to have their chromatin spin out into fine threads, often branching, without the formation of vesicles in or around them. This method is combined with vesicle formation in the generalized illustration Fig. 35 (*J*, left). Occasionally, even when chromosome vesicles are formed, they are distinguishable as separate objects during the interphase (Fig. 40).

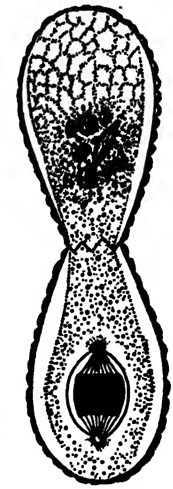

FIG. 43.—Intranuclear spindle in the protozoon Euglypha. (*From Wilson, "The Cell," after Schewiakoff.*)

Variations in Spindle and Cytosome.—A striking variation in the spindle is the lack of any centrioles in the cells of flowering plants (Fig. 41). In animal cells they may be very minute but are usually present. The rest of the spindle, that is, the fibers and radiating lines about the centrioles, may or may not be conspicuous. In Fig. 42 the spindle fibers and the rays around the centrioles are very conspicuous. But in the very flat cells in the outer layer of the skin of salamanders there is little or no sign of a spindle, even though the chromosomes are sharply defined.

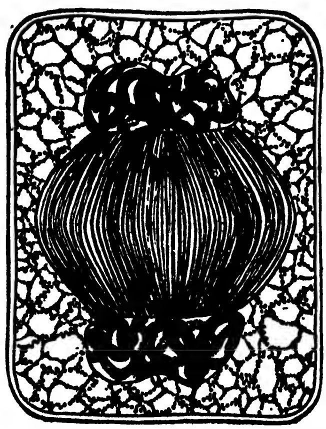

FIG. 44.—Formation of the cell plate in a dividing cell of the root tip of the hyacinth. The thickenings on the fibers of the spindle are the beginning of the process. (*From Dahlgren and Kepner, "Principles of Animal Histology."*)

The place where the spindle forms is different in different organisms. In Fig. 35 it is shown forming outside, but near, the nucleus. This is its usual origin. But in certain protozoa and some multicellular animals it forms within the nucleus. In such animals the spindle may be well developed and the chromosomes arranged on it, or the chromosomes may even be moving toward the ends of the spindle (Fig. 43), before the nuclear membrane disappears.

With respect to the cytosome, the principal variation is the way in which the two cells produced by division are separated from one another in plants as compared with animals. Instead of dividing by means of a furrow around the cell, plant cells form a group of nodules on the middle of the spindle

(Fig. 44). These lumps increase in size until they coalesce into a plate, which forms a new wall dividing the cell into two.

Amitosis.—*Amitosis* is a type of cell division which involves no complicated visible mechanism. The word means, literally, not mitosis. Many supposed examples of amitosis are merely distorted forms of mitosis, the distortion being due either to faulty preparation or to natural degenerative changes in the cells. Preparations of cells have in some cases been so defective that cell division was at first regarded as amitotic, but better technique revealed some of the features of mitosis. Also, in certain degenerate animals it appears that the process itself has become so modified that even the most perfect preparations of dividing cells resemble amitotic division very closely.

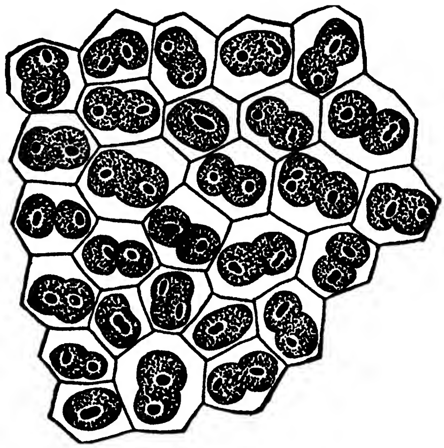

FIG. 45.—Amitotic division of the nuclei in the follicle cells of the cricket's ovary. Various stages of nuclear division are shown. (*From Conklin.*)

Confusion has arisen from the fact that the nucleus of a cell may divide without any subsequent division of the cell body. This division is often called amitosis of the nucleus, but it is not amitotic cell division. Follicle cells in the cricket's ovary (Fig. 45) show nuclear division of this sort.

Genetic Significance of Mitosis.—The longitudinal duplication of the chromosomes and the equal distribution of sister chromosomes to the cells in division, to which attention has been called, has a greater significance than has yet been indicated. The chromosomes contain the units of heredity, which are called *genes* (Chapter 17). It is these genes, more than anything else, which are arranged in longitudinal pattern in the chromosomes. In the division of the chromosomes, the greatest importance attaches to the duplication of the genes. The necessity of distributing a complete set of chromosomes to each cell rests on the necessity of having a complete set of genes in each cell. Incidentally it is the genes in the chromosomes which make the word duplication preferable to division in describing the formation of two chromosomes from one, for the genes may be single protein molecules. As such they could not be divided and retain their identity; they could, however, be duplicated.

How the cells in different parts of a multicellular animal become and do different things when they contain identical chromosomes and genes is a question which must be postponed until embryonic development is studied. The even greater importance of genes and chromosomes in reproductive cells, and a different type of cell division which manipulates the genes in germ cells, must likewise await the discussion of embryology.

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CHAPTER 6

FROM ONE CELL TO MANY CELLS

Knowledge of the structure, function and multiplication of single cells should pave the way for an understanding of the more intricate structure, function, and interrelations of the complex animals or *metazoa*. As a step toward such an understanding it will be useful to reflect upon some of the consequences of the differences between the complex and the simple.

Insight into the nature of multicellular organisms would be furnished by some certain knowledge of how they became multicellular. It seems clear that living things have not always existed in the highly complicated form that many of them now show. There must have been an origin of complex beings from simpler ones. This conclusion is often couched in the statement that multicellular organisms must have arisen from unicellular ones, but it would be somewhat safer, as we shall see, not to imply that cells were involved in the change. Some biologists hold that a step comparable to a change from one cell to many was made before these living things had arrived at a genuinely cellular constitution. But whatever the origin of multicellular organisms was, if we knew that origin we should have an important clue to some of their other characteristics.

Relation of Parts to the Whole.—Two schools of thought have arisen concerning the relation between multicellular animals and the cells of which they are composed. One school has held that the whole is the sum of its parts; hence that many-celled organisms are what their cells make them. If cells of a certain structure and certain capacities are assumed, any body composed of them will have the combined structures and capacities of those cells. The other school has regarded the whole as superior to its parts. A living thing is a whole first of all; its parts are secondary. Animals and plants are not determined by the cells composing them. Instead, they impress upon their cells certain properties because the parts of the given whole must have those properties. The former view is the more easily understood of the two, though probably only because in the physical and industrial world about us we see many examples of construction of wholes, such as buildings, out of units, such as bricks, whose properties are predetermined and do not change, just as bricks do not change when they are set in a wall. We are not accustomed to building materials whose nature depends on the kind of structure to which they contribute.

Two Contrasted Theories of Multicellular Origin.—In consequence of these two views of the relation of parts to wholes, two general theories of the origin of multicellular organisms have been entertained. According to one theory, parts have joined to make wholes; cells have joined to make many-celled bodies. According to the other theory, wholes have been divided into parts. Organisms became complex, then divided into cells whose qualities were dictated by the nature of the whole from which they were produced.

Which of these theories contains the greater element of truth it is impossible to say. As applied to the origin of metazoa, both have received ardent support from biologists. Both have certain physiological facts in their favor. On the one hand, as a purely logical deduction, it is obvious that the function of an organ is the sum of the things which its component cells do. But that deduction means nothing if the single cells are doing things which are dictated by the whole. On the other hand, it is known from the development of embryos that cells become certain structures because they occupy a certain place among their fellows. But there is no certainty that this is in any sense a consequence of a property of wholeness in the embryo. The two theories must be left, therefore, with the mere statement of their import, without any attempt to judge between them.

When, however, one considers the step-by-step consequences of the possible evolution of higher organisms by the one or the other of these general methods, the two concepts rest on different planes. Biologists have usually held that, in the evolution of any line of descent, many branches of the group have arisen, some of which have advanced farther than others. If all of these branches could be collected, they could be arranged in such an order as to give at least a hint of the steps by which the evolution of the most advanced branches had reached their ultimate condition. The less advanced types might, of course, become extinct and so destroy the evidence of the successive stages, and in actual evolution it is certain that such extinction has often occurred. On the chance, however, that some of them have survived, biologists have frequently sought among existing relatively simple organisms approximate representatives of the conditions through which the more complex ones have gone in their evolution. The attempt to reconstruct lines of descent by means of series of modern organisms must be done with caution, and no very close correspondence between modern forms and ancestral types can be expected.

In a reconstruction of the origin of the metazoa by means of a series of modern organisms supposed to represent the evolutionary steps, the two theories of the relation of parts to wholes fare very unequally. Only a few modern representatives of the one type of change may be selected, while very many are available to represent the other.

The Organismal Theory.—The organismal theory is that which treats living things primarily as wholes, to which the parts are subordinate. In accord with this theory, the evolution of complex organisms from simple ones should start with an increase in complexity in some animal or plant while it is still a single cell. Much differentiation in the structures of the cytosome must have occurred. It would be expected also that the nucleus would have divided into many nuclei without corresponding divisions of the cytosome. That is, a multinucleate cell would have arisen out of a uninucleate one. Protoplasm containing many nuclei without separating cell membranes is known in a number of animals and plants and is called a *syncytium.* Voluntary muscle cells (page 95) in the higher animals have many nuclei, and the developing eggs of insects (Fig. 172) pass through a stage in which there are many nuclei before cell membranes begin to appear. One cannot, however, think of these very complex metazoan structures as remnants of an evolutionary stage which most of the other metazoa have passed. To have any possible significance as representative of a step in evolution, the syncytium should be some rather simple organism. Vaucheria (Fig. 46), one of the simple plants, is syncytial, and there are several other plants. Good examples are lacking among animals. The organismal theory is thus not well supported by living representatives of the stages for which it calls, though this lack can hardly be regarded as a fatal objection to the theory.

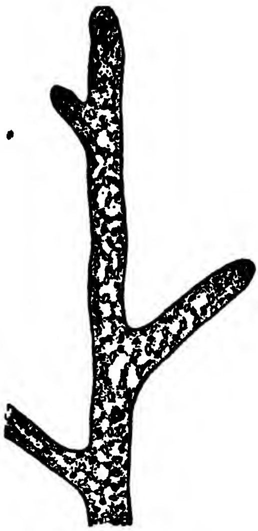


FIG. 46.—Vaucheria, a simple plant illustrating a syncytium or multinucleate cell. (*From Sharp, "Introduction to Cytology."*)

The Colonial Theory.—If one regards organisms as the sum of their component parts, the natural supposition is that multicellular animals and plants arose through some form of colony formation. Cells multiplied by division and then, instead of falling apart as they do among the protozoa, they clung together in groups. Such colonies could be formed before any of the cells became any more greatly differentiated than the single cell had been. The differentiation and increase in complexity could then follow in a succession of steps. The multicellular condition comes first, the complexity later, reversing the order expected from the organismal concept. This way of deriving the metazoa has the advantage—if advantage it be—of being capable of illustration by organisms now living. The series of types used to illustrate it must still show considerable gaps, and the representation is sure to be only approximate; but the imagination can easily fill the vacant places. Let us consider what these representative living organisms may be.

Types of Colonies.—The adherence of the two cells produced by division should require no more explanation than the physical connection and the mode of separation seen in mitosis in multicellular animals. The fact that protozoan cells should regularly separate is quite as remarkable as that metazoan cells should regularly cling together. Protozoan species in which the cells remain attached exist in colonies. Sometimes no more than two cells adhere; sometimes the number is thousands. The manner of adherence varies. An envelope of jelly may help hold the cells together, or they may be joined by stalks, or the cells may cling to one another merely by small areas of contact.

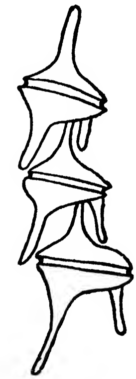


FIG. 47.—A linear colony, *Ceratium candelabrum.*

Colonies take various forms. In Ceratium (Fig. 47), the cells are in a single row, making what is called a *linear* colony. This type is rare in animals but common in the simple plants (algae), in which cylindrical cells are set end to end in long fine filaments. In some species the cells do not touch one another but are joined by branching stalks (Fig. 48),

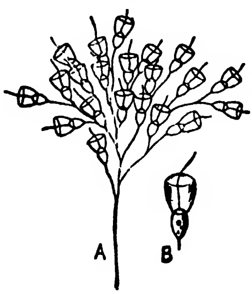


FIG. 48.

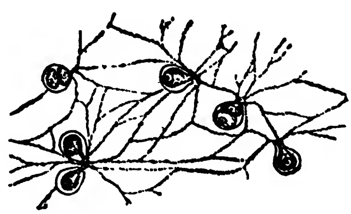


FIG. 49.

FIG. 48.—*Codosiga cymosa* Kent. *A*, treelike colony; *B*, individual cell in detail.

FIG. 49.—A gregaloid colony, *Microgromia socialis.* (*From Calkins, "The Protozoa," The Macmillan Company.*)

forming a treelike or *dendritic* colony. These branching colonies are of many degrees of complexity, from those in which two cells fork off from a single common stalk to ones in which the stalks branch and rebranch and end in hundreds of cells. These organisms are all aquatic. The branched stalks and cells may be quite exposed to the water, so that currents of water pass freely among them, or they may be imbedded, stalks and all, in a mass of jelly. Such colonies may be as large as walnuts, or even baseballs.

A third type of colony is the *gregaloid*, in which the cells are irregularly placed in a mass of jelly. These cells may be loosely arranged and in

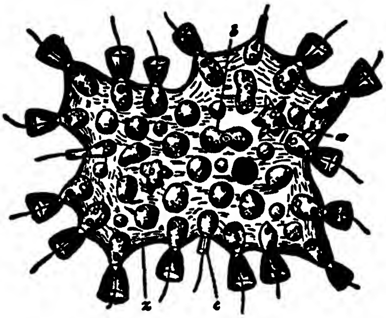


Fig. 50.

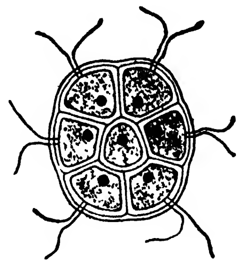


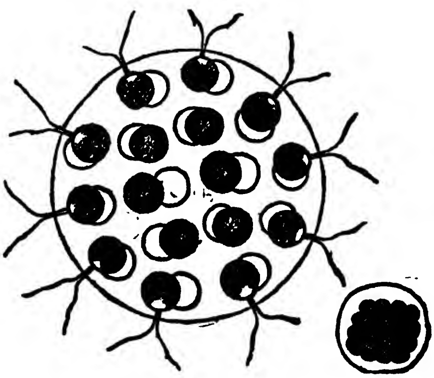
Fig. 51.

Fig. 50.—A gregaloid colony, *Proterospongia haeckeli.* (*From Hegner's "College Zoology," The Macmillan Company.*)

Fig. 51.—*Pandorina morum,* a spheroid colony.

contact with one another by means of fine processes branching out from them (Fig. 49), or they may be quite separate with only the jelly to hold them together (Fig. 50).

Somewhat more compact and more regularly arranged are the *spheroid* colonies. In these there is usually a mass of jelly nearly spherical in



A B

Fig. 52.

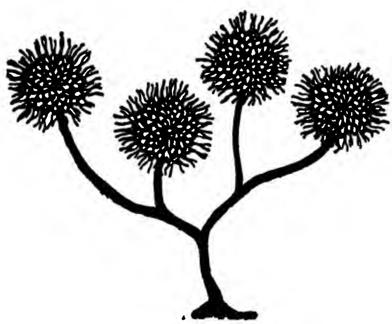


Fig. 53.

Fig. 52.—A spheroid colony, *Eudorina elegans.* *A,* adult colony, ×475; *B,* daughter colony, ×730. (*From West after Goebel.*)

Fig. 53.—*Anthophysa vegetans.* Spheroid colonies arranged on a branching stalk, thus combining two types of colonies. (*After Kent.*)

shape, in which cells are imbedded in a layer near the surface, but none is in the center. The cells may be actually in contact, or nearly so (Fig. 51), especially in young colonies (Fig. 52*B*), or widely separated, as in most such forms when older (Fig. 52*A*).

In some organisms two of these types of colonies may be combined. The cells may be in globular masses (spheroid type), though not imbedded in jelly, and several of these masses joined by a branching stalk (Fig. 53).

Choice of Colony to Illustrate Metazoan Origin.—If it is assumed, in tracing probable lines of descent, that the colonial theory is correct, which of these colonial types is most likely to represent the early evolution of the metazoa? The massive compact form of most of the metazoa suggests that the linear and dendritic colonies may be left out of consideration. Of the other two types, each has something in its favor. The fact most favoring the gregaloid colony is that in one of the best known organisms of that kind, Proterospongia (Fig. 50), each cell at the surface bears a delicate protoplasmic collar around its one flagellum. Such a collar, surrounding a flagellum, is found on certain internal cells of the sponges (Fig. 33, page 52), which constitute one of the simplest groups of metazoa. Some biologists have inferred from these collared cells that the earliest metazoa may have been in some degree spongelike and that they came from colonies somewhat like present-day gregaloid colonies.

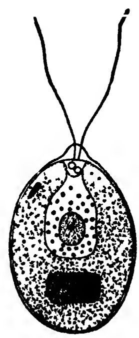


FIG. 54.—Chlamydomonas, illustrating a primitive type of organism from which colonies and later metazoa may have arisen.

The spheroid type of colony is favored by its greater abundance at the present time. Most of the spheroid colonies consist of cells bearing flagella, and many students of protozoa have held that the flagellate forms are the most primitive of the single-celled animals, which is another pair of facts in favor of the spheroid colony. Furthermore, the spheroid colonies lead directly to other forms that may, as we shall see, be used to illustrate later steps in the evolution process.

This reasoning may not be correct, but many biologists in the past have followed it and concluded that the metazoa probably arose from a single-celled organism, bearing some resemblance to modern flagellates (Fig. 54), through the formation of colonies.

The First Differentiation.—In all the colonies described, the cells of one group are all alike, at least potentially. In Proterospongia (Fig. 50) they may seem to be of two kinds, since the cells in the interior of the jelly mass do not have collars. This is not a real difference, however, for the cells take turns coming to the surface, where they feed, and while at the surface develop a collar and flagellum, which they lose when they retreat to the interior.

Now, the chief distinguishing mark of the metazoa is that their cells are not all alike. In the evolution of the multicellular organisms there must have been a differentiation of the adhering cells into two or more kinds, if the colonial theory of origin is correct—or a differentiation of the parts of the cell which later became distinct cells, if the organismal theory is correct. Following only the colonial origin, what differentiation shall we expect?

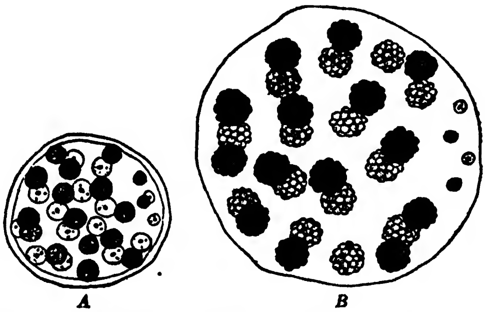


FIG. 55.—*Pleodorina illinoisensis*, consisting of 28 reproductive and 4 sterile cells. *A*, young organism; *B*, reproductive stage. The sterile cells may be regarded as the beginning of a soma.

If we are to draw our answer to this question from the animals and plants that live at present, we should look for those in which there has been only one differentiation—in which, as a consequence, there are only two kinds of cells. The only organisms which exhibit a single differentiation among their cells are those in which some cells have lost the power of reproduction, while others retain it. Pleodorina is an example. In one

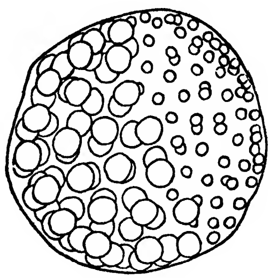


FIG. 56.

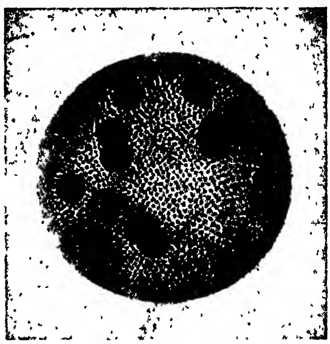


FIG. 57.

FIG. 56.—*Pleodorina californica*, with small sterile cells almost as numerous as large reproductive ones.

FIG. 57.—*Volvox weismannia*, with 10 reproductive cells and thousands of sterile cells. (*From Powers, in Transactions of American Microscopical Society.*)

of its forms (Fig. 55), which may be only a variety of *Eudorina elegans* (Fig. 52), it consists of 32 cells in a jelly matrix. Four of these cells, placed at that side which moves foremost as the organism swims, are smaller than the rest. These 4 cells are sterile, while the remaining 28 may reproduce. Any of the 28 larger cells may divide to form a group of 32 cells which escape from the jelly and lead an independent existence or form special cells which reproduce the group in another way; but none of the 4 small cells can do this. In another species (Fig. 56) the cells are more numerous, and the sterile and reproductive cells are more nearly equal in number; but they are again of two sizes, the smaller ones being sterile. Volvox (Fig. 57) is another, though much larger, form in which there are sterile and reproductive cells; but here the sterile cells greatly outnumber the reproductive. The two Pleodorinas and Volvox, taken in the order in which they are used here, show an increasing number of the sterile cells.

The existence of such forms as these suggests that the earliest differentiation between the cells of a colony, on its way to becoming a metazoon, was the loss of reproductive powers by some of the cells. The group of sterile cells in these organisms corresponds to the *soma*, or body, as contrasted with the *germ cells*, or reproductive cells, of the metazoa.

Further Differentiation.—In the organisms just studied, all the sterile cells are alike in structure and function, except in Volvox, in which the cells on the front side, as the organism swims, differ slightly in color and the size of certain of their structures from those on the rear side. This is quite at variance with the higher metazoa, in which the cells of the soma are of very many markedly different kinds. There is no way of knowing which of the many types of somatic cells originated earliest; hence no clue as to what kind of modern animal we should look for to illustrate that step. The best we can do, if we are to pursue this plan of choosing present-day representatives, is to select some animal in which the differentiations among the somatic cells are not too numerous. A suitable form is the fresh-water Hydra, in which half a dozen kinds of somatic cells are found. A brief description of the body as a whole must precede the study of these cells.

Fig. 58.—Hydra, showing general form of body, with bud.

The form of Hydra is essentially cylindrical (Fig. 58) when extended and more or less globular when contracted. Ordinarily the body is attached by one end, the *foot*, to a solid object. At the tip of the free end of the body the *mouth* is located. Near the mouth is a circlet of long contractile *tentacles* which have arisen from the body by an outpushing of the body wall. By means of the tentacles Hydra captures and thrusts into its mouth minute aquatic animals. The conical eminence between the mouth and the tentacles is the *hypostome*.

The body of Hydra is hollow (Fig. 59), the interior space being a digestive cavity. Its wall is composed of two layers of cells, the outer known as the *ectoderm*, the inner as the *endoderm*. The endoderm cells are all essentially alike, being tall and slender and bearing flagella. Their function is the digestion of food. The ectoderm has differentiated into several kinds of cells. The bulk of that layer is made up of nearly cubical cells called the *epithelial* cells. Some of these epithelial cells, at the side toward the endoderm, are drawn out into long slender processes which serve both to contract, like muscles, and to convey impulses, like nerves. They are accordingly called *neuromuscular* cells (Fig. 60). Between the bases of the epithelial cells are numerous smaller rounded cells which, from their location, are named *subepithelial* cells. These give rise, at intervals, to very specialized cells, the *cnidoblasts*, which travel toward the surface of the ectoderm and produce within themselves a threadlike stinging apparatus called a *nematocyst*. As the nematocysts are consumed in attacking other animals or in defending the Hydra, other cnidoblasts migrate to the surface and produce new stinging threads. At the foot of the animal the epithelial cells have the ability to produce a sticky substance by which the body is made fast to other objects and may therefore be called gland cells.

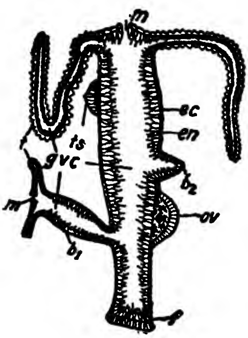


FIG. 59.—Hydra, diagrammatic representation of a lengthwise section. b_1, b_2, buds in different stages of growth; *ec*, ectoderm; *en*, endoderm; *f*, foot; *gvc*, gastrovascular or digestive cavity or coelenteron; *m*, mouth; *ov*, ovary; *t*, tentacle; *ts*, testis.

Hydra has also reproductive cells, which are included in the ectoderm layer and which at intervals develop into the mature cells, *eggs* and *spermatozoa*. The former, which are the female cells, raise the ectoderm into a rounded lump called the *ovary* (Fig. 59*ov*); the latter, the male cells, elevate the ectoderm into a conical mound called the *testis* (*ts*). Hydra also reproduces by buds (Fig. 59b_1, b_2), into which all the various body cells in the region of the bud enter.

It is thus apparent that Hydra, like Pleodorina and Volvox of the preceding section, possesses germ (reproductive) and somatic (sterile) cells. The existence of a budding process in Hydra, by virtue of which the somatic cells may share in the production of new individuals, does not alter the fundamental contrast between one class of cells which retain the typical mode of reproduction and another class of cells which have lost that power. Unlike Pleodorina and Volvox, however, Hydra has not stopped with this one differentiation. It has gone farther and differentiated its somatic cells into five or six different kinds.

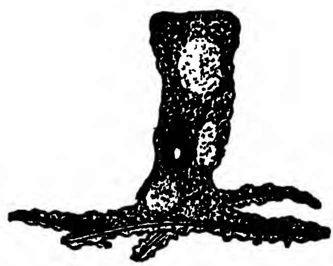


FIG. 60.—Neuromuscular cell of Hydra. (*From Schneider.*)

Parallel between Foregoing Series and Individual Development.—Some biologists have favored the foregoing series of colonial protozoa and simple metazoa as representative of the course of evolution of the metazoa because it finds a parallel in the development of the individual among the metazoa. Whether this parallel has any particular significance, or is of interest only as part of the historical development of evolution theory, is uncertain, but the comparison is interesting.

Individual development begins with a single cell, the egg, which is comparable to the supposed protozoan ancestor of the metazoa. This egg divides repeatedly (Fig. 61*II–IV*) to form a group of cells, which may be likened to the protozoan colony. As the division of the egg proceeds farther, it yields a hollow ball of cells, the *blastula* (*V*, *VI*), which has a form very much like that of Pleodorina and Volvox. It will be recalled that in these organisms the cells are all near the surface, no cells being at the middle of the jelly. The next step in development is the indentation of one side of the blastula to form a two-layered embryo, the *gastrula* (Fig. 62*A*, *B*). When a diagram of Hydra is placed beside a diagram of a gastrula (*B* and *C*, Fig. 62), they are seen to be built on the same general plan—that of a two-layered sac open to the exterior at one end. At a stage quite as early as these, some animals show the distinction between germ and somatic cells (Fig. 63), just as Pleodorina, Volvox, and Hydra do. The germ cells are usually larger than the somatic

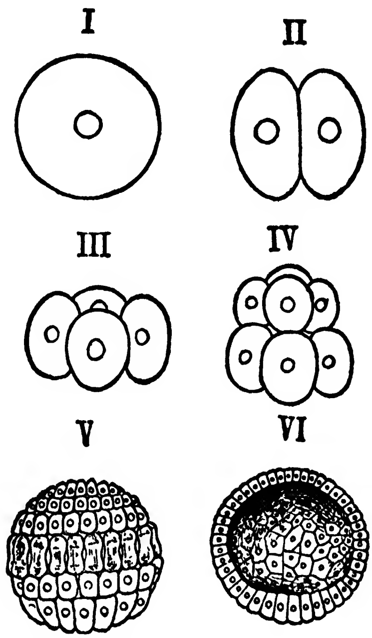


FIG. 61.—Early metazoan development. *I*, undivided egg; *II–IV*, successive segmentation stages; *V*, blastula, exterior view; *VI*, blastula in section to show hollow interior or blastocoele. (*From Wilder, "History of the Human Body," Henry Holt and Company, Inc.*)

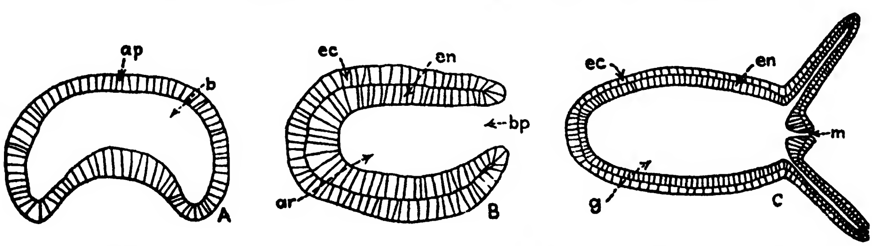


FIG. 62.—Gastrula compared with Hydra. *A*, beginning of gastrula formation; *B*, completed gastrula; *C*, diagram of Hydra; *ap*, animal pole; *ar*, archenteron; *b*, blastocoele; *bp*, blastopore; *ec*, ectoderm; *en*, endoderm; *g*, gastrovascular cavity; *m*, mouth.

cells, when they can be distinguished at all, and sometimes contain granules of a peculiar sort. Finally, to complete the comparison, development of the embryo need be followed only a short way to observe differentiation of the somatic cells into at least as many kinds as Hydra possesses.

A Conclusion, and Caution in Adopting It.—The principle of using embryonic development to discover the course of evolution is known as the *biogenetic law*. According to this generalization, the development of an individual repeats the history of its race. This law is seriouly questioned by many biologists and vigorously opposed by some. Also, the use of series of modern organisms to illustrate what may have taken place in evolution must be made, if at all, with great care. Both of these comparisons have been made, however, by biologists in the past, using the organisms referred to in the preceding pages. The conclusion to which they lead is that metazoa have arisen through (1) the adherence of protozoan cells to form a colony, (2) the loss of reproductive powers by some of the cells of this colony, and (3) the differentiation of these sterile cells into a number of kinds. These are the fundamental steps; the details of cell structure and the general form of the colony are immaterial.

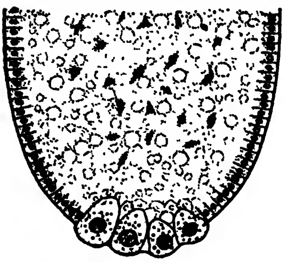


FIG. 63.—Posterior end of developing insect egg. Large cells at tip are reproductive cells, all others somatic.

This conclusion, it will be observed, accepts the colonial and rejects the organismal theory. It rather favors spheroid colonies over the gregaloid type because the modern organisms available for a series of representative types are spherical, and because the blastula of embryonic development is a hollow ball. Many biologists hesitate to recognize these reasons, and reference to them here is in no sense a pronouncement in favor of the mode of origin of the metazoa which they appear to indicate. Nevertheless, that origin is not improbable. And even if the scheme of evolution described should be far from correct, a consideration of it has led to an understanding of the relation of parts to wholes and a glimpse of some of the situations which many-celled organisms have to meet.

What Is a Colony, What an Individual?—When any change is effected by a number of graduated steps, as the origin of metazoa from simpler organisms must have been, it is difficult to say just when any stage that may be named is reached. When, for example, has a metazoon been evolved out of a protozoon? How far must the change go to be recognized as having reached that goal? No matter what process led to the metazoa, the answer to this question must be a matter of definitions. If the organismal theory is correct, was the animal with numerous nuclei but no cell membranes around them a metazoon? If not, was it a metazoon as soon as the cell membranes were formed? If not then, was it a metazoon after some differentiation among those cells had occurred? If the colonial theory is correct, was the first group of adhering cells a metazoon or only a colony of single-celled animals? Would a group of a thousand cells be a metazoon, while a group of four was only a colony of protozoa? If number makes no difference, would differentiation among the cells constitute the mark of a metazoon?

Whatever the event that marks the advent of a metazoon, the organism that has experienced that event is an individual. Without that characteristic, it is a protozoon or a colony of protozoa, depending on the nature of the origin of the metazoa. Biologists have differed in their definition of the individual. To some, a group of cells that shows any differentiation becomes a metazoan individual. Since in actual cases when only one type of differentiation exists it is that between reproductive and sterile cells, as in Pleodorina, defining the multicellular individual as any group of cells in which differentiation exists is equivalent to saying that the individual is any group in which sterile cells are set apart from reproductive cells. Other biologists have insisted that a group of cells is not an individual unless its sterile cells are differentiated into several kinds, as in Hydra. Under the former definition Pleodorina and Volvox are individuals; under the latter they are colonies of unicellular organisms exhibiting division of labor, since some reproduce and others do not.

The distinction between reproductive and sterile cells is more fundamental than the distinctions among several kinds of sterile cells. In this respect the former definition has the advantage. It is also preferable for the reason that the criterion of individuality is, according to it, always the *same* thing—loss of the capacity to reproduce by some of the adherent cells—while under the latter definition the criterion of the individual would presumably be a *different* distinction between sterile cells in every line of descent. But definitions are arbitrary, and there is no tribunal except usage which can choose among them.

Further Organization.—Beyond the stage at which they are barely entitled to be called metazoa, most of the higher animals have gone long distances. They have increased the number of their cells so that even a moderate-sized animal contains literally billions of these units. With increase in size, they have usually developed a framework or shell of some sort which provides protection or aids locomotion. Special devices are created for the providing of food and the elimination of waste materials. With large volume, they have had to provide means of communication by which substances may be quickly transported from one part to another. Structures of different sorts capable of effecting movement have arisen. Unified control and the harmonious working together of the various parts have been provided in different ways. So multifarious are these characteristic developments that a group of chapters, immediately following, must be devoted to them.

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CHAPTER 7

BASIC ORGANIZATION OF THE METAZOA

Beyond the evolutionary stages traced in the last chapter, ending with the differentiation of the somatic cells into a number of kinds, the metazoa have gone various ways in great groups. Within each group there is much in common, both in structure and in physiology; but between groups there are many differences. Scarcely anything is common to them all. There are a few features, however, that are characteristic of several or many of the great groups. Some of the more important of these frequent structural conditions should be passed in review.

Symmetry.—Symmetry is an arrangement of parts in relation to planes, straight lines or points. A point is a position in space; it has no dimension or size. A straight line is the shortest distance between two points; it has only one dimension, length. A plane is, in common words, a flat surface; more precisely it is a geometric figure of two dimensions—length and breadth but no thickness—such that if any two points in it be connected by a straight line that line is everywhere within the figure.

Symmetry is defined as a correspondence in shape or arrangement of parts on opposite sides of a dividing line or plane, such that if the portion on one side were viewed in a mirror it would appear identical with the part on the other side. A symmetrical surface is divided into the corresponding parts by a straight line; solid (three-dimensional) objects, including animals, are divided into their equivalent parts by a plane. The plane which divides a body into its corresponding halves is called the plane of symmetry. Objects have different types of symmetry (Fig. 64) depending on the number of planes of symmetry which may be passed through them. If only one such plane is possible, the symmetry is *bilateral.* Most animals (including all the higher ones) are bilaterally symmetrical. They possess anterior and posterior ends which differ, right and left sides which are alike except for the reversed order, and a dorsal side (at or toward the back) and a ventral side (literally pertaining to the belly, hence opposite to the dorsal side). The plane of symmetry passes through the two ends, through the dorsal and ventral surfaces, and between the right and left halves.

Some animals possess a number of planes of symmetry. If these planes all have a certain straight line in common, that line is the axis of symmetry. An axis is a line around which something rotates, or around which things are placed. The planes of symmetry may be thought of as rotating on the axis of symmetry. Symmetry of this sort is known as *radial.* In one of the major groups of animals (Fig. 65) the

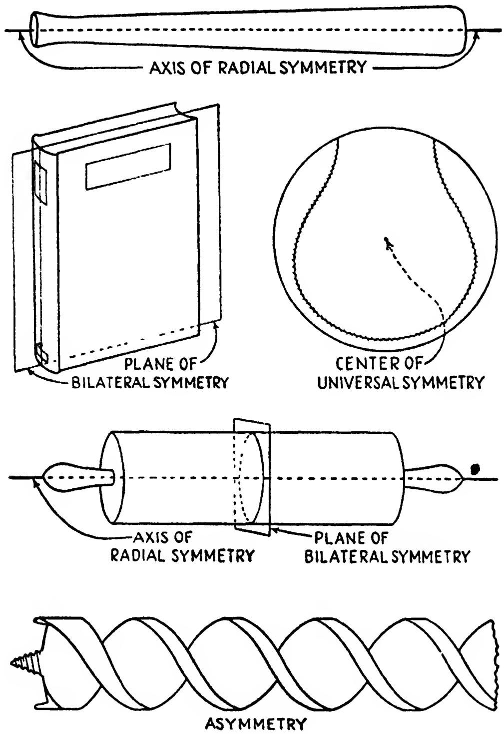


FIG. 64.—Types of symmetry illustrated by familiar objects.

bodies regularly possess radial symmetry. The arms or tentacles of the animals of that group limit the number of planes that divide them symmetrically; in practice the symmetry is called radial if there are two or more such planes all having the axis line in common.

Sometimes there are many planes of symmetry having, not a line, but a point in common. Symmetry is then said to be *universal,* and the common point is the center of symmetry. In a sphere, any plane that passes through the center is a plane of symmetry. Not many animals have a spherical form, but Eudorina (Fig. 52) approaches it.

An object may possess symmetry of two types. A football, for example, has radial symmetry around its long axis, but bilateral symmetry in relation to the plane halfway between its ends. Some cells have approximately that form, as do also some protozoan colonies.

In general, animals which move rapidly or are capable of well coordinated movements are bilateral. The radial animals are usually slow movers and frequently are attached to fixed objects. Universally symmetrical animals are aquatic and progress with a rolling movement.

Asymmetry.—Any object which cannot be divided into corresponding halves by any plane is said to be asymmetrical. Many of the protozoa are made asymmetrical by a groove running spirally part way round the body. The coiled shell of a snail is asymmetrical.

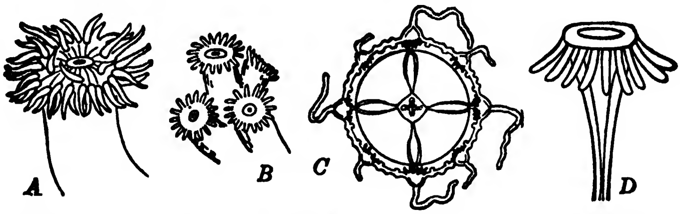


FIG. 65.—Various coelenterates, showing their radial symmetry. *A*, sea anemone; *B*, group of coral polyps; *C*, the medusa, *Mitrocoma cirrata*, ventral view. *D*, polyp of the hydroid, *Perigonimus serpens*. (*A and B after Jordan, Kellogg, and Heath; C after Mayer; D after Allman.*)

Many animals which are externally symmetrical may have their internal structures arranged on an asymmetrical plan or on a plan of symmetry different from the external plan. Examples are the heart, stomach, and other parts of the alimentary tract and the lobes of the liver in man, which are arranged asymmetrically. Many animals which exhibit asymmetry in certain of their adult organs are symmetrical in early stages of development. The flatfishes (halibut, flounder, and sole) which have two eyes placed on one side of the head, are in their early embryos bilaterally symmetrical, but one eye migrates through the head to its new position.

Metamerism.—Animals exhibiting metamerism are composed of a linear series of body segments fundamentally alike in structure. These units are called *somites* or *metameres*, and animals so constructed are said to be *metameric*. In simple metameric animals the somites closely resemble one another in size, form, and the arrangement of organs. In no animal, however, are all somites entirely alike because some of them have become specialized and perform special duties.

The common earthworm (Figs. 135, 137) is a metameric animal. It is composed of a series of ringlike somites outwardly much alike. The limits of the somites are marked on the outside by grooves, and on the interior by the septa (cross partitions) which lie immediately under the grooves. The segmental arrangement extends to both external and internal structures and involves organs of locomotion and excretion, muscles, blood vessels, and the nervous system. The sexual organs also have a segmental arrangement, although they are limited to a few somites.

Certain other organs are repeated in only a few segments, but in general the earthworm's structure is that of a metameric animal.

In complex animals the metameric arrangement has often become obscured through fusion of somites, loss of organs, and centralization. The primitive arrangement, however, is readily seen in the embryos of such animals. Thus the embryos of the vertebrates generally reveal a well-marked metamerism in certain organs (the muscles, for example), in which this arrangement is later partly or completely lost. Not all metamerism has been lost even in the adult vertebrates, however, for it may be seen in the vertebrae and ribs (Fig. 79), spinal nerves and ganglia (Fig. 117), and branches of the dorsal artery.

Body Cavities.—Most of the higher animals have a cavity of some sort in their bodies, but these cavities are of several kinds. In Hydra (Fig. 59)

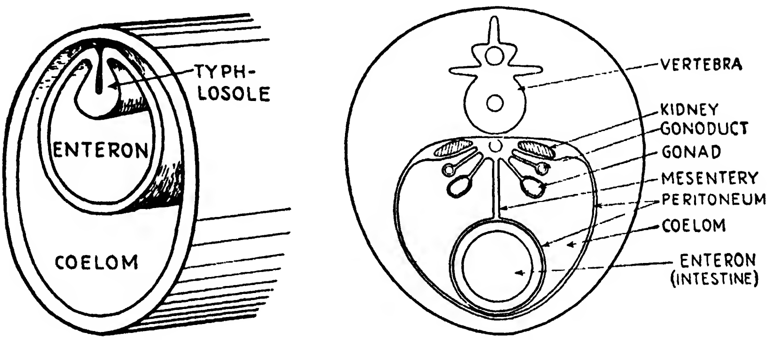


FIG. 66.—Relations of body cavities (enteron and coelom). At left, the earthworm; at right, cross section of a vertebrate animal.

there is but one cavity, which is open at one end, the mouth, and closed at the other end. A cavity so constructed is called a *coelenteron*, though in Hydra, in recognition of its function of digestion and its assumption of some of the tasks of a blood system, it is often named the *gastrovascular cavity*. Flatworms also have a coelenteron. Undigested food must, in such animals, be ejected through the mouth.

In most of the metazoa there are two cavities. One is in the digestive tract, the other lies between the digestive organs and the body wall. The digestive cavity in most complex animals is open at both ends and to distinguish it from the closed sac in Hydra is known as the *enteron*. The space between the digestive organs and the body wall is the *coelom*. These relations are shown diagrammatically for the earthworm in Fig. 66 (left). In vertebrate animals (right) the cavities are in the same relative position; the coelom appears to be filled with many organs. These, however, are merely pushed into it from the outside. Since some animals (the lobster, for example) have irregular spaces among their organs, filled with body fluids, there is sometimes difficulty in deciding whether a cavity is a coelom or not. In general, the coelom must be lined by a definite layer of cells, the *peritoneum*, which is lacking around the spaces in the lobster, and the principal reproductive organs (*gonads*) are suspended from its walls.

Tissues.—In practically all metazoa in which the several kinds of somatic cells are very numerous, those of any one kind are grouped together, not necessarily all in one place but usually in a number of places. In Hydra (Fig. 59), as we have seen, all endoderm cells together form a continuous layer constituting the inner part of the body wall. The epithelial cells are similarly placed together in the ectoderm. The secreting cells of the foot are together in a small group. The other somatic cells of Hydra are not conspicuously grouped, since the subepithelial cells and the cnidoblasts derived from them do not form a continuous layer.

FIG. 67.—Connective tissue, consisting of cells, matrix, and fibers.

In most metazoa the somatic cells of any given sort are more conspicuously assembled in layers or masses than in Hydra. Such groups or masses of like cells are called *tissues*. A tissue may be defined as a number of cells of the same kind forming a continuous mass. Ordinarily they perform some function in common, but it is not necessary to know their function to consider them a tissue. Tissues may be classified on the basis of both structure and function. In the vertebrate animals these classes are *sustentative, epithelial, contractile, nervous, vascular,* and *reproductive.*

Sustentative Tissues.—The sustentative tissues are primarily those which support. The typical sustentative tissue is ordinary connective tissue which binds the skin to the flesh beneath or holds the muscles of the thigh together in a mass or helps suspend the intestine from the body wall. It contains scattered cells (Fig. 67), but the serviceable part is made of things secreted by the cells. These things are a gelatinous *matrix*, or ground substance, and large numbers of tough fibers imbedded in the matrix. It is the latter that give connective tissue its strength.

Certain connective tissues of very great strength are given special names. The ligaments binding bones together at the joints, and the tendons joining muscles to the bones which they move, are examples. The essential features of connective tissue—cells, matrix, fibers—are present in both, but the fibers far outbalance the other parts.

Cartilage and bone are likewise specialized forms of sustentative tissue. They are alike in having their cells more or less scattered in a substance, the matrix, which the cells have secreted. In cartilage the cells are entirely separate from one another, though often placed in pairs, trios, or quartets (Fig. 68) resulting from recent divisions of an earlier cell. The matrix is firm or pliable, contains much gelatin, and is used as a buffer to absorb shock or in places requiring flexibility. In bone the cells possess numerous slender projections, some of which, probably, are always in contact with similar projections from other cells (Fig. 69). The hard bony material of the matrix, consisting largely of calcium carbonate

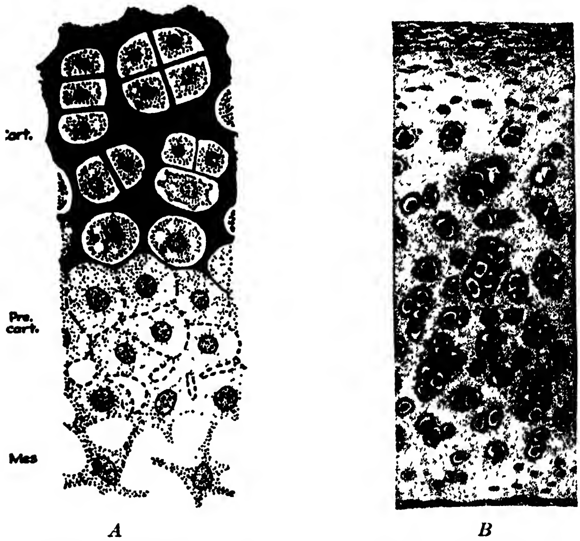
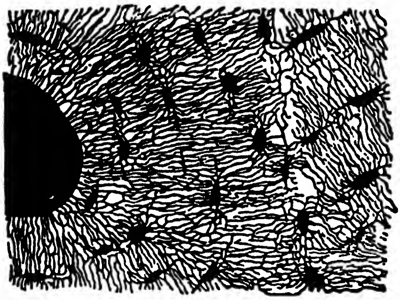


Fig. 68.—Sections through cartilage. *A*, development of cartilage (top) from mesenchyme (bottom); *B*, hyaline cartilage. (*From Lewis-Stöhr, "Textbook of Histology," The Blakiston Company.*)

and calcium phosphate, is secreted by these cells; consequently there are always spaces in the bone for the cells and their slender processes.

Fatty or adipose tissue is regarded as sustentative, but rather because of its original similarity to connective tissue than from any mechanical function which it may serve. The cells are numerous and closely packed, not scattered as in other sustentative tissues. The fat itself is in globules of small or large size contained within the cells. It is reserve food; hence fatty tissue fluctuates greatly in volume, depending on the state of nutrition of the organism. Favorite places for the deposit of fat are in the abdominal wall and beneath the skin at many other places.

In many embryos, and in the adult of certain lower animals, such as the flatworms, there is a tissue known as *mesenchyme*, which should be included with the sustentative tissue, though chiefly because of its structural resemblance to some of the supporting tissues. It is a very loose tissue whose cells are irregular, often star-shaped. These cells are not closely packed but touch one another only by their corners or the tips of their projections (Fig. 70). Considerable space is thus left among the



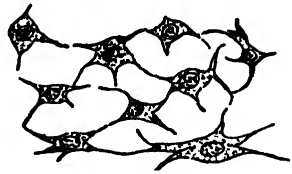


FIG. 69. FIG. 70.

FIG. 69.—Section through bone, showing the stellate spaces in the matrix occupied by cells, and at left part of the space occupied by a blood vessel. (*From Hill, "Manual of Histology and Organography," W. B. Saunders Company.*)

FIG. 70.—Mesenchyme from umbilical cord. (*From Hill, "Manual of Histology and Organography," W. B. Saunders Company.*)

cells, which is filled with some more or less liquid substance. This spongy structure is everywhere characteristic of mesenchyme.

Epithelial Tissue.—An epithelium is a layer of cells covering some surface, either the outside of an organ or the lining of the wall of a cavity.

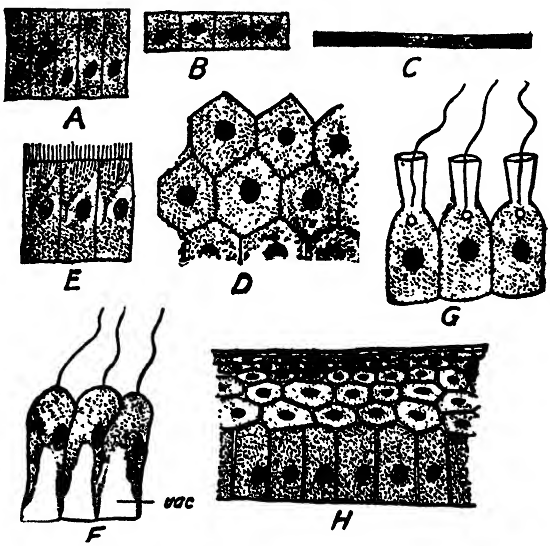


FIG. 71.—Types of epithelium. *A*, columnar; *B*, cubical; *C* and *D*, squamous (side and surface views, respectively); *E*, ciliated; *F*, flagellate; *G*, collared; *H*, stratified; *vac*, vacuole.

The endoderm and ectoderm of Hydra, already described, are epithelia. Others likely to be observed in laboratory studies are the outer layer (hypodermis) of the body wall of the earthworm, the lining of the intestine of any animal, the peritoneum which covers the intestine and lines the abdominal cavity (coelom) of vertebrate animals, the outer layer (epidermis) of the skin, and the inner or secreting layer of any gland.

An epithelium is designated *cubical, columnar,* or *squamous,* according to the shape of its component cells (Fig. 71*A–D*), the last term meaning flat and tilelike; *ciliated, flagellated,* or *collared,* if the free ends of the cells bear any of the structures indicated by these words (*E–G*); and *stratified,* if the layer is several cells thick and the cells at different levels have different shapes (*H*).

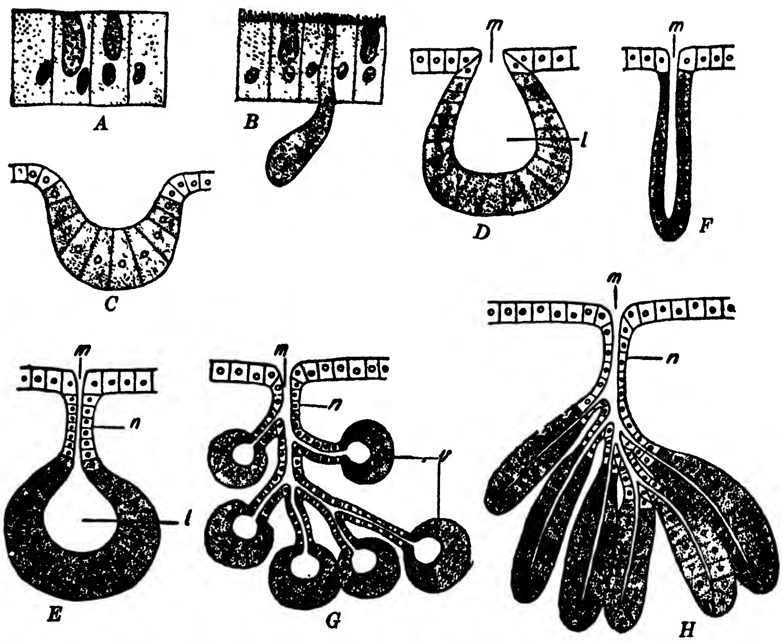


FIG. 72.—Types of secreting surfaces and glands. *A*, scattered gland cells (two goblet cells containing secretion in the darkly stippled *goblets*); *B*, gland cell enlarged and dropped below general level; *C*, group of secreting cells dropped slightly below the general level; *D*, a simple multicellular gland; *E*, alveolar gland with neck; *F*, tubular gland; *G*, compound alveolar gland; *H*, compound tubular gland; *l*, lumen; *m*, mouth; *n*, neck; *v* acini. Secreting portions of the glands are stippled.

Epithelia on the outer surfaces of organs are usually in some degree protective. When they line a cavity, they often have the function of secretion. The lining membrane of the intestine in vertebrate animals is secretory, and in all glands the secreting portion is epithelium. If a gland consists of a single cell, that cell is in an epithelial layer (Fig. 72*A*, *B*). If the gland is multicellular, its secreting cells may dip below the general level of the surface, but still it is part of the epithelium (*C*, *D*). When the secreting cells thus indented form a channel of nearly uniform diameter, the gland is said to be *tubular;* if the deepest portion is expanded like a flask, the gland is *alveolar*. Such an indented epithelium may branch, that is, form subsidiary indentations (*G*, *H*), and then the gland is termed *compound*, as contrasted with *simple* glands in which the tube is not branched. Nearly all glands, in the higher animals at least, have other tissues, including blood vessels, collected around or spread among the epithelial part; but in every case it is the epithelium that does the actual secreting.

The Other Tissues.—The two types of tissues described in the preceding sections are distinguished largely on structural grounds, while the functions performed by different samples of them may be quite unlike. The remaining tissues of those listed on page 81 are, however, highly specialized for specific functions. They are so much more important in connection with those functions than with respect to their structure that descriptions of them are deferred to later chapters. Contractile tissue includes mainly the voluntary and involuntary muscles; nervous tissue comprises all the nerve, brain, and ganglion cells; vascular tissue includes the blood and the more fluid parts of the blood-producing organs (red marrow, spleen); and reproductive tissue consists of the germ cells and their forerunners.

Organs and Systems.—An *organ*, generally speaking, is any structure which performs a given function. In this general sense, a single cell may be an organ, as in the case of single secreting cells scattered through an epithelium. Usually, however, cells that do a certain thing are grouped. Thus the secreting cells of Hydra which provide the adhesive substance that holds the animal fast to other objects are all located on the foot. Also, the stinging cells of Hydra show a tendency to be collected in patches, particularly on the tentacles. Where such patches are sharply marked off, as the glandular foot of Hydra, each group could be considered an organ.

Some biologists, however, reserve the term organ for a collection of tissues acting together to perform some function. The stomach of a vertebrate animal is a suitable example. The inner epithelium, just one cell thick, does the secreting of the digestive fluid or fluids. Outside this layer is a connective tissue layer rich in blood vessels and lymph spaces by which the materials for secretion are brought in and the digested foods are carried away. Covering this layer are two layers of muscles, running in different directions and together serving to churn up the contents of the stomach and mix them with the digestive fluids. The several tissues are structurally unlike, but each contributes in some way to the digestion of the food. The stomach is thus an organ in this more restricted sense.

When a number of organs are occupied with different phases of a complicated general process, they constitute a *system* of organs. The mouth, esophagus, stomach, intestine, and several glands associated with these organs are all concerned in some way with digestion. They constitute the digestive system. The heart, arteries, veins, and capillaries propel or convey the blood and so make up the circulatory system. In like manner the brain, spinal cord, ganglia, and nerves compose the nervous system. The term system is sometimes applied to a group of organs of a single kind, when these are the only organs concerned with that function. Thus, as will be explained in a later chapter, the excretory organs of some of the simple animals (the earthworm, for example) are all alike, but there are many of them. There is no objection to speaking of these organs collectively as a system; but in all the more complex animals the systems are everywhere made up of unlike parts, each contributing a different portion of the general process.

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CHAPTER 8

PHYSICAL SUPPORT AND MOVEMENT

In many animals the characteristic activities could be performed only in the presence of hard parts which may collectively be termed the *skeleton.* A skeleton is any more or less firm framework on or within which the softer fleshy parts of the body are placed. The services performed by the skeleton are chiefly of three types: (1) it provides support for soft organs whose relations to one another could not otherwise be maintained; (2) it protects delicate structures; and (3) it furnishes a mechanism through which different types of movement may be executed. Skeletons are widespread, from the protozoa to the largest mammals. Such prevalence is testimony to their usefulness; yet some large groups of animals (flatworms, roundworms) and some members of other groups (jellyfishes) get along without them.

Support Furnished by Skeleton.—It is not practicable to separate mere mechanical support from protection in many cases, though an attempt will be made to choose examples where this may be done at least in principle. Sponges of all kinds possess narrow channels, lined in places by collared cells (Fig. 33, page 52) which take in food. Currents of water are constantly maintained in these channels by the flagella of the collared cells, and it is essential that the passages be prevented from collapsing. While conceivably the canals might be kept open by cells of firm consistency, they actually are kept open by means of a skeleton. In the so-called bath sponges, this skeleton is a network of horny material; in other kinds the skeleton is made of numerous limy or siliceous rods or variously shaped objects called spicules (Fig. 73).

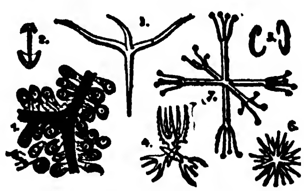

FIG. 73.—Elements of sponge skeletons. 1, spongin fiber surrounded by cells; 2–7, spicules of different types. (*From Van Cleave after Hertwig.*)

Fresh-water mussels and marine clams bear on the outside of their bodies a bivalve shell, consisting of two saucerlike pieces hinged together at one edge and opening like a book. Between the edges of these pieces, at certain places, water must enter and leave by fixed routes in order to bring the animal its food and oxygen and remove its wastes. The actual channels for the water are formed by the fleshy parts of the mussel, but these fleshy parts must be kept in their proper positions. In many of the mussels they are too soft and delicate to do so unaided, and it is the shell which holds them in place.

The importance of the skeleton is closely related to size of body and the place where the animal lives. A large animal may exist in the sea and, because the body is of about the same density as the surrounding water, be buoyed up in such a way as to allow its parts to function. Cuttlefishes, for example, lead active lives in marine waters but washed up on shore are helpless and shapeless. On land, however, even moderate-sized mammals, because the medium around them, the air, is so much lighter than themselves, would be unable to maintain the physical relations of their parts to one another sufficiently to enable them to function if they were made of mere protoplasm. Some form of mechanical support other than a skeleton might have been evolved; but large size without such support, along with physiologies of the general sort exhibited by modern land animals, would have been out of the question.

Skeletons and Protection.—Nearly every skeleton may be regarded as a source of protection, though often there is little definite information to show what injuries might result in the absence of the skeleton. Those sponges which have a skeleton of limy spicules generally bristle all over with long shafts projecting from the surface cells (Fig. 74). How much they are thus protected from predatory animals can only be conjectured. In some marine animals known as hydroids, having the general structure of Hydra but existing in branching colonies, there is a horny tubular sheath covering the various branches and main stem of the colony. This skeleton enables the hydroids to stand out more or less firmly instead of being lashed against other objects by the waves. In insects, crayfishes, spiders, and their allies there is a skeleton of a horny substance known as *chitin* which covers the entire body on the outside. This does not protect them from predatory animals, since members of this group, particularly the insects, are abundantly eaten by other animals; but it must serve to ward off mechanical injuries of other kinds. The limy wall, or test, of sea urchins and the shells of clams are presumably likewise protective structures. In the vertebrate animals some of the most delicate and vital organs are within bony cases—the brain within the skull, the spinal cord in a canal running through the backbone, the heart within the framework of the chest, and such sense organs as the ears and eyes either imbedded in solid bone or set in among projecting ridges or other prominences.

FIG. 74.—A simple sponge. (*From Hegner, "College Zoology," The Macmillan Company.*)

Skeletons which serve only the functions of support and protection may often be rigid one-piece structures. Some of the protozoa have a solid limy shell surrounding the whole cell, and corals rest in limy cups which they have secreted. Most skeletons serving other functions are either flexible or jointed.

Function of Hard Parts in Movement.—Only occasionally are the hard parts of much service in movement among the simpler animals. One of the best examples of such use is the earthworm, which is provided with a number of spines, or *setae*, projecting from the body in each segment except a few at the ends. These setae are operated by muscles attached to their inner ends and sloping off in different directions (Fig. 75), like the ribbons of a Maypole, to the body wall. When the worm crawls forward, the outer end of the seta is tilted backward, so as to catch the soil, and in crawling backward or holding fast in the worm's burrow the seta points forward.

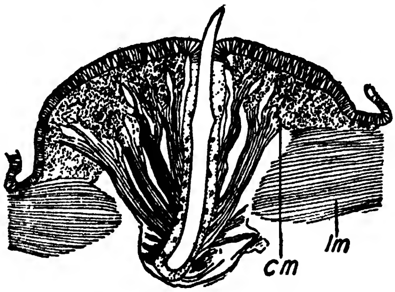

FIG. 75.—Seta and muscles in the earthworm, drawn from a longitudinal section anterior to the clitellum; *cm*, circular muscles, and *lm*, longitudinal mucles.

Sea urchins also have movable hard parts, which, however, are not precisely a part of the locomotor equipment. The fleshy parts are enclosed in a round shell, or test, the surface of which is studded, porcupinelike, with a host of spines (Fig. 76). These spines are capable of movement in any direction and, when the animal is thrust over on its side or back, may give it an irregular motion that helps it right itself. But the main movement is effected by fleshy tubes ending in suckers.

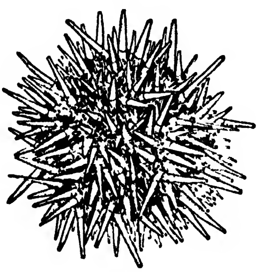

FIG. 76.

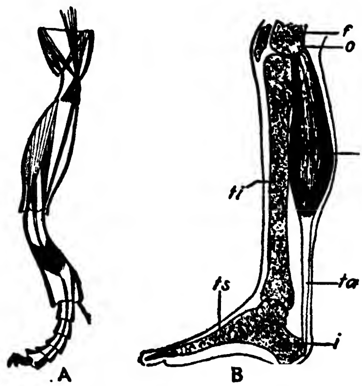

FIG. 77.

FIG. 76.—A sea urchin, covered with a test and spines. (*From Haupt ,"Fundamentals of Biology."*)

FIG. 77.—Relation of muscle to hard parts in appendages of insect and man. *A*, leg of insect; *B*, leg of man; *f*, femur; *fs*, skeleton of foot; *i*, insertion of muscle; *m*, muscle; *o*, origin of muscle; *ta*, tendo-Achilles; *ti*, tibia. (*A after Berlese; B after Hesse and Doflein.*)

The fullest use of skeletal parts for movement is found in the insects and their allies and in the vertebrate animals. In both groups the hard parts are joined by curved surfaces, which permit free movement of one upon another. Sometimes these curved surfaces are such as to permit movement only in one plane, as in a hinge, while other joints allow a rotary motion. The skeleton of insects and that of vertebrates differ, however, in one important respect. In the insects it is on the outside, covering all the fleshy parts, and here is known as an *exoskeleton.* In vertebrate animals the skeleton is on the inside, everywhere covered by flesh, hence of a type called an *endoskeleton.* The muscles which operate the movable parts must work from the inside in the former but from the outside in the latter (Fig. 77).

Skeleton of Vertebrates.—To illustrate the main features of a typical skeleton, that of the vertebrate animal is chosen. This skeleton is composed of bones and cartilages united partly by ligaments, is covered

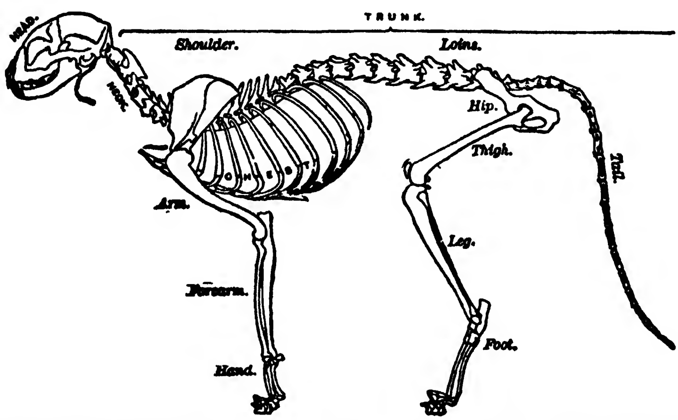

Fig. 78.—Regions of the vertebrate skeleton (cat). (*From Jayne, "Mammalian Anatomy."*)

by the soft parts of the body, and is supplied with blood vessels and nerves. It may conveniently be divided into regions as indicated in Fig. 78. On more fundamental anatomical grounds it is also subdivided into the *axial* and the *appendicular* skeleton. The former lies in the longitudinal axis of the body, and to it the latter is appended; hence the names.

Axial Skeleton.—The axial skeleton (Fig. 79) is made up of the *skull, hyoid apparatus, vertebral column, ribs,* and *sternum.* The skull furnishes a case for the brain, capsules for the organs of hearing and smell, and orbits for the eyes. It also includes the bones of the jaws. To it is attached the hyoid apparatus which is a bony or cartilaginous support for the base of the tongue.

The vertebral column is a jointed structure composed of a number (different in different species) of vertebrae placed end to end. Together they form a tube enclosing the spinal cord, and their outer surfaces form attachments for ligaments and muscles. The vertebral column is structurally differentiated into five regions, the *cervical*, *thoracic*, *lumbar*, *sacral*, and *caudal* (see Fig. 79). The plan of a vertebra is shown in Fig. 80. It is composed of a heavy ventral portion, the *centrum*, from which arises a bony arch, the *neural arch*. The latter encloses the *neural canal* which is occupied by the spinal cord. From the sides of the arch two *transverse processes* project, and from the apex of the arch arises the

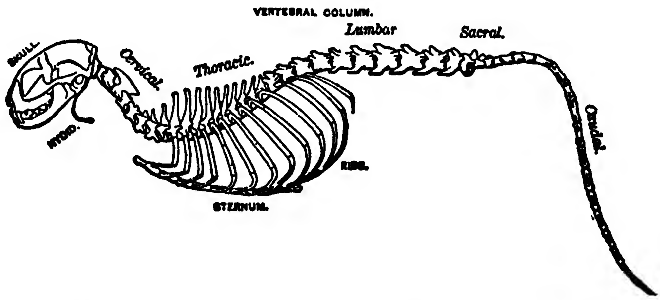

FIG. 79.—Axial skeleton of the cat. (*From Jayne, "Mammalian Anatomy."*)

neural spine. One pair of articular processes or *zygapophyses* projects anteriorly and another posteriorly from the sides of the arch. The relations of the anterior and posterior zygapophyses and the articular faces of the centra of adjoining vertebrae are made clear in Fig. 80 (right).

The forms of the vertebrae in different regions of the vertebral column are very different, as shown in Fig. 79. In the thoracic region of an

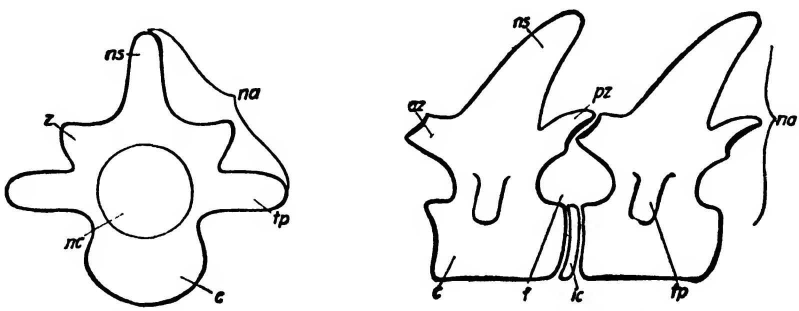

FIG. 80.—Diagram of a typical vertebra viewed from in front or behind and from the left side: *az*, anterior zygapophysis; *c*, centrum; *f*, intervertebral foramen through which nerves and blood vessels pass; *ic*, intervertebral cartilage; *na*, neural arch; *nc*, neural canal; *ns*, neural spine; *pz*, posterior zygapophysis; *tp*, transverse process; *z*, zygapophysis.

animal having ribs the vertebrae have faces for the articulation of the ribs. In the sacral region the vertebrae in some animals are considerably thickened without great change in form, while in others they are much flattened and more or less fused into a platelike structure, the *sacrum*. In the sacral vertebrae the neural canal is reduced in size and in the caudal vertebrae it is entirely absent. The spinal cord does not pass into the latter region.

Vertebrae articulate with each other chiefly by means of the centra. The articular surfaces of the centra may be concave or convex. Commonly one of the surfaces of a centrum is concave and the other convex, the convex surface of one vertebra fitting into the concavity of the next. But in some vertebrae both surfaces are concave and the space between the centra is filled with a lens-shaped pad of cartilage. Biconcave vertebrae are called *amphicoelous* (*amphi* = both and *koilos* = hollow). In the concavoconvex type of vertebra, if the concavity is directed toward the head, the vertebra is said to be *procoelous*, but *opisthocoelous* if the concavity is directed posteriorly. These types of vertebrae are illustrated in Fig. 81.

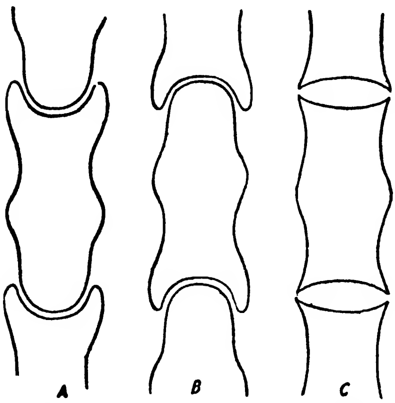

Fig. 81.—Three types of vertebrae. Only the centra and lateral processes are shown. Upper end is anterior. *A*, procoelous; *B*, opisthocoelous; *C*, amphicoelous.

Ribs are usually attached to the vertebrae in such a manner that they can be moved. Some of the hindermost ribs are free at their ventral ends, while others are connected to the sternum or breast bone more or less directly by means of cartilage. The sternum is a bony or cartilaginous structure which lies in the median ventral part of the thorax. The number of pairs of ribs varies in different species, being 12 in man.

Parts of Appendicular Skeleton.—The appendicular skeleton consists of the shoulder or *pectoral girdle*, the hip or *pelvic girdle*, and the *fore* and *hind limbs*. The generalized plan of the girdles and limbs of animals higher than the fishes is shown diagrammatically in Fig. 82. In these appendicular skeletons each of the girdles is composed of three pairs of bones which are similarly arranged in the two girdles. Each side of the pectoral girdle is composed of a flat bone, the *scapula*, or shoulder blade, directed dorsally, a *coracoid* bone connecting the scapula and the sternum (the latter not shown), and a *clavicle* which in some vertebrates also connects the scapula and the sternum. There may be a cartilage, the *precoracoid*, affixed to the posterior edge of the clavicle. A cavity, the *glenoid fossa*, located at the junction of scapula and coracoid, serves as the surface of attachment of the fore limb. Each side of the pelvic girdle consists of an *ilium*, *ischium*, and *pubis*. These three bones in a generalized skeleton are arranged similarly to the bones of the pectoral girdle. The cavity at the junction of the three bones is the *acetabulum*. In it is seated the head of the femur (thigh bone).

The bones of the arm and leg or fore and hind limbs are arranged according to the same plan and may be compared bone for bone, *humerus* with *femur*, *radius* and *ulna* with *tibia* and *fibula*, respectively, *carpal* (wrist) bones with *tarsal* (ankle) bones, *metacarpals* with *metatarsals* (body of hand and foot, respectively) and *phalanges* (bones of the digits) of the hand with those of the foot. Vertebrates with primitive limbs have five digits on fore and hind feet, but the limbs of specialized animals have undergone more or less extensive modifications from the original five-fingered and five-toed plan. In them usually the number of digits has been reduced.

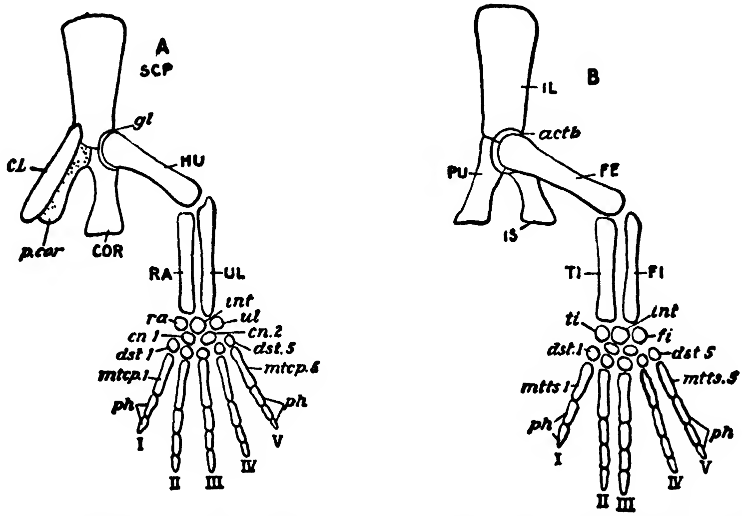

FIG. 82.—Diagrams of generalized fore (*A*) and hind (*B*) limbs with limb girdles: *actb*, acetabulum; *CL*, clavicle; *cn.* 1, *cn.* 2, centralia; *COR*, coracoid; *dst.* 1–5, distal row of carpals and tarsals; *FE*, femur; *FI*, fibula; *fi*, fibulare; *gl*, glenoid fossa; I–V, digits; *HU*, humerus; *IL*, ilium; *int*, intermedium; *IS*, ischium; *mtcp.* 1–5, metacarpals; *mtts.* 1–5, metatarsals; *ph*, phalanges; *p.cor*, precoracoid; *PU*, pubis; *RA*, radius; *ra*, radiale; *SCP*, scapula; *TI*, tibia; *ti*, tibiale; *UL*, ulna; *ul*, ulnare. (*From Parker and Haswell, "Textbook of Zoology."*)

The Motive Power.—The movement of structures in the higher animals, whether these structures contain parts of the skeleton or not, is all effected by muscles. Protoplasm in general has the power of contracting, and in the protozoa there are motile structures, the cilia and flagella, which have already been described (page 52). The muscles are, however, much more specialized than any of these.

In general, the muscles are arranged in opposing pairs or sets. In the earthworm, in which crawling is effected by alternate contraction and expansion of the length of the animal, there is one set of muscles running lengthwise, another passing circularly around the body. With the front end of the worm holding to the soil with its sloping setae, a wave of contraction of the lengthwise muscles draws up the rest of the body.

Then the circular muscles contract, while the longitudinal ones relax. Since the body cavity (coelom) is filled with a fluid and cannot reduce its volume, contraction of the circular muscles forces the body to elongate, thus pushing the front end forward to take a new hold upon the soil. The setae, as previously explained (page 89), are tilted forward or backward by opposing muscles. In vertebrate animals, bones are moved by muscles and tendons placed on opposite sides of the bones at or near the joints. The arrangement at the knee joint in man is shown in Fig. 83. The *flexor* muscle bends the joint, the *extensor* straightens it. When

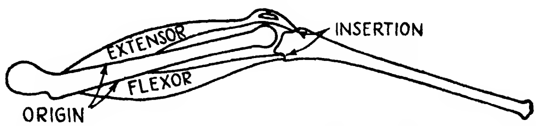

FIG. 83.—Diagram of knee joint in man, illustrating opposed muscles.

one of these muscles contracts, the other must relax if movement is to be produced. If both contract the leg is merely made tense. The area of attachment of the less movable end of the muscle (usually that nearest the body) is called the *origin* of the muscle, that of the more movable end its *insertion.* In such boneless movable parts as the eyelids and lips, one set of muscles, operating to pull radially away from the openings which these structures surround, is opposed by circular bands of muscles which close the openings. The stomach and intestine of vertebrate animals possess longitudinal and circular muscles which operate much as do those of the earthworm. Everywhere muscle is opposed by muscle.

FIG. 84.—Smooth-muscle cells.

The necessity of this arrangement arises from the fact that, while muscle contracts vigorously, its expansion is entirely passive. It can force movement in one direction but can only permit it in the opposite direction.

Muscle.—Muscles constitute the contractile tissue referred to in the preceding chapter (page 81). They are nearly always plates or bundles of cells, not single cells. Three types of muscle cells in vertebrate animals may be recognized, known respectively as *smooth, striated,* and *cardiac.*

Smooth muscle is composed of cells each of which is provided with a single nucleus. The cytosome contains well-marked longitudinal fibrils. These cells (Fig. 84) have the form of slender spindles with unbranched tips or in certain organs the tips may be branched. They are found in the walls of the digestive tract, urinary bladder, gall bladder, arteries and veins, and in certain glands and their ducts.

Striated muscle differs greatly in its structure from smooth muscle. For one thing, it has many nuclei in each cell. The cells of an embryo from which striated muscle cells develop have only one nucleus apiece, but after a time the nucleus divides a number of times without an accompanying division of the cell body. Many nuclei are thus present in the muscle cells of the adult. The striated muscle cell is roughly cylindrical in form and usually very long. It is covered by a firm membranous sheath, the *sarcolemma*. Within this is the rather liquid proto-

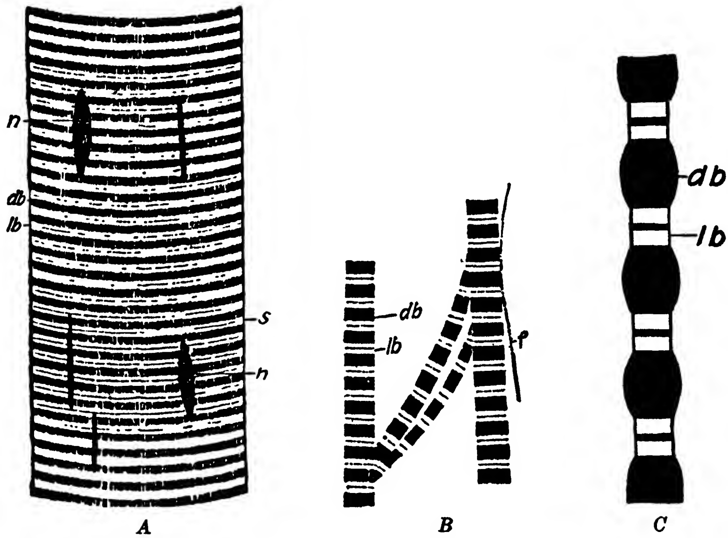

FIG. 85.—General appearance of striated muscle. *A*, part of a muscle fiber of a frog; *B*, part of a fiber teased out to show myofibrils; *db*, dark bands; *lb*, light bands; *f*, myofibril; *n*, nucleus; *s*, sarcolemma; *C*, a myofibril, diagrammatic; *db*, dark band; *lb*, light band with a thin band of dark material dividing it into two portions. (*A and B from Parker and Haswell, "Textbook of Zoology."*)

plasm called the *sarcoplasm*. Imbedded in the sarcoplasm, and forming a large part of the bulk of the cell, are numerous slender strands, the contractile *myofibrils* (Fig. 85*B*, *f*). Each myofibril consists of alternate segments of different substances, light and dim in appearance. In the muscle cell these myofibrils extend parallel to each other and to the long axis of the cell and are so aligned that the dim segments are side by side, and light segments are side by side. Collectively they give the whole cell the appearance of being marked by light and dark transverse bands (Fig. 85*A*). These are the marks to which the term "striated" refers. Little is known of the chemical or physical properties of the substances in the light and dim bands, but when they are examined with polarized light it is found that the dark substance is doubly refractive.

Cardiac muscle is found only in the heart of vertebrate animals. It contains fibrils somewhat resembling those of striated muscle, and has cross striations which these fibrils confer on it. However, the strands of heart tissue interconnect in a network, and there is little or no blocking off of the protoplasm into cells. The heart is thus practically a large syncytium (page 66).

The actions of the three kinds of muscle are very different. Smooth muscle is capable of only relatively slow movement. It is not directly subject to the will, hence is sometimes called *involuntary* muscle; but this is not a distinctive designation, since the heart is also free from

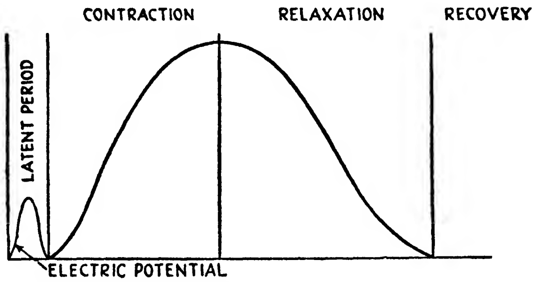

FIG. 86.—Curve illustrating the course of a single muscle twitch.

conscious control, and even striated muscle sometimes acts involuntarily. Striated muscle acts very strongly and very rapidly; and since its movement is regularly initiated by act of will, it is known as *voluntary* muscle. Heart muscle acts without control of the will, as do other vital organs. Its rhythmic action can be maintained for long periods after removal of the organ from the body, as determined by a mechanism to be described in a later chapter. Because of its syncytial nature, waves of stimulation pass rapidly over the whole heart, and the organ tends to act as a single unit.

Muscle Contraction.—In the living animal, contraction is stimulated only by nerve impulses, though in laboratory experiments artificial stimuli can be given. A single nerve cell may govern only a few muscle cells, or as many as 150. The group of muscle cells controlled by one nerve fiber constitutes a *motor unit.* It is characteristic of motor units that, if they contract at all, they do so to their fullest capacity, in accordance with the all-or-none law already stated (page 53). Since muscles are made up of many motor units, some contracting, others usually not, an entire muscle may experience many degrees of contraction. How many motor units act depends on the intensity of the nerve stimulus, a strong stimulus activating many of them, a weak stimulus few.

A single stimulus to a striated muscle results in a single quick twitch of the muscle. If the muscle is attached to a movable pointer, which traces a line on smoked paper on a revolving drum, the single twitch is recorded by a curve of characteristic form (Fig. 86). The twitch as a whole lasts about 0.1 second in the frog. It takes a very short time (0.01 second) for the muscle to start to contract. This brief period of inaction is known as the latent period; by the time it is ended the change

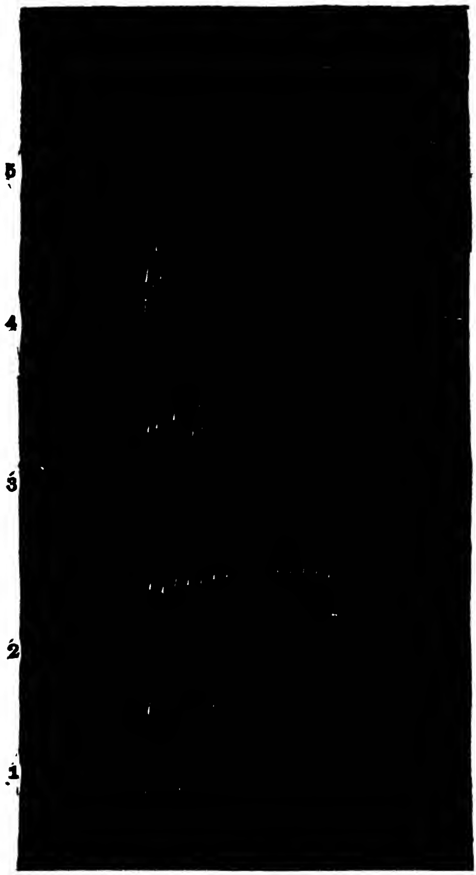

Fig. 87.—Curves of contraction of muscle in response to repeated stimuli. Rate of stimulation is slow at the bottom, but gradually increases toward the top. *(From Howell, "Textbook of Physiology," W. B. Saunders Company.)*

of electric potential which is the sign of stimulation has usually reached a peak and subsided. Then the muscle contracts for about 0.04 second, and the succeeding relaxation lasts about 0.05 second. Following the twitch there is a period of recovery lasting a number of seconds in which the muscle returns to its previous condition. If stimuli are applied repeatedly before the recovery is complete, the muscle shows fatigue and its responses are weaker. Smooth muscle, as in the intestine, reacts much more slowly, the contraction lasting about 20 seconds. The relaxation of any muscle is purely passive; the ends of the muscle fibers do not push.

Single twitches are not, however, the commonly observed type of muscle action. During ordinary contraction, nerve impulses are delivered in rapid succession, beginning, say, at 4 or 5 per second and increasing in frequency to 40 or 50 per second. These rapidly repeated stimuli may be shown experimentally to be the most effective method of getting strong and sustained contraction. The nature of the contraction resulting from stimuli repeated at different rates is shown in Fig. 87. In the lowest curve the stimuli were given at a slow rate, and after each one the muscle relaxed almost to its former state. But when the stimuli were given more and more rapidly, as in the remaining curves of the figure, complete relaxation did not have time to occur between them, and the total contraction gradually increased.

In striated muscle the cells act separately and do not communicate stimuli to surrounding cells. In smooth muscle, however, stimulation at one point may lead to a wave of contraction passing over a whole sheet of muscular tissue, showing that the stimulus is communicated from cell to cell.

The efficiency of muscle, that is, the ratio of work done to energy consumed, is rather high. For a single twitch, including the recovery period following, this ratio is about 50 per cent. For sustained contraction, however, the efficiency is much less—around 25 per cent.

Chemistry of Muscle Contraction.—Just what happens in a striated muscle when it contracts is only partially understood. It is the myofibrils that do the contracting, but the important thing to know is the set of physical or chemical conditions which cause them to shorten. Clues have been furnished by chemical analysis of fatigued muscle. Most of the glycogen, which in rested muscle amounts to about 3 per cent of the weight, has disappeared in fatigue, as has also much of the oxygen. At the same time the inorganic phosphates (produced out of organic phosphates) have considerably increased; so also has carbon dioxide. If under experimental conditions oxygen is excluded there is also an increase of lactic acid. How the glycogen is lost is known; combining with water, it is converted into glucose and lactic acid. Something must also have been oxidized to account for the increased carbon dioxide. Under ordinary conditions the lactic acid does not persist, for part of it is oxidized to obtain energy with which the rest of the lactic acid is reconverted to glycogen. Formerly it was thought that the breaking down of glycogen or the oxidation of one of its products furnished the energy for muscle contraction; yet conversion of glycogen may be prevented by certain poisons, and the muscle still be able to contract. It seems necessary to conclude that the energy comes from decomposition of organic phosphates; such phosphates are known to release energy with almost explosive speed when they are decomposed. The organic phosphates must be reconstituted, ready for the next contraction, and the energy for this reconstitution comes from oxidations. The oxidations are thus accessory phenomena; instead of furnishing the energy for the contraction itself, they provide for the restoration of the phosphates, and the latter on decomposition furnish the energy for contraction.

The mechanism of the contraction itself is probably the sudden folding of long protein molecules arranged lengthwise in the myofibrils. Since the most abundant protein in muscle is *myosin*, this may be the responsible agent. Myosin extracted from muscle exercises a strong catalytic action on the decomposition of organic phosphates, and this action may be a part of the contraction process.

A muscle in which there is no more organic phosphate nor glycogen, and in which much lactic acid has been accumulated, is incapable of contraction; it is "fatigued." In living animals as distinguished from laboratory preparations, however, the common source of fatigue is not in the muscle itself, but between the muscle fibers and the nerve which delivers the commands to contract. Some substance there, at the junction of nerve with muscle, experiences a change in response to repeated stimulation such that it no longer transmits the stimulus or does so more weakly. The nerve fiber still conducts, and the muscle is still able to contract. The nature of the failure of the junction is not known.

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CHAPTER 9

SOURCES OF ENERGY AND MATERIALS

Muscular action and the other activities of an organism entail destruction of living substance, which must be steadily replaced. In growing animals, not only are repairs necessary, but provision must be made for new construction. The general source of material for growth and replacement is food. How this material is utilized in single cells has already been described; how it is transformed in multicellular animals is now our concern.

Since most food is not in a form that can be transported through protoplasm, it must usually be converted in some way. In large part the conversion consists of making it soluble. But even some soluble foods are unable to pass through tissues, because of the selective action of protoplasm which will receive some substances and not others. The conversion is accomplished by the process of digestion which, in multicellular animals, is carried on in some sort of digestive system.

The Locus of Digestion.—In the protozoa digestion is an intracellular process. Amoeba engulfs food by flowing around it at any part of the cell. Paramecium takes the food in at a particular place, through a permanent gullet. In either case the food is surrounded by a droplet of liquid, which is acid in reaction at first, and presumably enzymes are secreted into this fluid. The food vacuole thus formed is the digestive apparatus. These features of protozoan digestion were described earlier but are repeated here in the first two parts of Fig. 88 for contrast. Among the multicellular animals, sponges retain the intracellular type of digestion. Through the channels and cavities which are characteristic of sponges, water flows, kept in motion by the flagella of collar-bearing cells in some of the channels (Fig. 33). From the water the collared cells seize organisms, after the manner of Amoeba, and digest them. Products of this digestion are passed on to other cells by diffusion or osmosis, so that nutrition in sponges is on a cooperative basis; but just as in protozoa, digestion is done within the cells.

In all metazoa other than sponges digestion is performed partly, even chiefly, in cavities of organs—surrounded by cells, but not in cells. The process is at least begun in these cavities, and in the higher animals is almost completed there. The more complicated types of food are rendered quite simple before they leave these cavities. Some foods are rendered completely soluble and immediately ready to enter into the metabolism of protoplasm. Other foods leave the digestive cavities lacking still one or two of the simplifying steps which are necessary. The cells which receive these incompletely digested foods finish the process themselves. Indeed, all cells which use these kinds of foods in their metabolism must have the power of taking these last digestive steps. Thus some of the primitive digestive activities characteristic of protozoa are not lost by any active cells in any organism.

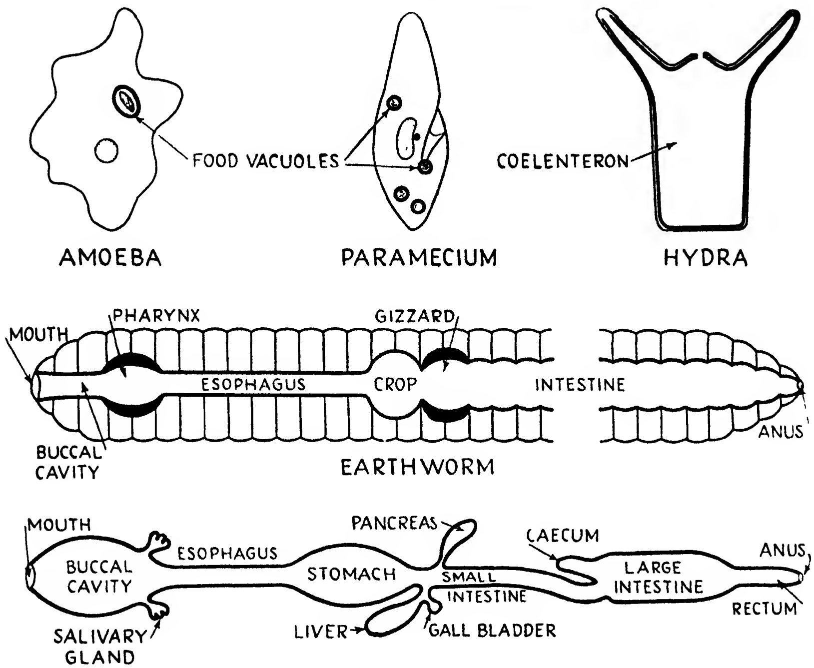

FIG. 88.—Diagrams of several types of digestive systems in metazoa, compared with protozoa.

Simple Digestive Systems.—The simplest system in which digestion occurs in a cavity is that known as a *coelenteron*. Hydra (Fig. 88) has such a system. A coelenteron has only one opening to the outside, usually called the *mouth*, although besides taking in food that opening must also be the place of exit of undigested matter. The coelenteron of Hydra is in the main a simple sac, though it is branched into the ring of tentacles near the free end of the body. A less diagrammatic representation of Hydra's coelenteron is given in Fig. 59, where it is labeled the *gastrovascular cavity* and the cells forming its wall are the *endoderm*. Flatworms also have a coelenteron. In some of them (Fig. 89, above) it is as simple as in Hydra, but the simplicity is not primitive;

it is a result of degeneracy. Other flatworms have a three-branched coelenteron, each part of which is extensively branched (Fig. 89, below).

As animals rise in the scale of complexity the digestive system becomes a tube open at both ends. One end is the mouth, which ingests food, the other end the *anus* through which undigested, mostly indigestible, matter is ejected. In the course of the tube it is differentiated into organs. In the earthworm (Fig. 88), following the mouth, there is a short *buccal cavity*, a *pharynx* with strong muscular walls, an *esophagus*, a *crop* in which food may be stored, a *gizzard* with thick muscular walls and a chitinous lining by means of which food may be finely ground, and an *intestine* with secreting and absorptive cells. An internal ridge, the *typhlosole*, formed by an infolding of the dorsal wall of the intestine (Fig. 66), gives increased surface. About the exterior surface of the intestine is a layer of brown cells, the chloragogen cells, which have been thought to serve as a digestive gland, possibly as a liver.

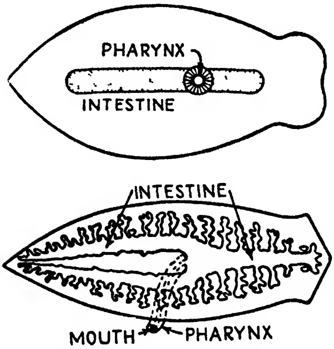

FIG. 89.—Digestive system (coelenteron) of a rhabdocoele flatworm (above) and a triclad turbellarian.

Digestive Systems in the Vertebrates.—In the vertebrates the digestive system reaches its highest development. Here it consists not only of an alimentary canal, subdivided into regions, but also of highly developed glands which produce digestive secretions. A diagram representing vertebrates in general fairly well, but more particularly the mammals, is at the bottom of Fig. 88. The system in the frog is slightly more simple (Fig. 90, left). In the mouth the upper jaw bears *teeth* which serve to hold the prey when caught. Attached to the anterior portion of the floor of the mouth is a prehensile *tongue* which is provided with many *glands* that produce a sticky secretion. The *buccal cavity* or *mouth cavity* leads backward into the short broad *esophagus* through a distensible opening, the *pharynx*. The esophagus leads into the muscular *stomach* which in the frog, as in most vertebrates, is a curved organ usually lying somewhat to one side of the middle line. The walls of both the esophagus and stomach are provided with highly developed *glands* which secrete digestive solutions. The stomach opens into the *small intestine* through a muscle-encircled passage, the *pylorus*. The small intestine of vertebrates is usually subdivided into three portions named, respectively, the *duodenum*, *jejunum*, and *ileum*. Of these the duodenum and ileum alone are recognized in the frog. These regions as a rule merge imperceptibly into one another, yet each shows certain characteristic structural features and each occupies a certain portion of the intestine. The duodenum receives the secretions of two large digestive glands, the *liver* and the *pancreas*. In the frog the secretions of these two glands are discharged through the *common bile duct* into the middle region of the duodenum. A reservoir, the *gall bladder,* attached to the liver and connected with the bile duct, serves as a storage place for the *bile*, one of the secretions of the liver. The small intestine is connected at its posterior end with the *large intestine* which in the frog is subdivided into two portions, namely, the *rectum* and the *cloaca*. The term cloaca is used to designate that portion of the large intestine which is used as a common passage for undigested materials from the

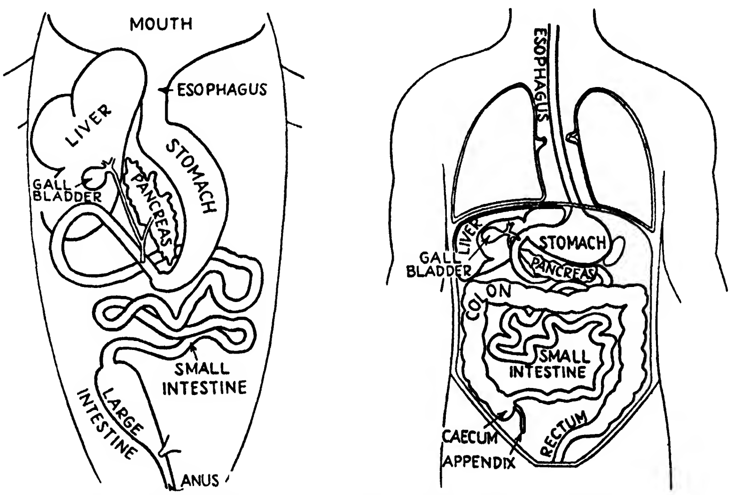

FIG. 90.—Digestive systems of the frog (left) and man, somewhat simplified.

alimentary tract, for urine, and for reproductive cells from the urinogenital system. It occurs in a few mammals and in most other vertebrates. The large intestine opens to the exterior by means of the *anus*.

The human digestive system differs little enough from that of the frog that the illustration in Fig. 90, right, should suffice without further description. That figure, however, omits the mouth and its associated salivary glands, and the small intestine is greatly shortened.

It is worthy of note that the intestine of the frog is relatively short. This condition is found in flesh-eating animals in general. Animals which feed entirely or largely upon vegetable food have long intestinal tracts and frequently have a large *caecum* (a blind pouch) at the junction of the small and large intestines. The rabbit and muskrat have a large *caecum* with a *vermiform appendix* at its end; the chicken and dove have two caeca. In man the caecum is small, rudimentary, with a vermiform appendix. Highly specialized modifications of the stomach occur in ruminants (animals which chew the cud) and in seed-eating birds.

Digestion in Man.—Inasmuch as the digestive process as it occurs in man has been much more intensively studied than in any other animal, the discussion of digestion which follows will be based on the human system. In the mouth, food is broken up, during which process the three pairs of salivary glands pour out their secretion (*saliva*) which is mixed with the food. The saliva contains an enzyme, *ptyalin,* which is able to transform starch, particularly cooked starch, into certain sugars. The breakdown of starch occurs by degrees, the intermediate products being various dextrins, but in no case does the digestion in the mouth go farther than to maltose, which is not one of the simple sugars. It is still a disaccharide (page 40) and not readily diffusible through protoplasm. Ordinarily, because of the short sojourn of the food in the mouth, little starch digestion actually takes place there; and since ptyalin acts only in an alkaline medium, its action is stopped by the acid of the stomach when the food reaches that organ.

In the stomach, the food is acted upon by the secretion of the gastric glands which are small branched or simple tubular glands located in the inner layer of the stomach. The movement of the muscles of the stomach mixes the food with the gastric secretion, which contains *hydrochloric acid* and two important enzymes, *pepsin* and *rennin.* The hydrochloric acid affords a suitable medium for the action of the enzymes and incidentally stops the action of the ptyalin descending from the mouth. The rennin coagulates milk, a fact made use of in cheese factories where a preparation of rennin made from calves' stomachs is used to separate the curd from the whey. Pepsin as it comes from the gastric glands is in an inactive state in which it is called *pepsinogen.* Pepsinogen is activated (converted into pepsin) by the hydrochloric acid, which is secreted in a concentration of about 0.4 to 0.5 per cent. Pepsin acts only on proteins, converting them to peptones and proteoses, which are also proteins but simpler than most proteins taken as food. Ordinary fats are not acted upon in the stomach.

Absorption of foods in the stomach is negligible. Alcohol is absorbed there, which may account for its quick action on mental and other physiological processes.

Secretin.—When the acid stomach contents are ejected through the pylorus, the acid acts upon a substance in the lining epithelium of the duodenum and changes this substance to *secretin.* The secretin is absorbed by the blood and is carried to the pancreas and liver which are thereby stimulated to secrete their fluids. Secretin belongs to a class of activators known as *hormones.* Normally, the pancreas and liver are also controlled in part by nerve impulses. Nevertheless, these glands discharge their secretions even after the nerves which innervate them are cut.

The Pancreatic Juice.—The pancreas produces a thin watery secretion containing three enzymes, which act upon proteins, carbohydrates, and fats, respectively. The protein-splitting enzyme is inactive when it emerges from the pancreatic duct and is then known as *trypsinogen;* but, when it comes in contact with the duodenal surface, it is quickly rendered active. The conversion of trypsinogen is initiated by the enzyme *enterokinase*, produced in the lining of the duodenum. This enzyme acts upon the inactive trypsinogen, changing it to the active form called *trypsin.* The trypsin splits proteins, proteoses, and peptones from the stomach into simpler and simpler compounds. The end products of protein digestion are amino acids (page 41) and several other compounds. Trypsin works in alkaline, neutral, or even acid media. It completes the work begun by the pepsin and works more rapidly and breaks up the protein more completely than does the pepsin.

The carbohydrate-splitting enzyme of the pancreas is *amylopsin.* Unlike trypsinogen, it requires no activation. It converts starches, dextrins, and complex sugars (with the aid of so-called inverting enzymes) into simple sugars (glucose and others), which are in condition to be absorbed.

The fat-splitting enzyme of the pancreatic juice is *steapsin.* Steapsin splits fats into glycerol (glycerin) and one or more fatty acids (page 41). These substances are soluble and are absorbed in this condition.

The Secretion of the Liver.—Bile, the secretion of the liver, contains no enzyme. It contains water, bile salts, and certain excretory materials. The discharge of bile is stimulated, as explained above, by the hormone secretin in the same manner as is the secretion of pancreatic juice. Bile is ordinarily stored in the gall bladder until the partially digested acid food is ejected by spurts from the stomach, but it has been shown in some animals that such a temporary storage place is not essential to the proper production and ejection of the bile. Each ejection of food into the intestine stimulates a flow of bile through the bile duct. The bile salts break up the fats into very fine droplets, thus greatly increasing the surface through which the fat-splitting enzyme may attack them. If the bile is artificially prevented from entering the intestine, a large share of the ingested fat is not digested and may be recovered in the feces.

The Intestinal Secretion.—The secretion of the small intestine is produced in small tubular glands which are local evaginations of the lining layer. This secretion consists of enterokinase, *erepsin,* several other enzymes, and secretin. Enterokinase, as stated above, converts inactive trypsinogen into active trypsin. Erepsin is a protein-splitting enzyme which, although unable to digest the original proteins, attacks the peptones which result from digestion in the stomach, reducing them to amino acids. It thus supplements the action of trypsin. The other enzymes convert maltose and the dextrins (resulting from the operation of ptyalin and amylopsin upon starches) into glucose and other simple sugars.

Secretin, as indicated above in connection with the stimulation of the pancreas, is not an enzyme but a hormone. It exists in the wall of the duodenum as *prosecretin* which is stable and does not affect the pancreas. The acid from the gastric juice mixed with the food coming from the stomach changes the prosecretin into secretin which is absorbed and carried by the blood to the pancreas and the liver, which are thereby stimulated to secrete pancreatic juice and bile, respectively.

Digestion in the Large Intestine.—The large intestine produces no enzyme. Water and some of the products of digestion are absorbed here. Bacteria flourish in the large intestine. Many of these attack proteins, while others attack the cellulose of plant cells and perhaps so break it down that some sugars are recovered from it. Bacteria which attack proteins are not numerous, however, when the products of protein digestion are removed with normal rapidity. Bacteria may also supply an important vitamin, as is indicated later.

Absorption.—In the more complex animals absorption occurs along the portions of the alimentary tract. In such simple animals as Hydra all the endodermal cells are bathed in the products of digestion or carry on digestion in themselves, and through these cells absorption takes place. Some of this material not used by the endoderm is passed on by diffusion to the ectodermal cells. In animals with a circulatory system the simpler substances pass through the absorbing cells directly into the blood stream.

In man, as stated earlier, there is little absorption in the stomach. Most of it occurs in the small intestine, whose inner surface is enormously enlarged by the fingerlike protrusions called *villi* (Fig. 91). Amino acids and simple sugars are absorbed directly into the blood, which carries them through the liver before delivering them to the general circulation. Glycerol and the fatty acids are absorbed, but in the process are at least partly reconverted into fats. Since fats are insoluble, they exist in the form of droplets and are delivered thus, not to the blood, but to the lymph vessels. However, since the lymph vessels empty into the blood stream (in the left shoulder, page 131), the entrance of fat into the blood is merely delayed.

While absorption by the intestinal wall is partly simple diffusion, some selection is practiced by the absorbing cells, so that certain substances are passed readily, others are retarded or rejected. This selective action may even send substances *against* the diffusion gradient—that is, cause them to go from places of lower to places of higher concentration.

Storage of Food.—Carbohydrates, in the form of glucose or other simple sugars, are ordinarily present in the blood to the extent of less than 0.1 per cent. After a meal they may increase perceptibly, but when they rise above 0.14 per cent they begin to be excreted by the kidneys and are lost. Protoplasm contains some glucose, mostly in combination with other compounds, and to that extent carbohydrates contribute to the

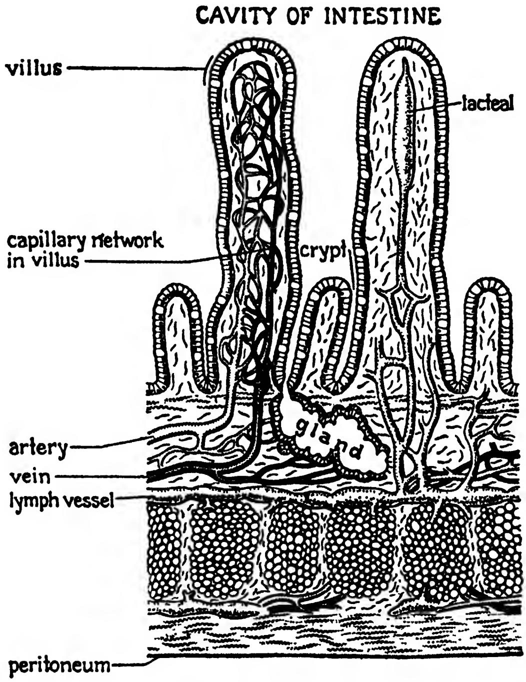

FIG. 91.—Diagram of section through wall of small intestine, showing two villi and their enclosed blood and lymph vessels. (*From Storer, "General Zoology."*)

architecture of the living substance. Much carbohydrate material is stored in the form of glycogen, which is made up of many molecules of simple sugars combined. · The main storehouse of glycogen is the liver, from which it is withdrawn when current supplies are inadequate.

Lipids enter into the construction of protoplasm, particularly at the surfaces of cells, where they play an important role in determining permeability of the cell membrane. Since the need of these materials is continuous, while the supply from digested food is intermittent, lipids must be stored. The ones so deposited are chiefly fats. All cells store them to some extent, but connective tissues between skin and muscles and among the muscles, and the mesenteries of the intestine and other organs, are particularly devoted to this function.

Storage of indiffusible substances such as glycogen or fats necessitates redigestion of them when they are to be used; consequently enzymes for carbohydrate and fat digestion must be produced or producible in all cells which store these products.

Proteins are not stored in animals, as carbohydrates and fats are stored. The supply of protein foods must therefore be rather steady; that is, they should be included in the diet almost daily. Amino acids enter the blood after the digestion of protein foods and are taken up by the cells which require them. When the diet is deficient in proteins, requirements of amino acids in vital situations are supplied only by breaking down body proteins elsewhere, as happens in starvation.

Energy Requirements.—Any balanced diet must provide two things, energy and materials. Energy is measured in the units known as calories, one calorie being the amount of heat necessary to raise the temperature of a kilogram of water 1°C. Each gram of a carbohydrate or protein food utilized in metabolism yields about 4 calories, a gram of fat about 9 calories. A relaxed, fasting human body of average size and shape, in prone position, requires about 1600 calories daily. More than half of this energy goes to maintaining the body temperature. The rest is expended by the vital organs such as the heart and the muscles performing breathing movements. If food is taken, so that muscles of the digestive tract are also active, the daily energy requirement is about 1800 calories. For sedentary workers leading normal lives it rises to about 2400 calories, while manual laborers need 3000 to 5000 calories, depending on how hard and long they work. If an average person consumes much more energy than is proper to his mode of life and occupation, he may have an overactive thyroid gland or a fever. If the energy consumption is much less than normal, the cause may be a deficient thyroid or pituitary or adrenal gland, or low nutrition.

So far as mere quantity of energy is concerned, it may be obtained from any of the types of food. High protein diet requires more work of the kidneys because of the increased nitrogenous wastes, but the kidneys are capable of much more than an average load if they are healthy. An excess of fat is objectionable chiefly because fats do not oxidize very completely unless carbohydrates are being oxidized at the same time. To some extent the human body can alter the proportion of the different kinds of compounds derived from its food, for amino acids can be converted to glucose, and carbohydrates to fat; but there is little conversion of fat to carbohydrate, and only the simpler amino acids can be made from nonprotein foods.

If the food currently taken does not provide the required energy, stored foods are consumed. The carbohydrates (glycogen of the liver and muscles) are used first. Fats are used simultaneously with the carbohydrates but usually last until after the carbohydrates are exhausted. Then the materials of the protoplasm itself are used, first those of the less essential organs, then of the brain, spinal cord, and heart. Death usually follows quickly upon such extreme starvation.

Materials Required.—Besides furnishing energy, food must also provide materials with which to build protoplasm and such secreted products as the hard parts of bone and teeth. One of the most urgently required materials is water—2000 cc. a day in an average person. Certain salts must be regularly supplied, since about 30 grams are lost per day, mostly in urine and sweat. Most ordinary foods contain about the right proportion of the various salts, though vegetable foods are deficient in sodium chloride (NaCl). This is the reason for the common use of table salt. Any one sweating profusely because of heavy labor in hot places must usually drink salt water to avoid muscular spasms.

There are certain minerals which are necessary. The ones most likely to be poorly represented in the diet are iron, calcium, and iodine. The hemoglobin of red blood cells requires iron, and this is adequately provided in liver, meats in general, eggs, and many vegetables and fruits. Calcium is needed for bone and teeth, and is obtained from milk, cereals, peas and beans. Iodine is necessary for the hormone of the thyroid gland. It is abundant in sea foods; and in inland communities health authorities often require that potassium iodide be introduced into table salt. Other minerals, including copper, zinc, manganese, and cobalt, are essential for the production of important enzymes, but the amounts needed are exceedingly small and natural diets usually contain enough of them.

For construction of protoplasm proteins are steadily required—a minimum of 50 grams a day for an average adult person. A variety of amino acids is necessary, and since only a few of the simplest ones can be synthesized from other substances, the others must be included in the diet. Foods which supply all the necessary amino acids are the proteins of eggs and lean meat, the glutenin of wheat, and the lactalbumin of milk and cheese. Most other protein foods lack, or include too small quantities of, certain amino acids. Some fat is also required; for though most of the fatty acids can be synthesized from carbohydrates, the ones which the human body can not synthesize are quite essential, and these must be received ready-made.

Vitamins.—One group of required specific substances deserves separate treatment. It has long been known that a diet consisting of purified proteins, carbohydrates, and fats leads to serious trouble. Natural foods evidently contain something that does not occur in the purified foods.

These essential substances were given the collective name of *vitamins* before anything was known of their identity. These substances, in small quantities, are needed for healthy activity or growth. If any of them is lacking, or present in too small amount, a *deficiency disease* results. The disease is specific for each of the vitamins.

The earliest known and recognized of the deficiency diseases was scurvy. Before the end of the sixteenth century an officer of the English

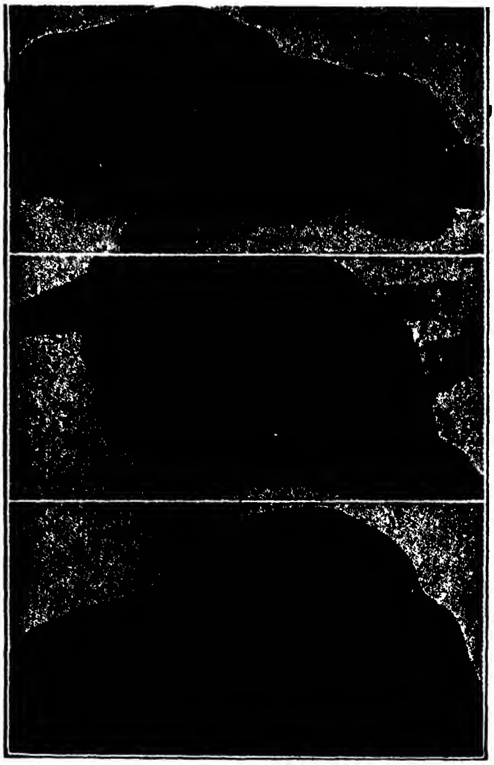

FIG. 92.—The need of vitamin A. Upper two dogs show xerophthalmia caused by deficiency of vitamin A. Lower figure, one of same dogs after 10-day treatment with cod-liver oil. (*From Steenbock, Nelson, and Hart in American Journal of Physiology.*)

navy observed the bruised skin, bleeding gums, and general anemia of his crew after they had been many months at sea and fresh foods had been exhausted, and he discovered that these symptoms could be completely prevented by giving his men a small amount of lime juice daily. The essential feature of the lime juice was long designated vitamin C, though its nature was unknown. In 1933 this vitamin was separated out in pure form, and was found to be *ascorbic acid*, of the chemical formula $C_6H_8O_6$. It is abundant in citrus fruits (oranges, lemons, limes, grapefruit), many other fruits, tomatoes, and many vegetables. Diets which include raw plant food are generally adequate, but cooking in vessels exposed to air usually destroys much of the antiscorbutic effect.

Vitamin A, itself colorless, can be split off, in the human body, from the yellow pigment *carotene* found in carrots and many yellow and green vegetables. Its formula is $C_{20}H_{30}O$. Severe lack of it in the diet leads to a dry, ulcerated condition of the cornea of the eye known as xerophthalmia (Fig. 92). Milder deficiencies cause abnormalities of epithelial membranes and retard growth. Vitamin A is also used by the retina of the eye in the synthesis of *visual purple*, one of the light-sensitive pigments, and was administered during the war to night-flying pilots to improve their vision. Being soluble in fats (as are two other vitamins, D and E), vitamin A is obtainable in liver oils and in such foods as milk, butter, and egg yolk. Manufactured butter substitutes are usually fortified by the addition of this vitamin.

What was originally called vitamin B eventually proved to be a collection of different substances, enough alike to be hard to separate, and occurring mostly in the same natural foods. This group, consisting of seven or more vitamins, is now known as the *B complex*. Only the more important of these can be mentioned here. Lack of *thiamin* (B_1) causes polyneuritis, which in man is usually named beriberi. This disease involves degeneration of the nerves, causing progressive paralysis. Along with paralysis go retarded growth and loss of appetite and vigor. Intravenous injection of B_1 into polyneuritic animals restores normal muscular movement in as short a time as one hour. The formula of thiamin is $C_{12}H_{16}N_4SO$. One of its sources in food is in cereals, especially the outer seed coats. For this reason polished rice, in which the seed coats are removed, and highly refined wheat flours (as contrasted with whole wheat) are poor in thiamin. It is common practice now to add thiamin in the manufacture of white flour. Other natural sources of thiamin are meats, especially pork, and yeast.

A second member of the B complex is *riboflavin* ($C_{17}H_{20}N_4O_6$), called also B_2. It is found in the same foods as B_1 and the other vitamins of this group. Lack of it induces a predisposition to cataract, loss of weight, and scaliness of skin around the ears and mouth.

Closely associated with the other B vitamins is *niacin* ($C_6H_5NO_2$), or *nicotinic acid*. Lack of it is the principal cause of pellagra, which is characterized by dermatitis (eruption of the skin) and diarrhea. As a pellagra preventive, niacin has come to be called vitamin P-P. The disease is still common in southeastern United States, where corn, molasses and meat are the staple diet. Niacin is manufactured and is available to prevent pellagra, but is not yet in sufficiently wide use. The dermatitis feature of pellagra may be due to lack of B_6, or *pyridoxin*, which is frequently absent from the pellagra-producing diet.

Rickets, the imperfect growth of bones and teeth, is caused by a deficiency of vitamin D. This substance is now known to be *calciferol* ($C_{28}H_{44}O$). It is produced from a closely related substance, *ergosterol*, regularly present in the skin, by ultraviolet radiation. In summer time the conversion of ergosterol to calciferol is usually adequate in most regions, but in winter it is often advisable to supply vitamin D artificially. The common foods containing it are butter, milk, and the oils of liver and other animal tissues. So well understood are the preventive properties of these foods, or the manufactured vitamin, that rickets, once a common disease, is seldom observed in most communities.

Reproductive disturbances in some animals are caused by lack of vitamin E, *α-tocopherol* ($C_{29}H_{50}O_2$). In its absence female rats do not retain the embryos in the uterus, and male rats do not produce functional spermatozoa. No such effects have yet been shown in man. Vitamin E occurs widely in plant and animal oils, particularly in the germ of wheat.

Failure of coagulation of the blood may be caused by lack of vitamin K, whose formula is $C_{31}H_{46}O_2$. In its absence the body does not produce enough *prothrombase*, from which the clotting enzyme is produced at wounds. Vitamin K is regularly administered before child-birth, with a considerable decrease in mortality from bleeding in both the newborn children and their mothers. Natural food sources of the vitamin are leafy vegetables; it is prepared commercially from alfalfa.

Vitamin P, not yet identified chemically, is closely related to ascorbic acid (C) and is involved in scurvylike weakness of the walls of blood capillaries. Its status is still unsettled.

The necessary amounts of vitamins are so small (0.01 gram or less daily) that they cannot be regarded as sources of energy. They must be in some way essential in protoplasmic structure. Three of the vitamins, thiamin, riboflavin, and the antipellagra factor, are known to enter the composition of important oxidative enzymes; that is, they furnish the nonprotein part of the enzymes. What other structural contributions the vitamins make is not known.

The need of vitamins in food differs greatly in different animals. Rats, for example, need no ascorbic acid in their diet, since they synthesize it in their metabolism; rats never have scurvy. Man can get along with little or no thiamin in his diet; but bacteria in his large intestine must then supply it. As stated above, man probably does not require vitamin E, or else produces it in normal metabolism.

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CHAPTER 10

RESPIRATION AND RELEASE OF ENERGY

The total requirements of energy and the general source of it in the food have already been discussed in connection with nutrition. How energy is released from food is a separate problem.

Derivation of Energy.—Ultimately most energy comes from sunlight. Many plants and a few of the simplest animals have chlorophyll, which utilizes solar energy to make sugars. In these sugars, energy is bound up in chemical structure. As sugars are converted into starches, or fats, or proteins, by combining them with other substances, still further energy is stored in these higher products. When plants are devoured by animals, the latter take possession of this potential or stored energy. So it is that all energy of life is traceable to sunlight. Indeed, most other energy in the world comes from the same source. Coal and oils used for fuel got their energy from ancient sunlight. Even the energy of waterfalls came from the same source, for it was the energy of the sun which lifted the water to its higher level. About the only energy expended on the earth which is not traceable to sunlight is that of the tides.

Animals derive some of their energy directly from the sun, for sunlight is one of the most potent of health-giving agencies. In the main, however, they obtain it from food, and for this they are directly or indirectly dependent on plants. To get energy from foods, it is necessary that the latter be chemically decomposed. The foods must be changed into simpler substances whose content of potential energy is smaller. In general, complex substances with large molecules have more energy bound up in their constitution than do simple substances with small molecules. Nearly all chemical reactions which split up molecules into smaller and simpler ones may therefore be depended on to release a certain amount of energy. Proteins, carbohydrates, and fats, on being decomposed, even in the process of digestion, liberate energy.

There is, however, one type of energy-yielding chemical reaction which is so much more abundant than any other that it is common practice to speak of energy as coming from that source. That type of reaction is oxidation (page 37), the union of oxygen with other elements. The commonest of these unions is that of oxygen with carbon, because carbon is abundant in all the classes of organic compounds—in proteins, but especially in carbohydrates and fats. Carbon dioxide, a very stable compound which ties up very little potential energy, is a product of these oxidations, so that the amount of carbon dioxide which an animal produces is often taken as an indication of the quantity of energy it uses.

Respiration.—How is all the oxygen for these oxidations obtained? There is not enough of it in the substances to be oxidized. The common carbohydrates contain only about half enough oxygen to oxidize their own carbon, even if all their oxygen were available—which it is not—for that purpose. Fats, the other main source of energy, have even less oxygen than the carbohydrates. The oxygen must therefore be introduced from external sources. For land animals that source is the air, about one-fifth of which is oxygen. Aquatic animals of most kinds secure the oxygen which is dissolved in the water about them.

The obtaining of oxygen is included in the process known as *respiration.* In small animals—unicellular and small multicellular ones—oxygen is absorbed more or less directly by the cells that use it. In the larger animals, those in which most of the cells are too far away from the surface to rely on this simple diffusion, respiration is a double process. That is, the oxygen must first be got into their bodies, a process known as *external* respiration, and then be conveyed to the cells where it is ultimately used. Its absorption by these cells, often far within the organism, is called *internal* respiration. In the protozoa, external and internal respiration are merged into a single process, to which neither name may be properly applied.

Whether an animal must have any special devices to carry on its external respiration depends on its oxygen requirement in relation to its surface. A large animal has much less surface relative to its volume than a small one has; hence, in general, the larger animals must have structures which greatly increase their absorptive surfaces. Warm-blooded animals consume much more oxygen than do cold-blooded ones, and active animals much more than sluggish ones. Even as large an animal as the earthworm, which is cold-blooded and not very active, is able to absorb enough oxygen through its general surface. Many smaller animals, however, because they are active, require some sort of respiratory organ for their external respiration.

Types of Respiratory System.—Probably the earliest external respiratory organs developed in animals were *gills.* These may be employed by aquatic animals, and by aerial animals having some way of keeping them moist, for oxygen cannot be absorbed through dry surfaces. A gill, like any other respiratory organ, must furnish a large surface, since the amount of oxygen taken in increases with increase of surface. It may consist of branching or treelike projections (Fig. 93), or of bunches of fine tubes, or of clusters of flat plates, or of numerous ridges or fingerlike projections, or of sievelike sheets through which water passes. In every such organ the first essential is an increased surface, and the different forms of gill merely represent various ways of attaining that end. Among animals that use gills are fishes, some salamanders, crayfishes, clams, some marine worms, and young stages of many insects.

Lungs are internal cavities into which air is drawn for absorption of its oxygen. Notwithstanding their internal location, lungs are organs of external respiration, since the bulk of the oxygen they absorb is not used for energy release in the cells of the lungs themselves but is passed on to other cells of the organism.

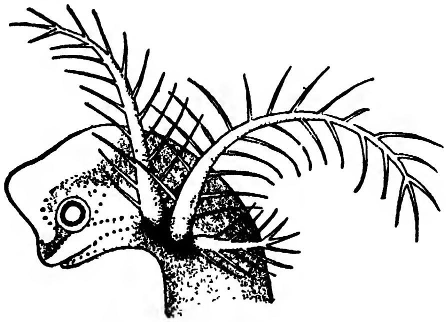

FIG. 93.—External gills of the amphibian, *Epicrium glutinosum*. (*From Wiedersheim after Sarasin.*)

The lung in lower amphibians is a baglike organ with a large central cavity (Fig. 94*a*); but in higher amphibians it becomes more complex since its inner surface is thrown up into corrugations with cross corrugations forming boxlike spaces (*b*, *c*). These corrugations increase the respiratory surface. In higher vertebrates the lung (*d*) is entirely subdivided into minute air spaces which are in indirect connection with one another through

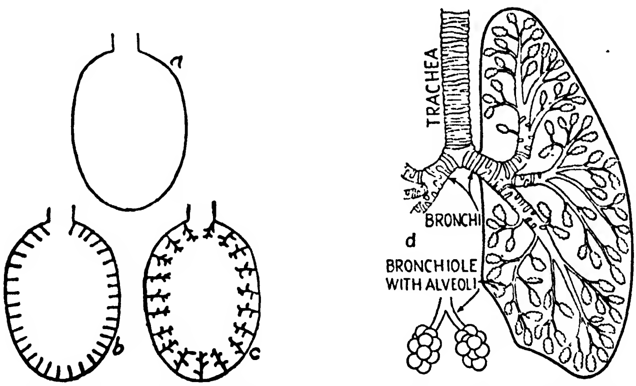

FIG. 94.—Diagrams of types of lungs. *a*, amphibian lung with plain surface; *b*, amphibian lung with low folds making simple alveoli; *c*, amphibian lung with higher folds which are themselves folded making more numerous alveoli; *d*, human lung.

large tubes, the *bronchi*, and their branches, the *bronchioles*. The bronchi unite in a single large tube, the *trachea*, which is present in the higher vertebrates, but absent in some of the lower forms, as the frog. The trachea opens into the mouth through a slitlike *glottis*. The trachea and bronchi have cartilage rings in their walls, so they do not collapse. The bronchioles end in expanded chambers, the *alveoli,* which are in close contact with blood capillaries. The aggregate interior surface of the alveoli in man (Fig. 94*d*) is more than 1000 square feet or about fifty times as great as the general surface of the body.

In most insects, air is taken in by *tracheae.* These are tubes opening at the surface of the body at various points. The tracheae branch, tree-fashion, in such a way as to reach all parts of the body (Fig. 95). No part of any insect tissue is more than a few cells away from the nearest tracheal branch. Formerly it was thought that air pulsed back and forth, into and out of these tracheae. It is now known for some insects, however, that air goes in at certain tracheae, out at others, thus implying a circulation of the air. The tracheae are connected with one another by branches, so that such a circulation is possible.

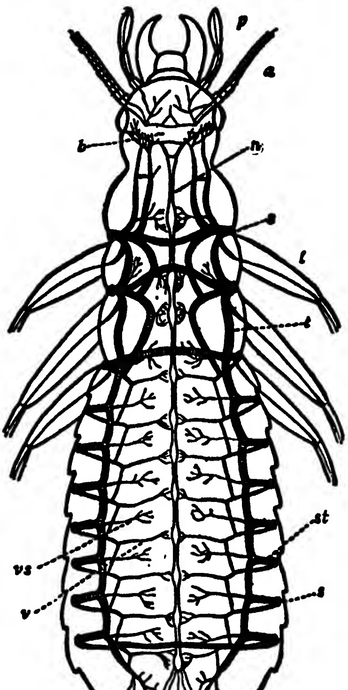

FIG. 95.—Tracheal system of an insect. *a*, antenna; *b*, brain; *l*, leg; *n*, nerve cord; *p*, palpus; *s*, spiracle; *st*, spiracular branch; *t*, chief tracheal trunk; *v*, ventral branch; *vs*, visceral branch. (*From Folsom, "Entomology," after Kolbe.*)

The young stages of May flies, dragon flies, and some beetles live in the water, yet respiration is carried on by tracheae. Instead of *opening* at the surface of the body, such tracheae begin in fine *closed* branches which spread out in external gills (flat plates or tubes), from which they receive their oxygen by absorption. Such gills richly supplied with tracheae are known as *tracheal gills.*

Breathing Movements.—Whatever mechanism an animal possesses for the absorption of oxygen, it is necessary that there be a continuous supply of oxygen to absorb. An animal that lives fully exposed but attached to some object in swiftly flowing water usually requires no special device to ensure that supply. But one that lives in still water and remains motionless soon absorbs all the neighboring oxygen; and since oxygen diffuses only very slowly through water, the supply is not quickly renewed. Fishes swim about; but since the gills are under a protective plate (the *operculum*) at each side just behind the head, mere moving about does not suffice. Renewal of the oxygen supply next to the gills is effected by taking water into the mouth and then pumping it out through clefts among the gills. The opercula are raised to allow the water to pass out but settle back immediately after, so as to prevent water from entering there. The action is repeated, and a pulsating current of water is kept up. Lobsters have a fanlike structure at one edge of the gill chamber, and by its movement a continuous stream of water is kept flowing over the gills.

Land animals have various devices acting to the same end. Insects expand their chitinous exoskeleton by muscular movement, and air rushes in: the skeleton collapses, and the air is forced out. Valves at the entrances of the tracheae determine which ones shall receive air. In general the air chambers or passages have, of themselves, no power of either expansion or contraction; they are manipulated by something else. The lungs in man are expanded at all times, to fill the cavity of the thorax, merely by the air pressure within them. If the chest expands, more air is forced in from the outside to equalize the pressure. In inspiration, the volume of the chest is increased by two means: (1) raising the ribs, and (2) lowering the *diaphragm*. The ribs are movably joined to the vertebral column, from which they slope downward both laterally and forward. The muscles between the ribs contract, so that all ribs are lifted, the lowest ones most of all. Since the ribs slope downward, elevating them pushes them outward (sidewise and to the front), thus enlarging the chest in both directions. The diaphragm, a muscular sheet across the bottom of the thorax, is convex like an inverted bowl. When its muscles contract, the diaphragm is flattened, thus further increasing the size of the chest cavity. Air pressure in the lungs is thus reduced, hence air is forced in to restore an equilibrium. In expiration, the rib muscles relax, and the ribs drop, largely by their own weight. Both width and depth of the thorax are thus decreased. When the muscles of the diaphragm relax, tension of the muscles of the abdominal wall presses the viscera up against it and the diaphragm rises. With the accompanying decrease in the size of the thorax, air is forced out of the lungs.

All such movements designed to ensure a continuous supply of oxygen, whether in air or water, are termed *breathing* movements. To supply the right amount of air, these movements must vary in vigor as the animal's activities change. In man, the rate of breathing is controlled by a nerve center in the medulla, posterior division of the brain. The action of this center depends on the amount of carbon dioxide in the blood. If muscular activity increases, much more carbon dioxide enters the blood from the tissues; this extra quantity stimulates the respiratory center in the medulla, and breathing becomes more rapid. Panting is an extreme response to such stimulation. If the breath is voluntarily "held" for a short time, carbon dioxide accumulates in the blood to such an extent that restoration of breathing is forced. No will power can resist the urgent demand of the respiratory center that breathing be resumed.

Mechanism of Oxygen Collection.—It has already been stated that oxygen does not spread through dry surfaces. This is because the movement of oxygen in entering an organism is a process of diffusion, which can occur freely only when the oxygen is in solution. Aquatic animals, except a few air-breathing types like whales and other swimming mammals, never meet oxygen except in solution. When air comes in direct contact with an animal, its oxygen cannot enter unless it is first dissolved. All that is necessary is to have the surfaces moist; oxygen dissolves in the film of moisture, then passes readily inward through the membranes. Lungs and tracheae have no difficulty in maintaining this moisture, since they possess internal cavities in which there can be little evaporation. Land animals with gills, however, must either live in places that are perpetually moist, such as swamps, or must prevent evaporation in some way. Land-dwelling crayfishes protect their gills from drying by means of chitinous flaps of the exoskeleton (page 90) and have the habit of burrowing in the soil until moisture is reached.

The passage of oxygen through moist membranes depends on the same principle as that which causes water to flow down hill, or winds to blow from areas of high atmospheric pressure to those of low pressure. Oxygen goes from places of high oxygen pressure to those of lower pressure. This pressure is not entirely a matter of quantity, for a small amount of oxygen dissolved in a certain volume of water may exist at a greater pressure than does a greater amount in the same volume of air. When oxygen enters the gills of an aquatic salamander, it is because the oxygen in the water is at greater pressure than is the oxygen in the gills. In a land animal with lungs, the oxygen in the [redacted]gs is at higher pressure than in the tissue of the lungs. In the human lungs the air in the remote alveoli, being diluted with waste products there, exhibits an oxygen pressure somewhat lower than the oxygen pressure of open air; and yet it is nearly three times as great as the oxygen pressure in the tissues of the lungs; hence the transfer to the tissue. From the cells lining the alveoli of the lungs it is a very small step to the blood, for the capillaries are closely applied to the alveoli. Oxygen enters the plasma, the liquid portion of the blood, again in response to a pressure gradient: pressure is lower in the plasma. Pressure is constantly kept lower in the plasma, because the red blood cells contain a protein which takes up quantities of oxygen in chemical combination. Moreover, the blood is circulating; blood that has absorbed oxygen is continually being replaced by blood that has little of it. So a perpetual transfer of oxygen to the blood is set up in the lungs.

Internal Respiration.—When the oxygen is finally presented to the tissues or cells in which it is to be consumed, its introduction to those cells is again dependent on relative pressures. Oxygen is at higher pressure in the plasma of the blood than in the adjoining tissue cells, which have used their oxygen. As the plasma gives up its oxygen to the cells its oxygen pressure is lowered; and in response to this reduction, oxygen is released from chemical combination in the red cells, and is dissolved in the plasma. The plasma thus maintains a higher oxygen pressure as long as there is oxygen in loose combination in the red cells; and before the red cells have lost all their loosely combined oxygen, the blood has passed on and been replaced by fresh blood which has not yet been called upon to give up its oxygen. So there is a continual diffusion of oxygen from the blood to the tissue cells. The transfer is very rapid, for the oxygen pressure in the blood is reduced by half in one second of time. The cells nearest the capillaries pass some of their oxygen on to cells farther away, again in response to differences in pressure but aided by a fluid (see next chapter) bathing the cells, and no cell is very far from the nearest blood vessel.

Respiration Also an Excretory Process.—While we are not yet ready to discuss the general phenomenon of removal of wastes, it should be pointed out in passing that certain wastes are removed in respiration. These wastes are carbon dioxide and a small amount of water. Carbon dioxide results from the very abundant oxidation going on everywhere in living things. It leaves the tissues where it is produced because its pressure is higher than in the near-by blood plasma. The resulting increase of pressure in the plasma causes the chief protein of the red cells to combine with carbon dioxide. Delivered by the blood to the lungs, the carbon dioxide is at greater pressure in the blood than in the air of the lungs; hence the plasma gives up carbon dioxide to the air on the other side of the two thin walls which separate blood and air, and red cells yield more carbon dioxide to the plasma. Since the blood moves on, no equilibrium can be reached; always carbon dioxide passes from blood to air in the lungs. This elimination of carbon dioxide is regarded as part of respiration, even though it is also excretion. Excretion in general is treated in another chapter.

Release of Energy.—Energy for all sorts of work in living things is obtained, as stated earlier, by combustion of foods. These substances are literally burned, just as coal is burned in a boiler, with the difference that combustion in living things is carried on at relatively low temperatures. The reason for the ability of animals to burn their fuel without great heat lies in their possession of enzymes. The burning is simple oxidation, and the enzymes serve to bring oxygen and the foods together in chemical reaction. One of the chief functions of respiration is to furnish oxygen, just as one of the principal ends of digestion is to provide foods, for this reciprocal reaction whose object is the release of energy.

Carbohydrates require less oxygen from outside sources for their combustion, because they furnish some of their own. The carbon of the sugar molecules unites with the oxygen which the same molecules contain and with oxygen of respiration. Carbon dioxide, the end product of this combustion, contains little stored energy. Most of the energy residing in the sugar is thus liberated.

Fats, which are also primarily fuels, are burned in the same way; but since they contain relatively little oxygen, more oxygen of respiration is required for their combustion. Again carbon dioxide is the energy-poor end product. As stated in the preceding chapter, fats are not readily burned unless carbohydrates are being oxidized at the same time; the reason for this connection is not known.

Proteins, which are primarily material for construction, may also be burned. To some extent they are utilized as a normal source of energy, but in times of starvation this use is stepped up markedly. Since proteins are not stored to any extent in animals, combustion of them is at the expense of the body tissues. Animals literally burn themselves at such times. Part of the living organism is being destroyed to maintain the rest of it. Proteins are intermediate between fats and carbohydrates in the amount of outside oxygen they require for their oxidation.

Heat.—One of the important uses to which energy is put in some animals is the development of heat. This heat comes mostly from oxidations occurring in muscle. If the amount of heat is regulated in some way, so that a fairly constant temperature is maintained, an especially advantageous situation is produced. Many physiological processes bear a time relation to one another, and the speed of most such processes is accelerated by high temperatures and retarded by low ones. If the speeds of various processes are not equally affected, a change of temperature destroys a nice adjustment among them. Hence a constant temperature is an advantage.

Many invertebrate animals have no heat regulation; and, when their muscular movements are slight, as in clams and snails, their temperatures are almost identical with that of other things around them. Such animals are said to be cold-blooded. Among the vertebrates, the fishes, amphibia, and reptiles are all regarded as cold-blooded because their temperatures rise and fall with changes in external temperature; but some, perhaps most, of them have temperatures somewhat above that external to them.

The higher mammals, including man, are warm-blooded (as are also the birds) and have very marked regulation of temperature. The temperature of the human body in health seldom rises much above 38° or falls much below 37°C. Regulation works in both directions. When the internal temperature falls to a certain degree, shivering is caused, and heat is produced by the additional muscular movement. When the temperature rises too far, there are several ways of checking it. Rapid breathing serves to cool the lungs, and with them the whole body. More blood flows to the skin; hence there is greater loss of heat by radiation. And in man and horses, but not so much in many other mammals, sweat exudes upon the surface, where its evaporation serves to lower the temperature. In the dog there are no sweat glands except on the nose and on the foot pads. In this animal rapid ventilation of the lungs in panting is the chief source of control; whatever cooling is caused by evaporation occurs in the open mouth and on the lolling tongue.

Regulation of temperature is governed by a nerve center in the thalamus of the brain. When this center is warmed, the nerves going to the blood vessels in the skin cause the latter to enlarge, and the sweat glands are stimulated to excrete. On cooling the nerve center, these actions are reversed, and muscle tension is increased, all of which leads to a rise of temperature.

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CHAPTER 11

TRANSPORTATION SYSTEM

Only in small animals can oxygen be taken in, digested food distributed, and carbon dioxide and other wastes eliminated by mere diffusion. In large animals the distances are too great for these slow-moving processes. In such animals there must be a system of transportation connecting all parts of the body. This communication is furnished by the circulatory system.

Open and Closed Circulatory Systems.—In crayfishes, insects, and their allies there is a heart which forces blood into a small number of major blood vessels. These vessels or their branches open into small or great spaces among the cells and organs, so that the blood comes into contact with the tissues directly. Food is carried to the cells, and wastes are removed, by direct contact. From the intercellular spaces the blood is passed through the gills, and finally returns to the heart. Circulation in such an open system must be slow because of the resistance offered by the tissues.

Any system of fluid communication must, like that of the crayfish, reach the cells rather directly. To retain this necessary direct contact and at the same time speed up the circulation, the vertebrate animals have evolved two separate yet cooperating systems: (1) a *blood* system in which there are smooth, closed tubular vessels in which the flow is very rapid, and (2) a *lymph* system in which movement is slow but the cells are reached directly. These systems are connected, and the fluid in the latter is derived largely from the former.

The Blood System.—A closed blood system consists of a set of tubes which branch so extensively as to bring all parts of the body very near to the circulating liquid. The blood is propelled through these tubes by a contractile organ, the *heart.* In some animals the walls of the blood vessels are contractile, and waves of contraction pass along them in the direction of circulation. When these vessels are especially large, and when their contraction is more marked than those of other vessels, as are those at the sides of the esophagus in the earthworm, they may properly be called hearts. In the higher animals, vessels conducting blood away from the heart are called *arteries;* those returning it to the heart are *veins;* and the fine tubes leading from the arteries to the veins are called *capillaries.* The arteries have strong walls capable of withstanding considerable pressure, and they are firm enough to stand open even when empty of blood. The veins are not called upon to endure such pressures as are the arteries; their walls are comparatively thin and collapsible. Moreover, in the veins there are at invervals valves, consisting of membranous flaps directed forward (in the direction of flow), which close and stop the blood if it starts at any time to flow backward (Fig. 96). The capillaries are of various sizes, the smallest ones being just large enough to allow the blood cells to pass along single file. They have very thin walls, only one cell thick. Being thin, they are collapsible, and at times of rest, when the circulation is slow, many of them are closed.

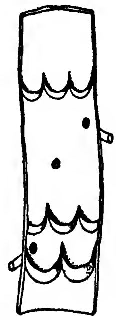

Fig. 96.—Vein slit open to show valves. Course of blood is upward.

Blood is kept coursing through these vessels by the motive power of the heart. Any muscular activity is apt to exert pressure on near-by veins, and this in conjunction with the valves in the veins helps to keep the blood moving; but the heart action is the main source of power.

Chambers of the Heart and Course of Circulation.—The hearts of various vertebrates have two, three, or four chambers, and the course of the circulation is in part related to this feature of heart structure. A diagram of the circulatory system in the dogfish, an animal with a two-chambered heart, is shown in Fig. 97. This diagram indicates that the blood of animals with gills and a two-chambered heart passes from the *ventricle* of the heart through the gills and then forward to the head or backward through the *dorsal aorta* to the organs of the body, where it passes through capillaries and returns to the *auricle* of the heart by means of the veins.

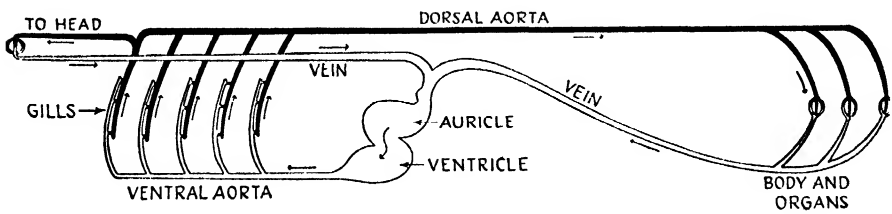

Fig. 97.—Simplified diagram of the circulatory system of the dogfish.

Except for the fact that the blood in the arteries is distributed to different organs, from each of which it returns independently to the veins, the blood of a fish covers only one circuit. It passes through two sets of capillaries, one in the gills and another in the head or some body organ or tissue, and goes to the heart *only once* in each circuit. This course is a consequence of the two-chambered construction of the heart.

In animals with lungs and a heart of more than two chambers the circulatory system is more complicated. The heart of amphibians and reptiles, except crocodilians, has three chambers in place of two as in the heart of fishes (Fig. 97), and the heart of mammals, birds, and crocodilians has four chambers. The four-chambered heart is composed of two halves, right and left. Each half is made up of two chambers, a thin-walled auricle and a thick-walled muscular ventricle. There is no passage between the two halves of the heart but there is a broad passage guarded by valves connecting each auricle with the ventricle of the same side. The relations of the parts of a four-chambered heart may be understood from Fig. 98.

The circulation in such an animal is a double one. Beginning at the left ventricle (see Fig. 99 for the human scheme), the blood is driven into the large artery which, with its divisions, leads to the body in general, including the head. In these parts the arteries divide into capillaries, which are collected again into veins. The veins gather into two large veins which enter the heart by the right auricle. The circuit just described from left ventricle through the body to right auricle, is called the *systemic circulation.* The blood now goes from the right auricle, through valves, to the right ventricle, thence is forced to the lungs. After passing through the capillaries of the lungs it returns by a large vein to the left auricle of the heart, thence to the left ventricle. The circuit through the lungs is called the *pulmonary circulation.* In a complete circulation, therefore, the blood passes through the heart twice, once through the left side, once through the right. The blood has no alternative in this course, except that in the systemic circulation it may go to any one of a number of parts of the head, trunk, extremities, or abdominal organs. When it has gone through the systemic circuit, it has no choice but to go to the lungs.

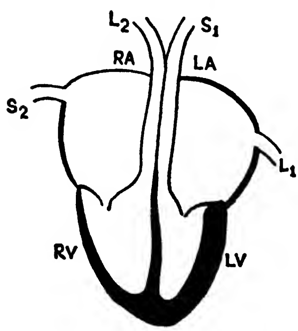

FIG. 98.—Diagram of a four-chambered heart. *LA*, left auricle; *RA*, right auricle; *LV*, left ventricle; *RV*, right ventricle; L_1, vessel from lungs; L_2, vessel to lungs; S_1, vessel to system; S_2, vessel from system.

The doubleness of this circulation is a consequence of the four-chambered heart, that is, of its complete separation into right and left halves. In animals with a three-chambered heart, as in a frog, this distinctness does not prevail, for while there are two auricles there is but a single ventricle. There is therefore some mixing of the blood in the ventricle; but the structure of the ventricle with its deep recesses and the operation of valves in the principal artery are such that the mixing of venous and arterial blood is partially prevented.

In general, when the heart has four chambers, the blood passes through only one set of capillaries in each circuit. There is only one set

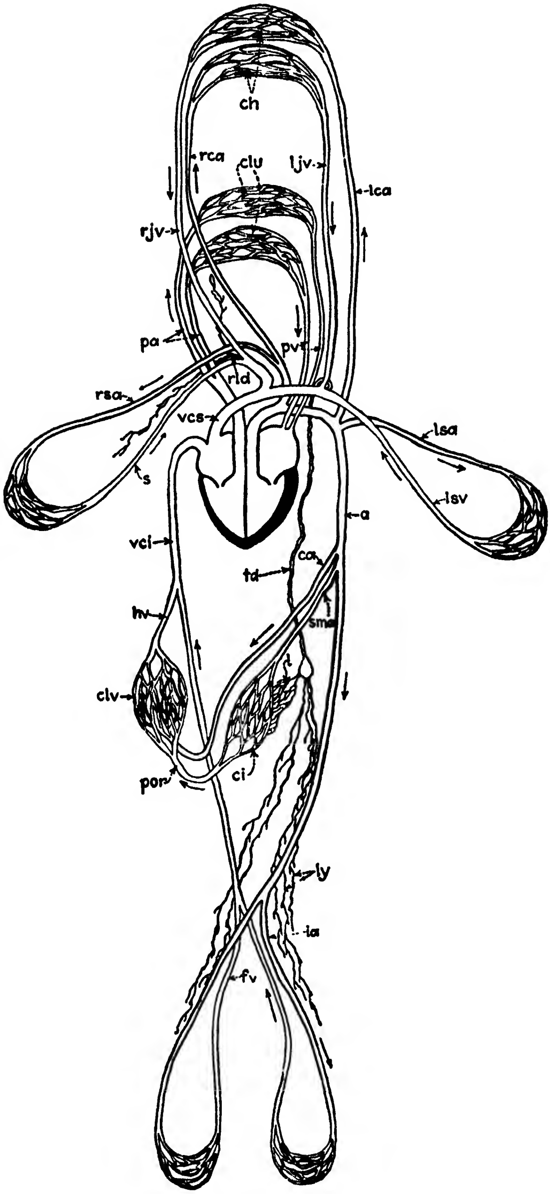

FIG. 99.—Diagram of human circulation: *a*, aorta; *ca*, celiac artery; *ch*, capillaries of head; *ci*, capillaries of intestine; *clu*, capillaries of lungs; *clv*, capillaries of liver; *fv*, femoral vein; *hv*, hepatic vein; *ia*, iliac artery; *l*, lacteals (intestinal lymphatics); *lca*, left carotid artery; *ljv*, left internal jugular vein; *lsa*, left subclavian artery; *lsv*, left subclavian vein; *ly*, lymphatic capillaries; *pa*, pulmonary arteries; *por*, portal vein; *pv*, pulmonary veins; *rca*, right carotid artery; *rjv*, right internal jugular vein; *rld*, right lymphatic duct; *rsa*, right subclavian artery; *s*, subclavian vein; *sma*, superior mesenteric artery; *td*, thoracic duct; *vci*, vena cava inferior; *vcs*, vena cava superior.

in the pulmonary circulation, and for the bulk of the blood there is only one in the systemic course. There are, however, certain exceptions. The blood which traverses the stomach, intestines, pancreas, and spleen collects into a vein (Fig. 99 *por*) leading to the liver; in the liver it passes through a second set of capillaries, then enters the large vein returning to the heart. A circuit beginning and ending in capillaries is known as a *portal* system, and that going from the abdominal viscera to the liver is the *hepatic portal* system. Fishes and amphibia have a portal system leading to the kidneys also, but that is lacking in man and mammals in general.

It has been estimated that about 7½ per cent of the weight of the human body is blood. From the amount ejected from the heart at each beat, it may be calculated that the speed of the blood is such that an entire circulation, both systemic and pulmonary, requires on the average only about 23 seconds.

Composition of the Blood.—The blood consists of a liquid known as the *plasma* and a number of kinds of cells or cell derivatives. The

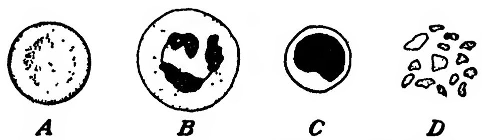

FIG. 100.—Formed elements of human blood. *A*, red corpuscle; *B*, *C*, two forms of white cell; *D*, platelets.

plasma floats the cells, and in addition carries a number of kinds of substances in solution. Among these substances are some temporary ones such as the products of digestion (glucose, amino acids, neutral fats, glycerol, fatty acids), waste materials (urea, uric acid), the respiratory gases (oxygen and carbon dioxide), hormones (secretin and others), and various enzymes, which are introduced and removed at certain places in the system. Other substances are permanent. Of these, proteins make up about 7 per cent of the weight of the plasma; one of the proteins is *fibrinogen* which features prominently in the clotting of the blood. Inorganic salts are about 1 per cent of the weight of the plasma; an important one is a bicarbonate which carries carbon dioxide in its negative ions (HCO_3^-). Finally, there are antibodies which the tissues of the body have produced in reaction to and protection against foreign proteins, including disease-producing organisms.

The visible objects in the blood are of three general kinds: (1) *red cells*, (2) *white cells*, and (3) *platelets* (Fig. 100). The red cells are flat disks, circular in form and thin in the center in man and most of the other mammals, but elliptical in other vertebrates. There are about 25 trillion (25 million million) red cells in an average human being. The human red cell has no nucleus when in the blood, but in its developmental stages in the red marrow of the bones, by which it is produced, it has a nucleus. Red cells contain an important protein substance known as *hemoglobin*, which gives the cells their red color. From the rate at which hemoglobin is disintegrated in the liver, it is estimated that at least 5 per cent of the red corpuscles are destroyed every day. In other words, more than 10 million of them disappear *every second.* Hence there must be a rapid replacement of them by the marrow.

The white cells are of half a dozen kinds. Two-thirds of them belong to one type having an irregularly lobed or even divided nucleus (Fig. 100*B*), the power of movement like Amoeba, and the ability to engulf bacteria. These cells may creep out of the capillaries, through small crevices between the cells of the capillary walls (Fig. 101). They emerge from the capillaries in great numbers at the site of an infection, to engulf the infecting organisms. In their battle with the bacteria many of the white cells are killed, and their bodies make up a large part of the

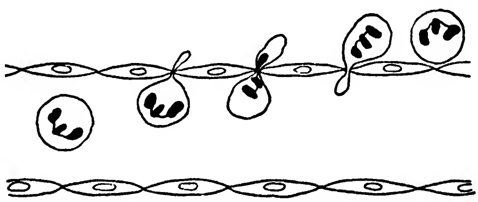

FIG. 101.—Successive stages in the emergence of a white blood cell from a capillary.

pus which collects in an abscess. White cells of this kind originate in bone marrow. The next most numerous kind, about one-fourth of the total, originate in lymphoid tissue (lymph glands, spleen). The remaining types are recognized by different staining reactions as well as by their size and nuclear structure; some of these devour bacteria, others do not, but their functions are not well understood. All kinds of white cells together number about 30 to 40 billions in an average human being.

The platelets are not cells, but pieces of cells. They come from certain large cells in the bone marrow by fragmentation. They disintegrate so rapidly when the blood leaves the capillaries that it is difficult to count them. By special techniques it has been estimated that there must be from one to three trillion of them in a human being. Only the mammals are certainly known to have them. Their disintegration on leaving the blood vessels yields a substance which is important in the clotting of the blood.

Regulation of Heart Beat.—Because the heart is histologically practically a unit, it beats also as a unit. It is one of the best organs with which to demonstrate the all-or-none principle, because of this unity and the constant vigor of its contraction. Several other features of its beating are of the utmost importance.

The heart has a long refractory period. Any muscle, after it has contracted, will refuse to respond to a subsequent stimulus until a certain time has elapsed. This interval of rest, known as the refractory period, is exceedingly short (0.005 second) in skeletal muscle, but very long in the heart. This prevents the heart from responding to any abnormal nervous condition by remaining continuously contracted. It contracts once, then must wait an appreciable time, during which it relaxes, before it can contract again.

Contraction of the heart is initiated by a mass of rather embryonic tissue located in the right auricle, near the point where the great veins enter. This tissue is known as the *sinus node* (Fig. 102). When this node is stimulated, the right auricle starts to contract, and a wave of contraction spreads to the left auricle. This wave is momentarily blocked at the margins of the ventricles but is carried over to them by another node located on the partition between the two auricles, a bundle of whose tissue is distributed through the ventricle walls.

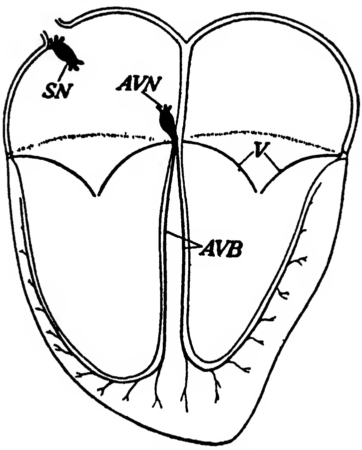

FIG. 102.—Pacemaker of human heart, the sinus node (*SN*). *AVN*, auriculoventricular node, with its extension in auriculoventricular bundles (*AVB*). *V*, valves between left auricle and left ventricle.

The sinus node is the "pacemaker" of the heart. It responds to an increase of carbon dioxide in the blood by causing the heart to beat faster. An increase of temperature, acting through the sinus node, also leads to faster beating. For both of these reasons, exercise accelerates the circulation of the blood.

The pacemaker is in turn partly regulated by nerves. A pair of accelerator nerves comes to it from the spinal cord in the chest region and a pair of inhibitor nerves from the medulla of the brain. The inhibitors are working constantly, exerting a continual drag on the heart. Against this braking effect the accelerators act to variable degree. Excitement and various reflexes (page 146) stimulate heart beat through the nervous control of the sinus node.

Blood Pressure.—The pressure of the blood against the walls of the vessels is greatest in the arteries near the heart, declines moderately in the more distant arterial branches, drops markedly in the minute arterioles and capillaries, then declines slightly in the veins (Fig. 103).

In the veins next to the heart it is on the average less than atmospheric pressure; that is, a "suction" is present there when the auricles relax.

The high pressure in the arteries is necessary to drive the blood through the capillaries where the resistance is great. It is also needed to send the blood above the pumping organ, as to the head in man. Pressure drops in the capillaries because of the great increase in the aggregate cross section of these numerous vessels, but there must still be a small pressure beyond the capillaries to push the blood (against gravity in much of the system) on to the heart.

Blood pressure is elevated if heart action is accelerated, also if resistance in the vessels is increased. This resistance depends on the diameter

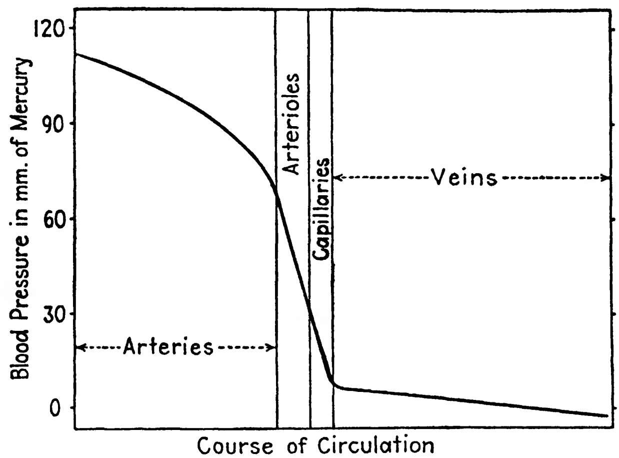

FIG. 103.—Curve showing decrease of blood pressure in course of circulation in man.

of the vessels, which is under the control of a nerve center in the medulla. A slight increase in the carbon dioxide in the blood stimulates this center, the vessel walls contract, and pressure is raised. However, in an active muscle, where the excess carbon dioxide is being produced, there is an opposite effect, a local dilation of the vessels, perhaps a response to higher acidity caused by the extra carbon dioxide or extra lactic acid. The net result is a shunting of the blood to the active organ where it is needed.

A special situation in the great artery from the left ventricle regulates the heart beat by stimulating it (through a nerve) when the pressure in the artery falls, depressing the heart when this pressure rises. Other stimuli are associated with these, but they all work together to check activity when it becomes too great, stimulate it when it lags. Highly adaptive controls thus depend upon automatic responses of organs to stimuli which the organs themselves help to create.

Coagulation.—One property possessed by blood, as a protection for its own operations and the life of the organism, is its power to clot. When blood vessels of small size are broken, the gap may be stopped by the coagulation of the blood, thus preventing loss of excessive amounts of blood. The clot consists of a tangled mass of threads of a substance known as *fibrin*, in which are trapped multitudes of red corpuscles. The fibrin is produced from fibrinogen, already mentioned as an important protein component of the plasma. Conversion of fibrinogen into fibrin is accomplished by the enzyme *thrombase*. This enzyme cannot exist in the blood during normal circulation, but its forerunner, called prothrombase (page 112), is regularly present. The conversion of prothrombase into thrombase is induced by a substance known as *thromboplastin* which is liberated partly from the damaged tissue cells at a wound, partly from the blood platelets which promptly disintegrate in exposed blood. The chain of reactions here described in reverse quickly leads to the precipitation of the fibrin network. Some other things are necessary to that chain. Calcium ions must be present, and clotting may be prevented in shed blood by precipitating its calcium with an oxalate or citrate. Vitamin K (page 112) also aids coagulation. Clotting can be artificially checked in surgical operations by injecting something (*heparin*, for example, extracted from liver and muscle) which inactivates thrombase. People afflicted with hemophilia have a very slow coagulation and bleed a long time from minor wounds. One feature of their blood is the slowness with which blood platelets disintegrate, so that production of thromboplastin is delayed, but there must be other factors.

The fibrin network traps most of the blood cells, and as it contracts it squeezes out a clear yellowish liquid, the *serum*, which is nearly identical with the plasma minus its fibrinogen.

Lymph and the Lymphatic System.—As a means of fluid communication between all parts of an animal, the blood system alone is not quite sufficient. The blood as a complete entity is confined to the blood vessels, and diffusion of substances held in it, even from the capillaries, is too slow to meet all needs. Moreover, the diffusion of water itself from the capillaries must be a one-way movement because of the pressure of the blood. Some of these inadequacies of the blood system are overcome by the second of the great networks of vessels (page 122), the lymph system.

Because of the considerable pressures which are maintained in the blood, there is a tendency for any of its components to escape if they can do so. The capillaries, with their thin walls, are the only place where this is possible. The liquid part, the plasma, filters out rather readily, passing into the spaces (Fig. 104) among the tissue cells. Some of the dissolved parts of the plasma (chiefly proteins) are held back by the walls of the capillaries, as happens in osmosis, and some other things may be added to it by a sort of secretion as it passes through those walls. The white corpuscles may crawl between the cells and escape (Fig. 101), and now and then a red cell may also pass out. The fluid which escapes from the capillaries is thus very little different from blood minus its red corpuscles and minus about two-thirds of its proteins. It is called *lymph*.

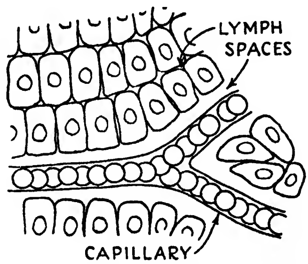

Fig. 104.—Diagram showing lymph spaces adjoining capillary and among cells.

The lymph carries with it most of the blood substances which can be dissolved in water, including most of the digested foods and a small amount of oxygen. It bathes the cells, which take any of the substances that are required. These cells also lose to the lymph any of their soluble wastes, principally carbon dioxide and urea. There is some diffusion of the various substances directly through the protoplasm of the cells, so that lymph is not the sole means of communication between the blood capillaries and the surrounding tissues.

Lymph cannot continue exuding from the capillaries unless it is somehow removed, and it cannot return to the blood vessels from which it came, because of the blood pressure. Instead, it is drained off by another set of vessels known as the *lymphatic system*. Very small *lymph capillaries* pass among the cells everywhere, and the lymph moves into them, mostly by diffusion, though minute solid particles are somehow able to get into them. These capillaries collect into larger vessels, which eventually empty into a vein. In man there are two main lymphatic trunks, one which receives lymph from the entire lower portion of the body below the chest and from the left side above that level, the other from the right side of the chest and head and the right arm (Fig. 105). These large vessels empty into certain veins, one at the base of the neck, the other in the left shoulder (Fig. 99*td*, *rld*). The lymph is thus returned to the blood system from which it came. In the course of the lymph capillaries there are valves (Fig. 106) which prevent backward flow, and there are valves at the two points where the main lymph ducts enter the veins. While these valves, together with pressure exerted by muscles, help maintain the flow of the lymph, the main cause of movement is the pressure of the blood behind it, and that is furnished by the heart. Because the source of pressure is distant and the resistance is great, the flow of lymph is sluggish. It takes an hour

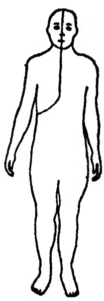

Fig. 105. Very unequal portions of human body supplied by the two main lymphatic systems.

or more to flow from the leg to the vein in the shoulder, as compared with less than a minute for the blood to make a complete circuit from heart to heart.

Interrupting the lymph vessels are numerous enlargements made of connective tissue, called *lymph nodes*, which filter out or otherwise remove the solid particles in the lymph. In these nodes one of the kinds of white blood cells (Fig. 100*C*) is created. In the nodes any bacteria which escape destruction by white corpuscles at the seat of infection are apt to be destroyed, and nodes are often swollen during an infection.

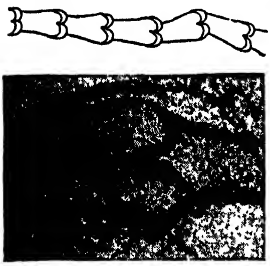

FIG. 106.—Lymph capillary, diagram of short segment above, photograph of single valve below. (*Photograph by courtesy of General Biological Supply House.*)

Connected with the lymph vessels is a set of tubes which originate in the walls of the small intestine. These are the *lacteals* (Fig. 99*l*), which are part of the lymphatic system. They extend into the minute fingerlike projections (the villi, Fig. 91) in the walls of the intestine and are especially useful in absorbing digested fats. These lacteals collect into larger vessels and finally merge with the lymph vessels of the lower part of the body, at a point shortly below the lowest rib. Their contents are thus disgorged into the left one of the veins which receive lymph.

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CHAPTER 12

DISPOSAL OF WASTES

Substances which cannot be built up into protoplasm, or do not yield energy when decomposed, or do not act as vehicles for important substances, or do not stimulate cells to activity can be of little use to animals. Such substances must be eliminated if they are incidentally acquired, as are the indigestible parts of various foods, or if they are produced as a consequence of physiological processes. Indigestible portions of objects taken in as food are removed as feces by the digestive tract itself. Those which result from the life processes are thrown off by the general process of excretion. It is only the latter group, the wastes which originate within the organism, that are dealt with in this chapter.

Origin of Wastes.—Since oxidation (page 37) is the main source of energy in living things, some of the principal wastes result from that process. Carbon is abundant in all protoplasm and in all the classes of organic foods (proteins, carbohydrates, lipids). Oxidation of these things results therefore in quantities of carbon dioxide (CO_2). This substance, as previously explained, is very stable and contains very little potential energy, besides being toxic in large quantities; hence it is waste matter. Water must be taken in as a vehicle for other substances, but in larger quantities than can be retained; the excess is waste. Destruction of proteins, whether those of protoplasm or unutilized food, must yield some nitrogenous wastes, the principal one being *urea.* There are minor substances of many kinds, but these three—carbon dioxide, water, and urea—form the bulk of the material that has to be removed.

Gaseous Wastes.—The removal of carbon dioxide has already been mentioned (page 119) as part of the process of respiration. Cells accumulate quantities of this substance as a result of their own oxidations and in man usually contain it at a pressure equivalent to about one-fifteenth of an atmosphere, or more. Since this pressure is double the pressure of the same substance in the blood of the capillaries, carbon dioxide diffuses from the cells into the blood. In the lungs, the pressure of the carbon dioxide in the blood is distinctly greater than in the air of the lungs; hence diffusion is outward. Gills operate in the same way as lungs, but the differences in pressure are smaller; hence the rate of elimination of carbon dioxide is slower.

Small quantities of other gases, especially those arising from bacterial action in the intestine, or from defective digestion, are also removed by the lungs. Considerable water (about one-tenth of the total water loss of the human body at rest) is also there removed in the form of vapor. Excretion through the lungs, therefore, involves only gaseous wastes.

Water and Urea.—Urea is a solid substance; hence by most organisms it can be excreted only in solution. Many other substances besides urea contain nitrogen and are produced by decomposition of proteins, but nearly all of them are solids that require to be eliminated in dissolved form. As just stated, only about a tenth of the excess water taken in by man can be removed as vapor, so that the bulk must leave as a liquid. These two groups of wastes may thus be removed by a single operation. The urea and the other nitrogen-containing substances are dissolved in water, and all are eliminated together. The amount of these wastes is much greater than that of all other wastes combined, and their removal

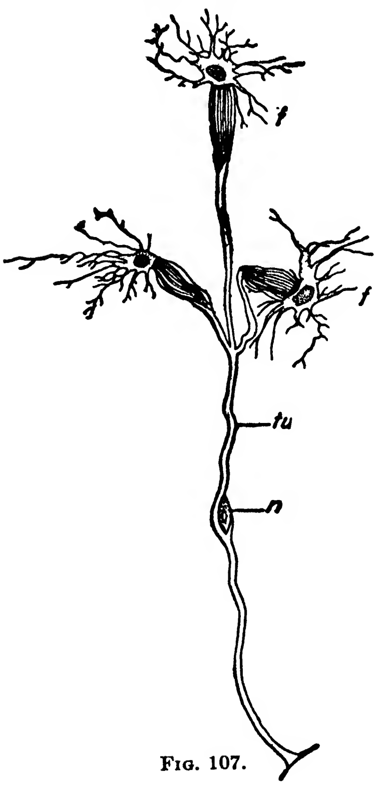

FIG. 107.

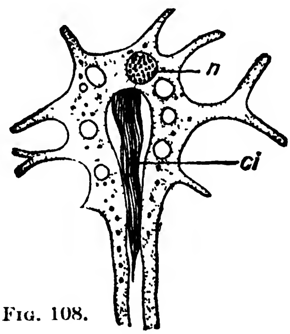

FIG. 108.

FIG. 107.—Portion of a protonephridial system from the tapeworm *Taenia crassicollis*. *f*, flame cell; *n*, nucleus of excretory tubule; *tu*, excretory tubule. (*From Hesse and Doflein after Bugge.*)

FIG. 108.—Flame cell of a protonephridium of a flatworm: *ci*, cilia within funnel-shaped cavity of flame cell; *n*, nucleus. (*From Hesse and Doflein after Lang.*)

is the chief task of what is called the excretory system of the multicellular animals. The excretory system is often aided by the skin, and there are other minor ways of removing water.

Excretory Systems of Invertebrate Animals.—The excretory system varies considerably in different animals. In the flatworms and some others it consists of *protonephridia*, which are fine tubes rising in *flame cells* and discharging to the exterior. A portion of such a system is shown in Fig. 107, and the structure of a flame cell in Fig. 108. The flame cell is somewhat stellate or irregular in shape, hollowed out to form a funnel-shaped cavity within itself. A number of long, slender cilia (the "flame") take their origin from the body of the cell and hang freely into the funnel-shaped cavity. In life, the cilia beat continuously and by their beating cause currents in the liquid which is excreted into the funnel by the cell.

Nephridia.—In the annelid worms each segment or somite (with some exceptions) is provided with a pair of more or less coiled tubes, the *nephridia*, which have a ciliated opening, the funnel or *nephrostome*, which projects through the septum into the cavity of the somite ahead. There it opens directly into the body cavity or coelom. The other end of the coiled tube is connected to the body wall where it has an opening to the exterior, through the *nephridiopore* (Fig. 109). Through much of its course this tube is surrounded by a network of capillaries, a feature of the excretory organ of all the higher animals. In its operation, the nephridium takes in fluid from the coelom through the nephrostome. This fluid contains wastes exuded into it by the various tissues, but it also contains some usable substances, one of them being glucose. As the fluid passes along the tube, the glucose and other useful substances are absorbed by the tubule walls and are carried away in the capillaries to be used elsewhere. Excess water is also thus reabsorbed into the blood, and the fluid finally ejected at the nephridiopore is highly concentrated.

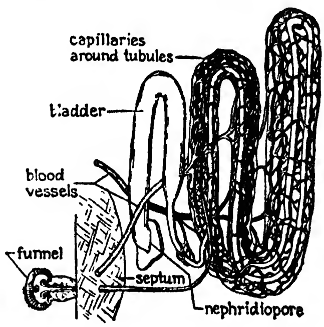

Fig. 109.—Nephridium of earthworm. (*From Storer, "General Zoology."*)

Kidneys.—In embryos of the higher animals the excretory system starts in a form which is comparable to a row of nephridia in the earthworm. It consists of a series of *uriniferous tubules*, a pair in each segment, the inner ends of which open into the coelom. The outer ends, instead of opening to the outside independently, all empty into a pair of tubes, one on each side, and these open to the exterior. In the course of development the coelomic openings, with a small portion of the tube, are closed off. Minute networks of blood capillaries are pushed into the sides of the tubules near the coelomic ends, and in the adult organ the tubule ends at that point. The tubule wall has grown almost completely around the invading group of capillaries, to form a double-walled cup through the open interior of which a blood vessel passes. This cup and the blood vessels in it are together known as the *renal corpuscle* (Fig. 110). The walls of the cup are *Bowman's capsule*, and the contained blood vessels are the *glomerulus*. The renal corpuscles with the uriniferous tubules are the essential excretory units in the vertebrate animals generally.

In the lower vertebrates (up to the amphibians) much of this embryonic state is retained in the adult, particularly the repetition of the tubules in a serial arrangement. In the higher vertebrates the segmental arrangement is completely lost in the gross form of the system. Yet in all of them the uriniferous tubule with its renal corpuscle is the functional unit.

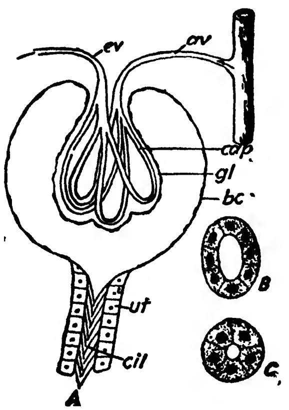

Fig. 110.—Structures from vertebrate kidney, diagrammatic. *A*, renal corpuscle; *B* and *C*, cross-sections of uriniferous tubules at different levels; *av*, afferent vessel; *bc*, Bowman's capsule; *cap*, capillary; *cil*, cilia (found in amphibia, not man); *ev*, efferent vessel; *gl*, glomerulus; *ut*, neck of uriniferous tubule.

The adult kidney in the frog, in cross section, is arranged as in Fig. 111. The renal corpuscles are located toward the ventral side. The uriniferous tubules from them pass upward, downward, and upward again, with many convolutions, and empty into *collecting tubules*, a number of which traverse the kidney near the dorsal surface. The collecting tubules begin in *Bidder's canal*, which extends along the median (inner) edge of the kidney, and end in the *ureter*, which extends along the lateral edge of the kidney, and then on to the *cloaca* and *bladder*. At the ventral side are nephrostomes, remnants of the embryonic openings into the coelom, but ending blindly in the adult. An important additional feature of the kidney is the abundant supply of blood vessels; the tubules are everywhere in close contact with capillaries.

The corresponding system in man is shown in Fig. 112. The kidney is bean-shaped, with the ureter emerging from the "eye" of the bean

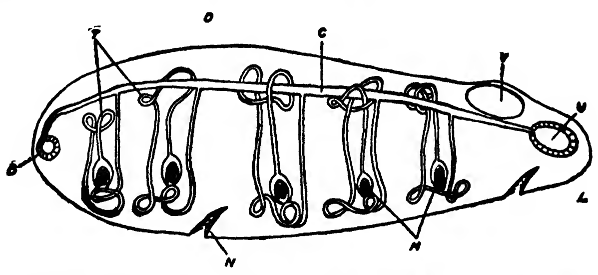

Fig. 111.—Diagrammatic representation of a cross section of the kidney of a frog. *B*, Bidder's canal; *C*, collecting tubule; *D*, dorsal, *L*, lateral margin of kidney; *M*, renal corpuscle; *N*, nephrostome; *T*, uriniferous tubule; *U*, ureter; *V*, renal portal vein. (*Modified from Holmes, "Biology of the Frog."*)

and discharging below into the bladder. A copious blood supply is furnished by branches of the main artery and vein. Inside the kidney are typical uriniferous tubules. Their renal corpuscles are massed toward the convex outer surface of the organ (Fig. 113). From there the course of the tubules is in general two convoluted stretches, with a more or less straight-limbed loop between them. The collecting tubules into which they empty converge toward the branches of the ureter, in pyramid-shaped groups. The ureters empty into the bladder, and this discharges through the *urethra*.

Excretion by the Kidney.—The elimination of waste by the kidney involves two general processes: (1) filtration of a great deal of liquid under pressure from the blood in the glomerulus into the tubule at the renal corpuscle, and (2) resorption of the greater part of this liquid by the uriniferous tubules in the rest of their course. The liquid forced out of the glomerulus, through the inner wall of Bowman's capsule into the

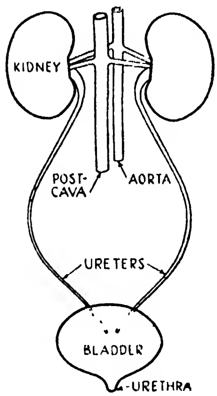

FIG. 112.—Excretory system in man.

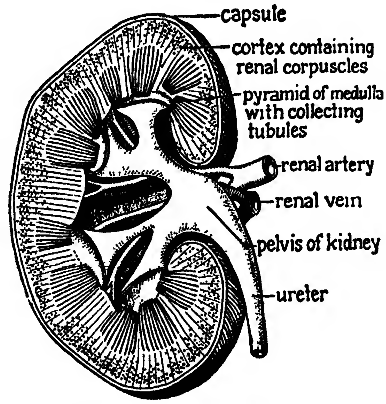

FIG. 113.—Human kidney, bisected. (*From Storer, "General Zoology."*)

tubule, consists of water, urea, glucose, amino acids, and the salts of the blood plasma, in about the same proportion as these things exist in the blood. The proteins of the blood, however, are not allowed to pass; nor are the other colloidal substances, such as the lipids, nor the blood cells. These are all retained in the blood vessels. The amount of fluid thus filtering into the tubule is about 1 per cent of the liquid of the blood passing through the glomerulus.

Then the resorption of much of this material occurs as the liquid passes along the tubule. The glucose in it is taken back into the blood capillaries, unless there is already too much glucose in the blood. The salts are also partially resorbed, not necessarily in equal fractions, but in proportion to the need of them in the blood. Amino acids return in like manner to the blood; so also does about 99 per cent of the water. What remains in the tubule is therefore a rather concentrated solution of the waste substances, mostly urea and uric acid. This liquid is the *urine*. About 1500 cc. of it leaves the kidneys daily in an average adult person under average conditions. Urine consists of about 96 per cent water, 2 per cent urea, 0.5 per cent uric acid, and 1.5 per cent inorganic salts.

A small amount of waste material may be added to the forming urine in the tubules, by excretory action of the cells of the tubules; but this addition is unimportant in relation to the amount filtering in at the renal corpuscle.

The Skin as Excretory Organ.—Excretion in the skin is done by the sweat glands, of which there are about two millions in man. These glands are of the simple tubular type (page 84), the deeper portion of the tube being closely coiled, while the outer part forms a duct which empties on the surface. Around the coiled bottom is a network of capillaries (Fig. 114). The amount of sweat excreted varies greatly with the temperature and the amount of muscular exertion; in mild weather and with moderate or slight exercise, about 600 cc. may be produced in a day, but five times that amount is not uncommon in hot weather and with great exertion.

Fig. 114.—Human skin, dissected to show sweat gland. At left, complete gland, much coiled at bottom. At lower right, network of capillaries from the midst of which the coiled portion of another gland has been removed.

Sweat is much more dilute than urine, about 99 per cent of it being water. Of its solids, sodium chloride is the most important. Urea is not very abundant; at the minimum production of sweat (600 cc. per day) only about 1.5 per cent of the total urea is lost through the skin in man. Other soluble wastes, of the same kinds as are eliminated by the kidneys, are found in the sweat, but in much smaller amounts. Since the sweat evaporates as rapidly as it is formed under ordinary conditions, these solids dry on the surface of the skin. As is pointed out on page 121, in connection with heat regulation, many mammals have only a few sweat glands, or none at all. In them the kidneys bear the whole burden of urea elimination. The sweat glands even in man are not an important excretory device. Their chief service is regulation of temperature.

Other Means of Excretion.—The liver shares in the excretion of urea, since it helps convert protein wastes into urea. When proteins are broken down, ammonium salts are among the products. These salts are converted into urea partly in the liver, but the actual excretion is elsewhere. The liver performs, however, a primary act of excretion in the removal of the hemoglobin of worn-out red blood corpuscles. The bile pigments are produced from this hemoglobin and are eliminated with the bile into the intestine, where they eventually pass out with the feces. Cholesterol is another waste substance excreted by the liver and eliminated into the intestine with the bile.

Other glands producing liquid secretions have some chance of casting out soluble wastes. Thus in the saliva there are traces of urea; but since most of the saliva is retained within the body, the occurrence of urea in it hardly amounts to excretion. Drugs injected into the veins can often be tasted owing to a similar excretion of them in the salivary glands. The wall of the large intestine is able to excrete small amounts of unusual foreign substances occurring in the blood or of ordinary substances when present in excessive amounts, as calcium and magnesium sometimes are. These substances are removed from the intestine with the feces.

None of these other excretory organs is important as a substitute for the kidneys; not even all of them combined could take over the job of the kidneys. Fortunately the kidneys have a wide margin of safety, for a kidney and a half may be removed and the necessary excretion still go on. There is no recovery, however, from overdestruction of kidney tissue, for the renal tubules do not regenerate.

Some organisms, principally plants, excrete wastes by simply rendering them insoluble and then retaining them within or between the cells. Insoluble substances can do no harm and, when they are not abundant, are not greatly in the way. Among animals, sea urchins are said to store insoluble excretions.

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CHAPTER 13

INTEGRATION OF ACTIVITIES

When many different operations are performed by the same machine, it is essential that they bear some definite relation to one another. Living organisms are subject to the same necessity. Their processes must dovetail into one another. When unusual exertion increases consumption of energy and output of carbon dioxide, it would be disastrous were the circulation not speeded up to provide oxygen and remove wastes. When the circulation is accelerated, it would be inefficient not to hasten the breathing movements to introduce more oxygen. In the digestive system it would be wasteful to have saliva, bile, and other digestive fluids secreted all the time, yet they must be produced when foods require digestion. If in warm-blooded animals the temperature increases above the most favorable point, it is important that the sweat glands of the skin or the breathing movement act to stop the rise. Even so simple an act as walking involves so many muscles that cooperation among the several units is necessary. The various organs cannot simply be wound up and, clocklike, run at the same speed, thereby ensuring proper timing, for many activities are carried on in response to external conditions and these change at irregular intervals.

Some means of coordination is necessary. Animals in general have contrived two devices—one nervous, the other chemical—to serve this end. The former has assumed the larger burden, but both are essential. While it has been necessary, in describing the action of the heart, the respiratory movements, and the production of digestive fluids, to refer to the controls which keep these processes in tune with the rest of the organism and with the environment, it is desirable now to examine the mechanisms of control more specifically.

Rise of the Nervous System.—The advantage or necessity of a nervous system is attested by its very general presence in widely different animals. Only a few groups are without it. It is made up of specialized types of cells, whose arrangement in the body exhibits an increasing complexity as other anatomical features become more complicated. Animals which have simple systems of other kinds have, in general, simple nervous systems.

The simplest form of nervous system is that of Hydra. The cells which are specialized for conduction in this animal have long, slender projections, usually branching (Fig. 115) and joining one another to form a network. The spread of these cells through the ectoderm is fairly uniform, though they are slightly more abundant at the foot and among the bases of the tentacles and around the mouth. Hydra's close relatives, the jellyfishes, have a ring of nerve cells around the edge of their cuplike bodies, with a loose network over the remainder.

Animals successively higher than the jellyfishes show a progressive tendency to collect their nerve cells into masses or strands. In the flatworms there is a mass of them, which may be called a *ganglion*, in the anterior region (Fig. 116), and from this mass two long strands or cords pass back on either side of the body. From both the ganglion

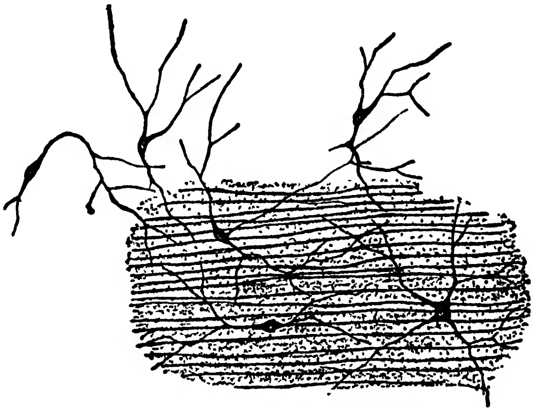

FIG. 115.—Nervous mechanism of Hydra. The long fibrils in the background are the contractile parts of neuromuscular cells lying in the mesogloea. (*From Schneider.*)

and the cords slender threads called *nerves* extend to all parts of the organism.

Invertebrate animals above the flatworms generally have two longitudinal nerve cords, but these are usually joined into a single cord in which the two components are still easily recognizable. In the earthworm (Fig. 116) these cords separate in the anterior region, pass upward around the digestive tract in the form of a collar, and become enlarged above the tract to form the bilobed *brain*. The rest of the double cord in the earthworm is swollen into a moderate ganglion in each segment, and from this ganglion two pairs of nerves emerge. The ganglia of the main nerve cords are much larger in the crayfish (Fig. 116) and its allies, with the larger ganglia located toward the front.

The tendency to mass the nerve tissue in a head region is carried much farther in vertebrate animals. In them there is always a distinctly enlarged brain. In the frog it is moderately larger than the cord behind it, which in the vertebrates is known as the *spinal cord*. The relative size of the brain increases up through the vertebrate group, reaching its maximum in man, whose brain includes more nerve tissue than all the rest of his nervous system together.

There is thus a tendency, in the animal scale, for complexity in general to be accompanied by a massing or centralization of the nerve tissue, and to emphasize this massing in the head region. The suggestion is near that somehow a concentrated system is better fitted to serve as a mechanism of control of a complex body than is a diffuse system. Additional reasons for reaching this conclusion will appear as the arrangement of cells in the larger masses of the system are examined.

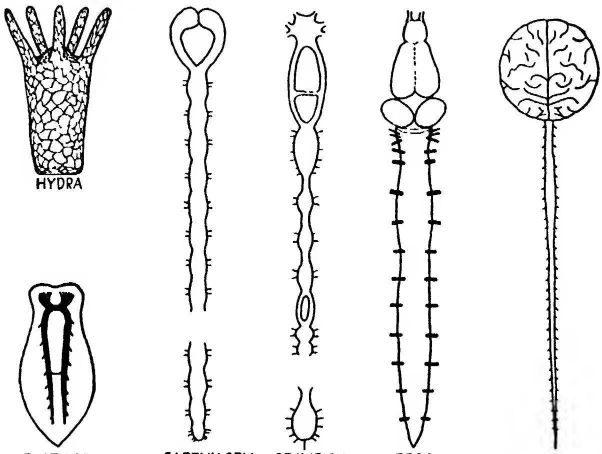

Fig. 116.—Diagrams of nervous systems illustrating centralization and massing in the head region.

The large masses of the nervous system, particularly the brain and spinal cord, constitute the *central nervous system.* The position of the central system in the body, and its structure, constitute fundamental differences between vertebrate and invertebrate animals. In the invertebrates the nerve cord is below the digestive tract, in the vertebrates above it. The cord is a double one (or there are two separate cords) in the invertebrates, single in the vertebrates. Finally, the cords are solid in invertebrates, hollow in vertebrates (resulting from the system's embryonic origin as a groove in the ectoderm which is pinched off below as a tube).

Peripheral Nervous System.—The nerves which pass out from the central system and branch to all parts of the organism are collectively called the *peripheral nervous system.* Of the principal nerves, a number (10 in amphibia, 12 in the higher animals) arise from the brain within the cranium; these are called *cranial nerves.* From the spinal cord there emerge, between the vertebrae, pairs of *spinal nerves* (31 of these in man). Each of the spinal nerves arises from the cord by two roots, a dorsal and a ventral, which join in a single nerve trunk a short distance from the cord (Fig. 121). The dorsal root includes a ganglion which contains a host of nerve-cell bodies. The relation of the peripheral to the central system in the frog is illustrated in Fig. 117.

A special part of the peripheral system is known as the *autonomic*

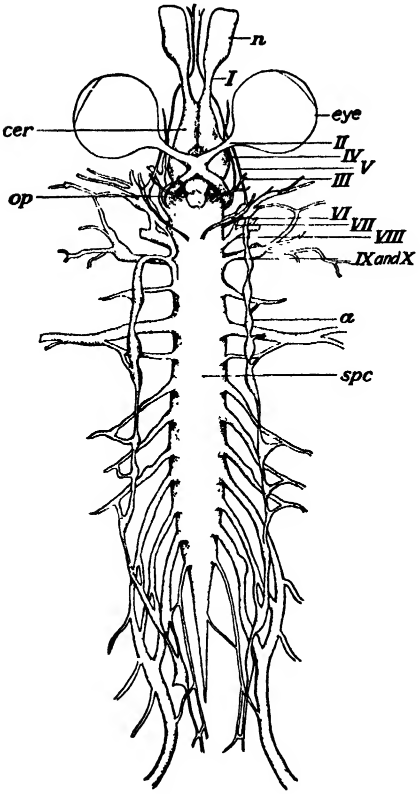

FIG. 117

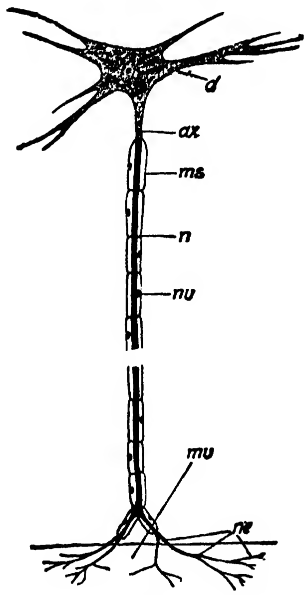

FIG. 118

FIG. 117.—Nervous system of frog, ventral view. *I–X*, cranial nerves; *a*, autonomic system; *cer*, cerebrum; *n*, nasal sac; *op*, optic lobe; *spc*, spinal cord. (*After Wiedersheim.*)

FIG. 118.—Diagram of a typical neuron. *ax*, axon; *d*, dendrite; *ms*, medullary sheath; *mu*, muscle; *n*, node; *ne*, nerve endings; *nu*, nucleus of cell of neurilemma.

nervous system because of its control, entirely free of the will, of many vital functions. It consists visibly of a pair of ganglionated cords on either side of the vertebral column, lying exposed in the body cavity. The ganglia are connected with the spinal cord by nerve fibers passing through the ventral roots of spinal nerves. In the extreme anterior and posterior parts of the autonomic system, however, there are nerve fibers which pass directly from the central nervous system to the organs controlled without connections in centrally placed ganglia.

Unit of Structure of Nervous System.—The unit of structure of the nervous system is the *neuron*. The neuron is a cell possessing a number of fine projections which sometimes extend to great lengths. The cell is compact in the embryo like most other cells, and the processes can be seen to grow out from it, passing among other cells and dodging obstacles, until they reach the organ to whose action they are to be related. These projections are of two kinds, distinguished from one another not by structure but by their normal functioning. Those which normally conduct impulses toward the body of the neuron are called *dendrites;* those which convey impulses from the body of the neuron are *axons.* Figure 118 diagrammatically represents the parts of a typical neuron, and three very different kinds of neurons are shown in Fig. 119.

These cells, which are strictly speaking the only constituents of the nervous system, are bound together by connective tissue, and the masses thus formed are supplied with blood vessels.

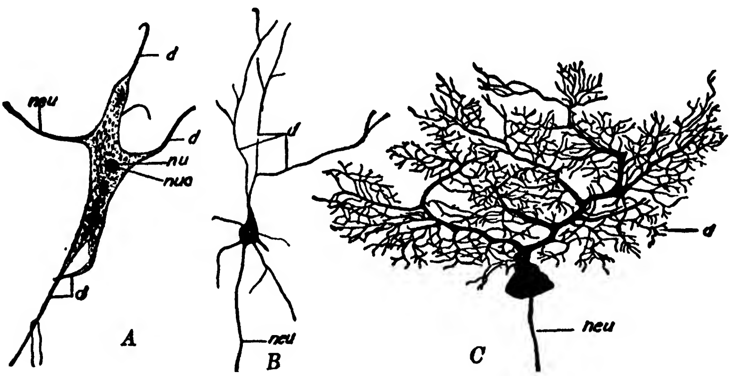

FIG. 119.—Three kinds of nerve cells. *A*, from ventral horn of spinal cord of an ox; *B*, from cortex of cerebrum of a cat; *C*, Purkinje cell from cerebellum of a cat; *d*, dendrite; *neu*, axon; *nu*, nucleus; *nuc*, nucleolus. (*B and C from Golgi preparations.*)

Functional Unit.—In the operations of a nervous system, the functional unit is a group of neurons called a *reflex arc.* These neurons are so related to one another that, following a stimulus or excitation, they induce some sort of action. One end of the arc is in some tissue or organ capable of receiving a stimulus, the middle of it is in the central nervous system or an associated ganglion, and the other end of the arc is in a tissue or organ capable of responding, such as a muscle or gland. The arc consists of at least two neurons, usually more. Leading from the sense organ is a nerve fiber (neuron) which, on being stimulated, conducts an impulse toward the central nervous system. This neuron is called an *afferent* fiber, the name meaning literally "bearing toward"—that is, toward the central system. It is also appropriately called a *receptor* neuron; very commonly, also, it is called a *sensory* neuron, though the result of the impulse it carries is not always sensation. The opposite end of the reflex arc consists of a neuron whose tip is applied to a muscle, or gland, or some organ capable of responding to a stimulus. This neuron carries the impulse away from the central nervous system, hence is designated an *efferent* fiber. It is also called an *effector* neuron, often a *motor* neuron though the action produced may be something else than movement.

If the reflex arc consists only of an afferent and an efferent fiber, these two neurons are in contact with one another by a minute surface known as a *synapse*. The axon of the afferent touches a dendrite of the efferent, and the surface of contact is the synapse. An arc of this simple two-neuron type is represented above, at the right, in Fig. 120. The afferent

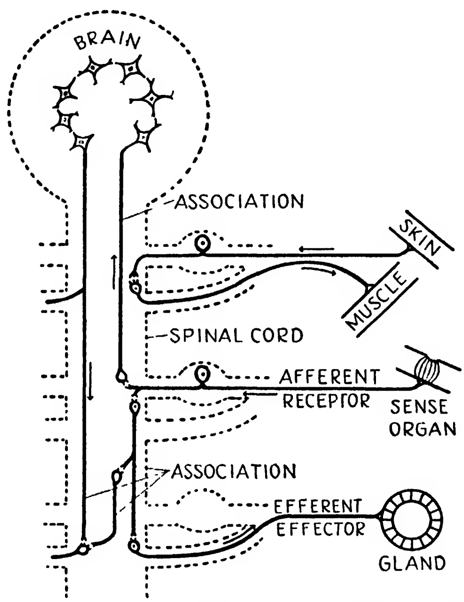

FIG. 120.— Diagram of simple reflex arcs in the vertebrate nervous system.

neuron enters the spinal cord through the dorsal root of a spinal nerve, in whose ganglion the body of the neuron lies. Within the spinal cord the axon synapses with the dendrite of another cell whose body lies within the cord. The axon of the latter cell passes out through the ventral root of the spinal nerve, and its tip is applied to the responding organ (muscle in the diagram).

Most reflex arcs consist of more than two neurons. The extra ones are interpolated between the receptor and effector neurons. These connecting neurons are known as intermediate or *association* neurons. The spinal cord is the seat of vast numbers of them. The association fibers are especially useful in carrying the arc over considerable stretches of the central system. In the lower right half of Fig. 120 is a reflex arc whose afferent fiber enters the cord by one spinal nerve, while the efferent fiber leaves it by way of the nerve next below. The lower level is reached by an association neuron between the receptor and effector. This same receptor is represented as connected also with an effector neuron on the opposite side of the spinal cord. A second association fiber establishes this connection. Some association neurons take the arc through the brain, across a number of cells, and back down the spinal cord again. Many arcs much more complicated than these exist. In all cases the first neuron in the chain is an afferent, the last one an efferent. All the contacts between any of the neurons are synapses, axon touching dendrite.

The response to a stimulus carried over a reflex arc is called a *reflex action.* Many of these actions are inherited. The vital organs in the chest and abdomen are controlled by innate reflexes, as are also the con-

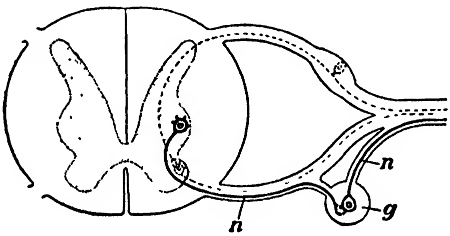

FIG. 121.—Chain of efferent neurons in human autonomic system, in chest region. *n*, the neurons; *g*, ganglion. Dotted lines represent neurons of ordinary spinal reflex arc.

traction and dilation of blood vessels and the action of sweat glands. Other reflexes are learned—"conditioned" is the usual descriptive term applied to them. Habitual movements of all sorts are conditioned reflexes.

Functions of Autonomic System.—The reflexes for which the autonomic nervous system is responsible are of such vital importance and are related to one another in so remarkable a manner as to call for separate description. Attention will be directed only to the efferent fibers of the reflex arcs, because it is their control of the vital organs with which we will be concerned. The system in man is the one used for illustration.

The neurons of the autonomic system lack a myelin sheath. Between the central system and the organ innervated there are always at least two, and often only two, neurons. In the chest region the body of the first neuron of such a chain is in the lateral part of the H-shaped gray matter of the cord (Fig. 121), and its axon passes out through the ventral root of one of the spinal nerves. It leaves that root, however, close to the cord and enters a special ganglion. Here the first neuron terminates, its axon synapsing with the dendrite of the second neuron of the chain.

This second neuron may then join the mixed spinal nerve at the same level of the cord, or pass up or down to nerves at other levels, in which it goes out to the organ which it controls.

The autonomic system is divided functionally into two major regions. One centers in the middle portion of the spinal cord (chest and small

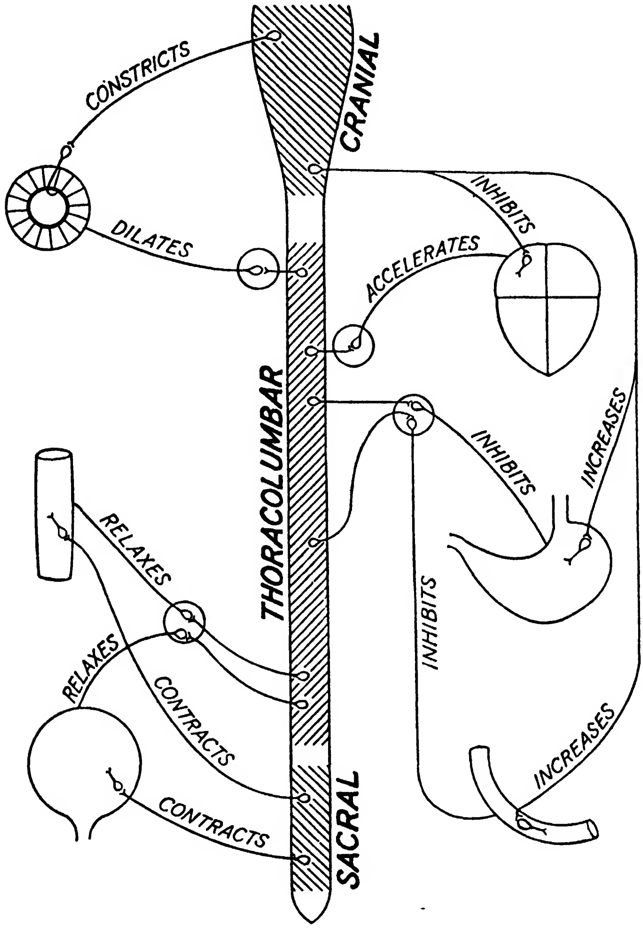

FIG. 122.—Autonomic nervous system of man, in part, showing double innervation of each organ and the action of each nerve. Organs on the left, iris of eye, rectum, and bladder; on the right, heart, stomach, and small intestine. Small circles are ganglia.

of back) and may be called the *thoracolumbar* system. The other has its center partly in the brain, partly in the lower end of the spinal cord, and is called the *craniosacral* system (Fig. 122). The chain of neurons described above belongs to the thoracolumbar. The ganglia of the craniosacral system lie in general much farther from the spinal cord, sometimes actually in the organ that is controlled.

Each organ governed by the autonomic system is innervated twice, one nerve coming to it from the thoracolumbar system, one from the craniosacral. One of these nerves is an activator, the other a depressor. Each organ is thus accelerated by one of the major divisions of the autonomic system, inhibited by the other; but neither division is exclusively excitatory or wholly inhibitory, each division exciting some organs, depressing others. The thoracolumbar system accelerates the heart but inhibits movement of stomach and intestine. The iris of the eye is constricted by the craniosacral, dilated by the thoracolumbar.

The excitation or inhibition is apparently accomplished by producing a chemical substance, and the organ responds to this substance. According to current theory, all the nerves belonging to the craniosacral system produce the same substance, which is probably *acetylcholine.* In like manner, the thoracolumbar nerves produce one substance which has been called *sympathin.* Acetylcholine inhibits the heart, increases stomach movement and secretion, contracts the rectum and urinary bladder, dilates the vessels of the salivary glands, and constricts the iris of the eye. Sympathin produces the opposite reaction in each of these organs.

Nerve Impulse.—The impulse which is carried along a neuron like that in Fig. 118 travels at a speed of about 120 meters per second in mammals, about one-fourth of that velocity in a frog. The rate is in some way related to the presence or absence of a sheath around the branches of the cell, and to the structure of that sheath if one is present. The axon of the cell in Fig. 118 is surrounded by a white layer of noncellular fatty substance known as the myelin (medullary) sheath, which is divided into segments by irregularly placed nodes. Not all neurons possess such a sheath. Those of the autonomic system do not, and in them the impulse travels much more slowly—only 10 or 12 meters per second. Among myelinated nerve fibers, those with the longer segments of myelin between nodes conduct, in general, more rapidly than those with short segments of the sheath. There is some reason from experiment to believe that the impulse jumps from node to node; the longer the segments between nodes, therefore, the faster the impulse travels.

According to present view, the nerve impulse is a surface phenomenon. The membrane of a nerve fiber—not the cellular covering or *neurilemma* and not the myelin sheath, but the outer film of the nerve cell itself—is charged positively on the outside, negatively on the inside. The charges are really borne by ions, which are located on opposite sides of the somewhat impermeable membrane. This membrane keeps them apart and so prevents them from neutralizing one another (Fig. 123). The impermeability prevents neutralizing, and the separation of the ions in turn is supposed to help keep up the impermeability. If, now, something (a stimulus of some sort) destroys the impermeability of the membrane at one point the polarization there is lost; the ions get together and neutralize one another. Such neutralization could then proceed to adjoining parts of the nerve fiber as rapidly as the impermeability is lost. No material thing moves along the nerve, but a wave of neutralization and permeability proceeds at considerable speed.

Waves of some sort pass over other organs, as over the heart when it contracts, over skeletal muscle, and over glands. It seems likely that

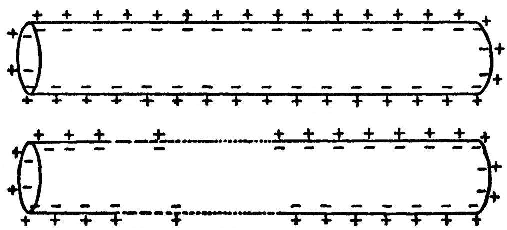

FIG. 123.—Propagation of nerve impulse, a wave of permeability associated with neutralization of positive and negative ions. Dotted lines, permeable membrane.

in all these structures essentially the same changes in polarization of surface membranes are taking place.

Initiation of and Response to Nerve Impulses.—Though the impulses carried by all nerves are the same, no matter where they begin or end, the things that start them and the actions they induce are quite different. The impulse is initiated by a receptor of some kind, that is, a specialized nerve ending which is exceptionally sensitive to some one sort of stimulus. In the retina of the eye the receptors (rods and cones) are sensitive to

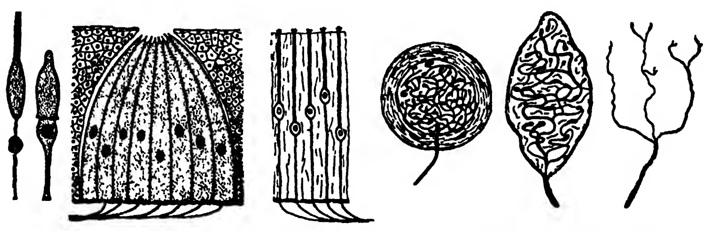

FIG. 124.—Various receptors: left to right, rod and cone of retina of eye, taste bud of tongue, olfactory cells of nasal lining, and cold, touch, and pain endings in skin.

light, the taste buds of the tongue and the olfactory cells in the lining of the nose (Fig. 124) are sensitive to chemical substances. Certain nerve endings in the skin are sensitive to cold, others to touch, still others lead to pain; the several kinds are structurally different from one another. These receptors are not interchangeable, each does its own work, no other. If a cold spot on the hand is stimulated in some other way than by low temperature—mechanically, for example—the sensation is still that of coldness.

The response which a nerve impulse elicits depends on the nature of the structure to which it is delivered. An impulse delivered to a motor unit in a muscle causes contraction; an exactly identical impulse carried to a gland causes secretion. It is probable that in each instance a chemical substance is produced at the nerve ending, and that it is this substance rather than the nerve impulse itself which really stimulates the responding organ. At least that is true of responses of some of the internal or visceral organs.

An impulse from one of the sensory endings in the skin leads to a certain center in the brain, and the appropriate sensation is there produced. The nerve fibers from the retina go to one region of the brain, neurons from the olfactory area in the nose go to another, fibers from the pain endings in the skin lead to a third. These regions of the brain are indicated more fully later; the important point now is that for each activity there is a special kind of receptor, located at a particular place or places, and a certain organ or region of the nervous system where the appropriate response is given. The nerve impulse which goes from the place of stimulation to the place of response is everywhere the same.

Direction of Impulse.—When a neuron is stimulated at its receptor ending, the impulse thus started travels toward the other end; there is no place else to go. Experimentally, however, and sometimes in special situations naturally, a neuron may be stimulated in the middle of the length of its axon or dendrite. When this happens, impulses travel in both directions to the limits of the neuron itself; but in one of the directions it goes no farther than the end of that particular neuron. The difference lies in the synapses at the ends of the axon and dendrite. Each synapse is a one-way conductor. An impulse can go over it from axon to dendrite but never from dendrite to axon. This is the reason why nerve impulses always go in one direction over such a chain of neurons. As stated above, when a neuron is stimulated somewhere in its middle, the impulse moves in both directions from that point to both ends of that neuron. In the "forward" direction, arriving at the terminus of the axon, it goes over to the dendrite of the next neuron and continues the propagation, because the synapse there permits passage in that direction. But in the "backward" direction the impulse is blocked when it reaches the tip of the dendrite because the synapse will not carry it over to the adjoining axon.

What gives the synapse this power of distinguishing direction? While the answer to this question is not certainly known, a possibility is suggested by what is known of responses to stimuli in general. We are familiar with the control of such organs as the heart by a double innervation, one nerve acting to stimulate, the other nerve to inhibit. Each nerve presumably produces a chemical substance to which the organ directly responds. It is not unlikely that an impulse arriving at a synapse from an axon produces an activating substance so that the wave is initiated anew in the adjoining dendrite, while an impulse going backward over a dendrite to a synapse produces an inhibiting substance so that further propagation is prevented.

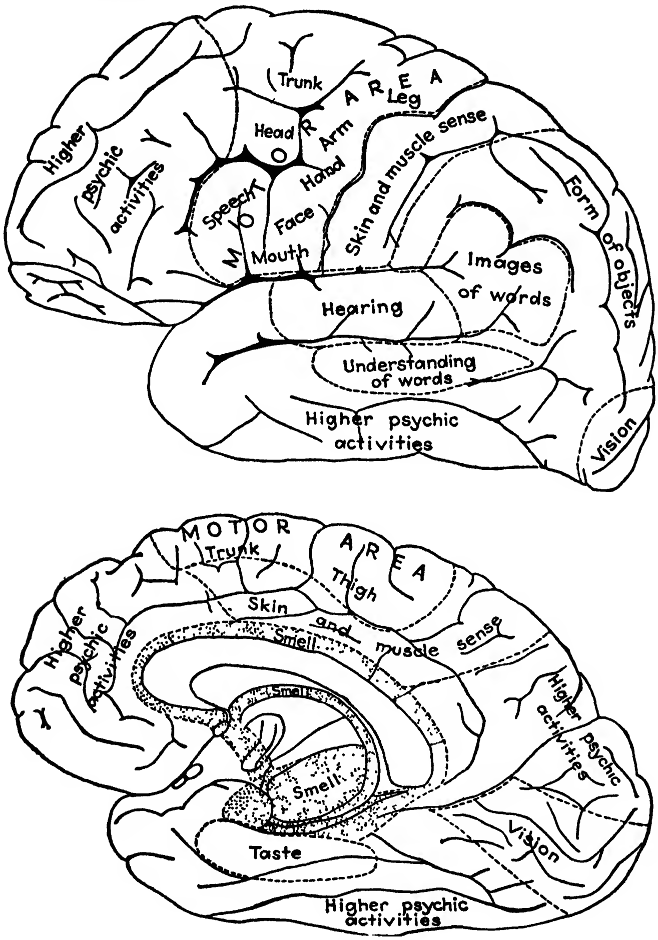

FIG. 125.—Functional areas of human cerebrum. Above, lateral surface from left side. Below, median surface viewed from left. The olfactory area, because it is discontinuous, is dotted. All boundaries are only approximate.

Localization in Brain.—It is more difficult to ascertain the function of different parts of the brain than to determine the role of nerves, because those parts cannot be isolated and experimented upon wholly separately. Knowledge of the regions where different brain functions are performed comes from destruction of certain areas in laboratory animals, artificial stimulation of brain areas in anesthetized animals, the consequences of lesions due to accident or disease in man, and, recently, the study of "action potentials," which mark the path of nerve impulses from the point of stimulation to their center. The latter method is particularly useful in locating functional areas in the cerebrum. To understand what follows, it is necessary to know the general structure of the brain.

As it originates in the embryo, the central nervous system is a tube, wider in front where the brain develops (page 208), narrower behind in the spinal cord. The brain tube enlarges moderately in three regions known as the fore-, mid-, and hindbrain. This tubular structure remains in the adult as the "brain stem," but the forebrain expands enormously upward, laterally, and backward, to form the *cerebrum* (divided into two hemispheres), while the hindbrain develops the *cerebellum*. Behind the latter is the *medulla oblongata,* which is usually counted a part of the brain but is really the somewhat enlarged anterior end of the spinal cord.

The cerebrum has a gray surface layer, the *cortex*—gray because of the cell bodies which it contains—which in man and the mammals generally is greatly increased in extent by folds and furrows. It is the cortex which has been the subject of much of the localization study, because it is the seat of those psychic qualities which tend to distinguish man from the beasts. By the methods outlined above, the functions of various parts of the cerebral cortex have been found to be roughly as portrayed in Fig. 125. The best established of the areas there shown are the motor area and the area of skin sensation which together form a transverse band halfway between the front and rear, the areas for hearing at the sides, and that for vision at the extreme posterior part. The rest of the cerebrum is largely given over to what may be termed associations, some of the particular forms of which are indicated in the illustration. The association areas deal with integration of individual sensations into a whole. The cortex is not responsible for pain except to localize it, and it is not concerned with any visceral sensations such as hunger and thirst. Pain is a function of the thalamus, in the stem region of the forebrain.

The cerebellum serves to coordinate muscular actions. Destruction of it results in irregular, jerky, fumbling, or reeling movement, or in thick slurred speech. The middle portion influences muscles of the trunk, neck, and head; each side of the cerebellum acts on muscles of the same side of the body, but there is not much other known localization.

The more important functions of the medulla in controlling the heart and digestive canal, the contraction and dilation of blood vessels, and the movements in breathing have already been described in this and earlier chapters.

Chemical Regulation.—The control of vital actions by the medulla is exercised partly at the behest of accumulated carbon dioxide. It has been necessary in earlier chapters to point out some of the initiatory actions of this substance which may be here recalled. Increased concentration of carbon dioxide in the blood causes centers in the medulla to increase breathing movements and to contract the blood vessels. Here the effect is produced through the nervous system. Sometimes carbon dioxide may act directly, without mediation of nerves, as when it stimulates stronger heartbeat by direct action on the sinus node, and almost directly when, perhaps by increasing acidity, it locally causes dilation of blood vessels. There is thus an important chemical regulation of muscle action, partly through, partly independent of, the nervous system. Coagulation of the blood is also initiated by chemical substances liberated from disintegrating platelets and injured tissue cells, in conjunction with certain substances in the blood plasma. There are some physical agents, also, which exercise regulatory control either directly or through the nervous system. Thus slightly higher temperature of the blood, warming the thalamus of the forebrain, starts activity of the sweat glands, which lowers the temperature; and higher blood pressure in the great arteries, acting through nerves, slows down the heartbeat. And, finally, greater warmth of the blood, influencing the sinus node directly, not through nerves, accelerates heart action. All these influences have been discussed before.

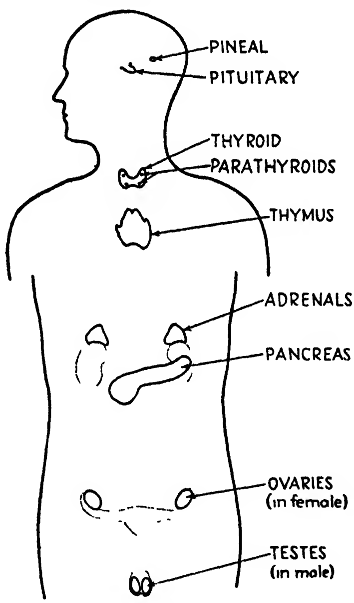

FIG. 126.—Location of endocrine glands in human body. Dotted lines represent kidneys (above) and oviducts and uterus (below) to show positions of glands.

Besides these chemical and physical agents, which are all part and parcel of the general physiological mechanism of the higher animals and which mostly serve other ends besides regulation, there is a group of chemical substances which have no other known function than to exercise control over something. These substances are known as *hormones*. In general they are produced at one place, but stimulate action at another, to which they have been carried by the blood. One of the earliest of these substances to be discovered was secretin, whose action in stimulating the pancreas and liver has been described (page 104).

While it is possible that most tissues produce substances that have some influence elsewhere, the marked and well-known instances of hormone action are those exhibited by certain definite glands. These glands do not have ducts, or, if they do, the hormone is not ejected through the duct. All hormones diffuse directly into the blood. Such ductless glands are known as *endocrine* glands, and the hormones are also called endocrine secretions. The best-known hormonal actions are those of man, so the account here given must draw heavily upon the facts ascertained for human endocrine glands. The names and locations of most of those which are known or believed to be endocrine are shown in Fig. 126.

Endocrine Glands and Their Work.—One of the best-known hormones is that of the thyroid gland, a bilobed structure lying beneath and beside the trachea in the neck in man. Its hormone, called *thyroxin*, has been isolated and has the formula $C_{15}H_{11}O_4NI_4$. The direct effect of thyroxin is to increase the rate of metabolism. Deficiency of this hormone in children or young animals retards their development. If this influence starts early enough it leads to *cretinism*, in which body and limbs are dwarfed and distorted, and mental development is arrested. Some regions of the world have little iodine in the soil, hence little in crops, and the inhabitants are unable to produce adequate thyroxin, which includes that element. Cretins were common in such regions until public health measures, such as the requirement that potassium iodide (KI) be added to table salt, were adopted. Deficiency of thyroxin in adults often causes endemic goiter, a swollen condition of the thyroid caused by an accumulation of a colloid fluid in the capsules of the gland. A more serious effect of deficient thyroid is myxedema, with its low metabolism, a state of lethargy, and puffed skin. Excessive thyroxin commonly causes exophthalmic goiter, with its increased metabolism, high blood pressure, and protruding eyeballs; removal of part of the thyroid, the proportion depending on how much the metabolic rate has been raised, is one of the cures.

Closely associated with the thyroid (imbedded in it in man) are the *parathyroids*. There are four of these bean-shaped bodies in the human thyroid. Separate experimentation with them has been hindered by their position. Their primary effect is upon calcium and phosphorus metabolism, and the calcium deposit in bones is reduced when the parathyroids are deficient. Complete removal of the glands causes violent muscular convulsions.

The *adrenal* glands rest on the kidneys (above them in man). They consist of a central part or medulla, which arises in the embryo as an outgrowth of the nervous system, and an outer part or cortex, which comes from the lining of the coelom. The two parts produce different hormones, that from the cortex being the more critically important. About one-fifth of the cortex suffices for normal processes, but if the whole cortex is removed prostration and death soon follow. Deficiency of its hormone interferes with carbohydrate metabolism, and the blood loses most of its glucose. Sodium chloride is also lost from the plasma, the osmotic properties of the blood are changed, and so the volume of blood is diminished and blood pressure falls. Development of reproductive cells is also stopped, and Addison's disease is partly caused by a cortical defect. Many substances have been extracted from the cortex, the potent ones all being chemically related to one another. The name cortin has been given to the active principle, but it has not been identified or isolated.

The adrenal medulla produces the well-known *adrenalin* ($C_9H_{13}O_3N$). This hormone has been synthesized artificially. Its effect is to strengthen and accelerate heartbeat, increase the glucose in the blood, whiten the skin, dilate the pupils of the eyes, and erect the hair. In general its action is the same as that of the thoracolumbar part of the autonomic nervous system. One theory of adrenalin is that it is a stand-by for emergencies. By its control of glucose in the blood, it has been supposed to increase muscular power and resist fatigue. In fear and rage and great excitement, adrenalin is increased, and the body is supposed to be able to perform feats under such emotions which it could not normally do.

The pancreas, though a digestive gland whose digestive secretion flows through a duct, also produces a secretion which must diffuse out to the blood. This secretion is called *insulin*. It is produced in certain groups of cells, the *islands of Langerhans*, which in the embryo were budded off from the digestive tubules but which lose all connection with the duct. The function of insulin is to control sugar metabolism. Failure of the supply of this hormone causes the disease known as diabetes mellitus, excess of sugar in the blood and hence its presence in the urine. The disease may be relieved by administering insulin extracted from other animals, but it has to be injected into the blood vessels, not taken by mouth, for insulin is destroyed by the digestive enzymes. Also, its effect lasts only a few hours, hence it must be used frequently.

The *pituitary* gland, at the base of the brain, consists of two parts. The anterior lobe is derived in the embryo from the roof of the pharynx, the posterior lobe from the floor of the brain. The connection with the pharynx is lost in the adult, but that with the brain persists. The anterior lobe produces a variety of hormones, one affecting growth, several affecting the sex organs, others acting on the thyroid, adrenal cortex, and mammary glands. Because of this multiple activity, particularly in control of other endocrine glands, the anterior pituitary is sometimes spoken of as the "master gland." The growth hormone was first isolated in 1944 as a pure protein. Oversupply of this hormone produces giants—

8- or 9-foot stature with disproportionately long limbs. Too little of it produces midgets, with disproportionately short limbs. The hormones related to the sex organs and mammary glands are to be described in a succeeding section. The hormones affecting the thyroid and adrenal cortex have not been isolated; but in an animal whose pituitary has been removed these glands experience degenerative changes; and when additional pituitary extract is injected, the thyroid and adrenal cortex are enlarged.

The posterior lobe of the pituitary produces at least two substances, one of which stimulates contraction of the uterus in the reproductive system, the other constricts the smaller arteries and so raises blood pressure. Neither of these substances has been isolated. Injury to the posterior lobe also deranges the uriniferous tubules of the kidneys, so that they no longer resorb the great quantities of water from the filtrate entering through Bowman's capsule. A large volume of dilute urine is produced under these circumstances.

The primary reproductive organs, ovaries and testes, produce hormones which are responsible for the development of the secondary sex characters, such as the beard and baritone voice in man, long tail feathers in cocks, and the contrasted features of the females. They also govern the mating behavior, and determine parental instincts. The principal hormone in the male is *testosterone* ($C_{19}H_{30}O_2$), isolated as a crystalline compound. It is produced by the *interstitial cells* of the testis, not by the germ cells nor the tubules which produce germ cells. The corresponding hormone of the ovary (sometimes called *estrogen* though the name has varied) is produced by the *follicles*, blastulalike spheres of cells surrounding the mature eggs.

Other hormones may be produced by the *pineal body* above the brain, which regulates the speed of sexual development, and the *thymus* in the upper part of the chest, which is in some way related to sex development and appears to control the production of the hard shell on bird eggs. Both of these organs are present in children, but the former degenerates into a fibrous structure and the latter disappears in youth.

Reproductive Cycle.—The influence of the pituitary on other endocrine glands, mentioned above, hints at interrelations much more extensive. Presumably not all the interrelations between the glands are known, but one group of them has received considerable attention because of its bearing upon medical practice. This is the group of glands and other secreting structures which control the reproductive cycle in female mammals.

These females show a rhythmical change in their behavior, in that periods of sexual excitement occur at regular intervals, separated by periods of apathy. This rhythm of behavior depends on an alternation of production and disappearance of certain hormones; to understand these, it is necessary to know the operations of the female reproductive system. The following account is limited to the mammals.

The female reproductive cells, in different stages, are contained in the ovary. Each cell is surrounded by liquid enclosed in a layer of cells known as the follicle. The cells (one or more at a time) ripen with considerable regularity, every 5 days in the rat, each 28 days in man, twice a year in the dog. In the maturing of a cell the follicle grows and approaches the surface of the ovary (Fig. 127). The follicle is there ruptured, and the egg escapes into the open end of the oviduct. The cells of the broken follicle become converted into a yellowish mass called the *corpus luteum*, while the egg moves down the oviduct. If the animal has mated, spermatozoa may have moved through the uterus and into the oviducts, and the egg may be fertilized there. If it is not fertilized,

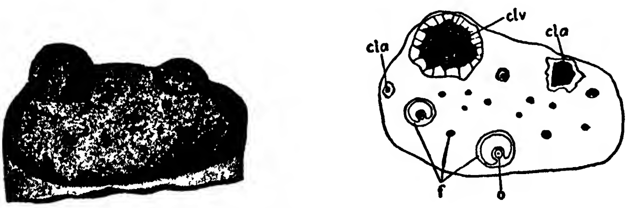

FIG. 127.—Human ovary to show follicles and corpora lutea. At left, surface view, with two follicles of different ages protruding. At right, section showing *cla*, two degenerating corpora lutea of different ages; *clv*, fresh corpus luteum; *f*, follicles; *o*, ovum.

the egg disintegrates or passes out to the exterior. If it is fertilized, it sinks later into the wall of the uterus and proceeds to form an embryo. To receive the fertilized egg, the wall of the uterus must become thickened, glandular, and supplied with an extra amount of blood. This preparation is all wasted if the egg is not fertilized, for then the uterine wall recedes to its "resting" condition. The corpus luteum degenerates (in about 2 weeks in man) if the egg is not implanted in the uterus but continues throughout pregnancy if implantation occurs.

What governs all these events, to ensure that they occur in the proper relation to one another? In general, it is an interplay of hormones from the reproductive organs and the pituitary gland, one gland stimulating the other and then being inhibited when its product increases to a certain concentration. The pituitary, by means of a hormone, stimulates the growth of the egg follicle; the follicle then produces a hormone which induces the thickening of the uterus just described. When the follicle is ruptured, its hormone is no longer produced, but another hormone is produced by its successor, the corpus luteum, which continues the preparation of the uterus. No other follicle is growing in the meantime, for the hormones of the follicle and corpus luteum inhibit the pituitary, so that no follicle-stimulating hormone is forthcoming. If the egg is not implanted in the uterine wall, the corpus luteum degenerates, and its hormone is no longer produced. The thickening of the uterus consequently disappears, and the pituitary is relieved of its inhibition. The latter gland therefore begins to produce its follicle-stimulating hormone, and the cycle is started all over again.

Why the corpus luteum persists if the egg is implanted is not entirely clear, but its hormone is essential to the continued development of the embryo, and the pituitary gland is in some way responsible for its persistence. Some have supposed that a hormone from the placenta guides the pituitary in this particular function, but this is not established. Increase in the size of the mammary glands during pregnancy, with their secretion of milk at birth, is also caused by a hormone of the pituitary, but the persistent corpus luteum seems to be the mentor of the pituitary in this control.

The cycle in other vertebrate animals is likewise controlled by hormones, but, since their young are developed outside the mother's body and are not nourished with milk after birth, much of the complexity of the reproductive rhythm is wanting in them. In the amphibia, the reproductive cycle is an annual one. Eggs ripen during the winter and are laid in early spring. During the summer the ovaries are small flabby organs, in which the oöcytes gradually increase in size into the fall, but normally none is liberated until the next spring. If, however, an extract of the anterior lobe of the pituitary gland is injected into one of these animals in the fall, eggs are released from the ovary in three or four days.

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CHAPTER 14

REPRODUCTION

A new animal or plant comes into existence only by the transformation of some part of a previously existing organism. While reproduction must have been understood for man and his domesticated animals from time immemorial, it is not so long since it was popularly believed there were other ways whereby new individuals could arise. Among the ancient Greeks it was common belief that leaves could be converted into fish or birds, mud into frogs, dead flesh into bees. In the Middle Ages barnacles were thought to be transmuted fruit of a tree, and to give rise in turn to geese. As these notions were abandoned, the idea was transferred to the smaller organisms which improved microscopes were revealing. It was only comparatively recently that the view that bacteria arose *de novo* from nonliving matter was given up. The supposed origin of living things from nonliving matter was called *abiogenesis* or *spontaneous generation*. While in the evolution of life there must once have been a beginning of the living out of the lifeless, it is not likely that such changes are happening now. Certainly there is no production, from nonliving substance, of new individuals belonging to recognized present-day species of animals or plants.

Increase in numbers of individuals, or replacement of losses, is provided for by a variety of reproductive methods which fall into two general categories, namely, *sexual* and *asexual* reproduction. Sexual reproduction as a rule involves two parents and the union of two germ cells, or of two cells of some kind, or of two nuclei of different cells. Asexual or nonsexual reproduction includes all forms of reproduction not involving germ cells or any of the unions just named.

Sexual Reproduction.—Sexual reproduction is a well-nigh universal method of reproduction. It is employed by representatives of every great group of animals and by many of them to the exclusion of the asexual method. It is also used by the plants, except the bacteria.

In one of its very common forms, sexual reproduction is the union of two cells to form a single cell, the *zygote*, which by its subsequent divisions produces a new individual (in the metazoa) or a new series of individuals (in the protozoa). Not all cells are capable of uniting in this way, and cells which are capable of this act are called *gametes*. Certain gametes are relatively large, contain a considerable amount of nutritive material, and are nonmotile; these are called *ova* (singular, *ovum*), or *eggs*. Other gametes are minute, often a very small fraction of the size of the ova of the same species. These are poorly supplied with nutritive material, have a very small cytosome, and usually are motile; they are known as *spermatozoa* (singular, *spermatozoon*). The individuals in which eggs develop are females, and those in which spermatozoa develop are males.

Sexual Reproduction in Metazoa.—In metazoa the germ cells (ova and spermatozoa) are the only cells which retain the power of uniting to initiate the development of a new metazoan individual. All other cells have completely lost this power. As the time for sexual reproduction draws near, the germ cells undergo a certain process of develop-

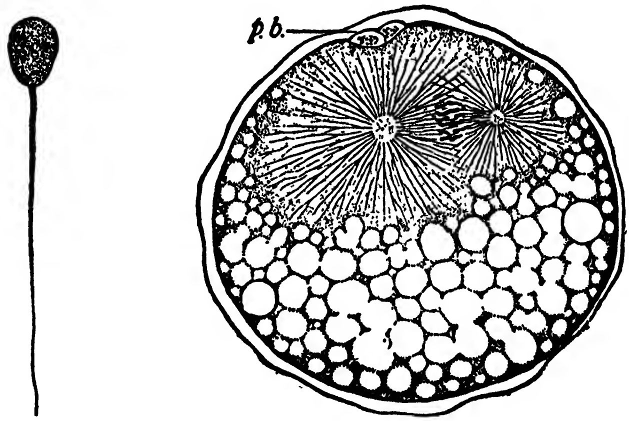

Fig. 128.—Sperm cell and ovum. *A*, spermatozoon of rabbit; *B*, fertilized ovum of Nereis with two polar bodies, *pb*. (*B from Wilson, "The Cell."*)

ment or of preparation for the sexual act. This preparatory process is described in detail in Chap. 16, but its essentials may be stated here. In the ovum it consists in the main of two cell divisions by which three or four cells are produced. Of these cells one is much larger than the others, and its nucleus has one-half the usual number of chromosomes. The small cells are called *polar bodies* and are nonfunctional. In the sperm cell the process does not differ essentially from that in the ovum, except that it results regularly in the formation of four relatively small cells of about equal size, all of which are usually functional. Like the eggs they have half the usual number of chromosomes. The male germ cells must then be transformed, by a striking change of shape, into spermatozoa. A sperm cell and an ovum with polar bodies are illustrated in Fig. 128.

When mature spermatozoa and eggs of the same or closely related species are brought together, the actively motile spermatozoa meet and penetrate the eggs. Usually but one sperm cell can enter an egg. After its entrance other spermatozoa are excluded, either by a change in the surface of the egg or by some other mechanism. The spermatozoan nucleus and egg nucleus arrange themselves side by side; and, as the zygote begins to divide in development, the chromosomes of the two nuclei mingle in such a way that their separate sources are as a rule completely obscured. A new cell has arisen from two cells, and out of it comes a new individual derived from two parents.

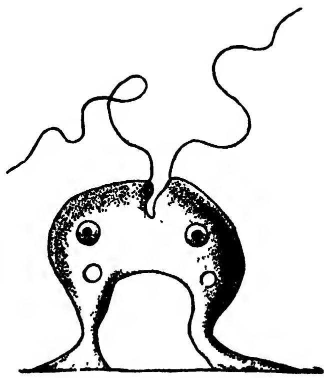

FIG. 129.—Isogamy in *Heteromita lens*. (*After Kent.*)

Sexual Reproduction in Protozoa.—In some of the protozoa, sexual reproduction involves union between two cells that are alike, which are accordingly known as *isogametes* (Fig. 129). In other unicellular organisms the cells that unite are necessarily of different kinds and are then known as *anisogametes*. In *Eudorina elegans* the difference is one of size; fusion is always between a large cell and a small one (Fig. 130). These might at first seem comparable to the egg and spermatozoon of

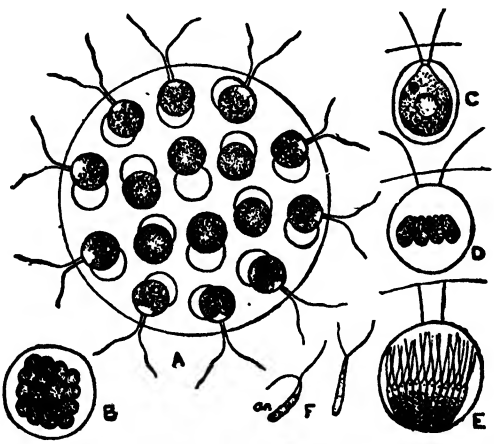

FIG. 130.—Reproduction in *Eudorina elegans* Ehrenberg. *A*, adult colony × 475; *B*, daughter colony produced by division of one of the cells of such a colony as in *A*, × 730; *C–E*, development of spermatozoa from a mother cell; *F*, separate spermatozoa. (*From West after Goetel.*)

metazoa, but both the large and the small gametes in Eudorina have flagella and are therefore motile. In Volvox and Pleodorina there are likewise differences in size, and the large cells are nonmotile. Still, the parallel between these large cells and the eggs of metazoa is not complete, because in Volvox and Pleodorina the reduction in the number of chromosomes occurs, not just before the cells are ready for reproduction, but a long time earlier. Indeed, all the cells of these organisms have the half number of chromosomes; only the zygote from which they spring has the full number. In *Pandorina morum* (Fig. 131) there is a curious combination of isogamy and anisogamy; it has reproductive cells of two sizes, and union may occur between two small ones or between a large and a small one, but not between two large ones.

In the foregoing examples, union of gametes is a fusion of whole cells. In some of the ciliated protozoa, however, it is only the nuclei of the cells which fuse. In the species in which this occurs, there are

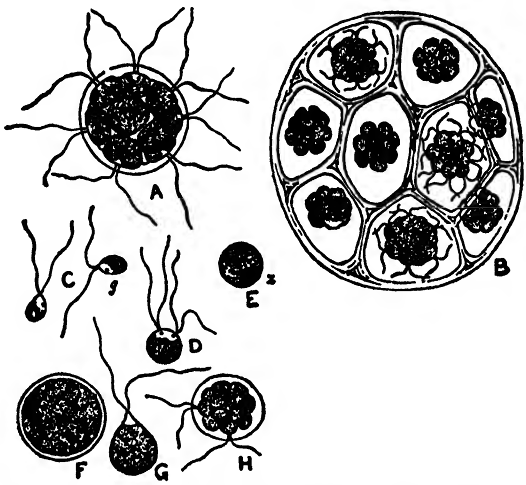

Fig. 131.—Reproduction in *Pandorina morum* Borg. *A*, vegetative colony; *B*, asexual reproduction; *C*, gametes (*g*); *D–E*, union of gametes to form zygote (*z*); *F–H*, development of zygote. (*From West after Pringsheim.*)

two nuclei in each individual, a large one called a *macronucleus* and a small one, or *micronucleus*. Only the micronuclei are involved in the union, and it is justifiable to regard these nuclei, rather than the whole cells, as the gametes. To effect this union, the cells must come together temporarily and make an exchange of nuclei. Temporary union of two protozoan individuals for exchange of nuclei is called *conjugation*. Since the process is rather complicated, it is best illustrated by a specific example, for which Paramecium is selected.

At the time of conjugation (Fig. 132*A*) two individual paramecia come together with their oral surfaces in contact. They are held in this position for a time because of the stickiness of the protoplasm on those surfaces. While they continue to swim about, internal changes in the micronucleus and macronucleus of each individual take place. The micronucleus of each paramecium divides by mitosis (*B*, *C*, *D*), and then each half divides again. Thus each micronucleus gives rise to four micronuclei (Fig. 132*E*). Of these micronuclei, three undergo degeneration, and the one remaining in each paramecium divides again into two parts, usually of unequal size (*F*). The smaller micronucleus of each individual now passes over into the other individual (*G*), while

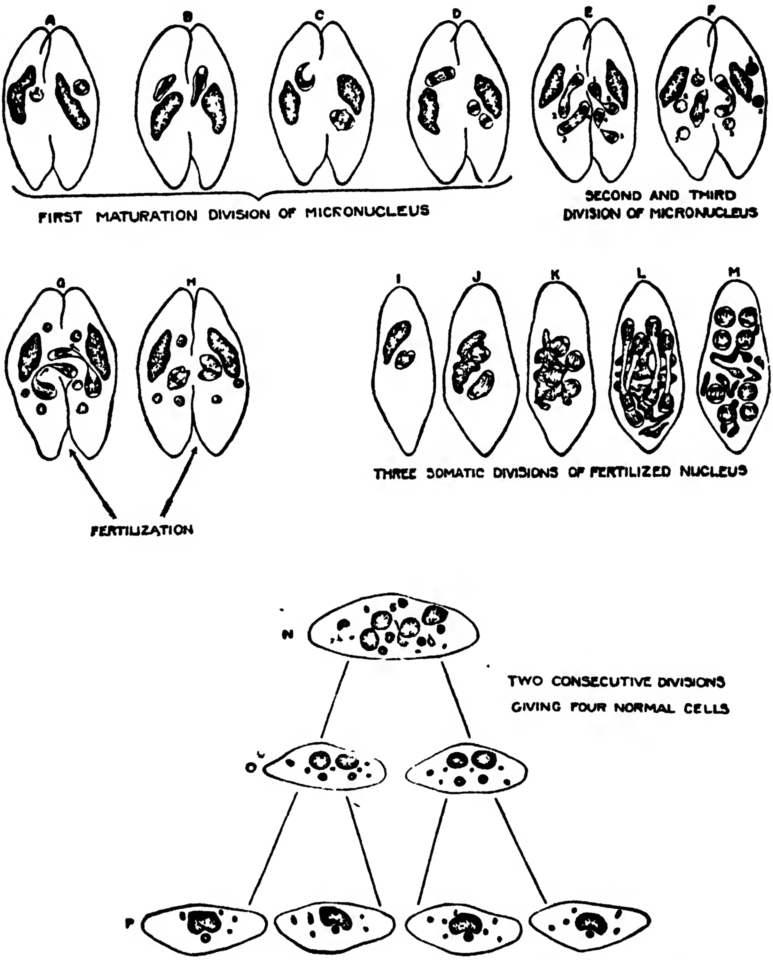

FIG. 132.—Diagram of the process of conjugation in Paramecium. The reference to maturation in the figure will be clear only after a perusal of the section on oögenesis in Chap. 16. (*From Calkins, "Biology of the Protozoa."*)

the larger one is retained. The two pieces, one derived from each individual, now fuse to make the fusion micronucleus (*H*). During these stages of the process the macronucleus has been undergoing fragmentation and sooner or later its parts degenerate completely. Soon after the exchange of micronuclei the individuals separate and the process of conjugation itself is completed. Fusion of the micronuclei, however, initiates a series of changes covering a long period. These processes in one of the exconjugants are essentially as follows. The fusion micronucleus divides three times (Fig. 132*I–M*), resulting in the formation of eight micronuclei. Of these, four enlarge and become macronuclei, while the other four remain micronuclei. The exconjugant then divides twice (*N–P*), each new individual receiving one micronucleus and one macronucleus. After a growth period each cell divides by fission (page 169) in the ordinary manner and at intervals of 16 to 24 hours thereafter for a considerable period, when again conjugation usually occurs. The part of this process which corresponds to fertilization is the exchange of micronuclei and the formation of a new nucleus from the two parts.

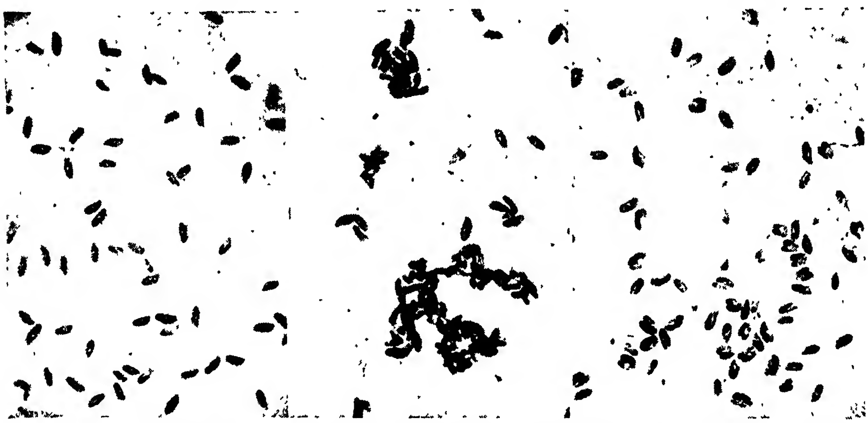

FIG. 133.—Conjugating strains of paramecia: at left, single strain, no conjugation; middle, two strains mixed; right, clumps sorted out, mostly into pairs. (*From Wichterman in Turtox News.*)

The repeated divisions of the cells following conjugation are to be likened to segmentation of the fertilized ovum of the metazoa.

A most interesting fact is that there are different strains of Paramecium, so organized physiologically that members of the same strain will not conjugate with one another, but all of them will conjugate with those of certain other strains. When members of two strains which will conjugate are mixed, they first form large clumps (Fig. 133). These aggregations slowly disintegrate and after a few hours are sorted out, mostly into pairs. Some biologists have been tempted to regard this distinction between strains as sex, despite the difficulty of deciding which of two conjugating strains is female, which male. Since each member of a pair receives a micronucleus from the other, they would seem rather to be hermaphrodites (see page 166).

Parthenogenesis.—In an earlier paragraph it was said that sexual reproduction usually involves two parents and the fusion of two germ cells. It is not uncommon, however, to find species of invertebrates among which, for considerable periods of time, no males can be found. The females produce eggs which develop into new individuals like the parent, although fertilization by spermatozoa does not occur, since no males are present. By their origin and division and nuclear changes the cells giving rise to new individuals are ova; hence the method is regarded as a sexual one. Development of an egg without fertilization is known as *parthenogenesis.* There are many animals which employ parthenogenesis. Some insects which do so are the plant lice, or aphids, and many ants, bees, and wasps. The method has also been observed in a few moths, a few of the scale insects, and commonly among the flower-inhabiting insects known as thrips.

The females of many parthenogenetic species produce, for a number of generations, only females. At intervals, frequently in the fall, males are also produced which fertilize the eggs. These zygotes usually differ from the unfertilized eggs in being provided with hard shells and in being resistant to the rigors of a winter season. The fertilized eggs hatch in the spring into parthenogenetic females which repeat the cycle as outlined. Many species of aphids and of the lower Crustacea have cycles of this type. In certain insects the bisexual reproductive phase is apparently entirely omitted, and reproduction is exclusively parthenogenetic. Thus the black flower thrips *Anthothrips niger*, the brown chrysanthemum aphid *Macrosiphum sanborni*, many species of scale insects, and some gall-producing and parasitic insects never produce males. In the ants, bees, and wasps, both males and females are usually produced. The female lays both fertilized and unfertilized eggs, in some way controlling fertilization of the eggs by the release or retention of spermatozoa stored in the seminal receptacles. Among bees the males (drones) are derived from unfertilized eggs, the females (queens and workers) from fertilized eggs.

Fertilization, where it occurs, has a dual function, that of (1) stimulating the egg to develop, and (2) introducing the hereditary properties of the male parent. In parthenogenesis there is only one parent; hence no paternal qualities can be transmitted, and the eggs are able for some reason to start development without any stimulus from a spermatozoon.

Parthenogenetic development has been induced in the eggs of a number of animals which ordinarily require fertilization. The methods have been various. Bathing the eggs with weak solutions of chemical substances, shaking them vigorously in a bottle, heating them, or pricking them with a fine needle, all have started division in certain eggs. Most of the individual animals whose development was started in this artificial way have died in early stages, but a few frog eggs pricked with a needle and moth eggs raised to a high temperature have yielded adult offspring.

Paedogenesis.—Although sexual reproduction is usually carried on only by adults, this is not always the case, for there are certain species whose members have the remarkable power of reproducing sexually while they are in the larval[1] state. This reproduction by a larval animal is called *paedogenesis.* Paedogenesis may be either parthenogenetic or bisexual.

Parthenogenetic paedogenesis occurs in certain species of flies. The larvae in these species (Fig. 134) produce ova which develop by parthenogenesis into larvae before the oviducts are present. The latter generation of larvae escapes from the parent larva by rupture of the body wall. This results in the death of the parent. Several generations may be produced in this fashion; then the larvae of one generation pupate and emerge as normal adult male and female flies.

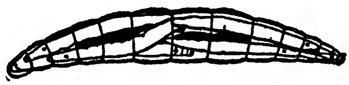

FIG. 134.—Paedogenesis in the fly Miastor. The parent, itself a larva, contains a number of larval offspring. (*From Folsom after Pagenstecher.*)

Paedogenesis of the bisexual type occurs in the well-known axolotl *Ambystoma tigrinum,* or tiger salamander. Under certain conditions this animal attains sexual maturity and breeds while it is still in the larval form having gills. In some of the Mexican lakes this is said to be the usual occurrence, while in Kansas and Nebraska it is rare, and in many localities it probably does not occur at all.

Hermaphroditism.—Most animals—a very great majority of the metazoa—possess either male or female organs of reproduction but not both. Species which have the sexes thus separate are said to be *dioecious* (living in two houses), while those species whose individuals produce both eggs and spermatozoa are called *monoecious* (living in one house). Individuals with both male and female organs are said to be *hermaphrodites.*[2] Two common species of Hydra are hermaphroditic, as are most of the flatworms, most snails, and some roundworms. In many monoecious species the spermatozoa are produced first and later the ova, but in some species this condition is reversed. By developing the sexual products at different times, cross-fertilization, that is, fertilization of eggs by spermatozoa from another individual, is assured. In the earthworm, eggs and spermatozoa are produced in the same individual and

[1] A larva is a young independent individual which differs from the adult in the possession of organs not possessed by the adult, or in lacking certain organs which are present in the adult (for example, a frog tadpole).

[2] The word monoecious is also applied to individuals, and is then synonymous with hermaphrodite; but the corresponding word dioecious cannot well be applied to individuals.

at the same time. Cross-fertilization is assured in this case by the arrangement of the generative organs and by the method of mating. In mating, the bodies of two worms are closely applied by their ventral surfaces, the heads pointing in opposite directions and the thickened band or *clitellum* of each worm approximately opposite segments 7 to 12 of the

Fig. 135.—Copulation of earthworms. (*Courtesy of General Biological Supply House.*)

other worm (Fig. 135). In this position each worm secretes a *slime tube* (Fig. 136) which sheathes its body. Spermatozoa are discharged into the space between the slime tube and the body of the worm, are carried backward within the slime tube by the muscular contractions of the body, and finally are picked up by the seminal receptacles of the other member

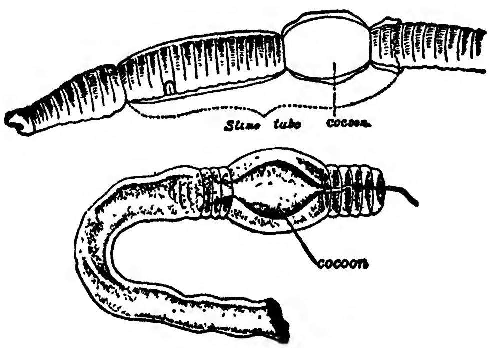

Fig. 136.—Slime tube and cocoon of earthworm: above, in process of formation; below, after slipping off the worm. (*After Foot.*)

of the pair. A cocoon is secreted around each worm, and eggs are laid in it. The cocoon with the eggs in it is then slipped off over the head end, along with the slime tube, and spermatozoa are discharged into it as it passes the seminal receptacles (see page 168). Fertilization occurs in the cocoon.

To work in this manner, the ducts discharging the germ cells must be in front of the clitellum, by which the cocoon is secreted. Their arrangement is shown in Fig. 137. The male organs are two pairs of *testes*, three pairs of *seminal vesicles*, and one pair of *vasa deferentia.* Male germ cells are originated by the first of these organs, are developed in the second, and are discharged through the third. The same worm also possesses a set of female reproductive organs consisting of one pair each of *ovaries*, *ovisacs*, and *oviducts* and two pairs of *seminal receptacles.* The eggs, after leaving the ovaries, are held temporarily in the ovisacs and then discharged through the oviducts. The seminal receptacles receive spermatozoa from another worm and hold them until a cocoon passes by their openings.

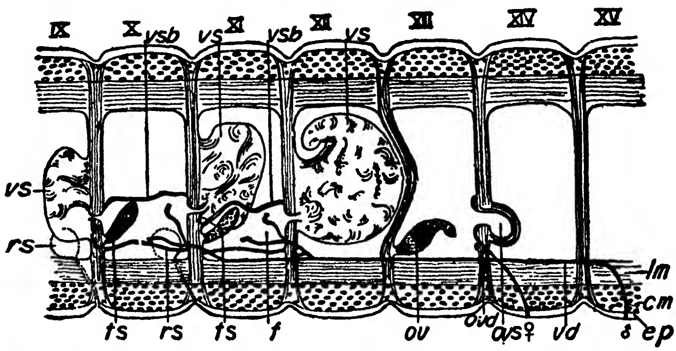

FIG. 137.—Reproductive organs of the earthworm, schematic representation of the side view: *IX–XV*, numbers of somites; *cm*, circular muscles; *ep*, epithelium; *f*, funnel of vas deferens; *lm*, longitudinal muscles; *ov*, ovary; *ovd*, oviduct; *ovs*, ovisac; *rs*, receptaculum seminis; *ts*, testis; *vd*, vas deferens; *vs*, vesicula seminalis; *vsb*, base of vesicula seminalis; ♀, opening of oviduct; ♂, opening of vas deferens. (*Modified from Hesse.*)

While in the earthworm and in some other hermaphroditic species an elaborate mechanism ensures cross-fertilization, in other hermaphroditic species no such devices exist and, indeed, self-fertilization (fertilization of eggs by spermatozoa of the same individual) is well known either as a regular or occasional occurrence. Some plants as wheat and beans regularly self-fertilize. Other plants as the violet produce some flowers which are regularly cross-fertilized and others which can only be self-fertilized. Among parasitic flatworms (tapeworms and flukes) and among snails both cross- and self-fertilization have been observed.

As stated in an earlier section, Paramecium is to be regarded as hermaphroditic. One individual conjugates with another for exchange of micronuclei. Besides this, at intervals there is, without conjugation, a reorganization of the nuclei of a single individual which results in reinvigoration, but which seems not to correspond to self-fertilization since there is no fusion of nuclei.

Asexual Reproduction: Fission.—Fission is a common reproductive method among the protozoa, and occurs less commonly among the metazoa. The essentials of fission are that the parent cell or the parent body (if a metazoon) be divided into approximately equal parts, each of which grows and regenerates the missing parts and thus comes to resemble the parent. The parent disappears as an individual and two new individuals take its place. The plane of fission may be longitudinal or

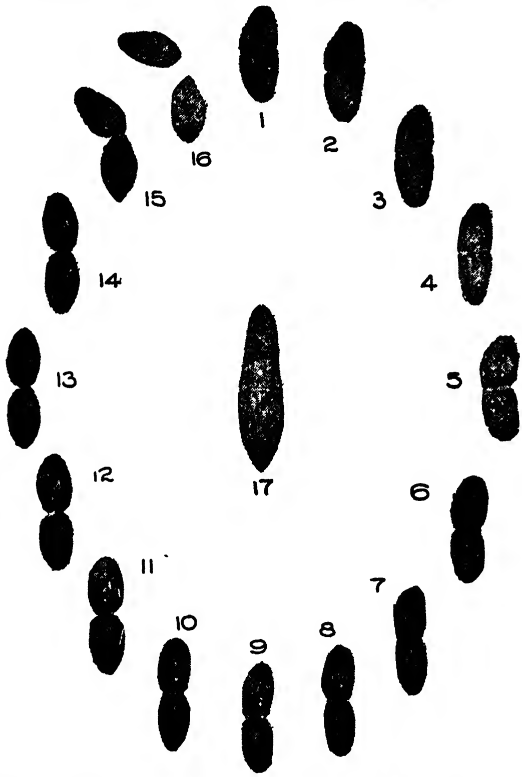

FIG. 138.—Successive stages in the fission of a single paramecium. (*Courtesy of Ralph Wichterman and General Biological Supply House.*)

transverse. Transverse fission, the more common type, is illustrated in Fig. 138, which shows, step by step, the division of *Paramecium caudatum*. Structures which extend across the plane of fission are divided, and the missing portion regenerated. Other structures go with that portion in which they are located before fission, and corresponding structures arise anew in the other portion. Thus in a paramecium with two contractile vacuoles, one placed anteriorly, the other posteriorly, one vacuole goes to each new individual and a second vacuole arises anew in each, usually before division is completed, as in the figure. In forms which have both macro- and micronuclei, both nuclei elongate and finally divide, a half going to each new individual. After the separation into two individuals, regeneration is completed and each individual grows in size. As stated on page 164, fission occurs every 16 to 24 hours in a healthy line of paramecia.

In the reproduction of certain parasitic protozoa the nucleus of a large cell may divide many times without the division of the cytosome. Later the cytosome divides, not by successive equal fissions but by many simultaneous divisions, into as many pieces as there are nuclei, thus forming a number of small cells at the same moment. This process is sometimes called *multiple fission* and sometimes *sporulation*. It occurs regularly in the complicated life history of the organism of malaria.

Budding.—When an organism divides unequally, the reproduction is termed budding. The larger portion may be regarded as the parent, the smaller one as the offspring. Usually, also, there is a definite protru-

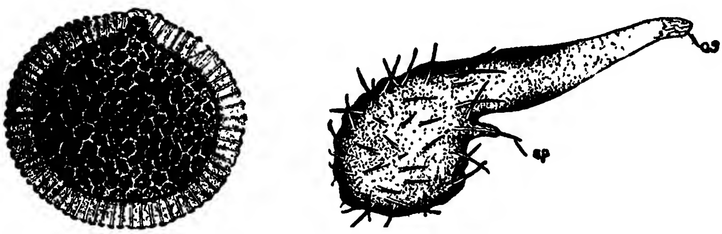

FIG. 139.—Gemmule of fresh-water sponge (left), and young sponge recently emerged from gemmule: *os*, osculum; *sp*, spicule. (*Gemmule after Hesse and Doflein.*)

sion of the bud, which is small at first but grows larger. The bud usually develops organs similar to those of the parent and either becomes independent of, or remains attached to, the parent. Budding is a rare reproductive process among the protozoa but is common in certain groups of the metazoa.

In the metazoa the budding may be either internal or external. In the former, the buds are formed somewhere within the body substance; in the latter, they are on the surface.

Internal Budding.—In fresh-water sponges, masses of cells collect in the jellylike middle layer of the body wall. Hundreds of cells are in each mass, and around them is a horny layer which often contains many spicules. Such a reproductive body is called a *gemmule* (Fig. 139, left). The gemmules are not shed, but when the parent's body disintegrates at the end of the season, they are left exposed on the log or stone to which the sponge was attached. They may remain there, or they may be transported considerable distances by water currents or perhaps by the feet or beaks of birds.

With the return of favorable conditions the bud enclosed within the outer coating of the gemmule begins to develop. There is an opening at one side of the gemmule (above in the figure), which is plugged shut during the resting stage. This plug is removed by the developing sponge, which then creeps out. It is greatly distorted while crawling out, for the aperture may be so small as to permit the sponge to pass only several cells abreast. Once out, however, it quickly takes on the form of a sponge

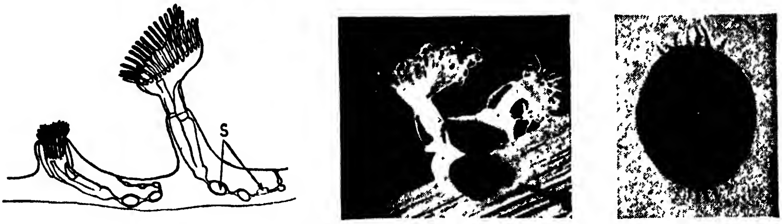

Fig. 140.—Diagram of bryozoan with statoblasts (s); also photograph of animals and (at right) a statoblast.

(Fig. 139, right). Gemmules allow sponges to live through winter and permit them to be carried to other bodies of water.

In the Bryozoa, or moss animals, the internal buds are called *statoblasts*. They appear at first as white or yellow spots along a stalk which joins the stomach of the animal to its body wall (Fig. 140). The oldest statoblasts are next to the stomach. In forming them a mass of cells

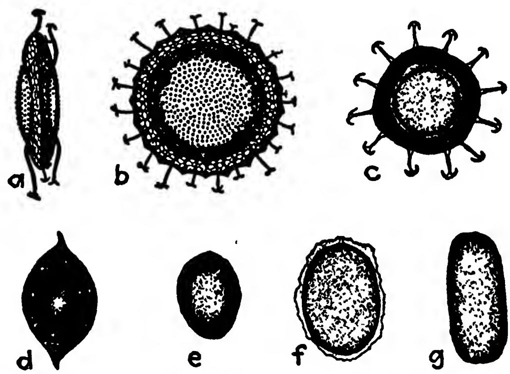

Fig. 141.—Statoblasts of several Bryozoa: *a* and *b*, two views of that of Cristatella; *c*, Pectinatella; *d*, Lophopus; *e* and *f*, floating and sessile types, respectively, of Plumatella; *g*, Fredericella. (*a and b from Sedgwick after Allen; c–g, from Ward's Natural Science Bulletin.*)

comes to be enclosed in a horny cover consisting of two valves, like two cymbals pressed together (Fig. 141*a*, *b*); or they may be of other shapes (*e–g*). These statoblasts escape by the degeneration of the body or some part of it. Some possess floats so that currents of water carry them, and some have hooks which tend to hold them fast to fixed objects. Some germinate late in the summer of the year in which they are produced; others remain undeveloped over winter. They endure long freezing with impunity, but complete drying for a few days usually kills them. When they germinate, the two valves are forced apart but may remain attached to the growing animal for a long time.

External Budding.—In external budding, the body wall is pushed out at some point and develops the characteristic features of the animal.

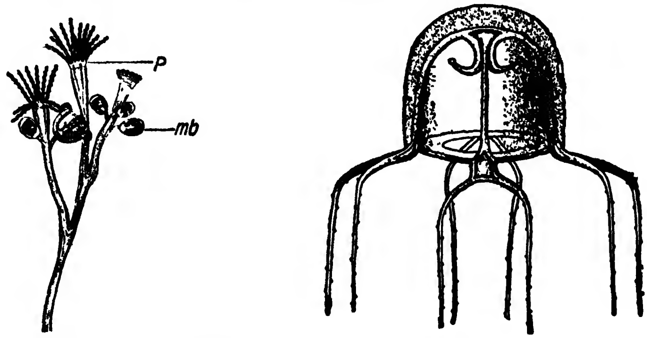

FIG. 142.—The hydroid, *Bougainvillea ramosa*, portion of a colony at left; medusa at right: *mb*, medusa bud; *p*, polyp. (*After Allman.*)

In some species the bud is eventually pinched off, as it is in Hydra (Fig. 58, page 71). This is doubtless the original method. In other species the buds remain attached, and colonies are produced, as is common in the hydralike animals called hydroids. A typical one of these, *Bougainvillea ramosa* (Fig. 142), forms a colony with a much-branched *coenosarc* (interior cellular portion) bearing at the ends of the branches flowerlike

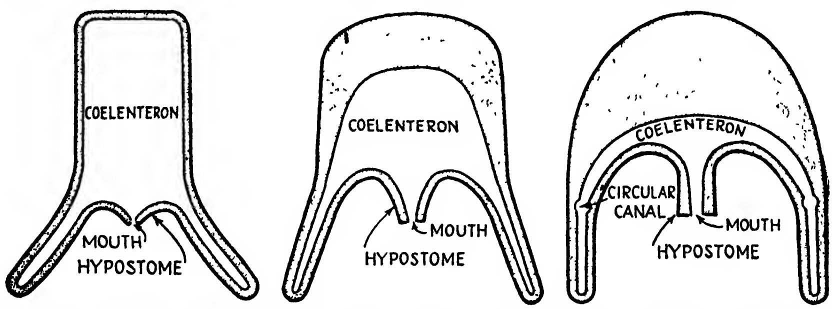

FIG. 143.—Diagram of structure of polyp (left) and medusa, with imaginary intermediate form between; the plan of structure is the same.

zooids, called *polyps* or *hydranths*. Each polyp is provided with a *hypostome*, a conical projection at the distal end, around which is a circlet of *tentacles*. The coenosarc is surrounded by the *perisarc*, a tough, lifeless cuticle secreted by the cells of the coenosarc. The colony arises from a branched rootlike structure, the *hydrorhiza*, which is attached to a solid body such as a rock or log. This colony is produced by budding without a separation of the buds from the parent. From the stalks of many of the polyps, *medusae* (jellyfishes) are formed by budding.

Medusae are bell-shaped individuals (right in figure) which after maturity become separated from the colony and swim freely in the water by means of rhythmic contractions of the bell. Each medusa produces eggs or spermatozoa. The fertilized egg develops into a ciliated free-swimming embryo which eventually attaches itself by one end to a rock and develops into a polyp. This polyp puts forth buds and thus a new colony is formed. Though polyps and medusae are so different in gross form as to have been regarded as different species before the production of one by the other was known, yet the general plan of their bodies is the same. In Fig. 143, by turning the polyp upside down, and introducing an imaginary form between, the scheme of structure is shown to be alike

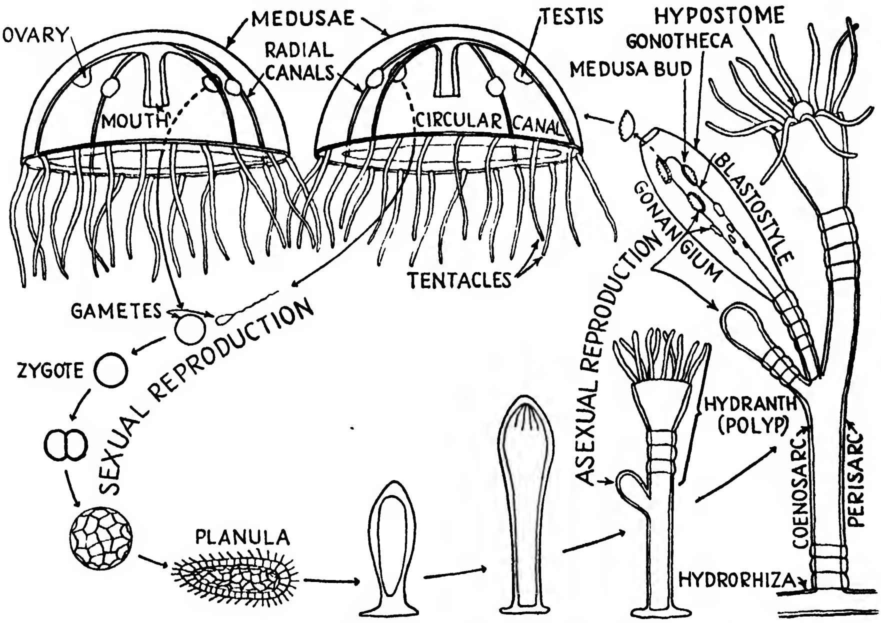

FIG. 144.—Diagram of life cycle of Obelia, illustrating metagenesis.

in both. The cavity or enteron does not always enter the tentacles; in some polyps and medusae the tentacles are solid chains of cells.

Obelia forms a colony somewhat resembling Bougainvillea. In Obelia, however, the medusa buds are produced by budding from the stalks of certain individuals (*blastostyles*) which, unlike polyps, have no tentacles. Each blastostyle is enclosed in a swollen chitinous sheath, the *gonotheca*. Blastostyle, attached medusa buds, and gonotheca together are often designated the *gonangium*. Obelia is thus composed of three types of individuals, two of which are sessile and incapable of sexual reproduction, while the other is a sexual free-swimming form (Fig. 144).

Species which, like Obelia, exhibit several forms of body are said to be *polymorphic* (literally of many forms). In Obelia, as in many other hydroids, polymorphism is accompanied in the life cycle by an alternation of asexual and sexual reproduction. The medusae, which are of separate sexes, produce eggs and spermatozoa. The fertilized egg, after fertilization, produces a larva or *planula* (Fig. 144). This settles

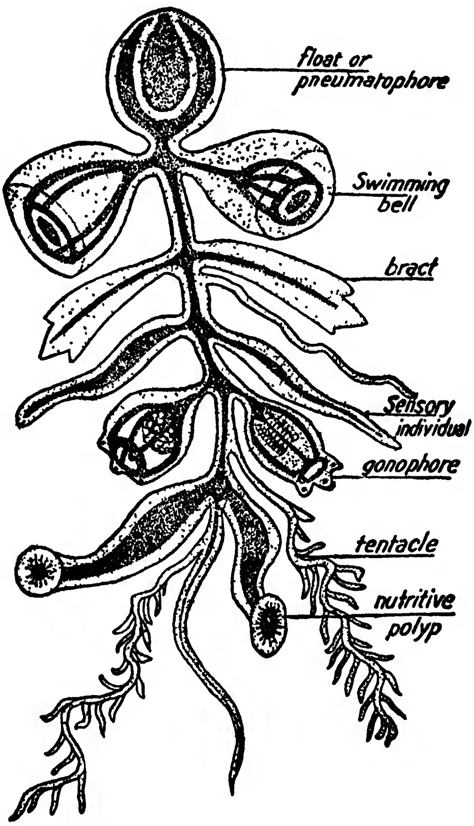

Fig. 145.—Diagram of a siphonophore colony composed of six kinds of individuals. (*Modified from Fleischmann.*)

down, grows into a polyp which buds off other polyps. The colony thus formed also buds off gonangia, whose contained blastostyles bud off medusae. These medusae are set free, and the cycle starts over again. In this cycle the medusae reproduce sexually; all other reproduction in it is budding, that is, asexual. It should be noted that the sexual individuals have a very different structure from the asexual ones. Such a combination of polymorphism with sexual and asexual reproduction is called *metagenesis*.

Extreme Polymorphism.—Remarkable examples of colony formation and metagenesis, accompanied by division of labor among the types of individuals that reproduce asexually, occur among the marine animals known as siphonophores, which have a structural similarity to Hydra. The siphonophores are free-swimming colonies of varying complexity. Each colony (Fig. 145) consists of a common tube of coenosarc which bears at one end a *pneumatophore* or float and along its length zooids of various forms. The float is the expanded end of the coenosarcal tube. It generally contains gas and serves to support the colony which hangs freely in the water. Near the float is a group of swimming bells (*nectocalyces*) which resemble medusae and whose function it is to propel the colony through the water by their alternate contraction and expansion. At intervals below the swimming bells occur *bracts*, or covering scales; feeding polyps which ingest the prey and digest it for the entire colony; sensory polyps which in some species at least also serve as digestive organs; *tentacles* (defensive and offensive individuals) provided with nematocysts (page 72); and *gonophores* (reproductive zooids) with or without bells. A first examination of a siphonophore might lead to the conclusion that it is a complex individual with half a dozen kinds of organs. By a careful study of selected forms, however, and by means of a comparison of these with such forms as Obelia, it may be determined that most of the structures which in a siphonophore resemble and function as organs are really much modified individuals, either polyp or medusa (Figs. 143, 144). In certain species the bracts contain remains of *radial canals* which are characteristic of medusae. The bracts, swimming bells, and gonophores are constructed on a medusoid

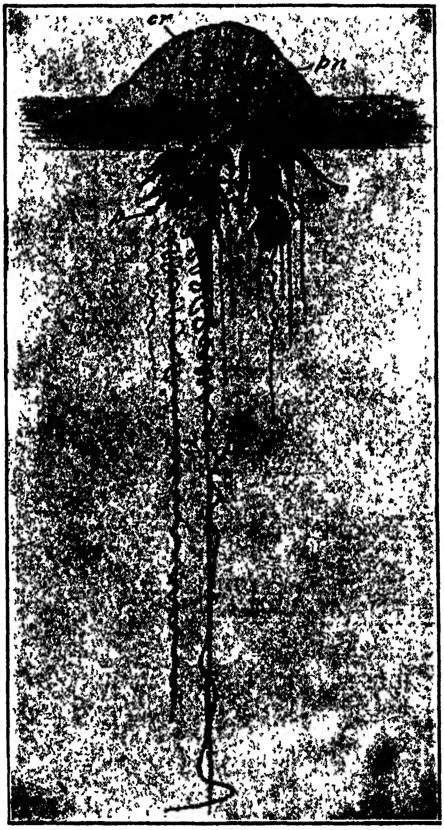

FIG. 146.—*Physalia*, the Portuguese man-of-war, drawn from live animal floating on the surface of the sea. *cr*, crest; *p*, polyp; *pn*, pneumatophore; *t*, tentacle. (*From Parker and Haswell, "Textbook of Zoology," after Huxley.*)

plan, while the feeding polyps, sensory polyps, and tentacles are constructed on the polyp plan. In a few species the gonophores may separate from the colony, as do the medusae in typical hydroids, but usually they remain attached.

The Portuguese man-of-war Physalia (Fig. 146) differs from the generalized form described above in possessing a float which sits high above the water and serves as a sail. It has no swimming bells or bracts.

Origin of Colony Formation.—Among the metazoa the formation of colonies, the integral union of individuals of the same species, occurs only in those groups which employ an asexual mode of reproduction such as budding or fission. Animals which employ the sexual method of reproduction alone do not form colonies. Colony formation, especially when it involves polymorphism and division of labor, may have made for greater efficiency in the performance of certain functions, but it should not be considered that efficiency is a goal toward which species have striven. It seems rather to have been an accident made possible by the existence of an asexual method of reproduction and to have been due to a failure of the mechanism by which budding or fission is normally completed.

Limits of Asexual Reproduction.—Asexual reproduction occurs only among the lower forms of life. It never occurs among vertebrate animals, and there are a number of great groups of invertebrate animals which never employ it. Even in those groups in which it occurs, there are many species which never use it. Nevertheless, asexual reproduction is very widespread. Because its mechanism is less complicated than that of sexual reproduction and because it is employed chiefly by animals of simple structure, it is regarded as the primitive method of reproduction. Animals must have reproduced asexually for ages before even the simplest arrangement for reproductive cooperation of two cells or individuals arose.

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CHAPTER 15

THE BREEDING BEHAVIOR OF ANIMALS

Reproduction in which both sexes are involved is dependent upon the uniting of the germ cells, proper conditions for the development of the fertilized egg, and conditions suitable for the development of the immature animal. The parents often do more or less to ensure these events and conditions, to guard against accident to the immature offspring, and to help it over the period of its own helplessness. These services of the parents are habitual and are known collectively as breeding behavior.

Breeding behavior in the animal kingdom is exceedingly varied. There are two apparent reasons for this variety. First, different forms have different modes of life, and the breeding habits must be suited to the manner of living if they are to accomplish their purpose. Second, the increasing complexity attained in the higher forms of life apparently necessitates in them a longer period of prenatal development. At least, the development before birth or hatching is longer in the complex forms than in the simpler ones. The differences in behavior are not characters that distinguish large groups of related animals from one another, for within these groups there is considerable dissimilarity in breeding habits. Even closely related tree frogs, for example, may employ very different means of assisting the processes of reproduction and development. Because of this diversity no attempt will be made to describe in detail the various breeding habits of animals, but rather to classify and summarize and to introduce just enough detail to illustrate in concrete manner the several types of breeding behavior.

Urinogenital Systems.—Since some features of the breeding habits of animals are dependent upon the structure of their reproductive organs, these must first be examined. In vertebrate animals the reproductive and excretory systems are intimately connected and together they comprise the *urinogenital* system. The excretory system of the frog has already been described (page 136). In both sexes of the frog the gonads (meaning testes or ovaries) develop ventrally to the kidneys and here they hang suspended in sacs of peritoneum. This relation is most plainly seen in the male and in young females whose ovaries have not yet become voluminous.

The oviducts are coiled tubes passing by the ovaries (Fig. 147, left). Each oviduct takes its origin in a ciliated funnel which lies near the heart and at the extreme anterior end of the coelom or body cavity. The posterior end of each oviduct is transformed into a thin-walled distensible bag, the *uterus*, which is connected by means of a narrow passage with the cloaca, in the same region as the opening of the *ureter*. The walls of the uterus and the ureter become united side by side in their lower courses, but their cavities remain distinct. Eggs are released into the body cavity by ruptures in the peritoneum covering the ovaries. They are carried forward to the funnels of the oviducts by the general body movements, assisted by pressure of the fore arms of the clasping male.

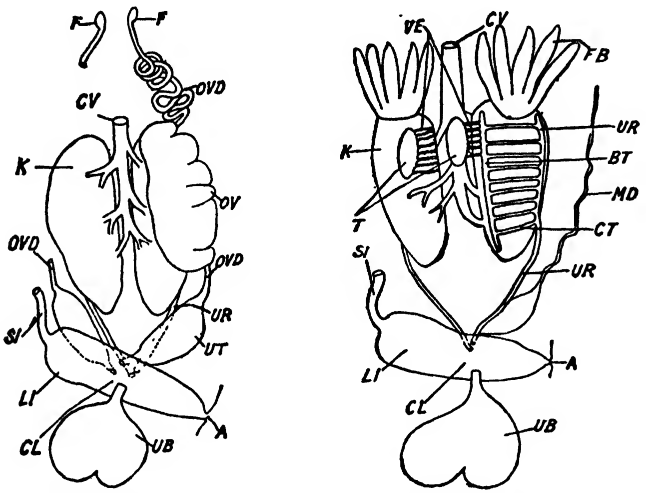


FIG. 147.—Urinogenital system of female (left) and male frog. Kidney at left in male is in surface view, that at right dissected to show internal tubes. *A*, anus; *BT*, Bidder's tube; *CL*, cloaca; *CT*, collecting tubule; *CV*, postcaval vein; *F*, funnel of oviduct; *FB*, fat bodies; *K*, kidney; *LI*, large intestine; *MD*, Muellerian duct; *OV*, ovary; *OVD*, oviduct; *SI*, small intestine; *T*, testes; *UB*, urinary bladder; *UR*, ureter; *UT*, uterus; *VE*, vasa efferentia.

Currents are also produced by the strong beating of the cilia which line the funnels of the oviducts. These currents sweep the eggs and other matter into the open funnels and down the oviducts. The remainder of the path to the exterior is indicated by the structure and arrangement of the organs.

In the male frog (Fig. 147, right) the testes are connected to the kidneys by means of fine ducts, the *vasa efferentia*. These fine ducts penetrate into the kidney and open into a longitudinal canal (*Bidder's canal*), which is a long tube running lengthwise of each kidney near its median border. Bidder's canal is connected with the ureter by means of a series of *collecting tubules* into which the uriniferous tubules (page 135) also open. Spermatozoa in the frog must therefore pass through the vasa efferentia, Bidder's canal, the collecting tubules, the ureter, and the cloaca on their way to the exterior. In some species of frogs, the lower end of the ureter in the male may be expanded into a *seminal vesicle* in which spermatozoa are stored until they are emitted at the time of breeding.

A comparison of the reproductive systems of male and female frogs reveals that in the male the reproductive organs are more intimately connected with the excretory organs than in the female. In reptiles and birds, the genital system, especially in the male, is more distinct from the excretory system, though in both of these groups, as in the frogs, both excretory and genital systems discharge into the cloaca.

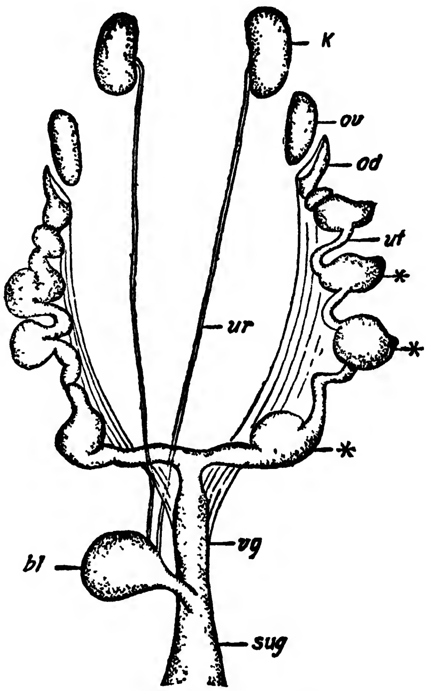


FIG. 148.—Urinogenital system of a female mammal having a bicornuate uterus, somewhat schematic. *bl*, urinary bladder; *k*, kidney; *od*, oviduct; *ov*, ovary; *sug*, urinogenital sinus; *ur*, ureter; *ut*, uterus; *vg*, vagina; *, position of embryos. (*Modified from Wiedersheim.*)

In most mammals, the genital and excretory systems open to the exterior through a common opening which is separate from the anal opening. That is, there is no cloaca. In the female, the funnel of the oviduct is close to the ovary but is not connected with it. The oviduct opens into the uterus in which the young are retained and nourished until birth. The form of the uterus differs in the different groups of mammals. That illustrated in Fig. 148 is common among the carnivores, rodents, and others which bring forth young in litters. The uterus is connected to the exterior by the vagina which is the copulation passage. The urinary bladder, which belongs to the excretory system, is connected to the lower portion of the vagina by means of the urethra. In the male the testes are connected by means of the *vasa deferentia* (singular, *vas deferens*) with the urethra, which extends from the urinary bladder through the *penis*.

Methods of Ensuring Fertilization.—In chronological order, the first event of the breeding process in bisexual animals is fertilization of the germ cells. From the nature of their reproductive systems it might be expected that this event would occur differently in hermaphroditic animals and those with the sexes separate, for in hermaphrodites self-fertilization is conceivable. This expectation is not usually realized, however. Relatively few animals are hermaphroditic, among them being some sponges, Hydra and a few animals similar to it, worms, and snails. Though hermaphroditism is often described in various kinds of vertebrate animals, the condition so named is usually merely the existence of egglike and spermlike cells in the same gonad. Since usually only one, if either,

FIG. 149.—Genital organs of a hermaphrodite animal, a common land snail *Polygyra albolabris* (Say). Note that some of the organs are characteristic of a male, others of a female. 1, atrium; 2, penis; 3, prepuce; 4, vagina; 5, spermatheca; 6, vas deferens; 7, free oviduct; 8, uterus; 9, spermatic duct; 10, talon; 11, hermaphroditic duct; 12, hermaphroditic gland; 13, penis retractor; 14, albumen gland.

of these kinds ever reaches maturity and since appropriate ducts for leading off both kinds of cells are not often present, such animals are not functional hermaphrodites at all. The reproductive system of a really hermaphroditic animal, a snail, is shown in Fig. 149.

Most hermaphroditic animals have some way of avoiding self-fertilization. In some of them, though both kinds of germ cells are produced, eggs predominate in some individuals, spermatozoa in others, and mere chance favors cross-fertilization. In other animals, the two kinds of germ cells are produced at different times, eggs first in some, spermatozoa first in others. Obviously there can be nó self-fertilization under these circumstances. In still others, the mating habits prevent self-fertilization, as has been described for the earthworm in the preceding chapter. Some of the roundworms, however, and Sacculina, which is a parasite attached to crabs, fertilize their own eggs regularly. No special act is necessary to bring eggs and spermatozoa together in these self-fertilizing forms, since they mingle freely within the body. Sometimes self-fertilization may occur accidentally, as in Hydra whose sperms are shed into the water, where they penetrate eggs still located in the ovaries. Since the spermatozoa find the eggs largely by chance, they may reach either an egg in the same individual or one of another individual.

Fertilization in Dioecious Species.—In many aquatic animals with separate sexes the sexual elements, or at least the spermatozoa, are simply discharged into the water and the germ cells come together by chance. Thus in the jellyfishes the spermatozoa are liberated into the water and may or may not happen to meet the eggs, which are retained in the ovaries of the females of some species just as in Hydra. In other animals there is congregation of the sexes at the breeding time, and the eggs and spermatozoa are liberated in proximity. Starfishes and sea urchins periodically congregate in this manner. This close association of the sexes undoubtedly greatly favors the meeting of the germ cells but still leaves to chance an important role, and many eggs are never fertilized. The hellbender (a salamander) is a form that congregates with its fellows at the breeding season. In certain other salamanders the male deposits the spermatozoa in a naked, nearly spherical mass resting on a gelatinous stalk which is attached to a leaf or some other object in the water. This structure, including the stalk, is called a *spermatophore* (Fig. 150). The mass of spermatozoa at its top is subsequently removed by the female with the lips of the cloaca, and the eggs are fertilized within her body.

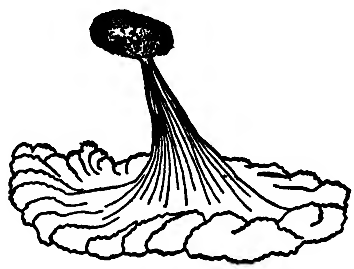


FIG. 150.—Spermatophore of *Notophthalmus viridescens viridescens* (Raf.), the common newt of eastern North America. The stalk is a clear gelatinous substance; the apical mass (dotted in the figure) is a snowy-white mass of seminal fluid containing spermatozoa. (*After* B. G. *Smith.*)

This last way of bringing eggs and spermatozoa together can be adopted only by animals that fertilize their eggs internally. In frogs and toads, fertilization occurs outside the body, and in these forms special behavior is designed to bring the sex cells together. In addition to congregating at the breeding season, the males practice clasping. The male grasps the female, with his forelegs around her body (Fig. 151), and pours out the fluid containing the spermatozoa as she lays her eggs in the water. One of the salamanders, *Notophthalmus viridescens*, shows a curious combination of methods, the value of which is obscure; the male first clasps the female, but instead of pouring out the spermatozoa into the water, he then deposits them in spermatophores, from which the female takes them into her cloaca as just described.

In many other animals the spermatozoa are introduced into the body of the female by direct act of the male, a process known as *copulation.* Fertilization then occurs internally. This method is employed

FIG. 151.—Clasping in a species of toad, *Bufo typhonius* (Linnaeus). The small individual is the male, the larger the female. (*Photograph by A. G. Ruthven.*)

by some parasitic worms, snails, fishes, and amphibia, and by all insects, reptiles, birds, and mammals.

Place of Development.—From the methods of ensuring fertilization, it will be seen that the eggs may be fertilized either before or after they are laid. That is, fertilization is either internal or external. When fertilization is internal the eggs may be retained for a long time after fertilization, or they may be laid very soon thereafter. Whatever period of time the eggs remain in the organs of the female after fertilization is utilized in development, so that the embryo may be far advanced before it is separated from the mother, or it may have attained only an early stage of development, or development may scarcely have started. Thus, in most of the insects and in all the birds the eggs are laid soon after fertilization. In these cases only a few divisions of the egg, or of its nucleus, have taken place at the time of oviposition, or it may not have divided even once. On the contrary, development may proceed until a well-formed embryo is produced, and then the eggs are laid; this occurs in some of the salamanders. Usually, if the eggs undergo more than a few cleavages while within the mother, they remain until a rather late larval stage, or until the form of the adult is attained. Some insects, some snakes, and the true mammals are of the last-named type.

Source of Nourishment of the Embryo.—Animals that lay their eggs are said to be *oviparous;* the eggs may be laid before fertilization, or, if after fertilization, while the embryos are still incapable of existence outside the egg membranes. Animals that retain the embryos until with proper care they are capable of independent existence are designated *viviparous.* Of viviparous species there are two general types. In one of these, the eggs are large and laden with yolk, from which the embryo derives its nourishment, just as in oviparous animals. The mother serves, in such cases, chiefly as a nest in which the eggs may develop. Viviparous animals in which practically the whole nourishment of the young is furnished by the egg itself are said to be *ovoviviparous.* Some reptiles are ovoviviparous (Fig. 152), the embryos being held in the oviduct of the mother until they are far advanced but receiving the food from the egg. The second type of viviparous animal is that in which the nutrition of the embryo is obtained from the mother, whose reproductive system is then of the general type represented in Fig. 148. The embryo, resting in the uterus, has as intimate a relation with the mother's blood vessels as do the mother's own tissues. Blood vessels of the embryo extend out through the umbilical cord, and branch profusely at the end in a highly vascular structure known as the *placenta* (Fig. 153, left). The placenta is furnished partly by the embryo, partly by the uterus of the mother. In it the blood of the mother and that of the embryo, while never joining in the same vessels, are separated only by the thin walls of their respective capillaries. In the human placenta the connection is even closer, for the walls of the maternal vessels become eroded away, so that the blood comes to lie in large sinuses, resembling the open blood spaces of the crayfish or insect circulatory system (page 122). In this lake of maternal blood the capillaries of the fetal system (branches of the

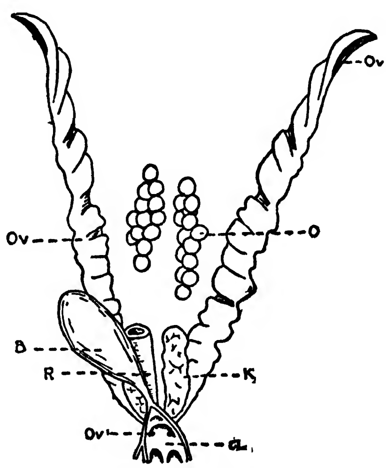


FIG. 152.—Urinogenital system of a lizard. *B*, bladder; *Cl*, cloaca; *K*, kidney; *O*, ovary; *Ov*, oviduct; Ov^1, cloacal opening of oviduct; Ov^2, abdominal opening of oviducts; *R*, rectum. The lizards are oviparous or ovoviviparous.

umbilical vessels) are bathed, as shown by the diagram at the right in Fig. 153. The physiological operation of the two blood systems is precisely like that of blood and adjoining tissue. Digested food and oxygen in the maternal blood are transferred to the fetal blood, because they are at higher pressure in the former. Accumulated urea and carbon dioxide go in the opposite direction because they are at greater pressure in the embryo. The fetus is thus being fed, and its wastes removed, as efficiently as if it were a rapidly growing tissue in the mother's own body. No blood cells are transferred in either direction, however; the exchange is entirely a process of diffusion and osmosis.

Forms in which the embryo is connected with the maternal uterus by a placenta are spoken of as truly viviparous. Hydra and some of

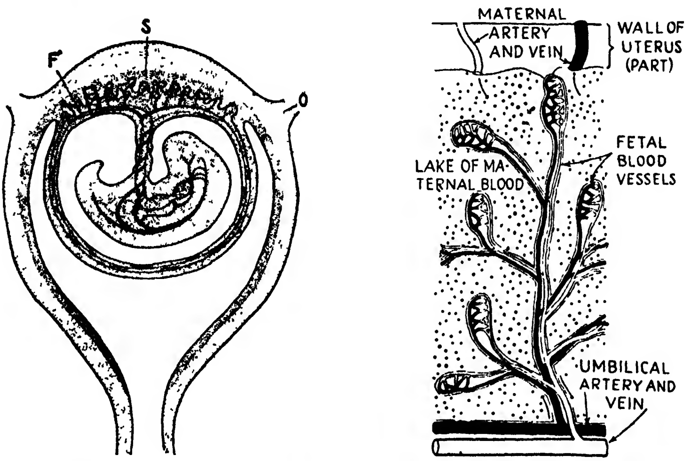


Fig. 153.—Position of fetus in uterus (left), with its attachment by umbilical cord and placenta to uterine wall: *F*, fetal placenta; *O*, opening of oviduct; *S*, maternal placenta. Rectangle shows approximate location of dissection of human placenta at right. (*Left after Kingsley, "Vertebrate Zoology," Henry Holt and Company, Inc.*)

the jellyfishes, among aquatic animals, exhibit something like viviparity, since only the spermatozoa are shed into the water. The spermatozoa in these forms find the eggs, largely by chance, while the eggs are still in the maternal ovary and penetrate the eggs in that situation, and the fertilized eggs develop there for a time. In these cases the eggs are large and presumably contain much of the necessary nourishment.

Intermediate between ovoviviparous and viviparous forms are those in which the young develops for a considerable time in the egg and later becomes attached to the body of the mother. Certain sharks (Fig. 154) exemplify this intermediate condition. The expanded end of the yolk sac becomes attached to the wall of the uterus, forming an organ like the placenta of mammals. The young receive nourishment through it from the mother.

No Evolutionary Sequence.—Since some of these types of breeding behavior are plainly much more specialized than others, one might be tempted to suppose that they exhibit some sort of evolutionary sequence. That is, it might be thought that the simpler habits would be employed by the more primitive groups of animals, while the complicated methods would be adopted by the higher forms. Such appears not to be the case, however, either as to assurance of fertilization or as to place of development. Thus, copulation, which is a specialized habit, is employed by some parasitic worms, some snails, the insects, reptiles, birds, and mammals. These groups are so diverse in structure that it is impossible to regard them as all primitive or all highly developed. Furthermore, most of the fishes and amphibia use either external fertilization with clasping or internal fertilization without clasping, while some members of each of these groups employ copulation. In general, the same breeding habits may occur in animals of widely different groups, and animals of the same group often have very different habits. The principal generalization concerning fertilization is that among aquatic or amphibious forms the habit prevails of depositing the spermatozoa and eggs freely in the water or in immediate proximity to each other, or of depositing the spermatozoa so that they can be secured later by the female; while in the groups composed mostly of land forms the habit of introducing them into the body of the female predominates. The latter method is essential to most land forms, since air is fatal to the delicate sexual cells, whereas in aquatic forms the eggs (at least after fertilization) can endure the water for a prolonged period.

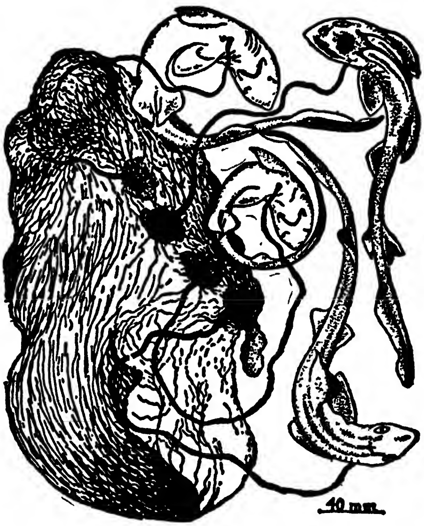


FIG. 154.—Embryo sharks of a viviparous species, *Mustelus mustelus* (Linnaeus), attached to the wall of the uterus, which is here dissected open. (*After Fowler.*)

In the method of bearing the young, also, there is no evolutionary sequence. Oviparity and viviparity are found in the vertebrates and the invertebrates. Certain conditions of reproduction itself, however, make one generalization possible. The forms in which the eggs are fertilized outside the body of the mother are necessarily oviparous; and it is only among forms with internal fertilization that viviparity, ovoviviparity, and the laying of fertilized eggs can occur. As a result, viviparity, ovoviviparity, and the laying of fertilized eggs prevail among land forms, where protection against evaporation of the eggs is necessary; and the habit of laying eggs before fertilization is mostly found among the aquatic species and the amphibious forms which lay their eggs in water.

Care of Fertilized Eggs.—Among oviparous species the methods of caring for the fertilized eggs are almost endlessly varied in their details.

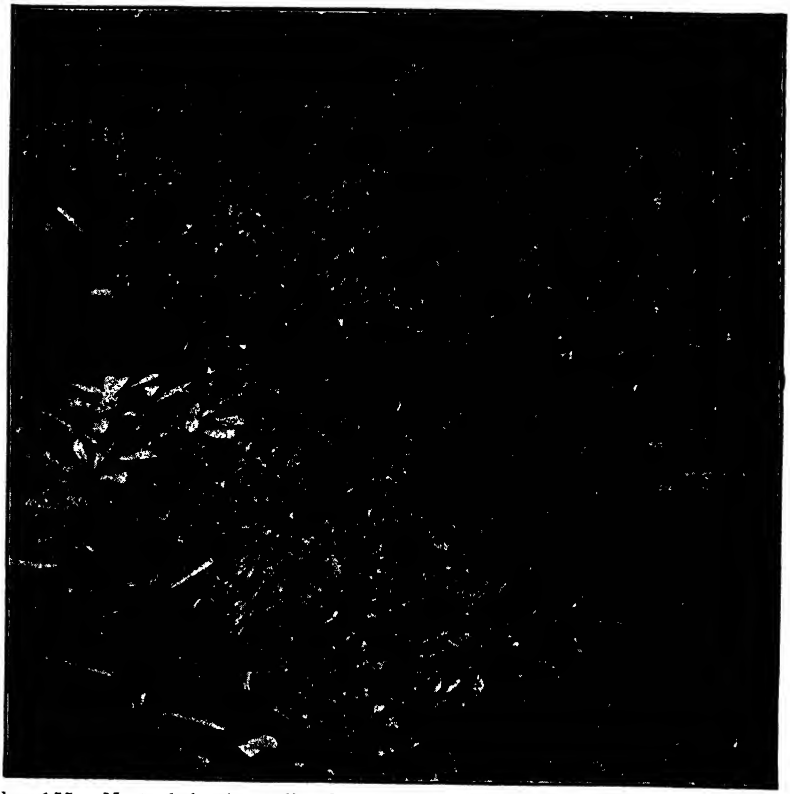


FIG. 155.—Nest of the Australian brush turkey, consisting of litter in which the eggs are buried to be hatched by the heat of the decomposing vegetable débris. The nest is the heap of débris in the lower half of the photograph. (*Photograph by E. R. Sanborn, loaned by the New York Zoological Society.*)

There are many animals which give no care whatever to the eggs. This is particularly true of aquatic species which pour the eggs and spermatozoa freely into the water to come together by chance. The starfishes and sea urchins and many other marine animals exhibit this lack of parental care. Other forms merely put the eggs in places where development is facilitated. Thus toads and certain salamanders which live on land in the adult stage lay the eggs in the water. Aquatic turtles come to land to lay eggs in the warm sand which hastens their development. Digger wasps, ichneumon flies, and certain other insects deposit their eggs in various places and provision them with living or dead animal food. Birds of one group, the megapodes, lay the eggs in a pile of decaying vegetation, the decomposition of which liberates heat that aids in development (Fig. 155). Again, many animals build nests. These nests may be very simple in construction. In the fishes, for example, many species merely hollow out a small area on the bottom of the stream by pulling out the pebbles and heaping them up on the downstream side of the nest. The eggs, when laid, drop into this hollow and among the loose stones. Birds build nests of a great variety of forms, from the loose collection of grass or straw put on the ground by the killdeer, or the

FIG. 156.—Blue-tailed skink, *Eumeces fasciatus* (Linnaeus), with eggs. This lizard buries its eggs (the white mass in the middle foreground) in decaying wood and stays with them until hatched. The curved white streak to the left of the center of the picture is the tail (blue in life) of the parent, and a part of the striped body can be seen to the right of the center. (*Photograph by A. G. Ruthven.*)

insecure litter of twigs set in the branches of trees by the mourning dove, to the elaborate hanging basket of the orioles. Still other forms enclose their eggs in cases, as was pointed out for the earthworm in the preceding chapter and as is true also of the leeches and some insects, snails, and spiders.

Among the nest-building forms the habit of caring for the eggs has usually been developed; that is, one or both of the parents in many species remain with the eggs until they are hatched. The habit of remaining with the eggs may ensure *incubation*, or the elevation of the temperature to a point at which development will proceed. Incubation by the parents is necessary in most birds and is an aid in some other animals. Remaining with the eggs does not, however, necessarily imply incubation. For example the common skink is a "cold-blooded" animal which remains with the eggs (Fig. 156). Its temperature is so nearly that of the surrounding air that the development of the eggs can scarcely be affected by the presence of the parent. Some other species apparently incubate the eggs to a small extent. The python, for example, coils about its

Fig. 157.

Fig. 158.

Fig. 157.—*Hyla fuhrmanni* Peracca, a South American tree frog that has the habit of carrying the eggs on the back. The female carries the eggs. (*Photograph by A. G. Ruthven.*)

Fig. 158.—A marsupial frog, *Gastrotheca monticola* Barbour and Noble, from Peru. The opening of the pouch and a protruding egg may be seen in the lumbar region. (*Photograph by G. K. Noble.*)

eggs, and as the temperature within its coils is a few degrees above that of the surrounding atmosphere, development is thereby probably somewhat accelerated.

The habit of carrying the eggs attached to the body is found in several groups, among both nest-building forms and others that build no nests. Thus, the female crayfish carries her eggs attached to the swimmerets under her abdomen, where she waves them back and forth. The movement of the eggs increases aeration, which is perhaps necessary. Fresh-water mussels keep their eggs in the chambers of the gills of the female, where they are furnished oxygen by the water that is constantly passing through the gills. In spiders the silken egg case mentioned earlier is often carried about by the mother. Certain frogs (Fig. 157) and insects bear the eggs glued to the back of one sex or the other. In other frogs the eggs are attached to the belly, or the egg masses are wrapped around the hind legs of the male or are held in the vocal sacs. One frog, the marsupial frog (Fig. 158), has a pouch formed of a fold of the skin on the back in which the eggs are carried. This habit is again found in the pipefish and sea horse (Fig. 159) which carry the eggs in a ventral pouch.

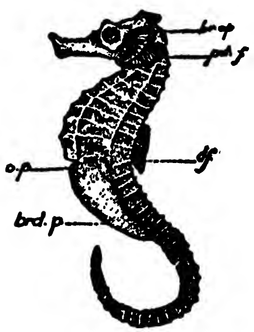


Fig. 159.—Hippocampus, the sea horse, male specimen showing brood pouch: *br. ap*, branchial aperture; *brd. p*, brood pouch; *df*, dorsal fin; *op*, opening of brood pouch; *pct. f.* pectoral fin.

Eggs thus carried in pouches may perhaps receive oxygen from the parent, but little is known on this subject. Either the male or female may carry the eggs, but usually only one sex does this in any given species.

Care of the Young after Birth or Hatching: Birth Stages.—After birth in viviparous forms and after hatching in oviparous species, the

FIG. 160.—The black swamp wallaby. The young are born in a very immature stage and are carried in a pouch (marsupium) on the ventral side of the mother. (*Photograph loaned by the New York Zoological Society.*)

young may or may not require protection and assistance in getting food. This is partly dependent upon the stage of development which the offspring has attained at the time of birth, but not entirely so.

The animal may leave the egg complete in all its parts and needing only the growth of the body and the maturity of the sex cells to attain the climax of its development. Among these forms the young may receive little or no parental care or they may be fed and cared for for many weeks or even months. Among the reptiles, for example, the young are left to their own devices as soon as they hatch or are born. Most fishes and invertebrates also throw off all parental solicitude after their offspring leave the eggs. Most birds, on the contrary, must feed and protect their young for a period of days or weeks; and mammals care for their offspring for weeks or years. In these cases, how long the young must receive aid depends on how far they develop before birth.

FIG. 161.—Recently hatched young of the chimney swift, *Chaetura pelagica* (Linnaeus), left, and spotted sandpiper, *Actitus macularia* (Linnaeus), right. These are examples, respectively, of altricial and precocial birds.

There are great differences in birth stages even in the same group. Thus among mammals the marsupials (opossums and kangaroos) give birth to young in a very immature state and carry them in a pouch (Fig. 160) until they are well formed; mice are born blind, hairless, and very helpless; rabbits are born blind but covered with hair; and guinea pigs are born in such an advanced stage that they are very shortly independent of the mother. Among birds are to be distinguished *altricial* and *precocial* forms (Fig. 161), the former usually, although not always, hatched blind and practically without feathers, thus requiring longer parental care; the latter covered with down and with the eyes open, requiring shorter care.

The common song birds are all altricial, while domestic fowls, partridges, most wading birds, and the various ducks are precocial.

There are also animals which escape from the egg so early that they lack important organs and must undergo extensive changes to attain the adult form. Or they may possess organs which they must lose before they become adults. Young animals, leading a separate existence but lacking certain organs of the adult or possessing organs not found in the adult, are known as *larvae*. The offspring of jellyfishes emerge from the ovary of the mother, where in some kinds as stated earlier the eggs are fertilized, as a simple ball of cells, almost at the beginning of development. They receive no care whatever thereafter. The embryos of sponges escape at a stage almost as early as the jellyfishes. The developing embryos of starfishes, sea urchins and their allies (Fig. 162), and marine worms are also capable of free-swimming existence at a very early stage. In the frogs and toads the tadpole is a larval form (Fig. 163), but it hatches at a much later developmental stage than do the larvae of the several preceding examples.

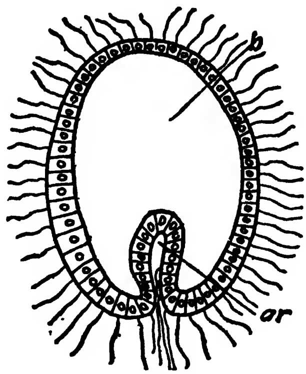


FIG. 162.—Free-swimming larva of the holothurian Synapta, leading an active independent existence at a very early stage of embryonic development.

Early development may be direct or indirect. In direct development the embryo develops directly toward the sexually mature condition, the organs being outlined and developed one after the other. In indirect

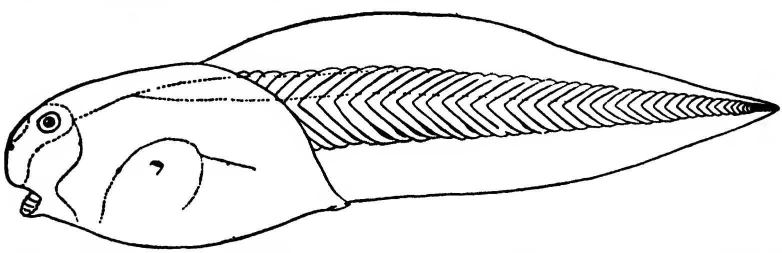


FIG. 163.—Tadpole of frog, illustrating a larval form. Organs are present that are lacking in the adult, and some organs are missing which the adult possesses.

development, on the contrary, organs belonging only to the immature stages and for that reason called *larval organs* are first formed and later destroyed. Thus the caterpillars (larval stage) of butterflies are distinguished from the adult not only by the absence of wings and compound eyes but also by the presence of anal feet and spinning glands which are absent in the adult butterfly; and tadpoles of toads and frogs (Fig.

163) are distinguished from the adult frog not only by the absence of lungs and legs but also by the presence of gills and tail. The transformation by which the larval organs disappear and the missing organs are constructed is known as *metamorphosis*. The more numerous the larval organs the more pronounced the metamorphosis becomes. This phenomenon is further described in Chap. 16.

Relation of Birth Stages to Parental Care.—That birth at an early stage of development necessitates parental care would seem at first contemplation to be obvious. That is not usually true, however, except for the animals of common daily observation. It cannot be said for animals in general that the stage of development at birth determines the amount of parental care necessary, for many of the lower invertebrates with incomplete larvae and many fishes which have very immature young give no care to the offspring, while other invertebrates with feeble young (for example, the ants) carefully guard and feed them. But it is noteworthy that, where no care is exercised, the young born in early stages are usually those of aquatic or amphibious forms, while the young of terrestrial forms are mostly born in relatively advanced stages or receive parental care. Furthermore, while many aquatic forms give some attention to the young, it is among the terrestrial forms that the greatest development in the habit of caring for the offspring is found. It may thus be concluded that, when aquatic animals, or amphibious forms with aquatic young, deposit the eggs or young in suitable habitats, they have done much to facilitate postembryonic development, but that land forms must usually give birth to young in an advanced stage of development or exercise parental care in proportion to the helplessness of the offspring.

CHAPTER 16

EMBRYONIC DEVELOPMENT

The minimum accomplishment of the reproductive processes is the formation of germ cells. With the aid of breeding behavior these germ cells are brought together in a favorable environment, where they are gradually converted into new organisms. Into this period of transformation of the fertilized egg into an active independent being is crowded a multitude of changes—analyses, reconstructions, rearrangements, growth, and differentiations—which constitute embryonic development. Embryology may properly treat of many of the things already described as breeding habit or reproduction; but there is left for examination in this chapter the whole series of structural changes and the chains of physiological events which lead to the formation of the new individual. The story may begin with the reorganization of the reproductive or germ cells.

Maturation of the Germ Cells.—The germ cells in a very young animal may remain for a long time in a relatively undifferentiated condition. Often it cannot even be stated whether they will become eggs or spermatozoa, yet in most animals, despite their lack of recognition marks, they are irrevocably destined to become the one or the other. During this time they divide frequently by ordinary mitosis, thereby multiplying in number. In this apparently unspecialized condition the reproductive cells are called, in a male animal, *spermatogonia* (singular, *spermatogonium*), in a female, *oögonia*.

As the time of reproduction approaches, the spermatogonia and oögonia undergo a series of remarkable changes called *spermatogenesis* and *oögenesis*, respectively. These changes consist typically of two rapidly succeeding cell divisions, in one of which the number of chromosomes is reduced to half. There are many variations in the process in different species, but the fundamental features are the same for nearly all the higher animals.

Spermatogenesis.—As soon as the spermatogonia reach the end of their multiplication period, that is, as soon as they have divided by ordinary mitosis for the last time, the cells are known as *primary spermatocytes*. The history of these cells in their further development is illustrated in Fig. 164, to which constant reference should be made throughout the following account.

During all of their history up to this time, the germ cells contain the same number of chromosomes as any other cells of the body. That number, barring differences in the sexes, is constant for the species. In an animal descended from two parents, these chromosomes, with certain exceptions that may for the present be ignored, come in equal numbers from the father and the mother. Half of the chromosomes in any cell may therefore be designated paternal, the other half maternal. These chromosomes may look precisely alike and may in fact be exactly

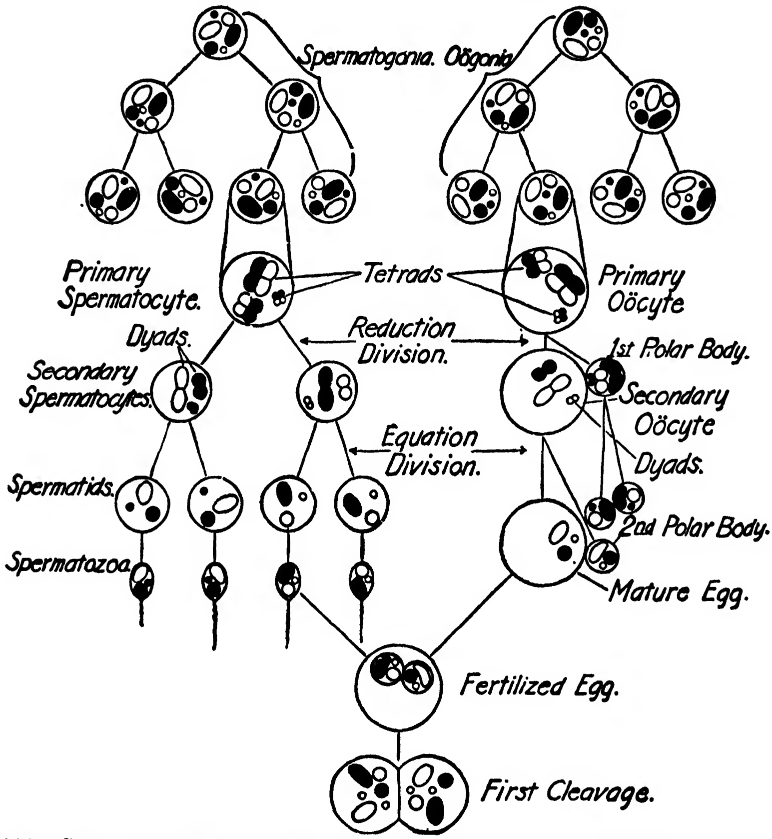


Fig. 164.—Spermatogenesis and oögenesis diagrammatically represented. The black chromosomes may be assumed to be of paternal origin, the white ones maternal.

alike; the terms paternal and maternal refer only to their source, not to their nature.

The spermatocytes grow considerably in volume, and at the same time their chromosomes come together in pairs. Each pair is composed of one paternal and one maternal chromosome. The pairing is not a purely fortuitous occurrence, for each paternal chromosome meets a particular maternal chromosome. As a result of this union of the chromosomes there are, of course, half as many pairs as there were chromosomes before.

While the chromosomes have been coming together, they may also have become duplicated; that is, each chromosome is in some way converted into two. Each pair thus comes to consist of four half chromosomes, and the quadruple body formed is called a *tetrad.* Owing to its origin, two of the parts of each tetrad are maternal, the other two paternal.

The Divisions in Spermatogenesis.—In the two divisions that follow, the tetrads are divided in two planes, first into double bodies called *dyads*, next into their single components. A spindle is formed on which the tetrads take their place. How the tetrads are divided depends on the way they are placed on the spindle. In some animals the tetrad may be turned so that its maternal half faces one end of the spindle, the paternal half the other end. In other animals the maternal and paternal halves of the tetrad may be turned toward the *sides* of the spindle (Fig. 165). In either position the tetrad is cut in two in such a way that the two parts facing an end of the spindle go to that end in the cell division. In Fig. 164 it is assumed that the tetrads were so placed that the maternal half was separated from the paternal half. It is a matter of chance, however, whether the paternal half is turned toward one end of the spindle or toward the other. It may happen, therefore, that all the paternal dyads go into one cell and all the maternal dyads into the other or, as in the figure, part into one cell and part into the other. The cells produced by this division are called *secondary spermatocytes.*

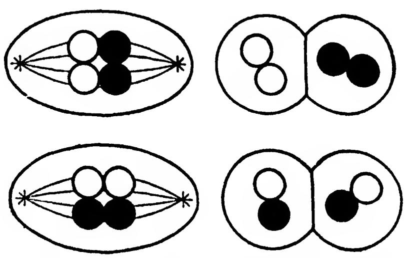


FIG. 165.—The two possible positions of a tetrad on the spindle of the first division in spermatogenesis, and the kinds of cells resulting from them.

It is important to note that in the division just described no chromosome has divided. The tetrads have divided, but merely by the separation of the two chromosomes which had previously come together. Such a division is called a *reduction division*, or *meiosis;*[1] it never occurs in divisions of somatic cells.

The secondary spermatocytes now divide by a mitosis in which the dyads are divided into two components. The resulting cells are called *spermatids.* A given spermatid may contain only paternal chromosomes, or only maternal, or both paternal and maternal in any proportion. The number of these chromosomes is only half that of the original spermatogonium.

[1] The term meiosis is sometimes applied to the whole process of spermatogenesis and oögenesis, including both divisions.

By a transformation in shape, the spermatid becomes a mature *spermatozoon.* This cell consists usually of a head and a whiplike tail, but the forms are very different in different animals (Fig. 166). The chromosomes are all contained in the head, the tail being merely a motile organ.

Oögenesis.—The ripening of the female germ cells is in most respects similar to that of the male. The early germ cells or oögonia undergo a period of multiplication in which they divide by ordinary mitosis. Eventually this ordinary division ceases, and the cells are ready to initiate

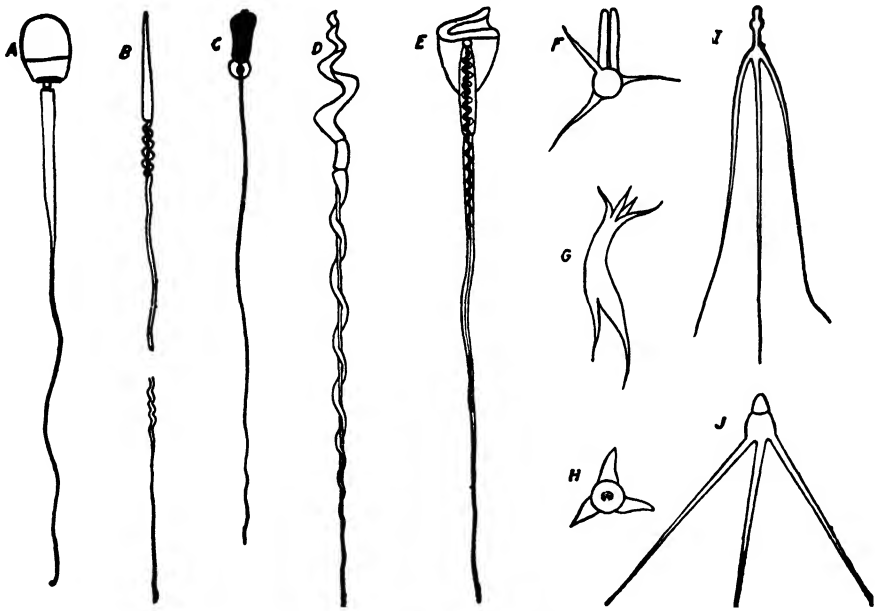


Fig. 166.—Different forms of spermatozoa: *A*, badger; *B*, sheldrake; *C*, sturgeon; *D*, flycatcher; *E*, opossum; *F*, lobster; *G*, crustacean Polyphemus; *H*, crab Dromia; *I*, crab Porcellana; *J*, crustacean Ethusa. (*A–D after Ballowitz; F after Herrick; G after Zacharias; H–J after Grobben. From Wilson, "The Cell in Development and Heredity." Courtesy of The Macmillan Company.*)

the maturation process. They are now known as *primary oöcytes.* These oöcytes grow rapidly to many times their original volume, the growth being much greater than in the male.

During growth the chromosomes meet in pairs, each pair, as in the male, being composed of one maternal and one paternal chromosome. Each chromosome may divide or be duplicated as they come together, so that the pair presents a quadruple body, the tetrad.

Divisions in Oögenesis.—These tetrads are divided in the remainder of the process, first into dyads, next into their single components, in a manner strictly comparable to the divisions in the male. When a spindle is formed for the first division, it appears not in the center but near the surface and is placed approximately perpendicular to the surface. The tetrads take their place on this spindle, again with their maternal and paternal halves either toward the ends of the spindle or toward its sides (Fig. 167). What kinds of dyads go into the two daughter cells depends

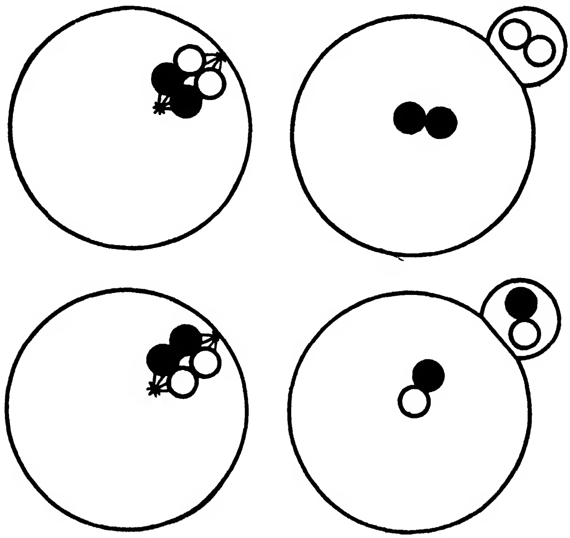


Fig. 167.—Two possible positions of tetrad on spindle of first division in oögenesis, and the kinds of cells resulting from them.

on which of these two positions the tetrads take. In Fig. 164 the tetrads are assumed to have been turned with their maternal half toward one end of the spindle, the paternal half toward the other, so that the first division was a reduction division. Each dyad formed is thus either wholly maternal or wholly paternal, although of the dyads in a given cell some may be paternal, some maternal.

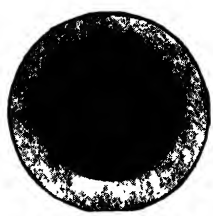


Fig. 168.—Starfish egg with polar body above. (*Courtesy of General Biological Supply House.*)

The two cells are of very unequal size. One contains nearly all the protoplasm of the primary oöcyte, the other very little indeed. The disparity between them is much greater than Fig. 164 indicates; the correct sizes for one animal are shown in Fig. 168. The larger cell is named the *secondary oöcyte*. The smaller cell is never functional and is called the *first polar body* or *first polocyte;* it eventually degenerates.

In most animals only the secondary oöcyte undergoes further division. In some species the first polar body also divides, and, to complete the comparison with the male, this occasional division is represented in Fig. 164, but the resulting two polar bodies are not functional.

The division of the secondary oöcyte involves the division of the dyads into their halves. The division of the cytosome is again very unequal, so that one small cell, the *second polar body* or *second polocyte*, and one large cell are produced. The large cell, unlike the final cells in the male, does not undergo any change of shape; its maturation is finished when the second division is completed, and it is therefore a *mature egg*.

Comparison of Oögenesis and Spermatogenesis.—Comparison of the maturation of spermatozoa with that of eggs reveals that with respect to

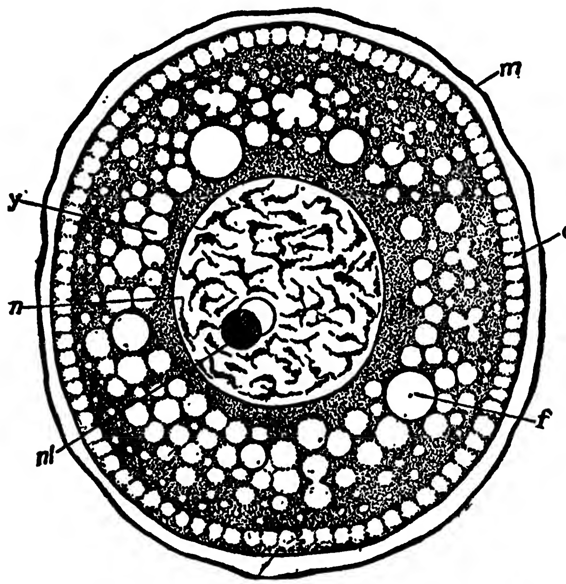


FIG. 169.—Homolecithal egg of the sandworm Nereis. *c*, cytosome; *f*, fat droplets; *m*, egg membrane; *n*, nucleus; *nl*, nucleolus; *y*, yolk spheres. (*After Wilson. Courtesy of The Macmillan Company.*)

the chromosomes the two processes are parallel. The chromosomes unite in pairs and are often at the same time duplicated so as to produce tetrads. Two rapidly succeeding divisions divide the tetrads into dyads and then single chromosomes.

The final cells contain half as many chromosomes as did the reproductive cell before the process began. These chromosomes may be paternal, or maternal, or paternal and maternal mixed in any proportion.

The striking feature in which the processes differ in the two sexes concerns the cytosome. In the female the divisions are very unequal, so that from each original cell there are produced not four functional cells as in the male but only one functional cell and two or three degenerate ones.

The Eggs.—The eggs of animals are typically spherical or nearly so. Often, however, one diameter is much greater than the others, or the egg may be elongated and curved, as in many insects. Internally the substance of the egg is in some way differentiated so that opposite sides or poles do different things. One side is known as the *animal* pole, the opposite side as the *vegetative* pole.

The food, or yolk, stored in an egg may be very meager and is in such instances rather uniformly distributed through the protoplasm. Sea urchins, marine worms (Fig. 169), and mammals have such eggs. In fishes, reptiles, and birds, and less

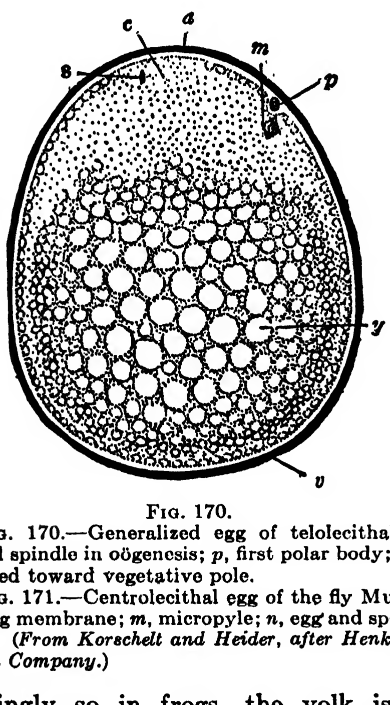


Fig. 170.

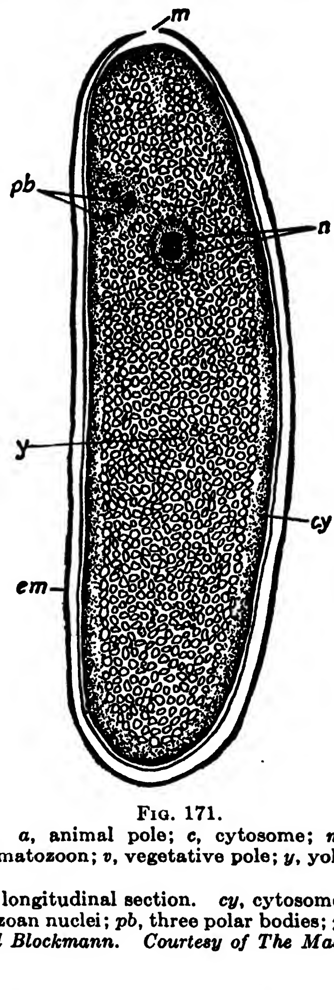


Fig. 171.

Fig. 170.—Generalized egg of telolecithal type. *a*, animal pole; *c*, cytosome; *m*, second spindle in oögenesis; *p*, first polar body; *s*, spermatozoon; *v*, vegetative pole; *y*, yolk crowded toward vegetative pole.

Fig. 171.—Centrolecithal egg of the fly Musca, in longitudinal section. *cy*, cytosome; *em*, egg membrane; *m*, micropyle; *n*, egg and spermatozoan nuclei; *pb*, three polar bodies; *y*, yolk. (*From Korschelt and Heider, after Henking and Blockmann. Courtesy of The Macmillan Company.*)

strikingly so in frogs, the yolk is crowded toward the vegetative pole, so that most of the protoplasm is at the animal pole (Fig. 170). In insects the yolk is in the central part, with a principal layer of protoplasm at the surface (Fig. 171). Eggs with little yolk are said to be *alecithal* or, from the uniform distribution of the yolk, *homolecithal.* Eggs with much yolk aggregated toward the vegetative pole are *telolecithal;* those with the yolk in central position, the protoplasm in a surface layer, are *centrolecithal.*

Eggs are very often enclosed in a membrane or shell, particularly among species that lay their eggs on land where evaporation must be retarded. These envelopes may be of a chitinous nature, as among insects, or composed of keratin which resembles chitin, or they may be impregnated with calcium salts. The shell of the egg of the domestic fowl is composed of three layers. The inner layer is composed of limy particles with conical faces pointing inward. These particles do not fit closely, and air may pass between them. Outside this layer is a compact sheet of calcareous strands which also permits the slow passage of gases. On the outer surface of the shell is a third layer, the cuticle, which appears to be structureless except that it is penetrated by pores. Within the shell is a membrane consisting of two layers of fibers crossing one another in various directions. The envelope as a whole is calculated to prevent excessive evaporation, and yet it permits the passage of gases necessary for the respiration of the egg and embryo. Indeed, air begins to penetrate the shell soon after the egg is laid and accumulates in a space between the two layers of the membrane within the shell at the large end of the egg.

Time and Mechanism of Fertilization.—Eggs and spermatozoa are brought together in fertilization by breeding behavior or some sort of affinity, as described in the preceding chapters. The time of their union, particularly in relation to the stage of oögenesis, is very variable.

In *Ascaris megalocephala,* a roundworm parasitic in the intestine of the horse, the spermatozoon enters the oöcyte about the time of the formation of the spindle of the first division. It remains in the oöcyte during the succeeding divisions. In the frog, rabbit, and some others the spermatozoon enters after the first polocyte is formed but before the second. In the sea urchin the spermatozoon does not enter until after both divisions.

In eggs having a shell at the time of fertilization, there is an opening through which the spermatozoon enters (Fig. 171*m*). In naked eggs, the spermatozoon may enter anywhere. Usually only one male cell penetrates an egg. Some change of a chemical or physical nature takes place in the protoplasm of the egg when a spermatozoon unites with it, such that no other spermatozoa can be drawn in. When by accident two or more spermatozoa gain entrance at the same time, abnormalities of development are likely to occur. However, in some animals numerous spermatozoa regularly enter the egg; but the nucleus of only one of them unites with the egg nucleus.

Cleavage.—Shortly after fertilization, within a time measured by minutes or hours in most animals, the fertilized egg begins to divide. This division, which is repeated in rapid succession until the egg is converted into many cells, is called *cleavage* or *segmentation.* In the following account of cleavage the egg may be likened to the earth with its two poles, so that a plane passing through the animal and vegetative poles may be spoken of as *meridional,* other planes as *equatorial* or parallel to the plane of the equator.

In alecithal eggs the early cleavage is very regular (Fig. 172, above). The first cleavage plane is meridional, passing through both animal and vegetative poles and dividing the egg into two approximately equal cells.

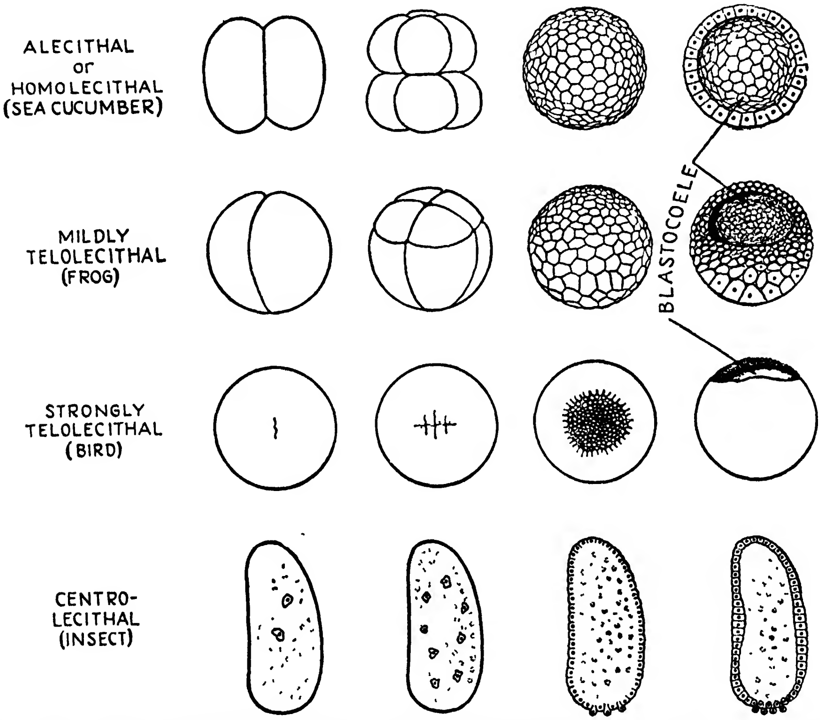


FIG. 172.—Cleavage of eggs, in relation to the amount and distribution of the yolk in them.

The second cleavage is also meridional and perpendicular to the first plane; four cells are thereby produced. The third cleavage is nearly equatorial, resulting in eight cells.

After the third cleavage there are two or more cleavage planes at the same time. The fourth cleavage passes through two planes, both of them meridional, and perpendicular to one another. The 16 cells thus formed then divide into 32, and so on. Up to the 32-cell stage, in such an egg, the divisions usually take place at the same time in all the cells; but irregularities occur later, and some cells divide earlier and more rapidly than others. By this cleavage the single cell (fertilized egg) is converted into hundreds of cells forming a nearly spherical mass, with a liquid-filled cavity in the interior. The whole embryo is now designated a *blastula,* the cavity within it the *blastocoele.*

In telolecithal eggs, cleavage is considerably modified. In general, the third cleavage is elevated toward the animal pole, so that the upper quartet of cells is smaller than the lower. Also the divisions occur earlier and require less time near the animal pole than at the vegetative pole, with the consequence that the smallness of the upper cells is accentuated. In some way connected with this difference between the poles, the blastocoele is eccentric in position, nearer the animal pole. All these features are shown in the frog cleavage (Fig. 172, second row).

In fishes, reptiles, and birds there is so little protoplasm in the yolk-laden vegetative part of the egg that no cleavage occurs there at any stage. Only the cap of protoplasm above the yolk segments and the blastocoele is bounded by a layer of cells above and by undivided yolk below (Fig. 172, third row). In the bird egg in the figure the animal pole is in the center of the first three illustrations, but at the top in the fourth.

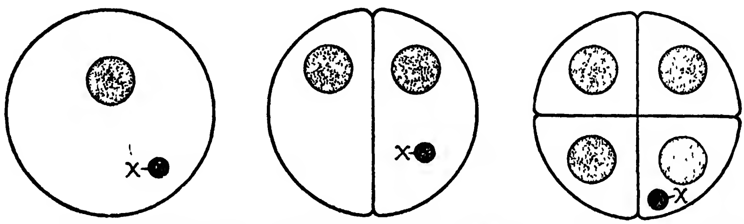


FIG. 173.—Cleavage in arrowworm Sagitta, showing x body (x), which identifies the germ cells.

In insects, cleavage is limited to the surface of the egg, where most of its protoplasm is located. A layer of cells is formed there (Fig. 172, below), while in the interior of the egg is undivided yolk. There is no hollow interior corresponding to the blastocoele at this stage in the insect egg.

First Differentiation during Cleavage.—Later stages of embryonic development are replete with differentiations of cells. Far in advance of them is a most important differentiation, that between sterile cells which go to form the body (*somatic* cells) and those which retain their reproductive powers and give rise to the germ cells. In some animals this distinction arises during cleavage, even in very early cleavage.

In the arrowworm Sagitta the egg contains a small object, the *x body,* which in the first six divisions goes undivided into one of the cells (Fig. 173). Thus in the 64-cell stage only 1 cell contains an x body. This is the forerunner of all the germ cells, the other 63 are somatic cells. After the sixth cleavage, the x body divides at each cell division, and every germ cell contains it.

In *Ascaris megalocephala* (page 200) the first distinguishing mark of somatic cells is their early division. In the second cleavage of the fertilized egg, one cell divides earlier than the other. Thus in Fig. 174*A*, *B* the left cell is ahead of the right in division, and it gives rise in later cleavages only to somatic (sterile) cells. The cell which lags behind gives rise to both somatic and germ cells. As the 4 cells derived from this cleavage begin to divide to produce 8 cells, a second mark of somatic cells becomes evident (Fig. 174*C*). The middle portion of each of their chromosomes breaks up into many small pieces, which continue

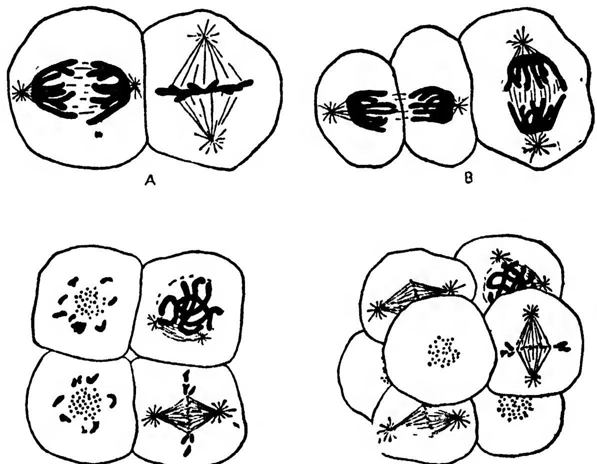


Fig. 174.—Cleavage of the fertilized egg in *Ascaris megalocephala*, showing distinction of somatic and germ cells. *A*, second cleavage, in which cell on left, in more advanced stage of division, is somatic; *B*, later stage of second cleavage, with cells in same relative positions and same relative states of advancement; *C*, third cleavage, with chromosomes of three cells (somatic) fragmenting and losing their ends, those of the fourth remaining intact; *D*, fourth cleavage, with chromosomes fragmented in six cells (one hidden), becoming fragmented in one (middle right), and remaining intact in one (upper right). All germ cells are descended from the last-named cell. (*Schematized from account by Fogg in Journal of Morphology and Physiology.*)

as chromosomes, while the ends of the original long chromosomes are thrown off into the surrounding protoplasm where they degenerate. Three of the 4 cells lose chromatin in this way, and all these give rise later only to somatic cells, while the one which retains its chromosomes intact (upper right in *C*) produces both germ and somatic cells. In each of the next two cleavages, in one of the cells that had retained whole chromosomes, these chromosomes break up into small fragments and lose their ends in the cytosome (*D*). Thus at the 32-cell stage there is only 1 cell with long chromosomes like those of the fertilized egg. In subsequent divisions of this cell there is no further loss of chromatin, and all its descendants become germ cells. The other 31 cells have fragmented chromosomes, and all their descendants are somatic cells.

In insects the germ cells usually either are larger (Fig. 175) or contain certain granules not found in somatic cells. In vertebrate animals the distinction between somatic and germ cells is not recognizable until a much later stage. In the embryos of a number of forms the germ cells are found as large cells in the lining of the digestive tract (Fig. 176), whence they migrate up through the mesentery and out to the place where the gonads subsequently develop. Whether germ and somatic cells have existed as distinct entities through the earlier embryonic stages is not known.

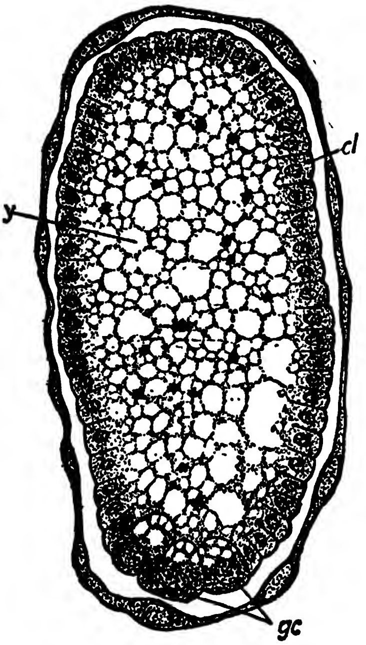


FIG. 175.—Early recognition of germ cells (*gc*) in the development of the egg of the fly Miastor, showing also the cleavage cells (*cl*) at the periphery and the yolk globules (*y*). (*After Hegner in Journal of Morphology.*)

Gastrulation.—When the blastula is well formed, it is converted into a two-layered embryo. The process by which this conversion is effected, already briefly outlined in Chap. 6, is called *gastrulation.* The simplest form of invagination takes place in those animals whose eggs have a small amount of yolk evenly distributed, that is, in alecithal or homolecithal eggs. In these the vegetative side of the blastula becomes flattened, then inturned (*invaginated*) (Fig. 177, above). The invagination proceeds until the inturned cells are in contact with the opposite side of the blastula wall. The embryo now has two layers of cells, an outer or *ectoderm* and an inner or *endoderm.* The blastocoele has been obliterated, but a new cavity, the *archenteron,* lies within the endoderm. This cavity has been pushed in from the outside, with which it is still connected by a small opening called the *blastopore.* The two-layered embryo of this stage is known as a *gastrula.* The endoderm of the gastrula becomes the lining layer of cells of the digestive tract of the adult.

The blastula produced from a mildly telolecithal egg could not well be invaginated directly from the vegetative side by flattening and infolding, because the layer of cells there is so thick. In such a blastula the invagination begins about midway between the animal and vegetative poles, where the cell layer is thinner (Fig. 177, below). It is mostly the cells above the blastopore which are invaginated, though there is some withdrawal of the whole yolk-laden mass of lower cells into the interior. The end result is, as in the alecithal embryo, a two-layered gastrula.

In the frog, whose gastrulation is of this type, the invagination appears from the exterior as in Fig. 178. The cells are inturned along a short crescent-shaped line, which becomes extended into a marked U, and finally completes a circle which diminishes in size to a mere pore as the yolk-filled cells are withdrawn inside.

Gastrulation in strongly telolecithal embryos, like those of birds, reptiles and most fishes, is so modified as to require an interpretation of events too difficult for presentation here. In insects there is an infolding which is usually called gastrulation, but the tissue turned in

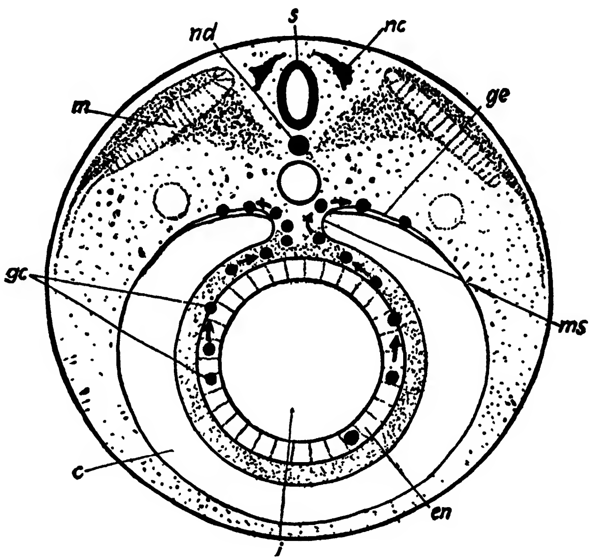


FIG. 176.—Earliest recognition of the distinction between somatic and germ cells in a vertebrate animal. Diagram of cross section of the body of the embryo, showing germ cells in the endoderm of the intestine and their path of migration (shown by arrows) to the site of the reproductive organs. How much earlier than this stage the somatic cells have lost their reproductive powers is not known. *c*, coelom; *en*, endoderm of intestine; *gc*, germ cells; *ge*, germinal epithelium which later covers the gonads and from which the germ cells issue; *i*, intestine; *m*, myotome, or muscle segment; *ms*, mesentery; *nc*, neural crest, from which nerves and ganglia develop; *nd*, notochord, forerunner of the backbone; *s*, spinal cord.

becomes not just the lining of the digestive tract but the whole internal structure of the body. These two types are omitted from the comparisons in Fig. 177.

Mesoderm Formation.—At the end of gastrulation at least two layers of cells, ectoderm and endoderm, are present. In most multicellular animals a third layer, the *mesoderm*, if not already present is soon formed between these two. In the fishlike amphioxus, a classical form in biology, the upper portions of the endoderm (Fig. 179) are turned outward in the form of grooves, shown dotted in cross section in the illustration (*A*). The edges of each groove meet and fuse, and the groove now in the form of a tube is completely separated from the endoderm (*B*). The two tubes thus formed are the mesoderm, and the slender openings in them constitute the body cavity, or *coelom*. In later stages of development the tubes expand, as in *C*, shown black. One side becomes a thin layer of cells applied to the digestive tract, while the other side lines the inside of the ectoderm.

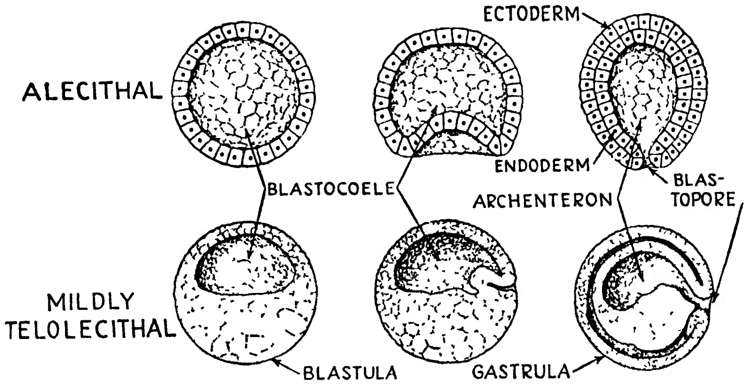


FIG 177.—Gastrulation of embryos, in relation to the quantity and distribution of yolk in them.

In the frog the mesoderm is formed simultaneously with the endoderm—indeed, almost before endoderm—during gastrulation. The cells which turn in over the dorsal rim of the curved blastopore, in its middle portion, form the mesoderm directly (Fig. 180). A band of these cells migrates forward from the blastopore, above the archenteron, to the front end of the future embryo. In late stages of gastrulation, cells

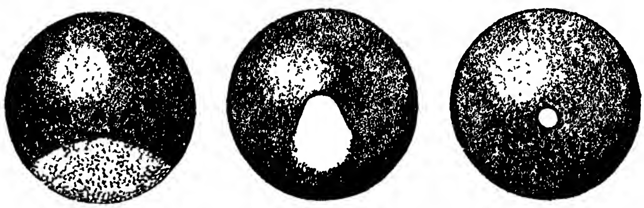


FIG. 178.—Gastrulation in frog, external view.

invaginated at the lower margin of the (now circular) blastopore also contribute to the mesoderm. The endoderm below the main sheet of mesoderm is in the form of an open trough. The upper rims of this trough (*a*) were originally continuous with the edges of the mesoderm, but they break loose and curve up under the mesoderm. They meet at the top, to enclose a tube which becomes the intestinal tract.

Subsequent Development of the Vertebrates.—The three layers of cells, ectoderm, endoderm, and mesoderm, are often called *germ layers.* They are so designated because certain organs are normally derived from each one, so that the layers may be thought of as containing the germs of those organs. They are not irrevocably destined to form these organs, for, as we shall see later, their fate may be experimentally altered in a variety of ways.

From the ectoderm ordinarily arise the epidermis of the skin, reptilian (but not fish) scales, feathers, hair, nails and claws, the nervous system including nerves and their endings, and some glands which discharge at the surface. From the endoderm comes the lining of almost the whole digestive tract and of all the organs which branch off from it, such as the lungs, liver, and pancreas, and of the thyroid gland which, though wholly separate in the adult, is an out-pocketing of the digestive tract

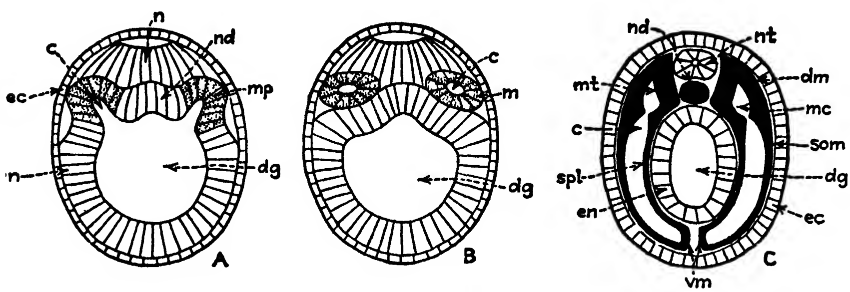


FIG. 179.—Mesoderm formation in the amphioxus, in cross section. *A*, evagination of ridges (dotted) at upper lateral regions of endoderm; *B*, these ridges pinched off as tubes; *C*, mesoderm (black) expanded so as almost to surround the digestive tract; *c*, coelom; *dg*, digestive tract; *dm*, dermatome; *ec*, ectoderm; *en*, endoderm; *m*, mesoderm; *mc*, myocoele; *mp*, mesodermal pouch; *mt*, myotome; *n*, neural plate; *nd*, notochord; *nt*, neural tube; *som*, somatic layer of mesoderm; *spl*, splanchnic layer of mesoderm covering the digestive tract; *vm*, ventral mesentery. (*A and B after Hatschek.*)

in the embryo. From the mesoderm are derived muscle, bone, connective tissue, blood vessels, and the thick inner layer of the skin.

The development of the several organs from the ectoderm and endoderm is in its early stages a bending or folding of these layers, which is called *invagination* or *evagination* according as the sheets of cells are bent into, or out from, some enclosed space. The following account of their origin is limited to the vertebrate animals.

The Early Embryo.—Several of the chief systems of organs are laid down at a very early time. One of the first changes visible externally is the appearance of two prominent ridges, close together, along the dorsal side of the future embryo. These extend lengthwise and are roughly parallel except at the anterior end where they diverge from one another (Fig. 181). In a cross section of the frog these ridges appear as in Fig. 182, *nf*. They are the *neural folds*, the beginning of the central nervous system. Where these folds are near one another, the spinal cord develops; the divergent folds in front form the brain. These ridges approach one another and fuse along their upper surfaces (Fig. 181*B*), cutting off a tube beneath the ectoderm. In longitudinal vertical section at this time, the nervous system appears as in Fig. 183.

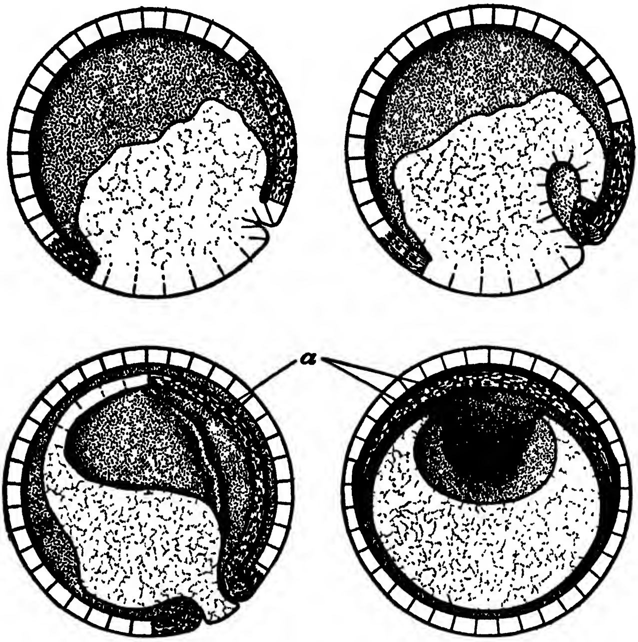


FIG. 180.—Mesoderm formation in frog. First three figures, median sections; last figure, cross section. The line-shaded cells on the outside, as they turn in, become the mesoderm. *a*, edges of trough of archenteron.

Beneath the nervous system a cylindrical rod of cells, the *notochord*, is formed out of the middle portion of the inturned mesoderm. Around it later is formed the backbone. The digestive tract has been present, as the archenteron, ever since gastrulation took place. At first it is usually enlarged in front and narrowed behind. These parts correspond roughly, in the frog, to the stomach and intestine. Posteriorly the intestine opens to the outside through the *anus*, which in some animals is the same opening as the blastopore but in others a passage produced anew after the blastopore has closed.

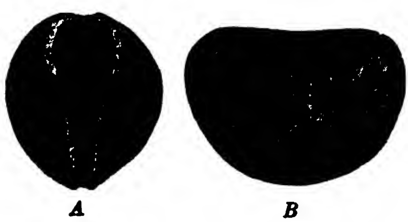


FIG. 181.—Neural folds of frog embryo. *A*, folds still separate, brain above, spinal cord below; *B*, folds fused, producing neural tube beneath surface.

As indicated earlier (page 206) and in Fig. 182, the mesoderm is early divided into two layers, one applied to the inside of the ectoderm, the other covering the endoderm. The peritoneum, which occupies approximately the corresponding positions in later stages, is derived from these layers. Above the endoderm, between it and the notochord, two layers of the mesoderm approach one another and form the mesentery (Fig. 176, page 205) which later suspends the digestive tract in a trough of peritoneum. In the longitudinal section (Fig. 183) the mesoderm is not represented above the digestive tract, since the section passes exactly through the median plane. But below the intestine the mesoderm occurs, divided into its two characteristic layers.

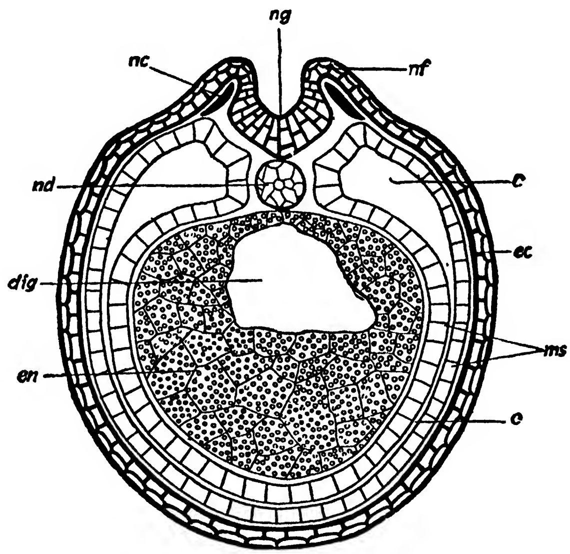


FIG. 182.—Cross section of the early embryo of a frog, diagrammatic. *c*, coelom; *dig*, digestive tract; *ec*, ectoderm; *en*, endoderm; *ms*, mesoderm; *nc*, neural crest; *nd*, notochord; *nf*, neural fold; *ng*, neural groove.

Anterior Digestive Tract.—The *gill pouches*, represented as seen from above in Fig. 184, are evaginations of the endoderm in the sides of the pharynx, or anterior part of the gut. Typically there are five of these protrusions on each side, but some of them are often rudimentary, or two of them may be nearly combined, so that the number frequently appears to be less. Successive stages in the evagination of the gill pouches are shown in *A*, *B*, *C*. They finally reach the ectoderm, with which they fuse. In fishes and usually in amphibians the ectoderm and endoderm both break open at the point of fusion, so that the pharynx is open to the outside. These openings are the *gill clefts*. They serve as channels for the passage of water, which enters at the mouth (not shown in the figure since it is at a lower level). The course of the water is indicated in the figure by arrows. In the fishes and in at least the young stages of amphibians, gills (organs of respiration) are developed upon the tissue (*gill bars*) between the gill clefts.

In the higher vertebrates the gill pouches do not open to the outside at all or do so only temporarily. They are to be regarded as to some extent vestigial organs, an inheritance of an ancestral condition in which functional gills were present. However, some of them are regularly converted during embryonic development into other functional or non-

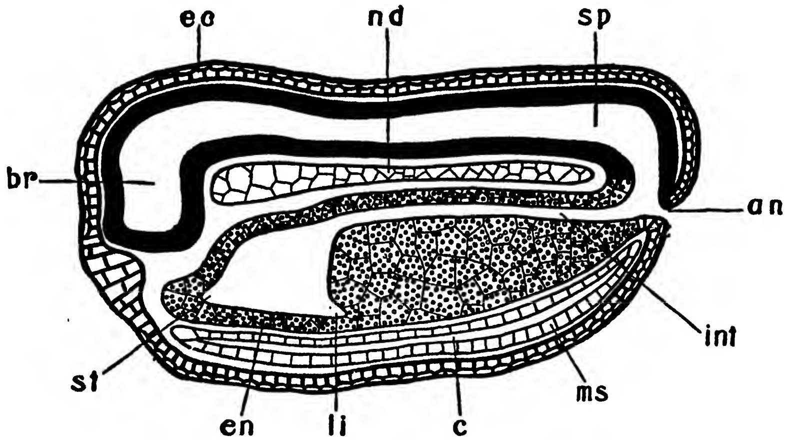


FIG. 183.—Longitudinal section of the early embryo of a frog, diagrammatic. *an*, anus; *br*, brain; *c*, coelom; *ec*, ectoderm; *en*, endoderm; *int*, intestine; *li*, liver; *ms*, mesoderm; *nd*, notochord; *sp*, spinal cord; *st*, stomach.

functional organs. Thus the first pouch becomes part of the Eustachian tube and middle ear. Certain of the bars share in the production of the tonsils, the thymus, and the parathyroid glands.

The *mouth* starts as an invagination of the ectoderm from the outside, as in Fig. 185*m*. For a time it is separated from the rest of the digestive system by a membrane composed of an outer layer of ectoderm and an inner layer of endoderm. This membrane later breaks, and part of the fore end of the gut is incorporated in the mouth cavity. That part of the mouth derived from the external invagination is of course lined with ectoderm.

Outgrowths of the Digestive Tract.—The *liver* appears at an early stage as an evagination from the lower side of the intestine just behind the stomach. In the frog the liver is present shortly after the fusion of the neural folds (see Fig. 183, *li*). An early indication of the liver is also shown in Fig. 185, *li*. This pouch grows in extent and soon becomes branched. One branch at the posterior side of the liver forms the gall bladder (*gb*). The rest are bound together by mesodermal tissue which collects about them, forming part of the body of the liver. The undivided basal portion of the original pouch remains as the *bile duct* (*bd*), through which the secretions of the liver are conveyed into the intestine. During all this development the liver has been covered by the layer of peritoneum (mesodermal) which invests the entire digestive tract. The adult liver is thus covered by peritoneum and suspended by mesenteries formed from the same layers of mesoderm.

The *pancreas* originates from two pouches evaginated from the intestine (Fig. 185). One arises from the dorsal side of the intestine nearly opposite the liver (*dp*); the other springs from the angle between the liver

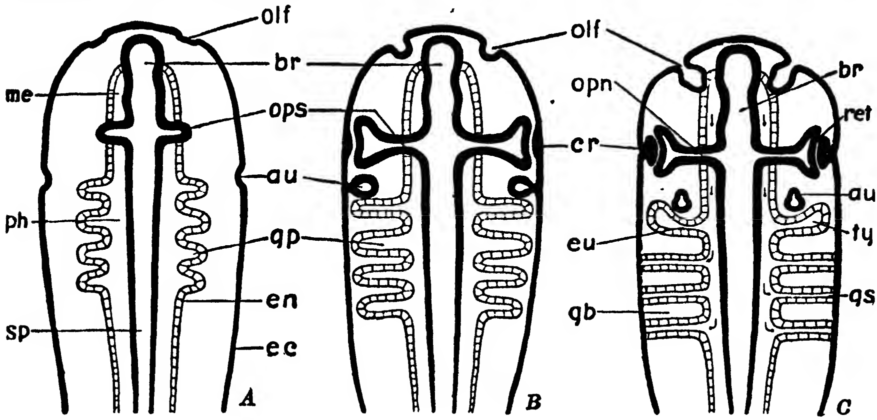


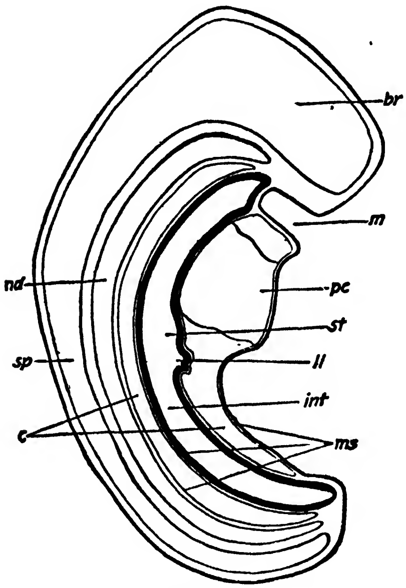
FIG. 184.—Diagrams showing the early development of some of the organs of vertebrate animals, as seen in section from above. The stages here shown are not contemporaneous in all cases. *A, B, C,* successive stages; *au,* auditory vesicle; *br,* brain; *cr,* crystalline lens; *ec,* ectoderm; *en,* endoderm; *eu,* Eustachian tube; *gb,* gill bar; *gp,* gill pouch; *gs,* gill slit or cleft; *me,* endodermal portion of mouth; *olf,* olfactory pit; *opn,* optic nerve; *ops,* optic stalk; *ph,* pharynx; *ret,* retina; *sp,* spinal cord; *ty,* tympanum or middle ear. Arrows in *C* denote current of water through mouth, pharynx, and gill slits.

and the intestine (*vp*). The two pouches intertwine their branches to form the pancreas, which is likewise invested with peritoneum.

The *lungs* take their origin from a protrusion from the ventral side of the gut some distance in front of the stomach (Fig. 185, *lg*). This pouch is at first single (Fig. 186*A*), but soon divides into two parts (*B, C, D*). As these grow in size they become branched. The undivided stalk of the lung rudiment is the *trachea,* the two principal branches are the *bronchi,* and the finer divisions are the air passages and alveoli within the lungs. Mesoderm is constantly pushed before the growing lung rudiments, so that the adult lungs are invested with a peritoneum. Other mesodermal tissue is incorporated in the lungs among the air passages, where blood vessels are abundantly developed.

It should be borne in mind that Fig. 185 is diagrammatic and does not represent a condition prevailing at any one time in embryonic development. For the sake of compactness, organs have been shown in the same figure in stages which do not occur simultaneously.

Nervous System.—It has already been pointed out, and shown in Figs. 182 and 183, that the early central nervous system is a tube formed by the fusion of two folds or ridges of the ectoderm. This tube is wide in the anterior region, where it forms the brain, and narrow posteriorly, where it produces the spinal cord. The thickening and folding of the walls of this tube,



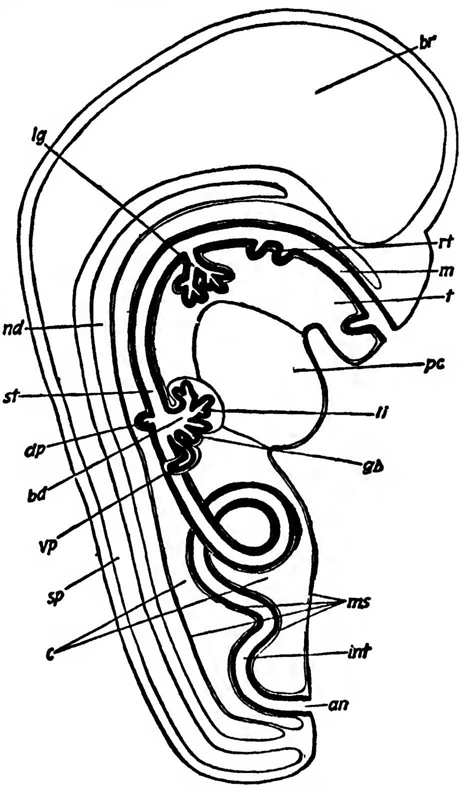


FIG. 185.—Diagram representing the development of some of the organs of vertebrate animals, early and later stages. The figures are a trifle to one side of the median plane. The stages shown are not necessarily contemporaneous. *an*, anus; *bd*, bile duct; *br*, brain; *c*, coelom; *dp*, dorsal rudiment of pancreas; *gb*, gall bladder; *int*, intestine; *lg*, lung; *li*, liver; *m*, mouth; *ms*, mesoderm; *nd*, notochord; *pc*, pericardial chamber; *rt*, root of tongue; *sp*, spinal cord; *st*, stomach; *t*, tongue; *vp*, ventral rudiment of pancreas.

especially in the formation of the lobes and cavities of the brain, are very complicated processes.

The nerves extending from the spinal cord take their origin in part from the *neural crests*. These crests are masses of cells budded off from the inner surface of the ectoderm at or near the region of the neural folds, as indicated in the cross section of the frog (Fig. 182, *nc*) and in Fig. 176.

As was pointed out in Chap. 13, the large nerves arising from the spinal cord are connected with the cord by two roots. The dorsal root is composed of afferent fibers and the ventral root of efferent fibers. The dorsal root is enlarged to form a *ganglion*.

The dorsal ganglion is in each nerve developed from one of the neural crests. The dorsal root is completed by processes of nerve cells growing inward from the neural crest and entering the dorsal part of the spinal cord, and by other processes growing outward from the same cells in the neural crest toward the periphery of the body, forming the afferent part of the spinal nerve. The ventral root fibers grow out from the ventral part of the spinal cord and join the fibers of the dorsal root at a point beyond the ganglion. The nerve fibers from these two roots remain distinct from one another but are enclosed in the same connective tissue coverings.

Sense Organs.—The principal sense organs are developed either as outgrowths from the central nervous system or as ingrowths, chiefly from the ectoderm, which come secondarily into connection with the nervous

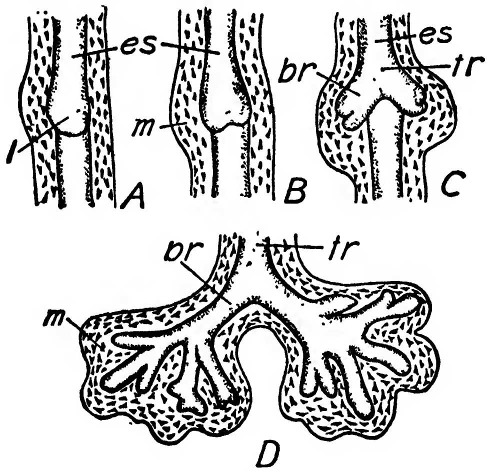


FIG. 186.—Successive stages in the development of the lungs. The esophagus is shown in *A*, *B*, and *C*, but not in *D*. As the lungs grow the mesoderm is pushed before them and thus comes to invest the adult lungs and to make part of the lung tissue. *br*, bronchus; *es*, esophagus; *l*, lung; *m*, mesoderm; *tr*, trachea.

system, or by a combination of these two modes of origin. The *eye* begins as an evagination from the side of the brain (Fig. 184*A*). This protrusion elongates and at the same time expands at its outer end into a hollow bulb. The bulblike expansion flattens on its outer side and is then invaginated to form a double-walled cup resembling a gastrula (Fig. 184*B*, *C*). The inner layer of this cup becomes the visual part of the *retina*, and the basal stalk on which the cup rests is the *optic nerve*. When the outgrowth from the brain comes near the ectoderm, the latter thickens and later invaginates, finally pinching off a rounded mass of cells (*B*, *C*). This mass becomes the *crystalline lens* of the eye. The ectoderm at the point where the lens was formed becomes transparent and with additions from the mesoderm in most vertebrates forms the *cornea*. The rest of the eye, including its muscles, is derived from the mesoderm.

The *ear* begins its development in the surface ectoderm, not, as does the eye, from the central nervous system. A patch of ectoderm on each side of the head region thickens and then invaginates (Fig. 184*A*), producing a pear-shaped vesicle. The vesicle is pinched off from the ectoderm and comes to lie within. It changes its shape, producing the characteristic semicircular canals and the (sometimes) coiled body of the inner division of the ear. Nerve cells growing out from the ganglion of the eighth (auditory) nerve join the vesicle with the brain.

The middle ear, which contains the bones of the ear, is derived at least in part from the first gill pouch (Fig. 184*A*, *B*, *C*). In the distal portion of this pouch the ear bones are developed out of mesoderm, while its connection with the digestive system, as already stated, forms the *Eustachian tube* which connects the middle ear with the pharynx.

The *olfactory organ*, like the ear, is at first a patch of thickened ectoderm on each side of the head far to the front. This ectoderm invaginates (Fig. 184, *olf*), but unlike the ear the pit thus formed does not close; it remains open to the outside as the *nostril*. The pit enlarges and protrudes inward to meet the front end of the digestive tract just behind the ectodermal part of the mouth. An opening is subsequently formed at this point of contact, and the nostril is thus connected with the deeper portion of the mouth cavity. Only certain parts of the ectoderm that forms the olfactory cavity become sensory. From these parts nerve processes grow toward the brain, thus forming the olfactory nerve.

Metamorphosis.—Besides the usual course of development, which is in large measure the same for all vertebrate animals, some members of that group undergo an additional series of changes called *metamorphosis*. Animals that metamorphose are born or hatched with one or more organs which they will not possess as adults, or lacking organs that will be developed before they become adult. It is the process of losing the larval organs and of gaining the missing adult organs which is called metamorphosis.

The transformation of a tadpole into a frog (Fig. 187) or toad is the classical example. The readily visible changes are the degeneration of the so-called "sucker" or attaching organ beneath the head; the development of the legs; and the absorption of the tail, the material of which is probably used elsewhere for growth. The external gills, hidden under a fold of skin called the *operculum*, disappear early, to be replaced by internal gills which are developed on the endodermal lining of the gill slits. The internal gills are lost later, and their function served by lungs, which have all the while been developing. The jaws are provided with a horny armature, serving as teeth, but these are shed and the mouth increases greatly in size. The intestine, from the early tadpole stage a very long and much coiled tube, is greatly shortened.

Other kinds of animals undergo metamorphosis, notably among the insects. In some kinds the changes are very small from stage to stage, as in the bugs (Fig. 188). These sucking insects shed their skins periodically as they grow, and at each change they are a little more like the adult. At the very beginning, however, they are easily recognized as bugs. Such a series of changes is scarcely metamorphosis at all but is usually

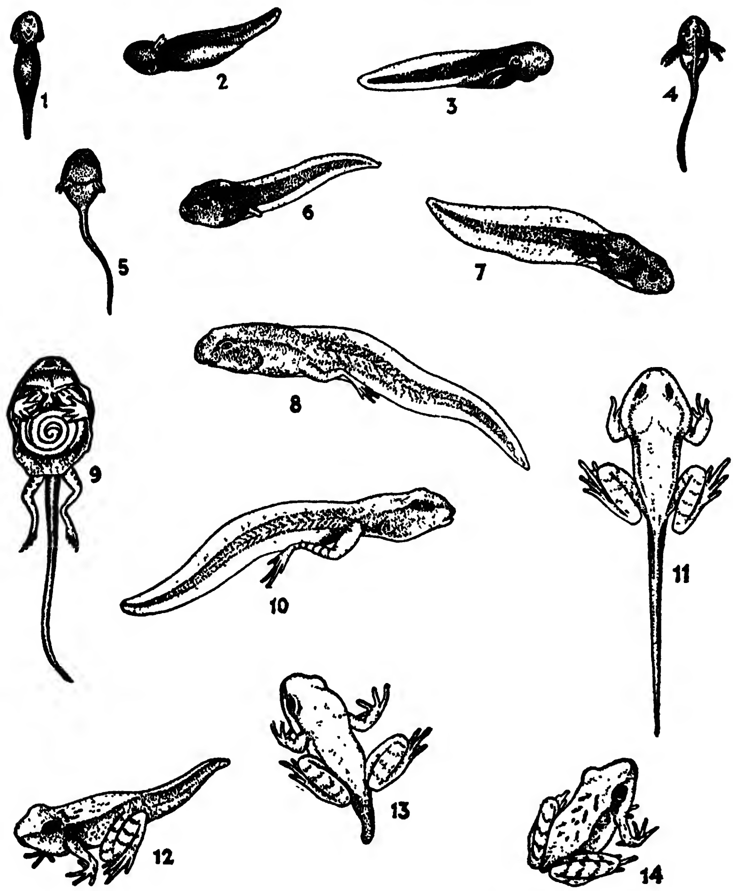


FIG. 187.—Metamorphosis of frog. 1–4, growth of gills; 5–6, covering of gills by operculum, degeneration of sucker; 7–10, growth of legs (9 shows greatly elongated intestine); 11, fore legs pushed through operculum; 12–14, degeneration of tail. (*Rearranged from Newman, "Outlines of General Zoology," by permission of The Macmillan Company.*)

called *incomplete* metamorphosis. Contrasted with this gradual transformation is the very marked one which flies, butterflies, bees, and beetles experience. In the flies (Fig. 189) the larva is a legless wormlike animal called a maggot. This changes, in a very brief operation, into a quiescent nonfeeding form, the *pupa*. After a definite (usually short) time there bursts from the pupa shell the adult insect. The development of the adult occurs gradually enough within the pupa, but the emergence of the fly is sudden. These marked and more sudden modifications make up *complete* metamorphosis.

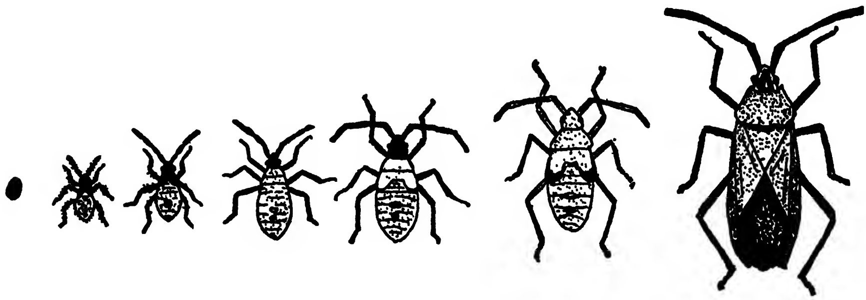


Fig. 188.—Incomplete metamorphosis of a bug. The most easily recognized change is the gradual growth of the wings. (*From Frost, "General Entomology."*)

Problems of Development.—The question naturally arises, how are all these complicated developmental changes brought about? This is the general problem which experimental embryologists have set themselves. Some progress in solving it has been made, but much remains to be done. The knowledge already gained has to do with such questions as why the embryo is placed in a given position in the seemingly indifferent material of the fertilized egg; how a structure is stimulated to develop, and how it is guided so as to acquire its characteristic form; the time at which the fate of any bit of tissue is settled, and whether the decision at that time is final or revocable; whether development is a sorting out and the loss of capacities, or a gain of new ones; the importance of the mere position of a

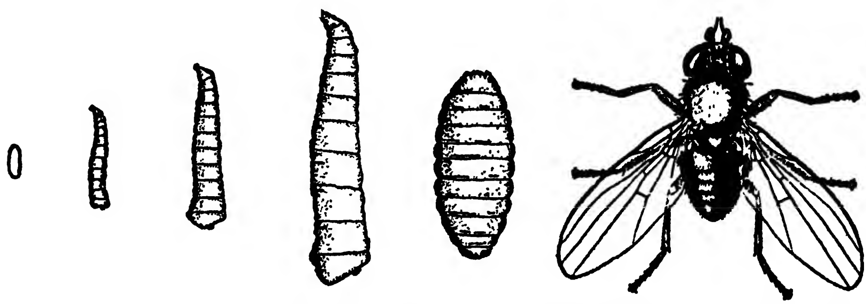


Fig. 189.—Complete metamorphosis of a fly. The successive stages shown are the larva. pupa and adult. (*From Frost, "General Entomology."*)

piece of tissue in the embryo, in deciding what it shall become; whether a tissue is passively moved about by some force, or actively assists in the change; whether the agencies which direct development reside within the cells, or impose their control from the outside; and the duration of any influence in relation to the period within which it can normally be effective. Some of these topics will be considered in connection with concrete illustrations.

Orientation of Embryo.—The higher animals are all bilaterally symmetrical; yet they all develop from an egg which is apparently radial. The animal pole is differentiated from the vegetative, and it is clear why development should commence in the animal portion. But so far as can be seen in an unfertilized egg, the head of the embryo might be turned toward any point in the circumference of the circle of which the animal pole is the center. What decides the position which it actually does take?

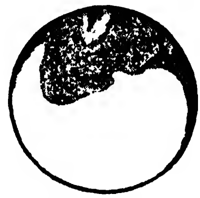


FIG. 190.—Section through frog's egg, in plane of first cleavage, showing at right the path of entering spermatozoon. (*Modified from Schultze.*)

In the frog, the median plane of the future animal is fixed by the point of entrance of the spermatozoon in fertilization (Fig. 190). The first cleavage of the egg passes through that point and also through the animal pole and vegetative pole. Up to the time of fertilization, any plane passing through the two poles may become the plane of symmetry. In some of the salamanders either the first or the second cleavage plane may become the median plane, and the entrance of the spermatozoon has nothing to do with fixing the positions of these planes. In fishes, sea urchins, and some other animals there is no connection between the early cleavages and later symmetry, and in them it is unknown how the median plane is determined.

After the position of the embryo is fixed, all later questions of orientation are settled in relation to it. When, by artificial methods, a second embryo is made to develop at the surface of the same egg, it is roughly parallel with the first, with its head pointing in the same direction. A patch of ectoderm in which gills would normally develop at its anterior margin may be cut out, turned halfway around, and made to grow in place. The gills still grow in the anterior portion, but this was originally the posterior part. Also, if the regenerating stumps of cutoff arm and leg rudiments be removed and their positions exchanged in transplantation, the anterior one becomes an arm, the posterior one a leg, which is the reverse of their normal fate.

Some biologists have suggested that a gradient of some sort is set up at the first orientation of the embryo. Perhaps a chemical substance occurs in gradually less and less concentration from front to back, or a physical phenomenon becomes less and less intense in that direction, and the position of structures is governed by this gradient. Little is known, however, that would establish this supposition.

Principle of Determination.—Another important question is why different parts of an embryo produce different structures. In the majority of animals there is no fundamental difference between the cells of different regions. For example, the cells of a sea urchin embryo, in the two- or four- or eight-cell stage, may be separated from one another, and each becomes a complete, though small, larva. If left in contact with the other cells, each cell would have produced only certain parts of a single animal, but it obviously has the capacity to produce all of it. In a few animals, however, the cells are in some respect different, for, if the cleavage cells are separated, each one gives rise only to a fraction of a larva. Animals of the former type are said to have *indeterminate* development, the latter kind *determinate* development.

The cells of indeterminate embryos take on their specific destinies at a much later time. This has been most completely shown for some of the salamanders. If, at a time shortly after gastrulation begins, bits of tissue are transposed, a group of cells that would normally become nervous system exchanging places with a group that would become epidermis, the fate of each is altered. The would-be part of a nervous system becomes epidermis, the prospective epidermis becomes nervous system. The exchange of regenerating stumps of fore- and hind limbs, described in the preceding section, is a similar example. The interchange of bits of tissue may be made between different species with equal success. One such interspecific exchange was effected between species differing in color, one very light-colored, the other quite dark. The cells retained their color characters but produced strange organs. In one experiment, presumptive brain cells of a dark species were transplanted to the region on a light species where gills develop. Now these species differ not only in color; their gills are of different shapes. The transplanted dark cells, while being converted into gills instead of brain, produced gills of the form characteristic of the dark species. The general fate of the cells may be altered, but their specific performance within the general field remains unchanged.

In all these examples the fate of the transplanted tissues had not yet been determined. For each of them, however, there comes a time after which such reversals of fate are no longer possible. After that time, transplanted parts become what they would have become in their original situation. If, for example, a patch of ectoderm including a portion of the neural folds (a stage shortly after the end of gastrulation) is placed on the side of the body, it becomes nervous system despite its strange location. Something has happened to these cells during the process of gastrulation which has deprived them of the capacity to respond to their position in the embryo and has fixed their fate regardless of location. An area of such determined ectoderm may even be cut out of the embryo and cultivated by itself in a suitable salt solution, and it still develops the sort of organ (nervous system, for example) which it was destined to become.

Organizers.—What induces this change in a tissue, destroying its apparent independence of action, and forcing it into a single further course? It is often some influence coming from other cells near it. In salamander embryos, the cells which roll over the dorsal lip of the blastopore and become the notochord and mesoderm (Fig. 180) exert such an influence. It is because of them that neural folds are produced in the ectoderm above the notochord. The mesoderm cells possess that power of inducing nervous system even before they are invaginated into the gastrula. This is beautifully shown by an experiment. If some cells are removed from the dorsal rim of the blastopore, before they are invaginated, and are inserted among the ectoderm cells of another embryo, at a place where only epidermis would ordinarily develop, they sink below the surface and are covered over by the ectoderm. From that ectoderm an additional nervous system is formed, so that the embryo has two nervous systems (Fig. 191). The transplanted cells would, in their own embryo, have been invaginated to form mesoderm and would have induced a nervous system in the ectoderm above them. That same influence they exerted on the strange ectoderm beneath which they were planted.

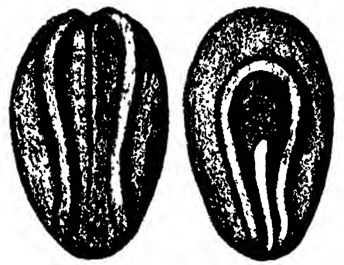


Fig 191.—Development of nervous system in response to transplanted cells. Left, neural fold of salamander, Triton, developing in its normal situation. Right, opposite side of same embryo, with additional neural fold produced because cells from the dorsal lip of the blastopore of another embryo were transplanted in that region. The transplanted cells were from a lighter colored species and form the pale streak in the middle. (*Modified from Spemann.*)

In a similar way, the eye stalk protruding from the side of the brain (Fig. 184), as it approaches the outer ectoderm, stimulates that layer to thicken and invaginate to form the crystalline lens of the eye. In some animals the ectoderm forms a sort of lens without such stimulus, as when the eye stalk is cut off; but the lens is seldom normal unless the optic stalk comes near it.

Something issues from the prospective mesoderm and the eye stalk, in the above examples, which causes the ectoderm to develop a certain structure. This something, whatever it is, has been called an *organizer.*

An important question arises, whether embryonic development is conducted by a series of such organizers, produced in succession in different structures. May one organizer ensure the development of a certain organ, and then a different organizer arise in that organ that would stimulate a third organ, and so on? Some slight indications of such chains may be found, but they are not general. The eye stalk often stimulates a lens, and the lens then helps to bring about the invagination of the optic cup to form the retina. A few other such chains of influences are known. In general, however, the events of *early* embryonic development appear to be more or less independent, though working in harmony. Probably they are helped to keep in the proper order of time by organizers that successively arise.

Nature of Organizers.—These organizers are not specific, not effective merely in their own species, since transplants between species show about the same consequences as those within species. This fact has encouraged a search for the nature of such influences, for the same ones must be fairly general and widespread. Almost certainly organizers are chemical substances. A number of organic acids have been shown to induce certain differentiations. Among them are several of the fatty acids, nucleic acid, and adenylic acid from muscle. There is some indication that the sterols (higher alcohols) have inductive powers. Glycogen is probably in some way connected with the power of induction in salamanders, for while the cells are being rolled over the rim of the blastopore during gastrulation (which is about the time at which these cells first acquire the power to induce nervous system), they rapidly lose their glycogen. What an organizer does to stimulate development, what happens between the stimulus and the response in differentiation, is unknown.

The power of an organizer to induce a certain event usually lasts much longer than there is any need of it in ordinary development. Thus, notochord and mesoderm, taken from embryos in which nervous systems have long since been irrevocably established above them, are still capable of stimulating secondary nervous systems in younger embryos into which they are transplanted. The power of the tissues to respond to organizers is, however, not so persistent. Usually they must be stimulated at about a certain time, or they cannot respond at all.

In general, it may be said that the inherent properties of the tissues to respond by developing are more important than the stimuli received from organizers.

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CHAPTER 17

GENETICS

The object of the study of embryology, as outlined in the preceding chapter, is to discover how animals become what they are. Mere observation shows by what steps the development proceeds, and experiments have revealed some of the physiological principles underlying these events. Embryology discloses these things satisfactorily for the major features of structure which are essentially alike in whole large groups of animals—satisfactorily, that is, if one does not require to know the fundamental causes of the different types and steps of development.

There are, however, many minor features of organization which are just as definitely fixed parts of animals as their digestive and nervous systems are, but which are different in different individuals. Color of eye, shape of hair, dimples, stature, complexion, and talents are different in different people, yet all through their embryonic development it is quite settled what these characters are going to be. No embryologist could tell what the outcome would be in any of these traits in the adult, but the die would have been cast before cleavage of the egg had begun.

These individual differences furnish another way of learning the rules governing the development of characteristics. This method consists of crossing individuals having different traits and observing the occurrence of these different traits among the descendants. This is the method of genetics. It would be impossible to use it to discover much about the structures with which embryology deals, for there is no difference between individuals with respect to the major features. Nevertheless when the mode of inheritance of minor characters has been discovered, it may be taken as certain that the inheritance of the major features follows the same scheme. Genetics uses minor features to discover the principles of heredity, with the conviction that the same principles apply to the major features as well.

Genetics has the further advantage, in the study of origins, that it reveals more fundamental causes. While embryology, when it employs experiment, may reveal physiological processes causing the developmental changes, genetics lays bare to some degree the causes of the physiological processes. It is today one of the biologist's most potent tools in delving into the fundamental nature of living things. Embryology is an aid because it reveals some of the visible mechanism of heredity, particularly in the maturation of the germ cells, but the crossing of unlike individuals demonstrates the nature of much that is invisible.

Modern Genetics.—The story of the Austrian monk Gregor Mendel as the leading figure in the beginnings of modern genetics has been recounted in the opening chapter (page 18). Before going into the details of hereditary transmission, it will be profitable to indicate briefly wherein his ideas of heredity differed from those which preceded him; for it must be remembered that Mendel was not the first student of heredity. Many before him had tried to solve its mysteries, and the mere fact of resemblance between parents and offspring, or even between more distant relatives, had been recognized from time immemorial.

One of the chief distinctions of the Mendelian system was the recognition that offspring do not necessarily inherit any particular character of either parent. Not only do the offspring not have to show such a character in themselves, they may even be quite incapable of transmitting it to subsequent generations. Prior to Mendel's time there had been a prevalent suspicion that any character which appeared in one or more individuals in a given line of descent might be expected at some future time to appear in any branch of their posterity. No one of the descendants was to be regarded as free from the possibility of that character's recurrence. According to this old notion, if in a given line of descent of horses there had once been a chestnut animal, there was a distinct expectation that some time or other the chestnut character would reappear in some individual of any branch of the descending family. According to the Mendelian scheme, it is now clear that this color *may* be bred entirely out of the descendants. It is almost certain to be bred out of some branches of the general relationship and *may* be lost to all of them; and chestnut is no more likely to occur after such elimination than it is in a line which never had a chestnut ancestor. Later we shall see why this is true.

Another distinctive feature of Mendel's contribution to knowledge of heredity was his discovery that characters may be transmitted quite independently of one another. Wing length is one character, eye color another, body color a third, and so on, each having its own inheritance. Because of their separateness, such characters have been spoken of as "unit" characters. Some degree of detachment of traits was, of course, popularly implied when it was pointed out that a child had its mother's eyes, its father's lips, and perhaps its grandfather's wavy hair. But complete scattering of one individual's characters in succeeding generations was not previously thought to take place—certainly not as a regular occurrence. Before Mendel's time there was a strong tendency to think of heredity in terms of the totality of characters exhibited by an individual; by Mendel himself emphasis was put upon the single characters.

Heredity, Mendel concluded, juggles characters, not individuals; it deals with traits, not ancestors and descendants. The complete independence which he supposed characters to have is illustrated by the peas which he studied. He found that shape of pod, color of seed, height of stem, etc., were entirely free to go to the various offspring without reference to the other characters. Thus there arose different combinations of the characters in different plants. One would have constricted pods, green seeds, and tall stems; another inflated pods, green seeds, and dwarf stems; a third constricted pods, yellow seeds, and dwarf stems; and so on. This freedom of assortment proved later, in heredity in general, to be less than Mendel supposed, but it is very widespread.

Mechanism of Heredity.—How heredity operates will be more easily understood if its mechanism is known. Inherited characters are represented in the cells of an organism by minute bodies called *genes*. These genes are located in the chromosomes and are demonstrated in some animals and plants to be in a row, from one end of the chromosome to the other. There are two genes representing each character in each cell, one of them derived from the mother, the other from the father. These two genes must, from their source, be in two different chromosomes, one of which has come from the individual's mother, the other from its father. The genes in one of these chromosomes all relate to the same characters as do the genes in the other chromosome. Two of the chromosomes in the cells of the vinegar fly Drosophila are diagrammatically shown in Fig. 192. Two chromosomes having corresponding genes, as these do, are said to be homologous with one another (see page 252 for homology). The genes in them are likewise homologous; the gene for yellow body is homologous with the gene for gray body, white eye with red eye, complete eye with bar eye, and so on.

All the chromosomes in a cell are members of such homologous pairs. One chromosome of each pair has come from the mother, the other from the father. The two homologous chromosomes come together in a pair in the oöcytes and spermatocytes early in the maturation of the germ cells, as in Fig. 164. In the reduction division they are separated again, one going to each of the cells produced by that division. Since the genes are in the chromosomes, the two homologous genes of every pair part company at the reduction division, one gene going to each of the cells produced. At the end of maturation in the male, each spermatozoon contains one gene of every pair, never both of any of them. In the female, each mature egg contains one gene of every kind, never both. Polar bodies receive their share of the genes, but these genes are lost as the polar bodies degenerate.

As a result of the reduction division, therefore, the mature germ cells have a single set of genes, one of every kind. Body cells, on the contrary, have a double set, two genes for each character. When egg and spermatozoon unite in fertilization, the zygote receives a double set of genes, and these are handed on as a double set to all the cells of the body of the individual produced from that zygote. With this understanding of the mechanism of heredity we may now turn to some concrete examples of its operation.

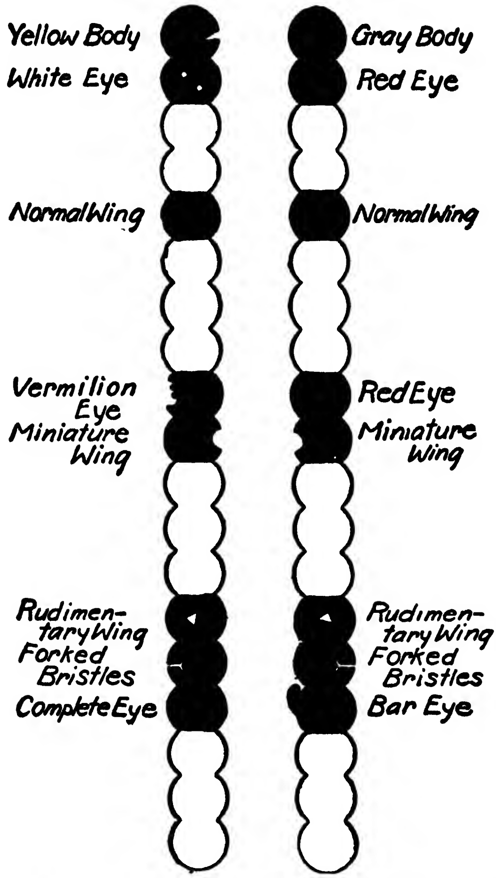

FIG. 192.—Diagrams of two homologous chromosomes of the vinegar fly Drosophila. Some of the genes are represented, and are in their proper order through the length of the chromosome. Homologous genes are located at the same level in the two chromosomes.

Simple Inheritance.—Among guinea pigs there are different color varieties which breed true so long as animals of the same color are mated with one another. One of these true-breeding strains is black (Fig. 193), another one is albino or white, from the absence of all of the ordinary pigments in skin and hair and the iris of the eyes. If a black animal is mated with a white one, the offspring are all black. This result is described by saying that black is *dominant*, white *recessive*. The hybrid generation is known as the F_1 generation (abbreviated from the words *first filial*). The white coat is not lost in the F_1 animals, however, for when they are mated together they produce an F_2 (*second filial*) generation consisting of some blacks and some whites. In a large collection

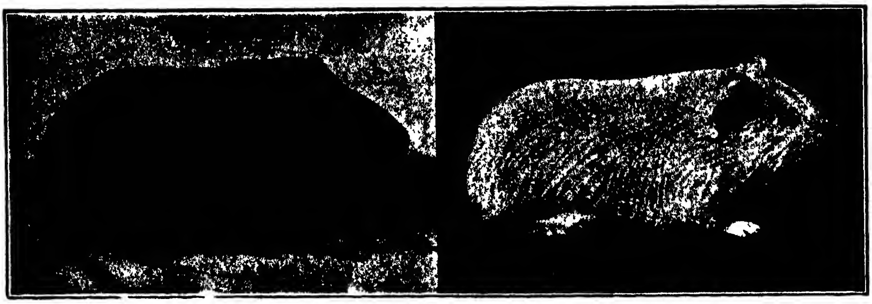

FIG. 193.—Black and white guinea pigs, with smooth coats. (*Courtesy of Professor W. E. Castle and the Harvard University Press.*)

of such F_2 families the black animals are found to make up about three-fourths of the total number, the whites about one-fourth.

These results are explained by the diagram in Fig. 194, where the genes involved are symbolized by letters—the white gene by *w*, the black gene by *W*. The two letters under each parent are its genetic formula, the single letter under these the formula of the germ cells of that parent. The F_1 generation has the formula *Ww*, and the animals are black because one gene *W* is capable of producing black pigment just as well as two *W*'s are. That ability of one gene to do the work of two is what is called dominance; *W* has that ability, *w* does not.

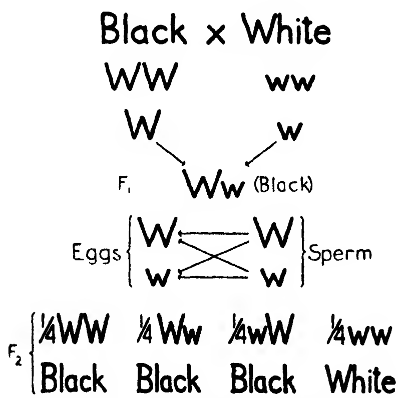

FIG. 194.—Inheritance of black and white color in guinea pigs: *W*, gene for black; *w*, gene for white.

When the reduction division occurs in F_1 animals, two kinds of germ cells are produced because the two genes are different. Some eggs and spermatozoa contain *W*, some contain *w*; and the numbers of the two kinds are about equal. When two kinds of eggs, equally numerous, are fertilized at random by two kinds of spermatozoa, equally numerous, four combinations result, also about equally numerous. These combinations are *WW*, *Ww*, *wW*, and *ww*, as shown in the F_2 line of the figure. The first three of these are black, the last one white—hence the 3:1 ratio of blacks and whites. The two middle formulas are identical, and would ordinarily be written the same way; they are written in opposite orders here merely to show that the gene which came from the egg in one came from the spermatozoon in the other.

Choice of the letters *W* and *w* to represent this particular pair of genes is in accord with a generally accepted convention that the name of the newer character should suggest the symbol. Without much doubt there were colored guinea pigs before there were white ones, hence white is the newer color. In accord with another convention the small letter is used for the recessive gene, the capital for the dominant.

To describe other types of matings, it is desirable to provide names for certain of the genetically different types of individuals. An organism whose two genes for any particular character are alike (*WW* or *ww*) is called a *homozygote;* one whose genes are different (*Ww*) is a *heterozygote.* The same animal may be, and usually is, homozygous for some genes, heterozygous for others.

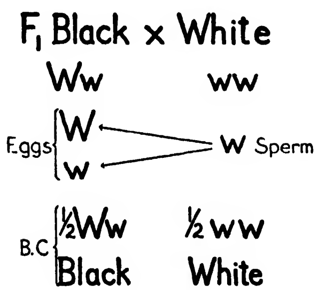

FIG. 195

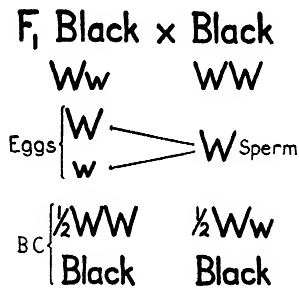

FIG. 196

FIG. 195.—Backcross of a heterozygous black guinea pig with a white animal.

FIG. 196.—Backcross of a heterozygous black guinea pig with a homozygous black animal.

Backcross.—Not always do experiments proceed from an F_1 generation to an F_2. A very useful kind of cross is that between an F_1 animal and another like one of its parents. Such a cross is a *backcross.* Essentially it is a mating of a heterozygote with a homozygote. Such a cross might well be made between a heterozygous F_1 black guinea pig and a white one exactly like the white parent. Figure 195 shows what happens when that is done. The heterozygous parent produces two kinds of eggs, in equal numbers, the white parent only one kind of spermatozoon (*w*). Consequently there are two kinds of offspring, heterozygous black (*Ww*) and white (*ww*) in equal numbers.

The backcross may also be made between an F_1 and the black parental type, as in Fig. 196. There are two kinds of offspring as before, with respect to their formulas; but they all look alike (black). The difference between these two backcrosses is that one was made to the recessive parental type, the other to the dominant type. The former cross is made often, the latter seldom because its two kinds of offspring cannot be distinguished.

Two Pairs of Characters.—Since every animal possesses probably thousands of different kinds of genes, any mating between individuals serves as a test of the mode of inheritance of any or all characters in which the two individuals differ. The experimenter may center his attention on as many or as few of these as he wishes. For most purposes, the smaller the number of characters studied simultaneously the better, for the interpretations are clearer. No more than two pairs of characters will be used in this book. For an example, we may add another pair of characters in guinea pigs to the black-white contrast already presented.

Ordinary guinea pigs have smooth coats of hair, since the individual hairs all slope in the same general direction in any part of the skin.

FIG. 197.—Two guinea pigs with rough coats. The hairs are in many places arranged in whorls, sloping away from the central point. (*Courtesy of Professor W. E. Castle and the Harvard University Press.*)

One variety, however, has a rough coat because, at a number of places on the body, the hairs slope outward in all directions from a central point like the radiating spokes of a wheel. These hairs push against other hairs sloping in other directions, producing an unkempt appearance (Fig. 197). Rough and smooth coat could be used in a single-pair cross, in which case rough would appear in F_1, and the F_2 would be three-fourths rough, one-fourth smooth. That is, rough is dominant.

The two pairs of characters, hair slope and color, can be combined in four ways, namely, rough black, rough white (these two in Fig. 197), smooth black, and smooth white (Fig. 193). To test the inheritance of the two pairs of characters simultaneously, the animals crossed must differ in both of them. Suppose one of the original parents is rough black, the other smooth white. The F_1 generation is rough black, since these are the two dominant characters. When these hybrids, which are heterozygous for both pairs of genes, produce their germ cells, the genes of each pair separate from one another in the reduction division and go to different cells. The two pairs undergo this separation independently, for they are in different pairs of chromosomes. As a result of this independent distribution, four kinds of germ cells are produced, *RW*, *Rw*, *rW*, and *rw*. There are these four kinds of eggs, about equally numerous, and the same four kinds of spermatozoa, equally numerous. In fertilization, random unions take place between each kind of egg and each kind of spermatozoon—16 combinations all told.

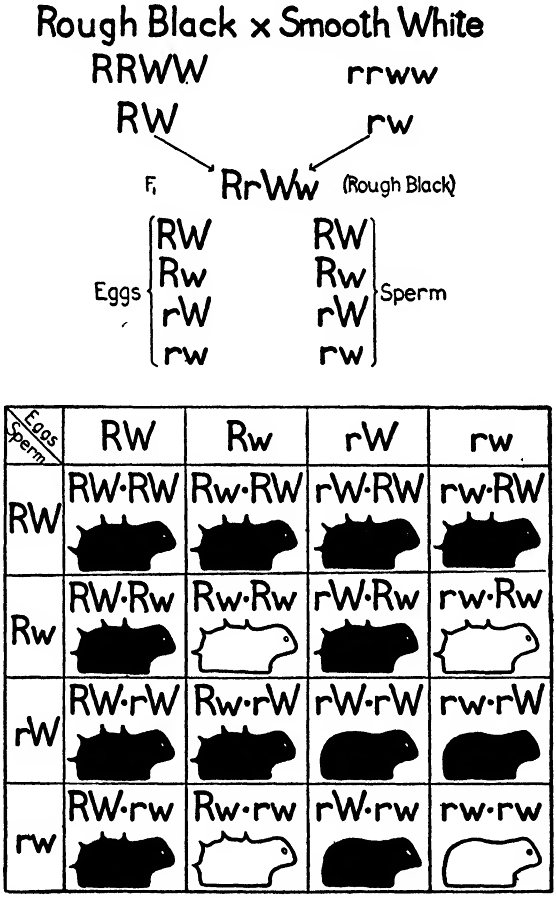

FIG. 198.—Inheritance of two pairs of independent characters in guinea pigs, black and white color, rough and smooth coat. The points on the backs of the animals indicate rough coat.

To write these 16 combinations in the F_2 generation without omission or duplication, it is convenient to use the Punnett square, so named from the English geneticist who devised it. Such a square is included in Fig. 198, which explains this cross. Each egg formula is written four times, in one of the columns of four spaces down the chart. They are put there to be fertilized by the four different kinds of spermatozoa.

Then each sperm formula is written four times in one of the rows of spaces across the chart. In each space are the genes found in one of the sixteen kinds of F_2 animals. They are written in the chart with the genes from the egg separated by a dot from the genes from the spermatozoon; but in other situations it is preferable to write the two genes of one pair together, followed by the genes of the other pair. Some of the sixteen formulas are identical with others, but they have been arrived at in sixteen different ways.

It remains only to indicate the appearance of the guinea pigs having these genes. The little figures accompanying the gene formulas are intended to do this. Nine of the sixteen are rough black, three rough white, three smooth black, and one smooth white. It should be remembered that these numbers are a ratio, 9:3:3:1, not absolute numbers. They are so many sixteenths of the total number in F_2. In a single litter the least frequent kind (smooth white, the double recessive) could easily be missing.

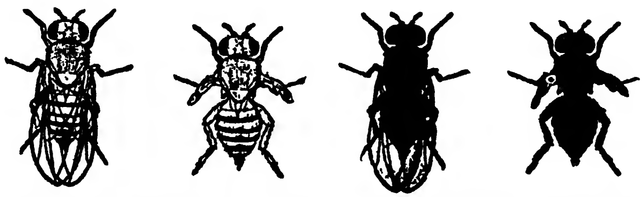

FIG. 199.—Gray and ebony body and long and vestigial wings in Drosophila, combined in the four possible ways.

A Two-pair Backcross.—As a basis of judgment of certain phenomena to be described later, a backcross involving two independent pairs of characters will be useful. The characters chosen for illustration are the color of the body and the shape and size of the wings of the fly Drosophila. The body is normally of a brownish gray, but there is a very dark variety known as ebony. The wings are ordinarily long and lie flat over the back of the fly when at rest; but in one variation of them, called vestigial, the wings are small and crumpled and project obliquely outward from the body. The vestigial wing is useless for flight; flies with such wings merely crawl or jump.

The four combinations into which these characters may enter are shown in Fig. 199. Suppose that the cross be made between a gray long-winged fly and an ebony vestigial-winged one. The F_1 generation is gray and long-winged, for these are the dominant characters of the two pairs. If these F_1 flies, which are heterozygous for both pairs of genes, are mated with ebony vestigial flies, which are necessarily homozygous for the two recessive genes, all four of the kinds of flies illustrated in Fig. 199 are produced. Moreover, they are about equally numerous;

about one-fourth of the backcross family are of each of these kinds. Figure 200 gives the explanation. The four kinds of eggs produced by the F_1 flies are about equally numerous because the two pairs of genes are distributed at random in the reduction divisions of their germ cells. Whatever ratio exists among these eggs must also prevail among the backcross offspring produced from them—hence the equal numbers of the four kinds of flies in that generation.

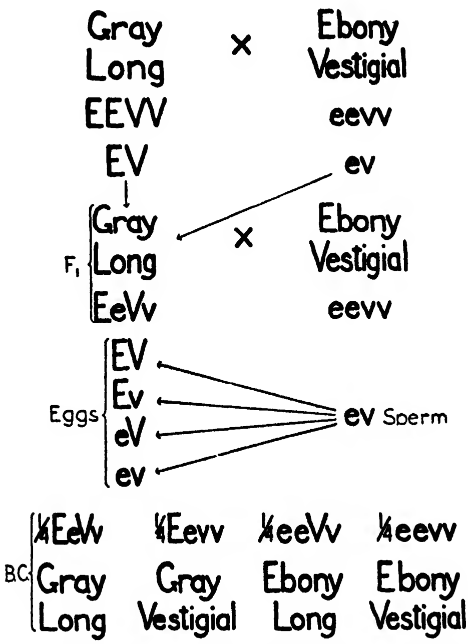

FIG. 200.—Inheritance of two pairs of characters in a mating between a double heterozygote and a double recessive. The characters are gray and ebony body and long and vestigial wing in Drosophila.

Interactions of Genes.—The two pairs of genes studied in guinea pigs, and the two in Drosophila, appear to be entirely independent of each other in the production of their characters. An animal with gene *W* is black, regardless of the slope of its hair; and one whose formula is *rr* is smooth, no matter whether it is white or black. A long-winged fly may be either ebony or gray, and an ebony fly either long- or vestigial-winged. Very often, however, the action of one gene is modified by some other specific gene if they are both present in the same individual. A striking example is found in the combs of fowls. When a pea-combed fowl (Fig. 201, upper left) is crossed with a single-combed one (lower right), their offspring are pea-combed, and the F_2 generation is three-fourths pea and one-fourth single. These results indicate that pea comb and single comb differ in just one pair of genes, with pea dominant. In like manner it is shown that rose comb (upper right) is dominant over single and differs from single by just one pair of genes.

What should be expected, then, if fowls showing the two dominant characters pea and rose, respectively, are crossed? No one could predict the result; it has to be determined by experiment. The hybrid proved to have a large rounded comb overhanging the base of the beak, as in the center of Fig. 201. From its shape this comb is called walnut. A clue to the nature of this remarkable character is obtained by breeding some of the F_1 walnut fowls together. They yield four kinds of offspring

Fig. 201.—Interaction of genes for combs in fowls. The gene for pea comb (upper left) interacts with that for rose comb (upper right) to produce walnut comb (center). Two of these F_1 walnut-combed fowls, bred together, produce four types of offspring. Single comb (lower right) is produced when neither the pea gene nor the rose gene is present. (*Rearranged from Punnett, "Mendelism." Courtesy of The Macmillan Company.*)

walnut, pea, rose, and single (lower row, Fig. 201). Very significantly, the ratio of these four types is 9:3:3:1 in the order named and pictured. This ratio indicates that two pairs of genes are involved. The pea-combed fowl must have had the formula *PPrr*, the rose-combed one *ppRR*, in which *P* is the gene for pea comb, *p* for no pea, *R* for rose comb, *r* for no rose. Single, which is "no pea" and "no rose," is *pprr*. The student is encouraged to work out the gene explanation for the F_1 and F_2 generations; any individual possessing both dominant genes *P* and *R* will have a walnut comb. Whatever effect these genes have, singly, on the physiology of comb development, together they interact to produce a very different effect.

Many other examples of interaction of genes belonging to different pairs have been discovered. Sometimes the relation is such that one of the genes in question cannot produce a visible result unless the other gene is present. Sometimes one gene suppresses the action of a gene of some other pair. Sometimes two genes, neither of which produces anything detectable by itself, combine to produce a visible result when they occur together in the same animal. When the interactions are between dominant genes, they result in F_2 ratios which are some modification of the fundamental ratio 9:3:3:1. This ratio is changed because two or more of the classes of individuals *appear* alike. To describe details of such interactions would go beyond the scope of a first study. The complexity is considerably increased by interactions among three, four, or five different genes. So many examples of combined actions have been found that it seems probable that they are universal. That is, every gene probably interacts with some—even many, or all—other genes. The phenomena of heredity *can* be very complicated.

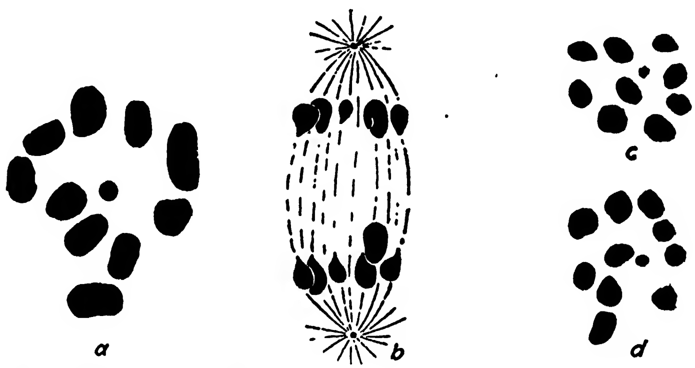

FIG. 202.—The divisions of the male germ cells of the bug Anasa: *a*, polar view of equatorial plate of first division; all the chromatic bodies are double except one and therefore represent 21 chromosomes, the somatic number; *b*, second division in side view, not all of the chromosomes shown; the single chromosome of *a* is going undivided to the lower pole; *c* and *d*, polar view of the two anaphase groups of the second division; 11 chromosomes go into one spermatid (female-producing), 10 into the other (male-producing). (*After Wilson in Journal of Experimental Zoology.*)

Inheritance of Sex.—A special genetic situation exists in the distinction between the sexes, for in a large number of animals and some plants the chromosomes of the male and female are in some respect unequal. Either one sex has one more chromosome than the other, or one of its chromosomes is larger than the corresponding chromosome of the other, or certain corresponding chromosomes are of different shapes. When the *number* of chromosomes is different, most species of animals have more in the female than in the male. An example of this condition is found in a species of bug whose chromosomes are shown in Fig. 202. The male has 21 chromosomes, the female 22. The figure shows the reduction division of the spermatocytes of the male. At the left (*a*) are the pairs of chromosomes, mostly so closely united that their double nature is not revealed. At the bottom of *a*, outside the circle of other chromosomes, is the odd chromosome not paired with any other. This unmated chromosome is called an X chromosome. In the division which follows (*b*), the paired chromosomes separate (not all of them are shown), while the X chromosome goes undivided to one end of the spindle (the lower end in Fig. 202). The two cells thus formed (*c* and *d*) have 10 and 11 chromosomes, respectively. These two numbers of chromosomes go into the final spermatozoa, so that there are two kinds of spermatozoa, one with 11 chromosomes (including an X), the other with 10 (without an X).

Now, the female of this species has 22 chromosomes, two of which are X chromosomes identical in composition with the one X of the male. Her eggs ripen in typical fashion, and every egg has 11 chromosomes, including one X. When an egg is fertilized by a spermatozoon containing an X chromosome, the fertilized egg has 22 chromosomes, two of which are X's, and it develops into a female. If an egg is fertilized by a spermatozoon without an X chromosome, the fertilized egg has only one X (21 chromosomes all told), and it becomes a male.

Whether there is a definite gene, or perhaps several genes, for sex in the X chromosome is not yet certain. They are in any case not the sole determiners of sex, for in Drosophila the other chromosomes contain genes modifying sex.

Sex-linkage.—If, in species in which the two sexes have unlike chromosome groups, there are genes for other characters in the chromosomes that are chiefly associated with sex, it is obvious that these characters will be differently inherited in the males and females. When the female has two X chromosomes, and the male only one X chromosome without any mate, any genes contained in the X chromosome will come to the male from only one parent (his mother), while the female will receive them from both parents. Furthermore, such genes even if recessive will produce their character in the male, because there is no other gene of the same pair to be dominant over it. The same situation exists in species in which the *number* of chromosomes is the same in both sexes, but the shape or physiological properties of one of them are different. In such species the male possesses what is called a Y chromosome corresponding to one of the X's of the female; that is, the male is XY, the female XX. The Y chromosome possesses few known genes and with respect to most characters might as well be absent.

Characters whose genes are in the X chromosome are said to be *sex-linked*. How sex-linked characters are inherited is shown in Fig. 203 which illustrates Drosophila in which the males have the XY constitution. The Y chromosome in this fly is shaped somewhat like a letter J. The character involved is white eye as contrasted with red. In the first cross (left) the female is white-eyed (*ww*), the male red-eyed (*W*). The female produces only one kind of egg (*w*); but the male, because of his Y chromosome which lacks any gene of this pair, produces two kinds of spermatozoa, one having the X chromosome (with *w*), the other the Y chromosome. The two combinations of eggs and spermatozoa produce the two sexes, respectively, of the F_1 generation. The males of this generation are white-eyed because there is no red gene (*W*) to dominate over their white gene. In the F_2 generation, as the figure shows, there are four combinations, two of which are red, two white. The marks of sex-linkage in this cross are (1) that the F_1 generation is of two kinds,

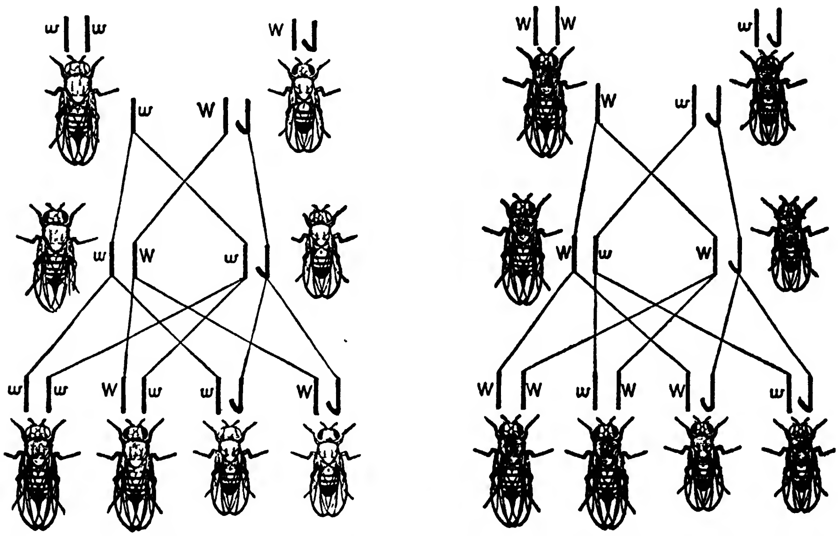

FIG. 203.—Sex linkage of eye color in Drosophila. Left, white-eyed female × red-eyed male. Right, the reciprocal cross. (*Modified from Morgan, Sturtevant, Muller, and Bridges, "Mechanism of Mendelian Heredity," Henry Holt and Company, Inc.*)

instead of only the dominant type, and (2) that the F_2 ratio of dominant to recessive is 1:1 instead of 3:1.

If the cross is made with the red eyes in the female and white eyes in the male, the results shown are as indicated at the right in Fig. 203. The F_1 males get their eye color gene from their mother as before but now are red-eyed, as are also the heterozygous F_1 females. In the F_2 generation there are again four combinations. Three of these are red-eyed; hence the F_2 ratio is 3 red: 1 white. However, the white-eyed F_2 flies are all males. This last feature is the only sign, when the cross is made this way, that the character being studied is sex-linked.

Any animal or plant whose sex is determined by chromosomes, and in which, as a consequence of this chromosome relation, the male produces two kinds of spermatozoa, may be expected to show sex-linkage of the kind just illustrated. Man is one of these animals. A modified form of this same phenomenon is found in birds, butterflies, and moths, for in these groups the sex-determining chromosomes are so arranged that the female produces two kinds of eggs and the male only one kind of spermatozoon. The distribution of the sex-linked genes in these animals is precisely like that in Drosophila except that the sexes are reversed. What is true of the male in Drosophila is true of the female in birds, for example. An opportunity to work out the situation in birds is afforded by one of the problems at the end of the chapter.

Autosomal Linkage.—The chromosomes other than X and Y are known as *autosomes*. When two genes for different characters are located in the same autosome, they have a strong tendency to remain together for a while, going to the same germ cells. How many successive generations they stay together depends on how far apart the genes are in the chromosome. The chromosomes break more or less at random and homologous chromosomes recombine their pieces in new ways. If the breakage occurs between two pairs of genes, the genes enter into new combinations. The genes which had been going to the same germ cells now go to different germ cells. Naturally the farther apart they are, the more often the breaks occur between them.

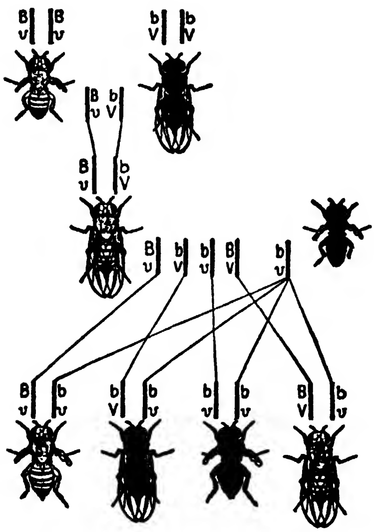

Fig. 204.—Linkage of body color and wing length in Drosophila. Left, above, gray vestigial-winged male; right, black long-winged female. (*From Morgan, "Physical Basis of Heredity," J. B. Lippincott Company.*)

Linkage operates to distort the expected ratios of different kinds of individuals. This effect is illustrated in Fig. 204. The two pairs of genes involved are *v* (vestigial wing) contrasted with *V* (long wing), and *b* (black body) as against *B* (gray). The chromosome composition of the two flies is shown at the top of the illustration. The chromosomes in their respective germ cells are pictured between the parents, and the F_1 female fly below. This F_1 fly is heterozygous for both color and wing length and affords an opportunity to discover the breakage of the chromosomes. It produces four kinds of eggs, as shown at its right. The first two of these (*Bv* and *bV*) are produced if the two pairs of genes are not separated; and the genes are néar enough together so that this happens in about 83 per cent of all cells. In the other 17 per cent the two pairs of genes are separated by breakage of the chromosomes, resulting in the other two kinds of eggs (*bv* and *BV*). The F_1 female is represented as mated to a black vestigial male, whose spermatozoa are necessarily *bv*. These spermatozoa fertilize the four kinds of eggs and produce four kinds of offspring which should be in the same proportion as the kinds of eggs. The first two kinds (gray vestigial and black long) together make up about 83 per cent of the family just as the *Bv* and *bV* eggs made 83 per cent of the eggs. The other two classes (black vestigial and gray long), coming from eggs containing broken and recombined chromosomes, constitute about 17 per cent. If these two pair of genes had been in different pairs of chromosomes and so had been independent of one another, the last generation would have exhibited a 1:1:1:1 ratio, each kind making about one-fourth of the total, as in the two pairs of characters in Fig. 200. The distorted ratio is the evidence that the genes are all in one pair of chromosomes.

Mendel's Law; Mendelian Heredity.—Gregor Mendel never stated his discoveries in the form of a concise principle, but this has been done by others since. Heredity as Mendel conceived it differed in two important respects from heredity as understood by his predecessors. A statement of these two differences is commonly spoken of as Mendel's law. Using present terminology, one might state this law as follows. *The genes of any pair separate from each other in the production of the germ cells, so that each germ cell receives only one of them; and the distribution of each pair of genes to the germ cells is independent of the distribution of other pairs.* The separation of genes of the same pair is effected by the reduction division in maturation. Independence of the genes of different pairs exists when the pairs of genes are in different pairs of chromosomes, since these pairs of chromosomes are independently placed on the spindle of the reduction division. As is indicated in the preceding section, this latter condition is not always met. Many pairs of genes are in the same pair of chromosomes. Autosomal linkage, which results from this association, is very common. Such linkage is a violation of the second part of Mendel's law. Apparently Mendel never witnessed this relation between any two pairs of genes.

Despite the fact that Mendel's law as stated does not provide for linkage, all the phenomena so far described are still regarded as belonging to Mendelian heredity. The concept of Mendelism has been widened to include them. Any heredity is now considered Mendelian if it is dependent on chromosomes. Most heredity is so dependent. Yet in some plants the plastids go over directly from one generation to the next, and whatever color characters these plastids determine are independent of chromosomal genes. Heredity of plastid colors in such plants is not Mendelian. Possibly, even probably, there are some other structural units which are transmitted directly like plastids.

Since the inheritance of linked characters is still called Mendelian, it would be better if the statement of Mendel's law could also be liberalized. A better formulation would be: *The fundamental units of heredity are distributed by means of the chromosomes.* This would exclude plastids. Also, to understand the law it would be necessary to know a good deal about chromosomes.

The Nature of Genes.—It is practically certain that the genes are chemical substances and that it is through their chemical properties that they control the development of the characters they represent. Presumably they are protein in nature. One reason for considering them protein is that the chromosomes give protein reactions, and the genes make up a fraction of the chromosomes. Moreover, genes are highly specific in their action; that is, they do certain definite things with considerable precision, and not other things. Highly specific reactions are characteristic of proteins in general, which would help to explain the functioning of genes if these be protein.

Moreover, genes are subject to change. Although any mechanism of heredity must have some degree of permanence—otherwise there would be no heredity—genes do not remain forever the same. One of the genes for red eye in Drosophila changed, and the eye color was then brown. A gene for gray body color in the same species changed, and yellow body resulted. A gene for uniform color in mice changed, and the mice in succeeding generations were spotted. Changes of this sort are known as *mutations.* They must be chemical changes of the genes, which would be not only possible but probable if the genes were proteins. The chemical structure of proteins is very complex, and occasional permanent change is more likely in complex substances than in simple ones.

It is a current concept that a gene may be a single protein molecule. One reason for so believing is the suddenness with which gene mutations occur. If a gene were composed of several molecules, any change in chemical structure would presumably, just as a matter of chance, affect only one of them. The argument is that, with a number of molecules to change, mutation might tend to be a gradual process. With only one molecule, any structural change must affect the whole gene at once.

Practical Applications.—Knowledge of heredity has been used for centuries to improve the economic situation of the human race. The classical field in which that has been done is the improvement of crops and farm animals. The knowledge upon which this improvement rested was, until comparatively recent times, little more than a knowledge that heredity existed. Its laws have been fairly well understood by breeders only in the present century, but by the year 1900 most of the development of domestic races had already been accomplished. The reason for this great success of the early breeders is that their method was practically the same as it is at present. That method is selection. Those animals and plants which were most valuable were selected for breeding, in the belief that their good qualities would be transmitted. If even only a few of these characteristics were inherited, long-continued selection would result in great improvement.

The discovery of Mendel's principles thus found mankind already in possession of very valuable varieties of animals and plants. Man had attained this result without knowing very much about how he did it. Improvement has, of course, gone on since then. It is now considerably plainer why certain results are obtained; and these results often come more quickly. Among the important domestic animals, poultry have probably yielded more to the newer Mendelian knowledge than any others. Considerably less has been done with pigs and sheep, and little has been revealed about Mendelian behavior of the valuable characters of cattle and horses. Undoubtedly the cost of experimenting with these larger animals and the long time involved, when one generation requires several years, are responsible for the lag of knowledge concerning their heredity.

Plants have revealed more of their hereditary constitution, partly because they are inexpensive to rear, partly perhaps because they are of simpler composition. The most important feature of most crops is yield, which is inherited, since varieties differ greatly in this respect. The principal factor contributing to yield which is being studied now more successfully than a generation ago is resistance to disease. The various bacterial and fungous diseases of the grains and fruits are receiving concentrated attention at most of the experiment stations, and the results attained are very gratifying.

Room exists for improvement of man himself, through the elimination or diminution of some of his defects. Every system of organs and every sense organ exhibits hereditary deficiencies in some individuals, such as feeble-mindedness, fragility of bones, a tendency to bleed, cataract of the eyes, atrophy of muscles, and baldness. Some of these defects are more important than others, but there is not one which the human race would not choose to banish if it could. The only method is to avoid reproduction by individuals possessing genes for the undesirable qualities. With respect to most defects, this avoidance must be voluntary, and it is uncertain how seriously men and women take their responsibilities. Some of the more serious defects, such as feeble-mindedness and epilepsy, are, however, frequently dealt with by law. At present 29 states of the United States have laws designed to prevent people afflicted with these infirmities from rearing families.

Theoretically, man should be able to improve himself by favoring those qualities, talents of various sorts, which it is particularly desirable to possess. Unfortunately, too little is known of the heredity of these traits to raise the hope that such improvement is imminent. No one as yet knows the formula for the production of genius at will.

Problems

1. A rose-combed fowl (Fig. 201, upper right) mated with a single-combed fowl produces only rose-combed offspring. If many of these offspring are mated together and produce an aggregate of 64 fowls, how many of the latter should be rose-combed?

2. Tall peas are dominant over dwarf peas. What would be the appearance of a plant heterozygous for tall and dwarf? If such a heterozygote were self-fertilized and produced 30 dwarf offspring, how many tall offspring should it yield?

3. Mating a red-eyed and a pink-eyed fly yields red-eyed offspring. If one of these red-eyed offspring is mated with its pink parent, and they produce 60 offspring, how many of these should be red-eyed?

4. Brown color in mice is dominant over albinism. In a given cross between a brown mouse and an albino, 6 of the offspring were brown, 5 albino. What was the formula of the original brown parent?

5. A long-winged fruit fly mated with one having vestigial wings (a recessive character) produced 28 long-winged and 23 vestigial offspring. What were the formulas of the parents? Of their long-winged offspring? Of their vestigial-winged offspring?

6. Snapdragons with bilaterally symmetrical flowers, crossed with plants with radial flowers, produce only bilateral F_1. If an F_1 plant is self-fertilized, what is the chance that one of its offspring selected at random will be radial?

7. Shepherd's-purse with triangular seed capsule is dominant over the variety with spindle-shaped seed capsule. If a homozygous triangular is pollinated from a heterozygous triangular, and 20 offspring are obtained from them, how many of these should have spindle-shaped capsules?

8. Starchy grain is dominant over sugary grain in corn. If, in a cross between these types, 58 of the progeny are sugary, how many of the progeny should be starchy?

9. A certain white-fruited squash, self-fertilized, produced some white and some yellow offspring. If there were 21 yellows, how many white would be expected?

10. Short hair is dominant over long hair in guinea pigs. A short-haired guinea pig, one of whose parents was long-haired, was mated with a long-haired animal. If, blindfolded, you selected one of their litter from the cage, what is the chance you would get a long-haired animal?

11. The offspring of a brown mouse and an albino are all brown. If the heterozygous brown mice are mated together and produce 80 offspring, how many of these should be albino? How many of the brown ones should be heterozygous? How could you tell *which* browns were heterozygous?

12. If gray color in an animal mutates to yellow, and in crosses between stocks of gray and yellow the offspring are yellow, what (according to accepted conventions) would be the symbol for the gray gene? For the yellow?

13. If an animal having the formula *Cc* produces 100 eggs, how many of these eggs should have the formula *C*? How many *c*? How many *Cc*?

14. A family consisting of 17 red-eyed and 15 purple-eyed flies probably came from a mating of parents whose formulas were *P*____ and ____. (Fill the blanks properly.)

15. Applying the conventions relating to choice of symbols for genes, make a number of matings between trotting horses *Pp* × *Pp*, and obtain 24 foals. How many of these should be pacers?

16. If two parents which have the same visible characters produce some offspring which are like the parents, some different, write the formulas of the parents using any symbols you choose.

17. In squashes, white fruit is dominant over yellow. From a certain cross between a white- and a yellow-fruited plant, 54 white and 59 yellow offspring were obtained. What were the formulas of the parents, if squashes were primitively yellow like pumpkins?

18. One flower of a white-fruited squash plant A is pollinated from another white-fruited plant B, and both white and yellow progeny are produced. Another flower of plant A is pollinated from a yellow-fruited plant and produces 44 offspring. How many of these should be white?

19. A third flower of plant A in problem 18 is self-fertilized and produces 44 offspring. How many of these should be white?

20. Two gray female mice are mated with a black male. In several litters the first female produces 12 gray and 10 black offspring, the second female 19 gray. What are the formulas of the two females? Use your knowledge of wild mice in determining part of your answer.

21. Pink eye in mice is recessive to the wild-type dark eye color. From a certain mating between two dark-eyed mice some dark- and some pink-eyed mice are obtained. The male is then mated with a pink-eyed female, and they produce, in several litters, 20 offspring. How many of these should be pink-eyed?

22. Uniform or self-color in mice is dominant over spotting. A self-colored mouse is mated with a spotted mouse, and their self-colored offspring are mated together. All the offspring of these crosses are mated to spotted mice. Assuming all matings to be successful, and the resulting litters of equal size, what fraction of the mice from the last matings should be spotted?

23. Mating a red-eyed fly with curved wings and a claret-eyed fly with straight wings yields an F_1 all red-eyed and straight-winged. If the F_1 flies are bred together and produce 96 offspring, how many of these should be claret-eyed and straight-winged?

24. Frizzled feathers in fowls are turned up at the end, smooth plumage lies down flat. Pea and single combs are illustrated in Fig. 201. If a cross between single smooth and pea frizzled yields pea frizzled, and if these are mated together and produce in the aggregate 48 fowls, how many of these should be single smooth? How many pea frizzled?

25. Self-colored rats (color distributed over the body) are dominant over hooded (color only on head, rest of body white). Albino rat is recessive to gray. Crossing a homozygous gray hooded rat with an albino having a pair of genes for self-color (which, of course, cannot show in an albino) would produce what kind of offspring in F_1? If the F_1 animals were bred together and produced 80 offspring, how many of these should be albino? How many gray hooded?

26. Two walnut-combed fowls, mated together, produce 9 walnut-combed and 3 pea-combed offspring, and no others. Assuming that no class of offspring is missing because of the small numbers, what were the formulas of the parents?

27. In cattle, black (B) is dominant over yellow (b), and polled (P) (hornless) is dominant over horned (p). If several homozygous black horned cows are mated with homozygous yellow hornless bulls, what will be the appearance of their offspring? If these offspring are mated with one another, and in a number of such matings 9 yellow polled animals are produced, how many black polled ones would be expected? How many yellow horned?

28. If a homozygous red mule-footed pig (toes grown together) is mated with a homozygous black normal-toed pig, their offspring are black and mule-footed. If the F_1 animals are crossed with red normal-toed ones and produce 80 offspring, how many of these should be red and normal-toed?

29. Black is dominant over white in sheep, and in certain breeds horns are dominant in males but recessive in females. A homozygous black hornless ewe of one of these breeds is mated with a homozygous white horned ram. If their offspring is female, what will be its appearance? If male, what appearance? If a number of F_1 males and females from such parents are mated together, and produce 32 offspring, equally divided between the sexes, how many of these will be black horned females? How many white horned males?

30. Red eye (B) is dominant over brown (b) in Drosophila, and pigmented ocelli (WO) dominant over white ocelli (wo). A certain brown-eyed fly with pigmented ocelli is mated with one having red eyes and white ocelli, and some of their offspring have brown eyes and white ocelli. What are the formulas of the parents?

31. In Drosophila, gray body is dominant over ebony, and straight wing dominant over curved. A certain gray-bodied curved-winged female is mated to a gray straight-winged male, and they produce some ebony curved offspring. Out of a total of 40 offspring, how many should be ebony straight? How many gray curved?

32. Each cell of the muscles of a certain male bug contains 27 chromosomes. How many chromosomes in its spermatogonia? How many in its mature spermatozoa? How many chromosomes in the body cells of the female of the same species? How many in her mature eggs? How many in fertilized eggs?

33. Can a male Drosophila be homozygous for a sex-linked character? From which parent does a male Drosophila receive his sex-linked genes? To which sex among his offspring does he transmit his sex-linked characters? If a gene were located in his Y chromosome, to what offspring would he transmit it?

34. Color blindness is a sex-linked recessive, and sex in man is determined essentially as in Drosophila. A girl of normal vision whose father was color-blind marries a color-blind man. What is the chance that their first child will be color-blind?

35. A woman of normal vision, whose father was color-blind, marries a man of normal vision whose maternal grandfather was color-blind. Among their three daughters how many should be color-blind?

36. A color-blind boy's parents and grandparents all had normal vision. What was the formula of his maternal grandfather? Of his mother? Of his maternal grandmother?

37. Yellow body (y) in Drosophila is a sex-linked character recessive to gray body (Y). A certain gray female mated with an unknown male produced some yellow and some gray offspring of both sexes. What was the formula of the original female? What was the appearance of the male to which she was mated?

38. A female fruit fly with sable body (s) is mated with a male having gray body (S). Their daughters are gray, their sons sable. In what chromosomes are the genes S and s?

39. A barred rock hen mated with a black cock produced black daughters and barred sons. Using B and b to represent the genes, give the formulas of the two parents.

40. The genes for purple eye (normally red) and curved wings (normally flat) in Drosophila are in the same pair of chromosomes, and the normal red eye and flat wings are dominant. A homozygous purple-eyed flat-winged fly is crossed with a homozygous red-eyed curved-winged fly. One of their daughters is mated with a purple curved male. What kinds of offspring will they produce, and in what proportions, assuming that 21 per cent of the pairs of chromosomes break between the genes for eye color and wing shape?

41. The character known as speck (*s*), a spot near the base of the wing in Drosophila, is recessive to no speck (*S*), and plexus (*p*), a tangled patch of wing veins, is recessive to no plexus (*P*). A doubly heterozygous no-plexus no-speck female (*PpSs*) is mated with a plexus speck male (*ppss*). Of their 200 offspring, 10 are plexus no-speck. How do you account for the smallness of this number? How many of the offspring should be plexus speck?

42. In four-o'clocks the red flower color is not wholly dominant over white, so that heterozygous flowers (*Rr*) are pink. What would be the appearance of the offspring of a self-fertilized pink-flowered plant? If the progeny of this plant numbered 100, how many red ones should there be?

43. If a pink-flowered four-o'clock is pollinated from a red one, and they produce 84 offspring, how many of these should be red?

44. In shorthorn cattle, the hybrid between red and white is roan (having white hairs and red hairs intermingled). What would be the nature of the offspring of a roan and a white animal? The offspring of a roan and a red animal?

45. In Drosophila, cinnabar eye is recessive to red, stripe (a mark down the back) is recessive to no stripe, and bent wing recessive to straight wing. A cinnabar stripe bent fly is mated with a homozygous red no-stripe straight (wild-type) fly, and their offspring crossed with cinnabar stripe bent flies. Of 288 offspring from this latter cross, how many should be red stripe straight?

46. If two F_1 flies from Problem 45 are mated together, and among their F_2 offspring there are 36 cinnabar no-stripe straight-winged individuals, how many wild-type flies would be expected in the F_2 generation? How many red stripe bent flies?

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CHAPTER 18

PRINCIPLES OF TAXONOMY

Objects of all kinds that have ever interested civilized man have been classified by him as soon as they became numerous enough to show similarities amid differences. Animals have not escaped this human propensity for cataloguing. Classification was not necessary when chiefly the large, conspicuous animals were known, and when travel and communication between regions was so meager that each naturalist knew only the beasts of his own land. But as knowledge enlarged through travel, and as microscopes increased the range of size of animals that could be observed, the method of describing animals and their habits and modes of life singly, without reference to other animals, became cumbersome. It was then that classification began.

The classification of living things is known as *taxonomy* (from the Greek *taxis* arrangement and *nomos* law), which means literally an orderly arrangement. Both animals and plants are classified, and the principle on which their grouping is based is the same in both; but the schemes adopted for these two great kingdoms are somewhat different. Taxonomy of animals is often called *systematic zoology*, that of plants *systematic botany*. Only the plan adopted for zoology is considered in this book.

Conceptions of Taxonomy.—An orderly arrangement of objects or facts presupposes a system of classification. The same objects or facts can usually be classified in different ways by the use of different characters, qualities, or relations as a basis. What qualities are chosen to form the basis of classification depends on the importance attached to those qualities. If their importance is not known, the classification depends on the purpose or bent of mind of the classifier. It thus happened that in the early taxonomy of animals there were likely to be various schemes of classification, because no settled convictions existed regarding the significance of such grouping. Some of the first schemes are described below, but it may be pointed out in advance that all but one of the systems of classification that have ever been in use have been essentially devices to save confusion. Things were put upon shelves, figuratively, and labeled and catalogued. As long as prevention of confusion was the chief aim, classification might be artificial and arbitrary. The one exception to this arbitrary basis of arrangement is found in the system of classification that prevails at the present time. The modern system serves two purposes instead of but one. It has fitted admirably the modern evolution doctrine, according to which species of animals are related to one another through common descent. Classification may now afford the convenience that was desired in the earliest attempts at organization and at the same time express the kinship which the evolution doctrine implies. It is rather by accident than by design that the modern system is both a convenience and an expression of the course of evolution, because the author of it did not subscribe to the evolution doctrine. The system of classification is a branching one, and evolution results in a branching scheme of kinship. When the evolution idea was adopted, therefore, it was easy to adapt the branching classification to the portrayal of evolution. The scheme had the further advantage of being capable of expansion; the successive branchings could be as numerous as was required in any line of descent. A classification which expresses evolutionary development is called a genetic or natural system—genetic because ancestries are involved, natural because the basis of it exists in nature, not just in the minds of men.

Ray and Linnaeus in Taxonomy.—It has been said that John Ray (1627–1705), an Englishman, was the first true systematist. Ray proposed a dichotomous systematic table of the animal kingdom, that is, a system which branched by twos. He used anatomical likenesses as the basis on which animals were grouped, and the soundness of his judgment of these characters is shown by the fact that several of his groups are still recognized as natural ones. It is Carolus Linnaeus (Fig. 205), 1707–1778, however, who is considered to be the real founder of classification. Linnaeus's most important work was the "Systema Naturae," which appeared in 12 editions between 1735 and 1768 and, after his death, in a thirteenth, edited by Gmelin. In this work Linnaeus completed a classification which Ray had established in part, giving names to important groups that Ray had left without appellations and describing animals in language which, unlike many of the writings of his time, could not be misunderstood. Linnaeus also had the courage to defy prejudice in such details as removing the whales from the group of fishes, to which Ray also knew they did not belong, and placing them with the terrestrial hairy animals called mammals. For, in the Linnaean classification, structural characters, rather than habits or external forms, were used as a basis. Six *classes* were employed, four of them vertebrate (borrowed from Ray) and two invertebrate. These classes were divided into *orders*, the orders into *genera*, and the genera into *species*. The lesser groups were usually much more inclusive than the groups now given these same ranks. Thus, a Linnaean genus occasionally includes three or four orders, as these groups are now reckoned. Moreover, the genus often contained animals now placed in widely separated categories. One genus was erected to include certain sea cucumbers, a worm, a colonial jellyfish, and several primitive near vertebrates; some of these are now placed near the bottom, others near the top, of the animal scale.

Later Temporary Systems of Classification.—Following Linnaeus, many naturalists concerned themselves with systematic zoology. Some of them adopted the Linnaean system in general but altered it to suit their tastes, sometimes improving it but quite as often not. Others invented new classifications. Georges Cuvier (1769–1832) established four major

FIG. 205.—Carolus Linnaeus, 1707–1778, at the age of forty. (*Courtesy of New York Botanical Garden.*)

groups, called branches, which he divided into classes, 19 in number; and some parts of his classification remained in vogue in his own country (France) for three-quarters of a century. De Blainville (1777–1850) in several instances happily discovered the structural characters that were of genuine importance in distinguishing natural groups. He proposed a classification involving three subkingdoms, distinguished by the arrangement of their parts about a center or axis. These subkingdoms were the *Artiomorphes*, having a bilateral form like the majority of animals; the *Actinomorphes*, with a radiate form like a starfish; and *Heteromorphes*, animals having an irregular form (chiefly protozoa and sponges). Lamarck (1744–1829) devised a classification based upon nervous sensibility and proposed three principal groups: the *apathetic* animals, those without nervous systems or apparent sensation among the invertebrates;

the *sensitive* animals, also among the invertebrates; and the *intelligent* animals corresponding to the vertebrates. Oken (1779–1851), who was a philosopher rather than a naturalist, advocated simultaneously at least two classifications, which were equally worthless. One divided animals into groups according to their systems of organs, as intestinal, muscular, sexual, respiratory, vascular, etc. His other classification was based on the senses. Thus, there were the *Dermatozoa* (literally, skin or touch animals), by which he meant the invertebrates; the *Glossozoa* (literally, tongue animals), the fishes; the *Rhinozoa* (nose animals) which included the reptiles; the *Otozoa* (ear animals), or the birds; and another class, which appears to have been called interchangeably the *Ophthalmozoa* (eye animals) or *Thricozoa* (hair animals), the mammals. It would be hard to name a set of distinctions less applicable as classification marks than most of these, but Oken did not engage in practical matters. Then there was a host of minor systematists the value of whose labors was diminished by attempts to force their classifications into some numerical system, as, for example, those who held that the number of orders in each class should be the same as the number of families in each order, or the number of genera in each family. The favored number was five in some classifications, less often three, four, or seven.

These early modes of arrangement of animals have been described not for any value that may attach to them as classifications but to form a background for the one system that has survived. It should be obvious, from the brief statements made, that most of the plans used were totally unsuited to the requirements which later developments of zoology would have imposed upon them. The system of Linnaeus, however, was happily capable of being adapted to the demands of the tenets of evolution, and it alone has persisted to the present time.

The Linnaean System.—That the Linnaean system was rapidly adopted in advance of the general acceptance of the evolution idea is doubtless due largely to the fact that it introduced a sharply defined grouping, a definite terminology, and brief, clear diagnoses. It also permitted early naturalists to group those forms that resembled each other, which would be a natural tendency in any classifier. And then, as stated earlier, came the added advantage that it equally well permitted the classification of forms according to their relationships. As stated above, Linnaeus recognized groups of four different values—the class, the order, the genus (plural, genera), and the species (plural, species). To these categories have been added the *phylum* (plural, *phyla*) and *subphylum* (assemblies greater than the class), the *subclass*, the *suborder*, the *family*, the *subfamily*, the *subgenus*, the *subspecies*, and others. Of these additional groups the phylum and family are now generally accepted, and every classification includes a named group of each of these ranks. So regular is this practice that if there were only one kind of animal in a phylum, it would probably be assigned also to a named class, an order, and a family, as well as a genus and a species. The other ranks named are used for some groups or by some naturalists. The rank of recognized categories may be expressed as follows:

Phylum. Example, *Chordata* (the chordates)
Subphylum. Example, *Vertebrata* (the vertebrates)
Class. Example, *Mammalia* (the mammals)
Subclass. Example, *Eutheria* (the placental mammals)
Order. Example, *Rodentia* (the rodents)
Suborder. Example, *Sciuromorpha* (the squirrellike rodents)
Family. Example, *Sciuridae* (the flying squirrels, marmots, squirrels, chipmunks)
Subfamily. Example, *Sciurinae* (marmots, squirrels, chipmunks)
Genus. Example, *Sciurus* (the arboreal squirrels)
Subgenus. Example, *Tamiasciurus* (the red squirrels)
Species. Example, *hudsonicus* (the Hudsonian red squirrel)
Subspecies. Example, *loquax* (the southern Hudsonian red squirrel)

In some groups "divisions" or "sections" are recognized by authors, but these categories have no definite place in the system; that is, they may be introduced to mark off a group of genera, an assemblage of orders, etc.

The Linnaean system designates the species by two Latin or latinized names, the *generic* name, a noun, and the *specific* name, usually an adjective. Thus Natrix is the generic name of a group of water snakes, and *Natrix rhombifera* and *Natrix sipedon* are two species of water snakes. This is known as the binomial system of nomenclature. When subspecies are recognized, three names are used—the generic, the specific, and the subspecific—thus: *Thamnophis sirtalis parietalis.* Subspecies must usually have somewhat separate geographic ranges, but they grade into the neighboring subspecies at their common boundaries. The term variety, sometimes carelessly used synonymously with subspecies, often means only a genetically different type of individual not having geographic separation, for which the word phase is a preferable designation. Thus, the cinnamon individuals that occur not infrequently throughout the range of the black bear, *Euarctos americanus,* to which species it belongs, may be called a phase or variety. Such varieties are not ordinarily named in the Linnaean scheme. However, the taxonomic rank of variety may be assigned to divisions smaller than subspecies, and in one group, the ants (family Formicidae), the systematists regularly recognize and designate divisions smaller than subspecies by name, using four names for each variety (for example, *Camponotus herculeanus ligniperdus noveboracensis,* the northern carpenter ant).

Rules of Nomenclature.—The binomial and trinomial systems of nomenclature have been of great convenience to naturalists. Before their adoption, common names were in use in the scientific world and led to much confusion, the same animals being known by different names and different animals by the same name. To make certain that each animal shall have but one scientific name and that no two animals shall have the same name, rules of nomenclature have been proposed at different times for the purpose of determining which name shall prevail when several have been or are likely to be inadvertently proposed for the same form. Linnaeus seems to have appreciated the necessity for rules and to have proposed a set. These rules were not sufficient, and several other codes have been proposed, the more important of which are the *British Association Code*, the *American Ornithological Union Code*, the *Code of the German Zoological Society*, and the *Code of the International Zoological Congress*. The code now almost universally in use is the *International Code of Zoological Nomenclature*, adopted by the International Zoological Congress and governed through a Commission on Nomenclature created in 1898.

The International Code.—Some of the essential features of the International Code are as follows. The first name proposed for a genus or species prevails on the condition that it was published and accompanied by an adequate description, definition, or indication, and that the author has applied the principles of binomial nomenclature. This is the so-called *law of priority*. Duplicate names which have to be rejected because not prior are called *synonyms*. The tenth edition of the "Systema Naturae" of Linnaeus is the basis of the nomenclature. Names given earlier and not used in that edition are not recognized. The author of a genus or species is the person who first publishes the name in connection with a definition, indication, or description, and his name in full or abbreviated is given with the name; thus, *Bascanion anthonyi* Stejneger. In citations the generic name of an animal is written with a capital letter, the specific and subspecific name with initial small letter. The name of the author follows the specific name (or subspecific name if there is one) without intervening punctuation. If a species is transferred to a genus other than the one under which it was first described, or if the name of a genus is changed, the author's name is included in parentheses. For example, *Bascanion anthonyi* Stejneger should now be written *Coluber anthonyi* (Stejneger), the generic name of this snake having been changed. It is common practice now for the author of a species to designate one particular specimen as the *type* of the species, and to indicate the museum or other collection in which it is placed. If the species is later divided, the original name goes to that part of it which includes the type specimen. Also the specimen can be inspected in case of doubt regarding the identity of the species. One species constitutes the type of the genus. This decides, in case the genus is later divided into two genera, which group shall receive the original name. One genus constitutes the type of the subfamily (when a subfamily exists), and one genus forms the type of the family. The type is indicated by the describer or, if not indicated by him, is fixed by another author. No two genera in the whole animal kingdom may have the same name—a rule still occasionally violated because the interested taxonomists have not proposed corrected names. The name of a subfamily is formed by adding the ending *-inae* and the name of a family by adding *-idae* to the root of the name of the type genus. For example, Colubrinae and Colubridae are the subfamily and family of snakes of which Coluber is the type genus. Names of subfamilies are accented on next to the last syllable, family names on the third syllable from the end.

The Basis of Classification.—Early systematists largely employed superficial characters to differentiate and classify animals, and their classifications were thus largely artificial and served principally as convenient methods of arrangement, description, and cataloguing. Since the time of the development of the theory of descent with modifications by Lamarck (1809) and Darwin (1859), as stated in an earlier section, there has been an attempt to base the classification on relationships. Very nearly related animals are put into the same species. They are related because they descend from a common ancestry. The common ancestry could not in most cases have been very ancient, otherwise evolution within the group would have occurred and the species would have been split into two or more species. Species that are much alike are included in one genus, being thus marked off from the species of another genus. The similarity of the species of a genus is held to indicate kinship; but since there is greater diversity among the individuals of a genus than among the members of a species, the common stock from which the species of a genus have sprung must have existed at an earlier time, in order that evolution could bring about the degree of divergence now observed. In like manner, a family is made up of genera which resemble one another more than they resemble other genera, and their likeness is again a sign of affinity. But to account for the greater difference between the extreme individuals belonging to a family, evolution must have had more time; that is, the common source of the members of a family must have antedated the common source of the individuals of a genus. Orders, classes, and phyla are similarly regarded as having sprung from successively more remote ancestors, the time differences being necessary to allow for the differences in the amount of evolution. This statement is, however, only in a general way correct. Since evolution has probably not proceeded at the same rate at all periods or in all branches of the animal kingdom at any one time, the time relations of the groups of high or low rank must not be too rigidly assigned. Thus certain genera in which evolution has been slow are probably much older than some families in which evolution has been rapid. The genus Lingula (a burrowing marine brachiopod found between tide lines) has evolved very little. The modern animals differ only slightly from fossil Lingula of Ordovician time, estimated by some to be 400,000,000 years old. This is an extreme instance of slow evolution: Lingula is probably the oldest living genus. Many families, even orders, and some classes must be younger than that. It is not improbable, also, that some genera are quite as old as the families which include them; but in no case can they be older. Furthermore, different groups are classified by taxonomists of different temperaments, so that groups of a given nominal rank may be much more inclusive (and hence older) in one branch of the animal kingdom than in another. On the whole, neverthe-

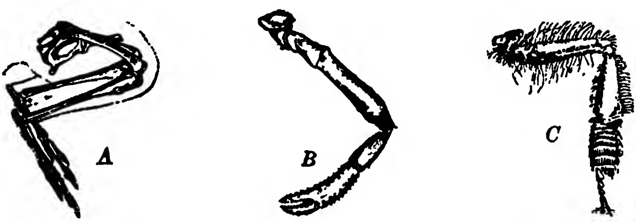


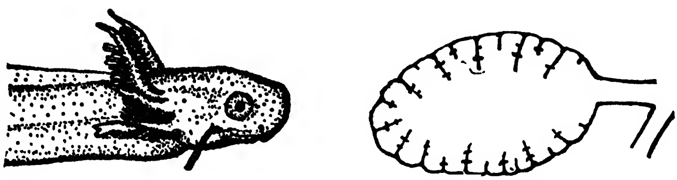
FIG. 206.—Analogous structures; legs of several animals. *A*, kangaroo; *B*, crayfish; *C*, honeybee. (*C from Metcalf and Flint, "Destructive and Useful Insects."*)

less, the groups of higher rank have sprung from ancestry more remote than that of the groups of lower rank.

Judging Kinship.—The means of recognizing the kinship implied in classification permit some differences of opinion. It is recognized that likeness in structural characters is the chief clue to affinities. However, similarity in one or several structures unaccompanied by the similarity of all parts is to be distrusted, since animals widely separated and dissimilar in most characters may have certain other features in common. Thus, the coots, phalaropes, and grebes among birds have lobate feet but, as indicated by other features, they are not closely related; that is, the lobes on their feet are *analogous*, meaning that they serve the same function. Analogy is widespread in the animal kingdom, since the same activities must be carried on by animals of very different structure. Locomotion, for example, is effected by legs of very different kinds. The legs of a kangaroo, a crayfish, and a honeybee (Fig. 206) are analogous, but their structure is unlike. The skeleton is within the flesh in the first of these but on the outside in the other two, and the materials of the skeleton are different. The crayfish and the bee, though alike in the position of the skeleton, differ in the number and character of the segments of the leg. Another case of analogous structures is that of lungs and gills

(Fig. 207). Both are used for absorbing oxygen but are wholly different in structure.

The foregoing analogous organs are so unlike in structure that no one would be led to classify together the animals that possess them. Not always, however, are the structural differences so obvious externally. A whale swims by means of paddles and a flattened tail which greatly resemble fins, and the early naturalists regarded whales as fishes. Yet the whale is a warm-blooded air-breathing animal with a four-chambered heart and some hair on the skin and has also the other characters of mammals, while the fishes are cold-blooded and aquatic, and have a two-chambered heart and scales in the skin. A close resemblance is also exhibited by certain lizards (Amphisbaenidae) to a group of snakes (Typhlopidae), because the former are blind and legless and have a short tail. These external similarities have apparently arisen in evolution



A B

FIG. 207.—Analogous structures; respiratory organs: *A*, gills of salamander; *B*, lung of frog. (*From Wieman, "General Zoology."*)

independently of one another and for that reason are not an indication of kinship.

Homology.—In judging of kinship by means of structural similarities, therefore, care must be taken to employ only those structures that have had similar origins in evolution. It is sometimes difficult to determine now whether similar structures in two groups of animals arose in evolution in the same way, or have converged for some reason from originally distinct beginnings. In general, if two or more groups of animals have one or a few structures in common while all others are different, it is safer to assume that the common structures arose independently, or at least that their *recent* evolutionary developments have been independent, and that the groups are therefore not closely related. The lobate feet of the several groups of birds mentioned above fall in this category. If, however, a great many features of two groups of animals are closely similar, the probability is that such similarities could only have come from similar or identical origins in evolution. The work of the taxonomist therefore becomes, in large measure, the recognition of those characters in different animals whose similarities are due to common evolutionary origin.

Structures that arise in the same way in evolution are said to be *homologous* with one another or to exhibit *homology*. Homology means similarity of origin in evolution. Unfortunately for the taxonomist the early evolution of the structures on which his classification is based took place in many instances millions of years ago. How can he ascertain, under these circumstances, whether the evolution of structures in two animals was similar or not? The answer to this question must usually be arrived at indirectly.

Homology Judged from Adult Structure.—The most reliable means of judging of similarity of evolution in two groups would be fossil members of those groups, if fossils could be obtained in sufficient numbers to establish a fairly complete history extending far back into their ancestry. Some such histories are given in Chap. 22. In most families of animals,

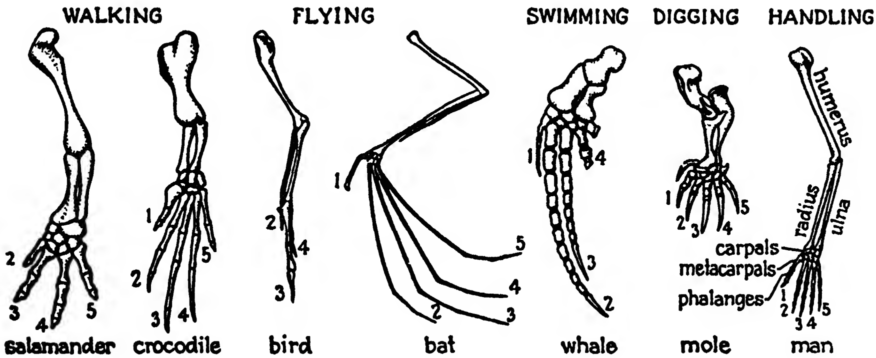


FIG. 208.—Homology in the bones of the fore limbs of vertebrates. Numbers 1–5 refer to digits, from thumb to little finger. (*From Storer, "General Zoology."*)

however, good fossil series are wanting, and the taxonomist must rely on what can be discovered from the living animals of today. In clear cases adult structure is sufficient, but only where many features are alike in the animals in question. A classical case of homology, judgment of which could safely rest on adult structure alone, is that which exists among the forelimbs of vertebrate animals (arms, wings, forefeet, etc., Fig. 208). Although the external forms of these forelimbs differ greatly in birds, seals, horses, whales, bats, and man, their skeletons are found to correspond very closely, bone for bone, at most points. It is believed that so many similarities could not be the result of accident or of convergence from originally distinct sources and that the likenesses are a sign of similar evolutionary origins. The nervous systems of vertebrate animals are equally good examples. The parts of the brain in fishes, amphibia, reptiles, birds, and mammals have a very obvious correspondence, and the origin and distribution of the cranial nerves are very similar in all of them. It is scarcely conceivable that these nervous systems could be alike in so many respects unless their evolutionary histories were largely the same.

Homology Ascertained from Embryonic Development.—Somewhat better evidence of homology than is afforded by adult structure can often be obtained from a knowledge of embryonic development. As was pointed out in Chap. 16, corresponding structures in vertebrate animals arise in essentially the same way in the embryo. The nervous system of one vertebrate begins with ridges that are much like those of another vertebrate embryo. The eye of a bird develops as does the eye of a frog. The early ear also is about the same, whether found in a reptile or a

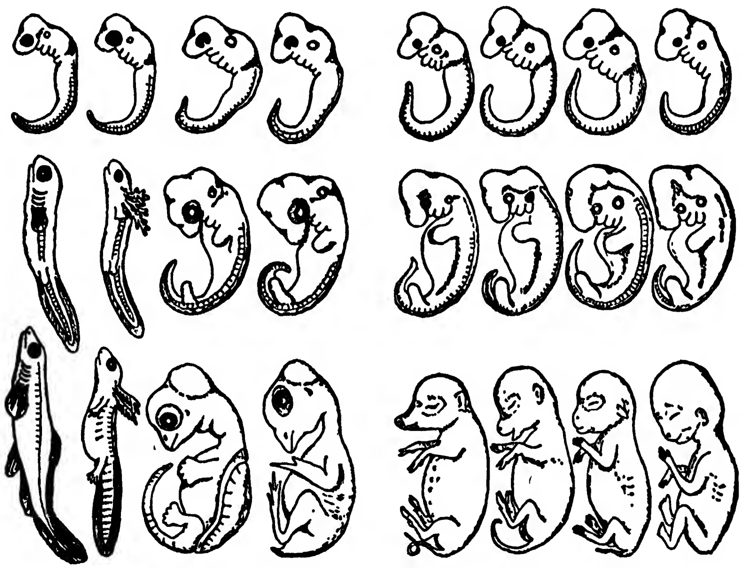


FIG. 209.—Homology of embryonic form, and particularly of gill clefts and bars, in vertebrates. (*From Haupt, after Romanes, "Darwin and After Darwin."*)

mammal. This similarity of the first appearance of embryonic structures occurs even when the adult organs are strikingly different. The arm of a man and the wing of a bird are different from one another in the adult condition, especially in the hands; but in the embryo the earliest limb buds are almost identical. An even greater difference exists between the adult fore- and hind limbs of a bird. When compared, bone for bone, there is scarcely a point at which there is not a distinct difference. Yet the wing and leg could be interchanged in the early embryo, and few observers would detect the substitution. Even the general form of the whole embryo is similar in the several classes of vertebrates (Fig. 209). This illustration also shows the common origin of gill clefts and gill bars, and their presence in the embryos of reptiles, birds, and mammals which do not have gills in the adult. Thus, on the whole, animals whose adult structure is similar resemble each other even more closely in embryonic stages. Similarity of embryos is particularly useful in taxonomy in those instances in which the adult animals, though closely related, have become so changed as to lose all similarity. An example of this kind is found in the parasite Sacculina described in Chap. 23. Biologists believe that similarity of structures in the embryo can be due only to similarity of the evolution of those structures; and because resemblance in the embryo sometimes remains after adult similarity has been diminished or destroyed, embryonic development is frequently better evidence of homology than is adult structure of the same animals.

The only known phenomenon which could preserve the similarities possessed by different animals is heredity. The likenesses of present-day animals must therefore be inherited from like animals of the past. Since it is scarcely conceivable that two identical organisms ever could have arisen independently of one another, inheritance from *like* ancestors must ultimately be inheritance from the *same* ancestors. Animals of different modern groups are held to possess like features in both adult and embryo because of this descent from a common source. This is the argument upon which the taxonomist relies when he classifies animals on the basis of supposed homologies.

Biogenetic Law.—The evident dependence of homology upon a common descent led, in the last century, to a conception comprised under the term *biogenetic law*, sometimes called by the more expressive and less committal name *recapitulation theory*. According to this law or theory (already stated page 74), the embryonic or other early stages of individual animals of today represent the condition of successive ancestors of these animals. That is, early developmental conditions represent very remote ancestors, later embryonic stages represent more recent ancestors. Some biologists held that the early embryonic stages are like the adult ancestors; others believed merely that the embryonic stages of the present are like the embryonic stages of the ancestors.

If this law were capable of rigid application, it would be easy to trace the evolutionary history of a race simply by studying the development of its individuals. In some cases this simple precedure is almost feasible. A series of fossil cephalopods (allies of the cuttlefishes) is a case in point. The fossil remains of these animals indicate that, in their racial history, their shells were at first provided with straight partitions, later with partitions whose edges were bent, crooked, and finally lobed in a very complicated manner (Fig. 210). Since in the fossils both the young and old stages of each individual shell are preserved, it is possible to compare the individual development with the racial development. When this is done, it appears that the individuals of the highly complex types passed through very similar stages, in which the partitions were first straight, then bent, crooked, and finally complicated.

Another suggestive and perhaps significant individual development is that of the decapod crustacea (lobsters, prawns, shrimps). The shrimp Penaeus hatches as a *nauplius*, and goes through several increasingly complex forms (Fig. 211), the last immature one being the so-called *mysis*

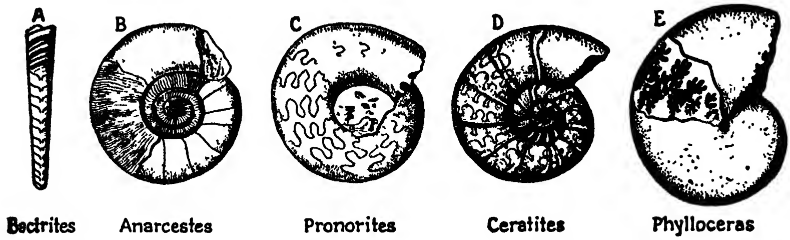


FIG. 210.—Biogenetic law illustrated by fossil cephalopods. Edges of partitions of shells start nearly straight and become increasingly crooked, in both evolution of group and development of individual ammonites (like Phylloceras, *E*). (*From Storer*, "*General Zoology*.")

stage. The appendages through all this development are two-branched. In the adult shrimp, however, the outer one of these branches on the five pairs of trunk appendages is considerably reduced. The lobster has shortened its individual development and hatches as a mysis which has two branches on all appendages; but the five pairs of walking legs have lost the outer branch completely in the adult. The support which these

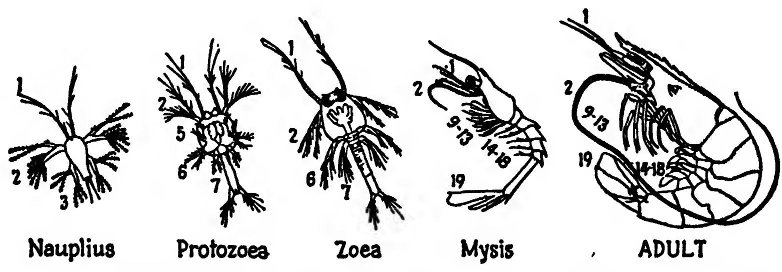


FIG. 211.—Larval stages and the adult of the shrimp Penaeus, perhaps illustrating biogenetic law. Numbers refer to successive appendages. (*From Storer*, "*General Zoology*.")

decapods give to the biogenetic law lies principally in the fact that there exists a present-day animal called Mysis (from which the larvae of other forms take their name) in which two well-developed branches persist on the trunk appendages of the adult. The lobster and shrimp thus pass through a developmental stage which resembles a supposedly more primitive animal.

In most animals embryonic development has undergone many changes, so that steps in development no longer represent accurately the steps in the evolution of their ancestors. That is, the biogenetic law is less generally applicable than it was formerly supposed to be. However, many important facts of evolution, of limited scope, have been discovered by an appeal to this law. A case in which the recapitulation theory is presumably correct is in the development of gill pouches in all the vertebrate animals. Gills are never developed in the reptiles, birds, and mammals; but gill pouches are formed in the embryo, and these may actually open temporarily to the outside as gill clefts, between which are the gill bars upon which gills are developed in fishes and amphibia. The production of gill pouches and bars in the higher vertebrates as well as in the lower, besides indicating a common ancestry of all these animals, points to the conclusion that the ancestor was an aquatic animal that respired by means of gills.

Practical Taxonomy.—The foregoing scheme of genetic classification is a goal toward which taxonomists in general strive. Application of it is attended with some difficulties. One obstacle is that before a satisfactory classification of even a small group can be made the species in it must be known. Judgment of kinships rests largely on a comparison of structures, and the characters of each species have an influence on one's judgment of the relationship among other species. Omission of some species tends to modify judgments concerning the whole group. Since there are usually many species in a family, or even a genus, the task of discovering and describing them is no small one. This work has been going on a long time, yet many species are still unknown. Every year many new species are described—few in the groups of large, conspicuous animals, but many in those less generally observed. Because of this still waiting task of describing species, many taxonomists, particularly in the past, have devoted their energies chiefly to naming and putting on record the newly discovered forms. They have had to concern themselves with kinship to the extent of putting species in the right genera, etc., but they have conceived their main task to be filling out the record. More and more, however, the genetic classification will have to be their aim.

The large number of species in existence is also a difficulty. Among well over a million, possibly over two million, species no one person can be expert on any considerable fraction. Each taxonomist must limit himself to one group, perhaps an order, often only a family. Names are given to these specialists according to the phyla or classes in which they have competence. An *entomologist* deals with insects, though he is never an expert in all the orders; a *protozoologist* studies the unicellular animals; an *ornithologist* knows birds, a *herpetologist* reptiles or amphibia or both, a *mammalogist* mammals, etc.

The other difficulties are mostly those which inhere in the animals studied. To know which characters best indicate kinship is the chief problem. In the higher ranks of the classification, those qualities which are constantly associated with one another are presumably best. Thus feathers are constantly associated with wings, a beak, claws, a four-chambered heart, and warm blood. These are the marks of one class, the birds. This principle may be pushed down to the lower ranks, the orders and families, but in less marked degree. When it is used for genera and species it is still valid but often difficult to apply. For species the uncertainties of its application are so great that some systematists have advocated abandoning it in favor of some more or less arbitrary scheme.

Relations of Taxonomy.—Classification has wide connections with nearly all other phases of biology. In a practical manner every biologist has occasional or frequent use for the technical knowledge of the systematist, and this requirement is not a purely formal one. Many investigations whose principal aim is entirely apart from classification must, nevertheless, constantly use the data of taxonomy. Thus the zoogeographer, as will be apparent in Chap. 21, is not primarily interested in classification; but in order to discover the principles which have guided migration or determined extinction in the past, he must be thoroughly conversant with the taxonomy of the group whose distribution he studies. The paleontologist also requires a knowledge of classification not only of extinct forms but of their living relatives. The work of the physiologist frequently involves the question of relationship, as does that also of the ecologist. Indeed, every biological field is in very close connection with taxonomy.

This intimate relation is not one-sided, for each of the phases of biology contributes to a knowledge of classification. Distribution and fossil forms supply information where morphology fails or may refute conclusions based on morphology alone. Physiological facts must be taken into account in explaining the formation of species. Ecological relations must be understood if certain taxonomic questions are to be correctly answered. In practice, this close relation between taxonomy and the other phases of biology is not always observed, but all of them suffer from its neglect.

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CHAPTER 19

THE GROUPS OF ANIMALS

In applying the principles of taxonomy systematic workers have often disagreed. This is inevitable because of the many judgments which must be made from meager evidence. When groups of facts seem to point to different conclusions, biologists may and frequently do weigh the conflicting data differently. Various schemes of classification have therefore arisen, all of them agreeing in many major features, differing from one another in less fundamental respects. The one here given may not be the best, but it is in common use.

The principal groups of animals are given, with brief descriptions and some well-known examples. The definitions are necessarily incomplete and are often not sufficient to distinguish all the members of one group from those of another. They will serve, however, to give a general concept of classification and a bird's-eye view of the animal kingdom.

Phylum 1. Protozoa.—These are single-celled animals, mostly of microscopic size, though some are visible to the unaided eye. Some species are colonial, but in these the cells are usually all potentially alike; that is, there is no differentiation among the attached cells to form tissues or organs. Protozoa live in very varied situations but usually require moisture. Many of them live in the soil. They are exceedingly common in ponds, streams, lakes, and oceans and may be attached to solid objects, be buried in mud or débris, or swim freely in the water. Many of them are parasitic in other animals. Some of the parasitic ones cause disease, as malaria, dysentery, and African sleeping sickness in man. Some protozoa live in other animals in a relation that is beneficial to the host as well as to the guests. A most remarkable example of mutual benefit is that received and conferred by certain protozoa in the digestive tracts of termites. These insects, whose food is wood, would be quite unable to digest the cellulose without the aid of the guest protozoa.

Untold numbers of protozoa live in the sea, and lived there ages ago. The great limestone beds, chalk cliffs, and quartzite and flint deposits are made up of shells of ancient protozoa. Noctiluca is a marine protozoon which is responsible for some of the remarkable phosphorescence observable in disturbed waters at night.

There are three principal modes of locomotion. Some protozoa thrust out pseudopodia, projections of their protoplasm, and then flow into them. This is characteristic of the class to which Amoeba (Fig. 212) belongs. Protozoa of this type have no constant characteristic form but are always changing. Others have at one end of the cell one or two long whiplike flagella whose lashing or sometimes wavelike motion propels the organism through the water. Euglena (Fig. 213) is one of these. Still others have the body covered by hundreds of cilia, short

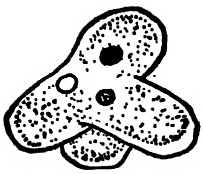

FIG. 212.—Amoeba.

FIG. 213.—Euglena.

FIG. 214.—Paramecium.

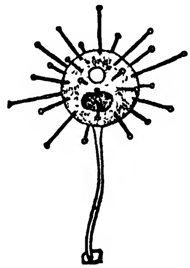

FIG. 215.—Podophrya, one of the Suctoria.

hairlike projections whose beating drives the body along, as in Paramecium (Fig. 214). Some protozoa, particularly the parasitic ones, have no locomotor structures. The classification of protozoa follows.

SUBPHYLUM I. PLASMODROMA. Protozoa that never have cilia in any stage.

Class I. Mastigophora. Protozoa with flagella, which serve for locomotion or for taking food. Euglena. (Figs. 34, 47, 48, 50, 51, 52, 53, 54, 129, 130, 131, 213.)

SUBCLASS I. PHYTOMASTIGINA
- Order 1. Chrysomonadina
- Order 2. Cryptomonadina
- Order 3. Dinoflagellata
- Order 4. Euglenoidina
- Order 5. Phytomonadina

SUBCLASS II. ZOOMASTIGINA
- Order 1. Protomonadina
- Order 2. Polymastigina
- Order 3. Hypermastigina
- Order 4. Distomatina
- Order 5. Cystoflagellata

Class II. Rhizopoda. Protozoa with pseudopodia or other changeable processes. Amoeba. (Figs. 16, 30, 43, 49, 212.)

- Order 1. Amoebina
- Order 2. Rhizomastigina
- Order 3. Heliozoa
- Order 4. Foraminifera
- Order 5. Radiolaria
- Order 6. Mycetozoa

Class III. Sporozoa. Parasitic Protozoa, usually without motile organs or mouth, reproducing by spores. Malarial organism.

SUBCLASS I. TELOSPORIDIA
- Order 1. Coccidiomorpha
- Order 2. Gregarinida

SUBCLASS II. NEOSPORIDIA
- Order 1. Cnidosporidia
- Order 2. Sarcosporidia
- Order 3. Haplosporidia

SUBPHYLUM II. CILIOPHORA. Protozoa having cilia in some stage.

Class I. Ciliata. Ciliophora with cilia throughout life. Paramecium. (Figs. 15, 132, 138, 214.)

Order 1. Holotricha
Order 2. Heterotricha
Order 3. Oligotricha
Order 4. Hypotricha
Order 5. Peritricha

Class II. Suctoria. Ciliophora with cilia in young stages, tentacles in adult. (Fig. 215.)

Phylum 2. Porifera.—The sponges are roughly radial in form and always diploblastic (two-layered), though many wandering cells are found in a jellylike substance between the layers. The body wall is always penetrated by many pores, which give the phylum its name. These pores lead to chambers within, which may be single cavities extending from outside to inside, or may branch or connect with other cavities in a complex system. The final opening through which the water leaves

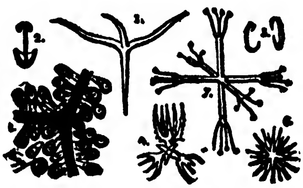

FIG. 216.—Elements of sponge skeletons. 1, spongin; 2–7, spicules.

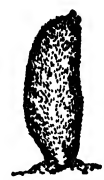

FIG. 217.[1] A sponge.

the body is called the *osculum*, and there may be many of these oscula. Some of the chambers are lined by collared cells (Fig. 33, page 52). The collared cells also possess flagella, by means of which a current of water is kept up continuously in the same direction. Food organisms and oxygen are brought, and wastes are carried away, by these currents. The collared cells seize the food, digest it, and pass along much of the nutrition to the other parts of the organism.

The sponges all possess a skeleton, which in some consists of a host of limy or siliceous spicules, in others of a network of horny (spongin) threads (Fig. 216). It is this latter horny skeleton which makes the ordinary bath sponge.

Members of this phylum are all sessile; that is, they are attached to other objects and do not move about. About a hundred and fifty species live in fresh water, where they sprawl in irregular form over twigs or logs. It is these fresh-water forms that reproduce by gemmules (page 170). The bulk of the phylum is marine, and they are found all over the world.

[1] Courtesy of General Biological Supply House.

A curious feature of the development of sponges is their "inside-out" gastrulation. It is the ciliated cells of the blastula that are invaginated and form the endoderm, whereas other gastrulas, if ciliated at all, regularly bear the cilia on the outside. Sponges also have remarkable powers of regeneration. Their bodies may be crushed, the separated cells sifted through a bolting-cloth net upon a surface under water, and there the cells gradually collect into lumps from which new sponges grow.

In the irregular, spreading, fresh-water and bath sponges, there has been some debate as to what constitutes the individual sponge. One concept is that each osculum is the center of an individual, and that the mass called a sponge is a colony. The boundaries of the individuals would then necessarily be indefinite, since all the oscula are parts of one system of canals.

There are three classes of sponges:

Class I. Calcarea. Sponges with spicules composed of calcium carbonate, monaxon or tetraxon in form. (Figs. 74, 139, 217.)

Order 1. Homocoela — Order 2. Heterocoela

Class II. Hexactinellida. Sponges with spicules composed of silicon, triaxon in form.

Class III. Demospongiae. Sponges with spicules composed of silicon, not triaxon in form, or skeleton composed of spongin, or with skeleton of both spicules and spongin.

Order 1. Tetraxonida — Order 3. Keratosa
Order 2. Monaxonida

Phylum 3. Coelenterata.—This phylum includes Hydra, the hydroids, jellyfish, sea anemones, and corals (Figs. 218, 219). Its members are radial in form and are all diploblastic. They possess a coelenteron (page 101), a cavity with only one opening, the mouth. There is no other body cavity. They have tentacles, and in the ectoderm are stinging cells used for offense and defense. Their nervous system is very diffuse, consisting of a network of scattered cells. While such a system provides for related actions throughout the body, the coordination is often imperfect and rather slow.

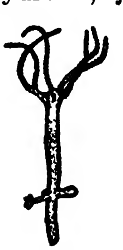

FIG. 218.—Hydra, with buds. *(Courtesy of Carolina Biological Supply Co.)*

There are in general two forms of body: (1) the polyp, which is typically tubular and elongated with tentacles around one end, and (2) the medusa or jellyfish, which is ordinarily compressed into a hemisphere or flat disk with tentacles around the edge. Polyp and medusa are really built on the same fundamental plan, as is readily understood if the mouth and the center of the convex surface of the medusa be imagined drawn apart so that the body is a long cylinder like a polyp (also see Fig. 143). The medusa is regularly free-swimming, though because it is produced by budding from the polyp form it remains in some species attached to its parent. The polyp is usually sessile, though sometimes, as in Hydra, it may become detached from one object and loop along to a new situation where it again glues itself fast.

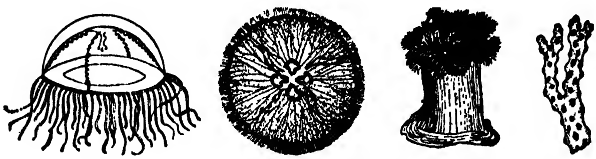

FIG. 219.—Various coelenterates: *A*, Gonionemus; *B*, Aurelia; *C*, sea anemone; *D*, coral. (*A–C from Carolina Biological Supply Co.; D from Wolcott, "Animal Biology."*)

Colony formation is common. Most of the hydroids are branching colonies. The corals have massive stony skeletons which in the aggregate may form reefs and atolls or other islands. The sea pens are colonies resembling a quill pen, with the pointed end thrust into the sand. Many of the colonial types are gorgeously colored and are responsible for some of the brilliance of tropical seas. The siphonophores (Figs. 145, 146, pages 174, 175) are free-swimming colonies.

Coelenterates exhibit a great deal of polymorphism. The polyp and medusa have already been mentioned as generalized types. Each may be considerably modified in different species and modified in several different ways in the same species. In the hydroids the medusa shows more variation than the polyp. It is free-living in some species, permanently attached to the hydroid colony in others. When attached, it may suffer considerable reduction; that is, it does not develop the full medusoid structure, which would be useless to an inactive individual. Sometimes the reduction of the medusa is so great that practically only the gonads are left (Fig. 220). Then the medusa looks like a reproductive organ belonging to a colony of polyps.

FIG. 220.—Hydroid, with reduced medusae. (*Courtesy of Carolina Biological Supply Co.*)

Much more marked polymorphism is found in the siphonophores (page 174). In them there are usually several kinds of structures which betray, sometimes in vague but often in unmistakable ways, their medusoid architecture and several other kinds which, in development or adult anatomy, are more or less like the polyp.

These polymorphic species often show that type of alternation of generations which is known as metagenesis (page 174). One or more kinds of individuals reproduce by budding (asexually), another kind by eggs and spermatozoa.

In some groups (Scyphozoa, Fig. 219*B*) only the medusoid generation exists, and in them its structure is different (see table of characterizations below).

Corals are the skeletons of two kinds of coelenterates, the Hydrocorallinae and the Madreporaria (see below), the latter being the more common. Aside from their use as ornaments, corals are of interest because of the long debate concerning the origin of coral reefs and atolls. The theories of their origin differ largely in whether the sea bottom on which they grew was assumed to be subsiding, stationary, or rising.

Class I. Hydrozoa. Coelenterates without stomodaeum and mesenteries; sexual cells discharged to the exterior; life history including hydroid form, or medusa (with velum), or both hydroid and medusa in same species. Polyps (including Hydra), a few corals, small jellyfishes. (Figs. 58, 59, 65*A*, 142, 144, 145, 146, 218, 219*A*, 220.)

Order 1. Anthomedusae
Order 2. Leptomedusae
Order 3. Trachymedusae
Order 4. Narcomedusae
Order 5. Hydrocorallinae
Order 6. Siphonophora

Class II. Scyphozoa. Coelenterates with only the jellyfish, not hydroid form; velum lacking; notches at margin of umbrella. Larger jellyfishes. (Fig. 219*B*.)

Order 1. Stauromedusae
Order 2. Peromedusae
Order 3. Cubomedusae
Order 4. Discomedusae

Class III. Anthozoa. Coelenterates without medusoid forms, with well-developed stomodaeum and mesenteries. Sea anemones, most corals. (Figs. 65*A*, *B*, 219*C*, *D*.)

SUBCLASS I. ALCYONARIA
Order 1. Stolonifera
Order 2. Alcyonacea
Order 3. Gorgonacea
Order 4. Pennatulacea

SUBCLASS II. ZOANTHARIA
Order 1. Edwardsiidea
Order 2. Actiniaria
Order 3. Madreporaria
Order 4. Zoanthidea
Order 5. Antipathidea
Order 6. Cerianthidea

Phylum 4. Platyhelminthes.—This phylum includes the planarians (Fig. 221), the flukes (Fig. 222), and the tapeworms (Fig. 223). The name of the phylum comes from the generally flat form of the body, and its members are commonly called flatworms even when the body is not flat. The body is bilaterally symmetrical, the only phylum so far mentioned to possess this form. The animals are triploblastic, the third layer being mesenchyme (page 82), which makes up the bulk of the body. The digestive tract is a coelenteron (page 80), opening only at the mouth, and there is no other body cavity. Parasitic forms may, however, lack the digestive tract completely. The free-living species have cilia on the epidermis, but the parasitic ones lack them. The excretory system is of the protonephridial type (page 134) ending in flame cells.

The planarias, which are free-living, live under stones or logs in fresh water. They have remarkable powers of regeneration, and have been used by many investigators to study the physiology of development and growth. The theory of gradients (page 217) in embryonic development originally grew out of studies on planarias.

The flukes are parasitic. Some of them are external parasites, as on the gills of fishes or other aquatic animals. Others—and these are the menacing ones—are internal parasites. Some of the latter pass through very complicated life cycles, in which the successive generations are totally different in form. Usually these different types of individuals must live in different hosts, one of which is a snail, the others being usually arthropods (Phylum 9, below) and vertebrate animals. One such life cycle involves four different hosts, following one another in a certain

FIG. 221.—Planaria.

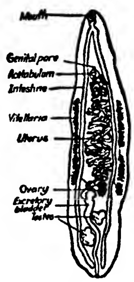

FIG. 222.—A fluke. (*From Van Cleave.*)

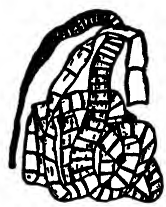

FIG. 223.—A tapeworm.

order. Sometimes the host, of any of the several successive general types, must be a particular species—a certain species of snail, a specific arthropod, a definite vertebrate species; in other trematodes there is a choice of species for host, but usually only a very limited one. Some degeneration (loss of eyespots, reduction of sense organs and nervous system) has been permitted by the parasitic mode of life, but the reproductive system is highly developed and specialized.

The tapeworms are parasitic in the digestive tracts of vertebrate animals. They consist of chains of rectangular individuals budded off from a small "head" which is attached to the intestinal wall of the host. There is no digestive tract, and no use for one since all food is absorbed already digested by the host. Longitudinal nerves and longitudinal excretory tubes pass along the margins of the "tape," common to all the individuals in it; but each individual has its own highly developed reproductive system which makes up most of the substance of the animal. Man gets his commonest tapeworms from insufficiently cooked pork; thorough cooking is the best guarantee against infection.

Class I. Turbellaria. Free-living flatworms with ciliated epidermis. Planaria. (Figs. 89, 221.)

SUBCLASS I. Rhabdocoelida
SUBCLASS II. Tricladida
SUBCLASS III. Polycladida

Class II. Trematoda. Parasitic flatworms without cilia but with a hardened ectoderm, usually parasitic and with attaching suckers. Flukes. (Fig. 222.)

SUBCLASS I. Monogenea
SUBCLASS II. Digenea

Class III. Cestoda. Parasitic flatworms with the body differentiated into a scolex, an enlargement usually provided with suckers and sometimes with hooks, and a chain of similar structures (proglottides), the whole being usually regarded as a colony. Tapeworms. (Fig. 223.)

Phylum 5. Nemathelminthes.—These are elongated, bilaterally symmetrical animals, commonly called round- or threadworms. They

A B

FIG. 224.—Important Nemathelminthes: *A*, Trichinella encysted in muscle; *B*, hookworm. (*A from photograph by General Biological Supply House; B from Rivas, "Human Parasitology," W. B. Saunders Company.*)

are triploblastic, and there is a "coelom" in the middle tissue layer. The digestive tract, unlike that of the two preceding phyla, is not a coelenteron, for it opens at both ends. There are no cilia on any part of the body. The sexes are separate; that is, some individuals are males, some females, none hermaphroditic.

This is probably one of the richest phyla in numbers of species, but its species are not proportionately well-known. Most of the members of this group are free-living, and they are found in all sorts of situations, in water or soil. Some infest plant tissues. Others are parasitic in animals. The dread human disease called trichinosis is caused by roundworms which are introduced in insufficiently cooked pork. The pigs get it by eating meat refuse or infested rats. The larvae get into the lymphatic vessels or bore out through the intestinal wall and enter the muscles, where they become encysted (Fig. 224*A*). Government inspection of meats is carried out in a few countries, but in some of those with the most rigid inspection the incidence of trichinosis is high. The reason is the habit of eating rare pork in those countries. Thorough cooking is the safest preventive; once the larvae are on their way to the muscles there is no cure. Members of another family of roundworms may cause elephantiasis by clogging the lymph passages.

The hookworm (Fig. 224*B*) of the southern states is also a member of this phylum. The larvae develop in moist soil. From there they enter the body through the skin of the feet, get into the blood, and thus reach the lungs and intestines. By feeding upon the blood and causing bleeding through an inhibition of clotting they produce an anaemic condition. Injury to the lungs predisposes the victim also to tuberculosis. The shiftlessness of the "poor whites" in the South is attributed in part to hookworm disease. An important feature of preventive measures is proper disposal of human feces, so as to prevent pollution of the soil, thus stopping further infection. Curative treatments are also available for those already diseased.

Phylum 6. Echinodermata.—Members of this phylum are radially symmetrical in the main, though usually some small feature is eccentrically placed so as to introduce slight bilaterality. Usually there are five rays, but the number may be very much greater. The skeleton consists of limy plates, either firmly joined into a globular shell or more loosely aggregated in the body wall so as to be readily movable on one another. There is a distinct coelom. Many echinoderms possess a peculiar method of locomotion by means of tube feet. These are hollow muscular tubes, ending in suckers and filled with water by which they are operated. The tube feet may be thrust out long distances by pressure on the contained water, attached to fixed objects by the suckers, then contracted, pulling the whole animal slowly along. Locomotion is more rapid in the brittle stars, since the slender arms of these animals can be bent rapidly and provide a sort of walking or running movement. Some of the feather stars are sessile, being attached by a jointed stalk to the bottom. All members of this phylum are marine.

Starfishes (Fig. 225*A*) have arms usually well marked off from the body disk. The brittle stars (*B*) have this distinction of arms from the body disk especially clearly marked. The name brittle star comes from the animals' practice of breaking off injured arms, which thereupon regenerate.

Sand dollars (*D*) have a nearly smooth margin, without division into arms. The sea urchins (*C*) are globular and without arms. Sea cucumbers (*E*) have no arms, but around the mouth is a series of branched tentacles. The arms of the feather stars are branched like a feather, and the branches are featherlike.

The starfishes have the peculiarity of digesting their food outside the body. They prey upon clams, forcing the valves of the shell open by a steady pull with the tube feet. The stomach is thrust out through the mouth, pushed between the separated valves, and wrapped around the exposed parts of the clam, which is then slowly digested. Oyster beds suffer considerably from these attacks. The other kinds of echinoderms take their food inside the body.

A curious habit is that of the sea cucumbers, of eviscerating themselves when irritated. If they are attacked, the body wall contracts so vigorously that it bursts, and a part (or even all) of the intestine is forced

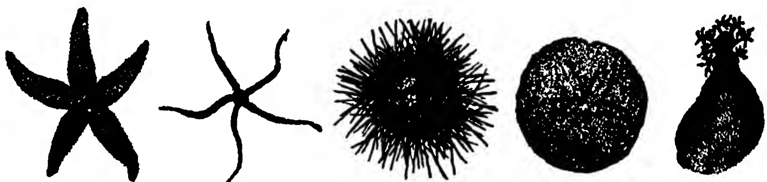

FIG. 225.—Various echinoderms: left to right, starfish, brittle star, sea urchin, sand dollar, sea cucumber. (*Courtesy of Carolina Biological Supply Co.*)

out, along with the branching respiratory organs that are attached to the cloaca. The tangled mass of viscera may so hinder (or perhaps appease) the enemy as to stop the attack. During a brief resting period the missing internal organs of the sea cucumber are regenerated.

Echinoderms are invaluable subjects in experimental laboratories because of the abundance of their eggs and the ease with which they may be obtained. Hundreds of studies of cytology, physiology of fertilization, and embryology have been made on the eggs of starfishes and sea urchins, and sometimes the other groups of echinoderms.

The relationships of echinoderms to the other phyla have been much debated because there is little clear evidence of them. Adult anatomy is entirely different from that of any other animals, and conclusions drawn from developmental stages have been various. There is less basis for establishing kinships of echinoderms than of almost any other group.

Class I. Asteroidea. Free-living, typically pentamerous echinoderms with wide arms moderately marked off from disk and with ambulacral grooves. Starfishes. (Fig. 225*A*.)

Class II. Ophiuroidea. Free-living, typically pentamerous echinoderms with slender arms sharply marked off from disk and no ambulacral grooves. Brittle stars. (Fig. 225*B*.)

Class III. Echinoidea. Free-living, pentamerous echinoderms without arms; test composed of calcareous plates bearing movable spines. Sea urchins, sand dollars. (Figs. 76, 225*C*, *D*.)

Class IV. Holothurioidea. Free-living, elongated, soft-bodied echinoderms with muscular body wall and tentacles around mouth. Sea cucumbers. (Fig. 225*E*.)

Class V. Crinoidea. Sessile echinoderms with five arms generally branched with pinnules, aboral pole usually with cirri, sometimes with jointed stalk for attachment to substratum. Feather stars, sea lilies.

Phylum 7. Annelida.—These are the true worms, as distinguished from Phylum 4 and Phylum 5 whose members are called flatworms and roundworms. The annelids are triploblastic, bilaterally symmetrical animals, with elongated body divided into segments. The segmentation is internal as well as external, for thin membranes divide up the body cavity or coelom. Corresponding with these segments, many of the internal organs are repeated in most of the segments, while some are repeated in only a few of the segments. The excretory organs, which are nephridia (page 135), occur in most segments; the nervous system, which is chiefly a long cord near the ventral side, typically has a ganglion and nerves in most of the segments; and the main blood vessels give off branches in each segment. Spiny projections or setae are common aids to locomotion.

Some of the annelids are hermaphroditic but do not fertilize their own eggs. Some of them (Fig. 226) also reproduce by budding or unequal fission. Many of them have remarkable powers of regeneration if cut into pieces. Some curious results are obtained by cutting off the head end of an earthworm; at certain levels the head structures are regenerated, while if cut at other levels a tail is developed in place of a head.

Despite the large size which many annelids attain, some of the larger ones respire only through the general body surface. Some others, no larger, have branched or filamentous gills which greatly increase the area through which oxygen is absorbed.

Some theoretical interest attaches to the larval stage of many marine annelids, which is known as a *trochophore*. It is pear-shaped or nearly spherical, with a circle of cilia around its equator. Similar larvae are found among the clams and snails, and adult rotifers may have roughly the same shape. Many biologists have considered that some relationship among these phyla is indicated by the trochophore larva or trochophorelike adult form.

Among the services to man performed by annelids may be mentioned the comminution and constant overturning of the soil by earthworms. These animals eat the soil, for whatever organic matter it may contain, and eject it from their digestive tracts. In making their burrows, much soil is brought to the surface from below. The burrows also leave the soil porous. Some annelids are also used for human food, notably the palolo of Samoa and other Pacific islands. These worms burrow in the coral reefs, and swarm in the open water in huge numbers just before the last quarter of the moon in October and November. They are captured in quantity by the natives at that time.

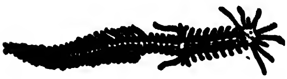

FIG. 226.—Autolytus, a marine worm.

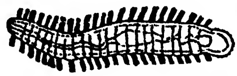

FIG. 227.—Aeolosoma. a fresh-water worm.

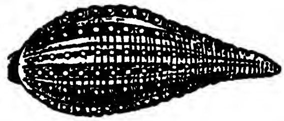

FIG. 228.—A leech. (*From Leunis.*)

Some of the annelida live in the soil (earthworms), many live in fresh water (Figs. 227, 228), and many are marine. Some of the leeches (Fig. 228) attach themselves to vertebrate animals by means of suckers and feed upon the blood of their host. Chaetopterus (Fig. 229) lives in a

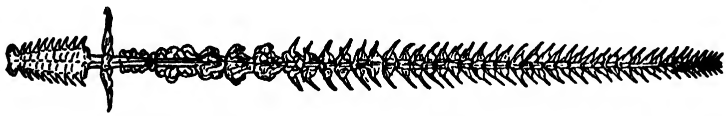

FIG. 229.—Chaetopterus. (*Courtesy of Carolina Biological Supply Co.*)

U-shaped parchmentlike tube in the sand under marine waters. The tube is open at both ends, and circulation of the water in it is maintained by flat appendages at the sides of the body.

Class I. Archiannelida. Marine Annelida with no setae or parapodia.

Class II. Chaetopoda. Annelida with setae and a perivisceral coelom; marine, fresh-water, or terrestrial in habitat. Earthworms.

SUBCLASS I. POLYCHAETA. With many setae. Marine worms. (Figs. 226, 229.)

Order 1. Phanerocephala Order 2. Cryptocephala

SUBCLASS II. OLIGOCHAETA. With few setae. Fresh-water and terrestrial worms. (Figs. 135, 136, 227.)

Order 1. Microdrili Order 2. Macrodrili

Class III. Hirudinea. Annelida without setae, and with anterior and posterior suckers. Leeches. (Fig. 228.)

Phylum 8. Mollusca.—This group includes clams, snails, and cuttlefishes. Their structure is so diverse that the phylum is difficult to define. Mollusks are triploblastic, unsegmented, and bilaterally symmetrical, though their symmetry is disturbed by a secondary spiral winding in some kinds. They have a coelom of restricted extent and usually possess a shell. The name mollusk refers to their soft bodies.

A structure called the foot is characteristic of the phylum but varies greatly in form. In the chitons (Fig. 230) it is like the sole of a shoe. In the clams and mussels (Fig. 231) the foot is a wedge which plows through the sand or mud. In the snails (Fig. 232) it is flat, and the animal creeps along on it, usually by rapid wavelike muscular contractions, but sometimes by means of cilia. The foot of a snail may secrete a mucous substance along which the animal creeps; a vertical roadway may thus be erected directly through the water without any support except at one end. The foot of the squids (Fig. 233), cuttlefishes, and nautili is transformed into a circle of arms bearing suckers.

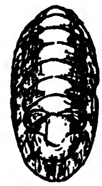

FIG. 230.—Chiton. (*Courtesy of Carolina Biological Supply Co.*)

The shell consists of two valves in the clams, oysters, and mussels; is spirally wound in the snails; is a row of movable plates in the chitons; is entirely embedded in the flesh in the cuttlefishes, squids, and most slugs; and is entirely lacking in certain marine mollusks called nudibranchs, which bear some resemblance to snails, and in a few species of several other groups.

The sexes are usually separate, but one class of snails is hermaphroditic, as are also some members of other classes. Among the latter, self-fertilization may occur, or two animals may mate.

The mollusks began as marine animals, then began to invade fresh water, and finally the land. Only the snails have gone on land, however,

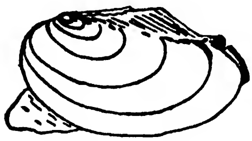

FIG. 231.—A clam.

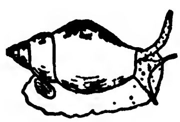

FIG. 232.—A snail.

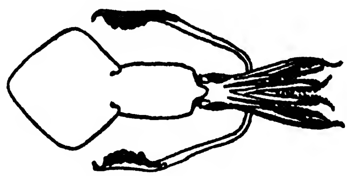

FIG. 233.—A squid.

and only the snails and clams into fresh water. The group as a whole has always been a successful one. It has maintained its abundance throughout geological time and is as well represented by number of species now as it ever has been. The evolution of mollusks has in general led to a reduction of the shell and the growth of the mantle over it, though one class has escaped these changes.

FIG. 234.—Teredo, the ship worm. (*Courtesy of Carolina Biological Supply Co.*)

Man has an economic interest in mollusks in several ways. Oysters and clams are important articles of food, the former being extensively cultivated. Pearls are made up of layers of nacre secreted around some irritating foreign object by the epithelial cells of clams. Such objects are deliberately inserted by pearl raisers, and pearls of any desired shape may be obtained. The same substance, nacre, on the inside of clam shells constitutes mother of pearl, which is used for buttons and knife handles. On the debit side of the ledger, the shipworm Teredo (Fig. 234, a mollusk, not a worm) bores into wharves and shipping and does considerable damage.

Class I. Amphineura. Mollusca with obvious bilateral symmetry, sometimes an eight-parted calcareous shell and several pairs of gills. (Fig. 230.)

Order 1. Polyplacophora　　Order 2. Aplacophora

Class II. Gastropoda. Mollusks with a head and with bilateral symmetry usually obscured by a spiral shell of one piece. Snails. (Fig. 232.)

SUBCLASS I. STREPTONEURA
Order 1. Aspidobranchia
Order 2. Pectinibranchia

SUBCLASS II. EUTHYNEURA
Order 1. Opisthobranchia
Order 2. Pulmonata

Class III. Scaphopoda. Mollusca with conical tubular shell and mantle.

Class IV. Pelecypoda. Mollusks without a head, with bilateral symmetry, a shell of two lateral valves and a mantle of two lobes. Clams, mussels. (Fig. 231.)

Order 1. Protobranchia
Order 2. Filibranchia
Order 3. Eulamellibranchia
Order 4. Septibranchia

Class V. Cephalopoda. Mollusks with distinct bilateral symmetry and a foot bearing eyes and divided into arms usually with suckers. Cuttlefishes, octopods. (Fig. 233.)

Order 1. Tetrabranchia　　Order 2. Dibranchia

Phylum 9. Arthropoda.—Members of this phylum have jointed bodies and jointed legs. Their skeletons are composed of a horny mate-

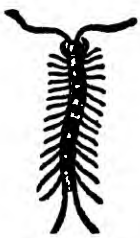

FIG. 235.—A centipede.

FIG. 236.—A beetle.

(*From Hegner, "College Zoology," The Macmillan Company.*)

rial on the outside of the body. This horny shell is burst and shed at intervals, and replaced by a new skeleton beneath, as the animal grows. Examples of arthropods are crayfishes, shrimps, centipedes (Fig. 235), insects (Fig. 236), and spiders (Fig. 237). They are triploblastic and bilaterally symmetrical. The blood system includes sinuses, which are merely spaces among the organs, into which the arteries open. The coelom is much reduced in size.

The number of different kinds of arthropods is almost unbelievably great. More known species belong to this phylum than to all other phyla combined. About half a million have been described, but the number must be several times as great. The insects furnish a greater share of these than all other arthropods together.

Arthropods are found in practically all situations that support life—in fresh and salt water, in mud, burrowing in soil, on the surface of the earth where they feed on animal or plant food, flying in the air, boring in trees or herbaceous plants, and parasitic in or on animals.

While most arthropods go through a fairly direct development, such that they are readily recognized at all stages even by the uninitiated, some of them, including many insects, have a striking metamorphosis involving larva, pupa, and adult. In the larva there are groups of cells forming the rudiments of the adult organs. These persist through the pupa, but the rest of the larval organization disintegrates into a milky mass which is doubtless partly used as nutrition for the growing adult structures.

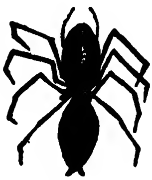

FIG. 237.—A spider. *(Courtesy of Carolina Biological Supply Co.)*

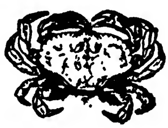

FIG. 238.—A crab. *(From Van Cleave.)*

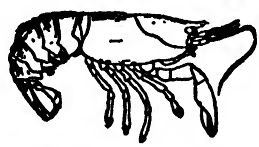

FIG. 239.—A crayfish.

Among the interesting features of arthropods is the social organization among some of the insects. The bees, ants, wasps, and termites have structurally different types of individuals which are also distinguished as social castes, sometimes in a very complicated system.

Worthy of note with respect to reproduction in the phylum is the rather frequent occurrence of parthenogenesis. In some of the smaller crustacea there is diploid parthenogenesis, in which the eggs do not experience a reduction division. Such parthenogenesis may be repeated for many generations but is usually interspersed with bisexual reproduction at intervals. In bees and many other insects there is haploid parthenogenesis, meaning that the egg which develops without fertilization has undergone chromosome reduction. The haploid individuals thus produced are regularly males.

Many members of this phylum are of economic importance to man. Lobsters, crabs (Fig. 238), in some regions crayfishes (Fig. 239), and shrimps are used as food, and bees collect honey in domestication. Small aquatic forms are common food for game fishes. Insects often pollinate flowers and are important to certain seed crops and fruits (figs). The silkworm moth is a valuable adjunct to the textile industry. Many species are injurious. They may destroy fruit or grain crops or shade trees or carry disease-producing organisms (mosquitoes, houseflies). Some of the insects are parasitic in domestic animals, and the mites may attack the skin of man ("jiggers"), poultry, or cattle. Barnacles injure bottoms of ships.

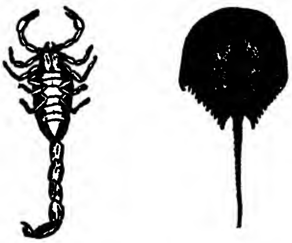

FIG. 240.—A scorpion (left) and king crab. (*From Carolina Biological Supply Co.*)

Relationship of the arthropods to the annelids has often been suggested, largely because of the segmentation of the body into a longitudinal chain of metameres. In support of this idea is brought the annelidlike Peripatus (class Onychophora, below). Peripatus has a body superficially like a worm and has segmentally arranged nephridia; but it has tracheae like insects, sinuses in the circulatory system, and no coelom. If Peripatus is a primitive form, which may be doubted, its value as a connecting link is considerable.

Class I. Crustacea. Arthropods breathing by means of gills, two pairs of antennae. Crayfishes, crabs, and shrimps. (Figs. 238, 239, 299, 300.)

SUBCLASS I. BRANCHIOPODA
- Order 1. Phyllopoda
- Order 2. Cladocera

SUBCLASS II. OSTRACODA

SUBCLASS III. COPEPODA

SUBCLASS IV. CIRRIPEDIA

SUBCLASS V. MALACOSTRACA
- Order 1. Nebaliacea
- Order 2. Anaspidacea
- Order 3. Mysidacea
- Order 4. Cumacea
- Order 5. Tanaidacea
- Order 6. Isopoda
- Order 7. Amphipoda
- Order 8. Euphausiacea
- Order 9. Decapoda
- Order 10. Stomatopoda

Class II. Onychophora. Primitive air breathing arthropods with tracheae and nephridia. Peripatus.

Class III. Myriapoda. Arthropods with tracheae, one pair of antennae, and many similar legs. Centipedes and millipedes. (Fig. 235.)

- Order 1. Pauropoda
- Order 2. Diplopoda
- Order 3. Chilopoda
- Order 4. Symphyla

Class IV. Insecta. Arthropods with tracheae, one pair of antennae, and three pairs of legs. Insects. (Figs. 95, 203, 204, 236, 303.)

- Order 1. Aptera
- Order 2. Ephemerida
- Order 3. Odonata
- Order 4. Plecoptera
- Order 5. Isoptera
- Order 6. Corrodentia
- Order 7. Mallophaga
- Order 8. Thysanoptera
- Order 9. Euplexoptera
- Order 10. Orthoptera
- Order 11. Hemiptera
- Order 12. Neuroptera
- Order 13. Mecoptera
- Order 14. Trichoptera
- Order 15. Lepidoptera
- Order 16. Diptera
- Order 17. Siphonaptera
- Order 18. Coleoptera
- Order 19. Hymenoptera

Class V. Arachnida. Arthropods with tracheae, book lungs or book gills and no antennae. Spiders, mites, scorpions, king crabs. (Fig. 240.)

Order 1.	Araneida	Order 6.	Palpigradi
Order 2.	Scorpionidea	Order 7.	Solifugae
Order 3.	Phalangidea	Order 8.	Chernetidia
Order 4.	Acarina	Order 9.	Xiphosura
Order 5.	Pedipalpi	Order 10.	Eurypterida

Invertebrate Groups of Uncertain Position.—Certain groups of invertebrates have not been assigned a definite relation to other groups. Opinion differs so widely as to their affinities that they may well be kept out of the classification for the present.

Mesozoa. Parasites apparently intermediate between the protozoa and metazoa. Not improbably degenerate relatives of the flatworms.

Nemertinea. Terrestrial, fresh-water, and marine animals resembling flatworms but with a proboscis, blood-vascular system, and alimentary canal with two openings.

Nematomorpha. Long threadlike animals with the body cavity lined with epithelium, a pharyngeal nerve ring, and a single ventral nerve cord.

Acanthocephala. Parasitic worms with spiny proboscis, a complex reproductive system, and no alimentary canal. (Fig. 241.)

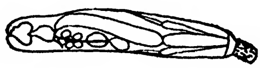

FIG. 241.—Echinorhynchus, one of the Acanthocephala.

FIG. 242.—Arrowworm, Sagitta.

Chaetognatha. Marine invertebrates with a distinct coelom, alimentary canal, nervous system, and two eyes. Arrowworm. (Fig. 242.)

Ctenophora. Triploblastic animals; symmetry partly radial, partly bilateral; eight rows of vibratile plates radially arranged. Sea walnuts or comb jellies. (Fig. 243.)

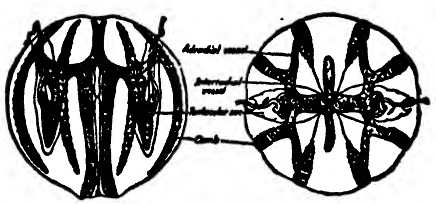

FIG. 243.—A ctenophore. (*From Van Cleave.*)

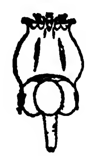

FIG. 244.—A rotifer. (*From Whitney.*)

Rotifera. Invertebrates with a head provided with cilia, usually a cylindrical or conical body often with a shell-like covering, and a tail or foot, bifurcated at the tip where it is provided with a cement gland. (Fig. 244.)

Bryozoa. Mostly colonial invertebrates resembling hydroids in form, with distinct coelom, and with digestive tract bent in the form of a letter U. (Fig. 140.)

Phoronidea. A single genus of wormlike animals having tentacles and living in membranous tubes in the sand.

Brachiopoda. Marine tentaculate animals with a calcareous shell, composed of two unequal valves, a dorsal and a ventral. (Fig. 245.)

Gephyrea. Wormlike animals of doubtful affinities.

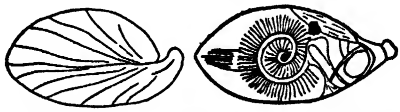

FIG. 245.—A brachiopod. Left, the shell; right, the animal.

Phylum 10. Chordata.—The animals of this phylum have at some stage a skeletal axis called the notochord, gill slits in the embryo or adult, and a nerve cord dorsal to the alimentary canal. (In preceding phyla when a nerve cord is present it is ventral to the alimentary tract.) This

FIG. 246.—Balanoglossus. (*From Carolina Biological Supply Co.*)

FIG. 247.—A tunicate. (*From Carolina Biological Supply Co.*)

phylum includes a number of degenerate animals such as Balanoglossus (Fig. 246) and the tunicates (Fig. 247) which must be included here because of the presence of the notochord in the embryo. It also includes the amphioxus (Fig. 248), a fishlike animal in which the notochord is the

FIG. 248.—Amphioxus.

FIG. 249.—Lamprey. (*From Carolina Biological Supply Co.*)

permanent skeletal axis. The remaining chordates are called vertebrates from the fact that the notochord becomes invested with cartilage which is segmented to form a vertebral column. In some lower forms the cartilaginous vertebrae and the notochord which they surround persist throughout the life of the animal, but in the higher forms the cartilage is replaced by bone and the notochord disappears.

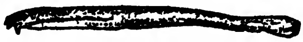

FIG. 250.—Hagfish. (*From Carolina Biological Supply Co.*)

FIG. 251.—A shark. (*From Carolina Biological Supply Co.*)

At the bottom of the vertebrate scale are the lampreys (Fig. 249) and hagfishes (Fig. 250) which are eellike in form but have no jaws and no lateral fins. The skeleton is made of cartilage only. Some of the lampreys inhabit fresh water and lay their eggs in nests made by pulling up stones from the bottoms of brooks. Next above these in the scale are the sharks (Fig. 251), skates (Fig. 252), and rays, whose skeletons are also cartilaginous but which have jaws. Their skin is armored with a type of scale having a tooth or spine mounted on a flat base. The dried and processed skin with these scales forms the leatherlike natural shagreen of certain costume accessories.

Above these are five major groups, the true fishes, amphibia, reptiles, birds, and mammals. Differences among these are found in the hard parts of the skin, the form of the limbs, the structure of the heart, and the means of respiration.

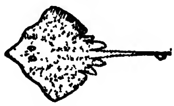

FIG. 252.—Skate.

FIG. 253.—A fish. (*From Carolina Biological Supply Co.*)

The fishes (Fig. 253) are aquatic, and respire by means of gills. The skin usually bears scales, but these are not toothed like the scales of sharks. The skeleton is at least partly of bone. Locomotion is effected by fins (and the bending of the body), and the heart consists of but two chambers (one auricle and one ventricle).

FIG. 254.—A salamander.

FIG. 255.—A frog.

The amphibia are the salamanders (Fig. 254), toads and frogs (Fig. 255), and certain legless forms called caecilians. Their skin is smooth, nearly always devoid of scales, though some fossil amphibia were heavily armored. They are nearly all aquatic at least in young stages, and some of them throughout their lives. Division of their habitats between water

FIG. 256.—A lizard. (*From Carolina Biological Supply Co.*)

FIG. 257.—A turtle. (*From Carolina Biological Supply Co.*)

and land is what gives the class its name amphibia. The heart is three-chambered—two auricles, one ventricle. Though the amphibia are of less value to man than are the fishes, frogs' legs are a table delicacy, toads devour many insects, and most orders have contributed material for important biological and medical investigations.

Reptiles include lizards (Fig. 256), snakes, alligators, turtles (Fig. 257), and such fossil forms as dinosaurs. Their skin contains scales or hard plates. They are cold-blooded in common with the fishes and amphibia but unlike the following two classes. They have no gills in any stage. The heart is three-chambered (approximately four-chambered in crocodiles, in which the ventricle is partially divided). Some snakes are poisonous, but most of them are beneficial to man (as are also the lizards) because they devour noxious animals. Some turtles are used for food.

The birds are characterized by feathers, which grow from pits in the skin, forelimbs adapted to flight, a four-chambered heart, warm blood (warmer than that of the next class, mammals), and a beak with horny covering but no teeth. The bones of the skeleton are extensively fused, particularly in the wings. The body is made light for its size by large air spaces, variously placed, some of them extending into the cavities of certain bones. These spaces connect with the lungs, but their walls are not made of lung tissue, though doubtless they do effect some exchange of oxygen and carbon dioxide.

Mammals are mostly quadrupeds. The skin is covered with hair —very sparsely in some. They breathe air even when they inhabit water. The heart is four-chambered, the blood warm. The red cells of the blood are devoid of nuclei except while they develop in the marrow. There is a muscular sheet or diaphragm between the thorax and the abdomen, important in breathing. The young are usually developed in the uterus of the female—a few lay eggs—and are nourished with milk from the mammary glands after birth. The most primitive mammals, the egg layers, live in Australia and neighboring islands. The marsupials, which give birth to their young in a very early stage and carry them for a long time in a pouch, are next most primitive. They live in the Australian region, in South America, and one kind (opossum) in North America.

SUBPHYLUM I. ENTEROPNEUSTA. Wormlike chordates of somewhat doubtful systematic position. (Fig. 246.)

Order 1. Balanoglossida Order 2. Cephalodiscida

SUBPHYLUM II. TUNICATA. Saclike marine animals with a cuticular outer covering known as a tunic or test. Tunicates. (Fig. 247.)

Order 1. Ascidiacea
Order 2. Thaliacea
Order 3. Larvacea

SUBPHYLUM III. CEPHALOCHORDA. Fishlike chordates with a permanent notochord composed of vacuolated cells. Amphioxus. (Fig. 248.)

SUBPHYLUM IV. VERTEBRATA. Chordates in which the notochord either persists or becomes invested by cartilage, segmented, to form a vertebral column, or disappears, the vertebral column being made up of bony segments.

Class I. Cyclostomata. Eellike vertebrates without functional jaws or lateral appendages. Lampreys and hagfishes. (Figs. 249, 250.)

SUBCLASS I. MYXINOIDEA SUBCLASS II. PETROMYZONTIA

Class II. Elasmobranchii. Fishlike vertebrates without air bladder, with jaws, and with a cartilaginous skeleton and placoid scales. Sharks, rays, and skates. (Figs. 251, 252.)

Subclass I. Selachii
Order 1. Squali — Order 2. Raji
Subclass II. Holocephali

Class III. Pisces. Aquatic, cold-blooded vertebrates breathing by means of gills, with air bladder, a two-chambered heart, and usually a dermal exoskeleton of scales. Fishes. (Figs. 159, 253.)

Subclass I. Teleostomi. Fishes with a skeleton consisting wholly or partially of bone, breathing by means of gills. True fishes.

Order 1. Crossopterygii
Order 2. Chondrostei
Order 3. Holostei
Order 4. Teleostei

Subclass II. Dipnoi. Fishes with a skeleton of cartilage and bone, and air bladder functioning as a lung. Lungfishes.

Class IV. Amphibia. Cold-blooded vertebrates breathing by means of gills in some stage, skin usually not covered with scales, heart of three chambers. Salamanders, toads, and frogs. (Figs. 93, 151, 157, 158, 163, 187, 254, 255.)

Order 1. Caudata
Order 2. Salientia
Order 3. Apoda

Class V. Reptilia. Cold-blooded vertebrates usually covered with scales, breathing throughout life by means of lungs. Lizards, snakes, crocodilians, turtles. (Figs. 156, 256, 257, 279, 281.)

Order 1. Testudinata
Order 2. Rhynchocephalia
Order 3. Crocodilini
Order 4. Squamata

Class VI. Aves. Warm-blooded vertebrates with the body covered with feathers, with the forelimbs usually modified as wings, and a heart of four chambers. Birds. (Figs. 161, 201.)

Subclass I. Archaeornithes
Subclass II. Neornithes
Order 1. Struthioniformes. Ostriches.
Order 2. Rheiformes. Rheas.
Order 3. Casuariiformes. Cassowaries, emus.
Order 4. Apterygiformes. Kiwis.
Order 5. Tinamiformes. Tinamous.
Order 6. Sphenisciformes. Penguins.
Order 7. Gaviiformes. Loons.
Order 8. Colymbiformes. Grebes.
Order 9. Procellariiformes. Albatrosses, petrels.
Order 10. Pelecaniformes. Pelicans, frigate birds.
Order 11. Ciconiiformes. Herons, storks.
Order 12. Anseriformes. Ducks, geese, swans.
Order 13. Falconiformes. Vultures, hawks, falcons.
Order 14. Galliformes. Pheasants, grouse, turkeys.
Order 15. Gruiformes. Cranes, rails.
Order 16. Charadriiformes. Shore birds, gulls, auks.

Order 17. Columbiformes. Pigeons, doves, sand grouse.
Order 18. Psittaciformes. Parrots, macaws.
Order 19. Cuculiformes. Cuckoos, plantain eaters.
Order 20. Strigiformes. Owls.
Order 21. Caprimulgiformes. Goatsuckers, oil birds.
Order 22. Micropodiformes. Swifts, hummingbirds.
Order 23. Coraciiformes. Kingfishers, hornbills.
Order 24. Piciformes. Toucans, woodpeckers.
Order 25. Passeriformes. Broadbills, ovenbirds, lyrebirds, songbirds.

Class VII. Mammalia. Warm-blooded animals which are covered with hair at some stage, suckle the young, and have a diaphragm between thorax and abdomen. Mammals. (Figs. 92, 160, 193, 197, 272, 294.)

SUBCLASS I. PROTOTHERIA. Egg-laying mammals. Monotremes.
Order 1. Monotremata
SUBCLASS II. METATHERIA. Pouched mammals. Marsupials. (Fig. 160.)
Order 1. Marsupialia
SUBCLASS III. EUTHERIA. Viviparous mammals. True mammals.

Order 1.	Insectivora	With claws	Order 10.	Artiodactyla	With hoofs
Order 2.	Dermoptera		Order 11.	Perissodactyla	
Order 3.	Chiroptera		Order 12.	Proboscidea	
Order 4.	Carnivora		Order 13.	Hyracoidea	
Order 5.	Pinnipedia		Order 14.	Xenarthra	
Order 6.	Menotyphla		Order 15.	Pholidota	
Order 7.	Rodentia		Order 16.	Tubulidentata	
Order 8.	Lagomorpha		Order 17.	Sirenia	Aquatic
Order 9.	Primates—With nails		Order 18.	Cetacea	

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CHAPTER 20

ANIMALS AND THEIR ENVIRONMENT

Ecology deals with the relations of organisms to the environment. It has to do primarily with those relations to environment which determine the organism's characteristics, its success, its mode of life, and its distribution. Ecology is also concerned with the environment itself. Since the things to which animals and plants are sensitive in the world about them are not everywhere the same, any organization which the environment may possess is of importance to living things. This organization is sometimes very intricate, and many an ecological study has been directed toward an understanding of the environmental system, without immediate reference to any particular organism.

The environmental relations of organisms may be approached from two different points of view: (1) that of the individual or single species, in which case ecology comes very near to a limited physiology, and (2) that of groups of species living in the same general situations and forming what are called associations or communities. These two points of view are successively adopted in this chapter.

Temperature.—Each kind of animal is capable of carrying on its metabolism only within a certain range of temperatures. At some point within this range, usually above the middle but sometimes below, the physiological processes work best. For most animals the lower limit is slightly above freezing, while the upper limit is usually below 45°C. Fish eggs develop best a few degrees above freezing, birds' eggs at about 40°C. Some animals possess remarkable powers of adjusting themselves to temperatures outside their usual range. Thus some of the protozoa which die when raised within a short time to a temperature of 23°C. will endure 70°C. if the temperature is raised very gradually.

Since temperature varies irregularly on the earth's surface from the equator to the poles, with elevation above sea level, seasonally, and as between day and night, it is obvious that animals must be so located that their permissible temperatures are present and that their limits are not overstepped. Ordinarily, species with a low optimum temperature must live in temperate or cooler zones, those with a high optimum temperature in tropical regions. The factor of dormancy also enters into the determination of geographic position. Most animals become torpid at sufficiently low temperatures, and some endure actual freezing. Many of them, however, cannot be dormant for any great length of time and still live. Such species have to live in tropical regions.

Some animals avoid the dangers of extreme temperatures by specialized habits. Certain wasps which dig in sand dunes cannot endure for long the high temperature at the surface of the sand on sunny days. They survive these temperatures by digging vigorously for a few seconds, then flying about a few inches above the sand where the air is much cooler, then returning to their digging for a brief period.

The regulation of body temperature by birds and mammals has already been described (page 120). This physiological feature enables animals of these classes to range widely so far as temperature is concerned. Among cold-blooded animals there is occasionally the ability to regulate temperatures in groups. Honeybees can do this in colonies, though each individual bee cannot. A certain amount of heat is liberated in their metabolism; and if this is conserved in masses of bees, the temperature may be considerably raised. Temperatures in their hives are much higher than those outside in winter.

One curious relation to temperature is the acceleration of metabolism by fluctuating as compared with constant temperatures. Grasshopper eggs develop much more rapidly at their optimum temperature if that temperature has been interrupted by a cold period. The acceleration is greater if the interruption by low temperature comes early than if it comes late in development. Eggs are laid by these insects in late summer and fall, over a period of many weeks. It would be expected that those laid early would be the first to hatch the following spring; but all the eggs hatch about the same time. Those laid late in the fall enter the winter in an early embryonic stage but are accelerated enough more in the spring to enable them to overtake their older companions and emerge at the same time. This is an important reaction to temperature, for if any of the young grasshoppers emerged much later in spring or summer they would miss the most favorable period of the year for passing through their immature nymphal stages.

Some animals change their reactions to other stimuli with changes of temperature. Thus one of the leaf-boring beetles studied by Chapman goes toward the light at high temperature and takes to flight if mechanically disturbed, but avoids light at low temperature and draws up its legs and falls if disturbed. These beetles live on a plant which grows in water, and during the warm part of the day they are out on the leaves. If their reactions were reversed and they were disturbed at this time, they would fall into the water, but instead they fly away. Disturbance during the cool part of the day, when they are hiding at the center of the plant, merely causes them to fall into the recesses at the bases of the leaves.

The structure of an animal sometimes depends on the temperature.

Among the aphids or plant lice some individuals have wings, other do not, and it has been shown that temperature helps to determine whether wings develop. No general rule can be given for the control of wing production, since different strains respond differently, even within the same species. In one strain maximum wing production is obtained if the parents are reared continuously at low temperatures. Since the aphids generally alternate between two host plants during a season, and since wings are the easiest means of effecting their migrations, it is important to them that wings develop in at least some individuals at the right time. Another insect that responds developmentally to temperature is the vinegar fly, Drosophila. One of its mutant varieties has vestigial wings (Fig. 204, page 236) which are quite useless for flight. At very high temperatures, however, the wings of this variety are nearly normal. This response happens to be of very little use to the flies for two reasons: first, the temperature which induces full wing development is so high that it is otherwise detrimental and flies seldom meet exactly that temperature, and, second, inability to fly is not this mutant's worst handicap, since it is physiologically weak and never matures so rapidly or in so large numbers as do the normal flies of the species. Color in butterflies is likewise known to be affected by temperature, and it seems certain that the differences between the northern and southern varieties of a species are sometimes thus determined.

Genetic and evolutionary effects of temperature are known in a few organisms. Mutations in Drosophila have been produced by heat in experiments by Goldschmidt and others. The amount of separation and recombination by characters in this fly due to breakage and reconstitution of chromosomes by exchange of pieces (page 236) is increased by high temperature. And Seiler has found that whether a given sex-determining chromosome in a certain moth goes into the polar body or remains in the egg at the meiotic division depends partly on the temperature. The effect is such that more females are produced at high temperatures.

Light.—The most obviously important influence of light upon the ecology of animals is its effect upon green plants upon which the animals feed. These plants are dependent on photosynthesis for their own nutrition and can maintain themselves only where sufficient light is present. Animals that live in caves must therefore subsist on plants that do not carry on photosynthesis or on other animals whose food chains do not end in green plants. In moderately deep lakes, as is pointed out later, green plants are limited to the surface water, if floating, and to a strip along the shore, if rooted (Fig. 258). Animals dependent on such plants for food must spend part of their time in the regions indicated.

Another influence that may be indirectly important for animals is the effect of daily duration of light upon the reproductive processes of plants. Many plants will come to flower only if they are exposed to a certain number of hours of light each day. A certain range of duration is always permissible. If the daylight period is longer or shorter than this required range of hours, the plant may grow vegetatively even more vigorously than usual but will not bloom. Unless a plant has some satisfactory asexual method of propagation, it cannot maintain itself in a region not affording the right duration of daylight. Probably no plant whose required amount of daylight is yet known is the sole food

FIG. 258.—Shore vegetation of lake, which is too deep elsewhere for rooted plants. (*Photograph by F. C. Gates.*)

of any species of animal, but the possibility exists that the range of some animal is thus limited by the length of day.

Of structural changes induced in animals by light, the most significant ecologically is probably the production of wings in aphids. In some strains of aphids, light has an even more important influence than has temperature, the effect of which is described above. In one of these strains, alternating light and darkness caused nearly every individual to be winged, provided the dark period was at least 12 hours long. Shorter periods of darkness, including continuous light, made most of the aphids of this strain wingless. Since temperate regions in summer do not have 12-hour nights, wing production must be considerably curtailed in such strains. Other strains respond differently to light, some of them directly reversing the behavior just described. The importance of wings in the migration of these insects from one host plant to another has already been mentioned.

The color of flatfishes, certain shrimps, and some other animals changes to correspond to the background on which they rest. When on a dark background, the pigment diffuses so as to fill the cells that contain it and in the aggregate makes the animal dark. When on a light background, the pigment collects into small knots, leaving much of the surface exposed; hence the animal is pale. These changes may be a concealing adaptation helping the animals to escape enemies.

Many animals respond to light with changes of behavior, some of which are of ecological significance. Isopods, the "pill bugs" or "sow bugs" that live under boards or stones or in other dark places, are driven into these places by their negative reaction to light. Such situations are generally moist, which is necessary for an animal which, like the pill bugs, respires by means of gills. Most other crustacea live in water, but some of the pill bugs have taken to land and have done so by utilizing damp places. Their crevices also doubtless give them some useful protection.

Some animals change their response to light according to certain other conditions. A species of thrips, a minute flower-inhabiting insect, crawls away from the source of light when it is quiet but is positive to light when mechanically disturbed. Under ordinary conditions these reactions drive the insect into the flower (a clover head, for example) where its food is; but if the flower is vigorously shaken, as by a grazing animal, it crawls out. Probably their lives are often saved by this behavior.

A more complicated adaptation involving response to light is exhibited by a parasitic copepod (crustacean) named Lernaeopoda. This animal is free-living in its larval stage but must attach itself to the gills or some other part of the brook trout to complete its development. During the day the larval copepod, because it is positive to light, swims near the surface of the water, but at night it sinks to the bottom because it is heavier than water. The brook trout likewise swims near the surface in the daytime, either in response to light or in deliberate search for food organisms which are located there, but at night settles to the bottom because of its high specific gravity. Day and night, therefore, fish and copepod are brought together—an arrangement highly satisfactory for the parasite but not so advantageous for the host.

Moisture.—All organisms contain in their protoplasm a certain amount of water, usually a very large amount. Without it they are unable to function as living things. Many of them are so constructed as to be unable to maintain this required water without living directly in water. Probably no animal can endure complete desiccation, though there are some that can exist for a long time in situations regarded as dry. Protozoa may secrete a thick wall (cyst) and lie in dry hollows (former ponds) or be blown about by the wind. Eggs of crustacea and rotifers, similarly covered with heavy shells, may likewise be dried without all being killed. One family of rotifers may be dried in the adult stage, as may also certain roundworms. Earthworms burrow deeper in the soil as moisture disappears near the surface, and eventually they roll up in balls to conserve their moisture.

Excess of moisture is often as injurious as dearth of it. Soil organisms may be drowned in wet seasons because the air is driven from the soil by water, and they are unable to obtain their required oxygen from water. The sugar-beet root louse suffers most damage from excess moisture at the time of hatching from the egg and at the periodic shedding of the skin as it grows. So much damage is done at these times that the louse multiplies in dry soil more than fifteen times as fast as in soil moistened from below, and nearly thirty times as fast as in soil moistened by water falling from above.

Insects that suck the sap of plants are more or less independent of moisture in the air around them, as long as their host plants can maintain themselves. Indeed, in such animals the water may be regarded as a waste material to be eliminated. The white fly, common on many greenhouse plants, ejects water from its rectum in frequent bubbles that burst and spray over the surrounding leaf surfaces at considerable distances. Aphids are similarly supplied with excess water.

Among the higher animals, the water requirements differ enormously. Mammals that lose much water through sweat (man, horse) or considerable excretion of urine or milk (cattle) must make good the loss by drinking. Most mammals are included in one or more of these categories, but some manage to get along with very little water except that taken with their food. Camels are the classical illustration of the ability to do without water, since they can subsist a week with only dry food, and if they are fed green plants they can avoid other water for a month or more. Mountain goats, prong-horn antelopes, mule deer, jack rabbits, gazelles, jumping mice, and some of the ground squirrels are said to use only the water that is eaten with other food. Such animals are peculiarly fitted for regions where there are few or no bodies of water.

One important ecological function of water in the protoplasm of animals is its modification of the effect of temperature. Relatively dry protoplasm endures high temperatures—even above that of boiling—without coagulation, and low temperature without freezing. It is not necessary that the water be actually removed from protoplasm to produce this effect, but merely that the amount of free water be reduced. Thus, in the pupa of the polyphemus moth, which is covered with a thick horny coat, there is little actual evaporation of the water, but as winter approaches more of the water is adsorbed on the colloidal (page 42) particles in the pupal liquids, leaving less water free. As a consequence of this condition, the pupa endures winter freezing for months.

Nutrition.—With very few exceptions, all of which are among the protozoa, animals are ultimately dependent on plants for their food. The green plants provide carbohydrates by photosynthesis, and a few microorganisms, including those forming nodules on the roots of clover and other legumes, can utilize the nitrogen of the air to produce nitrites and nitrates. Out of these primary substances animals can make any compounds they require, but plants have to make the start.

The manner of taking foods from plants is very variable. Many insects or their larvae eat the leaves or suck sap from the leaves, stems, or roots. Some eat the wood, though it is quite possible that fungi or other organisms growing on the wood or in the burrows form part of their food. Bees get carbohydrates (honey) from the flowers and proteins from pollen. Many animals grow on decaying logs or other plant matter, but it is likely that the microorganisms which are always present in such places constitute the actual food. Of the animals that do not feed directly upon plants but upon other animals, the larger ones usually, and the small ones often, kill their prey and eat its flesh. The larvae of the clothes moth eat hair or wool. Some insects live in the excrement of animals, but here again it is probably the microorganisms that furnish the food.

A very special way of obtaining nutrition is through *parasitism.* The host is usually not killed—at least until the parasite is past its parasitic stage—but contributes some of its substance to the parasite. The flukes and tapeworms are regularly parasitic, as are some of the roundworms and some insects. Parasites show a tendency to be degenerate, which they can afford to be, since in their protected situations and with their food often digested (page 265) before they receive it many of the usual organs are unnecessary. The advantages of parasitism accrue only to the parasite, none to the host.

Contrasted with this is the relation known as *symbiosis*, which is an association of two species with mutual benefit. A very striking example of symbiosis, in which food appears to be at least part of the advantage gained by both species, is that existing between termites (the so-called white "ants") and certain protozoa harbored in their intestines. The protozoa are so abundant that in some instances they weigh as much as the termite itself. The termites are wood-eating insects, and their normal food is cellulose. They are not themselves, however, able to digest the cellulose. This is done for them by the protozoa (page 259). These protozoa may be removed from the intestine artificially by high temperature or increase of oxygen or starvation, and after that the termites are no longer capable of subsisting on wood. Also, the protozoa are unable to survive outside the termites.

The amount of food and frequency of taking it vary greatly in different animals. A certain protozoon can swallow another protozoon ten times its own bulk, digest it in two hours, and be ready for another; while some insect larvae may eat a hundred times their own weight daily. Cold-blooded vertebrates, on the contrary, subsist on small quantities eaten at long intervals. Certain birds may go without food for four or five weeks, a lobster for months. Some insects do all their eating in the immature stages and take no food when adult; certain butterflies and May flies are examples. Male rotifers get all their food by eating done a generation in advance; for they take no food after hatching, all their nutrition coming from material stored in the eggs from which they hatch.

Structural characteristics in a few animals are determined or modified by their food. In the honeybee, for example, any fertilized egg may develop into a queen bee; but to attain that end the larvae must be fed on "royal jelly," which is predigested pollen prepared for and given to them by the workers. Other similar larvae denied this food become workers. A certain predatory bug acquires a yellow color by eating potato beetles, and the potato beetle gets the pigment from its food plant. The dependence of the queen bee on its food has an important ecological bearing, but no such significance is known for the other examples given.

How serious a problem food is in the ecology of a species depends on its food tolerance. An animal can live only where its food is obtainable, and it can be very successful only if its food is rather abundant. But some animals are omnivorous, being capable of eating a wide variety of other organisms, while others are very specialized. Many insect larvae live characteristically only on certain plants, numerous aphids are limited to two hosts (usually one at a time), and certain parasites are found only in one kind of animal in each (or some) of their stages. Such animals lead a precarious existence unless their food is abundant or widespread, or both.

Maintenance of Numbers.—There are other factors which enter into the lives of animals that help to determine their success of their distribution. Among them are altitude, as in mountainous regions, which affects temperature and density of the atmosphere, and pressure, as of the water in deep seas or lakes or of the air on mountains. The four discussed above are, however, among the most important, and they will suffice to illustrate the ecological situation of animals.

Each species of animal has a certain capacity to maintain itself, and this capacity is matched against an environment made up of all the factors that influence the life of the animals. If the net result of all these elements favors the species, it is successful.

An important part of the success of a species is the number of individuals it is prepared to pit against any unfavorable features of the environment. This number depends first of all on the rate of reproduction. In this activity, animals differ greatly. The larger mammals produce as a rule only one at a birth, and the period of development is long, so that successive offspring are separated by wide intervals of time. Rate of reproduction is slow in such animals. Contrast with them the small mammals. A mouse produces half a dozen at a litter, and several litters in a year, at which rate only a few years would be required for the descendants of one pair to overrun the earth. A shad may lay 100,000 eggs in a year, a tapeworm 100,000 eggs per day. A protozoon could, in seven years, produce a mass of protoplasm ten thousand times as large as the earth. One aphid could in a single summer give rise to 500 thousand million million descendants. Punnett has calculated that a female rotifer—which is parthenogenetic, lays 50 eggs, and requires only two days to reach maturity—would be able to produce in a single year, if all its potential offspring survived, a mass of rotifers large enough to fill the whole known universe and leave some over.

In bisexual animals, the sex ratio is significant in the maintenance of numbers, since the number of offspring is determined primarily by the females. A species with many females has an advantage over one with few. A short life history also favors large numbers, because there will be more generations in a given time.

Every species having great powers of reproduction is subject to enormous destruction. This is proved by the fact that it does not, in the long run, increase in numbers. Indeed, it may actually decrease. The rotifer for which the foregoing calculation was made, once an abundant object of biological experimentation, seems now to elude collection altogether; and the passenger pigeon, exceedingly abundant over most of eastern North America only a few decades ago, is now extinct. What keeps a species in check is not easily ascertained. Accidents reduce numbers to some extent, while predatory animals, disease, parasites, lack of food, and unfavorable climatic or other physical conditions must account for other extensive losses. The efficiency of a species in overcoming these obstacles determines its success. Rapid increase is not always a sign of efficiency, for species which become especially abundant in one season or over a period of several years must usually suffer a reverse later; and there are circumstances (such as exhaustion of their food) in which the greater the increase the more severe the following decline. Greater safety lies in a steady maintenance of numbers. This principle is illustrated by one of the most successful of birds, the English sparrow. A census of this species in the north central states over a five-year period showed a minimum of 9 pairs and a maximum of 13 pairs per 100 acres of land. In the northeastern states it was almost equally steady at a lower level—3 to 7 pairs per 100 acres. The number of eggs laid by the English sparrow is such that, starting with the normal number of pairs, about 260 individuals could have been produced in each 100 acres in one year. But in the long run the numbers did not increase at all, and at no time within the five years were the sparrows excessively abundant. Casual observation indicates that this stability is common over longer periods.

When some unusual event removes from the environment of a species one of its chief limiting factors, the number of individuals may increase enormously. Some of the best examples are found in the annals of economic entomology. An insect plant pest imported into a new region without the parasites which kept it in check at home may experience a remarkable outbreak. The end of such "explosions" has, in economic entomology, usually been brought about by introduction of the appropriate parasites. How they might end in the absence of help from man is problematical. The pest might exterminate its only food plant, resistant strains of the food plant might be developed through selection, or some other parasite might find the newcomer a suitable host.

Animal Communities.—Though the foregoing discussion deals mostly with single species in relation to their environment, more ecological information is often obtainable by a study of animal communities. A community consists of all the species living in one general situation. In a broad way, it is found that the species making up a community tend to be the same in many localities of the same kind. As will be seen later, similar ponds over a wide area have in part the same species in them; lakes of like size and depth not too far from each other are apt to contain many of the same species. These species are held together in a community by their requirement of practically the same set of environmental factors. Organisms requiring a given range of temperature, moisture, oxygen, and light herd together where these features are to be found. The constitution of communities is not rigid, for no two situations are exactly alike. One lake may have slightly more oxygen or lower temperature or clearer water than another. The difference may cause the communities of the two lakes to differ in certain species, though they are alike in most. Occasionally also two communities will differ in their component species by the mere accident that one or two species have been introduced into one but not into the other.

Sometimes species are held together by some very specific relation between them This relation may involve merely the nutrition of one of the species. Many plant-eating insects favor, or are practically limited to, a single species of plant: for example, an aphid that lives almost solely on the chrysanthemum. Carnivorous animals are less commonly or less rigidly limited; lady beetles nearly always feed on aphids, but accept a number of species, and can eat other small insects, such as thrips. They also devour insect eggs.

A highly specialized interspecific relation is parasitism, which has already been mentioned as one means of securing nutrition. It is referred to here again as an example of interspecific relations, because of the great lengths to which life cycles of parasites have sometimes gone in affecting other species.

In simple cases a parasite has only one host. The trematode Gyrodactylus is parasitic on the skin and gills of the goldfish. When it reproduces, the offspring become attached to the same or another goldfish. The liver fluke, however, employs two hosts. Its egg-producing stage is spent in the liver of the sheep, or certain other large mammals, but the offspring developed from these eggs must find a snail—any one of a number of genera. In the snail it undergoes a series of developmental changes, after which in a larval form it emerges from the snail and either floats in the water or becomes attached to grass. Here it is drunk or eaten by a sheep (or cow, or man) and the cycle is repeated.

A parasite in the human lung passes through three hosts in its cycle. Escaping in the sputum into water, it enters a snail. Then at a certain stage of its development it emerges into the water again, and penetrates the body of a crustacean. If the crustacean is eaten raw, as is the crayfish by people in Japan or sometimes shrimps in America, the human host is reentered and the cycle is concluded. And finally, the trematode Alaria passes through four hosts. From a carnivorous mammal, often a dog or a member of the mink family, it goes through a snail, then a frog, next a mouse or some other small mammal, and thence to a dog or other mammal which eats the mouse.

Ecological Succession.—No community of organisms is in a stable condition. It is to be expected that the component species will vary in relative abundance seasonally and from year to year. Occasionally a species seems to disappear, perhaps to return later, and other species may be added from some outside source. While these frequent changes are of interest, they are far surpassed in importance by the alterations known as succession. Ecological succession is an orderly sequence of substitutions of species in a community. Certain species increase in numbers, become perhaps dominant members of the group, then decline or even disappear. Other species rise in succession, enjoy dominance for a time, and then recede. Were this succession a purely random change, it would have little more meaning than do the irregular seasonal and sporadic fluctuations mentioned above. But in ecological succession, the species in any given type of habitat tend to follow one another in a certain order. This order of change of species is correlated with the order of change in the environment and in general is a change from instability toward a condition of equilibrium.

Plant communities of certain kinds have advantages for a study of succession, because in them the remains of earlier species are preserved. Thus, when peat is dug from bogs for fuel, successive layers of the material are well enough preserved to indicate what plants produced them (Fig. 259). The general order in such places seems to be aquatic plants, sedges, grasses, bog shrubs or alders, bog trees (larches), dry-ground

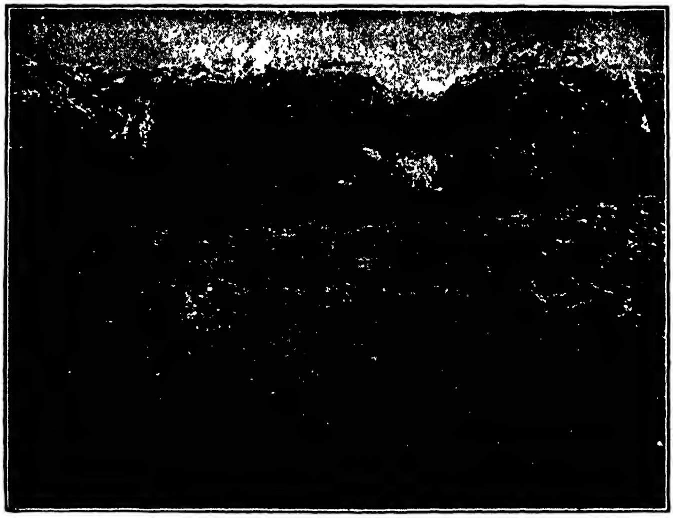

Fig. 259.—Section through peat bed. The types of plants that produced it at the different levels can be determined from the remains. (*From Weaver and Clements, "Plant Ecology."*)

forest. Successions starting on bare land begin with herbs and pass through shrubs to forests.

Animal successions are less easily ascertained and less simply described. Brief cycles may be demonstrated, such as the succession of protozoan types in laboratory cultures. These cultures are at first dominated by flagellate protozoa, then several types of free-swimming ciliates (nearly always in a given order), then the stalked ciliate Vorticella, and finally the amoebalike species. Following these protozoa come the simple plants or algae. Another succession much longer than the above, but short as compared with the plant series described, is that which is started by the wood-boring beetles that live in the trunks of living oak trees and gradually kill them. Larvae of another family, the long-horned beetles, enter the dying trees, utilizing the burrows of their predecessors. Darkling beetles come next and leave the bark separated from the wood by decaying material. Click beetles follow, bringing with them the wood-rotting fungi and bacteria. The trunk falls, and decay is gradually completed by various microorganisms. In the late stages of decay, spiders, small salamanders, and various other animals may use the log for shelter.

The longer successions of animals are too complicated for description here. The number of changes and the number of species belonging to the

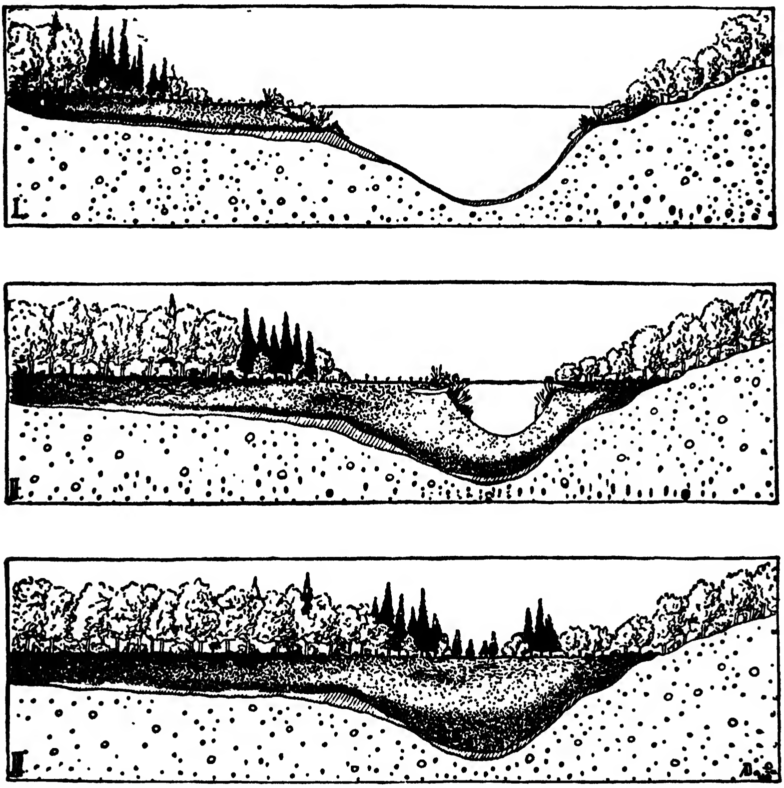

FIG. 260.—The filling of a lake with peat deposits; the succession of land plants is also shown. (*After Dachnowski in Bulletin of Geological Survey of Ohio.*)

successive communities are too great for simple summarizing. However, out of later sections of this chapter, in which various aquatic habitats are described, animal successions can be derived if the history of lakes is kept in mind. In general, lakes are being filled with washed-in soil and the remains of vegetation growing in them. They are generally converted into swamps or bogs, and finally dry land (Fig. 260). Under these circumstances, the animal communities characteristic of these situations may be placed one after another and together present a rough indication of the animal succession involved.

Fresh-water Habitats.—Of the many situations occupied by animals, the aquatic habitats have many advantages for purposes of ecological illustration. They are amenable to inexpensive study and have accordingly been thoroughly explored. They present a considerable variety of physical features and so accommodate very diverse communities. Moreover, they possess an organization which for orderliness is not easily matched in any terrestrial habitat. This organization depends on general principles which render aquatic situations capable of significant classification.

Besides the properties of water which make it an important constituent of protoplasm (see page 39), an excellent heat reservoir, and a solvent of gases, salts, and other chemical substances, it has certain characteristics which pertain to it in the bulk. These qualities become the qualities of the various bodies of water. It may be turbid or clear, which greatly affects the penetration of light. It has considerable weight; hence objects located at great depths are subjected to high pressures. And lastly, being liquid, it is highly mobile and is subject to waves, convection currents, and horizontal currents. Most organisms living in water are influenced by one or more of these features, some organisms by all of them.

The animals in water occupy different situations which are characteristic of different species. Some live on the bottom, others are free in the water and independent of the bottom. The latter include species that float passively or, if they swim, do so in an aimless, undirected fashion; and other species which, like fishes, swim actively and steer themselves in given directions. The other characteristics of aquatic animals are best described in connection with their several habitats.

Ponds.—Ponds are shallow—usually not over 2 or 3 meters in depth—and heat from the sun penetrates through all the water. The temperature is consequently nearly uniform from surface to bottom, though shading or resistance to currents by vegetation may cause differences of 5°C. between different parts of a pond. Although the water may be stirred completely by wind, wave action is so slight as to cause no important mechanical disturbance. The important gases are almost uniformly distributed through pond water; bright light and abundant algae may increase the oxygen content through photosynthesis, and, when crowded with animals, the water may contain excess carbon dioxide. Abundant rains dilute the chemical content and increase the turbidity temporarily.

Whether the bottom of a pond is covered with vegetation depends on its depth and turbidity; even when the water is fairly clear, there are few plants beyond 3 meters in depth. In most ponds, however, this permits vegetation throughout their area (Fig. 261). These plants furnish additional surface to which aquatic animals may cling. One of the chief characteristics of pond life is that it must be prepared to dry up. Typical pond organisms are those which spend part of their life cycles out

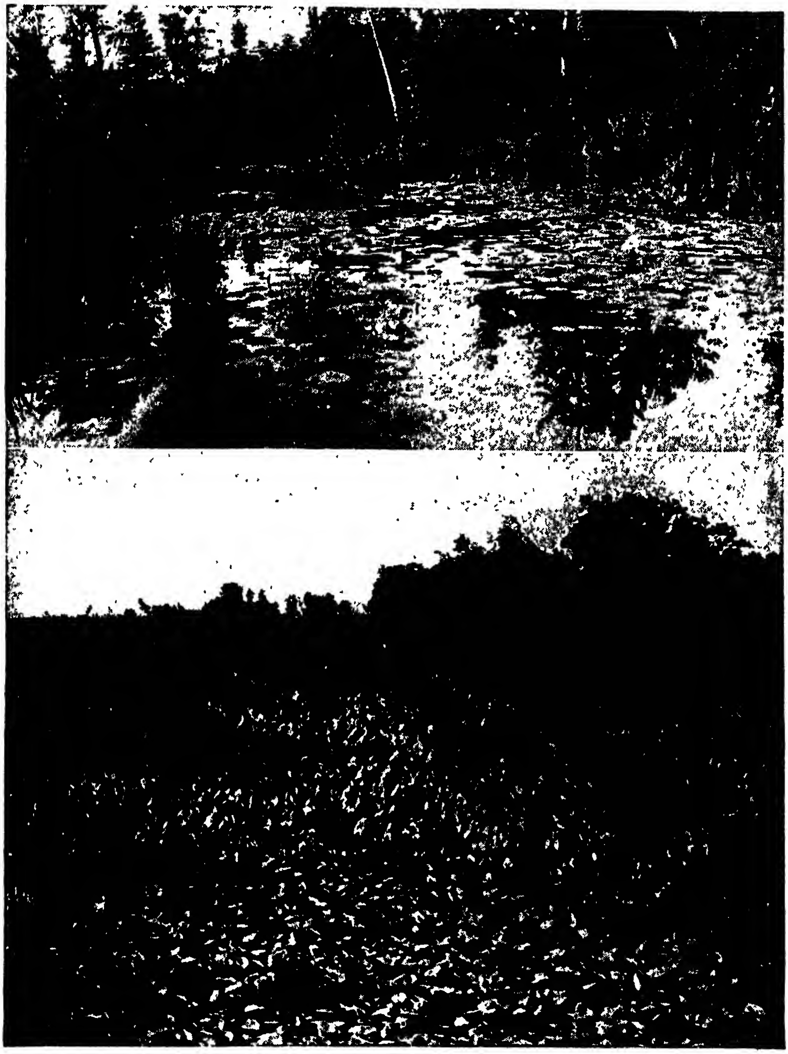

Fig. 261.—Ponds; large one above with vegetation practically throughout, small one below with heavy vegetation completely concealing the water. (*Photographs by F. C. Gates.*)

of water, either in a resting condition or actively in the air or on land. The larger ponds are permanent, and the organisms in these approach those of lakes in their characteristics. Ponds are temporary bodies also from a long-range point of view since, as explained above, they are being gradually filled in and converted into dry land; but that fact is of no importance in relation to the community of organisms existing in them at any one moment.

Animals of ponds are of too many kinds to be named with any completeness, but very characteristic ones are many protozoa; the fairy shrimp (particularly in temporary ponds); the immature stages of May flies, dragonflies, stone flies, and midges; mites or water spiders; snails and small bivalve mollusks; and often frogs, toads, and salamanders. Fish are uncommon; and occasionally muskrats build their houses in and over the water. Visitors are ducks, grebes, and other wading birds which feed upon the pond animals. Pond animals must produce many offspring, for the environmental toll is especially heavy.

Lakes.—Lakes differ from ponds chiefly in size, but this difference carries with it profound changes in all the principal factors of environment—light, temperature, and dissolved gases, with their effect upon nutrition. Lakes vary so much in their qualities, depending largely on size and geographic position, that what is said here will be limited chiefly to those of moderate size in the temperate zones. Two-thirds of the light falling upon a lake is absorbed by the first meter of water, and almost none penetrates farther than 3 or 4 meters. The bottoms of most lakes are therefore in total darkness. The heat received from the sun and from contact with warm air in summer affects only the surface water. The water near the surface is stirred up by the wind, and a layer of water of nearly uniform temperature extends down as far as wave action reaches. In a lake of moderate size this surface layer is apt to have a temperature around 20°C. in late summer, and to be 10 or 12 meters in thickness. Below this depth the water becomes rapidly colder with increasing depth, as shown in Fig. 262. This layer of rapidly falling temperature is known as the *thermocline*, and in the lake represented in the figure it extends from about 11 meters to about 20 meters in depth. Below the thermocline the water continues to become colder at lower depths, but at a very much slower rate. Since the warm water above the thermocline is less dense than the cold water below it, there is practically no intermingling, and the water below is rather completely cut off from any communication with the world above.

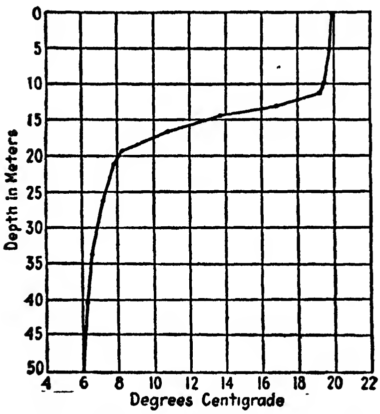

FIG. 262.—A thermocline; curve of temperature at different depths in a typical lake in summer.

In the fall the surface water becomes cooler, and the thermocline gradually disappears. When the surface water is of about the same temperature (and hence density) as the bottom water, the wind is capable of stirring the water from surface to bottom. Then the bottom water, which is held captive during the summer, may escape to the surface. In winter the surface water usually freezes to a very slight depth, but the bottom never freezes. Indeed, the bottom may be only 2 or 3° colder than in summer. The sheet of ice, if one forms, prevents wind action; and besides, water at or near 0°C. is not so heavy as that around 4°. Consequently there is no intermingling of surface and bottom water during winter. In spring, however, as the surface water warms, there is

Fig. 263.—Lake shore kept bare of vegetation by wave action. (*Photograph by F. C. Gates.*)

again a complete circulation of the water under the influence of the wind. As summer advances, the surface water is heated, and the thermocline is again produced.

Thus, twice a year, spring and fall, the water of moderate-sized lakes in the temperate zones circulates freely from surface to bottom; but at other times there is effective stratification, and surface and bottom waters do not mix. These facts have an important bearing upon the general ecological features of lakes. A lake is divided into regions whose properties are distinctly different not only in temperature but in light, gas content, and mechanical agents.

The region above the thermocline in summer is relatively warm, is well lighted near the surface, is subject to mechanical disturbance by waves, has no fixed objects to which organisms may be attached except near the shores, is well supplied with oxygen from the air (supplemented by that coming from green organisms carrying on photosynthesis), and is poor in carbon dioxide (a condition likewise accentuated by any photosynthesis going on there). The temperature of the shallow water along the shore is likely to fluctuate greatly between day and night, especially on the side of the lake toward the prevailing wind and among vegetation, where there is little agitation; but out in the open water in the middle of the lake temperature is much more nearly constant. Shore regions exposed to the wind are subject to vigorous wave action which usually prevents vegetation from gaining a foothold (Fig. 263).

Below the thermocline the water is always cold, often varying only 3 or 4° throughout the year. It is always dark. There is no wave action, and almost the only mechanical disturbance is that occasioned by the complete circulation of the water in spring and fall. A solid substratum is available for attachment. There is very little oxygen, sometimes none at all, for whatever oxygen is brought in by the spring and fall overturn of the water is consumed by decay of dead organisms that fall to the bottom, and there can be no photosynthesis in this dark region. Carbon dioxide is always abundant, likewise because of the decomposition of organic matter, except temporarily at the times of the spring and fall overturn.

The Organisms of Lakes.—It is obvious that the conditions described above have much to do with the types of organisms inhabiting lakes, and that different parts of a lake will have very different kinds. Plants can as a rule occupy only about 3 meters of the depth of a lake, owing to deficiency of light below that level. For plants springing from the soil, this means that they are limited to a narrow strip along the shore (Fig. 258). While a pond may have vegetation throughout, most lakes have plants over only 10 to 30 per cent of their area. This difference between ponds and lakes is indicated in Fig. 264. Since many animals depend on these plants, the abundance of the latter is important in the general ecology. Of the many animals found in such situations it is possible to mention only a few. In the shore region with the plants are usually snails and immature caddis flies, midges, May flies, and dragonflies. Where there is little or no vegetation because of waves, there are often mussels and young insects with flattened bodies and clinging habits (certain May flies). In the open water of the middle of the lake are sometimes floating plants, chiefly algae, so abundant as to reduce very materially the amount of light that enters the water. With the algae, and often feeding upon them, are many small animals, chiefly crustacea, protozoa, rotifers, and mites, abundant in numbers but not usually of many kinds in any one lake.

On the bottom of a lake, below the thermocline, are found those organisms requiring no light and little or no oxygen. Characteristic examples are the minute plants known as diatoms, some of the annelid worms, small bivalve mollusks, and the larvae of midges and of the mosquitolike Corethra. Such a place would not seem favorable to much life, yet Juday has found these animals make up a mass of over three hundred pounds per acre on the bottom of a typical lake.

The free-living population of a lake is subject to considerable fluctuation in amount and distribution. There is a daily variation in distribution caused by the reactions of these animals to light. Since most of them are positive to light, they accumulate at the surface during the day and settle away from the surface at night. Reference has already been made to this reaction in one of the parasitic crustacea (page 285). There is also great variation in the seasonal abundance of floating species. The algae generally have one maximum each year, occurring in midsummer, as have also certain protozoa. The diatoms, however, regularly

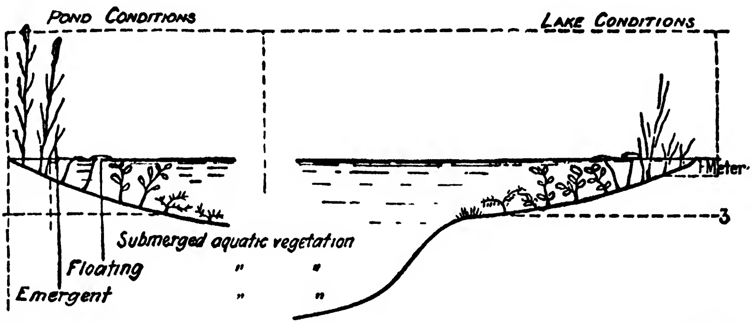

FIG. 264.—Section through pond and lake, showing contrast in extent of vegetation due to difference in depth. (*From Chapman, "Animal Ecology."*)

have two maxima, in spring and fall, respectively. The animals which feed upon these minute plants are naturally influenced by this seasonal fluctuation.

It will be observed that there is much overlapping in the general kinds of organisms living in lakes and ponds, respectively. This is largely due to the fact that the vegetated strip along the shore of a lake is not very different from many ponds. The most characteristic difference between lakes and ponds is in the swimming organisms. Fishes are common in lakes, but there are few ponds that contain them, and then only certain species. Comparison of ponds of different ages shows that the older the ponds the fewer the fish they harbor. In some regions the amphipod crustacean Gammarus appears also to be a distinguishing mark of lakes as compared with ponds.

Streams.—Water in motion has characteristics, as the habitat of animals, not possessed by standing water. The mechanical disturbance which it offers is very considerable in young streams (that is, those whose slope is steep) but much less in old streams. Soil may be carried in suspension; hence light penetration is periodically very low. Temperature is nearly uniform at various locations in a stream at any one time, but its variation seasonally for the stream as a whole is often extreme. The oxygen content of swiftly flowing water is generally near the saturation point, and most of the characteristic brook animals cannot be reared in a concentration of oxygen much below that level.

Since the chief feature of streams, as distinguished from lakes, is the movement of their water, consideration of their animals will here be limited to those whose currents are strong. This is the condition in most small streams or brooks. In such streams, animals have to be able to maintain their position; with the exception of the minute floaters, they cannot as a rule allow themselves to be carried along by the current and still be successful. One method of holding their places is to be attached to fixed objects. That is a feasible method in general, since animals do not have to travel in search of food, for it comes to them. In very swift water, one finds the larvae of the black fly, which hold fast by adhesive organs at the posterior end, while their appendages are so constructed as to strain minute organisms out of the water that flows through them. Some of the caddis-fly larvae spin nets on stones or other objects in rapids; they cling to the net, which also serves to catch food as the water goes through it. The other most abundant insects in brooks appear to be the larvae of midges, which live on or in the bottom, and May flies and stone flies of clinging varieties. In other animal groups there are snails, flatworms (planarians), amphipod crustacea, and mites. Some algae form incrustations on rocks and other objects. In the same brooks, but in the quieter water, are miller's-thumbs (fish) lurking under overhanging banks, catfishes which lie close to the bottom, and darters (fish) which are strong swimmers. The larger rivers contain larger animals, but they differ less from lake inhabitants.

The rate of reproduction of brook dwellers must be high, since the risks of loss are large. An individual that loses its station, if dependent on attachment, is not likely to become reattached until it reaches slow water, and there the conditions are not usually favorable. A single pair of midges, producing four generations a year, have a potentiality of nearly eight million descendants, but on the average only two are produced and live, in each generation, to do what their progenitors did.

Marine Conditions.—The oceans are so huge and are subject to so many variable influences in their various parts that no simple description of their environmental organization is possible. Their waters are a little heavier because of the salt content, hence offer more support to animal bodies than fresh water does. Deep water is at very high pressure, but this feature is of little significance to any animals except those fishes which have a closed swim bladder which is compressible. Very strong mechanical disturbance may be caused by waves and tides, and currents such as the Gulf Stream and the Labrador Current create special conditions of temperature and distribution. Temperature of surface waters varies little during the year in the open oceans (from 7 to 12°C. in one situation), but considerably in stagnant seas and bays (3 to 18° in the Baltic Sea). Deep water is always cold. Light of sufficient intensity to aid plant growth penetrates the first 30 to 100 meters of water but is detectable at 200 to 600 meters. Concentration of salt is increased by evaporation in the tropics, and diminished in summer in polar areas by the melting of ice. Ocean waters are also diluted by rivers, but these streams are more important for the materials

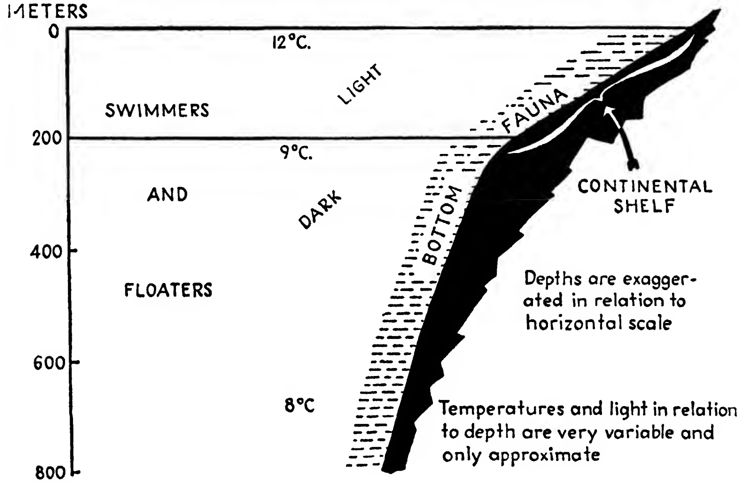

FIG. 265.—Vertical section through portion of ocean near the shore. Bottom fauna includes animals which are able to move briefly but must periodically come to rest.

they bring in from the land. The Atlantic and Arctic Oceans receive by far the greatest contribution from rivers, while the southeastern Pacific receives the least. The solubility of oxygen in marine waters is about 20 per cent less than in fresh water, and cold water (either salt or fresh) dissolves more than warmer water does. Deep waters, which are cold and which are replenished by a circulation from the polar regions, therefore have a good oxygen supply.

Ocean Bottom.—A great majority of marine animals live on, in, or near the bottom (Fig. 265). Near the shores the bottom is lighted; here it is that life is most abundant, and all groups of marine animals are found in this relatively shallow water (200 meters or less). The stock of animals in these coastal waters is generally regarded as having produced all the water-breathing aquatic forms, whether marine or fresh-water. Below the low-tide level there is abundant plant life if the bottom is one in which roots can take hold (clayey or sandy), and a rich animal population finds shelter, support, and oxygen among the plants. Where plants are lacking merely because shifting of the sand prevents their rooting, numerous animals (clams, worms, sea cucumbers, crabs) burrow in the bottom material and feed on remains of seaweeds and animals. Gravel bottom is practically without life, because movements of the pebbles in strong wave action destroy living things. Animals of this coastal area depend for food on the organic matter (largely dead bodies, including plant remains) brought in by rivers or produced in the coastal area itself.

Between low and high tide there are fewer animals, yet some are able to endure the twice-a-day uncovering, exposure to the heat of the sun in summer and temperature extremes in winter, and dilution of the

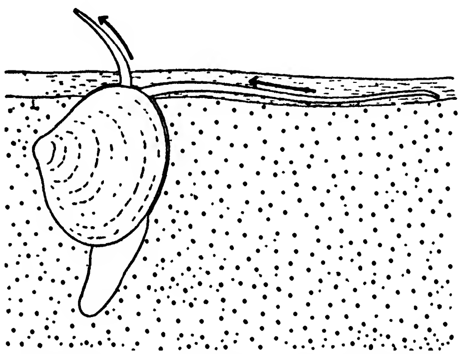

FIG. 266.—A burrowing animal between tide lines; the clam Scrobicularia.

water by rains. The clam Scrobicularia (Fig. 266) burrows in the sand and with its long inhalent siphon explores the surface around it for food-bearing water.

The ocean bottom below the effective penetration of light is less well populated. The organic remnants which serve as food here are the decaying bodies of swimming and floating animals and plants which settle down from above. The ooze thus formed has a pasty consistency. The most abundant bottom animals of the deep sea are sea cucumbers. Others are crustacea (amphipods and isopods), hydroids, sponges, clams, and worms. In general, deep-sea animals are smaller than their relatives near the surface. Also they may be more delicately constructed (fragile skeletons, thinner shells) because there is little motion of the water.

Animals of the Open Ocean.—Organisms of open water either swim or passively float. Floating life must have some way of reducing its specific gravity, since protoplasm itself is heavier even than salt water. One way is to take up much water, without the salt, into the tissues. Other ways are to develop fat, or gas chambers like those of the siphonophores or the swim bladders of fishes. The air-breathing whales, seals, and turtles are floated by their lungs. Animals having no floating mechanism must actively swim, if they are to avoid settling on the bottom; among vertebrate animals only the powerful sharks and a few bony fishes without swim bladders are capable of the incessant exertion necessary to prevent sinking.

Fewer groups of animals are represented in the open ocean than on the bottom. There are no sponges, no brachiopods, no bryozoans. Hydroids and other sessile coelenterates are missing, and there are few echinoderms (except larval stages), few worms, few clams and snails. The bulk of the swimming animals (90 per cent) are copepod crustaceans.

Ocean currents either come to an end by spreading out and slowing down to zero (Gulf Stream), or they form a closed circuit. The meeting of warm (Gulf Stream) and cold (Labrador) currents of the terminating type causes great mortality of organisms, and adds to the organic detritus used by bottom forms. The larger closed circuits take a year (North Atlantic) or two (South Atlantic) to bring their organisms back to any starting point. In the eddy enclosed by such a circuit there are often accumulations of seaweeds (Sargassum), perhaps torn loose by hurricanes, and in these weeds is a characteristic animal community (certain fishes, crabs, shrimps, hydroids). An eddy of this sort is known as a Sargasso Sea, and each of the great oceans except the polar ones has one or more of them.

Coral Reefs.—Coral reefs are built up from the bottom in tropical seas by two different groups of coelenterates, aided by a number of other lime-depositing organisms. They may be developed along the shore line (fringing reefs), out some distance leaving lagoons between them and the shore (barrier reefs), or at any distance from the mainland in the form of a ring or horseshoe (atolls). Various theories to account for reefs, beginning with those of Charles Darwin, have been proposed. The theories postulate the type of habitat in which corals will grow, the possible rise or fall of the land, differences in exposure to the open ocean, and long-time changes in the water level of oceans; but none of the theories is entirely satisfactory. About these reefs there are characteristic communities of other kinds of animals.

Geographic Areas in the Oceans.—Swimming and floating organisms requiring moderate or relatively high temperatures are limited to their respective oceans, being cut off from other oceans by the continents which they cannot pass around. Yet the animals of the Atlantic have a considerable likeness to those of the Indian and Pacific Oceans. In the copepods, even some of the species are identical. This likeness presumably resulted from the connection between the two areas across Central America in Tertiary time.

The colder ocean waters, north and south, have fewer species of animals, but more individuals in a given volume, than do tropical regions. There is a striking similarity of arctic and antarctic animals, the same genera and even species occurring in both oceans. This is presumably accounted for by the fact that there is a connection between them in the cold deep waters of the intervening ocean, which is kept cold by a north-and-south circulation of surface and bottom waters. Another possible explanation is that northern and southern species have evolved independently under the guidance of similar conditions.

Soil.—Different types of land environment represent different stages in the evolution and conquest of the earth. Starting with bare rock, the succession is roughly rubble, bare sand, sparse grass and other vegetation, herbs, shrubs, and trees. The soil may thus be in a variety of conditions, since it develops by weathering and by the action and contributions of the vegetation. In texture it may range from very fine particles, as in clay, to coarse stones, as in gravel. In a good loam suitable for plant growth, about half of the bulk of the soil is made up of spaces between the particles, and these spaces are occupied about equally by air and water. About 10 per cent of the solid matter is derived from plants; the rest is mineral.

The temperature of the soil varies most at the surface and is nearly constant below a depth of 1 meter. Surface temperature fluctuates much more if the ground is bare than if it is covered by vegetation. In very cold regions the soil may freeze so deep in winter that it is never thawed out in summer; nevertheless, vegetation may grow above this perpetual ice.

Water may be held loosely in the larger spaces between soil particles, in which case it tends to drain away by its own weight, or it may be retained by capillary action between the fine particles. Even "dry" soil has some moisture adsorbed on the small particles. Silt and clay retain much more moisture than does sand or humus.

The importance of the soil as an ecological unit may easily be underestimated, unless it is remembered that most animals spend at least part of their life cycle in the soil. Some animals spend their whole lives there, such as earthworms, some roundworms, and protozoa. Some live in the soil during one stage, such as the grub of May beetles or the pupae of many other insects. Others make their homes in the soil but spend much of their time on or above its surface, as ants and termites. Burrowing in the soil is the common mode of life of moles and shrews, while homes are built in the ground by many other vertebrate animals (ground squirrels, ground hogs, mice, etc.). In numbers of individuals, the roundworms are the most abundant group, reaching as many as half a billion per acre.

Most soil animals are near the surface, not deeper than 5 or 6 inches during the active season. Many species migrate downward annually to avoid frost and return in the spring. Earthworms have been found as deep as 6 feet, where they went to find moisture in dry seasons. Species which merely make their nests in the ground often go rather deep—gophers 2 feet, termites 5 feet, ants 9 feet, and the prairie dog as deep as 14 feet.

As a special type of soil environment may be mentioned sand dunes. The chief physical characteristic of dunes is the extreme variation of their temperature and moisture. Even in moderately moist regions, rain water drains out of sand quickly; and in the heat of midday the temperature may rise to 50 or 60°C. The hottest part of a sand dune, when the sun has been shining upon it, is directly at the surface. The air a few inches above it and the sand at a depth of several inches are cooler. Certain wasps which dig burrows are among the most characteristic dune animals; and with them are certain other insects parasitic upon the wasps. Many other animals are occasional visitors but have no particular dependence on dune conditions.

Associations in Vegetated Areas.—When vegetation has taken hold in the soil in abundance, the physical conditions are modified in several important ways. Sunshine is intercepted, thereby reducing the fluctuations of the temperature of both soil and air. The diminution of light by trees is much greater than that by shrubs or herbs, and the reduction by pine trees is much more than by larches or elms. In one forest it was found that the maximum daily temperature was 5 or 6° lower, and the daily minimum an equal amount higher, than in a near-by cutover area. Evaporation of water from the trees is one of the ways in which temperature is lowered. Some of this reduction of temperature is, however, nullified by stoppage of the wind by trees, so that open spots surrounded by forest may, when the sun shines long upon them, become warmer than they would if there were no trees. General evaporation is also reduced by this retardation of the wind, beech-maple forest exercising a much greater control than cottonwood, for example.

Introduction of vegetation modifies the characteristics of an area in very many ways, depending on what plants are present. As a consequence the animals become exceedingly varied. The nature of an animal association is determined largely by the plant association. Insects which feed upon the leaves of plants often utilize only one or a few species. Those which produce galls on leaves are commonly limited to one species of plant. Wood-boring and bark insects prefer certain trees. Soil is altered differently by different plants, and root-feeding animals usually specialize in certain roots. Rotten logs in various stages of decay contribute to the variety of situations. The general effect of vegetation on temperature, light, and humidity, described above, introduces much diversity. As a consequence of this heterogeneity, it is impossible to regard vegetated areas as single ecological units. They consist of a number of types mingled with one another. Attempts have been made to classify them on the basis of predominant types of plants, but in an elementary discussion it is not practicable to follow any of these schemes through.

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CHAPTER 21

GEOGRAPHIC DISTRIBUTION

The locations of species on the earth have been determined by two general sets of factors, the ecological and the historical. Animals must live in situations which are at least moderately favorable to them, but they are able to occupy suitable areas only if these are within reach. Many excellent sites are not occupied because they are far away, and there is no adequate means of transport. Moreover, most animals cannot be assumed to have purpose, and they cannot have knowledge of the conditions of life in other places. Accordingly, if they find new locations it must be as a result of normal activities, including some events which must be regarded as accidental.

The purely local distribution of species, which depends on ecological factors, has been discussed in the preceding chapter. While it will be necessary to point out relations to the environment in this chapter also, only such relations as bear on the history of distribution will be included. Let us see how animals have come to be where they are.

Interplay of Two Evolutions.—While present distribution of living things has often been used to prove that evolution has occurred, an understanding of zoogeography is most easily attained by reversing the arguments. If it be assumed that evolution has taken place, many peculiarities of distribution have a natural explanation.

There are two of these evolutions, independent of each other in their origins, but with intertwining results. One is the evolution of species of animals and plants, the other the evolution of the earth on which they live. New species have arisen out of older species, ever since life began. A group of individuals becomes different from their fellows, through mutation and recombination of genes and other events, and a new species is started. Usually the new species finds or at any rate occupies an area somewhat different from that of the other species. In time it gives rise to further new species, which take up their special locations. As more and more new species arise, there is a cleavage among them; some of them are much more alike, but differ strikingly from another group within which the species are rather similar. Genera are thus produced. As species change still more and more, there is cleavage among the genera, and families arise. Continued change of species results in divisions of higher ranks, the orders, classes and phyla all of which was described in the chapter on taxonomy. The whole evolution process is a change of species, carrying with it necessarily the changes of genera and higher categories.

An important feature of this process, as it relates to geographic distribution, is that new species have been arising all the time since living things first existed. New species are originating at this very moment, and may be expected to continue to come into existence in the indefinite future. Also important is the fact that new species have taken their origin everywhere, in all parts of the earth which support life. Time and place thus enter in an important way into all questions of present-day distribution. The range occupied by each species becomes a center of dispersal from which its descendants tend to spread, and these centers have existed all over the earth and through long periods of time.

Starting much earlier than the evolution of life was the development of the earth. With the early stages of this process we are not concerned; but those parts of the earth's evolution which were contemporaneous with the evolution of living things are very important in geographic distribution. The changes which affected distribution have been largely the rise and fall or other shifts of position of the land, and changes of climate. The question of permanence of continents is an important one. Most zoogeographers have held that the continents have always been, in general, about where they now are; but there is another theory, that of continental drift, according to which continents, floating on the plastic interior of the earth, have moved horizontally. A common example of this drift is the alleged separation of Africa and South America. Many European and some American geologists have supported the drift theory, but distribution of animals has seemed to most biologists to call for more nearly permanent continents.

Regardless of the general position of continents, their shapes have changed. Many areas of dry land teem with fossils belonging to classes which are strictly marine. Such areas must once have been under the sea. Michigan, for example, contains many extinct corals, though it is now hundreds of miles from any salt water. Even high mountains have arisen out of the ocean. Land has also sunk, and areas which were the shores of an ocean have become its bottom. Broken shore lines are a common result of the sinking of hilly or eroded land.

Changes of climate have also been frequent. Michigan and most neighboring areas have been under glaciers more than once. At the other extreme, more northern regions have been tropical, as indicated by luxuriant plant growth preserved as fossils. Humid areas have become dry, swamps have become dry plains, forests have been converted into grasslands. These changes must have affected the distribution of animals profoundly.

The timing of the changes of species and the changes of the earth must have had important consequences for living things. When a group of animals experienced the genetic changes which might lead to the formation of a new species, any changes of the land or climate occurring at the same time and in the same region could spell the difference between survival and destruction of the new group. When a region of the earth was undergoing a physical (perhaps climatic) change, any genetic change going on in a few individuals could decide whether any members of their species would survive the changes of environment. For the sake of emphasis these changes are described as sudden and radical; actually they have been very gradual. Interplay of the physical forces of the environment and the genetic forces of animal or plant life must have been crucial in the guidance of evolution, and in the determination of the location of resulting species and higher groups. Let us turn to some of the facts of distribution, to see how they fit into the general scheme just outlined.

Position of Ranges.—It is easily observed that species, families, orders, etc., have their characteristic places on the earth. With the exception of closely interdependent species, such as parasite and host, probably no two species have exactly the same range. The musk ox is arctic; the nine-banded armadillo ranges from Texas to South America; the North American alligator exists only in the extreme southeastern part of the United States. Among such vastly different groups, widely separated ranges do not occasion any comment. Within a single genus, however, the several species have their distinct areas. For example, in the genus of spadefoot toads, *Scaphiopus couchii* extends from Texas to Arizona, and into northern Mexico, including Lower California; *S. hammondii* ranges from Montana to Mexico and west to the Pacific states; *S. holbrookii holbrookii* occurs along the Atlantic from Massachusetts to Florida, and west to Louisiana, Texas and Arkansas; *S. holbrookii albus* is only in the Florida Keys, or possibly also the extreme tip of Florida; and *S. hurterii* is found only in Texas.

The location of a species range depends primarily on where the species started. The present range must usually be around or near the point of origin. Looking backward, one sees the "center of dispersal" of a species as some point in or near its present range. Most species have not lived long enough to have traveled far. Very old species, however, especially those which survive in only a few individuals, may be far from their places of origin. Such old and nearly extinct species may usually be recognized as such because no closely related species are anywhere near them. Species consisting of few individuals because they are very young are, on the contrary, surrounded by very similar types. Remnants of very old species are spoken of as *relicts*. Examples are the several species of Nautilus, sole survivors of a once flourishing family (the tetrabranchiate cephalopods), now found only at places in the Pacific and Indian Oceans.

Size of Range.—Equally striking are the different sizes of ranges occupied by the various forms. When groups of high and low taxonomic rank are compared, as orders with genera, inequalities are to be expected. One simple reason is that the higher groups are made up of a number of lower ones. When those of the same rank occupy very unequal areas, an explanation is not always easy. Particularly important in the theory of distribution are unequal ranges of species. Some ranges are very small. One species of ant is found only in the Garden of the Gods in Colorado, another species occupies much of North America. Kirtland's Warbler, not including its migration routes, exists only as a few individuals in a very limited area, while the American Robin numbers millions of individuals and covers a continent. Among plants, a species of Oenothera includes only 500 to 1000 individuals and is known only in a mountain range in southern New Mexico. One of the spadefoot toads, already mentioned, occurs only in the islands off Florida and perhaps at the extreme tip on the mainland, while another species of the same genus has a range a thousand miles wide.

When there appears to be no difference in the tolerance, rate of reproduction, or means of locomotion of two species, a tempting explanation is a difference in age. This is thought to be the reason for the very unequal ranges of four species of tree frogs (genus Hyla). *Hyla versicolor* is found from southern Canada to the Gulf states, and west to a line between Montana and central Texas; *H. squirella* extends from Virginia to Florida, west to Texas and Indiana; *H. gratiosa* from South Carolina to Florida and Mississippi; and *H. evittata* only along the Potomac and York Rivers in Virginia and New Jersey. The species believed to be the younger have the smaller ranges, and the explanation may be simply the shorter time they have had to spread.

This idea has been developed as the "Age and Area" hypothesis, and has been applied more to plants than to animals. In accord with it is the fact that on the average groups of higher taxonomic rank (orders, for example) occupy areas larger than those belonging to groups of lower rank (genera, let us say). In general, the higher groups are older, and have had longer time to disperse. Some paleontological support for it is also claimed, for when the ages of taxonomic groups can be judged from the geological periods which furnish their earliest known fossils, the older ones again have the larger average ranges.

There are known exceptions to the rule, however, and probably many which are not known. Two species of shepherd's-purse differ in the number of chromosomes in their cells, one having just twice as many as the other, and it is fairly certain that the one with the larger number sprang from the other by a doubling of the chromosomes. This is a well known method of origin of species in plants, and must apply to this example. However, the species with the double number of chromosomes (which must be the younger one) ranges much more widely than the one with the smaller number. One species is simply much more successful than the other.

Continuity of Range.—Because a group of animals starts at some point, from which its members tend to spread until barriers are reached on all sides, ranges are expected to be continuous unless something happens to break them up. Taxonomic groups of as high rank as families and orders have usually been developing long enough for that "something" to take place. Ranges of such groups are large, and living conditions may change sufficiently to extinguish the animals across the middle of the area, thus dividing it in two. The camel family, for example, is represented by the true camels in Asia and Africa, and by the llama and its relatives in South America, with the great land gap of Europe and North America between. Fossil camels, however, are found in the area now vacant. The genus Alligator is composed of two species, one in central China, the other in southeastern United States. Extinct relatives of the alligators once ranged widely in North America and Europe, showing how the modern range became discontinuous.

When the rangé of a species is found to be discontinuous, which is rare, the reason is not easily found. The skink, *Leiolopisma laterale,* is found in southeastern United States, in China, and in certain of the southern Japanese islands. Why is it not in the areas between? Only if the species is an exceedingly old one would it be likely that destruction of its members over a large portion of its former range could have occurred. So improbable is the division of a species range by extinction that every example of it raises the question whether the species may not have developed independently in two places. Such an occurrence is not impossible. Many mutations are known to be produced repeatedly, and among random recombinations of genes the same combinations could occur anywhere. If environment of a certain type tends to preserve certain genetic combinations, similar environments in two areas could guide evolution in the same direction. Such double origin of a species would not be a violation of the taxonomic concept that all members of a species are descendants of common ancestors, for the two groups from which the species arose would necessarily be much alike, both having come from the same ancestry. The common ancestry of a duplicated species would thus be simply pushed farther back. Nevertheless, this dual origin of a species is so unlikely that it is not to be lightly assumed as an explanation of discontinuity.

Physical Conditions of Ranges.—Lest the ecological factors be forgotten in the study of historical phenomena, it should be observed how different are the conditions obtaining in different ranges. A striking illustration of this is found in the distribution of vegetation. The general vegetation areas of North America are shown in Fig. 267. Coniferous

FIG. 267.—General vegetation areas of North America. (*From Burlingame, Heath, Martin and Peirce, "General Biology," Henry Holt and Company, Inc. Prepared by A. G. Vestal.*)

and deciduous forests are separated by physical conditions, largely temperature, and they in turn determine the location of many animals. The eastern deciduous forests are the home of the opossum, gray fox, fox squirrel, cardinal bird, Carolina wren, and yellow-breasted chat. The northern coniferous forests shelter the snowshoe rabbit, pine martin, northern jumping mouse, three-toed woodpecker, and spruce grouse. The open treeless areas of the west are inhabited by the prong-horn antelope, bison, ground squirrels and many others. So nearly are many of these animals limited to one type of vegetation area that it is difficult

Fig. 268.—Ranges of the North American flying squirrels, *Glaucomys volans* and *G. sabrinus*. (*After Howell, "North American Fauna," No. 44.*)

to avoid concluding that the conditions prevailing in such areas are paramount in their lives. Sometimes the maps of ranges of forest animals and of prairie animals appear to overlap, as if the vegetation were not of great importance. In one such case, however, the appearance of mixture was occasioned by the fact that a series of somewhat parallel streams with trees along their courses were separated by strips of grassland. The forest animals were along the streams, the prairie

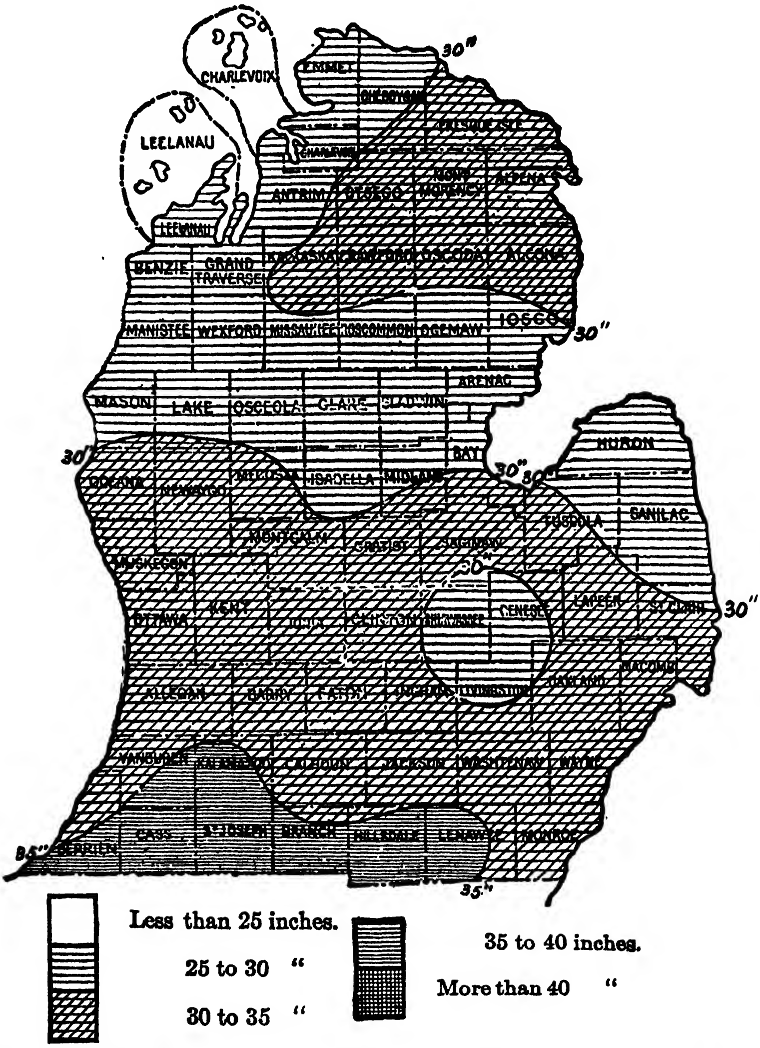

FIG. 269.—Annual rainfall in the lower part of the state of Michigan. This illustrates the differences in physical conditions which may prevail even in relatively small areas. (*After C. F. Schneider, Publication* 9, *Michigan Geological and Biological Survey.*)

animals between them; but on a map of moderate scale they appeared to be together.

An actual example of species definitely related to forests is the genus of North American flying squirrels. As shown in Fig. 268, *Glaucomys* *volans* is in general limited to the deciduous forests, while the range of *G. sabrinus* approximates that of the coniferous forests. Limitations of these species to forests is mostly caused by their feeding on nuts and seeds, to a lesser extent by their habit of "flight." Two animals that do *not* pay much attention to vegetation areas are *Rana pipiens*, the common leopard frog, which occurs all over North America east of the Sierra Nevada range; and the raccoon, *Procyon lotor*, which lives in deciduous forest areas and the prairie-plains region as well. The leopard

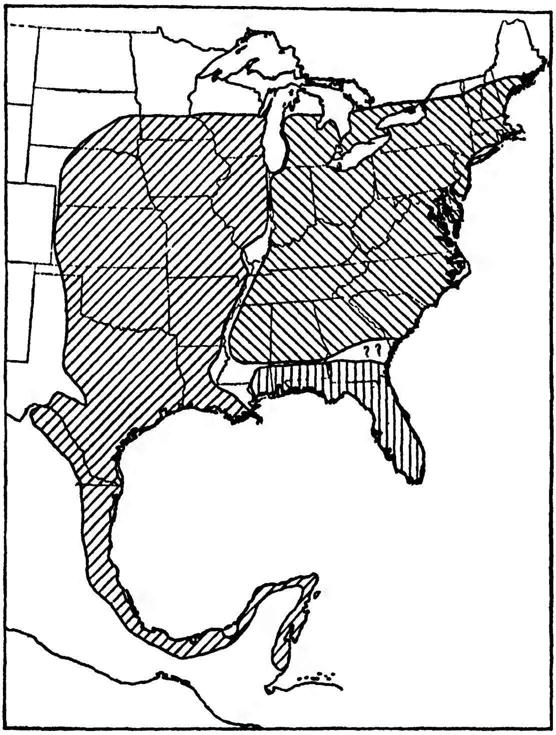

Fig. 270.—Proximity of ranges of three subspecies of one species of garter snake. West of the Mississippi and in Mexico, *Thamnophis sauritus proximus;* in Florida, *Thamnophis sauritus sackeni;* north of Florida, *Thamnophis sauritus sauritus.* (*Modified from Ruthven.*)

frog ignores forests because of its semiaquatic habits, the raccoon because of its tolerance of various conditions.

Besides vegetation, important physical conditions bearing on the distribution of animals are temperature and rainfall. Even in a limited area the amount of rainfall differs greatly, as shown in the map of Michigan in Fig. 269.

These several factors are sufficient to illustrate that geographic distribution is not wholly a historical development. Ecology and the time and place of origin of species have worked together.

Proximity of Related Forms.—If species originate from other species it would be expected that a very young species would still be near its progenitor. It would not have had time to travel very far. If the youth of species and the sources from which they have sprung be judged from the similarity between species, this expectation is in general realized. Those species of a genus, or those subspecies, which are most nearly alike are found geographically near one another. An example is found in a group of garter snakes known as ribbon snakes. The forms in question are three subspecies of one species, *Thamnophis sauritus*. One subspecies, called *proximus*, occupies a range west of the Mississippi River and along the east coast of Mexico (Fig. 270); another, named *sackeni*, is in Florida and on the Gulf Coast east of the Mississippi; the third, *sauritus*, is east of the Mississippi and north of Florida. The three ranges are practically in contact with one another; at any rate they are not separated by ranges of other garter snakes. Other species of garter snakes are at a distance.

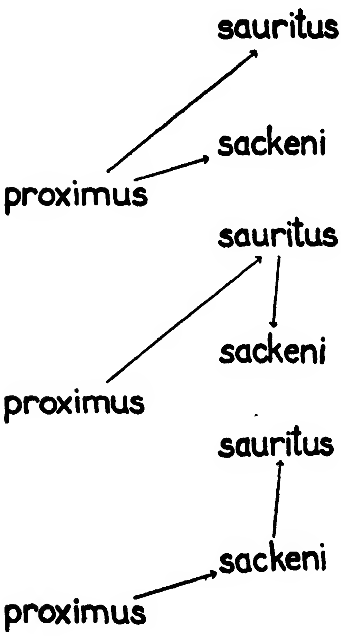

Fig. 271.—Three possible origins of subspecies *sauritus* and *sackeni* from *proximus*, in a garter-snake species. (*After Ruthven.*)

The earliest of these subspecies, as judged from their characteristics, appears to be *proximus;* from it *sackeni* and *sauritus* must have sprung. The order in which the latter two forms arose is in doubt. The possibilities are portrayed by Fig. 271; *proximus* may have given rise to *sackeni* and *sauritus* separately, or it may have produced one of them (either one), and this in turn produced the other.

The principle that nearly related (that is, similar) animals are geographically near one another is illustrated also in the higher taxonomic categories. The genera of mammals east of the Rocky Mountains in the United States have more similarities among themselves, and the genera of the Pacific coast area more mutual likenesses, than do the eastern genera to the western genera. The principle holds even for continents. The animals of one continent are usually more alike than they are like those of any other continent. Moreover, the faunas of neighboring continents are more alike than are those of more distant continents. The animals of North America and Eurasia are particularly good examples of this phenomenon. The similarity of these two faunas is believed to have been increased by a land connection between them across the Bering Strait and the adjoining Arctic Ocean, which would have permitted migration between them up to (geologically) comparatively recent times.

In all these instances the argument is that the similar animals have had more recent common ancestors, and there has been less time to migrate far away. The effect of a barrier, for example, the Rocky Mountains helping to keep eastern and western mammals apart, is merely to push back the time of the common ancestors of the less similar types, and so make their dissimilarities greater.

Normal Migration.—So important in the explanation of these peculiarities of distribution are the abilities of the members of species to spread, and the time they have had at their disposal to attain their present locations, that the means by which they have become dispersed should be examined. By far the most important method is what may be called their normal migration. This is best seen in freely moving terrestrial forms. The individual seeks food or shelter, avoids enemies, seeks a mate. How rapidly it moves depends on its powers of locomotion. Whether it goes alone or in flocks or herds depends on little understood psychology. These activities lead inevitably to the occupation of more territory, unless barriers forbid, and by a young species barriers are not as a rule reached very soon.

This spread by normal migration is ordinarily very gradual. Under special circumstances, however, it may be greatly accelerated for a time. The potato beetle, *Leptinotarsa decemlineata,* was long restricted to the Rocky Mountains and the plains east, as far as western Kansas and Nebraska. It could go no farther because its natural food, a wild species of Solanum, did not exist east of that area. As the western part of the Mississippi valley became settled, the range of the cultivated potato (*Solanum tuberosum*) extended farther and farther west, until between 1845 and 1850 it reached the range of Leptinotarsa. The beetle found the new Solanum a suitable food, so the eastern barrier was removed. In about 20 years it had reached the Atlantic seaboard, where it stopped until about 1918. Presumably in troop movements and shipment of food supplies in the war, the beetle was carried to Europe, where it has since existed despite efforts to eradicate it.

How effective normal migration may be in spreading species is indicated by some computations. For the slow-moving earthworms, Gadow calculates that if one pair produces enough offspring to occupy one square yard of soil in one year, their descendants in the time since the Ice Age (perhaps 30,000 years) would have choked the earth. Again, if a human family moved, gypsy fashion, only one day a week, and not more than three miles, then it would wander 156 miles each year; and the Mongolians, crossing Bering Strait, might at this rate have reached the Straits of Magellan in 50 years.

Periodic Migration.—Not all the movements of animals are of the slow, steady, progressive type just described. Many species move in large numbers from one place to another at different times of the year or at different times in their life history. The southward migration of many birds in the fall and their return in the spring is an example of seasonal migration. The great majority of bird species which may be found in the course of a year at a given place in the middle of the north temperate zone, for example, are seen there only at certain times. A small number of species spend the summer there, building their nests and rearing their young but disappearing southward in the fall. A still smaller number are winter residents, some of which have come south from a more northerly summer range. A much greater number are migrants, going north in spring to their breeding range and returning southward as cold weather approaches in the fall. What causes birds to migrate is one of the great biological enigmas. Migration starts before the situation where they spend the winter or summer becomes unfavorable. In some species the migrating is done correctly by young birds without previous experience and without guidance. Individual birds have often been found to return to the same nesting place in successive summers, but the way in which they are guided to the spot can only be guessed. It has been suggested that endocrine secretions (page 154), particularly those of the pituitary and of the gonads, and the duration of daylight may initiate migration, but how they could guide it is not clear.

Some other animals migrate seasonally in search of food. When the bison was abundant in the western plains, it wandered in droves north and south as grazing lands developed. The mule deer moves up and down the mountains likewise in search of vegetation. In these instances, however, there is no puzzle, for the animals move slowly, and they wait until the new feeding grounds are needed and are available. They do not anticipate events but direct their movements in relation to what can be actually seen.

In a few animals the migration is not seasonal but occurs once each direction in a lifetime. The fresh-water eel migrates at times separated by an interval of years. In its youth this animal ascends the rivers from the sea and lives there for years but does not breed; upon reaching maturity it returns to the sea to breed. The Alaska salmon shows a similar migratory habit.

Though *periodic migration* is important in the physiological cycle of individuals and in the economy of species, it is not known to have any influence on species ranges. There is no known peculiarity of distribution anywhere which seems to demand periodic migration as its explanation. The mere fact that the animals have to return from the place to which they periodically travel nullifies any effect which such movements might have on the size of the range. Migration would have to be accompanied by some physiological change in order to extend the area occupied.

Sporadic Migration.—Somewhat allied to periodic movements perhaps are the sudden outbreaks or irruptions of a species that may occur, during which the range is widely extended. The classic example is that of the Lapland lemming, a small rodent. The migration of this species has been described by Lyell as follows.

> "Once or twice in a quarter of a century they appear in vast numbers, advancing along the ground and 'devouring every green thing.' Innumerable bands march from Kolen, through Northland and Finmark, to the Western Ocean, which they immediately enter; and after swimming about for some time, perish. Other bands take their route through Swedish Lapland to the Bothnian Gulf, where they are drowned in the same manner. They are followed in their journey by bears, wolves and foxes, which prey upon them incessantly. They generally move in lines, which are about three feet from each other, and exactly parallel, going directly forward through rivers and lakes; and when they meet with stacks of hay or corn gnawing their way through them instead of passing around."

Another case of sudden movements is afforded by Pallas's sand grouse. This species inhabits the steppes of central Asia, extending into northern China and the Kirghiz Steppes north of the Aral Sea in the winter. At least since 1859 the bird has been in a restless and disturbed state and great waves of individuals have moved out from the normal range. In an irruption in 1859 some of them reached Poland, Holland, and the British Isles. Another outbreak in 1863 apparently involved thousands of individuals, and the birds reached Italy and the Pyrenees in the south of Europe, Scandinavia and Archangel in the north, and the British Isles and the Faroes in the west. Still another wave occurred in 1888 and at this time flocks appeared in England, Scotland, and Ireland. After each wave the species soon disappeared from the invaded countries. The extinction may have been due to slaughter by man; but while some of the invaders bred the first year, they were not so well established that they could have reared young.

Such sporadic outbreaks are apparently of the same nature as those which have been observed within the range of a species. An example is the mouse plague of 1907–1908 in the Humboldt Valley, Nevada. These mice (*Microtus montanus*), which live in scattered colonies in swampy places, are not usually abundant enough to attract notice. They produce half a dozen at a litter and four to six litters per year, but ordinarily are kept in check. In the year named, however, some element of control was removed, and the mice were produced in countless thousands. On some ranches there were as many as 12,000 per acre. Crops were destroyed, trees killed by injury to their roots, and banks of drainage ditches were riddled with their burrows. Great armies of mice moved on to new fields 5 miles or more from the point of first concentration. Then their hordes disappeared even more quickly than they arose. In the course of three months they dropped to only 200 to 500 per acre. No satisfactory explanation of either their increase or their disappearance was ever discovered.

Apparently *sporadic migration,* as these irruptive movements may be termed, does not usually result in an extension of range, for the species in the cases observed have not been able to maintain themselves in the invaded regions. However, it is possible that at times such irruptions have brought species into regions where conditions were favorable and thus enlarged the inhabited area. Instances of widely discontinuous range have sometimes been explained, whether correctly or not, by appeal to sporadic migration.

Accidental Dispersal.—Discontinuous ranges have been more often attributed to *accidental dispersal* than to sporadic migration. Animals are sometimes carried on rafts or floating logs or are blown by the wind beyond their normal range. Marine birds, such as the gannet, are occasionally during storms blown inland from the Atlantic Ocean as far west as Michigan, and a number of observers in the tropics have noted terrestrial animals on floating logs and rafts in the rivers and even out at sea. It has often been asserted that this method of dispersal is efficacious in extending the range. Islands may have received certain forms by accident, but there are many difficulties in accounting for the entire faunas of islands in this way. Some of these difficulties are (1) the inability of some forms to survive a long sea voyage, (2) the fact that many island forms, such as the giant tortoises, could not possibly be carried on rafts or blown by the winds, (3) the necessity that in the higher animals at least a pair of individuals or a pregnant female be landed if the form is to be perpetuated, etc. But the greatest obstacle to the acceptance of accidental dispersal as an effective method of extending ranges lies in the fact that actually observed cases of accidental dissemination beyond the range of a form are very few and mostly open to question. Possibly it may operate at rare intervals, for certain forms and over short distances.

Man himself is responsible for the introduction of animals and plants to new regions in a few instances that are well known. Sometimes it was done by design, more often by accident as in the transport of rats in ships. The animals carried by man have sometimes succeeded much better in their new locations than in the original ones, witness the rabbit in Australia, the cotton boll weevil in southern United States, and the English sparrow in America.

World-wide Scheme of Distribution.—Having so far examined some of the peculiarities of distribution, and the biological or geological processes needed to explain them, we may now attempt to see how these interlocking phenomena affect distribution on a large scale. One must usually limit such a study to a single major group of animals because of the different timing of evolutionary events in relation to changes in the earth. Zoogeographers have proposed different groups for this purpose. Mammals, snails, earthworms, birds, reptiles, insects, all have been urged as suitable. We shall use mammals, primarily because the different kinds are better known among nonbiologists, but partly because they are large, and the world has been explored enough to discover the location of most of them. They have one further advantage: their evolution has been rapid and recent, so that the effects of changes of the earth will be more readily discovered than in groups whose evolution has been slow and protracted.

The bulk of the land area of the earth is in the northern hemisphere. With the connection which must have existed across Bering Strait, this land was formerly a continuous body. From this area there project southward three great continental masses, South America, Africa, and Australia. The last is believed to have been connected with Asia across the Malay Archipelago prior to Jurassic time. South America, though now connected with North America, is held to have been separated from it in early Tertiary time. This is indicated by similarity of the marine animals on the east and west coasts of Central America, as well as by geological evidences.

Origin of Mammals.—Primitive mammals are believed to have arisen first in the northern continents. This conclusion flows partly from theory, since the great variations of environmental conditions characteristic of huge land masses should have been able to act selectively on almost any type of evolutionary change which happened to occur in living things. The northern continental mass as the place of mammalian origin is supported, moreover, by the fact that the most primitive fossils of the group have been found there, though it must also be said that more explorations have been made in that area.

These primitive mammals, resembling our monotremes and marsupials more than true mammals, must have spread in all directions. To the north barriers were soon reached, but to the south the three great prongs of land provided ample room; and they had a geological age or two in which to enter these.

Then the higher (true) mammals began to arise, also in the northern land mass. They proved to be superior to their predecessors, that is, more able to cope with the environment. This supposed superiority of the later mammals has been demonstrated in modern times by the introduction of northern true mammals into the southern areas, where they began to replace the primitive forms already there. This has happened very noticeably in Australia, where the dingo and rabbit were introduced. Something like a general principle must be involved here, for in other groups of animals northern forms have displaced southern ones when they have been brought together. This has happened in the case of birds (sparrow, starling, blackbird, and others) introduced into Australia, the goldfish in Madagascar, European ants and earthworms in all the southern continents.

The early mammals were thus driven out of the northern continents which they first occupied. With Australia then joined to Asia, and South America not yet separated from North America, they were free to fill all the southern land masses. Then the sinking of the land cut off Australia, so that the true mammals were not able to follow, and that continent was and is the principal home of the marsupials and monotremes. The severance of the Americas from each other checked the southward migration of the higher mammals, so that primitive types are relatively more common in South America. Restoration of the land connection at Central America has, however, permitted many of the true mammals to reach the southern continent. The traffic was not all in one direction at the isthmus, since the opossums and armadillos reached North America from the south over this restored land connection.

Primitiveness of Southern Faunas.—The scheme just outlined should have caused the faunas of the southern continents to be on the average more primitive than those of Eurasia and North America. For the mammals of Australia and South America this has already been shown to be true. To a less marked extent it is true also of Africa south of the Sahara; for there is the primitive little deerlike chevrotain, and there are the lemurs, the aardwolf, and the golden mole. In Madagascar is a host of lemurs; and if other groups of animals are to be considered, that island has the most primitive bird of the crane and rail group. Also outside the mammalia, Australia has the most primitive termites, the simplest insects of the butterfly-and-moth order, and some of the most primitive bees. The most primitive land snails are in the southern continents; indeed, the whole mollusk fauna of South America may be characterized as primitive. The three surviving genera of lungfishes are in the three southern continents, one genus in each. The lungfishes are well represented by fossils in North America and Eurasia, and the three living genera are plainly relicts.

Land Connections.—The connection and separation of land masses postulated in the foregoing account mostly are supported by geological evidence; that is, they have not been invented merely to explain animal distribution. This is particularly true of the changes in Central America or the Isthmus of Panama. These changes could be safely assumed on geological evidence alone.

Zoogeographers have not hesitated, however, to assume former land connections for which geology gives no support. Geologists have sometimes been the authors of such connections but have based them on the facts of modern distribution. North America and Europe have been assumed to be connected through a strip of land taking in Greenland, arching north of the Atlantic, and joining Europe through the Scandinavian Peninsula and the British Isles. An antarctic land bridge connecting the tips of South America and Africa with Australia was proposed by the British geologist Hutton to account for the large flightless birds in those areas. This bridge has been adopted by many others since, but it seems unnecessary, for the connection of the southern continents with the northern land mass is adequate to account for the degree of similarity of the animals. A land bridge has even been thrown across the middle of the Atlantic Ocean, from western Africa, say, to Brazil and the West Indies. This bridge has been employed by many students of distribution and is supported even now by reputable zoologists. The trend, however, has been away from extensive land bridges. They may have existed, but some of them seem geologically so improbable that zoogeographers are seeking other explanations for similarities of faunas, or are frankly leaving the facts unexplained rather than postulate the bridges.

Major Realms.—From the beginnings of zoogeography, many attempts have been made to divide the earth into half a dozen or so major realms which would have significance for all kinds of animals. Birds were first used for such a division, then mammals. For these two vertebrate groups the boundaries of the realms were somewhat similar, and the authors of the schemes believed that other animals would fit into the same divisions. Much of the work of zoogeography has consisted of fitting groups of animals into the realms and modifying the boundaries when necessary.

It has become increasingly clear, however, that different kinds of animals do not observe the same distributional limits, and that theoretically they should not do so. Each group must be delimited by a different scheme. New Guinea, with respect to its earthworms, belongs with eastern Asia; but in its other animals it is Australian. The earthworms of Ceylon, on the contrary, are of Australian types, despite the nearness of the island to Asia. Chile differs from the rest of South America in its mollusks, fresh-water fishes and earthworms, but agrees with other parts of the continent in its birds and mammals. It is true that in highly isolated areas like the Hawaiian Islands, Madagascar, and

New Zealand, the barriers are such as to affect nearly all animal groups; but they have done so to very unequal degrees.

One reason for the necessity of different distributional areas for the different kinds of animals is the very different history of evolution of each group. It makes a great difference whether, at the time of geologic isolation of an area, the animals in it are evolving rapidly or are rather stable. Madagascar, for example, is inhabited by mammals belonging mostly to families found nowhere else, but by amphibia, reptiles and insects belonging frequently even to the same genera as those of the African mainland. Australia is peculiar as to its mammals, but much like the Oriental realm (including southeastern Asia and some East Indian islands) in its lizards, butterflies, and earthworms.

It seems clear now that progress in interpreting the distribution of animals is to be made only by working out the history of each group separately.

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CHAPTER 22

FOSSIL ANIMALS

Many of the fundamental problems which exist in connection with living organisms may also be studied, and in some degree solved, with reference to beings, now extinct, which lived on the earth in times past. This biology of ancient life is termed *paleontology*. Paleontology may be defined as the science of fossil organisms.

Fossils.—A fossil is any trace of prehistoric life. Most organisms have left no trace because they were soft-bodied. Organisms with hard shells or skeletons had the best chance of being preserved, but even these were screened by a fine sieve of circumstances and most were lost. An animal whose bones are to be fossilized must usually be buried soon after death to prevent the destructive action of oxygen, water, freezing and thawing, and bacteria; and after it is seemingly safe the fossil is subject to the risk of heat and pressure which would alter it beyond recognition. Teeth are more likely to be preserved than bones, because they are highly resistant; teeth of mastodons are often saved when the bones of the same individuals have disintegrated.

A fossil need not be any part of an organism. It may be only an impression, a track, or even a burrow. A dinosaur walking on clay, not too hard or too soft, has left its footprints to the present time. A leaf leaves an imprint in the silt in which it is buried, and this impression is a fossil.

Similar objects buried only several thousand years ago are not regarded as fossils; that is a matter of definition. Fortunately not many objects belonging to the border line of prehistory are found, so that little difficulty arises from the stipulation that a fossil be prehistoric.

How Fossils Are Preserved.—Some animals in cold regions are preserved in the flesh. That happened to numerous woolly mammoths in Siberia (Fig. 272). They fell into crevasses in the ice, were covered with snow, and at the very low temperatures were quickly frozen. Even the undigested food in their stomachs is recognizable in some of them. These bodies have been frozen for probably 20,000 years. Some frozen mammoths have been found in Alaska also, but only fragments of the flesh were preserved. Other preservatives of flesh are oil in petroleum lands (Poland, Galicia) and the acids of peat bogs. Human bodies have retained their flesh, thoroughly dried and therefore resistant to bacteria, in the dry southwestern parts of the United States.

Soft parts have sometimes been preserved merely as films of carbon, which is the residue of the protoplasm. These films outline the body perfectly, around the skeleton which retains more nearly its original condition.

Entire insects in coniferous forests of the Oligocene epoch became immersed in the sticky resin on the bark of the trees, which then hardened, and may still show the delicate spines or the scales of the wings in butterflies as clearly as in the original.

More often only the hard parts are left—the tubes of corals (Fig. 273), the shells of clams, the bones of vertebrate animals. Usually these hard

FIG. 272.—Mammoth found frozen in Siberia in 1901. Most of the flesh was still on the body and intact. The skin is mounted in the museum of Leningrad in the posture in which it was found. (*From Lull, "Organic Evolution," courtesy of The Macmillan Company.*)

parts must be buried before disintegration has proceeded far. They may rest at the bottom of a lake, and be covered by silt carried in from the land; they may lie on flood plains of streams and be buried under deposits at times of high water; they may sink in the soft mud of bogs, be buried in wind-blown dust, or covered with volcanic ash. Very often the burying material hardens into rock by the cementing action of ground water carrying minerals; this is particularly true of under-water deposits. After such hardening, the shape of the buried object is usually maintained, regardless of what becomes of the material of which it is composed.

Sometimes the entire buried shell or bone is dissolved away by ground water, which usually contains some carbonic acid (carbon dioxide in solution). The cavity thus left is a *mold*. If this cavity is later filled by minerals deposited from the ground water, the mass thus formed (called a *cast*) has the external shape of the original structure (Fig. 274). Both molds and casts are fossils, though they include no part of any living thing.

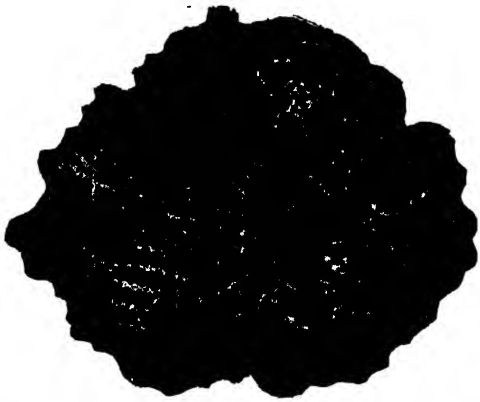


FIG. 273.—Fossil chain coral, Halysites, found in Michigan. (*From specimen in the Museum of Geology, University of Michigan.*)

Mud in which tracks were made hardened as it dried, and was resistant enough to keep its shape while new material was washed over it in the next freshet. New and old deposits hardened into rock, and the two slabs were readily separable at the level of the tracks. One slab bears molds, the other casts (Fig. 275).

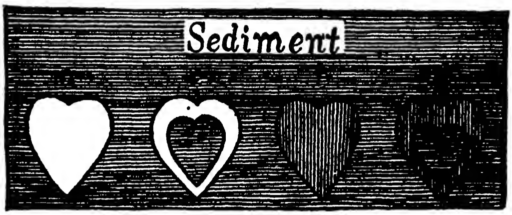


FIG. 274.—Diagram illustrating molds and casts. Horizontal shading represents sedimentary deposits, vertical shading the material subsequently filled in. *a*, mold of a shell which has been dissolved away by ground water; *b*, cast formed by subsequent filling in of the cavity of *a*; *c*, mold of a shell whose interior was filled with sediment; *d*, cast produced by filling the mold represented in *c*. (*From Schuchert, "Historical Geology," courtesy of John Wiley & Sons, Inc.*)

Many bones and shells were dissolved away and replaced piecemeal. That is, the most soluble parts were removed first and replaced by the least soluble minerals which the ground water then carried. Less soluble portions were removed later, and replaced by minerals then prevalent. Different parts of the original bone are thus replaced by different minerals, so that even the minute anatomy is preserved. Such objects are said to be *petrified* (the process being called *petrifaction*).

Large collections of fossils are sometimes found at ancient water holes, where animals congregated and died in periods of drought, or in asphalt pools where they were trapped and were probably attacked by predators which also were caught in the mire. The great collection of fossil bears, lions, saber-toothed tigers, horses, elephants, antelopes, and vultures at Rancho La Brea near Los Angeles was caught in a pit of tar. Caves are likewise the sites of numerous such collections. For the most part, however, fossil forms occur singly or in small groups, where they are discovered during excavations for buildings, by mine operations, or other accidental means.

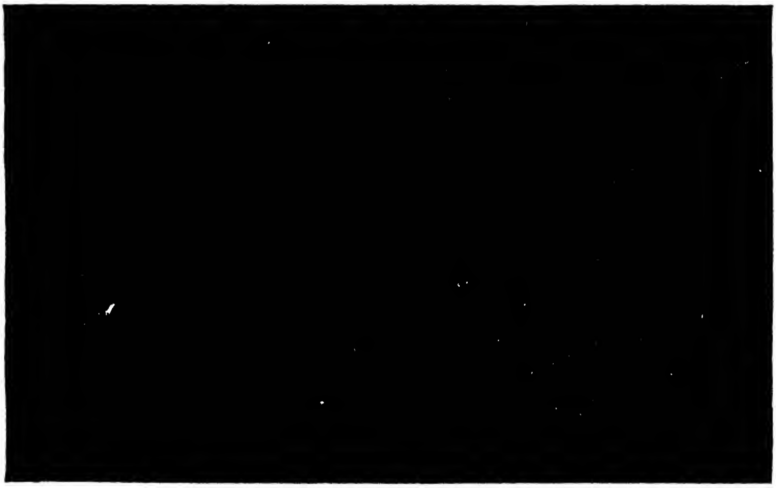


FIG. 275.—Natural casts of dinosaur tracks and rain imprints. (*From Schuchert, "Historical Geology," courtesy of John Wiley & Sons, Inc.*)

Paleontology Relates Two Evolutions.—Like zoogeography, paleontology treats of the interrelations of two evolutions, the evolution of the earth, and the evolution of living things. According to either of two prevalent theories of the origin of the earth, this planet was in some way derived from the sun, and went through a period of great heat. It is only the earth's history in the later cool period that concerns us in the study of fossils. Many of the superficial parts of the earth's crust are in strata of different kinds of rock. Obviously, where these strata are undisturbed, the lower ones were deposited first and are the oldest. In many places the strata have been compressed sidewise, and forced to rise in arches. With further lateral pressure, the arch may break, and the strata of one slope be shifted over the strata of the other slope. At the bottom of the overriding portion, an older stratum is above a younger one. Often this disturbance is readily recognized, but not always.

Considerable help in recognizing disturbed strata is given by the fossils they contain. While the earth's crust was changing, plants and animals were also evolving. Animals of one period were distinctly different from those of another. So characteristic of a given period are certain kinds of animals that the fossils are known as *index* fossils. Good index fossils must be abundant and widely distributed over the earth, and large enough not to be overlooked. Occurrence of an index fossil in a stratum at one place is not, however, a complete guarantee that any other stratum containing such fossils was contemporaneous with the first. These animals had to have a certain type of environment, and there are reasons to believe that similar environments occurred in different areas at different times in the earth's history. For example, the "red beds," made red by the oxidation of iron under certain climatic conditions, occur in the Conemaugh formation in Pennsylvania and West Virginia, and in the Wichita formation of mid-continental United States; but according to other evidence the Wichita is much younger than the Conemaugh.

While there are other ways of correlating rock strata of different regions, the changes in types of animals occurring simultaneously with changes in the earth are among the most reliable of the means of identification.

Divisions of Geological History.—Geologists use a classification of the earth's history which serves much the same purpose as does taxonomy for zoologists. The classification is known as the geological time scale. Major revolutions of the earth's crust caused elevation of great mountain systems, erosion on a grand and extremely rapid scale, and redeposit of the eroded material elsewhere. As a result of these great changes, layers of the earth's crust having very different characteristics and containing very different fossils lie next to one another. These contrasts, known as *unconformities*, are used to divide geological time into five great *eras*. Within each of these eras the land of continents sank in large areas so that the sea invaded the land, then rose again to push the oceans back. On the basis of such changes, each era is divided into *periods*. Minor and local changes of the same general type are used to divide the periods into *epochs*.

All the rocks belonging to a period constitute a *system*, those of an epoch make a *series*, while smaller divisions than the epochs have their rock *formations*. These terms are not generally used in this book, but are constantly met in geological works.

The accompanying table gives the geological time scale as far as the terms are needed in an elementary study of biology.

GEOLOGICAL TIME SCALE

Eras	Periods	Epochs	Dominant life
Cenozoic	Tertiary	Recent	Age of man
		Pleistocene Pliocene Miocene Oligocene Eocene	Age of mammals and modern floras
Mesozoic	Cretaceous Comanchean Jurassic Triassic		Age of reptiles
Paleozoic	Permian Pennsylvanian[1] Mississippian[1]		Age of amphibians and lycopods
	Devonian Silurian		Age of fishes
	Ordovician Cambrian		Age of higher (shelled) invertebrates
Proterozoic	Keweenawan Huronian		Age of primitive marine invertebrates
Archeozoic	Algoman Timiskaming Laurentian Keewatin		Age of supposed unicellular life

[1] Together constituting the Carboniferous (coal age).

Usually only a small part of this scale is represented in exposed strata at one place. One of the more extensive exposures of the crust is in the walls of the Grand Canyon in northern Arizona. The Colorado River at its bottom is cutting its way through granite at the rate of perhaps an inch in a century. Just above it in the slopes are Archeozoic rocks; the rim, a mile above, is Permian. Between these are mostly undisturbed strata in the order of the scale.

How old the strata are in years may be computed from the transformation of radioactive substances. The element uranium is being constantly transmuted into other simpler elements, the chain ending in lead and helium. The rate of change is constant, and independent of surrounding conditions. Where uranium is present, the amount of it and the amount of lead are ascertained as accurately as possible. If it be assumed that all the lead came from uranium, and that none of the lead has been removed, the time required for the transformation can be computed. On this basis, one computation gave certain Permian strata an age of about 220,000,000 years, late Cambrian 400,000,000 years, and several pre-Cambrian formations ages ranging from 900,000,000 to 1,800,000,000 years. The age of the earth itself has been variously estimated by the same method to be 3 to 6 billion years.

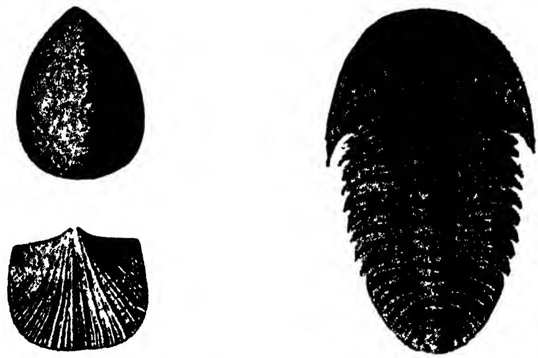


FIG. 276.—Cambrian brachiopods (left) and trilobite. (*From Hussey, "Historical Geology."*)

Change of Animal Life.—How animals have changed during the millions of years since life began can be indicated here only in a general way. Most of the Archeozoic rocks are igneous (once molten), hence could not bear fossils. Unicellular organisms are supposed to have existed then, but there is little evidence of them. In the Proterozoic, which witnessed two periods of glaciation at a number of places (Utah, Canada), there are limy deposits undoubtedly produced by unicellular

FIG. 277.—Ordovician graptolite (left) and snail. (*From Hussey, "Historical Geology."*)

plants. Sponges, spicules, and a jellyfish which have been reported are still somewhat in doubt.

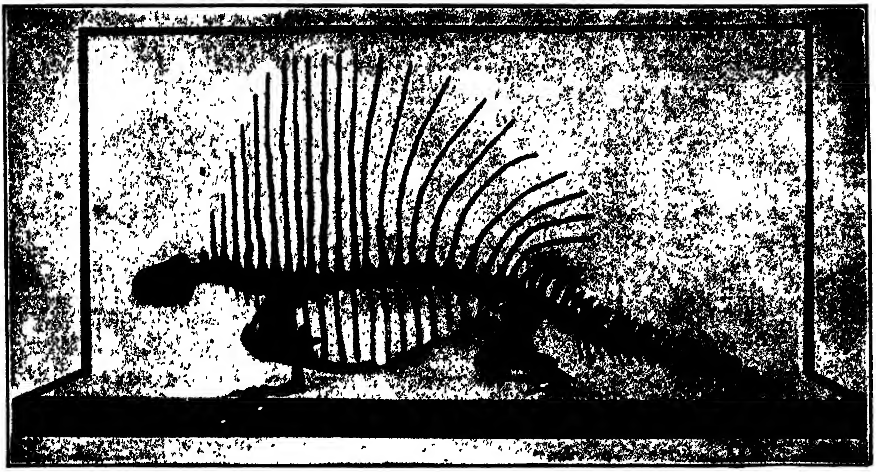
Cambrian presents a great outburst of animal life of many different kinds. Most characteristic and most abundant were the brachiopods and trilobites (Fig. 276). Some shale in British Columbia contains marvelously preserved jellyfishes, sea cucumbers, siliceous (glassy) sponges, annelid worms, and crustacea. There were so many kinds of Cambrian animals that the preceding era must have included many; but the long period of erosion between Proterozoic and Paleozoic destroyed whatever fossils there were.

Trilobites were even more common in the Ordovician, and brachiopods continued abundant but mostly with shells of lime instead of horn. With them in this period were graptolites, snails (Fig. 277), and others. The first vertebrate animals, the armored ostracoderm fishes, are found in Ordovician but must have existed long before. The following Silurian preserved few fossil fishes, but they must have been present, for that group blossomed out extensively in the Devonian; these two periods are known as the age of fishes (see time scale). Among the invertebrates of these periods were the brachiopods (now at their peak), trilobites (now on the decline), corals, snails, siliceous sponges, cup corals (Fig. 278), and the scorpionlike eurypterids.

FIG. 278.—Fossil cup coral found in Michigan. (*From specimen in the Museum of Geology, University of Michigan.*)

In Mississippian time the crinoids (stalked echinoderms) reached their climax (some of the best-preserved ones in Iowa), and declined greatly in the next period. Clams are preserved in Pennsylvanian with their actual shells; before this period the shells had dissolved away and the fossils were only casts. The latter period also had many insects, some of them giants having a wing spread of over two feet, also a number of amphibia chiefly of the armored type. The succeeding Permian had many of these armored amphibia, but was chiefly distinguished by its great variety of reptiles, some of which had curious bony spines in a sail over the back (Fig. 279).

The most characteristic invertebrate animals of the Triassic period were the ammonites, the most highly developed group of cephalopods whose evolution is described in a later section. These animals continued through the rest of the Mesozoic era but declined in the Cretaceous. Other invertebrates of the Mesozoic were crinoids, squids, and crustacea (particularly crabs). The great evolution of the Mesozoic, however, was in the group of reptiles. On the land were the dinosaurs, in the sea the ichthyosaurs (looking like porpoises or sharks) and the four-paddled plesiosaurs, in the air the pterosaurs. Dinosaurs often had curious rows of dorsal plates, as in the Jurassic Stegosaurus (Fig. 280), or shields and spines as in the Cretaceous Triceratops (Fig. 281). Some of them were of huge size, as the massive 75-foot Brontosaurus and the 10-ton Stegosaurus. Other points of interest concerning the Mesozoic are that true mammals were in existence, recognizable from their teeth and jaws, and the first birds appeared.



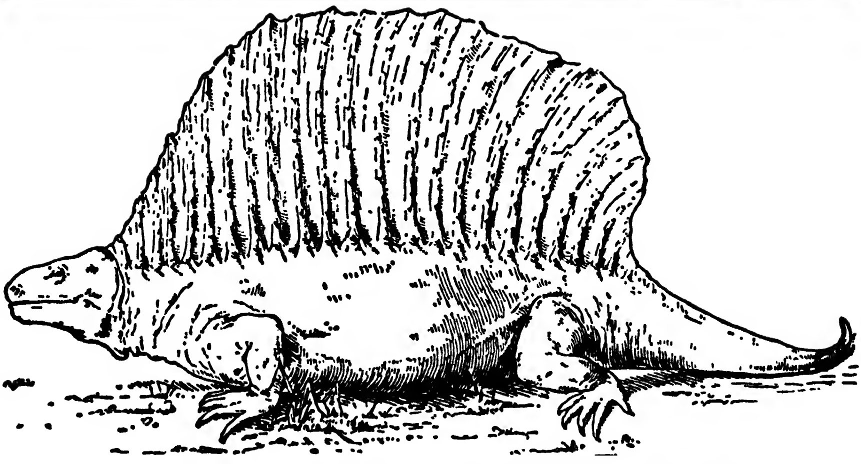


FIG. 279.—Permocarboniferous reptile, *Edaphosaurus cruciger;* skeleton above, restoration below. (*From specimen in Museum of Geology, University of Michigan; restoration by Prof. E. C. Case.*)

The outstanding feature of the Cenozoic is the tremendous development of the mammals, which rivaled that of the reptiles in the Mesozoic. No brief account can do them justice. The primitive members of this group are the marsupials, represented in North America by the opossum, which is little changed now from its Eocene form. Contrasted with these were huge forms (7 or 8 feet high) with bony protuberances on the head, represented in Eocene but long since extinct. This varied assemblage appears suddenly in the earliest Cenozoic deposits, indicating a long evolution before that era. The evolution of two mammals whose histories are most completely preserved is presented later in another connection.

The purpose of the brief account in this section is to show the general nature of the evolution of animals in relation to the evolution of the earth's crust. So far as it relates to the vertebrate animals the story

FIG. 280.—Skeleton of the armored dinosaur Stegosaurus. (*From Lull, "Organic Evolution," courtesy of The Macmillan Company.*)

is summarized by the diagram in Fig. 282. A similar chart for the more numerous kinds of invertebrates would be too confused for our purpose.

Lines of Evolution.—Out of the wealth of fossil forms barely hinted at above it is possible to select a few groups that show especially well the step-by-step changes which animals have undergone. These groups are particularly instructive because the relative ages of their members are not in doubt, and the differences between any two successive members are so small as to leave no question that they possess genetic continuity. Such a series of related forms is spoken of as a line of evolution.

The lines of descent of modern elephants, horses, and cephalopods are especially useful for illustration.

Evolution of Elephants.—The mastodon-elephant series shows a larger number of obvious changes than either of the other series named.

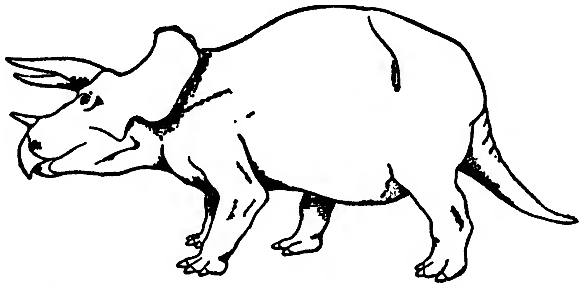


Fig. 281.—Restoration of horned dinosaur Triceratops. (*After Lull, from Schuchert, "Historical Geology," John Wiley & Sons, Inc.*)

Figure 283 will disclose the more striking steps of their evolution. The earliest animal recognized as belonging to the elephant series, Moeritherium by name, was recovered from late Eocene and early Oligocene

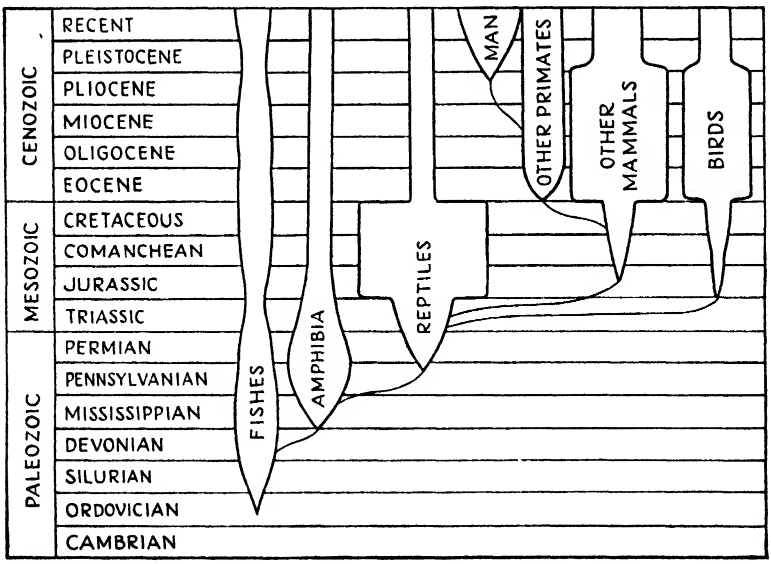


Fig. 282.—Diagram of the fossil history of the major groups of vertebrate animals. The width of the bands indicates abundance and number of kinds.

deposits of northern Egypt. It was slightly over 3 feet in height. The elephantine features are the high posterior portion of the skull (Fig. 283*F′*) composed of cancellate bone, that is, bone containing open spaces; the elongation of the second pair of incisors in each jaw to form short tusks; the indication of transverse ridges on the molar teeth (*F*); and the position of the nasal openings some distance back of the tip of the upper jaw,

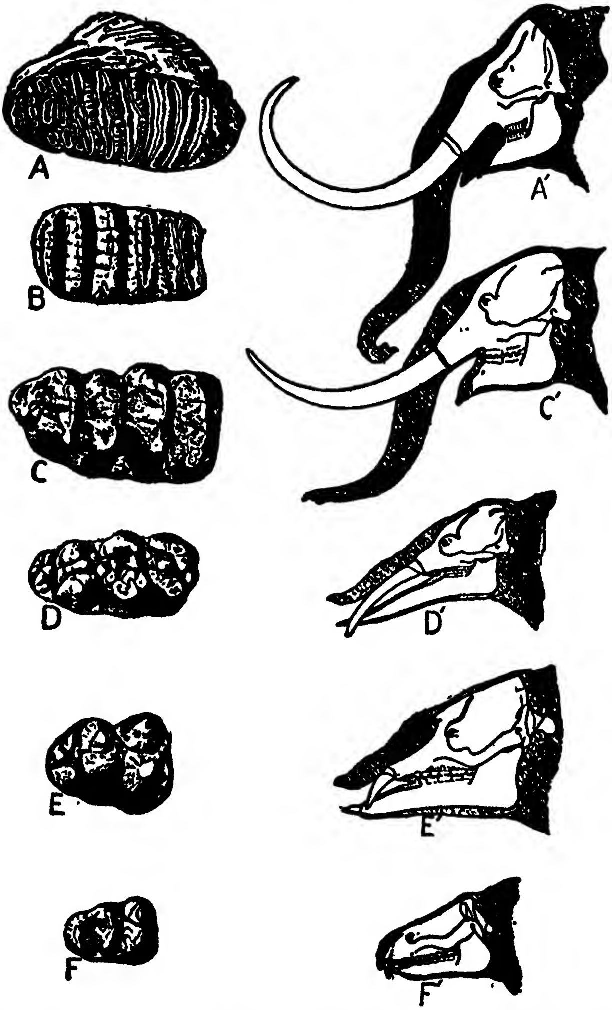


FIG. 283.—Evolution of the head and molar teeth of the mastodons and elephants. The shulls on the right are enclosed in the flesh in the form the latter is supposed to have had. *A*, *A'*, Elephas, Pleistocene; *B*, Stegodon, Pliocene; *C*, *C'*, Mastodon, Pleistocene; *D*, *D'*, Trilophodon, Miocene; *E*, *E'*, Palaeomastodon, Oligocene; *F*, *F'*, Moeritherium, Eocene. (*From Lull, "Organic Evolution," courtesy of The Macmillan Company.*)

indicating probably a prehensile upper lip. There were 36 teeth, and the neck was long enough to enable the animal to put its head to the ground.

Palaeomastodon, which lived in Egypt and India, dates from early Oligocene time. It was of somewhat larger size, the posterior part of the skull was distinctly higher (E') with a greater development of cancellate bone, and the neck was somewhat shortened. The upper incisors of the second pair were more elongated as tusks; the lower second incisors were present, but not enlarged; while all other incisors and the canines had disappeared. The molar teeth (E) resembled those of Moeritherium but were larger. The lower jaw was considerably elongated, and the number of permanent teeth was reduced to 26. The nasal openings had receded until they were just in front of the eyes, which is believed to indicate the existence of a short proboscis extending at least to the tips of the tusks.

Trilophodon, a great migrant and consequently widespread over several continents in Miocene time, was a huge animal, nearly as large as modern Indian elephants. The tusks were considerably longer (D'). The molar teeth were large and greatly reduced in number, so that only two were present at any one time on each side of each jaw. The surface of these teeth bore a somewhat larger number of transverse crests (D) than were present in the earlier forms. The lower jaw was enormously elongated, so that it projected as far forward as the tusks. There was a considerable development of cancellate bone in the skull, to which the supporting muscles of the neck were attached. The long lower jaw, which was not continued in later forms, has led paleontologists to conclude that Trilophodon was not in the direct line of descent, but that it was an offshoot. Dinotherium (Fig. 286, upper left), a contemporary of Trilophodon but with a strongly recurved lower jaw, is likewise regarded as a lateral branch.

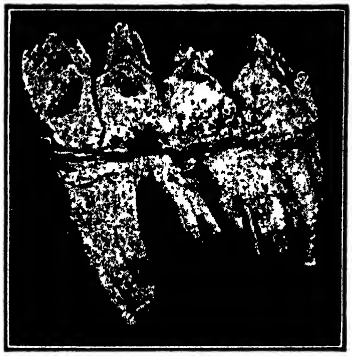
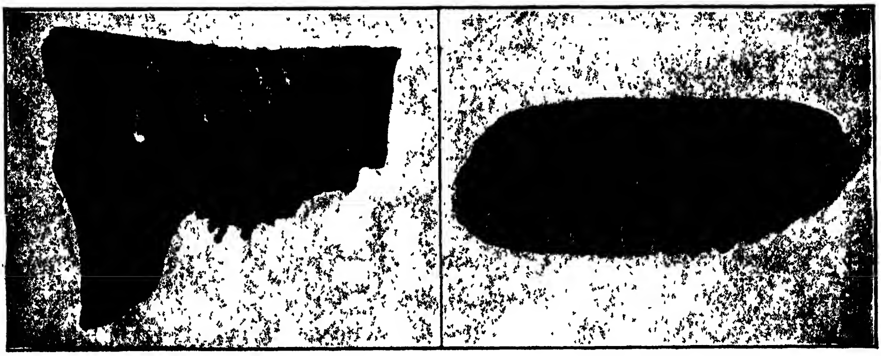


FIG. 284.—Mastodon tooth, showing the enormous cusps on the upper surface. (*From a California specimen in the Museum of Geology, University of Michigan.*)

The mastodons were somewhat larger than Trilophodon, being about the size of the Indian elephant. The tusks (C') were much elongated (9 feet or more), but the lower jaw was greatly shortened and the lower incisor teeth were reduced or wanting. The molar teeth (Figs. 283C, 284) were scarcely more complex than earlier forms and numbered 18 to 20 in the permanent set. They were still crushing teeth, and the food must have been tender twigs and succulent plants; indeed, remains of such objects have been found in the region of the stomach of some of the fossil mastodons.

Apparently arising from the primitive mastodons was Stegodon, known only from Asiatic Pliocene. Its molar teeth (Fig. 283B) had distinct transverse ridges, though not many of them, and its lower jaw was short.

The extinct elephants known as mammoths belong to Pleistocene time, while from them or directly from Stegodon have arisen two kinds still living, the Indian and the African elephant. The gross features of the elephants are their size, short neck, long proboscis, and heavy tusks. The skull is very high and short (Fig. 283*A*′), due chiefly to the development of cancellate bone. As in the earlier forms, the high skull affords the necessary leverage for the muscles that support the weight of the tusks. The molar teeth are distinctly grinding teeth (Fig. 283*A*; see also Fig. 285). Each tooth bears a number of transverse ridges, about 10 in the African elephant and 24 or more in the Indian species. These



A B

FIG. 285.—Tooth of mammoth (Elephas) from the Pleistocene, showing the flat grinding surface and the numerous plates of enamel bound together by cement. *A*, side view; *B*, surface view. (*From specimen discovered at Ridgeway, Michigan, in* 1912, *and preserved in the Museum of Geology, University of Michigan.*)

ridges are worn down by the chewing of harsh food, so that the upper surface displays the cross sections of a number of flattened tubular plates of enamel enclosing dentine and bound together by cement. While the tusks (incisors) are of two sets, one following the other like *milk* and *permanent* teeth of other mammals, the grinders succeed one another in continuous fashion. As the molar teeth that appear first wear down they move forward in the jaw and are replaced by others from behind. Three permanent molars may thus successively appear on each side of each jaw, but the wearing and movement are slow, so that the interval between the appearance of the second molar and that of the third may be 30 years. The total number of permanent teeth, including the tusks, is 14.

Correlated with the nature of the teeth of the elephants are their food and chewing habits. The ancestral forms whose molars bore prominent elevations lived on twigs and tender herbage which they *crushed* in mastication, but the mammoths with their flattened tooth surfaces devoured grasses, sedges, and other harsh vegetation which they *ground* with lateral motion of the teeth upon one another.

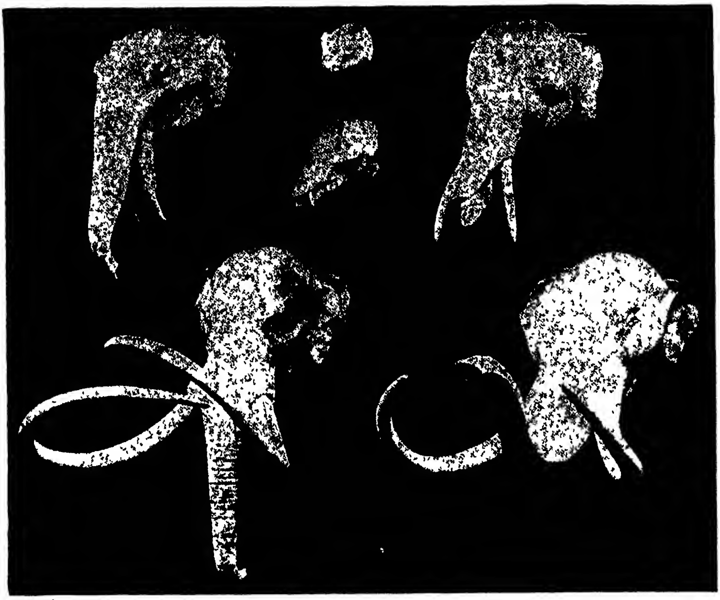
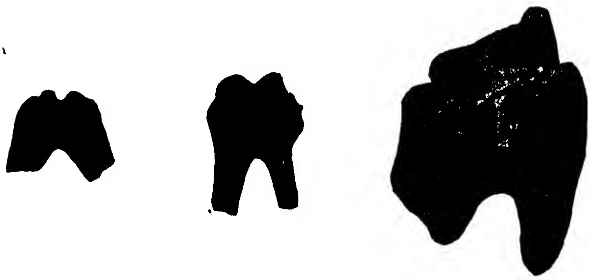


FIG. 286.—Restorations of heads of fossil elephantlike animals. Upper center, Moeritherium; below it, Palaeomastodon; upper right, Trilophodon; upper left, Dinotherium; lower right, Mastodon; lower left, Elephas. (*From models prepared by Ward's Natural Science Establishment.*)

The appearance of the heads of the series of elephantlike animals is imagined to have been as shown in Fig. 286. The ears are suggested by those of modern elephants, the proboscis by modern elephants and the position of the nasal openings, as already indicated. The general form of the head and tusks is, of course, accurate.

FIG. 287.—Restoration of Eohippus. (*From model prepared by Ward's Natural Science Establishment.*)

Evolution of the Horse.—Most of the development of the line of descent of the horse took place in North America. Eohippus, a lower Eocene form, is the first member of the series recognizable as ancestral to the horse, though it may also be regarded as approximately representing an ancestor of the tapirs and the rhinoceroses. It stood about 12 inches high and had a short head and neck (Fig. 287). The hind foot had three well-developed functional toes. On the outer side was a splint bone representing an additional toe, and on the inner side a rudiment of still another. Many living vertebrates have five digits on each hand or foot, and there is anatomical and embryological evidence that primitive vertebrates in general had five digits. These are numbered from the inside outward, the thumb or great toe being first, the little finger or little toe last. In the hind foot of Eohippus the functional toes are the second, third, and fourth, while the fifth is reduced to a splint bone



a b c

FIG. 288.—Fossil teeth of ancient horselike animals. *a*, tooth of Eohippus with the root broken; *b*, tooth of Mesohippus; *c*, tooth of Merychippus. (*Photographed from specimens in the Zoological Laboratory of the University of Michigan.*)

and the first is rudimentary. The forefoot had four functional digits, the first being wholly wanting, though some old figures erroneously include one. In the ancestors of the horse the first digits seem to have disappeared first, followed by the fifth. The teeth of Eohippus were short of crown and relatively long of root. The upper surface bore several conical cusps which, however, showed some sign of fusing to form transverse crests (Fig. 288). The skull (Fig. 289) was small, the lower jaw comparatively short, and the orbit was placed well over the teeth, making the face relatively short. Orohippus, which lived in middle Eocene time, resembled Eohippus closely but lacked the splint bone of the forefoot (Fig. 290, left).

FIG. 289.—Skull of Eohippus, about 3/10 natural size. (*From model prepared by Ward's Natural Science Establishment.*)

Mesohippus, an Oligocene form, was about 18 inches high. It had only three digits on each foot (Fig. 290), but on the outer side of the forefoot was a splint bone representing an extra toe (the fifth). Of the three well-developed toes, the middle one (third) was in each foot distinctly larger than the others. The skull (Fig. 291), except for its increase in size, had not changed materially. The crowns of the molar teeth were still low (Fig. 288) and were tuberculate, that is, provided with cusps on the upper surface, but the cusps were more distinctly united into ridges or crests. Miohippus, a little later in Oligocene, was somewhat larger, but otherwise much like Mesohippus (Fig. 290).

In Merychippus, a Miocene animal, the feet were all three-toed (Fig. 290), vestiges of the fifth toe being present in some specimens and wanting in others. The lateral toes, however, were high above the ground; the

FIG. 290.—Fore feet of fossil horselike animals; from left to right, Orohippus, Mesohippus, Miohippus, Merychippus, Pliohippus. Of each type there are represented the bones and the restoration in the flesh. (*From models prepared by Ward's Natural Science Establishment.*)

entire weight of the body was borne upon the middle (third) toe. The permanent molar teeth had moderately high crowns, and the upper surface was worn down to a flat grinding surface marked by sharp ridges of enamel set among dentine and cement (Fig. 288). Merychippus was evidently a grazing animal, whereas its predecessors must have fed upon succulent herbage which was crushed, not ground. The skull was

FIG. 291.—Skull of Mesohippus, about 3/10 natural size. (*From photograph of specimen in Museum of Geology, University of Michigan.*)

enlarged (Fig. 292), and the lower jaw was heavier in evident relation to the change of the teeth. The orbit of the eye occupied a more posterior position relative to the teeth, making the face longer. The orbit was also completely closed behind by a bar of bone which in the earlier forms was merely a process projecting down from above. The body had increased to a height of 3 or 4 feet.

Pliohippus (Pliocene) was not appreciably larger than the preceding member of the series but the two lateral toes had disappeared (Fig. 290), except as long splint bones. Pliohippus was thus the first one-toed horse. The teeth were moderately long-crowned and possessed grinding surfaces. The body stood about 48 inches high.

The fossil horses of Pleistocene time were so nearly like the living forms as to be included with the latter in the same genus (Equus). The recent animals are 60 inches or more in height and weigh many hundreds of pounds. Each foot has but one toe. Two lateral toes are evidenced

Fig. 292.—Skull of Merychippus, about 3/10 natural size. (*From model prepared by Ward's Natural Science Establishment.*)

by splint bones, and in rare cases a reversionary horse is born with externally visible digits articulated with one of these splints on each forefoot. The teeth are long and columnar and grow continuously during early and middle life, during which time the wear at the upper surface approximately equals the growth. The grinding surface is worn flat, except that the enamel resists the abrasion more successfully than do the dentine and cement, so that the enamel forms sharp cutting ridges. The position of these ridges changes somewhat as the tooth is worn to different levels and the pattern of the upper surface is indicative, in a general way, of the age of the animal. Later in life growth of the teeth practically ceases, and then the teeth may become quite short. The face is relatively longer than in the ancestral forms, since the eye is set well back of the teeth and the brain case has not been relatively enlarged.

Evolution of the Cephalopods.—An excellent fossil record among the invertebrates has been established for the tetrabranchiate (four-gilled) cephalopods (Mollusca), already used to illustrate the biogenetic law (page 255). This branch of the cephalopods is represented today by Nautilus, which lives in a coiled shell, externally resembling a snail shell. The animal lives in only a small portion of the shell near the aperture. The rest of the shell is divided by partitions into a number of chambers, from which the animal is excluded except for a small stalk that extends back through all of them. These partitions, or septa, represent the positions occupied by the animal earlier in its life. As the body grows,

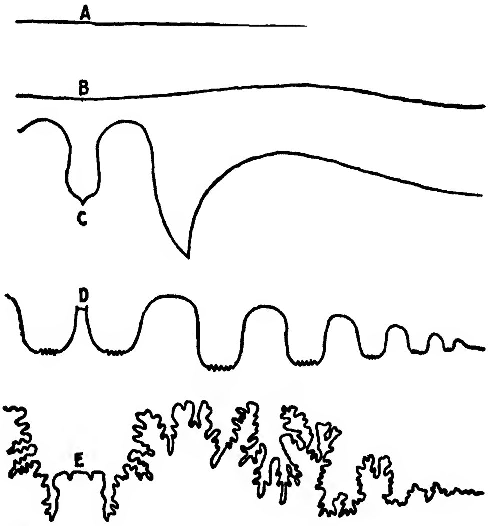


FIG. 293.—Diagrams of sutures of cephalopods, slightly more than half shown. *A*, orthocone; *B*, nautiloid; *C*, goniatite; *D*, ceratite; *E*, ammonite.

it moves periodically forward into the wider part of the shell and secretes a partition behind itself each time it moves.

Tetrabranchiate cephalopods have been found as fossils in Cambrian rocks. They became fairly abundant in early Ordovician time. At that time, unlike the modern Nautilus, their shells were straight cones (*orthocones*). All later forms appear to have descended from these orthocones.

The course of evolution was as follows. The shell soon began to bend and in many forms became closely coiled in flat spiral form (Fig. 210) like the shell of some snails. Owing to their resemblance to Nautilus these animals are called *nautiloids*. They were very abundant in Silurian time. Up to this period the septa across the shell were flat and saucer-like, and the *sutures*, the lines of junction of the septa with the wall of the shell, were nearly straight or only slightly curved. Later the septa became bent in various ways, at least at their edges, so that the sutures were curved or angular (see Fig. 293). Forms whose sutures were of this curved and angular form are called *goniatites*, and they were abundant in the Carboniferous period. These were to a large extent superseded in Triassic time by other genera, still tightly coiled but with sutures thrown into a number of regular curves and sawteeth, which may be described as "crooked." These forms with crooked sutures are known as *ceratites*, from a very common genus Ceratites. And finally, in the forms known as *ammonites*, the sutures became finely crimped in a compound fashion, often producing exquisite foliaceous patterns. Fossil ammonites are most abundant in the Jurassic to Cretaceous strata.

Though there were many irregularities and overlappings in the series of tetrabranchiate cephalopods, the fossils show on the whole clear evidence of progress from a straight shell to one tightly coiled, and from nearly straight sutures to sutures that were bent, augular, crooked, and finely lobed.

Prehistoric Man.—The human line of evolution is not complete enough to offer as an example of such lines, but it has an extraordinary appeal to the modern representatives of it. Man is one of the order of primates, other members of which are the lemurs, monkeys, and manlike apes. There is some reason to believe that the primates evolved from the insectivores, the group to which moles and shrews belong. If a series of fossils were available to show human evolution, it should, assuming our surmises to be correct, lead from the insectivore type, through forms resembling lemurs, monkeys, and apes. The later stages of this series would be especially useful as connecting the apes with man. Unfortunately, not many primate fossils have been found. The probable reason for the lack of fossils is that the primates have been tree-dwellers. Dead individuals would have dropped to the ground, and forested areas offer little chance for burial under either wind- or water-borne material. Fossils of man himself were not preserved in numbers until burial customs arose. As a result of these customs, more fossil men are known than fossil apes. Kinship of man and the apes must therefore be judged largely from homologies. Paleontology can begin to help only after considerable divergence has occurred. Nevertheless, the earliest manlike fossils show unmistakable leanings toward the ape structure in certain respects.

One of the most primitive of the fossils appearing to connect man with the apes, a form usually regarded as belonging to middle Pleistocene time, is *Pithecanthropus erectus*, uncovered in some excavations in 1891 in Java by a Dutch army surgeon. A femur, parts of the skull, and several teeth were in the original find, and parts of several skulls and jaws and additional teeth have been added from near-by locations since.

The cranial capacity is about 900 cc., which is intermediate between apes (600 cc.) and men of today. The straight femur indicates erect posture, since quadrupeds have doubly curved thigh bones. The heavy brow ridges, rounded chin, and protruding face are all apelike.

Also of middle Pleistocene time are a number of skulls and a few leg bones which were found in a cavern south of Peking, China, in 1928 and later explorations. Their massive brow ridges, low foreheads, and round chins are apelike, the average 1000-cc. cranial capacity intermediate, the straight femur human. Along with the remnants in this

FIG. 294.—Restorations of prehistoric men. Left, *Pithecanthropus erectus;* middle, *Homo neanderthalensis*, modeled on the Chapelle-aux-Saints skull; right Cro-Magnon man modeled on type skull of the race. *(From original busts by Prof. J. H. McGregor.)*

cave were crude flint implements, and charred bones of animals which indicated that Peking man was a hunter and knew the use of fire.

Piltdown man, so called from Piltdown common in Sussex, south of London, where it was found, might on the basis of associated fossils be assigned a slightly earlier time than the preceding ones, but had characteristics which are indicative, in part, of a later period. The find includes parts of two skulls and some loose teeth. Very much like man of the present were the cranial capacity of 1400 cubic centimeters, which is as large as many European skulls now, and the poor development of brow ridges. Like apes were the considerable thickness of the skull bones, the broad low nose, and the receding chin. The skull is a mixture of advanced and primitive features.

Neanderthal man, so named because the first-described specimens came from a cave in the Neander Valley near Düsseldorf, Germany, invaded western Europe in the warm period before the last of the great Scandinavian glaciers. Many skulls and nearly complete skeletons have been found in caves in a number of countries. These men were seldom as tall as 5½ feet, but were powerfully built. The cranial capacity was 1300 to 1600 cc., brow ridges were heavy, chin usually receding (though some had a small prominence). A restoration of Neanderthal man, with two other types here described, is shown in Fig. 294. The measurements of the skull are correct, but the thickness of the skin and underlying connective tissue at various places, and the amount of hair, can only be conjectured. Well-designed flint tools (Fig. 295) were their main weapons, scarcely adequate to kill the cave bear, mammoth, reindeer, and bison whose bones are found in the caves, so they may have used traps, pitfalls, and probably stones. Neanderthal men were not good housekeepers, for debris was allowed to accumulate. To this untidy habit and their burial customs we owe our very extensive knowledge of the anatomy and culture of this early human type.

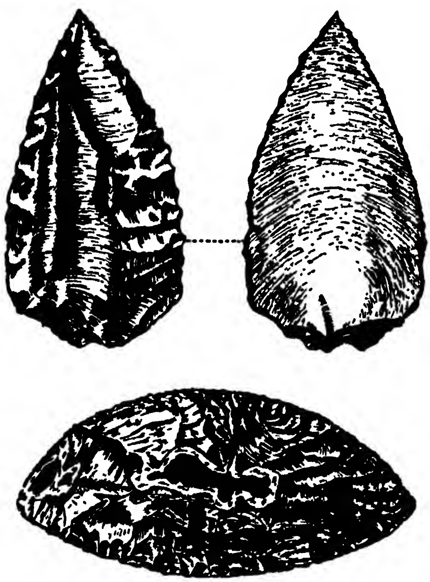


FIG. 295.—Neanderthal flints; point above, scraper below. (*From Hussey, "Historical Geology."*)

Toward the end of the last glacial epoch (late Pleistocene) Neanderthal man disappeared from Europe and was followed by the Cro-Magnon race. Probably it was a forcible displacement. The name Cro-Magnon comes from the cave in which the earliest-discovered skeletons of this type were buried. From these individuals it would be said that Cro-Magnon man was tall (6 feet or more), that his face was broad and flat (from prominent cheekbones), that his forehead was high (hence he was probably as intelligent as men of today), and that he was strongly built. But men elsewhere in southern Europe, who must presumably be assigned to any prevalent "type" of that time and region, were not all so tall, often had protruding faces, and even sloping foreheads. Thus there were tribes of Cro-Magnon man, just as there are tribes of American Indians, who are at the same time still Indians. The burials of these people were evidently conducted ceremonially. Bodies were placed in artificial positions, or were shrouded in garments of shells, or were painted, or community tombs were walled all around with certain bones, as the shoulder blades and jaws of mammoths. Flint tools were brought to perfection, but horn, bone, and ivory were also used for that purpose as being more easily worked. Sewing was done with bone awl and needle (Fig. 296). The bow and arrow had been invented, and these with the spear, thrown from a short holder which remained in the hand, were the principal weapons. Art had a considerable development, and pictures of animals were cut (Fig. 297) or painted on the walls of caves.

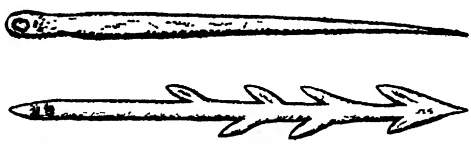


FIG. 296.—Cro-Magnon tools of bone; needle above, harpoon point below.

These murals also indicate the existence of witch doctors whose bizarre masks are there pictured, and of dome-shaped dwellings presumably made of skins stretched over a framework of wood.

Then new people began to appear from the East, from the plains of Persia or farther north. These newcomers migrated north of the Mediterranean, or south of it and across to southern Europe, or along the sea itself to the Atlantic Ocean and thence to the British Isles. They did not destroy the Cro-Magnons of southern Europe, but mixed with them, or by-passed and surrounded them. In southern France, elsewhere in Europe, and in the Canary Islands there are still people whose measurements are nearly identical with the Cro-Magnons of the first-found cave, and these are believed to be practically unaltered descendants of the Cro-Magnon race. With the coming of this eastern tide Cro-Magnon art declined, and the implement worker's skill deteriorated. But the Asiatic invaders had their culture, which included weaving of nets and baskets and, far more important, agriculture. In their Persian home they had learned to raise plants and animals for food—a step which made possible a tremendous increase in the number of people in a given area.

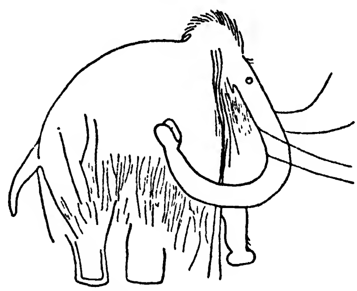


FIG. 297.—Cro-Magnon engraving of the woolly mammoth on the wall of a cave in France.

Continued migration from Asia, and evolutionary developments within Europe itself, led to the races and cultures that have succeeded one another to the present time. Since the white people of North America are the descendants of European immigrants, the history of man given above is the history of the bulk of people of the western continent also.

Man in America.—The American Indians are so plainly Mongoloids that they must have come from Asia; and the means of travel available to these people almost guarantees that they crossed the Bering Strait, which could have been dry. The Asiatics most like the American Indians are not the Chinese, but the more generalized people of central Asia, Tibet, or the East Indies. Migrations of these people extended to Patagonia on the south, and to the Atlantic seaboard, long before white men came to America. The Eskimos of the arctic region are more nearly like the Chinese and Siberians, and probably are the latest immigrants.

Important discoveries of arrow points with fossil bison in New Mexico in 1927 were followed in rapid succession by other revelations of culture in relation to such extinct animals as horses, camels, mastodons, and ground sloths. The making of pottery, an art which for some reason Cro-Magnon man never developed, has entered extensively into the later history of culture in America. The New Mexico points were interpreted as belonging to the late Ice Age, or perhaps 25,000 years ago, so the migration must have occurred earlier.

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CHAPTER 23

MODIFICATION OF SPECIES

At many places in the preceding chapters the assumption has been made that the kinds of living things on the earth have changed over periods of time. In Chap. 6 possible ways of deriving multicellular organisms from unicellular ones were postulated, in the belief that the complex life of today could not always have existed. In describing the varied breeding habits of animals (pages 185–186), it was assumed that animals had evolved, but it was pointed out that the evolution of their habits had not closely followed their structural evolution. In the classification of animals the basis of grouping is the supposed kinship of the various species, due to descent from common ancestors and ascertained from homology (pages 250*ff*). The environmental relations of animals were shown (page 283) to involve questions of evolution, since it was shown that temperature could produce permanent modification of races. All through the discussion of geographic distribution (Chap. 21) changes in species were assumed to have occurred, in order to explain the position, size, continuity, and proximity of ranges, and the differences between southern and northern continents. And, finally, fossil animals (pages 331–348) were regarded as giving positive evidence not only of evolution but of the direction which some evolutionary changes have taken. These frequent references to evolution in advance of its separate discussion indicate how intimately the idea of change of species is woven into the entire fabric of biology. It would have been impossible to discuss these phenomena adequately without relating them to evolution. Without repetition of the facts and discussions already presented, it is left to this chapter to summarize briefly with additions the reasons for believing such changes to have occurred, and the methods by which they may have been brought about.

Evidences of Evolution.—One of the most compelling reasons for assuming evolution is the existence of many similarities among species of animals and plants. Some of these similarities have already been detailed in the chapter on classification. To the homologies there described may be added that shown by the membranous labyrinths of the inner ears of vertebrate animals (Fig. 298). Each has a series of three semicircular canals set in different planes and attached to a central sac; but in each group of vertebrate animals there are characteristic differences that make it possible to recognize the group of animals by the labyrinth alone. The embryos of animals also show homologies. Every college course in embryology is a recognition of the existence of types of development; for the laboratory studies, based on one or two animals, are used to exemplify most of the classes in a phylum. The homology of embryos is more spectacular when it is discovered in species that are not alike in the adult. This situation is more likely to arise in

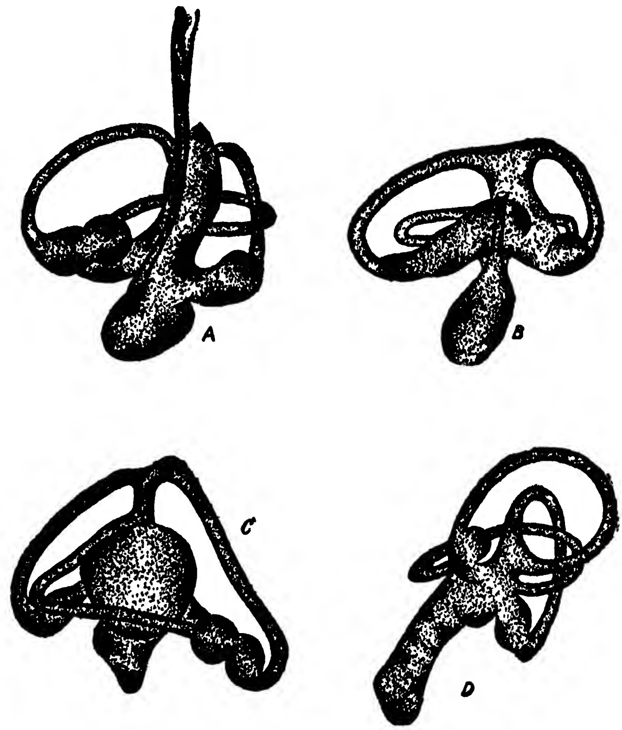

FIG. 298.—Membranous labyrinths of inner ear of various vertebrates. Each consists of a saccular portion from which three semicircular canals arise. *A*, of a fish; *B*, of a frog; *C*, of a reptile; *D*, of a bird. (*Modified from Retzius.*)

parasitic animals, since adult parasites are frequently very degenerate. An excellent example is a parasite, Sacculina, found attached to the underside of the abdomen of common crabs (Fig. 299). Sacculina, in the adult stage, is a rounded pulpy mass with practically no definite structure, except a host of rootlike processes which extend throughout the crab's body and absorb the body fluids. The embryo, however, is a three-cornered little animal with jointed legs which clearly marks Sacculina as one of the crustacea. It is, in fact, one of the barnacles, a group in which adult structure is usually quite complicated (Fig. 300).

Similarities in physiological properties are quite as abundant as are likenesses of structure. The enzymes of digestion are in general very much alike in different vertebrate animals. As a rule, protein-splitting enzymes are produced and used in corresponding organs in different vertebrates. Nervous and hormone control are in most respects alike. Even the composition of the blood shows close similarity between animals whose structures are alike; the hemoglobin (page 127) has nearly the same crystalline characters, and the serum has almost the same chemical composition as shown by precipitin tests. In using this precipitin reaction an animal is rendered immune to, let us say, sheep blood by repeated injection of sheep blood into its veins. This immune blood then pro-

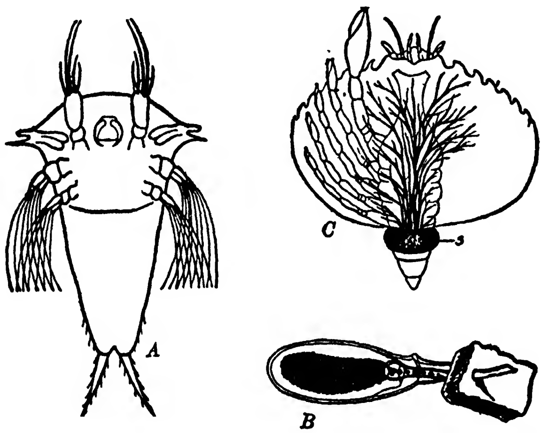

Fig. 299.—Sacculina, parasitic on crabs. *A*, young Sacculina, shortly after hatching. *B*, young animal shown attached to its host, the crab. The projection at the anterior end has penetrated the chitinous ventral wall of the abdomen of the crab, only a small piece of the chitin being shown. *C*, adult Sacculina (*s*), consisting of a pulpy mass on the under side of the crab's abdomen, and a host of branching processes in the host's body. *A* and *B* greatly but unequally magnified, *C* reduced.

duces a white precipitate when blood of a sheep or of an animal very similar to sheep is mixed with it, but not when blood of a very different sort of animal is mixed with it. The precipitate is formed only in response to blood of a given chemical composition, and similar composition has been found almost solely in the blood of animals that are structurally similar.

The argument from all these similarities, already advanced on page 255, is that only heredity—hence common ancestry—could account for them. But if two species of animals have come from a common source, any differences between them—and there always are differences—must have arisen since the time of the common ancestors. Emphasis is now to be put on these differences, for their origin constitutes evolution.

The other principal evidences of evolution are derived from fossils, from distribution of present-day organisms over the earth, and from observation of the process. The rather complete series of fossil animals leading up to modern horses and elephants, and the series of cephalopods ending with extinction, as described in the preceding chapter, need no comment as indications of evolution. To them may be added an immense amount of less complete data of fossils, all of which point to the same conclusion, namely, that species and larger groups of animals and plants have changed. Geographic distribution, as repeatedly shown in Chap. 21, likewise requires the assumption of evolution to be intelligible. It should not be necessary to comment further upon it here. The observational evidence will be referred to later.

Fig. 300.—Adult free-living barnacle of the genus Lepas, with half of its shell removed.

Evolution a Change of Species.—Though evolution has effected a separation of groups of high rank (orders, classes, phyla) from one another, it has accomplished this result entirely by modification of species. There is no such thing as single wide cleavages that at once produce even families or genera out of single common stocks. The divergence is everywhere a slow accumulation of small differences such as charactèrize species or varieties. When life originated, assuming that it did so only once, there was at first only one species of organism. When a change occurred in a part of this group, all experience indicates that the difference could have been no greater than that now existing between species—or more probably varieties. When further changes occurred, it is not likely that altogether the same changes took place in both varieties, so that each of them gradually broke up into two unlike sets of varieties or species. The two varieties produced by the first modification may thus have given rise to two species, later to two genera. By further change of species, each group of species pursuing a course somewhat different from the other, these two genera may be supposed to have been transformed into families. Still further changes in species within the families should have resulted in the degree of difference now held appropriate to orders. By continued change of species, the orders may have diverged from one another enough to be regarded as classes and finally to have attained the rank of phyla. The course of evolution has been not to create phyla and then to proceed to split them up into groups of lower ranks, ending in species and varieties; it has rather gone in the opposite direction, beginning with species and by repeated changes of species gradually converting them into groups of higher rank. The problem of evolution thus becomes that of the origin of species.

The Nature of Species.—To understand evolution it is necessary, therefore, to know how species are constituted. A species may be thought of as a group of individuals most of which have most of their inherited characteristics in common. Characteristics due to environment and differing in individuals solely because of different environmental influence are not considered. The difficulty in applying the foregoing idea lies in the word "most," for there is much disagreement among taxonomists as to how much it should include. Probably no species that can be recognized as a species anywhere in the world has all of its individuals alike in all hereditary qualities. It would be possible to assemble groups of individuals alike in all their genes (page 224), but such assemblages would be much smaller than the ones now recognized as species. To insist that species be entirely homogeneous would simply multiply the number of species and would solve no problem either of evolution or of classification. In practice, therefore, some heterogeneity is admitted. As far as taxonomists agree on the grouping, all individuals of a species have certain qualities in common; these qualities are held to characterize the species. Beyond this general heritage, there are other characters each of which is present in some individuals, but none in all of them. A certain amount of variation thus exists among the individuals of every species. Some of this variation is nearly always visible or otherwise capable of detection; but some of it is not seen, since it consists of recessive genes scattered through the population. These recessive genes, unless very numerous, are present more often in heterozygotes than in homozygotes (page 227) and do not greatly affect the species *visibly;* but they are a potential source of visible qualities in later generations.

Species do not as a rule cross with other species, though there are many exceptions. Also, species tend to occupy different areas from other species. These are marks which help the taxonomist to recognize species as distinct, and their intersterility is an important agent in making them distinct.

Origin of the Differences among Individuals.—What is the source of the minority of qualities in which the individuals of a species may differ? Since a species is ordinarily descended from a single individual, it would be expected, unless the ancestor had been an extremely heterozygous organism, that its descendants would possess practically the same genes throughout. The existence of a number of genes which are not alike in all individuals indicates that some of the genes have changed in some individuals. Such changes of genes are the mutations already referred to (page 238) in the discussion of genetics.

Mutations are not merely inventions to explain the variation within species; the visible changes due to them have been witnessed again and again in many animals and plants. Some of the first changes to be called mutations were observed by Hugo de Vries, one of the rediscoverers of

Mendel's law (page 18), in the evening primrose *Oenothera lamarckiana* before the year 1890. Since that time, individuals of this species and others of the same genus have continued to produce offspring unlike themselves in some permanent way. Not a year passes without the production of one or more new forms. Some of them represent changes

Fig. 301.—Mutation in Oenothera involving the length of the seed capsule. The two specimens at the left are *Oenothera reynoldsii* mutation *debilis*, a form which gives rise by mutation to the form represented by the two figures at the right, *Oenothera reynoldsii* mutation *bilonga*. (*Photograph by Prof. H. H. Bartlett.*)

in the seed capsules (Fig. 301), others the whole habit of growth. Some mutations are detectible only in the adult plant, others in the young stage known as the rosette (Fig. 302). The alterations arising in Oenothera are not the simplest examples of evolutionary change, for it has been found that most of them are due not to simple changes of genes but to rearrangement of large fragments of the chromosomes and regrouping of whole chromosomes that adhere to one another. Probably such changes should not be called mutations, but the name has been applied to them.

Modifications that are due to changes of single genes—and hence are true mutations—have, however, been abundantly witnessed in other organisms. Over a thousand alterations have occurred in pedigreed strains of the vinegar fly *Drosophila melanogaster*, and many of these

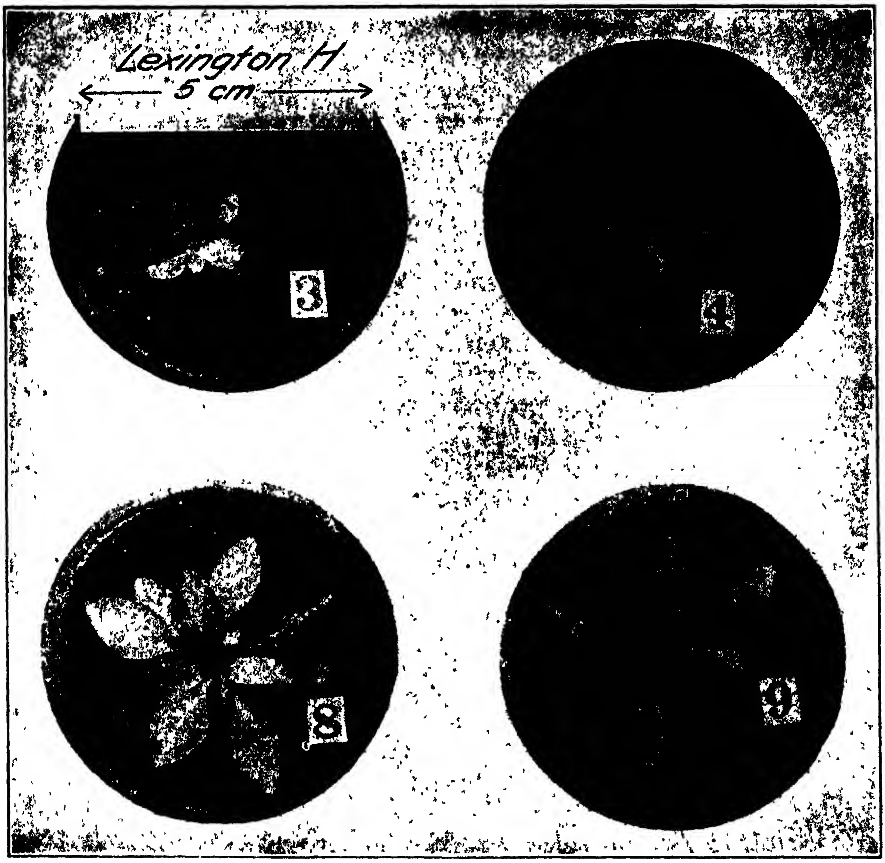

FIG. 302.—Mutation in Oenothera involving the rosettes, or young plants. Below (8 and 9), *Oenothera pratincola;* above (3 and 4), *Oenothera pratincola* mutation *nummularia*, a mutant of the preceding form. (*Photograph by Prof. H. H. Bartlett.*)

are presumably changes in single genes. The first of these mutations to be discovered was a change from red eye to white in one fly in the laboratory of Prof. T. H. Morgan in the year 1910. Since then there has been almost a continuous procession of mutations, affecting eyes, wings, body color, bristles, legs, antennae, and physiological properties (Fig. 303). Most of these mutants have been bred so that the mode of inheritance of their new characters was ascertained, and most of them turned out to be recessive to the wild-type characters from which they sprang. Smaller numbers of mutations have been observed to occur in other species of flies, and in wasps among insects; in mice, rats, rabbits, and guinea pigs among mammals; and in corn, barley, peas, and morning-glories among plants. So freely have these and other organisms mutated that the bulk of evolution may reasonably be assumed to follow from just such changes. True mutations may be supplemented by the breakage or duplication of chromosomes, but changes of this nature cannot be emphasized in an elementary discussion.

Causes of Mutation.—What causes mutations to occur under natural conditions is still unknown. The genes are almost certainly chemical, and it is likely that they are fundamentally protein. If these surmises are correct, mutations should be chemical modifications and of the sort

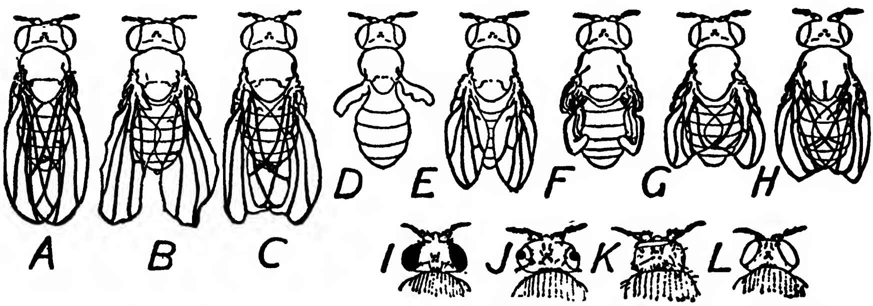

FIG. 303.—Mutations in the vinegar fly *Drosophila melanogaster*. *A*, normal wing; *B*, beaded wing; *C*, notch wing; *D*, vestigial wing; *E*, miniature wing; *F*, club wing; *G*, rudimentary wing; *H*, truncate wing; *I*, normal red eye; *J*, bar eye; *K*, eyeless; *L*, white eye. (*C from Morgan; D and L original; the rest from Morgan, Sturtevant, Muller, and Bridges, courtesy of Henry Holt and Company, Inc.*)

that proteins are capable of undergoing. A century and a quarter ago Lamarck (page 17), who was the first naturalist to propound a comprehensive theory of evolution, held that species changed in indirect response to the environment, effected through use and disuse. Lamarck knew nothing of the single character changes now called mutations; but, were his idea correct, it would mean that mutations are caused by environmental action. As Lamarck conceived the changes to occur, they constituted inheritance of acquired characters. For the individuals were supposed to be modified by the activity of the animals themselves which led to such things as overdevelopment of the muscles or stretching of the legs or neck. These changes were induced only in the soma or body at first, but he believed that the body was then capable of influencing the offspring in like manner. In the light of present knowledge, this influence of the body on the offspring would have to take the form of causing mutations in the germ cells while still in the body. It seems wholly unlikely that any such influence can be exerted. The organization of animals appears to offer no possible mechanism whereby an altered body can produce in the germ cells within it any modification such that offspring developing from them would have the same alteration. Moreover, though many experimental attempts to produce such changes have been made, no satisfactory evidence of their success has ever been adduced.

It seems necessary, then, to exclude somatic influence from the list of possible causes of mutation. When mutations began to arise under observation in experimental cultures, it was further observed that there was no apparent difference between the environment of the one mutant individual and all the rest. It was long supposed, therefore, that the cause of mutation was an unknown something within the animal, possibly in some way connected with its physiological processes. In recent times, however, it has been found that certain environmental agents are not stopped by the body but reach the germ cells directly. They may not influence the body in any detectable way yet produce modifications in the germ cells. The most potent of these known agents is X rays, and the most responsive organism is Drosophila. Hundreds of alterations have appeared *in the offspring* when the parents were exposed to the rays. Some of the modifications are visible structural changes; more of them have physiological effects. How much natural mutation may be due to such radiation is in doubt. Though there is always a certain amount of radiation from the earth, it appears much too feeble to account for the mutation that has occurred in laboratory cultures. Heat is the principal other agent that has been found to produce mutations, and again Drosophila is the subject. While some parts of the earth have as high temperature as was employed in these experiments, the temperate zones, where most of the thousand mutations of Drosophila have arisen in laboratories, are not among them.

On the whole, while it must now be recognized that external agents may produce mutations by direct action on the germ cells, the chief agents have not yet been discovered; and the possibility of wholly internal agents has not been exhausted.

Hybridization.—Given a number of genes in which various members of a species are different, an important other source of variation is at hand. If individuals having different genes are capable of crossing, as they nearly always are within a single species, the genes may be combined in different ways. How many recombinations may be produced depends only on the contrasting genes. If there are only 20 spots in the chromosomes at each of which, somewhere in the population, two different genes exist, it is possible to have over a million different kinds of individuals. Most species presumably have more than 20 mutant genes floating about in scattered members, and for each additional mutation the number of possible combinations is doubled. The importance of this sort of variability in evolution can scarcely be overestimated. A species that is confronted by a number of environmental situations may easily be in a position to take advantage of several of them. Its success would thereby be enhanced.

The variability that is due to combinations of genes in different ways is changed in its nature when genes of different pairs interact with one another to produce a character not like that produced by either one alone. An example is given on page 232 and in Fig. 201, where walnut comb is produced in fowls by a combination of the genes for pea and rose comb. The genes for brown and scarlet eye in Drosophila produce together a nearly white eye. Many such interactions between genes are known. It is indeed doubtful whether any gene fails to interact with those of other pairs in some way. Such interactions do not increase the number of different kinds of individuals which may result from recombination of genes, but they do introduce unpredictable qualities into the species. This feature may likewise be highly important to a species in a variable environment.

The hybridization referred to above is merely that occurring between slightly unlike individuals within the species. Whether hybridization occurs between two species or not depends partly on whether their chromosomes are similar and equally numerous. If the species has the same number of chromosomes and if the genes in them are in large measure alike, crossing is usually possible. The normal pairing of the chromosomes in the preparatory stages of germ cells depends on these two things. If the numbers of chromosomes are not equal, odd single chromosomes are left over from this pairing. And if corresponding genes do not exist in both species, the chromosomes do not unite readily. Many abnormalities result from these situations. The majority of species crosses fail to produce offspring, or the offspring are partially or wholly sterile. It seems unlikely, therefore, that any considerable part of evolution is due to hybridization between species.

The Direction of Evolution.—Evolution has taken by no means all of the courses that were theoretically open to it. Even if life originated only once, and even though the million or two species now probably in existence is a good round number of end products, this degree of differentiation is much less than might conceivably have occurred. The actual divergence of lines of descent has been considerably curtailed. What the other possibilities were that have not been realized, why certain species were produced and not others, why certain species that were produced survived and not others are problems to which we must now turn. Their solution is largely speculative but important.

The first element entering into the direction of evolution is the character of the mutations with which it starts. Some students of evolution have assumed that mutations are of every conceivable sort, just as a needle thrown on the floor may eventually, if thrown often enough, point in every horizontal direction. This seems an unreasonable assumption because, if genes are chemical in their nature, they should be no more free to enter into unlimited reactions than other substances are. Chemical substances are restricted to a certain range of reactions by the structure of their molecules. Furthermore, in organisms which, like Drosophila, have produced the greatest numbers of observed mutations, there is not so much variety among the mutations as a purely random determination of them should produce. They are too much alike, and some of them occur too often, to be the result of chance alone. It is more likely that each gene is capable of mutating in certain ways, and only in those ways. If this is correct, a species can evolve along any line which its possible mutations provide, but along no other. From these possible lines something has to choose.

With respect to the combinations of genes that result from hybridization within the species, chance probably plays an important role in the early stages of differentiation. When certain genes are present in a population in given numbers of individuals, certain combinations of genes are expected to occur in calculable proportions of individuals. Almost certainly, however, the expected proportion is never exactly realized. The accidental meeting and pairing of individuals will usually result in some small deviation from the expected result. A gene that ought theoretically to occur in 25 per cent of the individuals may easily happen to be in 28 per cent or only 22 per cent solely through chance. Should the deviation from expectation in the next generation happen to be in the same direction, the difference is accentuated. Different parts of a range may thus come to be inhabited by groups of individuals which, while still belonging to the same species, nevertheless have their genes in different proportions. These groups may look essentially alike, especially if the genes in which they differ are recessive and exist mostly in heterozygotes; but their potentialities for the future are distinctly different. Such differences tend to be preserved by lack of random mating. No individual travels the whole range of its species, so that it mates with one of its neighbors. When the genes become numerous enough to produce many homozygotes, or if they are or become dominant, the two groups of individuals show noticeable differences.

It is believed that varieties of a species may arise and come to occupy different parts of the range, entirely as a result of random wandering and the accidental union and fortuitous survival of certain gene combinations. Possibly even a divergence great enough to mark two separate species may take place in this purely random manner. Beyond this degree of differentiation probably other factors enter. The most important of such factors is believed to be natural selection.

Charles Darwin and the Natural Selection Idea.—Though Charles Darwin is often popularly credited with introducing the evolution doctrine, that is not correct, since, as shown in Chap. 1, the idea of evolution was already old in Darwin's time. His real contribution was the theory of natural selection. This theory made evolution seem so reasonable that opposition to evolution itself from intelligent people quickly fell away. From this fact, and from the confusion which exists between natural selection and evolution in Darwin's own writings, has no doubt come the popular misconception of Darwin's share in promulgating the evolution idea.

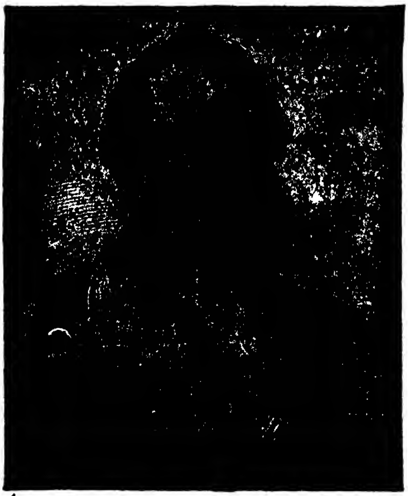

FIG. 304.—Sir Charles Lyell, 1797–1875.

The development of the natural selection concept in Darwin's mind is one of the fascinating romances of biological science. Darwin had come under the spell of the great English geologist Sir Charles Lyell (Fig. 304), one of whose principal teachings was that geological processes of the past were essentially the same as those in progress now. This doctrine, which has been called *uniformitarianism*, means specifically that erosion, warping of the earth's crust, rise and fall of the land, volcanic action, etc., had been continually occurring over long periods of time just as they are occurring now. By means of these present-day processes and no others, Lyell attempted to explain the development of earth features. Darwin was impressed with this method and was inclined to apply it to living things as well. When, therefore, from 1831 to 1836 he was privileged to accompany as naturalist an expedition that was traveling around the world on the ship *Beagle*, he was already in a frame of mind to reflect present occurrences back into the past to see what they might explain.

It was not until after his return from this voyage, however, that the idea of natural selection occurred to him. As he himself says, he got it from a book by Malthus, "Essay on Population," in which it was pointed out that human populations tended to increase rapidly, thus leading to a struggle for existence. Darwin quickly saw in this situation a means of modifying species of other organisms; for if individuals varied, and if they were competing with one another, any advantage possessed by certain types of individuals would tend to preserve them while less favored ones would either suddenly or gradually disappear. If the favorable qualities were hereditary, as he apparently assumed they would be, the result would be the formation of a new species.

For 20 years Darwin collected facts that seemed to bear on the possible correctness of this natural selection, but he published nothing. Only a few friends, including Lyell and the botanist Joseph Hooker, with whom he frequently discussed his views, knew what conclusions he was reaching. Then a curious coincidence induced him to put a synopsis of his work into print. Alfred Russel Wallace, a young naturalist then in the Orient, sent to Darwin a sketch of a theory of which he desired Darwin's opinion. To the latter's surprise, this theory proved to be none other than the theory of natural selection, or survival of the fittest; and, as Wallace afterwards related, he too had first got the idea from reading the work of Malthus, "Essay on Population." At first Darwin was inclined to withhold his own manuscript and allow that of Wallace to be published. But since Wallace's idea was admittedly a sudden one, in favor of which he had collected no facts whatever, whereas Darwin had long been gathering data relative to it, Darwin's friends protested. It was finally arranged to present extracts from both Darwin's and Wallace's manuscripts simultaneously to the Linnaean Society of London, which was done in 1858. Darwin's theory was developed at length in "The Origin of Species" in 1859. The book was written in language intelligible to the average reader without biological training. Furthermore, the time was ripe for such an advance. These facts, coupled with championship by T. H. Huxley (Fig. 305), who carried the evolution idea to the general public in lectures and popular articles, won a quick victory for the new doctrine. The history of the evolution idea in the last 60 or 70 years has been the accumulation of new facts in support of it, the development of theories to account for it, the grouping of animals on the basis of the relationship implied in evolution, and the application of corollaries of evolution to other branches of biology.

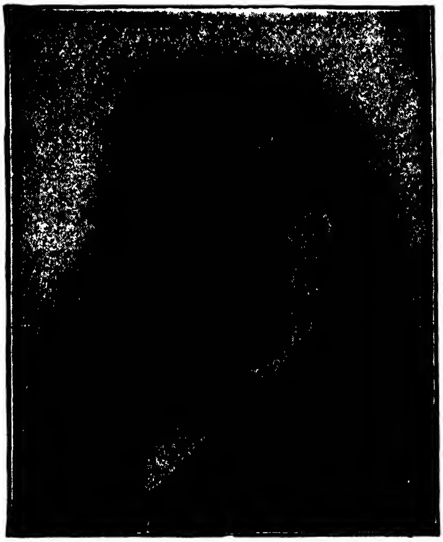

Fig. 305.—Thomas Henry Huxley, 1825–1895.

Operation of Natural Selection.—How natural selection is believed to work may be best illustrated from the standpoint of the genes. In any species in which a certain gene is becoming either more or less common, evolution is occurring. Even if the gene in question is recessive and even if it occurs only in heterozygotes so as never to produce a visible effect, if this gene is present in a gradually increasing or decreasing number of individuals, the species is evolving. Now most genes produced by mutation are recessive. They cannot at first affect the visible or physiological properties of the individuals, for these organisms are heterozygous. During this early period, pure chance must be responsible for the fluctuation of the prevalence of the new gene, as described above (page 359). Many a new gene is lost before it can become established. Most new genes are thus lost. Evolution would be going on at a tremendous rate in some species if even a majority of mutations succeeded. Out of the large number that occur only a few happen to become numerous enough to begin to show their effects in homozygotes. Then they are on trial. They may confer some advantage on their possessors, such as longer life, more rapid growth, or greater strength. If the advantage is one that enables them to leave more descendants, that gene tends to become more prevalent. If on the contrary the new gene is harmful, in such a way that its possessor leaves fewer descendants, it is checked in any increase which it might otherwise enjoy. Mere harmfulness cannot eradicate a gene altogether if it is recessive, for it may continue to exist in heterozygotes beyond the reach of natural selection; but a very harmful gene cannot become much more abundant than the level at which heterozygotes begin to meet and mate, thus producing homozygotes. A less harmful gene may become slightly more abundant than this, so that some homozygotes appear; but it cannot replace the alternative gene which is superior to it. A neutral gene, one conferring neither advantage nor disadvantage, is at the mercy of chance. As pointed out before (page 359), local races within a species may come into existence in different parts of a range by this accidental method.

A considerable degree of variability may thus exist in any species. Partly it is observable, as in the distinguishable local races; but much of it is hidden in heterozygotes. At any particular time it is to be expected that a species will exhibit approximately that part of its genetic composition which is most favorable; and "favorable" means conducive to large numbers of descendants. This most advantageous group of genes would be expected to show, because, if they were not expressed, natural selection would gradually bring them to expression. If, under these circumstances, the environment were to change in some respect, so that certain genes increased and their alternates decreased in *value*, without much question the species would change toward the genetic make-up that had acquired enhanced usefulness. Such changes would necessarily be slow; hence the alteration of the environment would have to be at least semipermanent to accomplish any important modification of the species exposed to it. Even a hundred thousand generations might well prove too short for any important change of a species under the selective action of the environment.

Among groups of organisms that differ in more than the mere proportion of certain genes, selection should work more effectively. Of the varieties that arise by chance within a species, one or more may well fit the environmental situation better than others. Unless these varieties are kept in their separate areas by different physiological responses to features of the environment, which is probably not often true, the favored variety or varieties should gain the ascendancy. They might or might not crowd out their fellow varieties; but even if they were only more abundant in individuals, they should have a greater share in determining any later evolutionary changes. In like manner, species must differ in their capacity to propagate, and the more capable ones should increase in numbers. Genera, families, orders, all higher ranks must be subject to this action of natural selection, but the action is always on the individuals that compose them.

Adaptation.—The guidance of evolution by natural selection should result in a considerable degree of fitness for the environment. If individuals and species are preserved in proportion to their ability to succeed, their success should grow with the passage of generations. The fact that natural selection offers a general explanation of adaptation is one of the chief reasons for the rapid acceptance of Darwin's theory among biologists. For adaptation is very widespread, and some of it is very remarkable. So abundant is it, and so marvelous are parts of it, that many naturalists have come to feel that adaptation is the outstanding feature of life requiring an explanation.

It would be easy, however, to overemphasize its frequency, its degree, and its necessity. Most species are not so well adapted to their situation as they conceivably could be, but they get along. Lack of satisfactory adaptation in certain species or larger groups seems to be proved by extinction. Moreover, obvious adaptation, as among taxonomic groups, is found most markedly in the groups of higher rank. Classes, orders, families are marked off from one another by such things as wings, gills, armor plate, webbed feet, and quills which perform definite functions in the lives of the individuals and often help to determine where they shall live. Such structures are highly adaptive. In lower ranks, however, this adaptiveness is much less common. Most genera of the same family do not make any particular use of the characters that distinguish them from one another, though there are exceptions. Among species of the same genus, almost never do the distinguishing characters seem to be of any particular value to the individuals possessing them. This lack or infrequency of adaptiveness of the so-called species and genus characters is one of the principal reasons for adopting the view, just described, that varieties and species may become separated from one another by accidental changes in genetic composition, while natural selection does not exert its most powerful influence until some degree of differentiation has been attained.

Pointing out the adaptations of animals has been one of the favorite pastimes of naturalists. Books and articles on natural history are full of examples, and recitation of the marvelous fitness of organisms to some special niche in the environment never fails to excite wonder. The several decades following the publication of Darwin's "Origin of Species" were marked by inordinate attention to the features of living things that enable them to cope with the environment, for to explain the development of any character through natural selection it was only necessary to find a use for it. The things most often regarded as making for success were ability to secure food, escape enemies, resist conditions of the physical environment, and attract the opposite sex. The supposed uses of spots and spines, colors and habits, to attain these ends were exceeded in marvelousness only by the ingenuity of the naturalists in devising them. In this period, what are probably the things of greatest importance, the physiological qualities, were relegated to minor roles. Comparatively little attention was given, for example, to resistance to disease and exceptional fertility. Either of these should influence the number of descendants more than most of the structural characters whose origins were sought. Plasticity, or the capacity of either an individual or a species to adjust itself to many types of environment, must be highly important but was seldom considered then. These mistakes of the early followers of Darwin led to a reaction against the natural selection theory over the end of the last century, but the doctrine has emerged again with a very different type of support, based on knowledge of mutations, the laws of heredity, and the mathematics of chance.

It should be pointed out that adaptation is a quality of an organism as a whole. While in some instances one feature of an organism stands out as supremely important, so that other characters all yield to it in determining success, in most living things fitness is composed of many things. The success of an individual is a product of them all. An animal has only one life to lose or preserve. If a frog perishes in the tadpole stage because it has not the requisite power to withstand desiccation, it cannot be preserved in the adult stage by any special agility in escaping from enemies. Likewise, an animal gives rise to only one set of descendants. If these are few because the animal's life is short, they cannot be numerous because it lays eggs rapidly. It is the totality of qualities, some favorable, some unfavorable, that determines success, and it is on this total product that selection acts.

Another point requiring emphasis is that, from the evolutionary standpoint, a successful species or individual is one that leaves many descendants. No quality is of any particular advantage to a species unless it entails numerous posterity. Long life may seem to be an advantage; but if it is merely a prolongation of activity after the reproductive period is over, the species gains nothing by it. Rapid growth is a good sign physiologically; but if it is expressed only in somatic tissue and does not result in more germ cells or more embryos or does not in some way enlarge families, it is useless as an element in the security of the species. On the whole, also, it is the far distant progeny, rather than the near generations, which are most important. A species so constituted that in its present environment it succeeds moderately but safely, but will in a much later environment thrive exceptionally, is more influential upon evolution than is a species which is exceedingly abundant now but dwindles in later time. These statements are, of course, merely definitions; it is not possible to apply them and say which present species are going to be successful later.

Isolation.—Many biologists have always believed that an important part of the divergence of species from one another is due to some sort of isolation. Attention was early called to the supposed effects of geographic isolation, as of terrestrial organisms living on an island. The species in such an isolated region are mostly different from those of the nearest other land areas. It is easy to see how, with different mutations happening to arise among island forms, and probably with a different sort of environment acting selectively upon them, there should be a gradual divergence of the two groups. Taxonomists, moreover, have generally held that the classification implies much more isolation than geographic features provide. Since species have presumably split up into varieties, which are free to cross with one another as far as they meet in the same area, and since by further divergence varieties are believed to advance to the rank of species, it might be supposed that hybridization between species would continue indefinitely. Now hybridization should operate to remove the distinctions between species. How, then, have arisen the generally rather sharp lines between species? For there are relatively few intermediate individuals that might be regarded as species hybrids.

The nature of the answer to this question is indicated by the discovery that most species are not fully fertile with other species, even with those most like them. While there are many exceptions, especially in plants, they are in a small minority. Some species, even within the same genus, cannot be crossed; that is, they cannot or do not produce hybrid offspring. Other species may be crossed, but the hybrid offspring are of low fertility or even completely sterile. Some species, if crossed, produce offspring only of the female sex, and these, since they are not parthenogenetic, cannot give rise to a new type.

What causes this sterility between species or in their hybrids is only partially known. Difference in numbers of chromosomes is one obvious cause, since there can be no complete pairing and meiotic division (page 195) of the chromosomes in a hybrid unless the chromosomes match. Rearrangement of the genes in the chromosomes, such as turning one segment of a chromosome end about, has a similar effect; for in a hybrid having two chromosomes alike in genes but differing in their arrangement the pairing of the chromosomes is not normal. Many other chromosome changes may occur. When an individual has two chromosomes of the same sort in each pair, even if both are aberrant, it may behave normally; and a group of such individuals may constitute a species. But when they attempt to cross with individuals having chromosomes differently constituted, abnormalities arise. Species are just as effectively isolated by such chromosome changes as they would be if separated by a thousand miles of ocean. Indeed, it is probable that separation of species from one another is often rendered complete by such chromosome aberrations.

Evolution of Domesticated Races.—One of the arguments used by Darwin in favor of natural selection is the fact that animals and plants under control by man have experienced enormous modifications. A very few years of selection by man have produced observable changes in cultivated plants, and herd records show similar though less striking changes in domesticated animals. The method is selection. The breeder preserves individuals most nearly approaching his ideals in the belief that they will transmit the desirable qualities, and sometimes they do. Darwin concluded that all that was necessary to accomplish a similar result in wild species would be some selecting agency to replace the breeder. That selecting agency could not be endowed with reason or foresight, but highly adaptive modifications could, he believed, be produced by selective action of the environment itself. The method, as conceived now, has already been outlined.

The written histories of domestic breeds do not go back far enough to show the source from which any of our principal types of animals came. Very early records show animals already in man's control, but not much information about them is given. The sources of the various animals have been conjectured from the qualities of breeds today and the characteristics of wild species, but nothing is certain. The breeds of poultry are believed to be descended from two wild sources, the jungle fowl and the Malay fowl, both of the Orient. Egg-laying qualities are thought to have come mostly from the former, while table birds have inherited more from the latter. The various breeds of pigs are all regarded as descendants of two wild boar species, one from Europe and Africa, the other from India. Dogs probably have a somewhat greater variety of wild ancestry, since their characteristics indicate contributions from the timber wolf of Russia, the jackal of Europe, the coyote of North America, and the dingo of Australia. Sea island cotton is probably derived from two wild species, upland cotton from at least three. Corn has an obvious relative in wild teosinte, but it is likely that other species of grasses are also ancestral to it.

All this modification of breeds is evolution of a sort. That Darwin was justified in concluding from it that selection has been likewise the guiding factor in nature, some biologists have doubted. For domestic breeds exhibit one important quality which is uncommon in natural species; they are generally interfertile. The several kinds of dogs differ from one another structurally quite as much as wild species do; but they can be crossed, while wild species usually cannot be. It has often been argued that if selection were responsible for species formation in nature, these species should be as fertile with one another as are domestic varieties. This criticism overlooks one difference between the selecting agents. Man is vitally interested in maintaining interfertility of his stocks, for his method requires that he cross them. If sterility had arisen between individuals, because of chromosome aberrations or for any other reason, those individuals would have been rejected. In nature, such individuals would have survived if lucky and if otherwise fit. By keeping his stocks fertile among themselves, and by crossing them frequently, man has speeded up the process of change far beyond any rate that might have occurred naturally. Man's goals have also been very different from those to which natural selection leads. But in no other important respect have the two processes been unlike.

Evolution of Man.—The fossil evidence of man's origin was briefly outlined in the preceding chapter. Whether there has been any important evolution in man since he attained the capacities of Cro-Magnon man, for example, is uncertain. There is no historical evidence of such change. It is often said that man has made no progress in physical or mental qualities in the last 10,000 years. This statement may be true, but there is no way to know. It would be expected that there had been some evolution during that time. Man is extraordinarily heterozygous, and there is much hybridization between stocks. Presumably also mutations arise in man. Unless all individuals survive, and all are equally fertile, it is difficult to see how evolution can fail to occur. Whether that evolution is progress upward or not is another matter.

Since man has guided the evolution of his flocks and herds, it would seem entirely possible that he should guide his own. The science of eugenics aims at improvement of the race by such methods. Assuming that man can judge correctly which of his qualities are most desirable and that he can subordinate his emotions to his reason, there is no apparent obstacle to progress as far as his present genes and future mutations make possible. How great this progress may be it is futile to estimate, for no one knows what new qualities may arise through interaction of genes already in existence, and certainly no one can guess what genes will mutate or how. Predictions regarding man's future evolution are accordingly meaningless.

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GLOSSARY

Pronunciations are indicated in the glossary as far as possible without the aid of diacritical marks, but the following symbols have been necessary:

H = the German ch;

N = the French nasal n;

ü = the French u, pronounced by shaping the lips for sounding long oo and the tongue for long ee.

Abiogenesis (*ab' i o jen' e sis*). The origin of living things from nonliving matter; same as spontaneous generation.

Absorption. The imbiding of a liquid by osmotic or capillary action.

Acanthocephala (*a kan' tho sef' a'la*). A group of parasitic wormlike animals sometimes included with the Nemathelminthes. For definition see Chap. 19.

Acetabulum (*as' e tab' u lum*). The socket on either side of the pelvic girdle for the head of the femur.

Acetylcholine. A substance produced by nerve endings of the craniosacral system and serving to stimulate certain organs, to inhibit others.

Acid. A substance which readily gives up hydrogen ions, H^+.

Actinomorphes (*ak' tin o mor' feez*). A group of animals in Blainville's early classification; animals with radiating parts, such as the starfish.

Adaptation. Fitness for the environment. In a concrete sense, an adaptive structure, habit, or function.

Adductor. One of the large muscles attached to the valves of a mussel shell, or the corresponding muscle of a glochidium; also, one of numerous muscles in other animals which draw a structure toward the median axis.

Adipose. Pertaining to fat.

Adrenal. One of two or more ductless glands in close relation with the kidneys in most vertebrates.

Adrenalin (*ad ren' al in*). A hormone produced by the adrenal medulla.

Adsorption. The adherence of molecules of gases or dissolved substances to the surfaces of other bodies.

Aeolosoma (*e' o lo so' ma*). A genus of worms, phylum Annelida, subclass Oligochaeta.

Afferent. Leading toward; said of nerve fibers which conduct impulses toward the central nervous system.

Aganides (*ag' a ni' deez*). A genus of extinct cephalopods with bent sutures of the goniatite form.

Agkistrodon piscivorus (*ag kis' tro don pis siv' o rus*). A species of snake, the cottonmouth moccasin.

Alanin (*al' an in*). A very simple amino acid.

Alecithal (*a les' i thal*). Containing little or no yolk; said of certain eggs.

Altricial (*al trish' al*). Hatched in a weak, helpless condition; said of certain birds.

Alveolar gland (*al ve' o ler*). A gland in which the lumen is inflated at certain points.

Alveolus (*al ve' o lus*). One of the microscopic air chambers to which the bronchioles lead in lungs.

Amblycorypha (*am' bli kor' i fa*). A genus of katydids.

Ambystoma (*am bis' to ma*). A genus of salamanders. **A. maculatum, A. tigrinum,** common species.

Amino acid (*am' i no*). One of a number of organic acids containing the NH_2 radical and having certain chemical properties. These acids enter into the composition of all proteins and are produced by the splitting of proteins.

Amitosis (*a' mi to' sis*). Cell division not involving the formation of chromosomes or a spindle.

Ammonite (*am' mo nite*). An extinct cephalopod having a coiled shell and complicated foliaceous sutures; so called from the genus Ammonites.

Amoeba (*a me' ba*). A genus of one-celled animals, a protozoon of the class Rhizopoda.

Amphiaster (*am' fi as' ter*). The figure produced by two asters and the connecting spindle in a dividing cell.

Amphibia. A class of Vertebrata embracing the frogs, toads, salamanders, and some others. For definition see Chap. 19.

Amphicoelous (*am' fi see' lus*). Having both ends of the centrum concave; said of vertebrae.

Amphineura (*am' fi nu' ra*). A class of Mollusca, the members of which are bilaterally symmetrical, have a shell of eight pieces or no shell at all, and many pairs of gills. Chiton is an example.

Amphioxus. A primitive fishlike animal belonging to the subphylum Cephalochorda of the Chordata.

Amphiuma (*am' fi u' ma*). A genus of salamanders.

Amylopsin (*am' i lop' sin*). A starch-digesting enzyme produced by the pancreas.

Anabolism. The aggregate of constructive processes comprised in metabolism.

Analogous (*an al' o gus*). Similar in function.

Anaphase (*an' a faze*). Any stage of cell division during the passage of the chromosomes from the middle to the ends of the spindle.

Anatomy. The science which treats of the structure of animals and plants as revealed by dissection. It more commonly deals with the grosser features, but the finest details of structure are not excluded.

Anaximander (*an aks' i man der*). A Greek physical philosopher and mathematician, pupil of Thales, who lived about 611–547 B.C.

Animal pole. That part of an egg in which the protoplasm is concentrated (in eggs with much yolk), and which in most animals produces the nervous system, sense organs, etc. Other features may also characterize the animal pole.

Anisogamete (*an' i so gam' eet*). One of two unlike cells which fuse in reproduction.

Annelida (*an nel' i da*). The phylum of animals comprising the segmented worms. For definition see Chap. 19.

Anodonta. A genus of fresh-water mussels.

Antenna (*an ten' na*) (*pl.*, **antennae**). One of a pair of jointed appendages projecting forward from the head of an insect or crustacean.

Anthophysa (*an' tho fi' za*). A genus of colonial flagellate Protozoa whose cells are borne in radiating masses on a branching stalk.

Anthothrips niger (*an' tho thrips ni' jer*). A species of insect of the order Thysanoptera, commonly called thrips.

Anthozoa (*an' tho zo' a*). A class of Coelenterata, comprising the sea anemones and most of the corals. They have no medusoid form in the life cycle.

Anus (*a' nus*). The posterior opening of the digestive tract.

Apoda (*ap' o da*). An order of Amphibia comprising the legless forms called caecilians.

Appendicular skeleton. The bones of the limbs and their attaching girdles in vertebrates.

Arachnida (*a rak' ni da*). A class of Arthropoda comprising the spiders, scorpions, and mites. For definition see Chap. 19.

Archaeozoic (*ar' ke o zo' ik*). Of the earliest geological era; the oldest known rocks are of this era.

Archenteron (*ark en' ter on*). The cavity within the endoderm of a gastrula. It communicates with the exterior.

Archiannelida (*ar' ki an nel' i da*). A class of primitive marine worms (Annelida) without setae.

Aristotle (*ar' is tot'l*). The most famous of the Greek naturalist philosophers, who lived 384–322 B.C.

Armadillo. An armored mammal of the order Edentata, which includes also the sloths and anteaters.

Arteriole. One of the smaller branches of an artery, leading to capillaries.

Artery. A blood vessel conducting blood from the heart.

Arthropoda (*ar throp' o da*). A phylum of animals, including the insects, crustacea, centipedes, etc. For definition see Chap. 19.

Articulate. To join; said of bones.

Artiomorphes (*ar' ti o mor' feez*). A group of animals in Blainville's early classification; it comprised the animals whose bodies are bilaterally symmetrical.

Ascaris (*as' ka ris*). A genus of roundworms (Nemathelminthes) parasitic in various animals. **A. megalocephala** (*meg' a lo sef' a la*), parasitic in the intestine of the horse.

Ascorbic acid. Vitamin C, the preventive of scurvy.

Asexual. Not involving germ cells or fusion of nuclei; said of reproduction, or of an individual employing such a mode of reproduction.

Assimilation. The conversion of digested foods and other raw materials into protoplasmic substances.

Association neuron. A nerve cell within the central nervous system, which helps to connect an afferent with an efferent neuron.

Aster. The starlike figure composed of a centriole and the radiating lines about it; or the centriole may be lacking.

Asteroidea (*as' te roi' de a*). A class of Echinodermata comprising the starfishes. For definition see Chap. 19.

Astral rays. The radiating lines surrounding a centriole in a dividing cell.

Asymmetry. Absence of any kind of symmetry.

Atoll (*at' ol*, or *a tol'*). A ring- or horseshoe-shaped coral island.

Atom. A unit of a chemical element, composed of one or more protons and electrons, and usually neutrons.

Auditory. Pertaining to hearing; applied to the nerve of hearing and the sensory part of the inner ear.

Auricle. The anterior chamber of the heart in fishes, and one of the two anterior chambers in higher vertebrates.

Autonomic nervous system. A system of ganglia and nerve fibers, comprising two mutually antagonistic groups, which center in specific parts of the central nervous system and regulate the involuntary responses of the heart, blood vessels, digestive tract, glands, and pupil of the eye.

Autosome (*aw' to some*). Any chromosome not closely associated with sex, that is, not an X or Y chromosome.

Aves (*a'veez*). A class of vertebrate animals comprising the birds.

Avoiding reaction. The behavior by which Paramecium avoids obstacles of various kinds. It consists of stopping, moving backward, turning through an angle away from the oral groove, and starting forward in a new direction.

Axial skeleton. The skull, vertebral column, ribs, sternum, and hyoid apparatus of vertebrates.

Axolotl (*aks' o lot'l*). The larval form of the tiger salamander *Ambystoma tigrinum* which reproduces while in the larval state.

Axon (*aks' one*). A projection from a nerve cell which ordinarily conducts impulses away from the body of the cell.

Backcross. A cross between an F_1 individual and one of its parent types.

Balanoglossus. A genus of wormlike animals doubtfully included in the phylum Chordata.

Bascanion. A genus of snakes, including the black snake or blue racer.

Base. A substance giving rise to free hydroxyl ions, OH^-, and thereby accepting hydrogen ions, H^+.

B complex. A group of related vitamins found in meats, seed coats of cereals, yeast, etc., including thiamin, riboflavin, niacin, and pyridoxin.

Biconcave. Having the centrum hollow both in front and behind; said of vertebrae.

Bidder's canal. A longitudinal tube near the median border of the kidney of certain Amphibia; into it the collecting tubules open.

Bilateral symmetry. An arrangement of the parts of an object or animal body such that the halves on opposite sides of a certain plane (only one in number) are mirrored images of each other.

Bile. The fluid secreted by the liver in vertebrates.

Bile duct. The tube through which bile is discharged into the intestine.

Binomial. Consisting of two names or terms. Applied to the system of nomenclature by which each species is given two names, one for the genus, the other for the species.

Biogenetic law. The doctrine that animals in their embryonic development repeat the evolutionary history of the race.

Biology. The science of life and of living things, whether plants or animals.

Bladder. A membranous sac in which urine is stored.

Blainville, Henri Marie Ducrotay de (*blaɴ veel'*). French naturalist, 1777–1850.

Blastocoele (*blas' to seel*). The hollow interior of a blastula.

Blastopore. The opening through which the archenteron of an early embryo (gastrula) communicates with the exterior.

Blastostyle. In hydroids, a nontentaculate individual which produces medusae.

Blastula (*blas' tu la*). An early developmental stage, consisting of a hollow ball of cells.

Blood platelet. One of the formed components of the blood, produced by fragmentation of certain cells.

Book gill. See **book lung.**

Book lung. A respiratory organ composed of flat sheets joined together like pages of a book, found in spiders.

Bougainvillea ramosa (*boo' gin vil' le a*). A species of marine hydroid.

Bowman's capsule. The expanded end of a kidney tubule, in which a glomerulus is located.

Brachiopoda (*brak' i op' o da*). A group of marine animals of uncertain rank or relationship. They have a bivalve shell, the two halves of which are unequal. Sometimes placed in a phylum with the Bryozoa and Phoronidea.

Bract. One of the covering (protective?) members of a siphonophore colony.

Bradypus (*brad' i pus*). A genus of sloths.

Bronchiole (*brong' ki ole*). One of the smaller branches of the bronchi, air tubes in the lungs.

Bronchus (*brong' kus*) (*pl.*, **bronchi**). One of the two main branches of the trachea in many vertebrates.

Brown, Robert. British botanist, 1773–1858.

Bryozoa (*bri' o zo' a*). A group of marine and fresh-water animals of uncertain rank and relationships, mostly colonial, bearing tentacles, and commonly known as moss animals. Sometimes placed in a phylum with the Phoronidea and Brachiopoda.

Buccal cavity (*buk' k'l*). The most anterior division of the digestive tract of an earthworm. Also the mouth cavity of other animals.

Budding. Division of an organism into unequal parts in reproduction.

Buffon, Comte de (*bü fon'*). French naturalist, 1707–1788.

Bufo. A genus of toads.

Byssus. A thread attached near the adductor muscle of a glochidium; or a bunch of threads attached to the foot of certain clams.

Caecilian. One of a group of legless, wormlike Amphibia of the order Apoda.

Caecum (*see' kum*). The blind pouch at the beginning of the large intestine.

Calcarea. A class of sponges (Porifera) whose skeletons are composed of spicules of calcium carbonate.

Calciferol (*kal sif' er ole*). Vitamin D, the preventive of rickets.

Calorie (*kal' o ri*). The quantity of heat required to raise the temperature of a kilogram of water 1°C.; this is a large calorie, equal to 1000 small calories.

Cambrian (*kam' bri an*). Of the earliest Paleozoic time.

Camponotus. A genus of ants.

Canaliculus (*kan' a lik' u lus*). One of numerous minute channels radiating from each lacuna in the matrix of bone, in which slender processes of the bone cells are located.

Cancellate (*kan' sel late*). Composed of a number of chambers separated by partitions; said of spongy bone.

Canine (*ka' nine*). A tooth located laterally to the incisors.

Capillary. One of numerous small vessels conveying blood through the tissues from arteries to veins or from one vein to another.

Carapace. The hard bony covering of a turtle; also the chitinous or calcareous covering of the cephalothorax of a crayfish or lobster.

Carbohydrate. Any one of a class of organic substances, embracing the starches, sugars, cellulose, etc., which are composed of carbon, hydrogen, and oxygen, with the number of atoms of hydrogen and oxygen regularly in the ratio of 2:1.

Carboniferous. The geological age to which the principal known coal beds belong; succeeding the Devonian, it is a combination of Mississippian and Pennsylvanian.

Carchesium (*kar ke' zi um*). A genus of colonial ciliated Protozoa, resembling Vorticella.

Cardiac. Pertaining to or near the heart.

Carnivore. Technically, a mammal of the order Carnivora, including the cats, dogs, and seals. In a popular sense, any flesh-eating animal.

Carnivorous. Flesh-eating.

Carotene. A yellow pigment found in carrots and many green or yellow vegetables; a source of vitamin A.

Carpal. One of a number of bones in the wrist in vertebrates.

Carpometacarpus (*kar′ po met a kar′ pus*). A compound bone in the wing of a bird, formed by the union of several of the metacarpals and carpals.

Cartilage. A flexible, somewhat translucent tissue composed of cells imbedded in a matrix, found on the ends of bones at joints and in other situations.

Cast. A mass of rock formed within a cavity, as the cavity of a shell or of a mold formerly occupied by an animal.

Catabolism (*ka tab′ o liz′m*). The aggregate of destructive processes comprised in metabolism.

Catalase. An enzyme which liberates oxygen from hydrogen peroxide.

Catalyst (*kat′ a list*). A substance which brings about a reaction but is not consumed in that reaction. It probably often participates in the reaction but is promptly reformed.

Caudal. Belonging to the tail.

Caudata. An order of Amphibia comprising forms with tails (salamanders, newts).

Cell. A mass of protoplasm containing a nucleus or nuclear material.

Cell doctrine. See **cell theory.**

Cell inclusions. Nonliving objects enclosed in cells.

Cell membrane. A thin sheet either of differentiated protoplasm, or of some substance produced by protoplasm, surrounding a cell.

Cell theory. The theory that all animals and plants are composed of similar units of structure called cells. The theory is now so well established as to be more properly called the **cell doctrine,** and other features concerning physiology, development, etc., may be included in it.

Cellulose (*sel′ u lose*). The substance, one of the carbohydrates, of which the cell walls of plants are commonly composed.

Cell wall. A nonliving structure secreted by a cell around itself. It is commonly composed of cellulose or chitin.

Cement. A binding material in the composition of teeth.

Cenozoic (*se′ no zo′ ik*). Pertaining to the most recent geological era.

Central nervous system. The brain and spinal cord.

Centriole. A minute body in the center of a centrosphere, and located at the end of the spindle of many dividing cells.

Centrolecithal (*sen′ tro les′ i thal*). Having the yolk in a central position, surrounded by protoplasm at the surface; said of eggs.

Centrosome (*sen′ tro some*). A minute body often present in a cell, usually near the nucleus in a centrosphere, related in some way to the process of cell division. By many writers the name is used interchangeably with **centriole.**

Centrosphere (*sen′ tro sfeer*). A differentiated portion of the cytosome of a cell, usually near the nucleus, and typically containing a centrosome or centriole.

Centrum. The massive portion of a vertebra ventral to the neural canal in which the spinal cord rests.

Cephalochorda (*sef′ a lo kor′ da*). A subphylum of Chordata, comprising the species of Amphioxus. For definition see Chap. 19.

Cephalopod (*sef′ a lo pod*). One of the group Cephalopoda, to which the cuttlefishes, squids, and nautili belong.

Cephalopoda (*sef′ a lop′ o da*). A class of Mollusca, comprising the octopi, squids, cuttlefishes, and nautili, animals in which the foot is developed into a headlike structure with eyes and a circle of arms.

Cephalothorax (*sef′ a lo tho′ raks*). A fused head and thorax, found in crayfishes and their allies.

Ceratite (*ser′ a tite*). An extinct cephalopod having a coiled shell and crooked sutures; named from the genus Ceratites.

Ceratites (*ser' a ti' teez*). A genus of extinct cephalopods with crooked sutures; the common name ceratite is derived from this genus.
Ceratium candelabrum (*se ra' shi um can' de la' brum*). A species of protozoon which forms linear colonies.
Cerebellum. A division of the brain of vertebrates developed on the dorsal side anterior to the medulla.
Cerebrum. The anterior division of the brain in vertebrates. In man it forms the greater part of the brain but is smaller in other vertebrates.
Cervical. Pertaining to the neck.
Cestoda. A class of Platyhelminthes, comprising the tapeworms. For definition see Chap. 19.
Chaetogaster (*ke' to gas' ter*). A genus of worms, phylum Annelida, subclass Oligochaeta.
Chaetognatha (*ke tog' na tha*). A group of marine animals of uncertain kinship, represented chiefly by the arrowworm Sagitta.
Chaetopoda (*ke top' o da*). A class of worms (Annelida) provided with setae, to which the earthworm and sandworm belong.
Cheloniidae (*kel' o ni' i dee*). A family of turtles.
Chelydidae (*ke lid' i dee*). A family of turtles.
Chelydridae (*ke lid' ri dee*). A family of turtles.
Chitin (*ki' tin*). A horny substance forming the outside skeleton of insects and many other animal parts.
Chiton (*ki' ton*). A genus of primitive mollusks, having a shell of several pieces.
Chloragogen cells (*klo' ra go' jen*). The cells of the outer layer of the intestine of the earthworm.
Chlorophyll. The green substance in chloroplasts through whose agency photosynthesis occurs.
Chloroplast. A green plastid.
Cholesterol (*ko les' ter ol*). A substance, one of the solid alcohols, found in many animal tissues.
Chordata (*kor da' ta*). A phylum of animals including the vertebrates and a few others. For definition see Chap. 19.
Chromatin (*kro' ma tin*). The deeply staining substance of the nucleus of a cell.
Chromoplast. One of several kinds of colored structures or organs found in many plant and some animal cells.
Chromosome. One of the rodlike or rounded bodies into which the chromatin of a nucleus is resolved at the time of cell division.
Chrysemys (*kris' e mis*). A genus of turtles.
Ciliate. A class of the protozoa, in which both young and adult stages are provided with cilia.
Ciliophora (*sil' i of' o ra*). A subphylum of protozoa, members of which are covered with a pellicle, have a fixed mouth, and are usually covered with cilia; example, Paramecium.
Cilium. A minute hairlike motile structure occurring on the surface of certain cells.
Circular canal. A channel passing around a medusa near its margin.
Circulation. The movement of the blood through a system of vessels.
Circumpharyngeal connectives (*ser' kum fa rin' je al*). Nerve cords in the earthworm connecting the brain with the ventral nerve cord; so called because they pass around the anterior end of the pharynx.
Citellus tridecimlineatus (*si tel' lus tri des' im lin' e a' tus*). A species of ground squirrel.
Class. A subdivision of a phylum; a group of higher rank than the order.

Clavicle. The collar bone in man. One of the bones of the ventral part of the pectoral girdle in vertebrates in general.

Cleavage. The division or segmentation of an egg.

Clitellum. A thickened glandular band encircling the body of an earthworm.

Cloaca (*klo a' ka*). A common passageway through which the intestine, kidneys, and sexual organs discharge their products in some fishes, in amphibia, reptiles, and birds, and in a few mammals.

Cnidoblast (*ni' do blast*). A cell containing a nematocyst or stinging thread in Hydra or other Coelenterata.

Coagulation. Hardening; specifically, the clotting of the blood.

Cocoon. A case in which eggs are stored and in which frequently the larvae are developed; also a silky covering around the pupa.

Codosiga (*ko' do si' ga*). A genus of flagellate Protozoa having a collar around the flagellum.

Coelenterata (*se len' ter a' ta*). The phylum to which Hydra, the hydroids, jellyfishes, and siphonophores belong. For definition see Chap. 19.

Coelenteron (*se len' ter on*). A cavity in forms like Hydra which have only one body cavity. It serves the digestive and circulatory functions and is therefore also called the gastrovascular cavity. It has only one opening.

Coelom (*see' lome*). The true body cavity, a cavity within the mesoderm on the walls of which the principal reproductive organs are located.

Coenosarc (*se' no sark*). The cellular living part of a hydroid, as distinguished from the perisarc.

Collared epithelium. Epithelium each of whose cells bears a collar.

Collecting tubule. One of a number of tubes leading across the kidney of the frog from Bidder's canal to the ureter.

Colloid (*kol' loid*). A mixture in which particles invisible through a microscope but greater in size than molecules are held in suspension in a liquid.

Colloidal (*kol loi' dal*). Contained in a liquid in aggregations submicroscopic in size but greater than molecules.

Colony. A group of individuals of the same species organically connected with each other.

Coluber. A genus of snakes.

Columnar epithelium. Epithelium in which the cells have one dimension distinctly greater than the others, that dimension being vertical to the surface covered by the epithelium.

Comanchean (*ko man' che an*). Pertaining to Mesozoic time prior to the Cretaceous; formerly called lower Cretaceous.

Common bile duct. The tube leading from the liver to the small intestine and serving to convey bile to the small intestine.

Compound. A substance produced by two or more elements in combination.

Compound gland. A branching gland.

Conemaugh (*ko' ne maw*). A rock formation of eastern United States, belonging to Permocarboniferous time.

Coniferous. Cone-bearing (as pine or cypress trees).

Conjugation. The meeting of two cells for exchange of nuclear material or (by extension of meaning) for complete fusion.

Connective tissue. A tissue composed of cells and certain other material produced by the cells, which in its simple form binds organs and other tissues together. In a broader sense it includes such modified tissues as cartilage, bone, tendon, and ligaments.

Contractile tissue. Any tissue capable of active contraction; as muscle.

Contractile vacuole. A vacuole whose contents are periodically ejected to the outside of the cell in which it is contained.

Copepod (*ko' pe pod*). Any one of a group of small Crustacea.

Copulation. The act of introducing spermatozoa into the body of the female.

Coracoid (*kor' a koid*). A bone of the ventral part of the pectoral girdle of vertebrate animals; a distinct bone in the bony fishes, amphibia, reptiles, birds, and lowest mammals, but fused with the scapula in the higher mammals.

Cornea. The transparent bulging membrane at the front of the eye.

Corpus luteum (*pl.*, **corpora lutea**). A mass of cells invading the space in an ovary from which an ovum has escaped.

Corpuscle. One of the cells of the blood.

Cortex. The layer of gray matter which covers the cerebrum and dips into its folds. Also, an outer layer on various other organs, as the kidney or adrenal body.

Cranial nerve. One of 10 or 12 pairs of nerves arising from the central nervous system within the skull.

Craniosacral system. That part of the autonomic nervous system which centers in the brain and posterior portion of the spinal cord. Each organ controlled by the autonomic system is innervated once from it.

Cretaceous. Pertaining to the late Mesozoic time; so named from the chalk deposits characteristic of it.

Cretinism. A developmental deficiency caused by inadequacy of the hormone thyroxin.

Crinoidea (*kri noi' de a*). A class of Echinodermata, including the feather stars and sea lilies. For definition see Chap. 19.

Crocodilini (*krok' o di li' ni*). An order of Reptilia comprising the alligators and crocodiles and their allies.

Cro-Magnon (*kro man yon'*). A rather highly developed race of men preceding the principal races of today. It dwelt, as far as known, in Western Europe.

Crop. In the earthworm, an enlargement of the digestive tract behind the esophagus and in front of the gizzard. In birds, an enlargement of the esophagus for the temporary storage of food.

Crustacea. A class of arthropods including the lobsters, crabs, water fleas, barnacles, etc. For definition see Chap. 19.

Crystalline lens. A rounded, transparent, refractive body situated behind the pupil of the eye.

Ctenophora (*te nof' o ra*). A group of animals of uncertain rank including the comb jellies and sea walnuts. For definition see Chap. 19.

Cubical epithelium. Epithelium in which the height and width of the cells are about equal.

Cuvier, Georges (*kü vyay'*). French naturalist, founder of comparative anatomy, 1769–1832.

Cyclostomata (*si' klo sto' ma ta*). A class of Vertebrata having an eellike form, a cartilaginous skeleton, no jaws, and no lateral fins; lampreys and hagfishes.

Cytology. The science which deals with the structure of cells.

Cytoplasm. The protoplasm of a cell exclusive of the nucleus.

Cytosome. The body of a cell as distinguished from its nucleus.

Darwin, Charles. Celebrated English naturalist, founder of the doctrine of natural selection, author of several works on evolution. Lived 1809–1882.

Deciduous. Falling off at maturity or at the end of a season; said of the leaves of trees which fall periodically. Applied also to trees whose leaves fall periodically.

Deficiency disease. Any disease resulting from the lack or scarcity of some specific substance in the diet.

Democritus (*de mok' ri tus*). Greek philosopher, known for his atomic theory, who lived about 460–357 B.C.

Demospongiae (*de' mo spun' ji ee*). A class of Porifera (sponges). For definition see Chap. 19.

Dendrite. A projection from a nerve cell which ordinarily conducts impulses toward the body of the cell.

Dendritic. Treelike.

Denticulate. Finely notched or toothed.

Dentine. The dense bony substance composing the bulk of mammalian teeth.

Dermatozoa (*der' ma to zo' a*). A group of animals (literally, the skin or touch animals) in Oken's early classification. It comprised the invertebrates.

Dero. A genus of worms, phylum Annelida, subclass Oligochaeta.

Determinate. Leading infallibly to a given end result from a given beginning; said of development in which each cleavage cell produces a certain structure and nothing else, regardless of experimental interference.

Devonian (*de vo' ni an*). Of middle Paleozoic age, next following the Silurian.

Dextrin. Any one of several related carbohydrates derived by hydrolysis from starch, among them being erythodextrin, achroödextrin, and maltodextrin.

Diaphragm (*di' a fram*). A partition; specifically, the partition between the thorax and abdomen of a mammal.

Diffusion. The spreading of the molecules of one substance among those of another.

Digestion. The conversion of food into soluble substances which may diffuse through protoplasm.

Dinosaur (*di' no sawr*). One of an order of extinct reptiles of Mesozoic time, mostly of large size.

Dinotherium (*di' no the' ri um*). An extinct elephantlike animal from the Miocene.

Dioecious (*di ee' shus*). Having the male and female organs in separate individuals; said of species.

Diogenes (*di oj' e neez*). Greek natural philosopher of the fifth century before Christ, born at Apollonia.

Diploblastic. Composed of two layers of cells.

Diploid (*dip' loid*). Double; specifically, the double number of chromosomes found in the somatic cells, and in germ cells before meiosis, in bisexual animals. *Cf.* **haploid.**

Dipnoi (*dip' no i*). A subclass of Pisces, fishes with an air bladder functioning as a lung; the lungfishes.

Disaccharide (*di sak' a ride*). A carbohydrate whose molecule can be split into two molecules of simple sugar (monosaccharide).

Dominant. Receiving expression when only one determining gene is present, and in the presence of the gene for a contrasted recessive character; said of inherited characters that are exhibited by heterozygotes.

Dorsal. Pertaining to the back; hence, usually, upper.

Dorsal aorta. A large artery formed, in fishes, by the union of vessels coming from the gills, and passing backward in the dorsal region.

Dorsal root. The dorsal one of two roots by which a spinal nerve is connected with the spinal cord. Its fibers are sensory in function.

Drosophila (*dro sof' i la*). A genus of flies, of which the vinegar fly (**D. melanogaster,** *mel' a no gas' ter*) is a common species.

Duodenum (*du' o de' num*). The first of three divisions of the small intestine.

Dutrochet, René Joachim Henri (*dü' tro' shay'*). French physiologist, 1776–1847.

Dyad. A double body formed by the division of a tetrad into two parts. Its two parts may be derived from the same chromosome or from different chromosomes.

Echinoderm (*e ki' no derm*). One of the Echinodermata.
Echinodermata (*e ki' no der' ma ta*). The phylum of animals including the starfishes, sea urchins, sea cucumbers, brittle stars, etc. For definition see Chap. 19.
Echinoidea (*ek' i noi' de a*). A class of Echinodermata, comprising the sea urchins, sand dollars, and heart urchins. For definition see Chap. 19.
Echinorhynchus (*e ki' no ring' kus*). An Acanthocephalan worm.
Ecology (*e kol' o ji*). The branch of biology dealing with the relation of animals or plants to their environment.
Ectoderm. The outer layer of cells of a gastrula, or the representative of this layer in later stages.
Ectosarc. The outer layer of protoplasm in cells in which the outer and inner protoplasm differ distinctly in structure, as in Amoeba.
Edaphosaurus (*e daf' o saw' rus*). An extinct lizardlike reptile bearing a spiny fin on its back, from Permocarboniferous rocks of North America.
Effector. A structure specialized for some specific response; also the nerve carrying impulses to such a structure.
Efferent. Leading from; said of nerve fibers which conduct impulses away from the central nervous system.
Elasmobranchii (*e laz' mo brang' ki i*). A class of Vertebrata comprising the sharks, skates, rays, torpedoes, and chimaeras. For definition see Chap. 19.
Electrolysis (*e lek trol' i sis*). Decomposition of an ionized substance in solution by passing an electric current through the solution.
Electrolyte. A substance which, because it ionizes, is in solution capable of conducting an electric current and of being decomposed by the current.
Electron. A unit of negative electric charge entering into the composition of atoms.
Element. One of the approximately 90 primary forms in which matter exists.
Elephas (*el' e fas*). A genus of animals including living elephants and their fossil relatives of Pleistocene time.
Elodea (*el' o de' a*). A genus of aquatic plants.
Embryo. An undeveloped animal while still in the egg membrane or in the maternal uterus.
Embryology. The science which deals with the development of the embryo, or young stages, of animals or plants.
Embryonic. Pertaining to an embryo.
Empedocles (*em ped' o kleez*). Greek philosopher and poet, born in Sicily. Lived about 490–430 B.C.
Emulsion. A mixture of two liquids or semiliquid substances, neither one soluble in the other, the one being in the form of separate droplets suspended in the other.
Emulsoid. A mixture consisting of a liquid in which are distributed particles of a liquid or semisolid substance which are exceedingly minute yet larger than molecules.
Emys (*e' mis*). A genus of turtles of the family Testudinidae.
Enamel. The very hard, polished calcareous substance forming the surface layer or internal plates in the teeth of mammals.
Endocrine secretion. A secretion which must leave the gland by diffusion, not through a duct.
Endoderm. The inner layer of cells of a gastrula, or the representative of this layer in later stages.

Endosarc. The inner mass of protoplasm in cells in which the outer and inner protoplasm differ in structure.

Endoskeleton. A skeleton within the fleshy parts, as in vertebrate animals.

Energy. The capacity for performing work. It is **kinetic** when employed in producing motion or heat, **potential** when stored in chemical combination.

Enterokinase (*en' ter o ki' nase*). An enzyme produced in the small intestine and serving to convert trypsinogen into trypsin.

Enteron. A digestive system open at both ends.

Enteropneusta (*en' te rop nu' sta*). A subphylum of Chordata, wormlike animals, of which Balanoglossus and Cephalodiscus are representatives.

Entomology. The zoology of insects.

Enzyme (*en' zime*). An organic substance which brings about a chemical reaction but is not consumed by that reaction. Probably it participates in the reaction but is promptly restored.

Eocene (*e' o seen*). Of the earliest Cenozoic and Tertiary time.

Eohippus (*e' o hip' pus*). The earliest known ancestor of the horse, an extinct animal of Eocene time.

Epidermis. The outer of the two principal layers of the skin. Also an outer layer of cells in general.

Epistylis (*ep' i sti' lis*). A genus of colonial ciliated Protozoa, resembling Vorticella. **E. flavicans** (*flav' i kanz*), one of the species.

Epithelial. Pertaining to an epithelium; as epithelial tissues or structures.

Epithelium. A layer of cells at the surface of a tissue or organ, or lining a cavity.

Epoch. One of the divisions of a period in the geological time scale.

Equation division. A division in which chromosomes are duplicated, producing two equal cells; said of one of the divisions of germ cells as contrasted with the other or meiotic division.

Equatorial. In the plane of a great circle halfway between the poles; said of a cleavage plane of an egg. Also, in a middle position in other objects.

Equatorial plate. The flattened group of chromosomes on the middle of the spindle of a dividing cell. Also, the plane which they approximately occupy.

Equus (*e' kwus*). A genus of animals including the living horse and some of its fossil relatives of Pliocene and Pleistocene time.

Era. One of the five major divisions of geological time.

Erepsin (*e rep' sin*). A proteolytic enzyme produced in the small intestine.

Ergosterol (*er gos' ter ol*). A substance, chemically a solid alcohol, obtained from ergot, a fungus. On irradiation with ultraviolet it possesses strong antirachitic properties.

Erosion. The wearing away (of rocks) through the action of water and other agencies.

Esophagus (*e sof' a gus*). In the earthworm, a narrow passage leading from the pharynx to the crop. In vertebrates, the passage between the pharynx and the stomach.

Estrogen. A hormone or group of hormones produced by the follicles of the human ovary; several other names have been applied to it.

Euarctos (*u ark' tose*). A genus of bears, including the western black bear.

Eudorina elegans (*u' do ri' na*). A species of colonial chlorophyll-bearing organism whose cells are imbedded in a spherical jellylike mass.

Euglena (*u gle' na*). A genus of green flagellate Protozoa.

Eustachian tube (*u sta' ki an*). A passage between the pharynx and the tympanum or middle ear.

Eutheria (*u the' ri a*). A subclass of Mammalia comprising the viviparous mammals.

Eutrephoceras (*u' tre fos' er as*). A genus of extinct cephalopods resembling Nautilus.

Evagination. The folding of a layer of cells outward from an enclosed cavity.

Evolution. The gradual or sudden change of animals or plants through successive generations.

Evolve. To change; to undergo evolution.

Excretion. The elimination of waste substances. Also a substance excreted.

Exhalent. Breathing out; applied to one of the siphons of a clam or mussel.

Exophthalmic goiter (*eks' of thal' mik*). A disease resulting from overactivity of the thyroid gland, and having as one of its symptoms the bulging of the eyes.

Exoskeleton. A skeleton on the outside of the body, as in the arthropods.

Extensor. A muscle whose contraction straightens a joint.

External respiration. The passage of oxygen from the surrounding air or water to the blood.

F_1 (*ef' wun'*). An individual or generation of individuals resulting from the crossing of two unlike parents. An abbreviation of the words *first filial.*

F_2 (*ef' too'*). An individual or generation of individuals resulting from the mating of two F_1 individuals as parents. An abbreviation of the words *second filial.*

Family. A taxonomic group of higher rank than the genus but below the order.

Fat. A compound of glycerol and one or more fatty acids.

Fatty acid. An organic acid entering into the composition of fats.

Fauna. Collectively, the animals of a given region or of a given period of time.

Femur. The single bone of the thigh in vertebrates above the fishes.

Feral. Escaped from domestication. Also, sometimes, wild.

Fertilization. The union of an egg with a spermatozoon, a process requisite, in the higher animals, to the development of the egg.

Fetus (*fe' tus*). The embryo of a mammal while still in the uterus.

Fibril. One of the longitudinal contractile threads of a voluntary muscle cell.

Fibrin. A substance in blood which forms much of the clot on escape from the vessels.

Fibrinogen (*fi brin' o jen*). A soluble protein carried in blood plasma, from which the insoluble fibrin of a clot is formed.

Fibula (*fib' u la*). The outer one of two bones in the lower leg of vertebrates except the fishes.

Fission. The division of an organism into two approximately equal parts; or, simply, division.

Flagellate (*flaj' el late*). Possessing flagella. As a noun, a flagellate protozoon.

Flagellum (*pl.*, **flagella**). A long whiplike motile projection from a cell.

Flame cell. A cell having a hollow interior in which a bunch of vibratile cilia are located, forming part of a protonephridium.

Flexor. A muscle whose contraction bends a joint.

Fluke. Any one of several species of trematode worms.

Follicle. A layer of cells surrounding some object, as an ovum in an ovary.

Foot. The basal muscular part of a clam or snail, variously modified in many other mollusks. Also the terminal part of a leg, the base of Hydra, etc.

Foraminal aperture (*fo ram' i nal*). In a sponge gemmule, the opening in the shell through which the young sponge escapes when it begins to develop.

Formation. The rocks belonging to one of the minor divisions (lower than epoch) of geological time.

Fossil. The remains, or other indication, of a prehistoric animal or plant.

Fructose. A simple sugar (monosaccharide) found in fruit juices, and one of the products (with glucose) obtained by breaking down sucrose (cane sugar); same as levulose.

Funiculus (*fu nik' u lus*). A muscular strand which draws the body of a bryozoan into a U shape.
Furcula (*fur' ku la*). The wishbone of a bird, consisting of the fused clavicles of the two sides.

Galactose (*ga lak' tose*). A simple sugar (monosaccharide) obtainable by breaking down lactose, or lipids of the brain.
Galen. Famous Greek physician and anatomist, born about A.D. 130. His writings were long the highest authority in medical science.
Gall bladder. A pouch in which the bile secreted by the liver is stored.
Gamete (*gam' eet*). A germ cell, or other cell which fuses with a second cell in reproduction.
Gametogenesis (*ga me' to jen' e sis*). The ripening of germ cells.
Ganglion (*gang' gli on*) (*pl.*, **ganglia**). A mass of nerve cell bodies, usually forming a thickening in the course of a nerve.
Gastric. Pertaining to the stomach.
Gastrocnemius (*gas' trok ne' mi us*). A large muscle in the calf of the leg in vertebrate animals.
Gastropoda (*gas trop' o da*). A class of Mollusca including snails and slugs, mollusks whose bilateral symmetry is often obscured by a coiled body and shell.
Gastrotheca. A genus of frogs.
Gastrovascular. Serving the functions of digestion and circulation.
Gastrovascular cavity. See **coelenteron.**
Gastrula (*gas' tru la*). An early developmental stage, formed from a blastula, commonly by the invagination of the vegetative pole of the latter. The gastrula consists of two layers of cells (ectoderm and endoderm) surrounding a cavity which communicates with the exterior.
Gastrulation. The formation of a two-layered embryo from a blastula, by invagination of the vegetative pole, by delamination, or otherwise.
Gemmule. A group of cells forming a reproductive body in fresh-water sponges.
Gene. Something in a germ cell or other cell which is responsible for a hereditary characteristic.
Generic (*je ner' ic*). Pertaining to a genus.
Genetics. The science of heredity, variation, sex determination, and related phenomena.
Genital. Concerned with reproduction.
Genus (*je' nus*) (*pl.*, **genera,** *jen' e ra*). A group of species having so many structural features alike that they must be regarded as having sprung from common ancestry; a group of lower rank than the family.
Geoffroy Saint-Hilaire, Etienne (*zho frwa' saN te lair'*). French naturalist, 1772–1844.
Gephyrea (*je fi' re a*). A group of wormlike animals of doubtful rank and relationships. They have sometimes been referred to the Annelida.
Germ cell. A cell capable of reproduction, or of sharing in reproduction, as contrasted with the somatic or body cells which are sterile; or, more strictly, a reproductive cell that has undergone, or will undergo, or whose cell descendants will undergo, oögenesis or spermatogenesis before participating in reproduction.
Germ layers. The embryonic layers, ectoderm, endoderm, and mesoderm; so called because, in a sense, each one contains the "germ" of certain adult structures.
Gill. A structure having a surface enlarged usually by branching or folding, which serves a respiratory function.
Gill bar. The tissue between two gill clefts.

Gill cleft. One of several openings from the pharynx to the sides of the neck or head of a vertebrate embryo or adult; derived from a gill pouch. Also called gill slit.

Gill plate. The thickened patch of ectoderm in an embryo from which gills are developed.

Gill pouch. One of several evaginations from the sides of the anterior part of the digestive tract in the embryos of vertebrate animals. In some animals they break open to the outside, becoming gill clefts.

Gizzard. In the earthworm, a thick-walled portion of the alimentary tract behind the crop. In birds, the posterior muscular division of the stomach.

Gland. An organ whose function is the secretion of something to be used in, or ejected from, the body.

Glaucomys. A genus of flying squirrels.

Glenoid fossa. The cavity into which the head of the humerus fits.

Glochidium (*glo kid' i um*). The young stage of a mussel, which becomes temporarily attached to fishes.

Glomerulus (*glo mer' u lus*). A coil of blood capillaries at the end of each tubule in the kidney of a vertebrate animal.

Glossozoa (*glo' so zo' a*). A group of animals (literally, tongue animals) in Oken's early classification. It comprised the fishes.

Glottis. A slitlike opening in the larynx at the anterior end of the trachea in vertebrates.

Glucose. Grape sugar.

Glycerol (*glis' er ole*). An alcohol entering into the composition of fats and having the empirical formula $C_3H_5(OH)_3$. Same as glycerin.

Glycine (*gli' seen*). The simplest of the amino acids.

Glycogen (*gli' ko jen*). Animal starch; a common form of stored carbohydrate food in animal tissues.

Gmelin, Johann (*gma' lin*). German botanist, 1748–1804.

Golgi apparatus (*gole' jee*). A structure of various shapes, often a network, and of unknown function, found in many cells, usually near the nucleus.

Gomphoceran (*gom fos' er an*). Any extinct cephalopod resembling Gomphoceras, whose shell was short and wide.

Gonad (*go' nad*). An organ in which germ cells (either oögonia or spermatogonia) are produced or lodged.

Gonangium (*go nan' ji um*). A reproductive structure in a hydroid, consisting of a blastostyle, its attached medusa buds, and a gonotheca.

Goniatite (*go' ni a tite*). An extinct cephalopod having a coiled shell and bent or angular sutures; so named from the genus Goniatites (*go' ni a ti' teez*).

Gonionemus (*go' ni o ne' mus*). A genus of jellyfishes.

Gonium. A genus of colonial flagellate organisms in which the cells are arranged in a flattened plate.

Gonophore. One of the reproductive members of a siphonophore colony. Also, a medusa or medusalike member of a hydroid.

Gonotheca. A transparent sheath forming the outer part of a gonangium of a hydroid.

Gopherus (*go' fer us*). A genus of turtles.

Grantia. A genus of calcareous marine sponges.

Graptemys (*grap' te mis*). A genus of turtles of the family Testudinidae.

Graptolite (*grap' to lite*). An extinct group of colonial hydroid coelenterates of Cambrian and Devonian time.

Graze. To eat grass or similar herbage.

Gregaloid. Loosely adhering in an irregular mass.

Grew, Nehemiah. English botanist, 1641–1712.

Gullet. A tube leading from the posterior end of the oral groove in Paramecium to the interior of the cell.

Habitat. The kind of place in which an organism lives.

Halogen. One of a family of chemical elements including chlorine, iodine, bromine, and fluorine.

Halysites (*hal' i si' teez*). A genus of extinct chain corals.

Haploid. Single; referring to the reduced number of chromosomes in the mature germ cells of bisexual animals. *Cf.* **diploid.**

Harvey, William. English physician and physiologist, 1578–1657.

Hemoglobin. A reddish protein contained in the red blood cells.

Heparin (*hep' a rin*). A substance extracted from liver, carbohydrate in nature with amino and phosphate components, used to prevent clotting of blood.

Hepatic portal system. The portal system leading from the stomach, intestine, pancreas, and spleen to the liver.

Herbivorous. Plant-eating.

Heredity. The occurrence, in organisms, of any qualities due to the nature of the protoplasm of which they are made.

Hermaphrodite. An organism possessing both male and female organs. Also (adjective), possessing the organs of both sexes.

Herpetology (*her pe tol' o ji*). The zoology of reptiles and Amphibia.

Heteromita lens. A species of flagellate protozoon.

Heteromorphes (*het' er o mor' feez*). A group of animals in Blainville's early classification; animals of irregular form, mainly sponges and Protozoa.

Heterozygote. An organism to which its two parents have contributed unlike genes with respect to some inherited character, and which in turn produces two kinds of germ cells with respect to that character.

Heterozygous. Of the nature of a heterozygote.

Hexactinellida (*heks ak ti nel' li da*). A class of Porifera (sponges) whose spicules are composed of silica.

Hipparion (*hip pa' ri on*). An extinct horselike animal of Miocene and Pliocene time in North America and Europe.

Hippocampus (*hip' po kam' pus*). A genus of fishes of bizarre form resembling in part the head of a horse.

Hippocrates (*hip pok' ra teez*). Greek physician, Father of Medicine, 460–359 (?) B.C.

Hirudinea (*hi' ru din' e a*). A class of Annelida comprising the leeches. For definition see Chap. 19.

Holothurioidea (*ho' lo thu' ri oi' de a*). A class of Echinodermata, comprising the sea cucumbers. For definition see Chap. 19.

Homo. The genus of animals comprising man.

Homolecithal (*ho' mo les' i thal*). Having little yolk, nearly evenly distributed; said of eggs.

Homologous (*ho mol' o gus*). Originating in the same way in evolution; said of organs or structures.

Homology. Similarity of origin in evolution; applied to organs that arise in the same way.

Homozygote. An organism whose two parents contributed to it similar genes for some inherited character, and whose germ cells are therefore all alike with respect to that character.

Homozygous (*ho' mo zi' gus*). Of the nature of a homozygote.

Hooke, Robert. English natural philosopher and mathematician, 1635–1703.

Hooker, Sir Joseph Dalton. English botanist, 1817–1911.

Hormone (*hor′ mone*). A secreted substance which stimulates activity in an organ.

Humerus. The single bone of the upper arm in Amphibia and the higher vertebrates.

Huxley, Thomas. English biologist and lecturer, 1825–1895.

Hybrid. The offspring of two parents unlike one another in some heritable character.

Hybridization. The process of crossing animals having unlike heritable characters, thereby producing animals possessing genes for the traits of both parents.

Hydra. A small tubular fresh-water animal with tentacles and stinging organs, belonging to the phylum Coelenterata.

Hydranth. A hydralike tentacle-bearing member of a hydroid colony.

Hydroid. A colonial coelenterate, the individuals of which resemble the hydra in certain respects.

Hydrorhiza (*hi′ dro ri′ za*). That part of a hydroid colony which is attached to the substratum.

Hydrotheca. The tough transparent sheath surrounding a hydranth of a hydroid; an expansion of the perisarc.

Hydroxyl ion (*hi droks′ il*). The radical OH^- produced in solutions of bases.

Hydrozoa. A class of Coelenterata, including Hydra, the hydroids, jellyfishes, and some corals. For definition see Chap. 19.

Hyla. A genus of tree frogs.

Hyoid. A bone or group of bones or cartilages located at the base of the tongue or in a corresponding situation.

Hypodermis. An external layer of cells beneath a secreted cuticle, as in the earthworm and in insects and Crustacea.

Hypohippus. An extinct horselike animal of Miocene time in North America.

Hypostome. A projection from the center of the circle of tentacles in a hydra or one of the hydroids. It is perforated by the mouth.

Ileum (*il′ e um*). The last and usually longest of three divisions of the small intestine.

Ilium (*il′ i um*) (*pl.*, **ilia**). The dorsal bone of the pelvic girdle in Amphibia and the higher vertebrates.

Incisor. One of the front cutting teeth of a mammal.

Incubation. The warming of eggs, resulting in acceleration of their development.

Indeterminate. Not leading necessarily to a given end result from a given beginning: said of development in which cleavage cells may, if disturbed, produce some structure other than that which they would have produced without interference.

Ingestion. The taking in of food.

Inhalent. Breathing in; applied to one of the siphons of clams and mussels, to certain pores of sponges, and to other passages.

Innominate bone. The single bone formed by the fusion of three bones of the pelvic girdle in man. This name is not usually applied in the case of other vertebrates, though fusion of the bones of the girdle commonly occurs.

Insecta. A class of Arthropoda having one pair of antennae, three pairs of legs, and tracheae for respiration; the insects.

Insectivore. Technically, a mammal of the order Insectivora, including the moles, shrews, and hedgehogs. In a popular sense, any insect-eating animal.

Insertion. The place of attachment of the distal end of a muscle or its tendon.

Insulin (*in′ su lin*). An endocrine secretion produced by the islands of Langerhans in the pancreas; its function is control of sugar metabolism.

Internal respiration. The transfer of oxygen from the blood to the surrounding cells; true respiration.

Interphase. The stage in the cycle of a cell in which it is not dividing: the so-called "resting" stage.
Interstitial cells. The cells of a testis which lie between the seminiferous tubules.
Intracellular. Within a cell.
Invagination. The folding of a layer of cells inward into a cavity.
Ion. An atom or group of atoms bearing an electric charge.
Ischium (*is' ki um*) (*pl.*, **ischia**). The posterior of two ventrally located bones of the pelvic girdle of vertebrate animals above the fishes.
Islands of Langerhans. Groups of isolated cells in the pancreas, which produce insulin.
Isogamete (*i' so gam' eet*). One of two gametes of equal size which fuse in reproduction.
Isogamy (*i sog' a mi*). Fusion of like gametes in reproduction.
Isolation. In evolution, the inability of species to cross with one another.

Jejunum. The second of three divisions of the small intestine.
Jensen, Zacharias. Dutch inventor of the microscope about 1591.
Jugular vein. A large vein returning blood from the head.
Jurassic. Of middle Mesozoic age; named from rocks in the Jura mountains.

Karyokinesis (*ka' ri o ki ne' sis*). Same as **mitosis.**
Kidney. The chief organ for the excretion of nitrogenous wastes in most vertebrates. Also an excretory organ in certain other animals.
Kinosternidae (*ki' no ster' ni dee*). A family of turtles.

Labial palp. One of two pairs of flattened organs beside the mouth of mussels.
Labyrinth. The inner ear of vertebrates.
Lacteal (*lak' te al*). One of the minute vessels leading from the intestine to the lymph ducts.
Lactose. Milk sugar, a disaccharide found in the milk of mammals.
Lacuna. A space in the matrix of bone which contains in life a bone cell.
Lamarck, de, Jean Baptiste, etc. Celebrated French naturalist and proponent of evolution, 1744–1829.
Lamella. A layer.
Lamprey. An eellike animal of the class Cyclostomata.
Lampsilis (*lamp' si lis*). A genus of fresh-water mussels.
Large intestine. The enlarged portion of the digestive tract following the small intestine.
Larva. A free-living developmental stage of an animal in which certain adult organs are still lacking or in which organs are present that are lacking in the adult.
Lateral fold. One of two ridges of skin along the back of certain species of frogs, extending lengthwise at either side.
Lecithin (*les' i thin*). One of a number of lipoid substances common in egg yolk, nerve tissue, and other kinds of cells.
Leeuwenhoek, van, Anton (*lay' ven hook*). Dutch naturalist and microscopist, 1632–1723.
Leiolopisma (*li' o lo piz' ma*). A genus of skinks (lizards).
Lemming. A rodent of the family Muridae, to which the rats, mice, and muskrats belong.
Lepas anatifera (*le' pas an' a tif' er a*). A species of barnacle (subclass Cirripedia of the Crustacea). The goose barnacle.

Leptinotarsa (*lep' tin o tar' sa*). A genus of leaf-eating beetles to which the common potato beetle belongs.

Leptodactylus (*lep' to dak' ti lus*). A genus of frogs.

Lernaeopoda (*ler' ne op' o da*). A copepod (Crustacea) parasitic on the gills of certain fishes.

Leucocyte. A white blood cell.

Linear. Arranged in a line or row.

Lingula. A genus of brachiopods, a group of uncertain relationships.

Linkage. The occurrence of the genes for two or more hereditary characters in the same pair of chromosomes.

Linnaeus, Carolus (*lin ne' us*). Swedish botanist and naturalist, author of the binomial system of nomenclature and an artificial classification of animals and plants, 1707–1778.

Lipid (*lip' id*). Any organic compound of the class including true fats, and the compounds of fats with other substances such as phosphates and sugars.

Liver. A gland which secretes bile and other substances.

Loxoceras (*loks os' er as*). A genus of extinct cephalopods of the orthocone type.

Lumbar. Pertaining to the loins, the region of the back posterior to the ribs.

Lumbricus terrestris (*lum bri' kus*). A species of earthworm.

Lung. A respiratory organ in the vertebrates.

Lycopod (*li' ko pod*). A club moss.

Lyell, Sir Charles. British geologist, 1797–1875.

Lymph. A clear fluid containing colorless cells found in lymph vessels. It is essentially blood without its red cells and with much less of the proteins.

Lymphatic system. A system of vessels conveying lymph in vertebrates.

Lymph capillaries. The smaller vessels of the lymphatic system.

Lymph node. A connective tissue enlargement in a lymph vessel, which removes solid materials from the lymph and produces one kind of white blood cell.

Macronucleus. The large nucleus in a cell or organism having two nuclei of unequal size.

Macrosiphum sanborni (*mak' ro si' fum*). A species of insect, one of the plant lice, living on chrysanthemum plants.

Malpighi, Marcello (*mahl pee' gee*). Italian anatomist, founder of microscopic anatomy, 1628–1694.

Malthus, Thomas Robert. English political economist, author (1803) of *Essay on Population*, who lived 1766–1834.

Maltose. Malt sugar.

Mammal. One of the Mammalia.

Mammalia. A class of vertebrates having hairy bodies, producing young within the body of the mother, and nourishing the young after birth with milk secreted by the mother.

Mammalogy. The zoology of mammals.

Mammoth. An elephantlike animal of prehistoric times.

Mantle. A sheet of tissue, typically quite thin, which secretes the shell in mollusks.

Mantle fibers. Fibers lying about the periphery of the spindle of a dividing cell and extending from the centrioles to the chromosomes.

Manubrium (*ma nu' bri um*). A projection from the center of the subumbrella of a medusa, corresponding to the hypostome of a hydranth, and bearing the mouth at its end.

Marginal bone. One of a ring of bones around the margin of the carapace of a turtle.

Marsupial. A mammal having a pouch in which the young are carried (for example, the opossum and the kangaroo). As an adjective, possessing a pouch; as the marsupial frog.

Mastigophora (*mas' ti gof' o ra*). A class of protozoa, characterized by flagella.

Mastodon (*mas' to don*). An extinct genus of elephantlike animals of Pliocene and Pleistocene time.

Maternal. Pertaining to or derived from the mother.

Matrix. The noncellular material in which the cells of bone and cartilage are imbedded.

Matter. That of which any physical object is composed; anything which can occupy space.

Maturation. A process which germ cells undergo before they become functional, consisting of one or two cell divisions; if of two divisions, the chromosomes remain unduplicated in one of them.

Medulla oblongata. The enlargement of the anterior end of the spinal cord in vertebrates, commonly regarded as the posterior division of the brain.

Medusa (*pl.*, **medusae**). A jellyfish; the free-swimming member of many hydroid species.

Megapode (*meg' a pode*). A bird of the family Megapodiidae, the mound birds and jungle fowls.

Meiosis (*mi o' sis*). Separation of maternal from paternal chromosomes in oögenesis or spermatogenesis. Also, according to some, the two divisions of oögenesis or spermatogenesis.

Mendel, Gregor. Austrian monk and plant breeder, founder of modern movement in genetics, and author of Mendel's law of heredity. Lived 1822–1884.

Mendel's law. The law that genes for inherited characters separate from one another and recombine in various ways in the germ cells.

Meridional (*me rid' i o nal*). Passing through the animal and vegetative poles; said of certain cleavage planes of an egg.

Merychippus (*mer' i kip' pus*). An extinct horselike animal of Miocene time.

Mesenchyme (*mes' en kime*). A tissue composed of cells of irregular shape, loosely joined in a network with extensive meshes.

Mesentery (*mes' en ter i*). A double sheet of tissue, continuous with the peritoneum, which supports an organ (such as the intestine) from the body wall.

Mesoderm. A layer of cells between the ectoderm and endoderm.

Mesohippus. An extinct animal of Oligocene time, ancestral to the horse.

Mesozoa. A group of degenerate animals of uncertain rank and relationship, once regarded as intermediate between protozoa and metazoa; hence the name.

Mesozoic. Pertaining to the geological era between the Paleozoic and Cenozoic, or the age of reptiles.

Metabolism (*me tab' o liz'm*). The sum total of the chemical processes going on in protoplasm.

Metacarpal. One of the bones forming the body of the hand or forefoot in vertebrates.

Metagenesis. The occurrence of two or more forms of individual in the same species, one of which reproduces sexually and one or more asexually.

Metamere. See **somite.**

Metamerism (*me tam' er iz'm*). The condition of being divided into a number of similar metameres or somites.

Metamorphosis (*met' a mor' fo sis*). The transformation of a larva into an adult.

Metaphase. That stage of cell division in which the chromosomes are in the equatorial plate. The chromosomes are typically duplicated in this stage.

Metatarsal. One of the bones forming the body of the (hind) foot of vertebrates.

Metatheria. A subclass of mammals including the marsupials or pouched mammals.

Metazoon. An animal composed of many cells. Although the term contrasts an animal with the protozoa, it is not a name of any taxonomic group of animals.

Miastor. A genus of flies; the larvae are often paedogenetic.

Microgromia socialis. A species of protozoon which forms a gregaloid colony in a gelatinous supporting substance.

Micronucleus. The smaller nucleus in a cell or organism having two nuclei of unequal size.

Micropyle. A small hole in the shell of an egg through which the spermatozoon enters in fertilization.

Microstomum (*mi kros' to mum*). A genus of rhabdocoele flatworms.

Microtus. A genus of field mice.

Miocene. Belonging to middle Tertiary time; succeeding the Oligocene.

Miohippus (*mi' o hip' pus*). An extinct horselike animal from the Oligocene.

Mirbel, Charles François (*meer bel'*). French botanist, 1776–1854.

Mississippian. The fifth period of the Paleozoic era, following the Devonian and preceding the Pennsylvanian.

Mitochondria (*mi' to kon' dri a*). Objects of unknown function and of various shapes (threadlike, rod-shaped, or granular) found in the cytosome of many cells.

Mitosis. Cell division involving the formation of chromosomes, spindle fibers, etc. Also called **karyokinesis.**

Moeritherium (*me' ri the' ri um*). An extinct animal from the Eocene of Egypt, probably an early ancestor of the elephants.

Molar. One of the grinding teeth of a mammal, back of the incisors and canines.

Mold. A cavity in a rock representing the form of an animal or plant or other object whose remains formerly occupied the cavity.

Molecule. Usually a group of atoms behaving as a unit of the substance which they compose. It is the smallest particle which possesses the chemical nature of the substance.

Mollusca. The phylum of animals including the clams, snails, cuttlefishes, etc. For definition see Chap. 19.

Mollusk. One of the Mollusca.

Monoecious (*mo nee' shus*). Having the organs of both sexes in the same individual which is thus a hermaphrodite; said of species.

Monosaccharide (*mon' o sak' a ride*). A simple sugar; one which cannot be broken down into simpler sugars.

Monotreme. One of the Monotremata (Prototheria); an egg-laying mammal having a cloaca.

Morgan, T. H. Leading American geneticist, 1866–1945.

Morphology. The branch of biology which deals with the structure of living things.

Motor. Pertaining to movement; applied to a neuron which conveys impulses resulting in muscular movement, glandular action, and the like.

Motor root. The ventral one of two roots by which a spinal nerve is connected with the spinal cord. So called because its fibers have a motor function.

Motor unit. The group of muscle cells innervated by a single nerve fiber.

Muellerian duct (*mül le' ri an*). A tube formed in the embryo of most vertebrate animals, becoming the oviduct in the female and degenerating (with few exceptions) in the male.

Muscle. An aggregation of contractile cells.

Mustelus mustelus (*mus te' lus*). A species of shark.

Mutation. A heritable modification arising in an organism.

Myelin. A fatty substance forming a sheath around many nerve fibers.

Myofibril (*mi' o fi' bril*). One of the contractile threads in a voluntary muscle cell.

Myosin (*mi' o sin*). A common protein in muscle.

Myotome. One of the segments into which certain muscles are divided.

Myriapoda (*meer' i ap' o da*). A class of Arthropoda having tracheae, one pair of antennae, and many unspecialized legs; centipedes and millipedes.

Mysis. A genus of crustacea having all appendages two-branched; also a larval stage of other crustacea in which all appendages are two-branched.

Myxedema (*miks' e de' ma*). A disease whose symptoms are puffy tissues, reduced metabolism, and mental depression, caused by deficient thyroid action.

Nacre. The pearly substance secreted by mollusks upon their shell or other objects.

Nais. A genus of fresh-water worms, phylum Annelida, subclass Oligochaeta.

Nasal pit. The ectodermal depression in an embryo which forms much of the nostril.

Natrix. A genus of snakes. **N. rhombifera, N. sipedon,** two of the species.

Natural history. A descriptive account of things in nature, particularly animals and plants, though the term is sometimes used to include minerals, rocks, climate, etc.

Natural selection. The survival of the fittest individuals or the fittest species in a variable population.

Nauplius (*naw' pli us*). The earliest larval stage of shrimps, barnacles, and some other crustacea.

Nautiloid. One of the extinct cephalopods resembling Nautilus.

Nautilus. An animal belonging to the Cephalopoda, living in a coiled shell divided into chambers.

Neanderthal man (*na ahn' der tahl*). A primitive man whose remains have been found in various places in Europe.

Necator. The genus of roundworms to which the hookworm belongs.

Nectocalyx (*nek' to ka' liks*) (*pl.*, **nectocalyces,** *nek' to ka' li seez*). One of the swimming members of a siphonophore colony.

Necturus. A genus of salamanders; the mud puppy.

Nemathelminthes (*nem' e thel min' theez*). The phylum of roundworms and their allies. For definition see Chap. 19.

Nematocyst (*nem' a to sist*). One of the stinging bodies of Hydra and other coelenterates.

Nematode (*nem' a tode*). Any roundworm of the class Nematoda, phylum Nemathelminthes.

Nematomorpha (*nem' a to mor' fa*). A group of wormlike animals of uncertain affinities. They have usually been doubtfully included in the Nemathelminthes. For definition see Chap. 19.

Nemertinea (*nem' er tin' e a*). A group of wormlike animals of uncertain relationships. They are regarded by some as a class of Platyhelminthes. For definition see Chap. 19.

Nephridiopore (*ne frid' i o pore*). The external opening of a nephridium.

Nephridium (*ne frid' i um*). An excretory organ of certain invertebrate animals (worms, mollusks, etc.), approximately corresponding in function to the kidney of vertebrates. It is commonly a coiled tube, as in the earthworm.

Nephrostome (*nef' ro stome*). The opening at the inner end of a nephridium as in the earthworm. Also an opening (originally like that in the earthworm) connecting the coelom with the blood vessels of the kidney in certain Amphibia.

Nereis. A genus of marine worms, phylum Annelida.

Nerve. A bundle of axons or dendrites of nerve cells or of both axons and dendrites.

Nervous tissue. Tissue capable of transmitting impulses; as the tissues of the brain, spinal cord, and nerves.

Net knot. A thickened portion of the chromatin of a cell nucleus.

Neural arch. That part of a vertebra above the centrum and neural canal.

Neural canal. The opening in a vertebra through which the spinal cord extends.

Neural crest. One of a number of groups of cells at the sides of the brain and spinal cord of an embryo, from which ganglia and nerves are developed.

Neural fold. One of the ridges of ectoderm forming the earliest development of the nervous system.

Neural groove. An elongated depression between the neural folds of an embryo.

Neural spine. A projection rising from the middle of the neural arch of a vertebra.

Neural tube. The tube formed beneath the ectoderm by the union of the neural folds along their crests.

Neurilemma. The thin cellular covering of a nerve fiber.

Neuromuscular. Combining the functions of contraction and the transmission of impulses.

Neuron (*nu′ rone*). A nerve cell.

Neutron. A particle, like a proton but without electric charge, entering into the composition of the nuclei of most atoms.

Niacin (*ni′ a sin*). The antipellagra vitamin, part of the B complex.

Nicotinic acid (*nik′ o tin′ ik*). Same as **niacin.**

Nomenclature (*no′ men kla′ ture*). A system of naming; terminology.

Nostril. One of the external openings of the nasal chamber.

Notochord (*no′ to kord*). A cylindrical rod of cells beneath the nervous system of an embryo (adult of some animals). It is the forerunner of the spinal column of the vertebrate animals.

Notophthalmus (*no′ tof thal′ mus*). A genus of salamanders.

Nuchal plate (*nu′ kal*). In turtles, the median plate of the carapace at the anterior end.

Nuclear membrane. A thin film of protoplasm surrounding the nucleus of a cell.

Nuclear sap. The liquid forming the bulk of the nucleus of a cell.

Nucleolus (*nu kle′ o lus*). A small, usually rounded body found in the nuclei of many cells, which is of different chemical composition from the rest of the nucleus. Its function is uncertain.

Nucleus. A highly refractive, deeply staining body of specialized protoplasm found within nearly all cells.

Nudibranch (*nu′ di brank*). One of a group of marine mollusks.

Obelia. A genus of hydroids, or colonial hydralike animals of the phylum Coelenterata.

Octopus. A genus of devilfishes (mollusks) having eight arms.

Oenothera (*e′ no the′ ra*). A genus of plants to which the evening primroses belong.

Oken, Lorenz. German naturalist and transcendentalist philosopher, 1779–1851.

Olfactory. Pertaining to the sense of smell.

Oligocene. Of early Tertiary time, between Eocene and Miocene.

Oligochaeta (*ol′ i go ke′ ta*). A subclass of Chaetopoda (Annelida), including chiefly terrestrial and fresh-water worms with relatively few setae which do not rest on fleshy outgrowths but project directly from the body wall. The earthworm is an example.

Onychophora (*on′ i kof′ o ra*). A class of primitive Arthropoda having tracheae and one pair of antennae. Peripatus is an example.

Oöcyte (*o' o site*). A female germ cell subsequent to the initiation of oögenesis and prior to the second division. An oöcyte is designated **primary** during the growth period and prior to the first division; **secondary** after the first division and before the second.

Oögenesis (*o' o jen' e sis*). The series of changes undergone by female germ cells in preparation for reproduction.

Oögonium (*o' o go' ni um*). One of the early germ cells of a female animal, prior to the beginning of oögenesis.

Operculum (*o per' ku lum*). A fold of skin covering the gills and gill clefts in some amphibian larvae; also a similar covering of the gills in fishes.

Ophiuroidea (*o' fi u roi' de a*). A class of Echinodermata, comprising the brittle stars. For definition see Chap. 19.

Ophthalmozoa (*of thal' mo zo' a*). A group of animals (literally, eye animals) in Oken's early classification. The term was synonymous with Thricozoa and comprised the mammals.

Opisthocoelous (*o pis tho see' lus*). Having the centrum concave behind and convex in front; said of vertebrae.

Optic nerve. The nerve of sight.

Oral groove. The spiral depression on one side of Paramecium, leading to the gullet.

Order. A group of animals forming a subdivision of a class, and being composed of one or more families.

Ordovician. Of early Paleozoic time, succeeding the Cambrian.

Organ. A group of cells or tissues performing some specific function.

Organism. A living being, whether plant or animal.

Organismal theory. The theory that parts of an organism owe their nature to the nature of the whole.

Organizer. A substance which controls some feature of embryonic development.

Origin. The place of attachment of the proximal end of a muscle.

Ornithology. The zoology of birds.

Orohippus. One of the earliest known ancestors of the horse, an animal of Eocene time in North America.

Orthoceras (*or thos' er as*). A genus of extinct cephalopods of the orthocone type.

Orthocone. One of the early cephalopods that lived in a straight shell.

Osculum. An opening through which water leaves the passages of a sponge.

Osmosis. The diffusion of a substance through a membrane in response to unequal distribution of that substance on opposite sides of the membrane.

Osmotic pressure. Objectively defined, the pressure that will just prevent diffusion of a solvent into a solution when the two are separated by a semipermeable membrane. Also, the pressure due to the greater kinetic energy of the molecules of a solvent on one side of a semipermeable membrane than on the other, due to the presence of a solute on the side exhibiting the lesser kinetic energy of the solvent.

Otozoa. A group of animals (literally ear animals) in Oken's early classification. It comprised the birds.

Ovary. The organ in which the immature germ cells of a female animal are lodged.

Oviduct. A tube through which the eggs of a female animal leave the body.

Oviparity. The condition of being oviparous.

Oviparous (*o vip' a rus*). Egg-laying.

Oviposition. The laying of eggs.

Ovisac. A chamber for the storage of eggs, being in some cases a lateral pouch of the oviduct, as in the earthworm.

Ovoviviparity (*o' vo viv' i par' i ti*). The condition of being ovoviviparous.

Ovoviviparous (*o' vo vi vip' a rus*). Producing young from eggs that are retained in the oviduct during their development, but without attachment to the oviduct, and wholly from nutrition stored in the egg.

Ovum. An egg; a relatively large passive cell which, in preparation for reproduction, has undergone one or two unequal divisions.

Oxidation. The chemical process of combining with oxygen.

Paedogenesis (*pe' do jen' e sis*). Sexual maturity in an animal otherwise immature; the capability possessed by some species of reproducing while in the larval condition.

Palaeomastodon (*pa' le o mas' to don*). A genus of extinct animals belonging to the elephant ancestry, found in the Oligocene of Egypt and India.

Paleontology. The science which treats of prehistoric life on the earth, now represented by fossils.

Paleozoic (*pa' le o zo' ik*). Pertaining to the geological era prior to the Mesozoic, when amphibia, fishes, and the higher shell-bearing invertebrates were the dominant forms.

Pancreas. A gland which secretes a fluid containing several digestive enzymes and discharges into the intestine.

Pandorina. A genus of colonial flagellate organisms in which the cells are held in a spheroidal jellylike mass. **P. morum** (*mo' rum*) is one of the species.

Paramecium. A genus of ciliated protozoa.

Parasite. An animal which lives in or on another species of animal (its host), at the expense of the latter.

Parasitism. The condition of being a parasite.

Parathyroid. One of a pair (or two pairs) of small ductless glands closely associated with the thyroid.

Parietal bone. One of a pair of bones on the posterior upper part of the skull of vertebrate animals.

Parthenogenesis (*par' the no jen' e sis*). The development of an egg without fertilization.

Parthenogonidia (*par' the no go nid' i a*). The asexually reproducing cells of Volvox.

Paternal. Pertaining to or derived from the father.

Pectoral girdle. A group of connected bones serving to attach the bones of the forelimbs of vertebrate animals to the rest of the skeleton.

Peking man. An early human type somewhat resembling the Piltdown and Neanderthal types, found in China.

Pelecypoda (*pel' e sip' o da*). A class of Mollusca having bivalve shells and a bilobed mantle; the clams and mussels.

Pellagra (*pel la' gra*). A condition of malnutrition accompanied by eruption of the skin.

Pellicle. A thin skin or film on the surface of a cell.

Pelvic girdle. A group of bones serving to join the bones of the hind limbs of vertebrate animals to the rest of the skeleton.

Penis. The copulatory organ in the male of many animals.

Pennsylvanian. The sixth period of the Paleozoic era, following the Mississippian and preceding the Permian.

Pentadactyl (*pen' ta dak' til*). Having five fingers or toes.

Pepsin. An enzyme of the stomach of vertebrate animals, whose function is digestion of many kinds of protein.

Pepsinogen (*pep sin' o jen*). An inactive substance from which the enzyme pepsin is derived.

Period. One of the divisions of an era in the geological time scale.

Periodic. Occurring at rather regular intervals; said of migration which depends on the seasons or on the age of the migrating animals.

Peripheral nervous system. In general, the nerves, collectively; the nervous system aside from the brain and spinal cord or other central cord.

Perisarc. The tough sheath surrounding the stalk and branches of a hydroid.

Peritoneum (*per' i to ne' um*). A sheet of cells covering the viscera and lining the body cavity in many animals.

Permeable. Permitting the passage of both liquids and dissolved substances.

Permian. Belonging to the close of the Paleozoic era.

Petrifaction. The piecemeal substitution of mineral matter for the body substance of dead animals or plants.

Phalanx (*fa' lanks*) (*pl.*, **phalanges,** *fa lan' jeez*). Any one of the bones of the fingers or toes in vertebrate animals.

Pharynx (*far' inks*). In an earthworm, the thick-walled portion of the digestive tract just posterior to the buccal pouch and in front of the esophagus. In vertebrates, the portion of the digestive tract at the back of the mouth, into which the gill clefts open.

Phoronidea (*fo' ro nid' e a*). A small group of marine animals, of which Phoronis is the only genus, of uncertain relationship to other animals. Sometimes placed in a phylum with the Bryozoa and Brachiopoda.

Photosynthesis. The construction of glucose from carbon dioxide and water by the energy of sunlight in the presence of chlorophyll.

Phylum. One of a dozen or more major groups into which the animal kingdom is divided; in general, the largest group of which it can be said that the members are related.

Physalia. A very complex colonial coelenterate, one of the siphonophores.

Physiology. The branch of biology which deals with the functions of animals and plants, and the processes going on in them.

Piltdown. A locality in Sussex, England, near which primitive human fossils have been found.

Pineal body (*pin' e al*). A structure on the dorsal side of the brain in vertebrate animals. Because of its similarity, in development, to the embryonic stages of an eye, it is often called the **pineal eye** and is believed by many to be a vestigial sense organ.

Pisces (*pis' seez*). A class of vertebrate animals including the fishes. For definition see Chap. 19.

Pithecanthropus (*pith' e kan thro' pus*). An extinct apelike and manlike animal believed to be closely related to the early ancestry of man.

Pituitary (*pi tu' i ta ri*). A glandular organ beneath the brain composed in part of nervous tissue.

Placenta. A vascular tissue dovetailing into the wall of the uterus on one side and connected with the umbilical cord on the other, thus forming an intimate nutritive connection betweeen the embryo and the mother in viviparous animals.

Planaria. A genus of flatworms, phylum Platyhelminthes.

Planula (*plan' u la*). A ciliated larva consisting of a solid elliposidal mass of cells, developed from the fertilized egg of a medusa or similar organism.

Plasma. The liquid part of the blood.

Plasmodroma. A subphylum of protozoa devoid of cilia.

Plastid. One of several kinds of protoplasmic bodies in cells, like the green bodies in plant cells, which are centers of chemical activity.

Plastron. The flat plate of bones on the ventral side of a turtle.

Platelet. See **blood platelet.**

Plato. A Greek philosopher, pupil of Socrates and teacher of Aristotle. Lived about 427–347 B.C.

Platyhelminthes (*plat' i hel min' theez*). The phylum of flatworms. For definition see Chap. 19.

Pleistocene (*plise' to seen*). Belonging to the epoch following Pliocene in the Tertiary.

Pleodorina (*ple' o do ri' na*). A minute spherical organism composed of cells of two sizes embedded in a jellylike substance. **P. californica** (*kal' i for' ni ka*), with numerous small cells; **P. illinoisensis** (*il' li noi zen' sis*), with four small cells.

Plethodon (*pleth' o don*). A genus of salamanders.

Pliny (*plin' i*). Roman naturalist (A.D. 23–79) and author of works on natural history.

Pliocene. Pertaining to the epoch of Tertiary time following Miocene.

Pliohippus. An extinct animal of Pliocene time, closely resembling the horse.

Plumatella. A group of fresh-water bryozoa.

Pneumatophore (*nu' ma to fore'*). A capsule enclosing gas, serving to float a siphonophore colony.

Podophrya (*po dof' ri a*). A protozoon belonging to the class Suctoria.

Polar body. A small nonfunctional cell, one of the two cells produced by each division in oögenesis.

Polarity. The condition of exhibiting or possessing different properties in different parts; the condition of a cell in which the protoplasm is unlike in different parts of the cell.

Pole. A differentiated part or extremity, as of an egg, or of the spindle of a dividing cell.

Polocyte. The small cell produced at either of the divisions of oöcytes in oögenesis. Same as **polar body.**

Polychaeta (*pol' i ke' ta*). A subclass of Chaetopoda (Annelida) including those marine worms having numerous setae borne on fleshy outgrowths at the sides of the somites. Nereis, the sandworm, is an example.

Polymorphic. Having a variety of forms.

Polymorphism. The existence of two or more kinds of individuals within a species.

Polyneuritis. A disease due to vitamin B_1 (thiamin) deficiency.

Polyorchis (*pol' i or' kis*). A genus of jellyfishes.

Polyp. One of the feeding individuals of a hydroid or coral colony or simple related form.

Polysaccharide (*pol' i sak' a ride*). A carbohydrate whose molecule can be split into many molecules of simple sugar (monosaccharide).

Porcellio. A genus of sowbugs (Isopoda, Crustacea).

Porifera (*po rif' er a*). The phylum of animals comprising the sponges. For definition see Chap. 19.

Portal system. A blood vessel or group of vessels beginning and ending in capillaries.

Postcava. A large vein leading to the heart from behind or below.

Poterioceras (*po te' ri os' er as*). A genus of extinct cephalopods of the gomphoceran type.

Precipitin (*pre sip' i tin*). A substance which produces a precipitate when two blood sera are mixed.

Precocial. Able to run about as soon as hatched; said of certain birds.

Precoracoid. A ventrally situated bone or cartilage of the pectoral girdle in Amphibia and some reptiles.

Primary. For application to spermatocytes, see **spermatocyte.** For application to oöcytes, see **oöcyte.**

Primate. A mammal of the order including man and the apelike animals.

Priority, law of. The rule that the name first given a species along with a description is the one that shall be accepted when different names have been applied to the same species.

Proboscis (*pro bos' sis*). The trunk of an elephant, consisting of the elongated nose and upper lip. Also a fleshy projection of other sorts.

Procoelous (*pro see' lus*). Having the anterior end of the centrum concave, the posterior end convex; said of vertebrae.

Procyon (*pro' si on*). The genus of Carnivora to which the raccoon belongs.

Proglottis (*pl.*, **proglottides,** *pro glot' ti deez*). One of the individuals in a chain of a tapeworm.

Prophase. Any early stage of mitotic cell division, prior to the equatorial plate.

Prosecretin (*pro' se kre' tin*). A substance in the walls of the small intestine from which secretin is produced.

Prostomium. A rounded projection overhanging the mouth of an earthworm.

Protein. One of many organic substances, compounds of amino acids, which therefore contain carbon, hydrogen, nitrogen, and oxygen and often other elements. The molecules are large and very complex. Lean meat and egg albumen contain quantities of proteins.

Proterospongia haeckeli (*pro' ter o spun' ji a hek' el i*). A species of protozoon which forms gregaloid colonies.

Proterozoic. Belonging to the era preceding the Paleozoic.

Proteus. A genus of salamanders.

Prothrombase. A substance from which an enzyme of clotting (of blood) is produced.

Proton. A particle bearing a positive electric charge entering into the composition of the nuclei of atoms.

Protonephridium. A primitive excretory organ consisting of flame cells and connecting tubes.

Protoplasm. The living matter of which animals and plants are essentially composed.

Prototheria. A subclass of Mammalia, including the egg-laying mammals such as the duckbill Ornithorhynchus and the spiny anteater Echidna.

Protozoa. One-celled animals. The phylum comprising the one-celled animals, including colonial forms in which the cells of the colony are, at least potentially, all alike.

Protozoology. The zoology of the protozoa.

Pseudemys (*su' de mis*). A genus of turtles of the family Testudinidae.

Pseudopodium (*su' do po' di um*) (*pl.*, **pseudopodia**). A blunt fingerlike projection thrust out by Amoeba and other rhizopods.

Ptarmigan (*tar' mi gan*). Any one of several species of birds related to the grouse and partridges.

Ptyalin (*ti' a lin*). The starch-digesting enzyme of the saliva.

Pubis (*pl.*, **pubes,** *pu' beez*). The anterior one of two ventrally placed bones in the pelvic girdle of vertebrate animals above the fishes.

Pulmonary circulation. The circulation of the blood through the lungs, as distinguished from that through the body in general (systemic).

Pulsating vacuole. Same as **contractile vacuole.**

Pupa. A quiescent stage in the development of an insect, just before the adult condition is reached.

Purkinje, Jan Evangelista (*poor keen' ya*). Bohemian physiologist in the University of Prague, 1787–1869.

Pus. A collection of white cells at a wound or place of infection.

Pylorus (*pi lo' rus*). The opening from the stomach to the intestine.
Pyridoxin. Vitamin B_6, the antidermatitis vitamin.

Quadrate. One of the bones of the skull; in birds and reptiles and bony fishes, the bone from which the lower jaw is suspended.

Race. A group of individuals having certain characteristics in common because of common ancestry.
Radial canal. One of four tubes extending from the middle to the margin of a medusa.
Radial symmetry. An arrangement of the parts of an object or organism such that it is capable of being divided into halves that are mirrored images of one another, by two or more planes all of which pass through a common longitudianl axis.
Radiating canal. One of a series of collecting channels surrounding the pulsating vacuoles of Paramecium and similar protozoa.
Radical. A group of atoms behaving as a unit in reactions.
Radio-ulna. The fused radius and ulna of frogs and toads.
Radius. The bone of the lower arm located on the thumb side in Amphibia and the higher vertebrates.
Rana. A genus of frogs. **R. cantabrigensis,** the wood frog; **R. catesbeiana,** bull frog; **R. clamitans,** green frog; **R. palustris,** pickerel frog; **R. pipiens,** leopard frog.
Range. The area occupied by a species or larger taxonomic group of animals or plants.
Ray, John. English naturalist, 1627–1705.
Reaction. Any response of an animal to a stimulus; also any chemical change taking place in a substance, particularly a change involving some other substance as well.
Recapitulation theory. See **biogenetic law.**
Receptor. An organ which is especially sensitive to certain stimuli and serves to initiate impulses in nerve fibers.
Recessive. Not being produced when the gene for a contrasted dominant character is also present; said of inherited characters that are not developed in heterozygotes.
Reciprocal. Involving the same types of individuals, but with the sexes reversed; said of two crosses, in one of which the female possesses the same characteristic as does the male in the other cross.
Rectum. The terminal portion of the large intestine in the higher vertebrates. In vertebrates with a cloaca, the term is sometimes applied to the part of the large intestine anterior to the cloaca.
Reduction. Cell division in which chromosomes are not duplicated but merely separated from one another after having previously come together in pairs, as occurs in one of the two divisions in the ripening of most germ cells.
Reflex. Same as **reflex action.**
Reflex action. An action performed as a result of an impulse which passes over a reflex arc.
Reflex arc. A group of two or more neurons, one of them afferent, another efferent, so connected as to be able to transmit impulses resulting in reflex actions.
Regeneration. The production of lost parts by organisms.
Relict. A living remnant of an otherwise extinct group of organisms.
Renal corpuscle. One of numerous bodies in the kidneys of vertebrate animals, each composed of the expanded end of a kidney tubule (Bowman's capsule) and an enclosed knot of blood capillaries (glomerulus).
Rennin. An enzyme produced by the gastric glands and having the property of coagulating milk.
Reproduction. The formation of new individuals among organisms.

Reptilia. A class of vertebrate animals including the snakes, lizards, crocodiles, turtles, and some others. For definition see Chap. 19.

Respiration. The gaseous metabolism of protoplasm, including elimination of carbon dioxide, usually absorption of oxygen, and, according to some physiologists, the chemical reactions which consume oxygen or produce carbon dioxide.

Retina (*ret' i na*). The sensitive inner layer of the eye of vertebrates and some other animals.

Retractile. Capable of being withdrawn.

Rhabdocoele (*rab' do seel*). A flatworm (Platyhelminthes) of the order Rhabdocoelida.

Rhinozoa (*ri' no zo' a*). A group of animals (literally, nose animals) in Oken's early classification. It comprised the reptiles.

Rhizopoda (*ri zop' o da*). A class of Protozoa having a form that is changeable through the production of pseudopodia; example, Amoeba.

Rhynchocephalia (*ring' ko se fa' li a*). An order of Reptilia, comprising only one living form, Sphenodon, of the New Zealand region.

Riboflavin (*ri' bo fla' vin*). Vitamin B_2, the preventive of scaliness of skin, tendency to cataract, etc.

Rodent. A gnawing mammal, a member of the order Rodentia (rats, mice, squirrels, etc.).

Rodentia. The order of mammals including the rodents (rats, mice, squirrels, etc.).

Rotifera (*ro tif' er a*). A group of animals (the rotifers) usually regarded as a separate phylum, but of uncertain position in the animal kingdom. For definition see Chap. 19.

Sacculina (*sak' ku li' na*). A degenerate crustacean, related to the barnacles, parasitic on crabs.

Sacral. Pertaining to the sacrum, the region between the hips.

Sacrum. A group of vertebrae, more or less fused, in the region between the hips.

Sagitta (*sa jit' ta*). A marine animal of small size, sometimes called the arrowworm, but not a true worm at all. Its relationship to other animals is obscure.

Salientia (*sa' li en' shi a*). An order of Amphibia including the tailless forms (frogs, toads).

Saliva. The fluid secreted by the salivary glands about the mouth.

Salivary. Pertaining to saliva, the fluid secreted into the mouth in mammals.

Salt. A compound, other than an acid or base, which in solution produces ions.

Sarcolemma. The membrane surrounding a striated muscle cell.

Sarcoplasm. The protoplasm of a striated muscle cell, as distinguished from the enclosed myofibrils.

Sargasso sea. A great eddy in an ocean, enclosing masses of seaweeds; with capitalized initials the name may be limited to the eddy of the North Atlantic Ocean.

Sargassum. A genus of seaweeds.

Scaphiopus (*ska fi' o pus*). A genus of spadefoot toads.

Scaphites (*skaf i' teez*). A genus of extinct cephalopods of the ammonitic form.

Scaphopoda (*skaf op' o da*). A class of Mollusca in which the shell and mantle are tubular, as in Dentalium.

Scapula. The shoulder blade; a bone of the pectoral girdle, located on or near the dorsal side of the body.

Schleiden, Matthias (*shli' den*). German botanist, 1804–1881.

Schultze, Max (*shoolt' sa*). German biologist and anatomist, 1825–1874.

Schwann, Theodor (*shvahn*). German physiologist and anatomist, 1810–1882.

Sciuridae (*si u' ri dee*). The family of rodents including the flying squirrels, squirrels, marmots, and chipmunks.

Sciurinae (*si' u ri' nee*). The subfamily of Sciuridae comprising the marmots, squirrels, and chipmunks.

Sciuromorpha (*si' u ro mor' fa*). The suborder of rodents comprising the squirrellike forms.

Sciurus (*si u' rus*). The genus including the arboreal squirrels.

Scolex. The enlarged attaching organ from which are budded off the proglottides of a tapeworm chain.

Scyphozoa (*si' fo zo' a*). A class of Coelenterata, jellyfishes of large size which have no hydroid form in the life cycle.

Secondary. For application to spermatocytes, see **spermatocyte.** For application to oöcytes, see **oöcyte.**

Secretin (*se kre' tin*). A substance produced in the small intestine and serving to stimulate secretion by the pancreas and liver.

Secretion. The act of producing from the blood or other fluids or substances in the protoplasm some new material to be used in metabolism or otherwise. Also the new substance thus formed.

Segmentation. Same as **cleavage.**

Self-fertilize. To fertilize the eggs of an individual by spermatozoa of the same individual.

Semicircular canal. One of several curved tubes forming part of the inner division of the ear in vertebrates.

Seminal receptacle. An organ in a female animal for the reception and storage of spermatozoa from the male.

Seminal vesicle. One of several bodies closely connected with the testes in the earthworm, in which a large part of the development of the spermatozoa takes place. Also, an enlargement in the vas deferens or similar duct in which spermatozoa may be stored in various animals.

Semipermeable membrane. A membrane which allows some substances to pass through it, but retards or excludes others.

Sensory. Pertaining to sensation; applied to a neuron which transmits an impulse resulting in sensation, or by extension to any other receiving neuron whether concerned with sensation or not.

Septum. A partition.

Series. The rocks, collectively, which belong to a geological epoch.

Serum. The yellowish fluid which escapes from a blood clot; it is approximately the plasma without any fibrinogen.

Sessile. Attached directly, as distinguished from stalked. Sometimes, also, attached, as distinguished from free-living.

Seta (*pl.* **setae,** *se' tee*). A spine; specifically, one of the spines projecting from the somites of an earthworm and used for locomotion.

Sex-linked. Associated with sex; said of hereditary characters the genes for which are in the X chromosomes associated with sex.

Sexual. Involving the production of true germ cells, or the fusion of nuclei; said of reproduction, or of an individual employing such a mode of reproduction.

Shoal. A shallow place in a body of water; also a sandbank or bar which makes the water shallow.

Silurian. Of middle Paleozoic time, between Ordovician and Devonian.

Sinus node. A mass of rather undifferentiated tissue in the right auricle of the heart which receives stimuli and initiates the heart beat.

Siphon. A passageway for currents of water; as the clefts between the halves of the mantle of mussels where the edges do not meet, or the tube on the ventral side of a squid or cuttlefish.

Siphonophora (*si' fo nof' o ra*). An order of Hydrozoa (Coelenterata), the members of which form highly polymorphic colonies. Example, Physalia, the Portuguese man-of-war.

Siphonops (*si' fo nops*). A genus of caecilians (Apoda, Amphibia).

Siren. A genus of salamanders.

Skeleton. A framework of hard parts serving for support, protection, or movement, or a combination of these functions, in animals.

Slime tube. A sheath of mucous material secreted on the surface of an earthworm at the time of mating.

Small intestine. That part of the intestine of vertebrates immediately following the stomach, as distinguished from the large intestine.

Smooth muscle. Muscle composed of nonstriated, uninucleate, spindle-shaped cells. It is common in the intestine, bladder, and glands of vertebrates.

Socrates (*sok' ra teez*). Greek philosopher who lived about 470–399 B.C.

Solanum (*so la' num*). A genus of plants including the common potato, nightshade, and many others.

Solution. A liquid containing another substance in the form of particles not greater than molecules in size.

Soma. The body, as contrasted with the germ cells.

Somatic. Pertaining to the body; when applied to cells, referring to the sterile body cells in contrast to the germ cells which are reproductive.

Somite. One of the segments into which the body of a worm or arthropod or other segmented animal is divided.

Species (*pl.*, **species**). A group of animals or plants so nearly alike that, in general, they might have sprung from the same parents. (The term is rather arbitrarily used, however.)

Specific. Pertaining to a species.

Sperm. One of the male germ cells in an animal or plant; also called sperm cell.

Spermary. See **testis.**

Spermatheca. See **seminal receptacle.**

Spermatid. One of the two cells formed by the second division in spermatogenesis. By transformation in shape the spermatids become mature spermatozoa.

Spermatocyte (*sper' ma to site'*). A male germ cell between the beginning of spermatogenesis and the second division in that process. A spermatocyte is called **primary** during the growth period and prior to the first division; **secondary** after the first division but prior to the second.

Spermatogenesis (*sper' ma to jen' e sis*). The ripening of male germ cells.

Spermatogonium (*sper' ma to go' ni um*) (*pl.*, **spermatogonia**). One of the early germ cells of a male animal, prior to the beginning of spermatogenesis.

Spermatophore (*sper' ma to fore'*). A mass of spermatozoa, sometimes resting upon a stalk or being otherwise attached, as in some salamanders.

Spermatozoon (*sper' ma to zo' on*) (*pl.*, **spermatozoa**). The male germ cell in animals.

Sphenodon (*sfen' o don*). A genus of reptiles of the order Rhynchocephalia. Only one living species is known.

Spheroid. Of nearly spherical shape.

Spicule. A body of various shapes commonly of calcareous or siliceous material, forming part of the skeleton of a sponge.

Spinal cord. That part of the central nervous system of vertebrate animals lying behind the brain and largely enclosed in a channel in the vertebrae.

Spinal nerve. One of the paired nerves arising by two roots from the spinal cord.

Spindle. A group of structures resembling threads, in the form of a spindle, formed in the cytoplasm of a cell during mitosis.

Spiracle. In frog tadpoles, an opening through which water passes out of the gill chamber on one side. In insects, one of a number of openings on the sides of the body through which air is introduced to or ejected from the tracheae.

Spireme (*spi' reem*). The coiled or tangled thread formed by the chromatin of a cell prior to division.

Spirostomum (*spi ros' to mum*). A genus of ciliated protozoa.

Splint. A bone at either side of the foot of the horse and some of its relatives, being the remnant of a lost toe.

Spongilla. A genus of fresh-water sponges.

Spongin. The horny material of the skeleton of the bath sponges.

Spontaneous generation. Same as **abiogenesis.**

Sporadic. Occurring at irregular intervals, often without apparent reason; said of migration of animals.

Spore. One of a great variety of reproductive cells usually having protective coverings. Often the term is limited to asexual reproductive cells. The word is often compounded with qualifying prefixes or preceded by qualifying adjectives.

Sporozoa. A class of protozoa, parasites usually without locomotor organs or mouth.

Sporulation. The formation of spores; sometimes applied to multiple division of the nucleus followed by fragmentation of the cytosome, which occurs in the spore formation of certain species.

Squamata (*skwa ma' ta*). An order of reptiles to which the snakes, lizards, and chameleons belong.

Squamosal. A bone of the posterolateral region of the skull of vertebrates. In the mammals it suspends the lower jaw, but not in the other vertebrates.

Squamous epithelium (*skwa' mus*). Epithelium whose cells are low and flat.

Statoblast (*stat' o blast*). A gemmulelike body by means of which many Bryozoa reproduce asexually.

Steapsin (*ste ap' sin*). The fat-splitting enzyme of the pancreatic fluid.

Stegodon (*steg' o don*). A genus of extinct animals, related to the elephants, from the Pliocene of southern Asia.

Stegosaurus (*steg' o saw' rus*). A genus of dinosaurs bearing rows of plates set vertically on the back, belonging to Jurassic and Comanchean time.

Stejneger, Leonhard (*sti' ne ger*). A living American herpetologist.

Stentor. A genus of ciliated protozoa.

Sternum. The breastbone; present in most vertebrates except fishes and some reptiles.

Stimulus. A change in the environment or some internal condition which produces a reaction in an organism.

Stomach. An enlargement in the anterior part of the digestive tract of many animals; certain phases of the digestion of food occur there.

Storeria. A genus of snakes. **S. occipitomaculata** (*ok sip' i to mak' u la' ta*); **S. dekayi** (*de kay' i*).

Stratified. Arranged in strata or layers; said of epithelia, geological deposits, etc.

Stratum (*pl.*, **strata**). A layer; specifically, a layer of sedimentary rock.

Stratum corneum. The thin outermost layer of cells in the skin of certain animals (as the frog).

Striated muscle. Muscle composed of cylindrical, cross-banded, multinucleate cells (except in the heart). Skeletal muscles in vertebrates are of this kind.

Striation. A stripe; as the crosslines of voluntary muscle cells.

Stylonychia (*sti' lo nik' i a*). A genus of ciliated protozoa.

Subepithelial cells. In Hydra, rounded cells lodged among the epithelial cells, often near the base of the latter.

Sucker. An attaching organ beneath the head of a frog tadpole; a similar organ on the scolex of a tapeworm colony; also the attaching organ of leeches.

Sucrose. Common table sugar, a disaccharide derived from cane or beets.

Suctoria. A class of ciliated protozoa which bear no cilia when adult, but have tube-like tentacles.

Surface phenomena. A group of physical and chemical phenomena characteristic of surfaces (of cells, particles, fine pores, etc.)

Sustentative (*sus ten' ta tiv*). Supporting; applied to connective tissue and other supporting tissues.

Suture. The line of junction between a septum of a cephalopod shell and the outer wall of the shell. Also the immovable joint between two flattened bones, as those of the skull.

Swammerdam, Jan (*swahm' mer dahm*). Dutch naturalist, anatomist, and entomologist, 1637–1680.

Sweat gland. One of the excretory organs of the skin.

Sylvius, Jacques Dubois. French anatomist, 1478–1555.

Symbiosis (*sim' bi o' sis*). The association of two species of animals for their mutual benefit.

Symbiotic. Of the nature of symbiosis.

Symmetry. The state of being symmetrical, or capable of being divided by a line or plane into two parts which are mirrored images of each other.

Sympathin. A substance produced by nerve endings of the thoracolumbar system and serving to inhibit certain organs, stimulate others.

Synapse (*sin aps'*). The point of contact of two neurons.

Synapsis (*sin ap' sis*). The pairing of maternal with paternal chromosomes early in the maturation of the germ cells.

Synapta. A genus of sea cucumbers.

Syncytium (*sin sish' i um*). An undivided mass of protoplasm containing several or many nuclei.

Synonym (*sin' o nim*). A taxonomic name which is rejected because it is a duplicate.

Synura. A genus of colonial flagellate protozoa.

System. A collection of organs concerned with the same general function, as digestion. Also, the rocks, collectively, which belong to a geological period.

Systematic botany. See **taxonomy.**

Systematic zoology. See **taxonomy.**

Systemic circulation. The circulation of the blood through the body in general, as distinguished from that through the lungs or lungs and skin (pulmonary or pulmocutaneous).

Tadpole. The larva of a frog, or certain other animals.

Tail. A slender posterior appendage. In a spermatozoon, the whiplike propelling organ behind the head and mid-piece.

Tamiasciurus (*ta' mi a si u' rus*). The subgenus of the genus Sciurus including the red squirrels. **Sciurus (Tamiasciurus) hudsonicus loquax** (*hud son' i kus lo'-kwaks*), the southern Hudsonian red squirrel.

Tarsal. One of a number of bones in the ankle of most vertebrate animals.

Tarsometatarsus (*tar' so met' a tar' sus*). A compound bone in the leg of a bird, formed of several of the metatarsals and tarsals.

Taxonomy. The science of the classification of animals or plants.

Teleostomi (*te' le os' to mi*). A subclass of Pisces comprising the true fishes. They have a skeleton partly or wholly of bone and respire by means of gills.

Telolecithal (*tel' o les' i thal*). Containing much yolk, crowded toward the vegetative pole; said of eggs.

Telophase (*tel' o faze*). The final phase of mitotic cell division, in which the nuclei are reconstructed.

Tentacle. One of a number of armlike projections from hydroids, Bryozoa, Nautilus, and other animals. Also one of certain elongated individuals of a siphonophore colony.

Termite. One of an order of insects called "white ants," but not really ants.

Terrapene (*ter' a pee' nee*). A genus of turtles of the family Testudinidae.

Terrigenous (*ter rij' e nus*). Derived from the land; as applied to lake bottoms, composed of material washed in from the land, as distinguished from material of organic origin.

Tertiary (*ter' shi a' ri*). The single period of Cenozoic time.

Test. A hard outer covering, capsule, or shell; as of a sea urchin.

Testis. The organ in which the male germ cells are lodged and developed.

Testosterone (*tes tos' ter one*). A hormone produced by the interstitial cells of the testis; it controls development of secondary sexual characters and sex behavior.

Testudinata (*tes tu' di na' ta*). An order of reptiles, comprising the turtles.

Testudinidae (*tes' tu din' i dee*). A family of turtles.

Tetrad. A quadruple body formed, during the growth period in the ripening of germ cells, from the union of two chromosomes which at the same time become duplicated.

Thales (*tha' leez*). Greek philosopher and astronomer who lived about 640–546 B.C.

Thamnophis (*tham' no fis*). A genus of garter snakes. **T. butleri** (*but' ler i*); **T. proximus** (*proks' i mus*); **T. sackeni** (*sak' en i*); **T. sauritus** (*saw ri' tus*).

Theophrastus (*the' o fras' tus*). Greek philosopher, founder of botany, who lived about 372–287 B.C.

Thermocline. A layer of water in a lake in which the temperature falls at least 1°C. for each additional meter of depth.

Thiamin (*thi' a min*). Vitamin B_1, the preventive of polyneuritis or beriberi.

Thoracic. Pertaining to the thorax or chest.

Thoracolumbar system. That part of the autonomic nervous system which centers in the middle portion of the spinal cord. Each organ controlled by the autonomic system is innervated once from it.

Thorax. A middle portion of the body of many animals, between head and abdomen.

Thricozoa (*thrik' o zo' a*). A class of animals (hair animals) in Oken's early classification. It comprised the mammals which Oken also called Ophthalmozoa.

Thrombase. An enzyme which brings about the conversion of fibrinogen into fibrin in the clotting of the blood.

Thromboplastin. A substance which converts prothrombase into thrombase in the clotting of the blood; it is found in blood platelets and many cells.

Thymus. A ductless gland located near the gill clefts, or in the neck, or in the anterior part of the thorax in various vertebrates.

Thyroid. A ductless gland located in the ventral part of the pharynx.

Thyroxin (*thi roks' in*). The hormone of the thyroid gland.

Tibia. The inner one of the two bones in the lower leg of vertebrates, except the fishes.

Tibiofibula. The fused tibia and fibula of some Amphibia.

Tibiotarsus. A compound bone in the leg of a bird, formed of the tibia and certain of the tarsal bones.

Tissue. A group of cells of similar structure forming a continuous mass or layer.

α-tocopherol (*al′ fa to kof′ er ole*). Vitamin E, the antisterility vitamin of rats.

Tonsil. A glandular organ at the side of the throat.

Trachea (*tra′ ke a*). The tube conveying air to and from the lungs in vertebrates. Also an air tube in insects and some other invertebrates.

Tracheal gills. Threadlike or leaflike projections in which tracheae have their beginning in certain aquatic insect larvae.

Trachelocerca (*tra′ ke lo ser′ ka*). A genus of ciliated protozoa.

Transverse process. One of a pair of projections at the sides of a vertebra in most vertebrate animals.

Trematoda (*trem′ a to′ da*). A class of Platyhelminthes, parasitic flatworms with suckers and without cilia.

Triassic. Of the earliest Mesozoic time.

Triceratops (*tri ser′ a tops*). A genus of three-horned dinosaurs of late Cretaceous time in western North America.

Trichinella (*trik′ i nel′ la*). A genus of parasitic roundworms, the cause of the disease trichinosis.

Triclad. Having the digestive tract divided into three branches; said of an order of flatworms.

Trilobite (*tri′ lo bite*). A primitive crustacean of Paleozoic time, having the body partially divided by longitudinal grooves into three lobes.

Trilophodon (*tri lof′ o don*). An extinct genus of animals from the Miocene of several continents; related to the elephants.

Trionychidae (*tri′ o nik′ i dee*). A family of turtles.

Triploblastic (*trip′ lo blas′ tik*). Composed of three fundamental layers of cells.

Triturus. A genus of salamanders.

Trochophore. A form of free-swimming larva characteristic of many worms, mollusks, and rotifers.

Trypsin. A protein-splitting enzyme produced by the pancreas.

Trypsinogen (*trip sin′ o jen*). The inactive substance from which the enzyme trypsin is produced.

Tube feet. Tubular protusions from the arms of echinoderms, which serve as organs of locomotion.

Tubercula pubertatis (*tu ber′ ku la pu′ ber ta′ tis*). Two thick glandular ridges on the clitellum of an earthworm near the ventral surface.

Tuberculate. Bearing cusps or conical prominences; said of teeth.

Tubular gland. A gland whose lumen is of about uniform bore throughout.

Tunicata (*tu′ ni ka′ ta*). A subphylum of Chordata, including the sea squirts, sea pork, salpas, etc. For definition see Chap. 19.

Turbellaria (*tur′ bel la′ ri a*). A class of Platyhelminthes, ciliated flatworms leading a free existence.

Type. In systematic zoology, an individual or group which is formally held to be typical of the species or larger group to which it belongs; as, the type specimen of a species, the type species of a genus, or the type genus of a family.

Typhlosole (*tif′ lo sole*). A ridge resulting from the infolding of the dorsal intestinal wall of the earthworm.

Ulna. The bone of the little-finger side of the forearm in Amphibia and the higher vertebrates.

Umbilical cord. A ropelike cord in which blood vessels pass between an embryo and the placenta in viviparous mammals.

Unconformity. A sharp contrast, often a lack of parallelism, between adjoining rock strata, caused by a long period of erosion.

Uniformitarianism. The doctrine that geological processes of the past were similar to those of the present time.

Unisexual. Involving but one sex, the female; applied to parthenogenetic reproduction.

Unit character. A hereditary trait that behaves as a unit in transmission, being capable of inheritance independently of other unit characters.

Universal symmetry. An arrangement of the parts of an object or organism such that it is capable of being divided into symmetrical halves by an infinite number of planes passing in any direction through a central point.

Urea (*u re' a*). A substance, $CO(NH_2)_2$, produced by the decomposition of proteins and some other substance in organisms.

Ureter (*u re' ter*). A tube conducting urine away from the kidney.

Urethra (*u re' thra*). The duct by which urine is discharged from the bladder.

Urinary bladder. A bag in which urine is stored.

Urine. The liquid waste excreted by kidneys.

Uriniferous tubule. One of the many coiled tubes making up the bulk of the kidney in vertebrates.

Urinogenital system. A group of organs concerned with both excretion and reproduction in vertebrates.

Uterus (*u' te rus*). A modified portion of the oviduct in which the eggs undergo at least part of their development. Strictly the term uterus is applicable only in animals in which the developing embryo becomes attached to the wall of the organ.

Vacuole. A region within a cell occupied by a liquid other than protoplasm, usually water with various substances in solution.

Vagina. The passage leading from the uterus to the exterior in many animals.

Valence. A measure of the number of other elements or radicals with which a given element or radical may combine; it is determined by the number of electrons in the outer layer.

Variety. In taxonomy, a division of a species; a group of individuals within a species that differ in some minor respect from the rest of the species.

Vascular tissue. Blood or lymph, or the more liquid parts of blood-producing organs.

Vas deferens (*vas' def' er enz*) (*pl.*, **vasa deferentia,** *vas' a def' er en' shi a*). A duct conveying spermatozoa from the testis to the exterior.

Vas efferens (*vas' ef' fer enz*) (*pl.*, **vasa efferentia,** *vas' a ef' fer en' shi a*). One of a number of minute tubes leading away from a testis, serving to convey the spermatozoa. They lead into a larger tube called in many cases the vas deferens.

Vaucheria (*vaw ke' ri a*). A multinucleate fresh-water alga.

Vegetative. Concerned with nutrition. When applied to an egg, meaning that side near which the yolk is accumulated (vegetative pole).

Vein. A vessel conveying toward the heart blood which has already traversed capillaries since leaving the heart.

Ventral. Literally, pertaining to the belly; hence, usually, lower.

Ventricle. The posterior chamber of the heart in fishes, amphibia, and some reptiles, and one of the two posterior chambers in higher vertebrates. Its function is the propulsion of the blood through the main arteries and connecting vessels.

Vermiform appendix. A narrow blind pouch forming a prolongation of the caecum.

Vertebrata. A subphylum of the phylum Chordata, comprising the backboned animals. For definition see Chap. 19.

Vertebrate. *adj.* Possessing a backbone. *n.* An animal having a backbone.

Vesalius (*ve sa' li us*). Belgian anatomist and court physician, 1514–1564.

Villus (*pl.*, **villi**). One of the fingerlike projections from the inner surface of the small intestine.

Virchow, Rudolf (*veer'* ʜ*o*). German physiologist and pathologist, 1821–1902.

Visceral. Pertaining to the viscera, or organs contained in some large cavity of the body; applied in the vertebrates chiefly to the organs of the abdomen, in clams to the digestive organs and glands above the foot.

Viscosity. The resistance offered by a substance to the relative movement of its molecules.

Visual purple. A light-sensitive pigment in the retina.

Vitamin. One of several substances common in leafy vegetables, animal fats, and elsewhere, which are necessary for specific aspects of metabolism in animals.

Viviparity (*viv' i par' i ti*). The condition of being viviparous.

Viviparous (*vi vip' a rus*). Producing young from eggs that are retained in the uterus of the mother, with the aid of nutrition derived from the mother through a placenta and umbilical cord.

Volvox. A small spherical organism composed of flagellated green cells embedded in jelly, in a single layer around a liquid interior. Sometimes regarded as an animal, though more properly included among plants.

Vorticella. A ciliated protozoon attached to a contractile stalk.

Wallace, Alfred Russel. English naturalist, 1823–1913.

X body. An object in the cytosome of some of the early cleavage cells of Sagitta, which marks the germ cells.

X chromosome. A chromosome closely associated with the determination of sex. In many animals the female has two of them, the male only one.

Xenophanes (*ze nof' a neez*). Greek philosopher who lived about 570–480 B.C.

Xerophthalmia (*ze' rof thal' mi a*). A dry, lusterless condition of the eyeball.

Y chromosome. A chromosome possessed only by the males of many species. It behaves in spermatogenesis much as if it were homologous with the X chromosome.

Yolk plug. The remnant of the vegetative cells last to be drawn into the interior of a gastrula in certain embryos.

Zoogeography. The branch of zoology treating of the geographical distribution of animals.

Zooid. One of the members of a hydroid or siphonophore colony. Often, in a restricted sense, a particular kind of individual, as a hydranth.

Zoology. The science of animals.

Zygapophysis (*zi' ga pof' i sis*). One of four short projections, two in front and two behind, extending from the upper portion of a vertebra. Those of the posterior pair articulate with the anterior pair of the vertebra next behind.

Zygote. A cell or individual produced by the fusion of two cells or their nuclei in the process of sexual reproduction.

CORRELATED LIST OF VISUAL AIDS

The following list of 16-mm. motion pictures and 35-mm. filmstrips can be used to supplement some of the material in this book. These visual aids can be obtained from the producer or distributor shown with each title. (The addresses of these producers or distributors are listed at the end of the bibliography.) In many cases these visual aids can also be procured from your local film library or local film distributor.

The running time (min) of the film and whether it is silent (si) or sound (sd), filmstrip (FS) or color (C) are listed with each title. All those not listed as color are black and white.

Each film has been listed only once, usually in the first chapter to which it is applicable. However, in many cases it can be used advantageously in several of the other chapters.

CHAPTER I. THE GROWTH AND SCOPE OF BIOLOGY

Eyes of Science (Bausch & Lomb 45min si).—Shows Galileo with his early telescope; Leeuwenhoek and his simple microscope; and today's lenses and tubes that have given scientists the "super eye."

Marvels of the Microscope (Gut 10min sd).—Microscopic studies of water plants and minute forms of animal life.

Unseen Worlds (Ganz 10min sd).—Explains the intricacies of the newly developed electron microscope.

CHAPTER III. SOME FUNDAMENTAL PHYSICS AND CHEMISTRY

Chemical Reactions (Brandon 20min sd).—Explains the composition of an atom; relationship between nucleus and electrons; chemical reactions.

Electrons (EBF 11min sd).—Shows phenomena associated with conduction of electricity in liquids, gases, and vacuums.

Molecular Theory of Matter (EBF 11min sd).—Molecular hypothesis illustrated by animation; behavior of molecules in various conditions; Brownian movement.

CHAPTER IV. THE FUNCTIONS OF PROTOPLASM AND CELLS

Protoplasm—the Beginning of Life (Bray 15min si).—Protoplasm shown in characteristic motion in one-celled and many-celled hosts.

Living Cell (EBF 15min si).—Shows single-celled organisms and many-celled organisms under the microscope.

Green Plant (EBF 15min si).—Shows that living things are dependent for food upon the green plant; the latter's processes of foodmaking and growth are diagramed.

Nitrogen Cycle (EBF 15min si).—Shows how nitrogen compounds serve as a key to the transfer of energy in nature and how animals depend upon plants for food.

CHAPTER VIII. PHYSICAL SUPPORT AND MOVEMENT

Body Framework (EBF 15min si).—Function of skeleton; structure, chemical composition, growth and repair of bones; main types of joints.

Muscles (EBF 15min si).—The structure and use of muscles are presented.

CHAPTER IX. SOURCES OF ENERGY AND MATERIALS

Digestion (EBF 15min si).—Covers complete digestive tract.

Digestion of Foods (EBF 10min sd).—A summary of the digestive process; shows relation of circulatory and nervous systems to the digestive process.

Alimentary Tract (EBF 11min sd).—Treats in detail motility phenomena of the gastrointestinal tract by means of actual photography.

CHAPTER X. RESPIRATION AND RELEASE OF ENERGY

Breathing (EBF 15min si).—Explains action of diaphragm, breathing, and lung structure and function.

Mechanisms of Breathing (EBF 10min sd).—The breathing mechanism in operation.

CHAPTER XI. TRANSPORTATION SYSTEM

Blood (EBF 12min si).—Illustrates the separation of plasma from blood cells, protein and salts from plasma, etc.

Circulation (EBF 15min si).—Traces circulatory system; compares human heart with that of the frog.

Control of Small Blood Vessels (Lutz 20min si).—Illustrates both the structural and physiological features of the arterioles, precapillaries and capillaries.

Heart and Circulation (EBF 10min sd).—Detailed explanation of the mechanics of the pulmonary and systemic systems.

CHAPTER XII. DISPOSAL OF WASTES

Work of the Kidney (EBF 11min sd).—Detailed exposition of the kidneys and their functions.

CHAPTER XIII. INTEGRATION OF ACTIVITIES

Reactions in Plants and Animals (Harvard 11min sd).—Characterizes the concepts of stimulus and reaction and presents a study of different types of reactions in plants and animals.

Nervous System (Brandon 150min si).—Study of development of nervous system with special sections on development of early nervous systems; reflex actions; spinal cord; the brain; conditioned reflexes and behavior.

Nervous System (EBF 10min sd).—Shows structure of the nervous system; nerve impulse.

CHAPTER XIV. REPRODUCTION

How Animal Life Begins (NYU 11min sd).—The fundamentals of reproduction in the rabbit; cell growth involved in animal reproduction is used to illustrate human reproductive processes.

In the Beginning (USDA 17min sd).—Prologue to life, shows ovulation, fertilization, and early development of mammalian egg.

Reproduction among Mammals (EBF 10min sd).—Presents the story of embryology, using the domestic pig.

Reproduction in Plants and Lower Animals (B&H 15min si).—Shows the process of fertilization, conjugation, and mitosis as well as reproduction by budding.

CHAPTER XV. BREEDING BEHAVIOR OF ANIMALS

Development of Bird Embryo (EBF 15min si).—Shows development from early stages to hatching.

Frog (EBF 10min sd).—Portrays life cycle of the frog and development of the embryo.

Salamanders and Their Young (Rutgers 15min si).—Shows the habitat and breeding of salamanders.

Snapping Turtle (EBF 11min sd).—Presents complete life story of this reptile.

Insects: Their Growth and Structure (USDA FS).—Shows types and kinds of insects; external anatomy; internal anatomy; and life cycles.

CHAPTER XVII. GENETICS

Heredity (EBF 10min sd).—Mendelian laws of inheritance presented.

CHAPTER XIX. GROUPS OF ANIMALS

Animal Life (Harvard 10min sd).—A review of the main types of animals: protozoans, sponges, coelenterates, echinoderms, worms, molluscs, crustaceans, insects, and vertebrates.

Parade of Invertebrates I–IV (Rutgers 10min si C).—In four reels; shows numerous types of invertebrates.

Microscopic Animal Life (EBF 15min si).—Shows four single-celled animals and one multicellular animal.

Marine Communities (Rutgers 15min si C).—Shows how many types of undersea life associate in communities.

One-celled Animals (EBF 15min si).—An excellent study of the protozoa.

CHAPTER XXII. FOSSIL ANIMALS

Lost World (EBF 15min si).—Exhibition in motion of extinct prehistoric animals recreated in full-scale, lifelike models.

History of Horse in North America (Cal 20min sd).—Demonstrates advancement of the horse in fifty million years.

Evolution (Gut 30min sd).—Presentation of theories of the origin and development of the earth and its living inhabitants; prehistoric animals.

Monkey into Man (NYU 20min sd).—A study of monkey life showing family and social life and variation in brain power among them; compares most intelligent of apes and man with a brief review of man's development from the primitive stages to modern evolution.

Fingers and Thumbs (NYU 20 min sd).—Traces the development of man's hands; evolution from earliest form of life to the ape is clearly depicted as well as the actual development of the hand in the ape family.

SOURCES OF FILMS LISTED ABOVE

Bausch & Lomb Optical Co., 635 St. Paul St., Rochester, N.Y.
B&H—Bell & Howell Company, 1801 Larchmont Ave., Chicago.
Brandon Films, Incorporated, 1600 Broadway, New York 19
Bray Pictures Corporation, 729 Seventh Ave., New York
Cal—University of California, Extension Division, Department of Visual Instruction, 301 California Hall, Berkeley, Calif.
EBF—Encyclopaedia Britannica Films, 1841 Broadway, New York 17
Ganz, William J. Company, 40 E. 49th St., New York
Gut—Gutlohn, Walter O. Inc., 25 W. 45th St., New York 19
Harvard Film Service, School of Education, Lawrence Hall No. 4, Cambridge 38, Mass.
Lutz, Brenton R., 688 Boylston St., Boston, Mass.
NYU—New York University Film Library, Washington Square, New York
Rutgers University, Box 78, New Brunswick, N.J.
USDA—U. S. Department of Agriculture, Motion Picture Division, Washington, D.C.

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