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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. (*Photo by A. G. Ruthven.*)

PRINCIPLES
OF
ANIMAL BIOLOGY

BY

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TO THE
Teachers of Zoölogy
who have beheld their subject outgrow
a pedagogical method

PREFACE

This book was made necessary by a radical change, several years ago, in the introductory course in zoölogy at the University of Michigan. When the dissection of animal types in the laboratory was replaced by exercises bearing on the larger questions and fundamental principles of biology, a textbook treating almost exclusively of the morphology of representatives of the phyla, classes and orders was obviously of small use. In the absence of any text which appeared to fit the new departure, a book was provided in temporary form by the organizers of the course. Until now the temporary volume has sufficed.

Were a textbook based on principles useful only in a course whose laboratory exercises were also based on principles, the authors would not now feel impelled to make the volume available to others. They have accepted, however, the judgment of other biologists who find that even in courses in which types are dissected in the laboratory, the textbook should deal largely with biological principles, and with classification and the morphology of types only as these subjects fit themselves into the principles of the science as a whole. The best teachers have, in fact, long been presenting to their students much of the material of this book in lectures and recitations. In the hope that a textbook based on principles will be thought better than those now commonly in use, even for courses which retain the dissection of types in the laboratory, this volume is presented to the teachers of zoölogy and biology.

It is believed, furthermore, that the general reader will find in its pages much that is of interest. Illustrations have been selected with a view to making the book intelligible, not only to college students, but to persons who are not pursuing laboratory work. The authors have made no attempt to write in popular style for the benefit of such readers, but have endeavored to make the exposition clear and in the main specific. They prefer to believe that the general reader is willing to labor for his acquisitions so long as his effort promises to yield commensurate results.

Advice and criticism have been freely asked and given in the preparation of many of the chapters. The authors desire to mention in particular Professors H. H. Bartlett and J. F. Shepard, Dr. L. V. Heilbrunn, Dr. O. M. Cope, Dr. P. O. Okkelberg and Margaret B. Shull.

A. Franklin Shull.

February, 1920.

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phology. The structure of embryos, or developmental stages, of animals is as much morphology as is the structure of adults. Various names, such as anatomy, histology, cytology, and embryology, have been given to the departments of morphology. They differ from one another in the size and nature or stage of the objects with which they deal, but all are primarily concerned with form and structure.

Anatomy which is the science of structure was at first concerned with the grosser structures of animals, those that were visible to the unaided eye, such as the divisions of the brain, the spinal cord, and the larger nerves and ganglia, the stomach and intestine and the larger glands and ducts in connection with them, the chambers of the heart and the arteries and veins, the individual bones of the skeleton, and so on. As aids to dissection gradually came into use, however, more and more minute structures were studied under the name of anatomy, so that today the anatomist considers nothing too minute to fall within his province. In practice, nevertheless, certain phases of morphology are still usually designated by other names.

Thus *histology* deals with the grouping of cells of a given kind into masses or layers called tissues. The epidermis of the skin is composed of cells of the same general kind grouped together; it is therefore a tissue. Muscle and bone are tissues, as are also tendons, many glands, and the components of the nervous system. *Cytology*, contrariwise, is concerned with the minute components of cells, the parts of the nucleus, the minute structure of the living matter, the nature of cell organs, and the like. *Embryology* has to do with the young or developmental stages of animals. When it is purely descriptive, dealing only with the structures of these young stages, not with the processes going on in them, it is morphological in its nature.

In creating subdivisions of zoölogy, the several morphological branches mentioned in the preceding paragraphs have occasionally been elevated to equal rank with the divisions described below; but since they do not differ in principle, all being concerned with structure, it seems better to combine all of them under the single head, morphology. Morphology is historically the oldest of the divisions of zoölogy, since in early times practically all that was known of animals was their structure.

Physiology.—The functions of organs, tissues, and cells, the processes carried on in them, are the subject matter of *physiology*. Not only the more obvious functions, such as digestion, circulation, and respiration, but the obscure chemical reactions involved in growth and repair, belong in this field. The conduction of nerve impulses, the origin of acts of will, the processes of thought, the behavior of animals under given conditions, all are the subject matter of physiology. Ordinarily one thinks of those processes which maintain the animal, get and prepare its food, secure a supply of energy, control repair and growth, or eliminate waste as being physiology. There is another aspect of the subject, however, which is not less fundamental, but of a different nature. The processes of development in embryos are included in this branch of zoölogy. The events which initiate the division of an egg, control the folding of cell layers, direct the migration of cells, and govern differential rates of growth in a developing embryo are physiological processes. Embryology thus has a physiological aspect, as well as a purely morphological one.

Physiology is also a very old branch of zoölogy although the subject remained in a crude state long after morphology, particularly the morphology of the higher mammals including man, had become fairly definite.

Ecology.—This branch of zoölogy has to do with the relations of animals to their environment. These relations may be manifold. The necessity for getting food puts an animal into relation to the things about it. Its method of locomotion is intimately related to the medium in which it lives. The presence of enemies and competitors is an almost universal condition of life. The possibilities of rearing young are important in every animal's environment. The very behavior of an organism especially in lower forms of life, as is pointed out in a later chapter, is dependent upon the nature of the surroundings, so that a minute change in the environment may completely reverse the organism's behavior.

Very often the study of ecology takes the form of determining the factors which govern an animal's choice of *habitat*, or place of abode. Animals of any species are found only or chiefly in certain types of environment, depending partly upon their structure and partly upon their physiological requirements. Often, also, their occurrence in a given environment is dependent on the presence of certain other animals. The factors which induce, or force, an organism to seek an aerial, aquatic, terrestrial, or subterranean abode are often quite obscure. One animal must have a pond, rather than a stream, and not all ponds are equally good; nor is every part of the same pond a suitable place. The reasons for these requirements are partly to be found in the animal, partly in the surroundings; or, more correctly stated, in the relations existing between the factors within the animal and those external to it. Thus, ecology involves much that is morphology and physiology, but only in so far as structure and function relate the organism to other things about it. It is the work of the ecologist to discover the structure and functions of an animal which are of significance in such relations, the features of the environment to which they are related, and the nature of the relation between them. Although every hunter, trapper or collector of animals has long been a practical ecologist, scientific work of this kind has only in comparatively recent years seriously occupied the minds of any considerable number of zoölogists.

Zoögeography.—The geographical distribution of animals, or *zoögeography*, is in some respects closely related to ecology. It deals with distribution, as does ecology, but in a much wider sense. It is concerned with regions, rather than kinds of environment. The regional distribution of a species is limited by the distribution of environments suitable for it, but no species of animal occupies all the regions of the world where the environment is right. Kangaroos, to cite a striking example, are found only in the Australian region, although many other places on the earth have a temperature, humidity, and other features very similar to those of Australia. Presumably kangaroos could live in most of these similar regions if introduced into them, but they are not there. On the contrary, rabbits were entirely wanting in Australia until taken there by man, since which time they have become, like the English sparrow when introduced into America, almost a scourge. The failure of a species to occupy a region in which the conditions of life are suitable for it usually means that it has been unable to reach that region, and this inability may have been due to the present topography of the region, to its geological history, or to the place of origin of the species. Thus, while zoögeography involves suitability of environment (ecology), it is also concerned with historical factors.

Paleontology.—In *paleontology* the zöologist studies the animals of the past. Parts of these ancient animals are preserved as fossils in the sedimentary rocks. The relative age of the fossils is determined from the relative depth of the rock strata in which they occur. The vast majority of animals, perhaps all of them, living on the earth in these early times were of different species from those alive today. Though there are numerous similarities, only a very few fossil animals were practically identical with living ones and the similarity of even these few must be stated with some reserve. Moreover, the deeper fossils are quite different from those in the upper layers. Past ages on earth were thus marked by very different groups of living beings. All of the problems which exist for animals today presumably existed for those of the past. Those animals had structure and functions, they were related to the environment, and they were distributed over the earth in various ways.

There is thus a zoölogy of the past just as there is a zoölogy of the present. The paleontologist is limited, however, in his study of ancient animals to what can be discovered from their remains. He is unable to experiment upon his subjects, nor can he rear them in his laboratory. It thus happens that paleontology is mostly concerned with structure and classification of fossil animals, and with their distribution in space and in time. Other things can be inferred concerning them such as their mode of life, the reasons for their migrations, or their relation to the environment, and such inferences are of much or little value according to the nature of the evidence which supports them. Paleontology is thus a limited sort of zoölogy.

In addition to the above features, which concern the past animals themselves, the paleontologist deals also with the relation of those animals to the animals of today. Whether the early beings were the ancestors of the ones now on earth, and if so, the probable lines of descent; what became of the extinct species and what brought about their extinction; what determined the succession of animals to the present time; these and similar questions of an evolutionary bearing are in the domain of paleontology.

Taxonomy.—The classification of animals, with the principles on which it rests, is known as *taxonomy.* As is pointed out later, classification is based on relationship, nearly related animals being placed together in the same group. This relationship is discovered from similarity of structure, from facts of distribution, or from the existence of certain fossils. A group in which the members are very closely related is apt to be a small one. Such a group can nearly always be shown to have certain similarities to one or more other groups which indicate that they are related to each other. The small groups are thus combined into a larger group of a higher rank, the component small groups still being distinguished from one another. A zoölogist whose chief interest is the classification of animals is usually called a systematic zoölogist. Ordinarily it is possible for one person to be familiar with the minute details of classification in only one group, or in a few groups, not in the whole animal kingdom. One who knows the birds thoroughly may be unqualified to classify reptiles or fishes. A student of insects usually knows insects of all groups in a general way, but can arrange in detail the members of only one order, for example, the butterflies and moths. As a rule zoölogists have various interests, and are called by different names. The student of birds is an *ornithologist;* of the insects, an *entomologist;* of the reptiles, a *herpetologist.* Systematic zoölogists may appear to have little in common; but if their work is well done, it rests in every case upon the relationship believed to exist among the animals of their special groups. That is, they are taxonomists. Although, as stated, one person can usually master the details of classification in only a small part of the animal kingdom, it is not a difficult task to learn the main divisions of all the principal groups of animals, and to be able to place almost any animal at sight in its proper group.

Evolution means the gradual or sudden change of animals through successive generations. Animals of today are not like those of a few million years ago, as is clearly proven by fossils. Since present-day animals must have descended from ancient forms, somewhere in the intervening generations offspring must have been unlike their parents. The difference may have been small or large, and may have occurred at frequent intervals or rarely. Supporting evidence of such changes is found in nearly every branch of zoölogy. Paleontology furnishes such evidence in the differences between animals of successive geological periods. Many facts of distribution are readily explained only by assuming evolution. The study of morphology and physiology by revealing similarities between different animals, indicates their relationship through a common origin, and the whole science of taxonomy has its basis in change with descent. More of the details of this evidence are pointed out in later chapters. Evolution is not, then, an isolated science, but is closely bound up with morphology, physiology, taxonomy, zoögeography, and paleontology; for in each of these fields valuable evidence of evolution is found, and the explanation of evolution and evidence of the course which it has taken are important parts of them all.

Summary and Comparison.—The seven fields of knowledge described in the foregoing paragraphs may be called the zoölogical sciences. Every fact of zoölogy may be referred to one or another of these subjects. They are not wholly distinct from one another, however, for not infrequently a single fact belongs to two or more of the sciences. That is, the fields overlap. The merging of evolution into the other problems of paleontology, zoögeography, taxonomy, and others has been pointed out. Ecology may very largely deal with physiological relations. Physiological facts are in most instances also morphological ones, since it is usually difficult to separate functions from the structures in which they are manifested. This overlapping and the merging of one subject into another, far from being confusing, is eloquent testimony of the unity of the whole field of zoölogy. There is also a unity of zoölogy and botany, which is the science of plants, for in botany the same seven subdivisions exist. There is a morphology, a taxonomy, an ecology, and an evolution of plants; and but for the immobility of most plants and the differences in their modes of life, the principles involved are largely the same as for animals. Paleontology and zoögeography have their counterparts in botany, but the study of fossil plants is often called paleobotany while the science of plant distribution is named phytogeography. This book, being a general discussion, will contain elementary facts and principles from each of the branches of the science. The student will find it a useful exercise, as he reads its pages, or discovers new things in the laboratory, to stop and reflect which of the divisions of zoölogy he is for the moment studying.

Although zoölogy of today comprises the seven sciences mentioned above, it would be a mistake to suppose that it has always been so inclusive. Some of the branches are much older than others. Morphology, as has been stated, is very ancient, while ecology is a mere infant. Physiology has been known for centuries, while the contemplation of evolution has been common for but sixty years. Zoölogy, then, has a history; and a knowledge of this history is as useful in accounting for its present content and tendencies, as is the history of a nation in understanding its present institutions and policies.

Conditions of Early Biology.—One who reads of the early ideas regarding animals is apt to conclude, unless warned in advance, that the science of zoölogy was much better developed among the early philosophers than it really was. The list of early writers who published biological doctrines is a long one, and unless it is pointed out that many of these doctrines were but a very small part of the works in which they were contained, and that the authors were often chiefly interested in religion, or theology, or astronomy, with their biological concern largely incidental, an exaggerated idea of their importance may be gained. When to this consideration is added the fact that these writings were often based, not upon observation or experiment, but upon speculation, anecdotes, rumor, or superstition, conservatism in appraising early zoölogy is more than ever necessary.

Although the ancient knowledge of animals was of little value in comparison with the zoölogy of today, the early students of the science should be regarded with lenience. Their advantages were meager. They could not be taught the subject, for they were pioneers. A sophomore now may know more about animals than did Aristotle, even though in intellect he would appear, beside Aristotle, as a candle to the sun. Nor could the pioneers easily remedy their benighted condition, since the absence of microscopes and other equipment closed to them many of the doors of investigation that are open now even to elementary students. Hence, while recognizing that ancient zoölogy was a very inferior science, as judged by modern standards, the early zoölogists must not be too harshly criticized. As will be seen, the best of them are to be credited with accomplishments which, in view of their handicaps, were truly remarkable.

The Early Greeks.—The earliest zoölogical writings that are known were produced by the Greeks. It is certain that these were not the earliest works, since they contain references to the "ancients," but they are the earliest that have been preserved. The earliest writers can hardly be called zoölogists. Often they were distinctly something else, even poets, and their shortcomings in biology need occasion no surprise. The early Greeks were inclined to the deductive method. They reached a conclusion quickly, with little evidence to support it, and then applied their generalization to discover what other things ought to be true. Naturally, if the generalization was incorrect, and it was likely to be incorrect, its application led to fallacies.

Surrounded as Greece is by warm waters, teeming with life, the country furnished abundant material for observation of animals. Some advantage was taken of this opportunity, or Greek writers would hardly have concerned themselves with biology so much in advance of other peoples. But the Greeks were of a philosophical bent, they preferred theorizing to the prosaic collection of facts. The origin of things in nature was particularly fascinating. Thales, an astronomer, conceived all life to have originated in the ocean, an idea that has its supporters today. Anaximander supposed that living things were first produced by the drying crust of the earth, which had been in a liquid state; and curiously enough, man was held to be the first of these products. He also believed that animals, of the kinds we know today, are produced out of inorganic matter, as eels from mud. This doctrine of the origin of living from non-living matter, known as *abiogenesis,* was held for centuries in the crude form adopted by the Greeks, but has been long since disproven and abandoned. Fossils were recognized as animal remains by Xenophanes, who correctly inferred from them that water once covered the land. Empedocles made some observations on embryonic development, the earliest ones, indeed, that are recorded. He also evolved a theory of the origin of animals, according to which heads, arms, trunks, necks, eyes, etc., were formed separately, and were kept apart at first through the force of hate. Then love triumphed, he supposed, and these parts began to combine. The combinations were purely fortuitous, and most of them were incapable of maintaining themselves. Others were more fortunate, and formed the animals now found on earth. Empedocles thus enunciated a crude form of theory of the survival of the fittest.

The Greek writers so far mentioned all lived in, ~~or~~ prior to, the fifth century before Christ. Their ideas were a curious mixture of truth and error, mostly the latter. A few have proven correct, or at least still have some support. But it can hardly be too strongly stated that these earliest notions, even when correct, were often not necessary deductions from observed facts, but happy conjectures.

Aristotle.—One of the Greek philosophers stands out in high relief, by reason of his correct methods and superior accomplishments. This was Aristotle, who lived in the fourth century before Christ. A portrait of him is given in Fig. 1. Aristotle was a man of high intellect and one of the greatest philosophers of ancient times. He was a pupil of Plato, and the teacher of Alexander the Great. Like other scholars of his time, he dealt with a great range of subjects and published hundreds of works, many of which are lost. He wrote treatises on philosophy, psychology, metaphysics, rhetoric and politics, but assumed the rôle of leader most distinctly in natural history. If one were to judge Aristotle by present standards the great philosopher might seem less notable, but it must be remembered that he was a pioneer, and that he lived at a period in the development of science when errors and crudities were to be expected. However, he recognized the things of importance and he adopted the right method in trying to advance knowledge. He

what to think. The clergy fostered this attitude, for they represented authority, and lived upon subservience. Obedience in intellectual as well as religious matters was proffered as a matter of course. Controversies upon insignificant matters, which could easily have been settled by a few first-hand observations, were referred to the books of Aristotle and others for decision. Those who chanced to make observations for themselves, and then found something in their favorite writings which seemed to refute their discoveries, refused to believe their own senses.

The period of deference to authority lasted many centuries. During this time interest in zoölogy was almost confined to the medical schools, where, in the form of anatomy, it had a practical value. But even anatomy was subject to the ills of the time. The works of Galen, a famous anatomist of the second century (A.D.), were the authority on which all teaching of anatomy was based. Galen himself was a talented observer and forceful writer, and it is not occasion for surprise that his works were accepted as the authority in questions of anatomy. He worked under a handicap imposed by the customs of his time, however, since human bodies could not then legally be dissected. As substitutes, other animals were used, and wherever these animals differed from man Galen was in error. In the absence of better works, Galen's books were read from the lecturer's desk, with occasional demonstrations of dissections—which, be it said, often belied the text they were supposed to illustrate. The negation, however, was never noticed, or perhaps was attributed to improper specimens for demonstration.

The Revival.—Slavish acceptance of authority could scarcely do other than breed revolt, and eventually prove its own undoing. Human bodies became increasingly accessible for dissection. And so, after more than a thousand years of servility, it is not surprising to find Mondino da Luzzi, a professor at the University of Bologna, in Italy, publishing in 1315 a work on human anatomy that was based, not on Galen's books, but on dissection. He dissected as many as three human bodies. Two hundred years later, Berengario, also of the University of Bologna, dissected a hundred or more bodies, and presumably taught anatomy from them.

It was reserved, however, for Vesalius, a gifted Belgian, to make the use of Galen's books alone unfashionable. Vesalius was a native of the city of Brussels, where he was born in 1514. A portrait of him is reproduced in Fig. 2. He appears to have inherited a passion for learning from an ancestry of physicians and scholars. His leaning was toward anatomy, and in his boyhood, besides securing the traditional schooling in Greek and Latin, he taught himself dissection, using the common animals about him. On entering the University of Paris to study medicine, it is said that he early became dissatisfied with the clumsy manner in which demonstrations were made in the lectures, that he pushed aside the barbers who were making the dissection, and demonstrated the structures himself. He finished his medical course at the University of Padua, in Italy, where he was subsequently appointed to teach anatomy. His teaching began with the time-honored method of reading Galen's books, but the independent spirit which he displayed in early life compelled him to discontinue the practice. He ended by teaching anatomy only as he himself found it by dissection, and only as he could demonstrate it to his students.

Unlike Mondino da Luzzi and Berengario, Vesalius was able to carry conviction to others. His students and colleagues recognized his worth, and other anatomists were gradually persuaded. Having probably no more facilities for original dissection than did Berengario and other anatomists of his time, Vesalius possessed what they probably lacked, a forceful personality. Opposition of the clergy, who had everything to lose and nothing to gain from a return to observation, did not daunt him. He was as adept in controversy as they—and Vesalius won. He did not live to see his method of appeal to nature universally adopted, but reform was rapid after his time, and to him belongs the chief credit for starting the reform.

Fig. 2.—Andreas Vesalius, 1514–1564. (*From Garrison's History of Medicine. W. B. Saunders Co.*)

The Experimental Method.—At the time of Vesalius zoölogy (anatomy, mostly) was an observational science. Every science has been observational in the early stage of its development. Observation represents on the whole the simplest phase of investigation, since it is possible to observe without any anticipation of the phenomena to be observed. The use of experiment is a later development in each field. It implies looking forward to a result, and the experimenter must formulate some problem and adopt a suitable procedure for its solution. Any branch of investigation, therefore, in which the experimental method is applicable may be regarded as mature or youthful, according as experiment has or has not come into common use. At the time of which we write, experiment had long been used in physics and chemistry. Experiment had been used occasionally in zoölogy even as early as Aristotle, but had been long since forgotten as a method. Its restoration was in large part due to the efforts of William Harvey, of England (1578–1657) (Fig. 3). Harvey is best known as a physiologist, sometimes called the founder of physiology. He is credited with the discovery of the circulation of the blood, though his claim to this honor has been disputed. Although in an account of the rise of physiology, which occupied centuries, Harvey would figure prominently in the early period, it is not indefensible to state that his chief service to zoölogy was not in his contribution to physiology but in his frequent use of the method of experiment. In his work in physiology he directly affected only one field of zoölogy; but in his adoption of the experimental method he influenced every branch of the science. For all of the zoölogical sciences today employ experiment as an important mode of investigation.

FIG. 3.—William Harvey, 1578–1657. (*From Garrison's History of Medicine.*)

The Microscope.—Prior to the time of Harvey zoölogists could concern themselves almost exclusively with objects of some size. Minute dissections were attempted, but were attended with difficulty and the results were uncertain, because there were no good microscopes. Of things that every freshman in a college class in biology may see a thousand times in a semester, the zoölogists of early times were wholly ignorant. Simple lenses existed from no one knows how early a period, and their value was understood. But in those days of the lack of specialization, there were no great designers and manufacturers of optical goods. Microscopes were planned and built by the scholars who needed them. An investigator could easily spend ten times as much energy in making and fitting his lenses, as in making observations with them once they were completed. Under these circumstances, it is no wonder the development of the microscope was slow. One of the products of this amateur manufacture of microscopes is illustrated in Fig. 4.

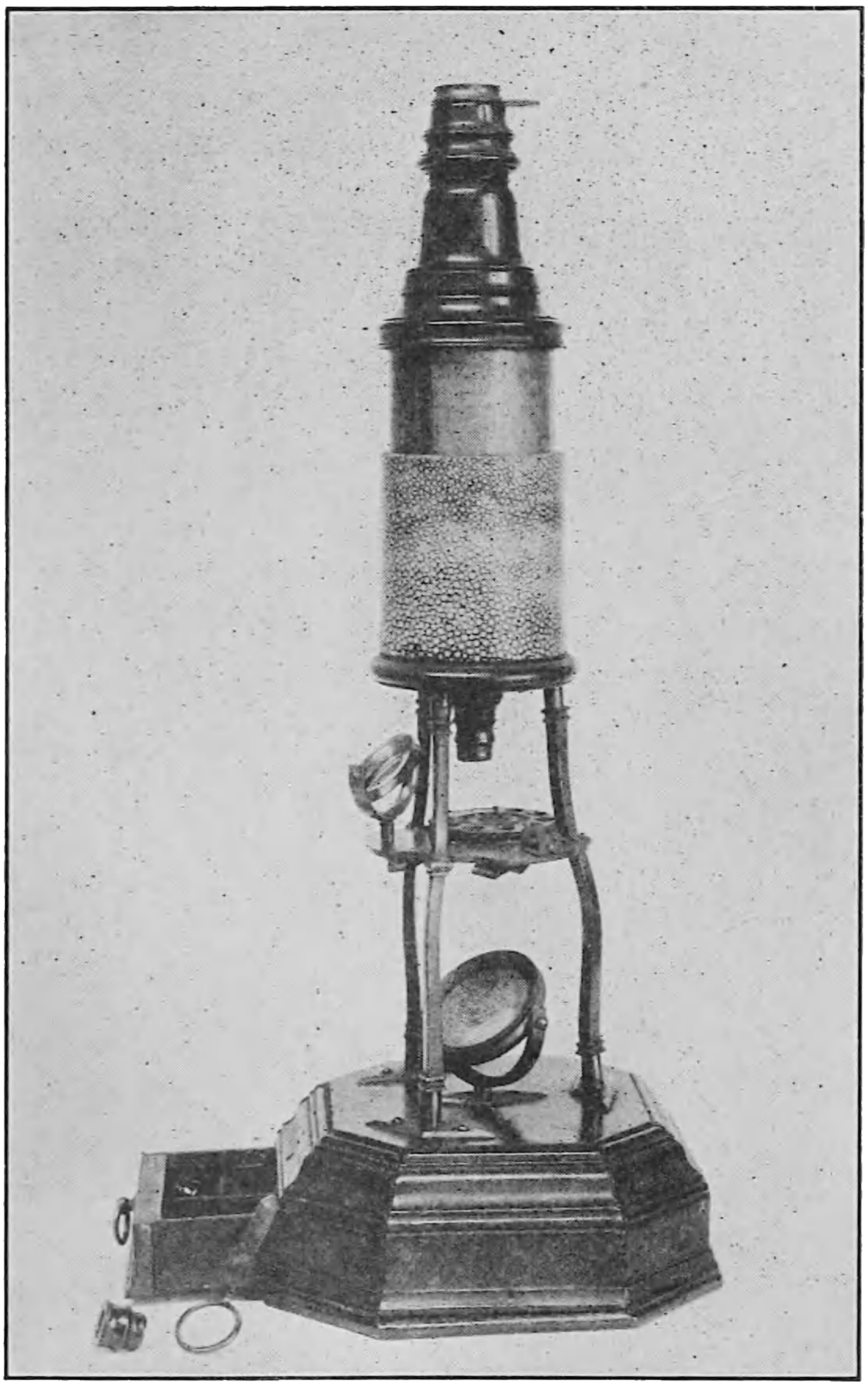

FIG. 4.—An eighteenth century microscope. (*Courtesy of American Museum of Natural History.*)

Among the early designers and users of microscopes are to be mentioned Hooke and Grew of England, Malpighi of Italy, and Swammerdam and Leeuwenhoek of Holland, all of whom flourished in the latter half of the seventeenth or early eighteenth century. Hooke was too versatile to be remembered much in zoölogy, except in connection with the development of the microscope and the incidental discovery of cells in cork. Grew did some good work in the anatomy of plants. The remaining three microscopists just named were much more productive in the strictly biological field.

Malpighi (Fig. 5) is famous for a treatise on the minute structure of the silkworm; for the discovery of the layer of cells at the base of the epidermis, which bears his name; for observations on the anatomy of plants; and for work in embryology. Swammerdam is known for his minute dissections of insects, snails, and clams. Leeuwenhoek (Fig. 6) studied blood capillaries, and the structure of muscles, and he saw and figured spermatozoa (the male germ cells) without at first knowing what they were.

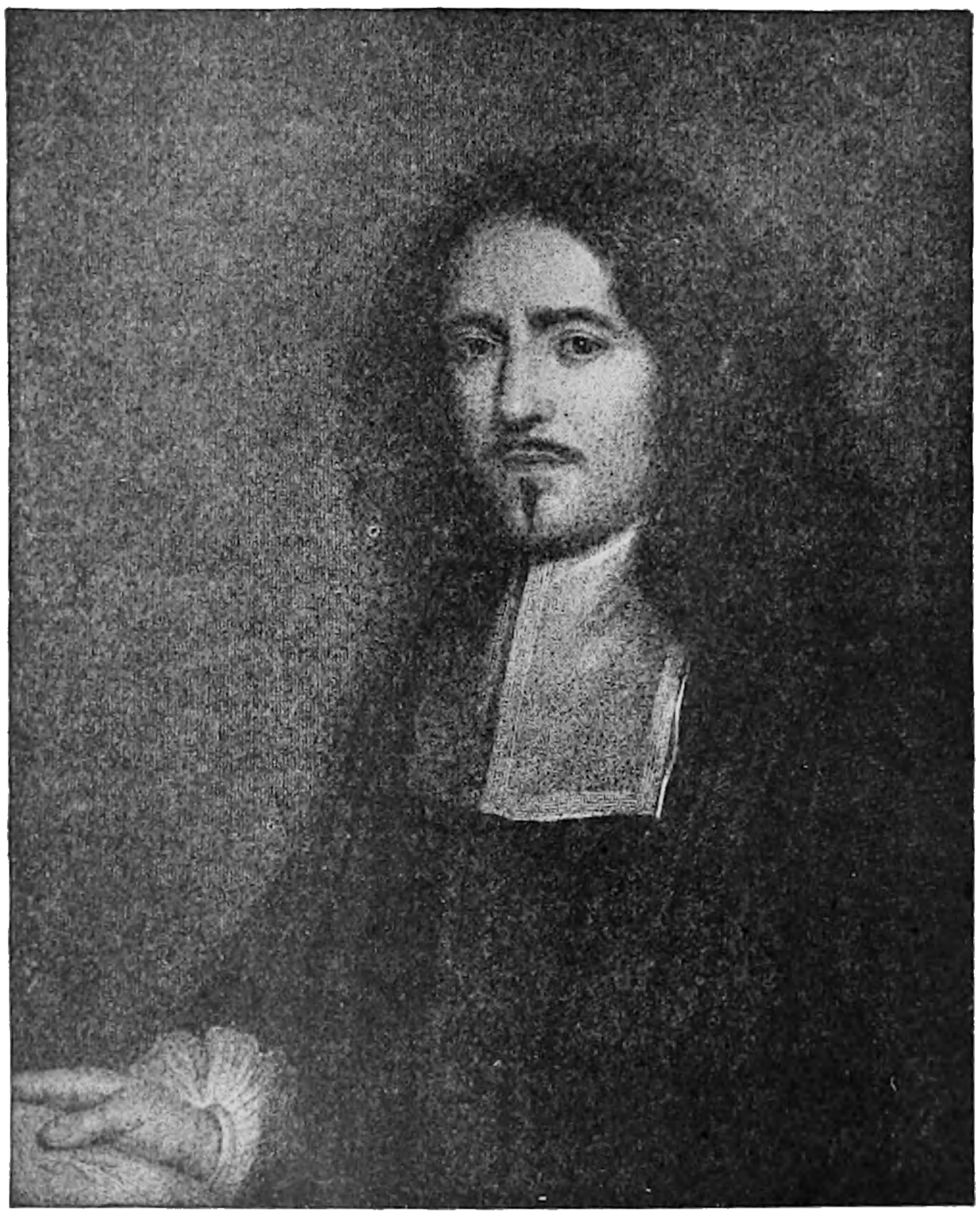

FIG. 5.—Marcello Malpighi, 1628–1694. (*From Garrison's History of Medicine, after the painting by Tabor, Royal Society.*)

Although the microscopes of the seventeenth century were not powerful, compared with microscopes of today, they opened up a large field for new discovery. Minute anatomy had its rise with the rise of the microscope. It is not important to name the many investigators who, with the aid of these instruments, studied the systems of minute organs in insects, or who discovered the small one-celled animals in pond water. No one of them stands out preëminently as a representative of this movement. It will be sufficient to point out that the steady improvement of the microscope in the two centuries and more since the time of Malpighi and his contemporaries has made it possible to study more and more minute structures. Progress in anatomy, in so far as it concerns the smallest structures, has at all times depended on, and kept pace with, the improvement of the microscope. The physiologist must often watch his experiment with the aid of a good microscope. Classification of animals and plants in many cases shifted to an entirely new basis when observation of minute structures became possible. Microscopic study of fossils reveals features of importance. Naturally, each of these subjects has grown as the microscope grew. From an instrument like that illustrated in Fig. 4, which is by no means the crudest one known, the microscope evolved step by step to the splendid optical aids of the present time. Today the biologist uses microscopes fitted with oil immersion objectives and condensers for increasing the illumination, lenses corrected for chromatic and spherical aberration, devices for delicate adjustments of focus, and other refinements. Whether further striking improvements are still possible is uncertain.

Fig. 6.—Antony van Leeuwenhoek, 1632–1723. (*From Garrison's History of Medicine.*)

Classification.—During all these centuries of observation, in the early Greek period and in the period following Vesalius, many kinds of animals came to be known. With the use of the microscope, hundreds more became visible. For a long time these thousands of species were a chaos, and with the improvement of the methods of study, and the increase in the number of travelers and naturalists, the number of known animals made the chaos intolerable. Systems of classification were used, but they were superficial and were devised for convenience only. It is true, even the early zoölogists knew that the quadrupeds were more like one another than any of them were like snakes, but no one had a comprehensive system of classification that included the whole animal kingdom. Nor was this the whole difficulty. Animals were often not named, but were known by cumbersome descriptions. Animals that were common enougn to have received names were differently named in different regions; and the same name was not infrequently applied in different localities to different animals.

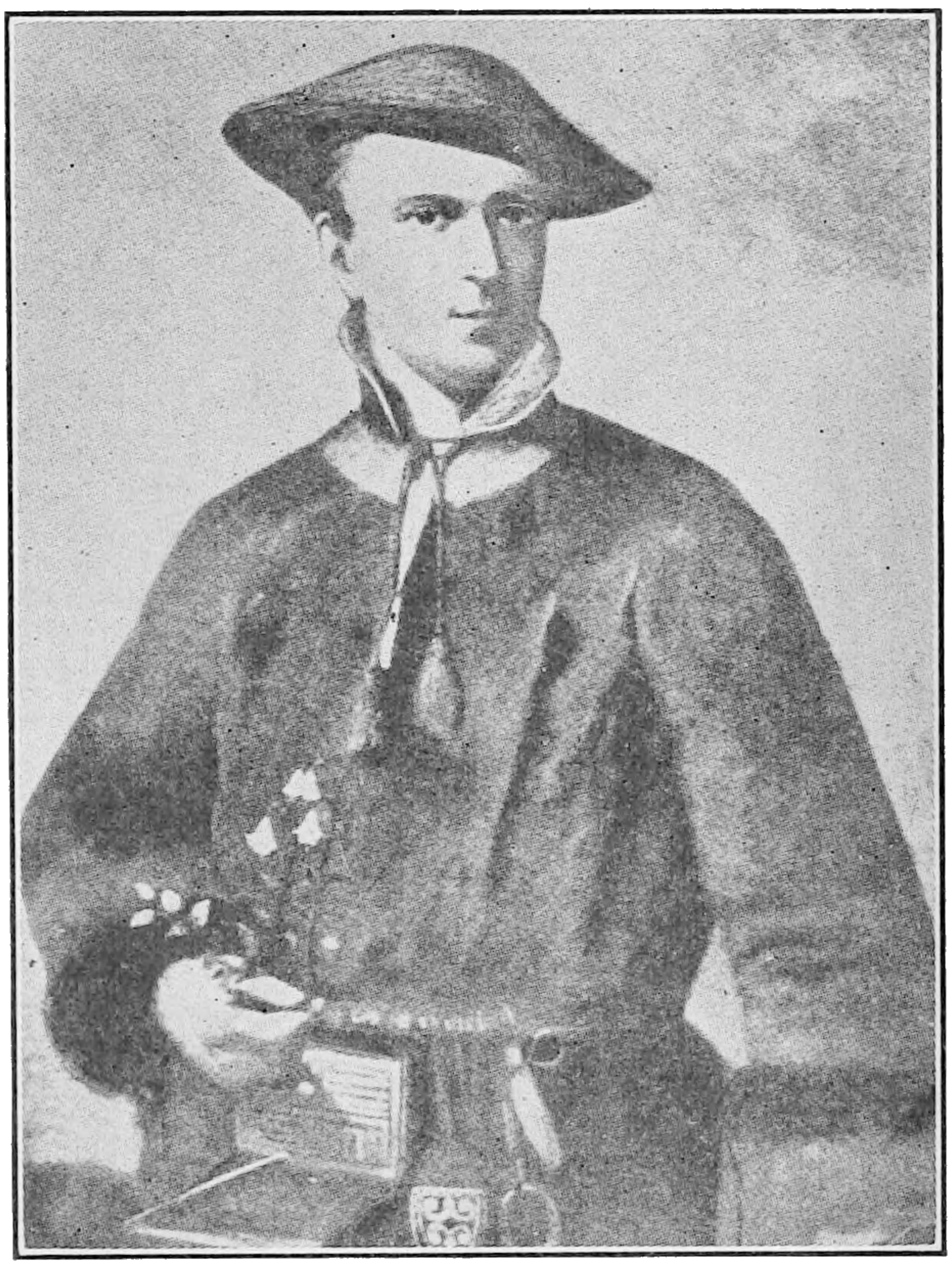

Fig. 7.—Carl von Linné (Carolus Linnæus), 1707–1778, in Lapland dress at the age of thirty. (*Courtesy of New York Botanical Garden.*)

Order has come out of this confusion largely through the initial efforts of Carl von Linné (or Linnæus as he is more commonly called), of Sweden, who lived from 1707 to 1778 (Fig. 7). Before his time John Ray of England, had taken one important step, by limiting the meaning of the word "species" to something like its present significance. Linnæus went further and gave each species a name which, being Latin, could be used the world over. The name of each species was a double one, the first name being that of the genus, the second that of the species itself. Thus,

molluscan type, the articulated type, and the radial type. He thus arrived at a scheme of classification based upon similarity of structure, which is even today the chief basis of classification. But curiously enough, Cuvier failed to see what every zoölogist now recognizes, that similarity of structure is owing to common descent. He even used his great powers of debate and his wide personal influence to combat the idea of common descent. The general acceptance of the idea of evolution was delayed many years by this error of Cuvier.

Following Cuvier was a long line of able anatomists in the nineteenth century, by whom comparative anatomy was raised almost to the rank of an exact science. Their names are everyday words to the trained morphologist, but no one of them stands forth preëminently, and they need not be mentioned here. The later ones recognized common descent as the key to similarity of structure, and comparative anatomy furnished some of the best of the early evidence of evolution.

FIG. 8.—Georges Cuvier, 1769–1832. (*From Locy's Biology and Its Makers.*)

The Discovery of Cells.—Early in the nineteenth century, before the end of Cuvier's career, the improvement of the microscope had resulted in such excellence that the study of the minute anatomy of animals and plants was becoming common among biologists. A number of investigators, some of them much earlier than the nineteenth century, saw in organisms minute divisions, arranged sometimes in orderly manner, sometimes in hit-or-miss fashion. Hooke saw box-like cavities in cork as early as 1665, Malpighi a similar pattern in other plant tissues in 1670.

Oken claimed to have witnessed "repeated vesicles" in animals and plants, in 1808, but it is not clear what he meant nor whether he actually saw them.

None of the writers mentioned appeared to regard these objects as units of structure, nor to attach any importance to them. However, in the hands of Schwann (Fig. 9) and Schleiden (Fig. 10), chiefly the former, repeated observation of these minute units of structure led to a great generalization. The units had been called "cells" since the time of Hooke, from a mistaken notion of their structure, and Schwann and Schleiden reached the conclusion that all animals and plants are built up of them. This generalization was called the Cell Theory. The correctness of their conception has since been abundantly verified, so that it should now rather be spoken of as the Cell Doctrine. Although Schleiden published his observations a little earlier than Schwann (1838 and 1839, respectively), it is only in the work of Schwann that the cell theory is stated, or that the words "cell theory" are used. So that, although Schleiden is usually named before Schwann in attributing to them the joint authorship of this theory, it is done so rather for the sake of euphony than from any desire to give Schleiden greater credit than, or even equal credit with, Schwann.

Fig. 9.—Theodor Schwann, 1810–1882. (*From Garrison's History of Medicine.*)

Fig. 10—Matthias Joseph Schleiden, 1804–1881. (*From Garrison's History of Medicine.*)

The importance of the cell doctrine can scarcely be over-estimated. It is taken as a matter of course, by beginning students, that all organisms are made up of cells; but when one reflects that all the things an animal is or does are what the cells are or do, the idea acquires tremendous significance. All growth, all development, all life processes, all reproduction, as will be pointed out in later chapters, are the results of cell activities. The universal occurrence of cells in organisms is, then, a fact of fundamental import.

Evolution.—While, on the morphological and purely observational side of biology, the cell theory was being built upon firm foundations, on the philosophical side new ideas were growing up which also marked progress in a different direction. Most zoölogists had become so well acquainted with animals as we know them at the present time that they conceived the various species to be fixed and constant. They believed each species to have been created in the form in which it exists now. Through a long period of biological history, however, there had not been wanting daring and inquiring naturalists who saw what they believed were indications that species had changed in the past, and were perhaps changing even at the present time. Vague ideas of evolution were held by some philosophers as early as the Greek period; but it was not until the end of the eighteenth century that any well-defined theory of evolution arose. Buffon (1707–1788) appears to have held evolutionary ideas, but was too timid to state them clearly. Erasmus Darwin (1731–1802) published in his *Zoönomia* in 1794 a comprehensive theory of evolution, but did not support his views by many facts.

FIG. 11.—Jean Baptiste Lamarck, 1744—1829. (*From Locy's Biology and Its Makers and Thornton's British Plants.*)

Lamarck (Fig. 11), 1744–1829, was the first to bring forward a theory of evolution that has retained a considerable following to the present time. Lamarck, like most of his contemporaries and predecessors, at first adopted the view that species were fixed and unchanging; but about 1800 his views changed. His theory is best explained in his *Philosophie Zoölogique*, published in 1809. Its two principal tenets were that the effects of use and disuse upon the parts of animals are transmitted to their offspring, and that the environment may produce changes in animals which are inherited by their progeny. Both of these views regarding the cause of evolution have been largely abandoned by the pure biologists, but are still held by some paleontologists, by numerous medical men, and by the laity.

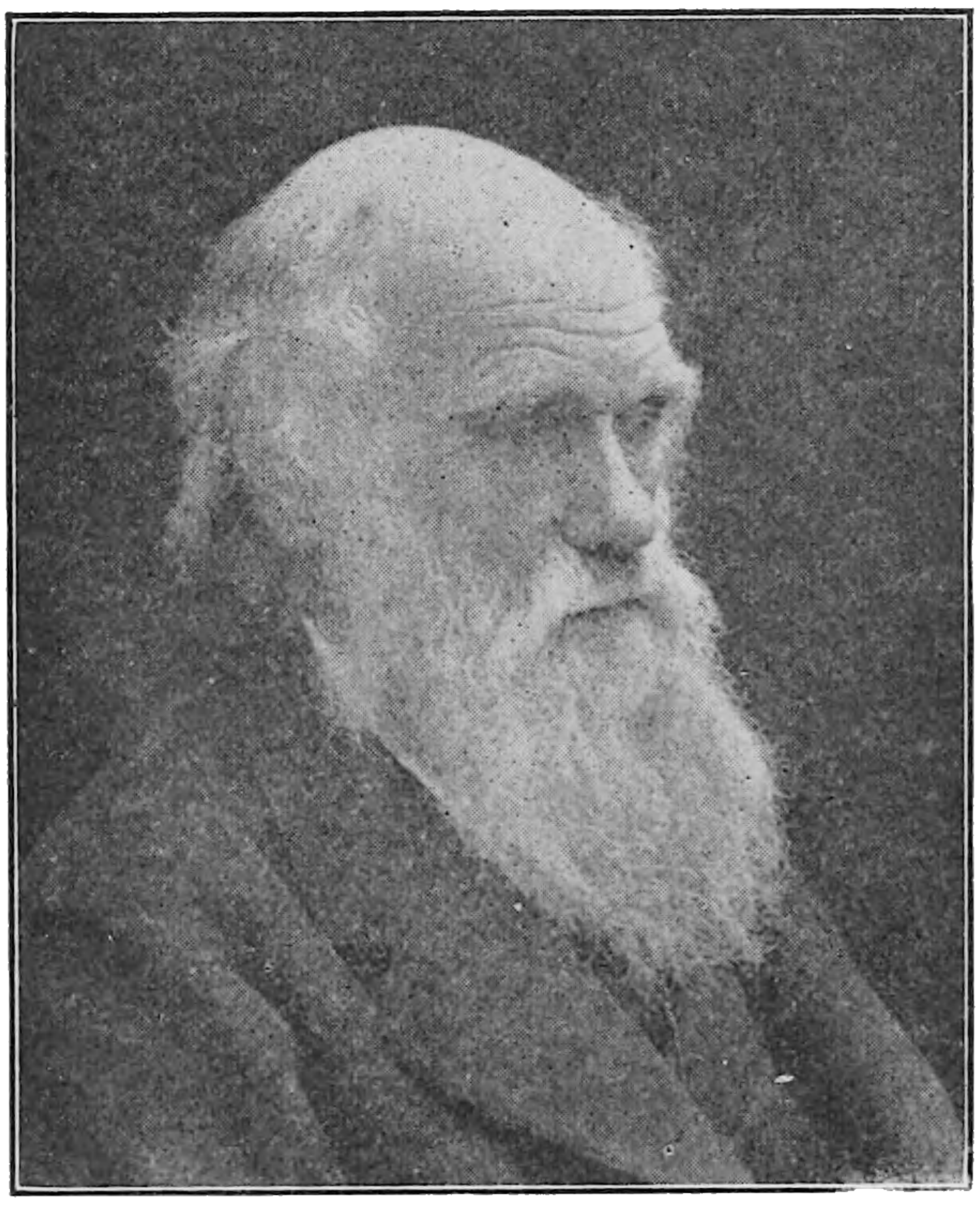

Fig. 12.—Charles Darwin, 1809–1882. (*From University Magazine. Photo by Leonard Darwin.*)

Lamarck's views were championed by the able naturalist Geoffroy-Saint-Hilaire (1772–1844). Cuvier, on the contrary, not only opposed the Lamarckian views of the cause of change, but ridiculed the idea of evolution itself. The attitude of the latter scholar is one of the incongruities of biological history, since Cuvier's own discoveries in the field of comparative anatomy constitute one of the best arguments in favor of the theory of evolution. Nevertheless, Cuvier adhered to the fixity of species, and in a famous debate in the French Academy of Science between Cuvier and Geoffroy-Saint-Hilaire, in 1830, the former was held to have won. Cuvier was in high esteem in government and social circles, and had a large following among the young men. As a result the rise of evolutionary thought was retarded for several decades.

Then came Charles Darwin (Fig. 12) grandson of Erasmus Darwin, with indisputable evidence of evolution. Cuvier was no longer living to combat the theory, and Darwin had laboriously collected a mass of supporting facts which could not be set aside. These he published in a series of books beginning with *Origin of Species* in 1859, and continuing to the end of his life in 1882. With them he proposed several theories to account for evolution which appeared so plausible that the whole thinking world was convinced of the fact of the mutability of species. The chief of these theories was that of *natural selection*, according to which, in the struggle for existence, the fittest survive. The theory of natural selection, as will be pointed out later, is still commonly held, though with diminished significance.

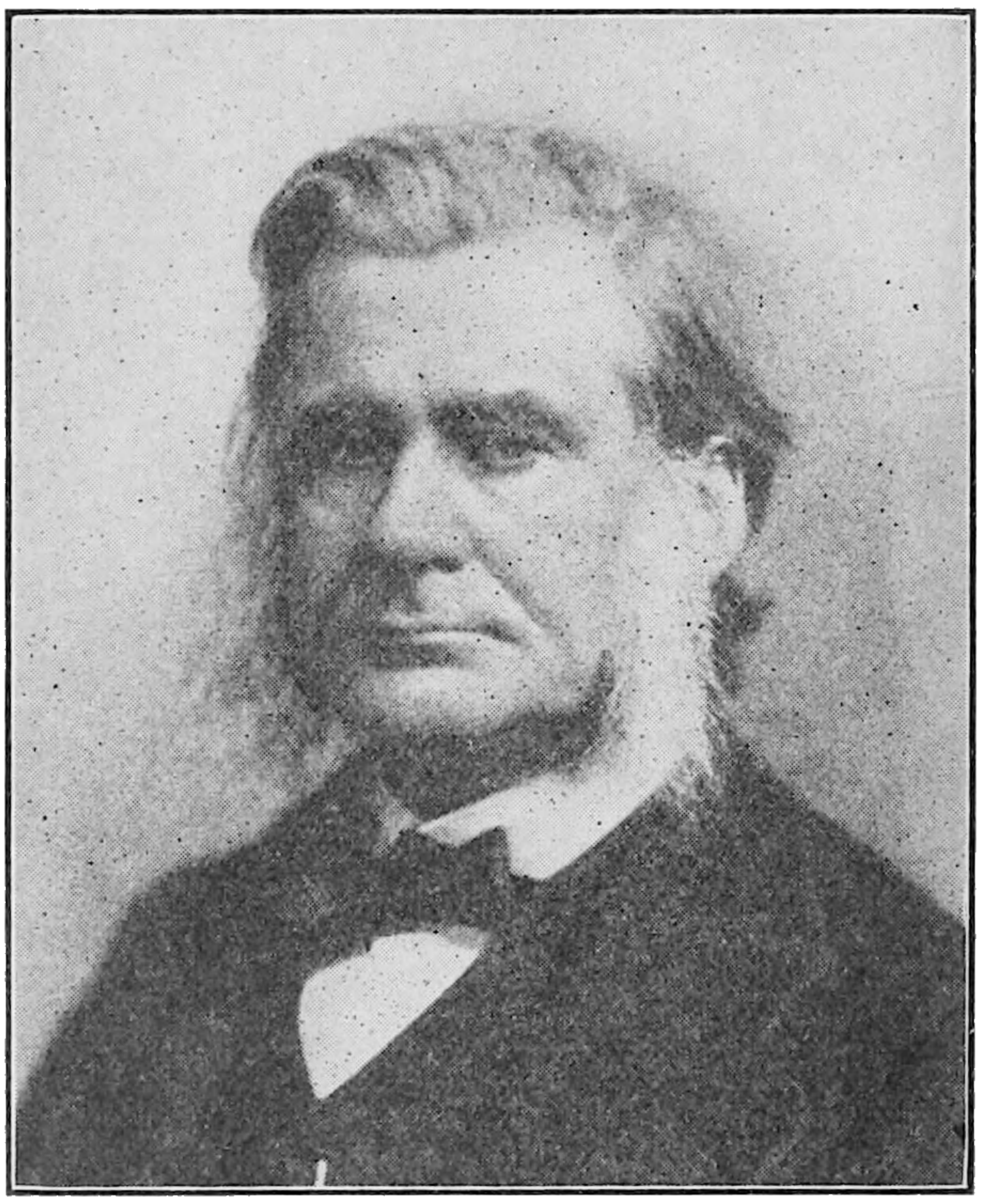

FIG. 13.—Thomas Henry Huxley, 1825–1895.

The doctrine of evolution was not accepted without opposition. However, with the aid of the powerful Thomas Huxley (Fig. 13), who spread the idea in forceful lectures among biologists and non-biologists alike, its victory was complete. With regard to the *fact* of evolution there are now no dissenters among thinking people. Whatever controversy still exists is concerned with the *causes* and *method* of evolution; evolution itself is admitted by all.

Genetics.—It will be noted that the theory of natural selection, by means of which Darwin sought to explain evolution, contained nothing to account for the *origin* of changes in species, but only for their *preservation.* So strongly did the theory of evolution and the theory of natural selection appeal to the imagination that another field of investigation, which would no doubt have gone far toward explaining evolution, was overlooked for a third of a century. This was the branch of biology now known as *genetics*, which includes heredity, variation, and related subjects.

A brilliant start was made in this field in 1866, by an Austrian monk, Gregor Mendel (Fig. 14). Mendel raised peas in the monastery garden, crossed a number of distinct varieties, and derived from them a simple law of heredity. So occupied were biologists with Darwin's theory of evolution, then in its infancy, that Mendel's writings remained unnoticed until 1900, when they were rediscovered. His simple experiments proved a tremendous stimulus to investigation, and much of the leading biological work of the present century has been in the field of genetics. Mendel's law of heredity has been amply verified and extended, but at the same time modified. At the present time the best work in genetics is being directed toward discovering the method by which hereditary traits are transmitted from parent to offspring. When that is finally discovered, it is not improbable that the causes of evolution will be more clearly understood.

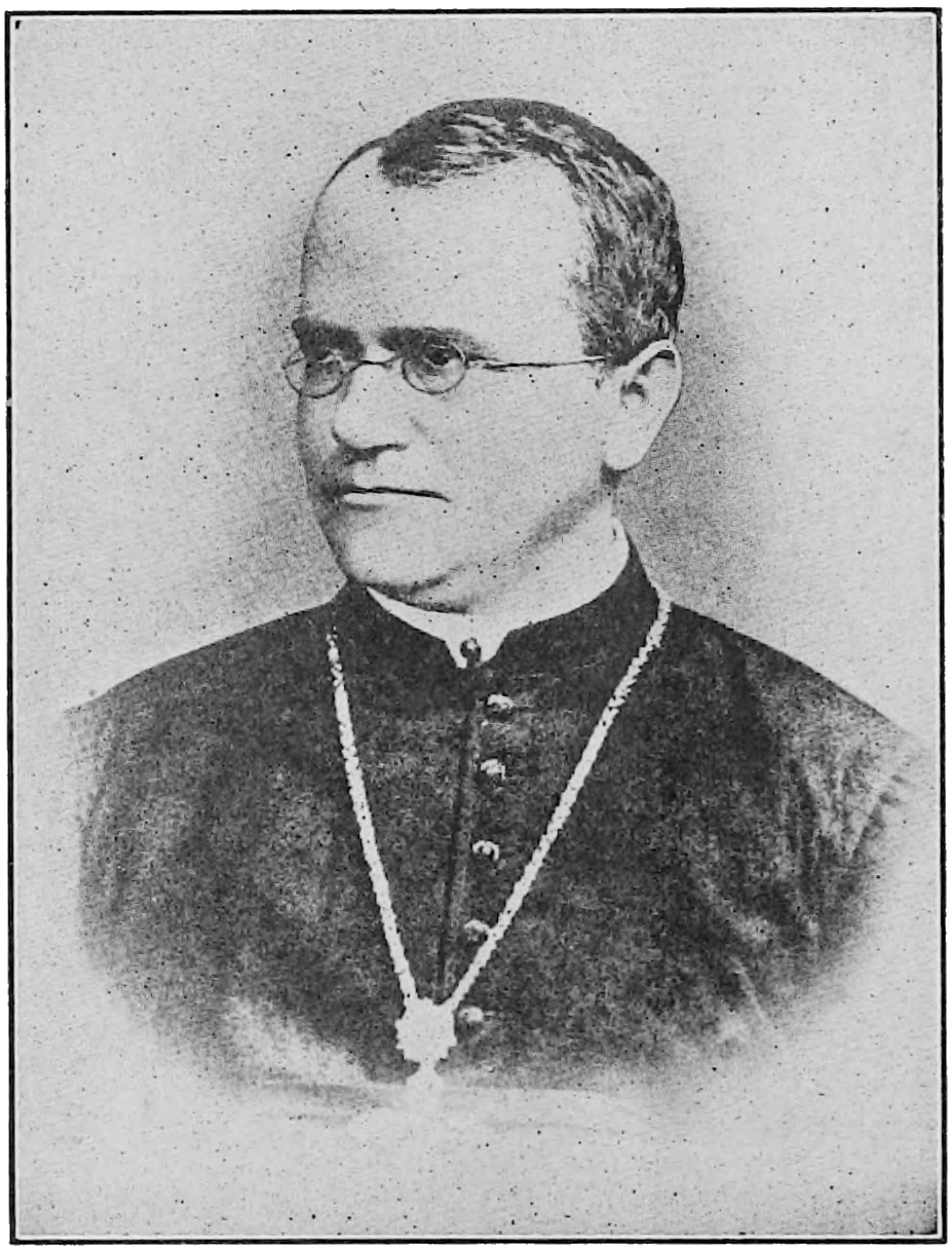

Fig. 14.—Gregor Johann Mendel, 1822–1884. (*From a photograph taken about* 1880. *Reproduced from the report of the Royal Horticultural Society Conference on Genetics,* 1906. *By permission of the President and Council.*)

Conclusion.—Although the foregoing account indicates the principal movements in the development of zoölogy, and the outstanding names connected with these movements, the "pure" science alone has been considered. It should not be forgotten that zoölogy has always had its practical applications. In the last half century these applications have been greatly multiplied. Medicine is applied zoölogy, applied directly to man and incidentally to those animals that are parasitic upon him or that are carriers of disease. Sanitation and public hygiene are matters of applied biology even more than matters of engineering. Crop-destroying insects and other pests are combated by the economic zoölogist. Improvement of breeds of domestic animals is the practical aim of the student of animal husbandry. The applications of zoölogy to practical ends are still probably in their beginnings. Its applications to man himself are particularly in a backward state. The improvement of human qualities, the maintenance of the best human strains, the effects of migration and intermarriage upon the races of men and their political development, and the effects of war upon racial qualities, are problems which still await solution.

Although zoölogy has had its fashions, though it has been developed in different directions at different times, these well-marked movements do not all bear the same relation to each other. The announcement of the cell theory stands in a peculiarly significant position. In itself the discovery of cells was not more important than some of the other developments of zoölogy. But it had and has unique possibilities as the foundation of other branches of the science. Animals are made up of cells, which is a purely morphological fact. But their physiology is what it is because of the nature of cells. Inheritance and evolution are cell phenomena. Relation to environment is dependent on the functions of cells. Even geographical distribution and classification are fundamentally dependent upon the cellular characteristics of animals. As a preface, then, to the discussion of the various branches of zoölogy in later chapters, a knowledge of cells is essential, and to that subject attention is now turned.

References

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haps intended to convey the idea of insignificance. Dujardin (Fig. 15), a French naturalist, appears to have thought it worthy of more attention, and described it in 1835 under the name "sarcode" (soft substance). He tested its solubility, and its behavior with certain reagents, such as alcohol and the acids, thereby satisfying himself that it differed from other jelly-like substances (gelatin, albumen, etc.) with which it might be confused. But either because Dujardin had studied the sarcode only in worms and Protozoa and a few other low forms of animal life, or because his diffidence forbade his making any larger claim for it, this substance was supposed to be found only in the lower animals. The general occurrence of this substance, however, could not long avoid discovery. Hugo von Mohl, in 1846, observed the living part of plant cells, distinguishing it from the walls and vacuoles, and called it protoplasm. This name, used earlier by Purkinje, von Mohl succeeded in bringing into common use. Gradually it dawned upon biologists that this matter is found in all living things, that it is in fundamental respects alike in all of them, and that this, rather than the walls, is the important feature of cells. In the absence of cell walls, this protoplasm is the cell. Of a number of investigators who contributed to this fortunate issue of the problem of the cell, mention should be made of Max Schultze (Fig. 16) who, probably more than any other one person, brought conviction of the truth of the idea just stated to the minds of all biologists.

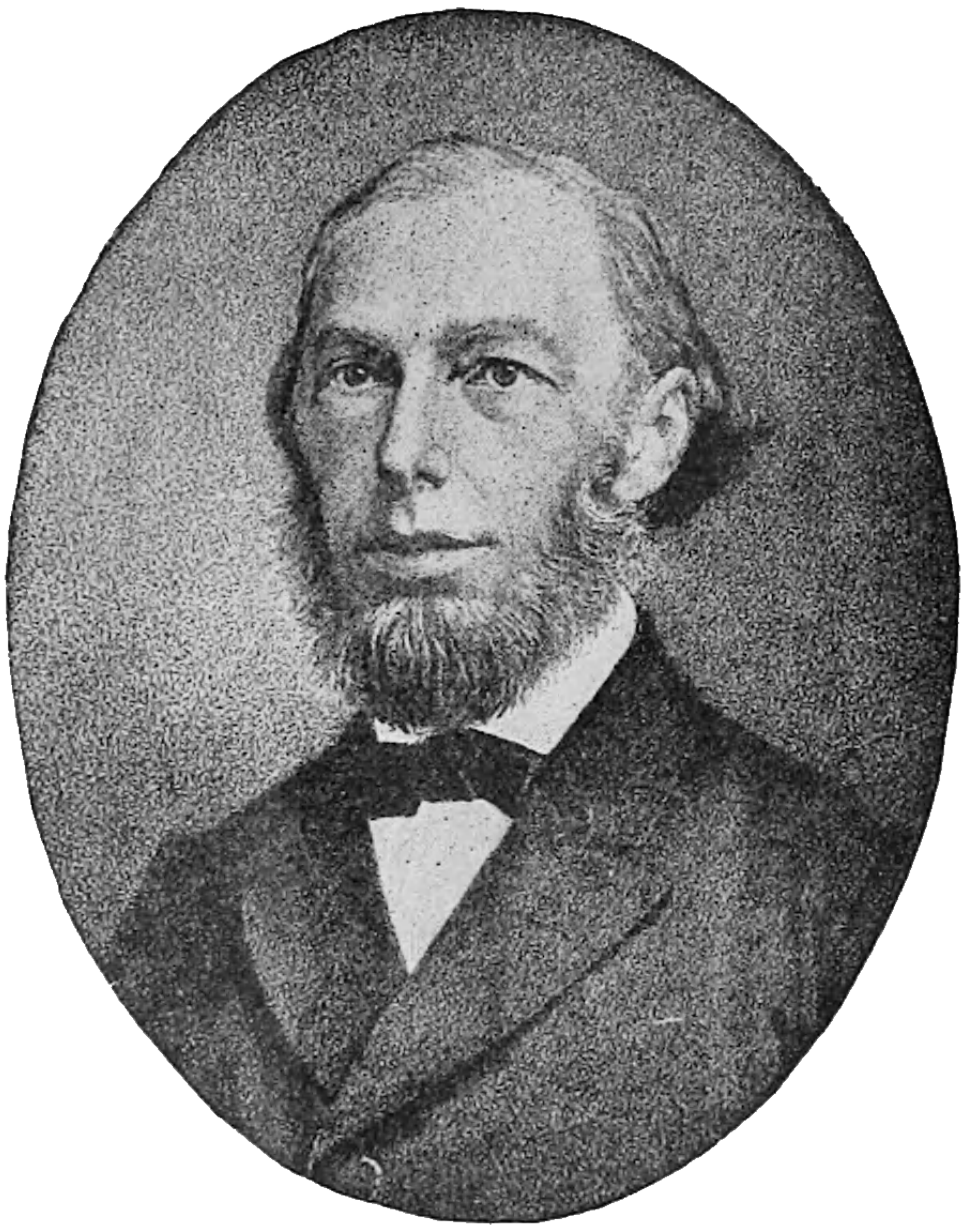

FIG. 16.—Max Schultze, 1825–1874. (*From Garrison's History of Medicine.*)

Additions.—The bare statement that all living things are composed of cells is also inadequate in at least one structural respect. It was early discovered that certain tissues are made up in part of structures and material that are not cellular, but that have been created by cells. The bulk of cartilage and bone is formed of a firm *matrix* not composed of cells, but lying between the cells. This matrix is produced by the cells as a secretion, in which the producing cells become imbedded. It is not changeless, since the cells may dissolve it away and build it in some other direction, but it is itself wholly inactive in this change. The matrix is not living matter. Connective tissue also contains elastic matter, in the form of fibers of several kinds, which are laid down as secretions by the cells. These fibers have a function, but it is entirely a passive one. Ligaments and tendons are in like manner largely non-cellular. Since animal bodies are so largely composed of such non-living material, all of it produced by cells, the cell doctrine should be made to specify that all living things are composed of cells *or cell products.*

With the corrections regarding the nature of nucleus, walls, and protoplasm, and the addition of cell products, noted in the preceding paragraphs the early statement of the cell doctrine would still be essentially correct as far as it goes. In that form, however, it would imply that biology is mostly a morphological subject. So it once was. But with the growth of the science, with its development in the fields of physiology and genetics, it becomes apparent that the cell doctrine can be extended to include more than the mere structure of animals and plants.

The life processes of living beings, fortunately now fairly well understood in some respects, have been shown more and more to be the life processes of their component cells. Without implying that the cells act independently of one another, it is still in a sense true that the activities of an organism are the sum of activities of its cells. Under favorable cultural conditions, cells may long continue their activities when removed from their association with other cells; and in many cases it has been possible to analyze the complicated processes of multicellular organs, and show that this thing is done by certain cells, that other thing by certain other cells, and so on. The cell has now come to be regarded as the *physiological unit,* as well as the morphological one; and some of the most important advances is zoölogical knowledge in recent years have been made in the field of cell physiology.

Almost as a part of the step by which the cell doctrine is extended to embrace cell physiology as one of its tenets, is the inclusion of development and heredity. The origin of a multicellular animal from a one-celled beginning (the egg) may be watched from first to last, and everywhere the process is a series of cell phenomena. Cell divisions, arrangement of cells into layers or tissues, the unequal growth of cells or parts of cells to form folds and protrusions, the migration of cells sometimes for long distances, the formation here and there of cell products, make up the complex process of *embryonic development.* All these changes are brought about *in or by the cells.*

Through this series of multiple changes there is built up an organism which, in most cases, closely resembles its parents. Here again it is found that the cells are responsible for each step and for the final result. The complete heritage of the eventual adult animal must of course be represented in some manner in the egg. The proper distribution of the *material of heredity,* whatever it is, through all of the divisions and rearrangements which the embryo undergoes, is at every point cared for *by the structure and functioning of cells.* What these structures and activities are cannot be stated here, even by name, but are dealt with in subsequent chapters.

An adequate statement of the cell doctrine, as must be apparent from the foregoing considerations, must do more than generalize upon the structure of living beings. It must include the fact that the cell is also the unit in physiological processes, including those of embryonic development and inheritance.

Influence of the Cell Theory.—The theory of the universality of cells was a great generalization. It would have been a most important milestone in biological progress, even if it had been in itself less fundamental. For zoölogy had had no great generalizations before the cell theory was brought forth. There was nothing in the field of biology to compare with Newton's laws of motion in physics. Biologists would have been pardoned for despairing of ever bringing the whole living world under one point of view in some specific regard. The cell theory, therefore, was a great unifying influence. Contemplation of it must have prepared biologists for other great generalizations. Less than half a century later, another fundamental proposition, the theory of evolution, had been accepted by practically the whole biological world; and it is not improbable that the idea of evolution was adopted the more readily because the cell theory had shown that basic unity was as much to be expected among living things as in physics and chemistry.

The knowledge that animals and plants are universally constructed of cells led to new problems. Comparative morphology could now extend its principles to an undreamed-of host of minute structures. All the components of cells, including those of the nuclei and specialized organs, which are mentioned in the description of a typical cell below, have been discovered since Schwann's time; and the occurrence of these in cells of widely different kinds courted comparisons. Physiology now became the physiology of cells, or was capable of such extension. General physiology, as distinct from the physiology of the organs of higher animals, has grown out of this discovery. A knowledge of the permeability of cell membranes, of the functions of electrolytes in living substance, of the release of energy by chemical reactions within the cells, are some of the products of this new physiology made possible by the cell theory. Heredity could now become a cell problem, and as is pointed out in a later chapter the chief discussion of heredity now has to do with the machinery by means of which cells produce hereditary characteristics. Not all of these developments of zoölogical investigation took place at once, after the cell theory was published, but they became possible, and a beginning was made. In numerous other ways the outlook of biology was changed and illumined by Schleiden and Schwann's epoch-making law. But in order to understand the influence of the cell theory on the development of the science, it will first be necessary to consider the structure of cells.

The Size of Cells.—All cells are composed of viscous or jelly-like material called *protoplasm*. The quantity of this material comprised in a single cell varies within wide limits. Many cells are so small as to be visible only with a good microscope. The vast majority of cells require considerable magnification to be seen. Not a few, however, are large enough to be visible with the unaided eye, as in the case of the larger Protozoa (animals composed of but one cell), while in muscles and nerves of the higher animals, the cells, though not of great diameter, may be inches or feet in length. This great variability does not exist, however, among cells of the same kind. The cells of the skin of a given animal, though not of uniform size, do not differ strikingly from one another; and cells that are arranged in definite layers, like that lining the intestine, are apt to be very nearly equal in size.

Gross Shape.—The shape of cells is also very variable. Theoretically, due to surface tension, a cell is typically spherical; but that shape is attained, even approximately, only in certain free cells, such as eggs and a few of the one-celled organisms, the Protozoa (animals) and Protophyta (plants). Cells take on other forms for various reasons. A free-living cell, as Amœba and other related Protozoa, may actively change its shape by thrusting out portions of the body into finger-like pseudopodia, Fig. 17. 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. Other free-living cells, of more or less constant form, are kept constant by a wall or pellicle that the cells themselves have secreted. 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. Good examples of such constant forms are found among the Infusoria (ciliated Protozoa), as in Fig. 18.

Cells that exist in aggregates 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. But other factors, such as unequal growth in different directions, and perhaps inequalities of surface tension, factors often not understood, combine to produce cells of a great variety of shapes. They may be rather regular rectahedrons, as in plants; long cylinders, as in voluntary muscle:

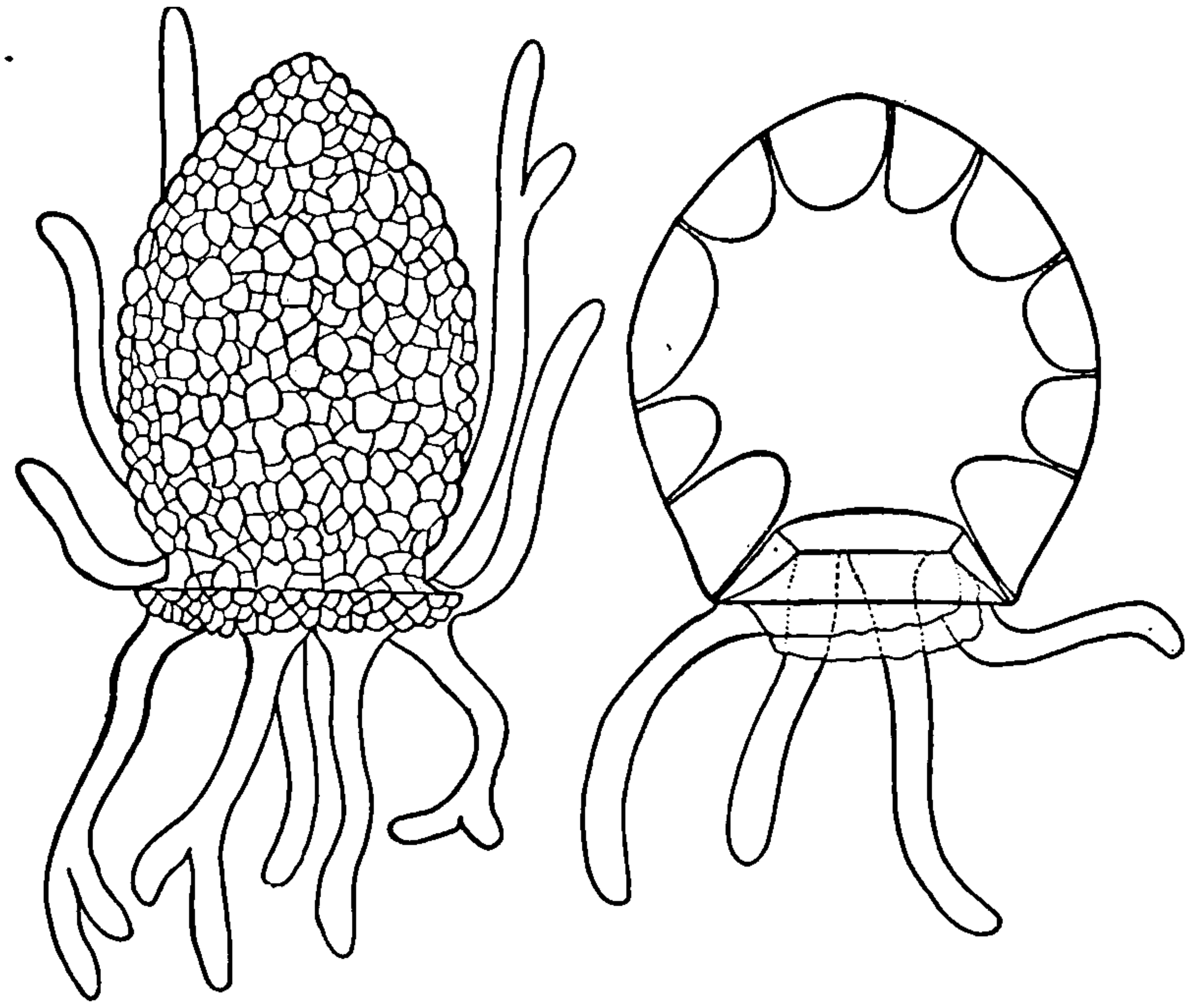

FIG. 17.—Two protozoa of the class Rhizopoda. The bodies are partly enclosed in shells, one made of sand, one of a chitinous substance. From these shells the protoplasmic body may be actively protruded in arm-like pseudopodia, which are afterwards retracted.

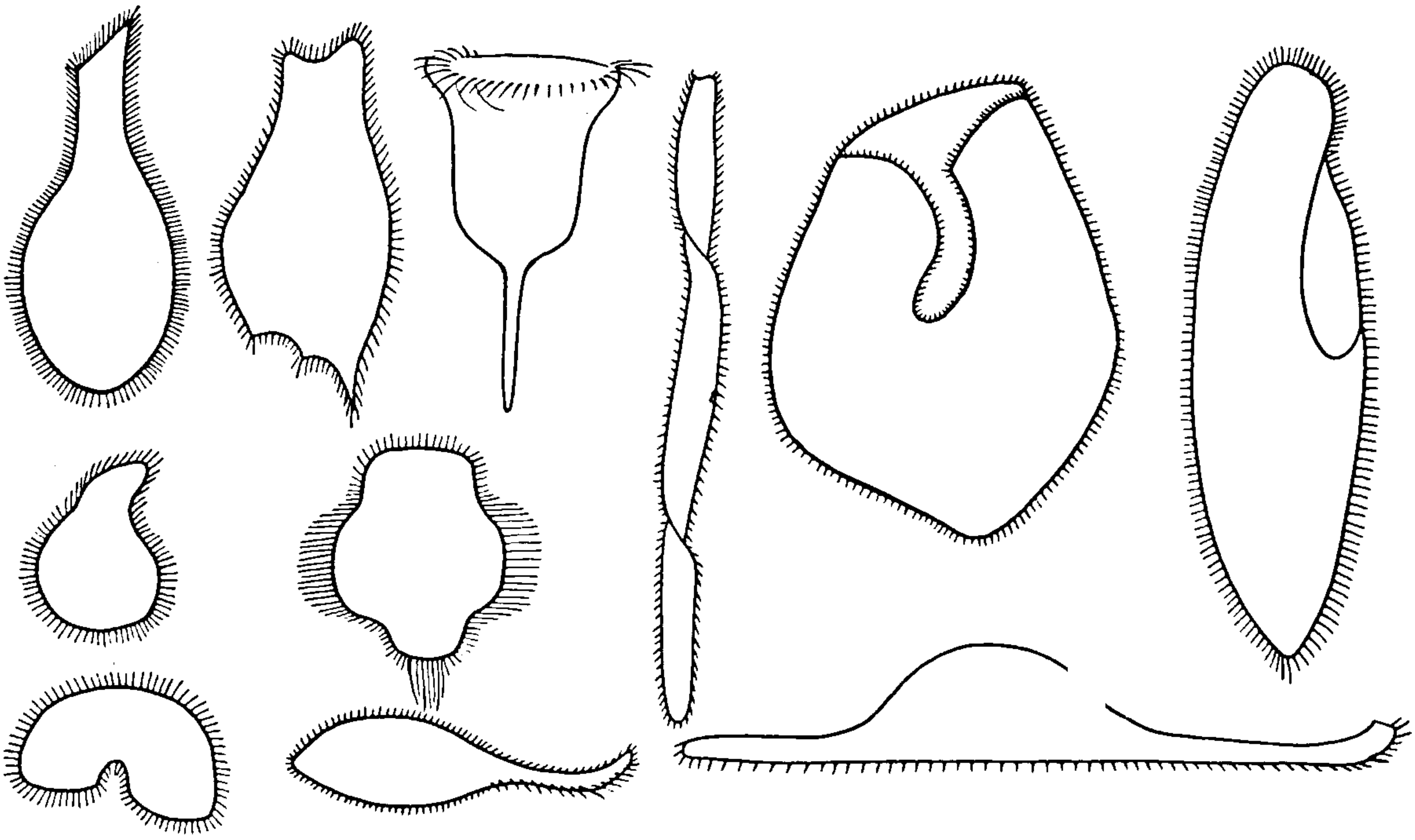

FIG. 18.—Various forms of Infusoria whose body shape is kept fairly constant by a surrounding pellicle. Though this shape may be altered by pressure, it is restored when the pressure is removed. Cilia project from the surface. (*Modified from Conn.*)

greatly flattened cells with their largest sides polygons, as in the outer layer of frog skin; somewhat flattened cells elliptical on their flat sides, as in the blood of many animals; circular and flattened or cupshaped, as in human blood; narrow and spindle-shaped, as in involuntary muscle; or finely branched, as in pigment cells of the skin of frogs and salamanders, or bone and nerve cells.

Nucleus and Cytoplasm.—This mass of protoplasm, regardless of its shape and other modifications, is usually differentiated into two distinct parts. There is a central body called the *nucleus* (Fig. 20, *n*) which, in prepared and stained material, is usually highly stained, since it is composed of substances which have a high affinity for most of the common dyes; but in living material the nucleus is somewhat transparent, nearly colorless, and highly refractive like a lens. The remainder of the cell, besides the nucleus, is called *cytoplasm* (Fig. 20, *cy*). Both nucleus and cytoplasm are composed of protoplasm, as the latter term is now commonly used.

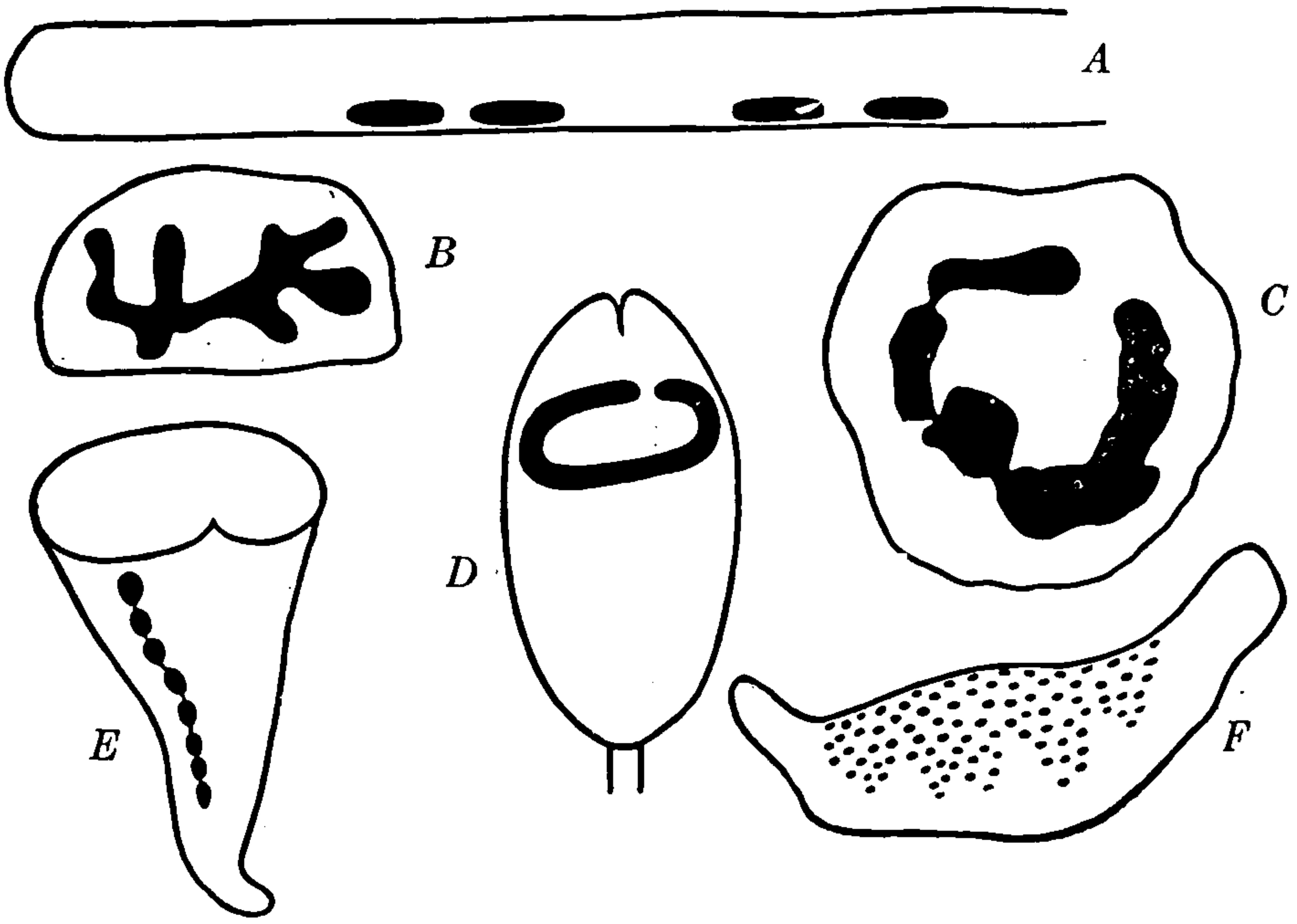

Fig. 19.—Various forms of nuclei in cells. *A*, part of muscle cell with multiple ellipsoidal nuclei; *B*, gland cell of butterfly with branching nucleus; *C*, marrow cell of rabbit with ring-nucleus; *D*, Epistylis with curved rod-like nucleus; *E*, Stentor with beaded nucleus; *F*, Trachelocerca with distributed nucleus. (*B*, *C*, *F*, *after Wilson. Courtesy of Macmillan Co.*)

The nucleus is typically spherical, owing, as in the case of the cell as a whole, to surface tension. But this shape is often altered by the shape of the containing cell, by physiological activity of the nucleus itself, or for reasons not yet understood. In long narrow cells the nucleus is apt to be ovoid or ellipsoidal, as in young voluntary muscle cells (Fig. 19, *A*). In highly active cells it may be branched (*B*) or otherwise irregular (ring-shaped, *C*). In some of the Protozoa it is rope-like (*D*), or beaded (*E*). There may be more than one nucleus, as in a number of Protozoa, and in voluntary muscle (*A*). Some cells have no nucleus of the usual structure, but possess the deeply staining nuclear material in the form of scattered granules. The bacteria and some of the Protozoa (*F*) are examples of this condition. Such scattered granules are spoken of as a *distributed nucleus*. In the red cells of human blood the nucleus is actually wanting, although in their developmental stages they possess nuclei which later disappear.

The form of the cytoplasmic mass is of course the form of the cell as a whole, as described above.

Other Bodies in the Cell.—As indicated in Fig. 20, a cell may possess other features. There is usually, perhaps always, a differentiated portion at the surface, whose nature is different in different cases, and which is variously designated. Often it is a lifeless secretion of the protoplasm, in which case it is called a *cell wall*. In plants and in some of the Protozoa, this cell wall is composed of *cellulose*, a substance related to the starches, but other substances as *lignin* or *silica* are often associated with it. In many Protozoa the wall is composed of nitrogen-containing substances resembling *chitin*, *keratin*, and *gelatin*.

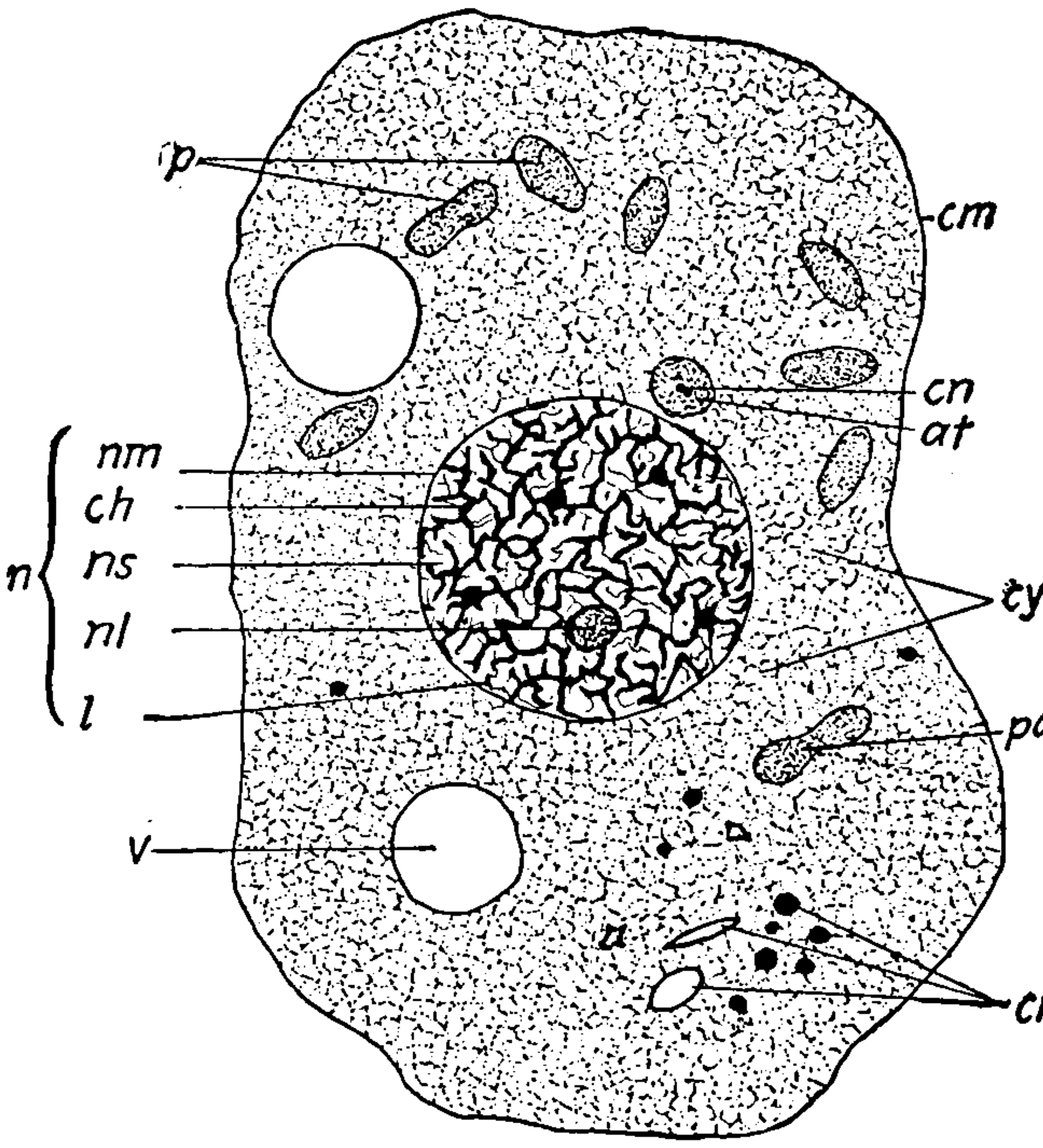

FIG. 20.—Diagram of a typical cell, with structures commonly present. *at*, attraction-sphere; *ch*, chromatin net-work; *ci*, cell inclusions; *cm*, cell membrane; *cn*, centrosome; *cy*, cytoplasm; *l*, linin thread; *n*, nucleus; *nl*, nucleolus; *nm*, nuclear membrane; *ns*, nuclear sap; *p*, plastids; *pdiv*, plastid dividing; *v*, vacuole.

Instead of a wall the surface of the cell may be covered with a thin, filmy sheet, called the *pellicle* or *cuticle*, the nature of which is uncertain. Probably the pellicle is to be regarded as a lifeless secretion, as is the cell wall. Such pellicles are found in the Infusoria (ciliated Protozoa) as described above (Fig. 18).

In cases where there appears to be no special covering, the surface layer of protoplasm is differentiated, at least with regard to its physical and probably also its chemical properties. Depending upon their effect

Polarity.—The structures described above are the chief features in which different parts of a cell are visibly distinguishable from one another. They do not, of course, constitute all of the organization which cells are known to possess; and other elements of organization are described below. But along with other general features is to be included an invisible organization which is termed *polarity.* In many cells, one portion is destined to perform certain functions, another portion certain 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 evidenced by their future activities, is the phenomenon which is called polarity. At either end of an axis the protoplasm is different.

A good example of polarity is found in the eggs of insects. One end of the egg, in some way different from the other end, always becomes the head. One side always is right, the other left. The polarity goes back into the ovary (reproductive body) for, at least in many insects, the same end of the egg always emerges first when the egg is laid.

Occasionally this polarity is recognizable in advance because the parts are differently colored; or one part may contain oil droplets, or some other cell inclusion, another part none. In many cases it has been definitely proven that these visible differences are not the cause of polarity, they are merely associated with it, or are signs of it. In other cases where proof is wanting that the visible bodies are not causal agents, it may still be doubted whether they are more than incidental phenomena. The polarity appears to be an invisible organization of the protoplasm itself.

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 surface phenomena.

In some cases, however, protoplasmic connections are known to extend from one cell to another. These have been demonstrated in the skin of the salamander (Fig. 21), are conspicuous in Volvox, and have been described for many kinds of animal cells. In plants, it is maintained that cell-bridges are usually present, the fine protoplasmic filaments passing through minute pores in the cell walls. This connection between cells opens up large possibilities of mutual influence. Some of the consequences of it are pointed out later.

Finer Structure of the Cytoplasm.—Protoplasm occurs in so many different forms, and undergoes so many changes during its normal activities, that agreement among careful students as to its intimate structure was long delayed. With this debate the student is only partially concerned. It seems now fairly safe to say that the most common form of protoplasm is that of an emulsion. That is, it is composed of minute spheres of liquid or semi-liquid matter suspended in another liquid or semi-liquid substance. A correct idea of the physical structure of protoplasm may be gained by imagining a quantity of marbles of various sizes poured into a vessel of syrup, and then supposing the marbles to become liquid without changing their relations to each other. The

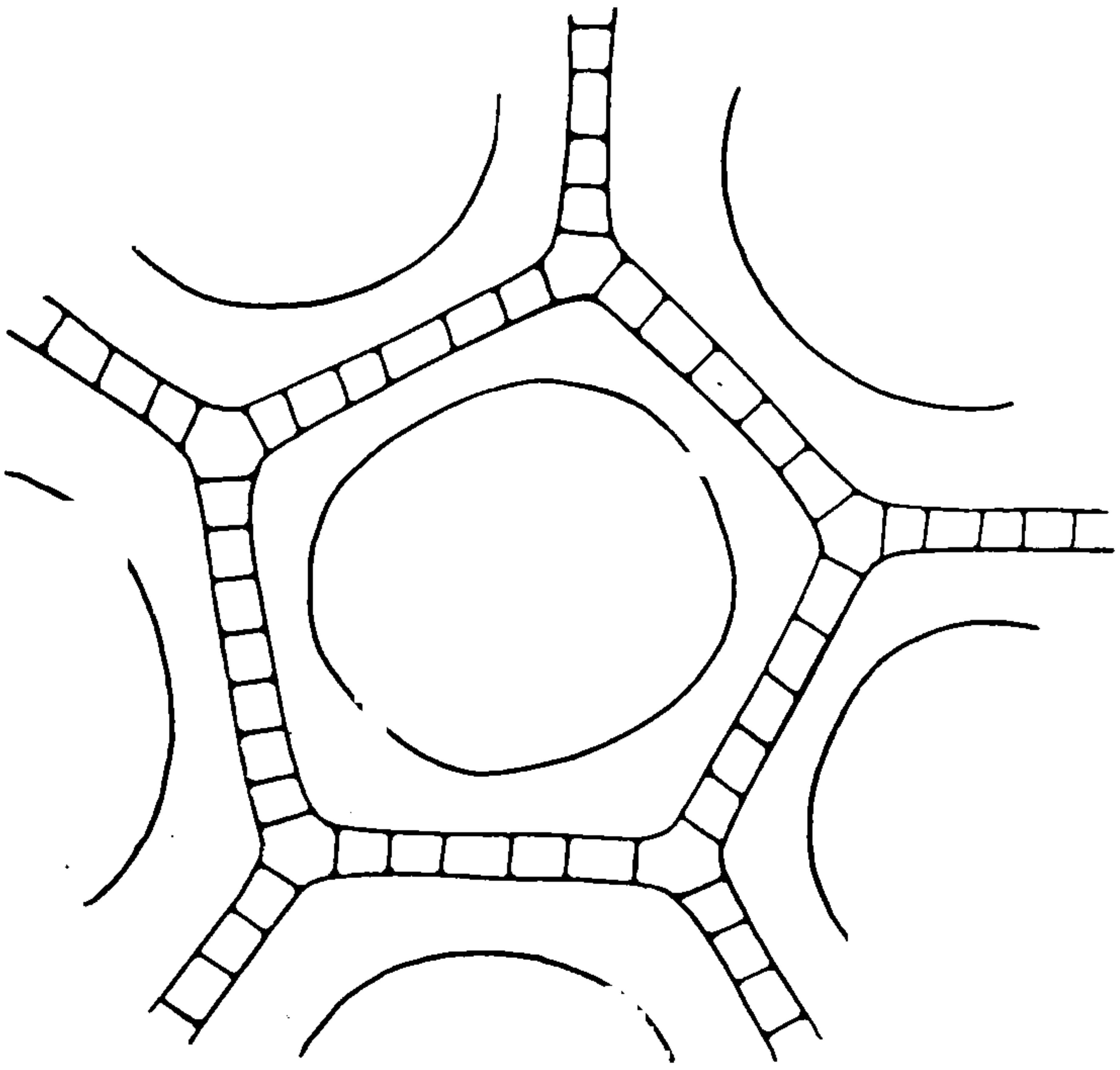

FIG. 21.—Cell bridges, or strands of protoplasm connecting the cells, in the skin of a salamander. (*After Flemming.*)

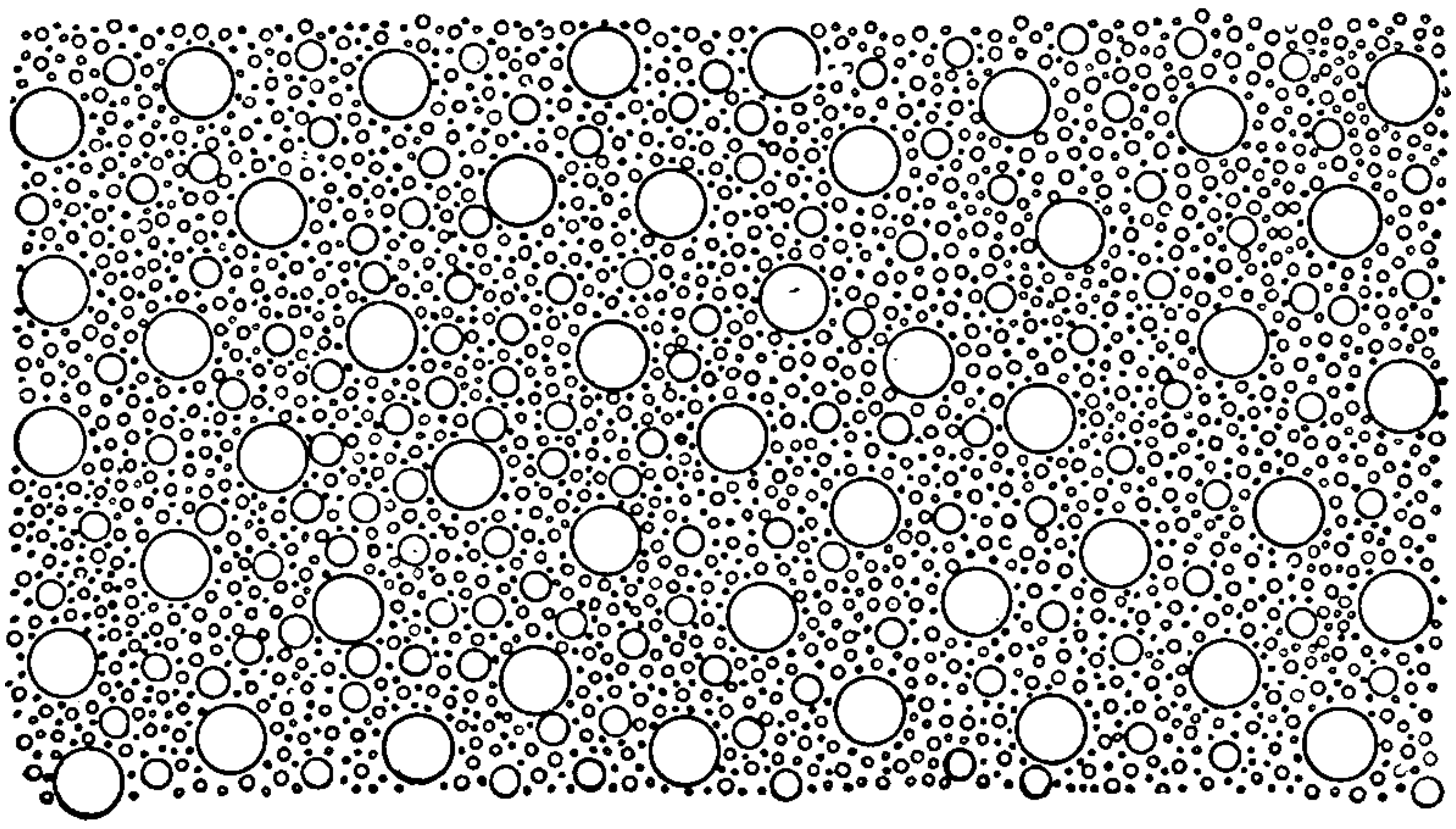

FIG. 22.—Diagram of an emulsion, illustrating the physical structure of a very common kind of protoplasm. The spheres are *alveoli*, the substance between them the *inter-alveolar substance.*

marbles are entirely separate from one another, being held apart by thin films of the syrup. It is not possible to pass from one sphere to another without passing through the supporting liquid; but all parts of the supporting liquid are directly continuous. These relations are shown in Fig. 22. Following the usual terminology, the separate spheres are called *alveoli,* the supporting liquid the *interalveolar substance,* and the structure of protoplasm (or of any emulsion) is said to be alveolar.

Protoplasm has also been likened to a foam, and the term foam is sometimes applied to it; but, strictly speaking, the alveoli of a foam are composed of a gas, not a liquid.

The alveolar and interalveolar materials are probably not homogeneous, nor uniform in all parts of the cell. Although the interalveolar material is continuous, and semi-liquid, diffusion must be slow in it, so that in different parts of the cell it is composed of different substances. In like manner, the alveoli probably differ from each other, and there is no assurance that a single alveolus consists of but one substance. Hence, although one sometimes speaks of the alveolar "substance," and the interalveolar "substance," they are not so in the chemical sense. They are not the same thing always, they have no chemical identity. Protoplasm is always a mixture. Of what this mixture consists and something of its chemical nature is stated below. But it is important even at this stage to state explicitly that protoplasm is living matter, not living *substance* except as the term substance is used to mean matter.

While the alveolar structure thus far described is the usual one in the protoplasm, there are occasionally found appearances that indicate other types of organization. Sometimes, even with the best microscopes, living protoplasm shows no alveoli, but appears to be entirely homogeneous. In some examples of apparently homogeneous protoplasm, the ultramicroscope, by means of oblique illumination against a dark background, has demonstrated a host of minute particles. This is taken to mean that the substance under examination is a colloid, that is, consists of multitudes of particles of greater than molecular size suspended in a liquid. But a colloid is thus in certain respects not very different from the emulsion just described, and some of the properties of a colloidal mixture are also those of an emulsion. Furthermore, from the colloidal nature of protoplasm that does not reveal an alveolar structure one may infer that at least the interalveolar substance of other protoplasm is probably colloidal.

Sometimes, and in some kinds of cells, fibers are also seen in the protoplasm. In certain instances these fibers are undoubtedly distinct structures immersed in the general emulsion. In other cases, as in dividing cells, they may result from a rearrangement of the alveoli. If the alveoli be placed in rows, the liquid between them will have the appearance of a fiber, an arrangement which is only temporary. Appearances must be interpreted with caution, however, for if an actual fiber is stretched through the emulsion the alveoli near it must be arranged in rows. Experiments with artificial emulsions indicate that this rearrangement does occur. As pointed out below, the nucleus also shows undoubted fibers. These observations led, in the early days of cell studies, to what were known as "filar" and "reticular" theories of protoplasmic structure. These threads are probably of importance, although their function is not well understood.

Killed, hardened, and stained protoplasm usually reveals multitudes of granules. These are coagulation products of the interalveolar material in most cases, the cut ends of fibers viewed on end in other cases, and sometimes cell inclusions.

The bulk of protoplasm is, as has been seen, an emulsion. The spheres and the liquid in which they float constitute what the physical chemist calls "phases" of a "system." Certain phenomena characteristic of such systems, particularly a variety of surface phenomena, are thus phenomena of protoplasm. The surface phenomena are intensified by the colloidal nature of the substances which are present even when the protoplasm does not appear to be an emulsion. Much of the activity of protoplasm is due to these surface phenomena.

Finally, it should be made clear that protoplasm is in a liquid or semi-liquid state. Solid particles, except as cell inclusions, are unknown in it. It is plastic. Substances may dissolve and diffuse in it. These physical properties are important in the consideration of the physiology of protoplasm, to be undertaken in the next chapter.

Structure of the Nucleus.—The nucleus differs, in its minute structure, from the rest of the cell. It is enclosed within a thin membrane, called the *nuclear membrane* (Fig. 20, *nm*), which is differentiated out of the general protoplasm. Its composition appears to be not always the same. Within this membrane the bulk of the nucleus consists of a liquid, the *nuclear sap* (*ns*), probably with various substances in solution. Stretched through this fluid is, in the most common cases, a network of fine, anastomosing filaments of a substance named *linin* (*l*). This substance stains only slightly, and is but dimly seen in most prepared cells. However, its position is made evident by another substance which is attached to, or imbedded in, the linin. This substance is called *chromatin* (*ch*), from its high affinity for dyes. In stained cells it is very conspicuous, and gives the nucleus its color in such preparations. The chromatin appears in the form of granules or minute masses called *chromomeres;* sometimes these masses are conspicuously larger at certain places than at others, and are known as *net-knots.*

The network of linin and chromatin is most commonly distributed throughout the nucleus without evident arrangement. Sometimes, however, it has a characteristic configuration. It may consist of a ribbon-like band in spiral form, as in some cells of insects; of a coarse rope-like strand surrounded by an occasional ring, as in the cells of the salivary glands of midges; or it may be so compact as to conceal all appearance of a network, as in many of the Protozoa.

The chromatin is the most important constituent of the nucleus, and indeed of the whole cell. It determines to a large extent, as is shown in subsequent chapters, the nature and activities of the cell. It is not a uniform material, but is differentiated into a number of chemically different substances. These different components are arranged in definite order in the chromomeres distributed along the linin network, and mechanisms operate in the division of cells and in the origin of reproductive cells to maintain this order, or to change it only in limited fashion.

Some nuclei contain, in addition to the sap and the network of linin and chromatin, a *nucleolus* (*nl*). 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 net-knots, which are sometimes unwisely 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 recently it has been regarded as a reserve food supply for the nucleus.

Chemistry and Physics of Protoplasm.—Not less important than the structural features of cells is the chemical composition of their protoplasm. This composition is so complex, however, that it must be described in rather general terms. It appears that the following elements are always present in every cell: carbon, hydrogen, nitrogen, oxygen, phosphorus, sulphur, sodium, potassium, magnesium, calcium, iron, and chlorine. In addition to these, aluminium, silicon, manganese, copper, fluorine, bromine, and iodine are sometimes present. These lists apply to the cell as a whole. When different portions of the cells are considered by themselves, it is possible to reduce the number of elements somewhat. Thus, it is commonly stated that the only elements always found in *protoplasm* (not cell) are carbon, hydrogen, oxygen and nitrogen; but that often phosphorus and sulphur are likewise present. Such statements, however, probably ignore the salts dissolved in the liquids of the protoplasm. It is unlikely that these salts are ever wholly lacking. However, since it is not the presence of certain elements, but the ways in which they are combined, that make protoplasm what it is, it is not important to agree on either the minimum or maximum number of elements that enter into its composition.

Proteins.—The principal constituents of protoplasm are substances of the class called proteins. These substances are abundant in lean meat, eggs, beans, and similar foods. Proteins are compounds of what are known as amino-acids, substances in which the NH_2 group and the COOH radical are always present. Thus the proteins contain the four elements carbon, hydrogen, oxygen and nitrogen, which are often named as the only elements necessarily present in protoplasm. In fact, the occurrence of all of these elements in every amino-acid, and hence in every protein, is the reason for naming these four elements as the minimum content of protoplasm. No chemical analysis of actual protoplasm ever yields these elements alone.

The amino-acids are combined with each other in various ways, with elimination of water, to form proteins. Other substances not in the amino-acid class may also enter into the composition of proteins. Since there are many kinds of amino-acids, and many kinds of other substances which may combine with them, the variety of possible proteins is numerous. Nearly all the proteins have huge molecules, composed of hundreds or even thousands of atoms, and the arrangement of these atoms is always complex. It has been impossible, up to the present time, to determine this arrangement for any but the simplest proteins. Structural formulas, by which the chemist aims to portray, not only the number of each kind of atom in the molecule, but also the position of these atoms relative to each other, are commonly used for inorganic and simple organic compounds. These structural formulas are derived from a knowledge of the behavior of the compound in reactions, and are designed to express that behavior. The absence of structural formulas for most of the proteins means, not that they have no molecular structure, but that the structure has not been discovered. Ignorance of their structural formulas is mute testimony to the complexity of those compounds.

Certain proteins, owing to their importance in vital processes, may be mentioned more particularly. The chromatin of the nucleus, which, as stated above, serves as a sort of cell-governor, is composed of nucleoproteins. These are compounds of nucleic acid and some other substances, and are characterized by an abundance of phosphorus. In view of the importance of chromatin in life processes, some one has said, figuratively, that we are what we are because of the phosphorus that is in us. The composition of the chromatin can be studied in quantity, because it resists peptic digestion; so that, when the cell bodies are dissolved away by the pepsin, the nuclei may be collected as a residue.

The complexity of protoplasm, which is largely a mixture of proteins, is necessarily much greater than that of any one protein. Protoplasm cannot, of course, have a structural formula, since it is not a substance in the chemical sense. But the uncertainty with regard to the nature of any one protein is small when compared with the ignorance which surrounds the nature of the protoplasm in its entirety. It will not occasion surprise, therefore, if in the following chapter the activities of protoplasm must be stated with caution and reserve.

Lipoids.—The term lipoids is applied loosely to a certain group of substances whose chemical and physical properties resemble those of fats. They are often sticky and waxy in consistency. The lecithins are some of the very common lipoids, found in quantity in the yolk of eggs; cholesterin is also usually included in this class of substances; and there are many others.

The structure of the lipoid molecule is simpler than that of the proteins, and in many cases it is well understood. Thus the lecithins are compounds of glycerophosphoric acid, substituted by two fatty acid radicals, with a base called choline. Since there are many kinds of fatty acids with which to make the substitutions mentioned there are also various kinds of lecithins. Although the lecithin molecules are large, containing often a hundred atoms, their empirical formulas (stating merely the number of atoms of each of the elements present) have been definitely determined. Moreover, their chemical relations are so well understood that there is no hesitation in ascribing to them definite structural formulas.

The principal elements in the lipoids are carbon, hydrogen, and oxygen; but phosphorus and nitrogen are often also present. On the whole they tend to lower the surface tension of cells, and therefore for reasons which cannot be explained here collect at the surface, forming part of the cell membrane.

Carbohydrates.—These substances are composed of carbon, hydrogen, and oxygen, and no others. The hydrogen and oxygen atoms are characteristically present in the ratio of 2 to 1, as in water. From this latter fact comes the name carbohydrate, which implies that the substances are hydrates of carbon. Ordinary cane sugar, glucose, the various starches, the cellulose of which cell walls are composed, and others are carbohydrates.

The soluble members of this class, as the sugars and allied substances, may exist in any part of the protoplasm, and may diffuse readily from one part of a cell to another, or from cell to cell. The insoluble carbohydrates are stored as solid particles in the cells, as glycogen (animal starch) in the liver and muscles, or starch grains in plant cells.

Fats.—The fats and oils are compounds of carbon, hydrogen and oxygen, as are the carbohydrates; but oxygen is usually less abundant than in the starches and sugars. Chemically the fats are compounds of glycerol and one or more fatty acids. They are not soluble in water, and are not thus capable of diffusion through the general protoplasm, but are stored. Most cells contain small quantities of fat in the form of droplets, while in the larger animals connective tissue may be heavily laden with it.[1]

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[1] Further characterization of proteins. carbohydrates and fats is given in the next chapter.

Probably even the food, while still undigested, should be regarded as extraneous matter.

Substances produced by the cell, on the contrary, such as starch grains or fat droplets serving as stored food, or the pellicle or wall secreted around the cell by the protoplasm itself, though not living matter, may properly be regarded as constituents of the cell. In defining the scope of the term protoplasm, even these intracellular products must probably be excluded. Anything that enters readily into the physiological activities of an organism may well be regarded as part of its living substance. Although stored starch and fat may affect the life processes, they have to be digested first, and there seems no reason why they should be included under the designation protoplasm when similar foods taken in from other sources are excluded. The cell wall, while possibly affecting life processes in many ways, does so only in a mechanical fashion, which scarcely entitles it to be included in the protoplasm.

Among the chemical substances found in protoplasm, it was once the tendency to regard the proteins as the living substance *par excellence.* The reason for this was doubtless the fact that the proteins form the bulk of protoplasm. But horns do not usually constitute an orchestra, even though they may outweigh and outvibrate all the other instruments. Though the activities of the proteins are of great moment, some of the other substances appear to be of much importance. The lipoids, once regarded as food material, are now known to enter into the constant or frequent functions of cells. As explained above, they tend to collect at the surface of the cells and many have supposed that they help to determine the behavior, particularly the permeability, of the cell membrane. Doubtless also the soluble carbohydrates influence the reactions of the protoplasm, but little that is definite can be said of them.

Whether the salts are part of the protoplasm, or in effect merely a medium in which protoplasm works, is perhaps immaterial to decide. The electrical charges borne by their ions are believed to play a rôle in certain phenomena, and the elements composing them must enter into many of the reactions of the proteins and lipoids.

Further consideration of this question would, however, lead far into the subject of cell physiology, the wide connections of which require treatment in a separate chapter.

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CHAPTER III

PHYSIOLOGY OF CELLS

Physiology treats of the functions or activities of living matter, that is, of the processes that are going on in the living substance, the part that each structure plays in the life of the organism, and the manner in which the organism as a whole lives and responds to the conditions of its environment. The general field of physiology may be variously subdivided, but the scheme followed in this book divides the subject into two parts, namely, physiology of the cell, and physiology of organs. Cell physiology, to which the present discussion is devoted, treats of the processes fundamental to all living matter, and since living matter, or protoplasm, is always arranged in the form of cells which occur singly or in aggregates a discussion of the functional relations of the parts of the cell to each other is included.

Physical and Chemical Processes of Living Matter.—Physiology is coming to depend more and more upon a knowledge of physics and chemistry for the solution of its problems. For this reason some of the topics usually studied in connection with those sciences are introduced here. These topics include diffusion, osmosis, the behavior of isotonic or isosmotic solutions, and the properties of true solutions and colloidal solutions.

Diffusion.—If two or more gases are placed in a container the molecules of each gas rapidly disperse. This dispersion continues until each gas reaches the limits of the container and becomes evenly distributed within the enclosed space. This action takes place without regard to the force of gravitation. The phenomenon of dispersion of the molecules of one substance among those of another substance is called *diffusion.*

If a crystal of common salt is dropped into water, minute particles of the salt separate from the crystal and, either as molecules or as ions into which molecules may divide, disperse until they are evenly distributed throughout the water. This also is diffusion. If a lighter liquid that is miscible with a heavier liquid is poured over the heavier liquid, care being taken not to mix them during pouring, particles of the heavier liquid notwithstanding its greater weight will rise into the lighter until there will be a homogeneous mixture of the particles of the two liquids. This process again is diffusion. The rate of diffusion of gases into each other is rapid, but that of a solid into a liquid or of a liquid into a liquid is much slower. Even particles of some solids which have been brought into contact with one another may diffuse to an appreciable extent provided the surfaces of the solids have been long enough in contact. The mixtures resulting from the diffusion of solids into liquids or solids, or of liquids into liquids, are known as *solutions*. When a solid is dissolved in a liquid, the liquid is called the *solvent*, and the solid the *solute*.

Osmosis.—As was said in the discussion of diffusion, miscible liquids diffuse into each other so that a homogeneous mixture is finally formed. If a semi-permeable membrane, by which is meant one that is permeable to solvents but more or less impermeable to dissolved substances, be interposed between water and a substance dissolved in water, it may be noted that the water passes through the membrane while the passage of the substance in solution occurs less readily, or not at all.[1] Animal membranes, such as the tissue of the urinary bladder, often do not even approximate the characteristics of an ideal semi-permeable membrane, yet they usually resist the passage of certain substances through them. If a piece of bladder is stretched over the open end of a funnel containing sugar solution, and the funnel is inverted in a dish of pure water (Fig. 23) the water will pass through the membrane causing the solution to rise in the tube, and some of the sugar may pass through to the water of the dish. The rise of solution in the tube is a measure of a pressure existing in the sugar solution. This pressure in the solution is known as *osmotic pressure*, and is due to the presence of molecules of sugar dispersed through the water.

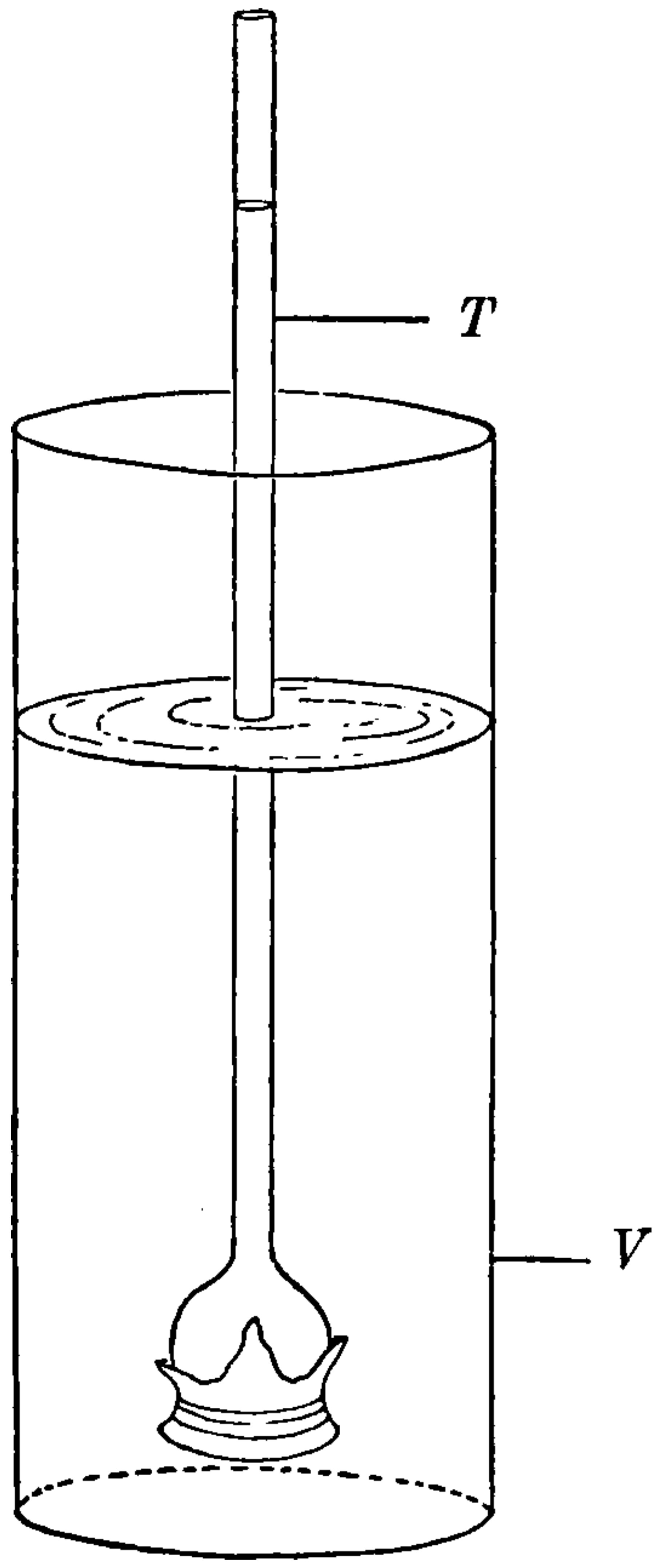

FIG. 23.—Diagram of apparatus used to illustrate osmosis. *T*, inverted thistle tube covered with animal membrane and containing a solution of sugar in water; *V*, vessel of water

Osmotic pressure is in fundamental respects not unlike gas pressure. As stated above, when a gas is placed in a closed chamber the molecules of the gas quickly disperse to fill the whole chamber. When dispersion is checked by the walls of the container, pressure is exerted upon those walls and throughout the gas. The nature of the mutual repulsion of the molecules of a gas need not be discussed, but the resulting expansion of the gas, and its pressure against any object preventing expansion

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[1] Ideally a semi-permeable membrane does not permit the passage of dissolved substances at all. Since, however, an ideal semi-permeable membrane probably does not exist, the term is loosely applied to membranes which greatly retard the passage of substances in solution and thus approximate the requirements of the definition.

and against other portions of the gas itself are matters of common observation. In like manner, when a substance is dissolved in water, the molecules or ions of the dissolved substance spread through the liquid until the limits of the liquid are reached. The liquid in this case sets the limit of dispersion of the diffusing substance. As in the case of the gas, pressure is exerted by the molecules and ions of the solute at all points within the solution. This pressure is what is called osmotic pressure. At a given temperature, the intensity of osmotic pressure depends upon the number of molecules and ions present per volume of the solution. Diluting a solution thus decreases the osmotic pressure. All the dissolved particles, regardless of size, whether molecules or ions, exert the same osmotic pressure, so that a substance which ionizes (that is, one whose molecules in solution divide into ions) to a large extent at a given concentration exerts a greater pressure than does another substance which ionizes to a lesser extent at the same concentration.

In the sugar solution referred to above and in Fig. 23, the molecules of the sugar exert a certain osmotic pressure. Were they free to pass into water surrounding the funnel they would do so, and the concentration (and hence the osmotic pressure) would be everywhere reduced; but the bladder, being approximately a semi-permeable membrane, largely prevents the passage of the sugar. However, water passes into the sugar solution, and dilution of the solution with the consequent lowering of its osmotic pressure results just as if the sugar molecules had passed out of the funnel. The passage of water and other substances through membranes is known as *osmosis*. Osmosis occurs in all living cells, and is an important feature of life processes. In higher animals, as is pointed out in a later chapter, it has much to do with the absorption of nutrient materials, with respiration, and with the elimination of wastes in excretion.

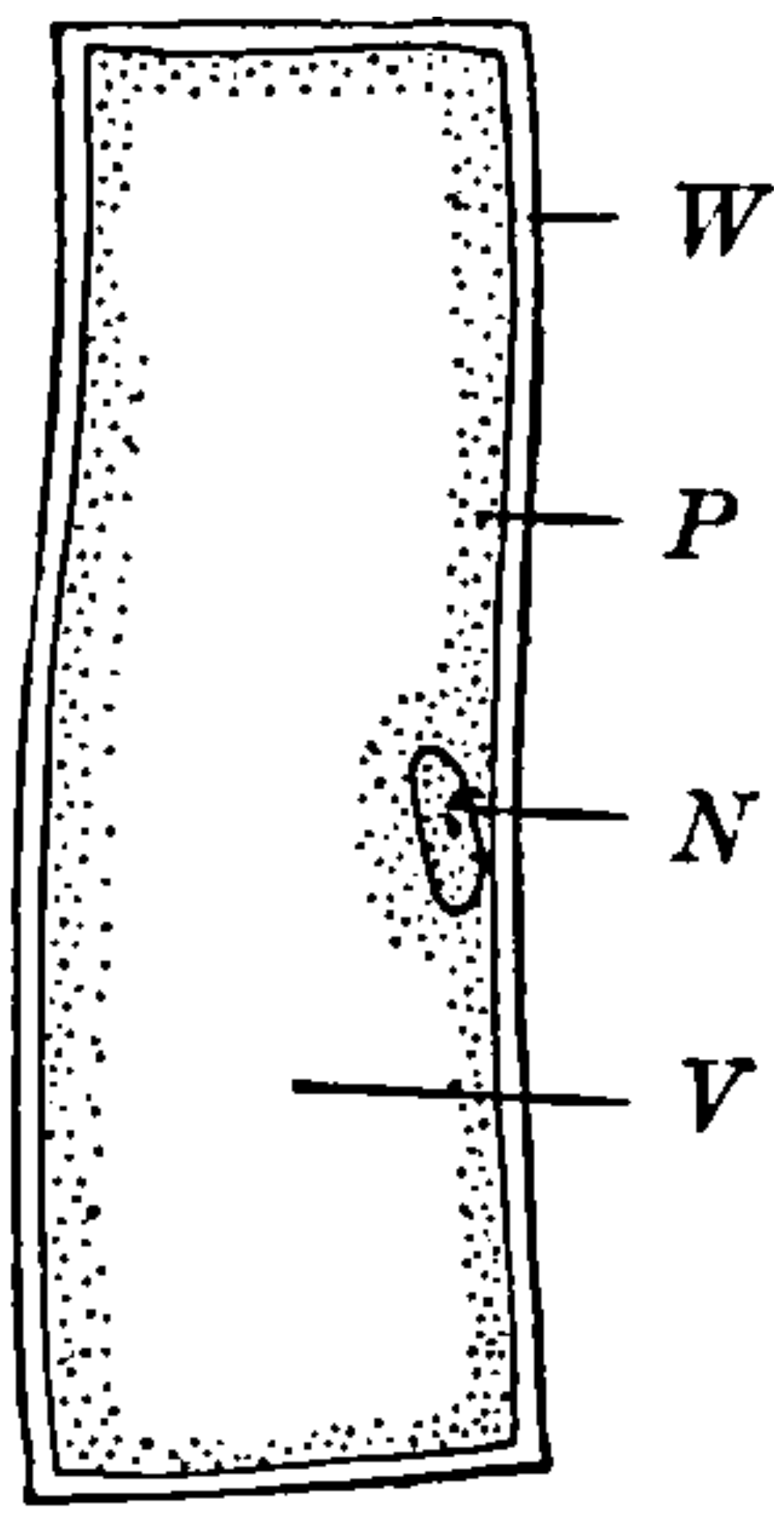


FIG. 24.—Diagram showing a plant cell as a bag of protoplasm encased in a cell wall and enclosing a solution in a vacuole *N*, nucleus; *P*, protoplasm; *V*, vacuole; *W*, wall.

Isotonic or Isosmotic Solutions.—Since in a plant cell the protoplasm occurs in the form of a bag encased in a cell wall and enclosing a solution, as shown diagrammatically in Fig. 24, such a cell may be used to compare the osmotic pressures of two solutions. The cell wall is permeable, but the protoplasm acts like a semi-permeable membrane. The effect of the solution on the cell can be observed under the microscope. If the cell contents shrink it is known that water has been withdrawn from the cell. If such cells be immersed successively in a series of solutions of very slightly different osmotic pressures, some of which cause shrinkage of the cells and others do not, the solution with the greatest pressure which does not cause shrinkage exhibits the same osmotic pressure as the cell contents, and is said to be *isotonic* or *isosmotic* with the cell contents. If a second solution is made isosmotic with the contents of the cell, it is also isotonic or isosmotic with the first solution.

Theories in explanation of osmosis, of the function of the membrane, and the retarding effect of the membrane upon the passage of substances in solution are numerous. None are wholly satisfactory and much needs yet to be discovered concerning various phases of osmosis.

True Solutions and the Colloidal State.—Substances placed in water or other solvents behave very differently from one another. In some substances the molecules separate from each other, and in many of these substances some of the molecules dissociate into ions. Such mixtures are known as *true solutions*. In a true solution the largest particles of the dissolved substance are single molecules. Most of the common salts, as sodium chloride, potassium nitrate, or magnesium sulphate form true solutions in water. Sometimes salts in solution form chemical compounds with water, but in such cases the molecules, although larger, exist in true solution.

Other substances in water do not separate into their single molecules, but into particles each of which is a physical aggregate of molecules. White of egg, gelatine, agar-agar and gum arabic are substances which, in water, exist in such molar aggregations. While these mixtures of a liquid and particles of greater than molecular size are sometimes called solutions, they are not true solutions. The "dissolved" substance is more properly said to be in a *colloidal condition*. Some substances may exist either in a true solution or in the colloidal state, depending in part on the solvent employed. Thus gamboge, a resinous substance, is truly dissolved by alcohol, but enters the colloidal condition when the alcoholic solution is poured into water.

True solutions exhibit an osmotic pressure whereas substances in a colloidal state show only a very low osmotic pressure or none at all. Colloidal systems involving water as a "solvent" also differ from true solutions in their affinity for water, in their electrical conductivity, and in a variety of "surface phenomena." The latter phenomena depend on the great amount of surface between the aggregations of molecules of the contained substance and the liquid in which they are held, but can not be further explained here.

Application to Living Organisms.—Protoplasm, as pointed out in the preceding chapter, is a colloidal system, and has the properties belonging to such a system. Many of the fundamental characteristics of living matter are due to the colloidal nature of the protoplasm, though only a few of them can be referred to in this book. Absorption and secretion, for example, as described in Chapter VII, are largely dependent upon the colloidal nature of the protoplasm. Colloidal systems may serve as semi-permeable membranes (imperfect ones, of course), and the protoplasm of cells shares in this general characteristic. Cell membranes act differently, in this regard, from the deeper protoplasm of the cell. An animal or plant tissue being composed of cells is thus made up of a multitude of minute semi-permeable membranes which, functioning alike, serve in the aggregate as a large membrane. Through the membranes of the body osmotic interchange of substances between solutions of various sorts is continually taking place.

Semi-permeable membranes composed of lifeless material (dead animal tissues or collodion films, for example) must always act in the same manner under a given set of external conditions. Living cell membranes, however, do not always act thus, nor do the cell membranes of various sorts of cells act alike. A membrane of living cells at one time permits the passage of certain substances and prevents the passage of others which would pass through dead membranes without difficulty. At other times some of the substances which formerly were denied passage are permitted to pass. It is evident that the cell membrane is capable of selecting (not consciously, of course) what substances shall pass through and what shall be denied passage, and furthermore that this selection may be varied. What is the cause of this variation in selection? The usual answer is that there is a change in permeability. The change in permeability is due to some change in the colloidal matter of the protoplasm. In some cases many have thought that some of the lipoids are removed from the surface layer and this induces greater permeability. The character of these changes and their causes are still subjects for investigation. It is known that in living protoplasm many of the colloids may be changed repeatedly from a liquid to a semi-solid condition and back to liquid again. This reversibility of coagulation of protoplasmic colloids may be of great importance in the chemical processes of the cell.

Metabolism.—The protoplasm of the cell carries on all the general processes of the living body. Within the cell 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 assimilated, built up into the living substance 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 one term *metabolism.*

Metabolism may be defined as the sum of all the chemical processes carried on within the organism. Perhaps also the contributory physical phenomena should be included in the definition. From the brief account of the activities of protoplasm outlined above it is obvious that metabolism may be divided into 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 properly includes all processes of synthesis by which substances are transformed into reserves of food. Catabolism, on the contrary, 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 continuous processes and both are of great importance. As long as anabolic processes are in excess of catabolic processes growth continues; but when catabolic processes are in excess the reverse of growth takes place. Thus in progressive emaciation due to starvation or under-nutrition catabolism is in excess of anabolism, reserves of food (carbohydrates and fats) are being consumed, and body weight decreases. It is a relatively easy matter to define the two phases of metabolism and to use the terms anabolism and catabolism in a general way, but it is a more difficult matter to apply the terms to specific processes. Some of the aspects of metabolism barely touched upon in the foregoing discussion are considered further.

Intake and Preparation of Substances.—Since the material intake of plants and that of all but a few simple animals is very different, and since animals are wholly dependent directly or indirectly upon plants as a source of food, the intake of substances in plants is considered first, although it is not desirable to separate from it entirely the subject of animal foods.

Intake in Plants.—Something in regard to the materials which plants take in may be learned by finding out the elements which compose their bodies, and the materials which they give off. Analysis of the dried substance of green plants shows that they always contain carbon, hydrogen, oxygen, and nitrogen. From the ash or burned bodies of plants sulphur, phosphorus, potassium, magnesium, calcium, iron, sodium, chlorine, and silicon are always recovered. Iodine, bromine, fluorine and many other elements may be found in the ash at times. All the elements used by the plant must be secured from the air, from water, and from the soil solution or the solution (for example, sea water) in which the whole plant is immersed. By experiments in which higher green plants are grown in water cultures containing known substances in solution it has been determined that these plants have a certain minimum chemical requirement and that if any of the required substances are not available normal development is impossible. These necessary elements are carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, calcium, magnesium, and iron. Except oxygen, these elements are never

blue is ineffective. The production of carbohydrates in this manner is called *photosynthesis*, literally, construction by means of light.

The first substance that can be readily identified in the process of photosynthesis is glucose, $C_6H_{12}O_6$. Various suggestions have been offered for the intermediate steps which occur in the formation of glucose. One of these is that the carbon dioxide and water unite to form carbonic acid which is in some way reduced, perhaps to formic acid, and the formic acid is then reduced to formaldehyde. In this process oxygen is set free. The molecules of formaldehyde then unite to form glucose. The formulas for these reactions may be written thus:

$$CO_2 + H_2O \rightleftarrows OH.COOH \text{ (carbonic acid)} \quad (1)$$

$$OH.COOH - O_2 = H.CHO \text{ (formaldehyde)} \quad (2)$$

By a rearrangement 6(H.CHO) becomes $C_6H_{12}O_6$ or glucose. By the condensation of n molecules of glucose and the elimination of $n - 1$ molecules of water, the glucose is changed into starch. Thus, approximately $n\ (C_6H_{12}O_6) - (n - 1)\ (H_2O) = (C_6H_{10}O_5)\ n$, the formula for starch. Glucose may be changed into other sugars, especially maltose ($C_{12}H_{22}O_{11}$), and the latter may be changed into starch. The sugars are soluble and in some plants may not be transformed into starch. Starch is insoluble and is temporarily stored in the form of starch grains in the chloroplasts. It is readily reconverted into a soluble carbohydrate (glucose) and in this form may be transported to other parts of the plant where again it may be converted into starch and stored in leucoplasts, or the glucose may be converted into cellulose, a form of carbohydrate used in cell walls.

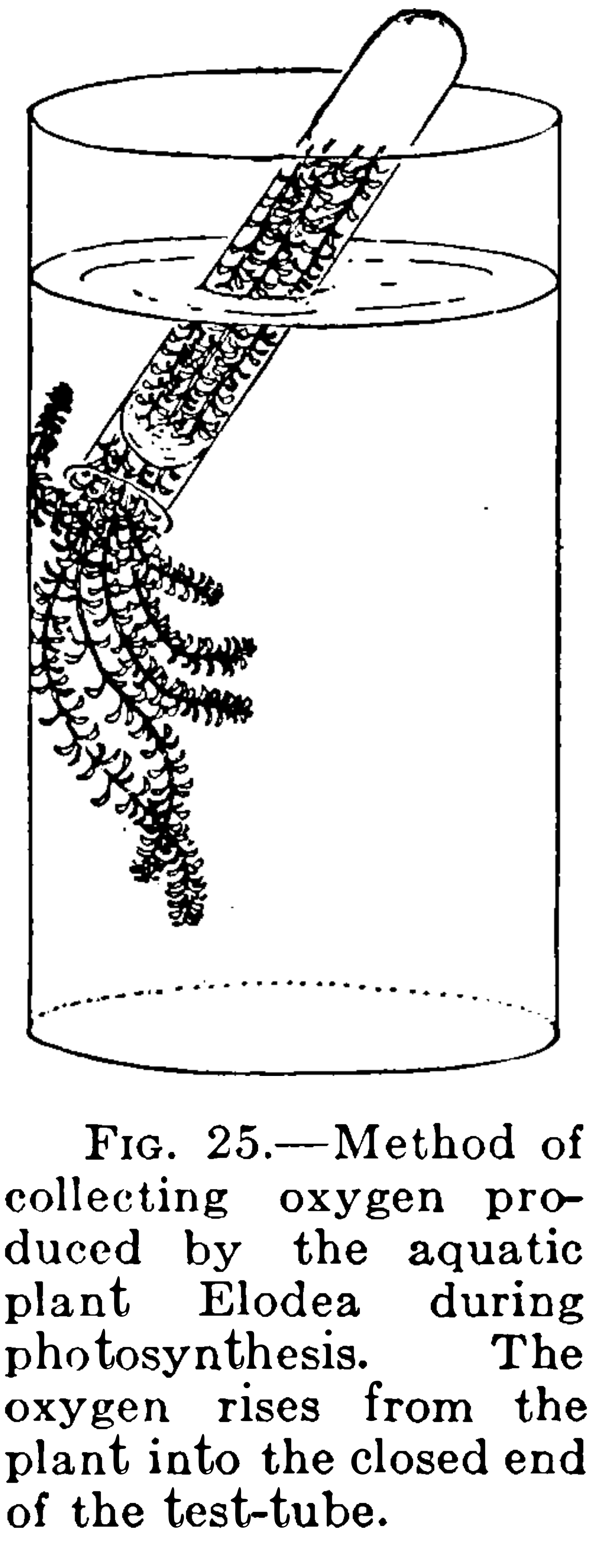
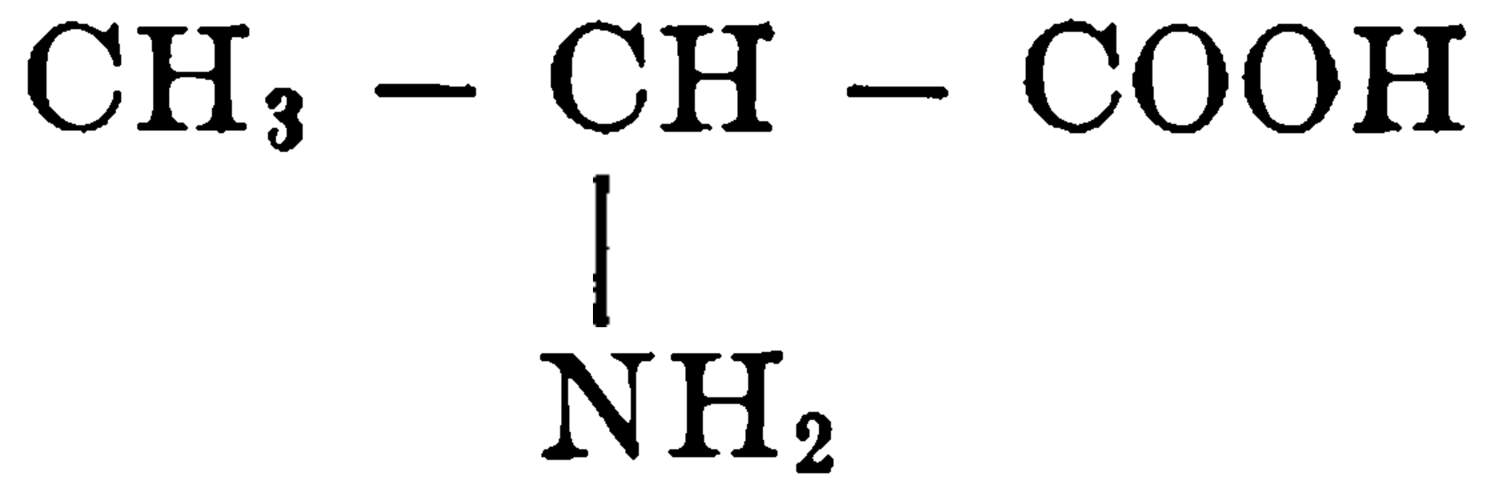


FIG. 25.—Method of collecting oxygen produced by the aquatic plant Elodea during photosynthesis. The oxygen rises from the plant into the closed end of the test-tube.

The oxygen released in the formation of carbohydrates, as in equation (2) above, may be readily recovered and tested, particularly if water plants are used for the experiment. 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 then the tube is inverted (Fig. 25). When the plants are placed in sunlight bubbles of gas escape from their cut ends and collect in the tube. The usual tests show the gas to be oxygen.

Protein Synthesis.—Proteins are formed by the linkage of molecules of various substances known as *amino-acids*. These acids all possess one or more *carboxyl* groups of atoms (COOH) which give the acids their acidic properties, and one or more *amino* radicals (NH_2) which give them basic properties. A simple example of an amino-acid is alanine, whose structural formula is



$$CH_3 - \underset{\displaystyle NH_2}{\underset{|}{CH}} - COOH$$

About twenty different amino-acids have been derived from proteins, all capable, because of their NH_2 and COOH groups, of acting either as bases or as acids or as both at once. The amino-acids readily combine with one another, the amino radical of one and the carboxyl group of another serving as the point of combination, thus:

$$-CO(OH\ \ H)NH-$$

A molecule of water (H_2O) is lost, and the bonds which formerly held the $-OH$ and $H-$ of the resultant water to their respective molecules of acid now hold these two molecules together, the point of union of the two molecules being represented as

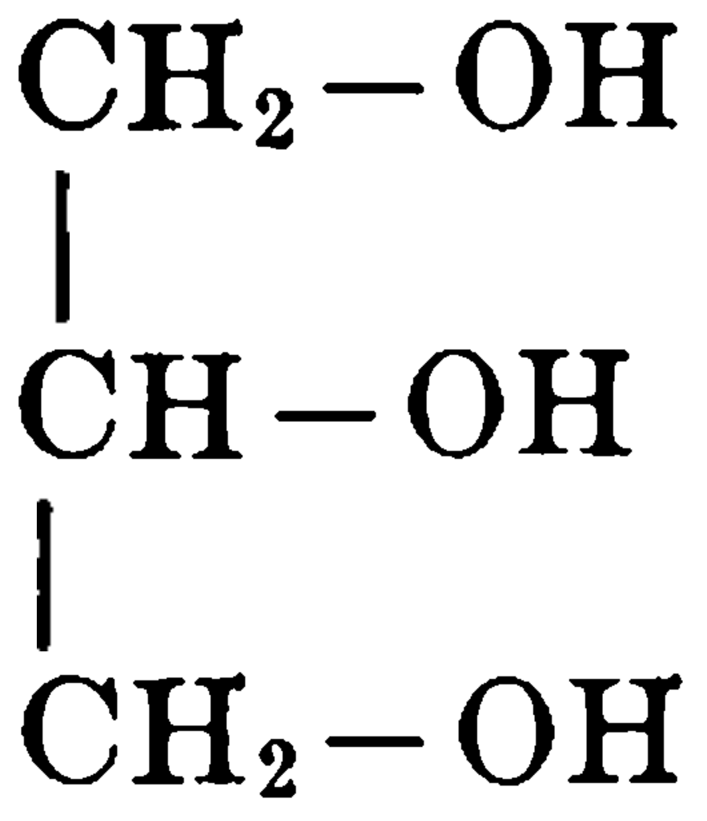
$$-CO-NH-$$

The two molecules thus joined may be of the same amino-acid, or of two different acids. Thus, from twenty amino-acids, a considerable number of new substances could be produced, even if the acids were combined only two at a time. However, the variety of combinations is not thus limited, for several or many molecules may be joined, and each molecule may be of a different acid, or the various acids may be represented in different proportions or the arrangement may vary. Furthermore, other substances than amino-acids may be joined to the combined product at various points, so that the variety of substances that can conceivably be created wholly or chiefly of amino-acids is almost unlimited. Add to this the fact that the arrangement of the molecules of the acids in the combined product may be different in different cases, owing to the fact that unions may often be made at any one of several points in the molecule, and the diversity of the possible aggregations is greatly multiplied. Other circumstances could be named which would lend still further emphasis to the fact that from a comparatively small number of amino-acids an enormous number of compounds may be produced, but the diversity of possible amino compounds has already been sufficiently indicated.

From such combinations of amino-acids and other substances all the proteins of plants and animals are constructed. This statement is not purely hypothesis, for the construction of *polypeptides*, as the compound substances described above are called, out of amino-acids, and the careful decomposition of proteins, have been carried to a point at which they meet. The brilliant work of Fischer and others in the synthesis of polypeptides has resulted in substances which are *identical* with substances that may be derived by the hydrolysis of natural proteins. Whether synthesis may ever be carried so far as to produce substances identical with the natural proteins themselves cannot be foretold; but already the synthetic work has yielded a large portion of the secret of protein structure. The importance of this revelation will become apparent in a later chapter when the digestion of the proteins is discussed. For in the process of digestion, by a process the reverse of Fischer's synthesis, that is, by hydrolysis or the *addition* of water, the protein molecules are dissociated into their amino-acid components.

The sources of the amino-acids from which the proteins of organisms may be constructed remain to be mentioned. Animals are almost wholly dependent upon other animals or upon plants, whose proteins they digest (hydrolyze) into amino-acids. Plants, on the contrary, are capable of synthesizing amino-acids from soluble carbohydrates and nitrates. The substitution of amino radicals (NH_2) for OH radicals of the carbohydrate is suggested as a step in the process. Fatty acids derived from fats may also be employed for similar amino substitutions.

Fat Formation.—Fats are compounds of a basic substance *glycerol* (glycerine) and various of the higher fatty acids. Glycerol has the formula

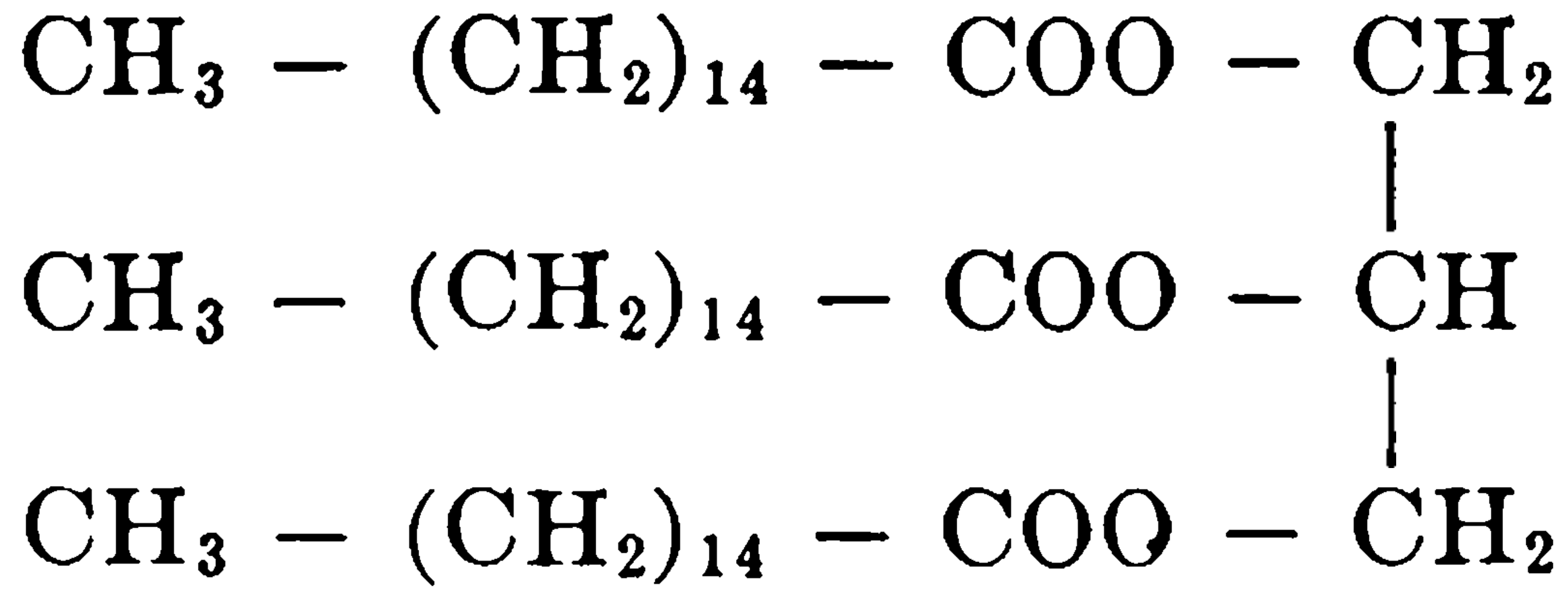


$$\begin{array}{l} CH_2-OH \\ | \\ CH-OH \\ | \\ CH_2-OH \end{array}$$

and all of the OH radicals are readily replaceable by fatty acids. The principal fatty acids in animals are palmitic, stearic, and oleic. The formula of palmitic acid, for example, ignoring the structure in part, is

$$CH_3 - (CH_2)_{14} - COOH$$

The H of the carboxyl group at the right is readily replaceable by the glycerol. If all three of the OH radicals of glycerol are substituted by molecules of palmitic acid, three molecules of water are lost and a substance called tripalmitin is produced, with the formula



$$\begin{array}{l} CH_3 - (CH_2)_{14} - COO - CH_2 \\ \qquad\qquad\qquad\qquad\qquad\quad | \\ CH_3 - (CH_2)_{14} - COO - CH \\ \qquad\qquad\qquad\qquad\qquad\quad | \\ CH_3 - (CH_2)_{14} - COO - CH_2 \end{array}$$

The substitutions need not all be made with the same acid, but may involve two or three different acids. Thus a variety of fats is possible

The formulas of the acid and fat just given are not in themselves important in this connection, but that fats are composed of glycerol and three molecules of fatty acid, and the method of combining these molecules, should be remembered.

The glycerol component of fats is readily produced in the organism from the carbohydrate glucose. The fatty acids are also undoubtedly derived, directly or indirectly, from carbohydrates. The details of neither process need be considered here. In animals both glycerol and fatty acids may be derived from fatty food, since in digestion as pointed out in Chapter VII the process of synthesis above described is reversed, and by hydrolysis (addition of water) fats are broken up into their components.

Foods for Plants.—Carbohydrates, fats, and proteins constitute the foods of plants. For purposes of building up protoplasm plants cannot make use of carbon dioxide, oxygen, water, and inorganic salts until these have first been combined within the plant into organic compounds. These inorganic substances which the plant takes in and uses as raw materials in the process of food manufacture may be called nutrient substances *but not foods.* The term *foods* must be reserved for the organic substances which the plant uses in building up protoplasm. Ordinarily the plant manufactures much more food than it can use and reserves are accumulated. These reserves of food are stored in fleshy roots, stems, leaves and seeds where they may be of use to the plant during the next growing season, or serve as nourishment for the young plant. Plants of the lower orders store very little food.

Foods for Animals.—The reserves of foods stored away by plants are of the utmost importance to animals since most of the latter do not have the ability to manufacture their food from the raw materials. Animals can use only the organic foods stored away by plants. This dependence on plant reserves in the case of herbivorous animals is obvious. It is not less real in exclusively flesh-eating animals which are dependent, through plant-eating animals, upon the activities of plants.

In addition to the carbohydrates, proteins or albuminous substances of various sorts resembling proteins, and oils or fats, all of which are secured directly or indirectly from plants, animals get from plants certain salts necessary to the well-being of the animal body. They also secure from plants certain substances of unknown chemical nature which are called *vitamines.* These substances are comparatively abundant in fresh vegetables, particularly leaf vegetables. They are less abundant in the cereals and are lacking in the vegetable oils. That these vitamines are of importance in the diet of animals is shown by experimental feeding. Animals which get foods deficient in vitamines suffer from malnutrition although they may get food of sufficient calorific value. If the diet of such experimental animals be changed so as to include sufficient vitamines the animals may recover. Flesh-eating animals get vitamines from the flesh of their prey and young mammals get vitamines from the milk with which they are nourished.

Further Characteristics of Carbohydrates, Fats, and Proteins.—An examination of the chemical formulas for carbohydrates stated in the paragraph on photosynthesis shows, as indicated also in part in the preceding chapter, that carbohydrates are composed of carbon, oxygen and hydrogen; and the hydrogen and oxygen are generally in the ratio of 2 to 1, as in water. Sugars as they occur in fruits and vegetables and in manufactured form, and starches as they occur in flour and in some fleshy roots, stems and fruits are good examples of carbohydrates. Carbohydrates burn (oxidize) readily with the release of considerable heat, and the liberation of carbon dioxide and water.

Fats are composed of carbon, hydrogen, and oxygen but as indicated above the ratio of oxygen to hydrogen is very low and the proportion of carbon is high. The character of a fat is determined by the fatty acid or acids entering into the composition. Fats are greasy and they leave a grease-spot on paper which does not evaporate. Good examples of fats are butter, lard and tallow derived from animal sources, and oils, such as olive, castor and cocoanut oils derived from plants. Fats combine readily with oxygen when burned and yield much more heat than do the carbohydrates. Thus a gram of starch yields about 4.19 large calories, while a gram of fat yields about 9.3 large calories. The products of the combustion of fats are carbon dioxide and water.

Proteins are always composed of carbon, oxygen, hydrogen, and nitrogen, and sometimes one or more other elements as phosphorus, iron, magnesium, sulphur, etc. The protein molecule is very complex. For this reason the analysis of proteins is very difficult and there may be considerable disagreement as to the empirical formula of the same protein. Two formulas for hemoglobin, a protein derived from the blood corpuscles, are $C_{712}H_{1130}N_{214}O_{245}FeS_2$, and $C_{600}H_{960}N_{154}O_{179}FeS_2$. Needless to say that the structural formulas cannot be given. Proteins coagulate upon heating or upon the addition of acids, alcohol or salts to form a firm clot which often is not soluble in water. The coagulum produced by neutral salts is soluble. Proteins have a large molecular weight, slow diffusibility, and high resistance to the passage of an electric current. Proteins burn with the release of considerable heat, and incomplete burning is accompanied by the production of a characteristic odor. The products of combustion are carbon dioxide, water, and certain nitrogenous compounds. White of egg, lean meat, and gluten derived from wheat are good examples of proteins. Seeds of leguminous plants and nuts are rich in proteins.

Digestion.—Living matter, be it plant or animal, cannot make use of foods until these foods have been rendered soluble and diffusible through protoplasm. In the plant cell starch, before it can be utilized in building up protoplasm, must first be brought into solution. Proteins and fats cannot be used while they remain proteins and fats for neither can diffuse through the colloids of the cell. In the animal cell the same state of affairs exists. Foods are rendered soluble and diffusible during the process of *digestion*. According to an accepted definition digestion is the process of bringing foods into solution and into a state of diffusibility by means of a chemical agent. The agents employed by plant and animal cells during the process of digestion are solutions elaborated by the protoplasm. The power of producing digestive solutions is possessed by all living cells. Digestive solutions are either alkaline or acid in reaction, and in addition to the acid or alkali present in the solution there are always one or more very important substances to which has been given the name of *enzyme*.

Enzymes.—Enzymes are substances whose exact chemical nature is yet unknown. Extracted enzymes may respond to protein tests, but this seems to be due to proteins associated with the enzymes, from which the latter have only occasionally been separated. Enzymes act like certain substances which have the property of hastening chemical reactions. These accelerating substances are called *catalyzers* or *catalysts* or *catalytic agents*, and the effect which they have in the reaction is called *catalysis*. Among inorganic substances which act as catalyzers may be mentioned finely divided platinum. So far as can be determined catalyzers hasten reactions by entering into the formation of intermediate substances from which they are promptly released. They are thus present undiminished at the end of the reaction. Enzymes also act somewhat in this fashion. Unlike the inorganic catalyzers, enzymes are affected by extremes of heat or cold. Most of them operate best at a temperature of 30–45°C. but are destroyed by temperatures of 60–75°C. Certain of them are rendered active by small quantities of free acid, others by alkali. The ions of certain metals inhibit their action. Enzymes may be extracted from plant or animal bodies, precipitated from their solutions, purified, and again brought into solution without loss of activity. A given enzyme may take part in only a single kind of reaction. This reaction, however, is reversible, that is, the enzyme may assist in the splitting of a substance into two others or it may serve as the agent for causing the combination of the two simple substances into the one. The limitation of an enzyme to a certain specific action is visualized by Fischer's famous "lock and key" hypothesis which assumes that the chemical configuration of the enzyme corresponds very closely to that of the substance on which it acts, and that the two are thus fitted to each other as a key is fitted to a lock. From the fact that many enzymes may take part in but one kind of reaction it may be inferred that to accomplish the multitude of chemical reactions that are going on continuously or periodically in the animal or plant a number of enzymes must be present in every living organism. A large number of enzymes have already been isolated and determined from plants and animals, and it is probable that many more will be found. An enzyme is named according to the substance which it acts upon or after the most important product of its action.

Important Enzymes and Their Action.—In both plants and animals there are three classes of digestive enzymes: the *amylolytic*, or carbohydrate-splitting; the *lipolytic* or fat-splitting; and the *proteolytic*, or protein-splitting enzymes. In plants the important amylolytic enzymes are *diastase* which acts on starch producing maltose, *maltase* which splits maltose into two molecules of glucose, and *invertase* which hydrolyzes cane sugar into glucose and fructose. There are also other enzymes capable of acting on other forms of carbohydrates. In animals *ptyalin*, produced by the salivary glands and acting on starch, and *amylopsin* which is contained in the pancreatic juice and changes starch to simpler carbohydrates are the most important carbohydrate-splitting enzymes. The lipolytic enzymes of both plants and animals break down the fats into glycerol and fatty acids both of which are diffusible. Soluble soaps are formed by combination of the fatty acids with bases, and these and perhaps some unaltered fats are absorbed. The proteolytic enzymes whether in plants or animals may be classed as *peptic* enzymes if they require the presence of acids to make them chemically active, or *tryptic* enzymes if they require an alkaline medium. The most important enzyme of the first group is *pepsin* which is produced by glands of the stomach in animals. This enzyme splits proteins into peptones and polypeptides. These substances are not diffusible and are further broken down by *trypsin*, the most important of the second group of proteolytic enzymes. Trypsin completes the splitting of the proteins into amino-acids and other compounds which are readily diffusible.

Digestion in Cells.—In unicellular animals digestion of necessity occurs within the cell. Food having been ingested comes to lie in vacuoles. Along with the food there is usually engulfed a small quantity of water. Into this water digestive solutions of acid or alkaline reaction are secreted by the surrounding protoplasm. These solutions contain enzymes, the nature of which may be inferred from the reaction of the solution. Obviously it would be quite impossible to secure a sufficient quantity of the digestive solutions of these minute animals to permit of analysis in the ordinary manner, but by making use of very dilute watery solutions of the dye *neutral red*, it is possible to determine the reaction of the digestive solutions in the living animals. The dye penetrates without killing the protoplasm, and the color changes may be observed in the vacuoles of the living animal by means of the microscope. Neutral red does not directly distinguish the enzyme which is present. Since, however, it is known that enzymes of the pepsin class operate

with the process of getting air into the body and out of it again. The latter process is only incidental to the real respiration which takes place in the cells.

Respiration results in the production of carbon dioxide and water or of certain other intermediate compounds, and in the release of energy, most commonly in the form of heat and motion.

In the simple animals and plants dissolved oxygen passes by osmosis 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 where it is used in oxidative processes. In many small aquatic multicellular animals and plants with few layers of cells the dissolved oxygen may readily diffuse through the intervening cells to those which lie deeper. The distribution of dissolved oxygen to the various cells in higher plants and animals is discussed in a later chapter.

Respiration and Photosynthesis.—The absorption of carbon dioxide and release of oxygen by green plants in sunlight are sometimes popularly but erroneously attributed to respiration, and have led to the mistaken notion that respiration in plants is the reverse of the corresponding process in animals. The behavior of the gases in green plants just referred to is, as pointed out above, due to photosynthesis. A comparison of the processes of respiration and photosynthesis shows that they are entirely distinct processes. Respiration is the same in both plants and animals. It is not a synthetic process but a destructive process yielding for the most part carbon dioxide and water as the end products. Photosynthesis is a constructive process in which carbon dioxide and water, as raw materials, are elaborated into carbohydrates by the chloroplasts which employ the energy of light for this transformation. By this process energy is stored. A by-product of photosynthesis is oxygen. In respiration, contrariwise, oxygen is consumed in the oxidation of elaborated foods, energy is released and the by-products are carbon dioxide and water. From this incomplete comparison it may be seen that these two processes are distinctly opposed to each other. In plants in the sunlight the two processes go on simultaneously but when photosynthesis is proceeding energetically the process of respiration is somewhat masked. In the dark photosynthesis stops while respiration continues.

Excretion.—The end products of the oxidation of carbohydrates and fats in respiration are carbon dioxide and water. When a protein is combined with oxygen there are formed some nitrogen compounds in addition to carbon dioxide and water. These nitrogen compounds differ according to the completeness of the oxidation but one of the principal ones is urea. The process of getting these substances out of the protoplasm is called *excretion* and the nitrogenous compounds and the carbon dioxide are waste materials or *excretions*. These waste substances pass through the cell membranes to the exterior, or in some of the Protozoa they are gathered up by the contractile vacuoles and voided through the outlets of these organs.

Plants in the course of their metabolic activities produce a number of substances, such as tannin and probably oxalic acid, which are often of no further use to the plant cells. Such substances may then be considered excretions which, however, the plants have insufficient means of eliminating. In some cases the cells render them inert by changing them from solutions to a crystalline form. Thus oxalic acid is neutralized by calcium salts in the cells with the formation of insoluble calcium oxalate. Salts are known to be exuded upon the surfaces of plants, where they are washed away by rain or dew, but it is not certain that these substances are to be regarded as excretions.

Secretion.—The cell is to be regarded as a laboratory or factory in which a multitude of chemical processes are taking place. Some of these processes have already been discussed. All cells produce certain chemical compounds which may be used in the chemical processes going on within the cell or in cavities adjoining the cells. Such products are *secretions* and the process of producing them is given the name *secretion.* Secretions differ from excretions in that they are used in performing some function for the body, while excretions cannot ordinarily be used by the organism. The actual processes involved in the production of excretions and secretions are very similar and the methods by which these substances are discharged from the cells of multicellular animals may be identical. 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 at the exposed end and then become liquid or gaseous. 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 are elaborated. Secretions are very diverse in their functions. Some aid in digestion, others give protection because of their odor or because of poisonous qualities, some serve as lubricating material, others oxidize readily with the production of light, and there are still other kinds performing other functions. The diversity of functions served by secretions is indeed very great.

Single-celled animals and plants produce all the secretions required for carrying on chemical processes within their single cells. In higher animals and plants specialized cells may be set aside chiefly for the production of certain secretions. Localized groups of these cells are called glands. The structure of glands is considered in Chapter VI.

Growth.—Growth is characteristic of living organisms. It is due to the conversion of foods into protoplasm at a more rapid rate than protoplasm is being broken down in catabolic processes. Cells are strictly determinate in size, the size of any particular kind of cell in any organism being fairly uniform. When the cell has reached the limit of its size it may divide. The half-sized cells then grow to normal size. Thus the growth of the cell is due to the increase in the quantity of protoplasm. Increase in size of many-celled organisms is usually due to multiplication of cells and to the growth of the half-sized cells to normal. The cells of a large frog are no larger than the cells of a small frog of the same species, but there are more cells in the large frog. Increase in the size of the cell 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. In every case where growth occurs it is due to the activity of the protoplasm. This is true in multicellular as well as unicellular organisms.

Reproduction.—Reproduction is likewise characteristic of living beings. In unicellular organisms, and only in these, reproduction is equivalent to cell division, for obviously a cell cannot reproduce its kind without a cell division of some sort. 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. An account of cell division is given in Chapter IV and a detailed account of reproduction in Chapter VIII.

Protoplasmic Movement.—One of the attributes usually ascribed to living organisms, distinguishing them from non-living matter, is the power of independent motion. This power resides in the protoplasm. Protoplasmic movement may result in locomotion, that is, change of position of the organism in space, or it may be confined to a change of position of particles of protoplasm within the cell itself with no resulting locomotion. 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 such as *streaming* or *flowing*. Naked plant cells and some forms of unicellular animals frequently progress by a type of protoplasmic movement which is so characteristic of the protozoön Amœba that it has come to be called *amœboid* movement. Other cells make use of *cilia* which are minute slender protoplasmic processes capable of rapid vibration. This movement of cilia is *ciliary* movement. Locomotion in most higher animals is due to the movement of appendages caused by contraction of special contractile cells, the muscle cells. Such movement is *muscular contraction*. The first three types of protoplasmic movement will be discussed here, the fourth in Chapter VII.

Flowing of Protoplasm.—In many living cells the protoplasm may be observed to be in process of circulation, particle following particle in a more or less definite course within the cell boundary. Such a movement involving not only protoplasm but also granules and food vacuoles which are swept along by the current may be observed in Paramecium and some other species of Protozoa. In many plant cells, as in Nitella, Chara, the stamen hairs of Tradescantia, leaf hairs of the tomato, and cells of aquatic plants like Elodea, a similar movement of protoplasm, sometimes involving the chloroplasts, may be observed. When the movement of the particles describes a definite closed circuit it is sometimes called *cyclosis* or *rotation*. In some plants, as in some of the fungi whose mycelia are not divided by cell walls, the protoplasm moves toward one end of the mycelium and then returns. This may be called *streaming* of protoplasm. Flowing of protoplasm of the kind described does not result in locomotion.

Amœboid movement.—When an amœba moves it thrusts out one or more lobe-like processes, called *pseudopodia*. Then the body is pulled forward or flows forward. Since there seem to be two methods of locomotion in Amœba both will be described. *Amœba verrucosa*, an amœba with a very viscous outer layer or ectosarc, puts out normally a single pseudopodium in contact with the substratum. The protoplasm of the upper surface flows toward the tip of the pseudopodium, while the protoplasm of the lower portion flows to the rear, thence to the upper surface and to the anterior end. Thus this amœba acts like an elastic sac filled with a viscous fluid. For an experiment in demonstration of this type of amœboid movement zoölogists are indebted to Jennings who mixed soot in water containing Amœba and then traced the path of the soot particles which adhered to the surface of the animals. Figure 26 illustrates Jennings's idea of locomotion in *Amœba verrucosa*. In *Amœba proteus* a number of pseudopodia may be thrust out. The anterior end is elevated, thrust out, and then brought in contact with the substratum with which it adheres. The posterior portion of the body is now brought forward by contraction of the protoplasm and this material now forms a new anterior end. Dellinger demonstrated this method of locomotion.

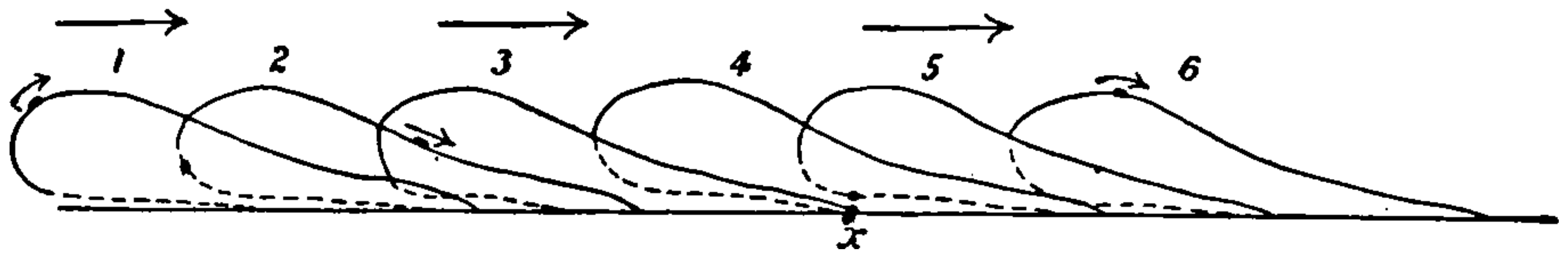


Fig. 26.—Diagram illustrating the movements of a particle of soot attached to the outer surface of *Amœba verrucosa*, in side view. *X* marks the location of the soot particle in position 4 of the amœba. In position 5 the particle is still at *X* but the figure has been raised a trifle in order to show the outline of the amœba. (*From Jennings.*)

He made an enclosure by cementing two cover glasses to the surfaces of a glass slide with a polished edge, so that the cover glasses projected over this edge (Fig. 27). Into this chamber amœbas were put and the chamber was mounted on the stage of a horizontal microscope. In this manner the amœbas could be observed from the side. Viewed thus their locomotion was shown to be a sort of walking (see Fig. 28). Both Jennings's and Dellinger's experiments show that protoplasm is contractile. Attempts have been made to show that amœboid movement is due to changes in surface tension and many experiments have been performed on non-living material to explain this form of movement. However, it appears that the currents of protoplasm in Amœba do not run in the way they should if movement were due to surface tension alone.

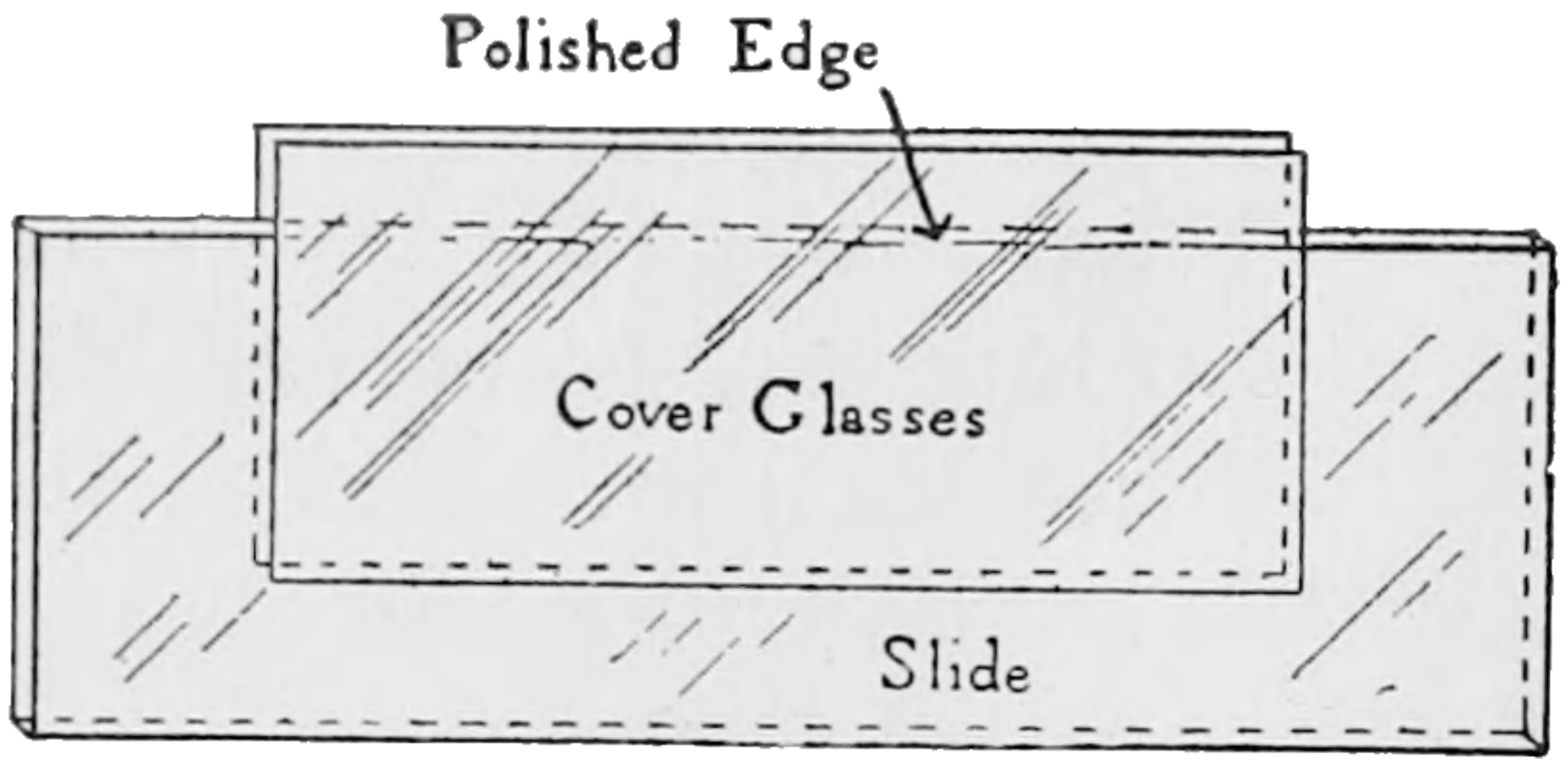


FIG. 27.—Apparatus for the study of locomotion in Amœba in side view. It consists of a glass slide with a polished edge and two projecting cover glasses which form a groove in which the specimens are kept. It is used on a horizontal microscope. (*From Dellinger in Journal of Experimental Zoölogy.*)

Amœboid movement occurs in the Protozoa provided with pseudopodia, in some naked plant cells, and in some cells of higher animals, namely, white blood corpuscles and pigment cells. Some other cells, as the germ cells, which originate in one location and migrate to another at some distance probably use this form of locomotion during their migrations.

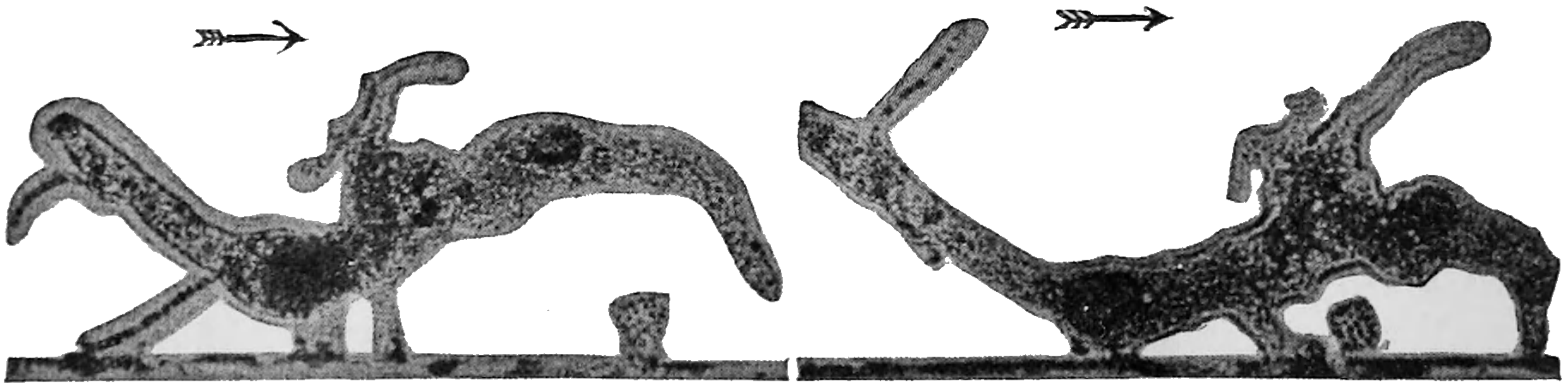


FIG. 28.—Locomotion in *Amœba proteus* as seen from the side with the apparatus shown in Fig. 27. *A* and *B* show the extension and attachment of a slender pseudopodium. Other pseudopodia are moving forward. (*From photomicrographs by Dellinger in Journal of Experimental Zoölogy.*)

Ciliary Movement.—Many small animals, such as the Infusoria of which Paramecium is the best known, wheel animalcules (rotifers), free-living flatworms, nemertean worms, and the aquatic larvæ of many animals are provided with numerous cilia, covering a portion or all of the surface of the body (Fig. 18). Each cilium has an elastic outer layer containing one or more contractile protoplasmic elements within it. The structure of a cilium of Stylonychia is shown in Fig. 29. Each large cilium of this and similar forms is regarded as being formed of several cilia of ordinary size fused together. Contraction of the protoplasmic elements on one side bends the cilium in that direction. The cilium because of the elasticity of the sheath returns to the original position as soon as the contractile elements relax. The active stroke involves the movement of the whole cilium while the return stroke begins at the base and like a wave runs along the cilium to its tip (see Fig. 30). The cilium thus presents the maximum friction in one stroke and the minimum in the reverse. Since the cilia move in unison or in waves in which the active beat is in the same direction, the difference in the friction of the cilia in the two strokes is sufficient to propel the animal.

Fig. 29.—Fibrillar structure of cilium of Stylonychia. (*From Dellinger in Journal of Morphology.*)

Many higher animals have inner surfaces covered with ciliated cells (*ciliated epithelium*) the cilia of which are not used for locomotion of the body but for the propulsion of liquids or minute solid particles which have lodged on these surfaces. Thus in the frog currents produced by cilia continually carry small particles and the mucous secretion of the mouth down the esophagus to the stomach. In the mammals and probably in most other air breathing vertebrates solid particles inhaled with the air are caught on the ciliated surfaces of the trachea and bronchi and are swept up into the throat by the action of cilia. So also phlegm or mucus is carried upward to the back of the throat whence it is expelled by "clearing the throat."

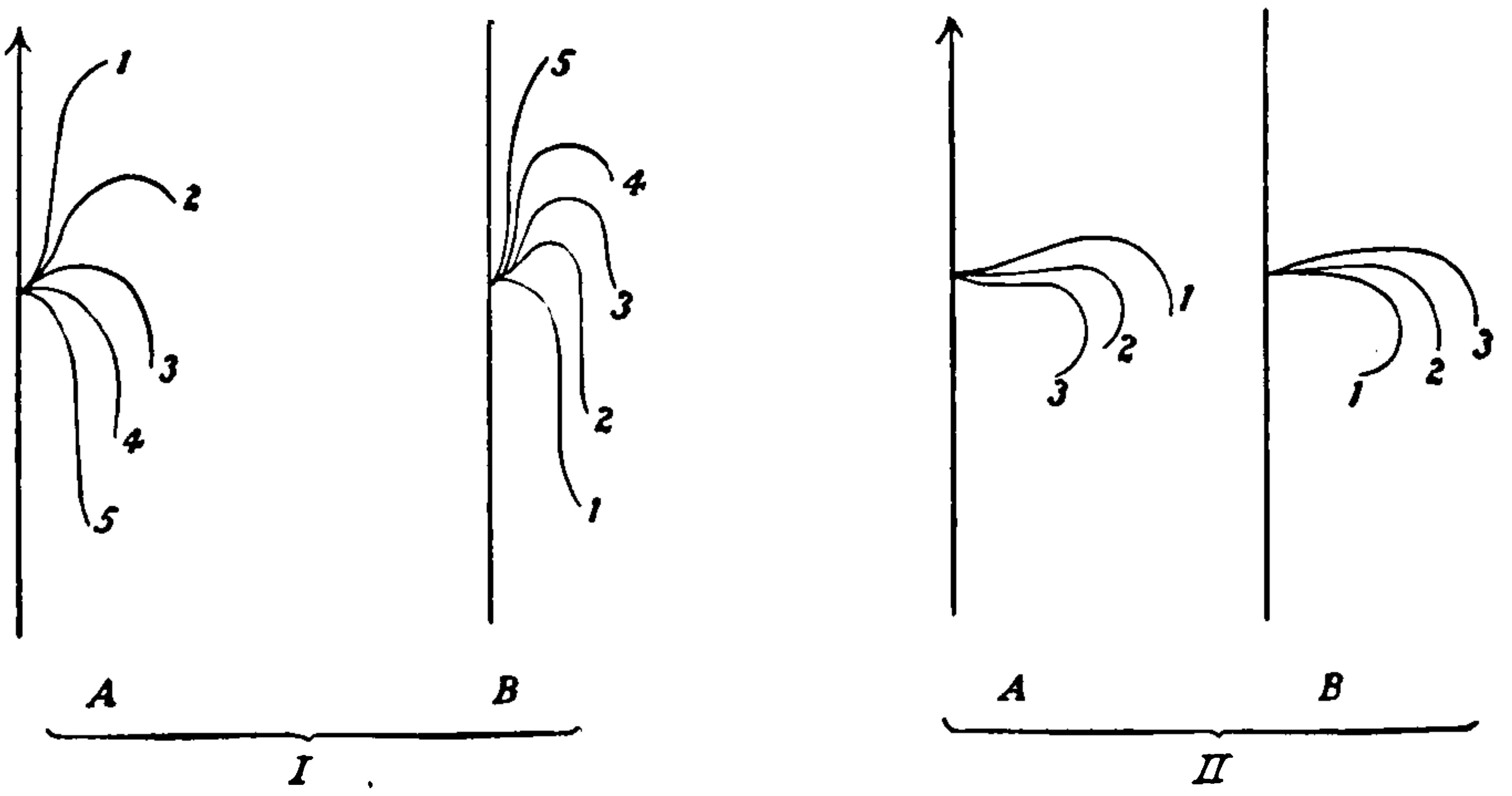


Fig. 30.—Diagrams showing successive positions assumed by cilia in locomotion. *A*, positions assumed from the beginning of the beat at 1; *B*, positions assumed during the return stroke beginning at 1. (*From Verworn.*)

Flagella.—Flagella are motor organs of the cell somewhat resembling cilia. They differ from cilia chiefly in their length and in the fact that when present they are few in number, there being from one to eight of these organelles (rarely more) to the cell. In cells that move always with the same end foremost, they are usually located at the anterior end of the cell. Cilia as a rule beat in one plane forward and backward.

Flagella may beat regularly in one plane, or they may have a rotary motion which may involve the whole flagellum or only the free end of it, or the movement may be irregular, involving any portion of the flagellum. Because of the diversity of these movements, a diversity which may be observed within a few minutes in the same specimen, it seems clear that the structure of the flagellum is not the same as that of the cilium. It has been shown for Euglena (Fig. 31) that the flagellum is composed of an elastic peripheral layer within which are several contractile threads extending throughout the length of the flagellum. The movement is due to the contraction of these threads. The return stroke is due to the elasticity of the outer layer or to the contraction of certain of the threads, or both of these factors may aid in the production of certain types of movement. The movement of the organism when propelled by one or more of these organelles is jerky or erratic. There is rarely the gliding movement which is characteristic of animals which employ cilia in locomotion. Flagella are the normal organs of locomotion in the Mastigophora or Flagellata, one group of the Protozoa. They are also the organs of locomotion in some plant cells. Flagella occur rarely as cell organs in higher forms. They occur singly on the endoderm cells of the Cœlenterata, and in Porifera (sponges) each cell of the radiating tubes (see Fig. 32) is provided with a flagellum and a protoplasmic collar surrounding the base of the flagellum. In these two groups of metazoan animals the flagella serve to create currents of water which circulate through the cavities of the animals. Cilia occur much more frequently as cell organs than do flagella, for in almost every group of animals some species may be found which have ciliated surfaces. Both cilia and flagella are protoplasmic structures whose functioning depends upon the contractility of protoplasm.

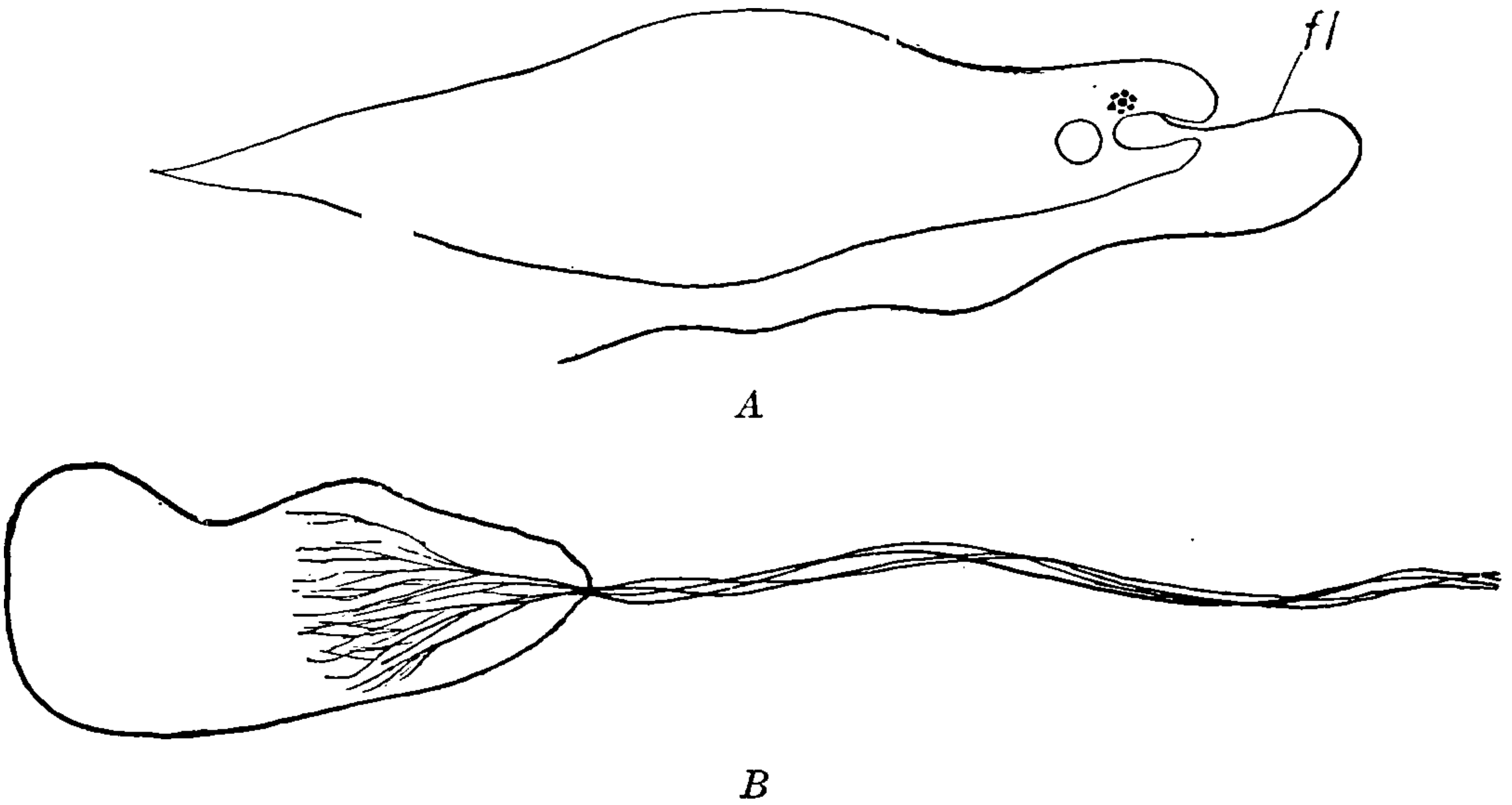


Fig. 31.—Euglena. *A*, outline showing flagellum (*fl*). *B*, the fibrils of the flagellum. (*A original*; *B after Dellinger in Journal of Morphology*.)

manner in which protoplasm is irritated and transmits impulses is unknown. From experiments on higher animals it has been ascertained that muscle may be stimulated to contraction after the nerve-connection has been cut and that the impulse may be transmitted from muscle cell to muscle cell. These experiments and others of similar nature show conclusively that irritability is a general property of protoplasm and not the property of any particular group of cells.

Relation of the Nucleus to Metabolic Activities.—In the discussion of cell physiology up to this point it has been assumed for the sake of simplicity that all parts of the cell were concerned in the functions discussed, with the possible exception of the chloroplasts in their function of photosynthesis. This assumption is not justified, for the greater number of functions of the cell are very complex, so complex, indeed, as to require the coöperation of several parts of the cell in their performance. In the present state of knowledge it would not be profitable to attempt a complete account of the interaction of the various parts of the cell in the different processes. It is possible, however, to point out one conspicuous phase of this coöperation, namely, the relation of the nucleus to the cytoplasm in certain types of function. It may be stated in advance that while cytoplasm alone may carry on neutral or destructive processes, the performance of constructive processes requires the presence of the nucleus. The evidence in support of this statement comes from a variety of sources.

Evidence From Regeneration.—One of the first and best of the indications of nuclear influence is the behavior of enucleated cell fragments. One experimenter found that if Oxytricha (a protozoön similar to Paramecium) were cut in two in such a way that one fragment contained all the nucleus, this nucleated portion quickly healed the wound and regenerated the missing parts. The fragment without a nucleus, however, soon perished. Stentor, another relative of Paramecium, showed similar results. In this animal the nucleus is a long body like a chain of beads (see Fig. 33), and it is possible to cut the body into several fragments containing large or small portions of the nucleus, or none at all. Gruber found that pieces containing much of the nucleus completely regenerated in twenty-four hours; those with smaller nuclear fragments regenerated more slowly; and those without any nuclear material, though the wound closed, underwent no regeneration, and later died. Polystomella, an Amœba-like protozoön with a perforated shell, may likewise be cut into fragments, one or more without nuclei. The piece with the nucleus is able to repair the shell, while non-nucleated pieces lack this power. Other experiments on Amœba and upon other Protozoa lead to concordant results. The non-nucleated portions may live and move for a time, and their pulsating vacuoles may continue to pulsate with little change; but they lack the power of digestion and secretion.

Evidence From Plasmolyzed Cells.—Similar evidence comes from plasmolyzed cells of leaf- and root-hairs. By placing these cells in certain salt solutions, the protoplasm, which normally rests chiefly against the cell wall and encloses a liquid in its otherwise hollow interior (Fig. 24), may be made to shrink up into much smaller volume by the withdrawal of the interior liquid. Frequently in this shrinkage the protoplasm is divided into several masses, which may be entirely separated from each other or may be joined by fine strands of protoplasm, as shown in Fig. 34. Those portions of the cell which contain the nucleus, or are connected with the nucleated piece by the fine strands of protoplasm, form about themselves a new cell membrane, grow, and live normally. Even a connection with a nucleated fragment of an adjoining cell, through fine pores in the cell wall, suffices to maintain the normal functions. The non-nucleated fragments, if entirely separated from nucleated

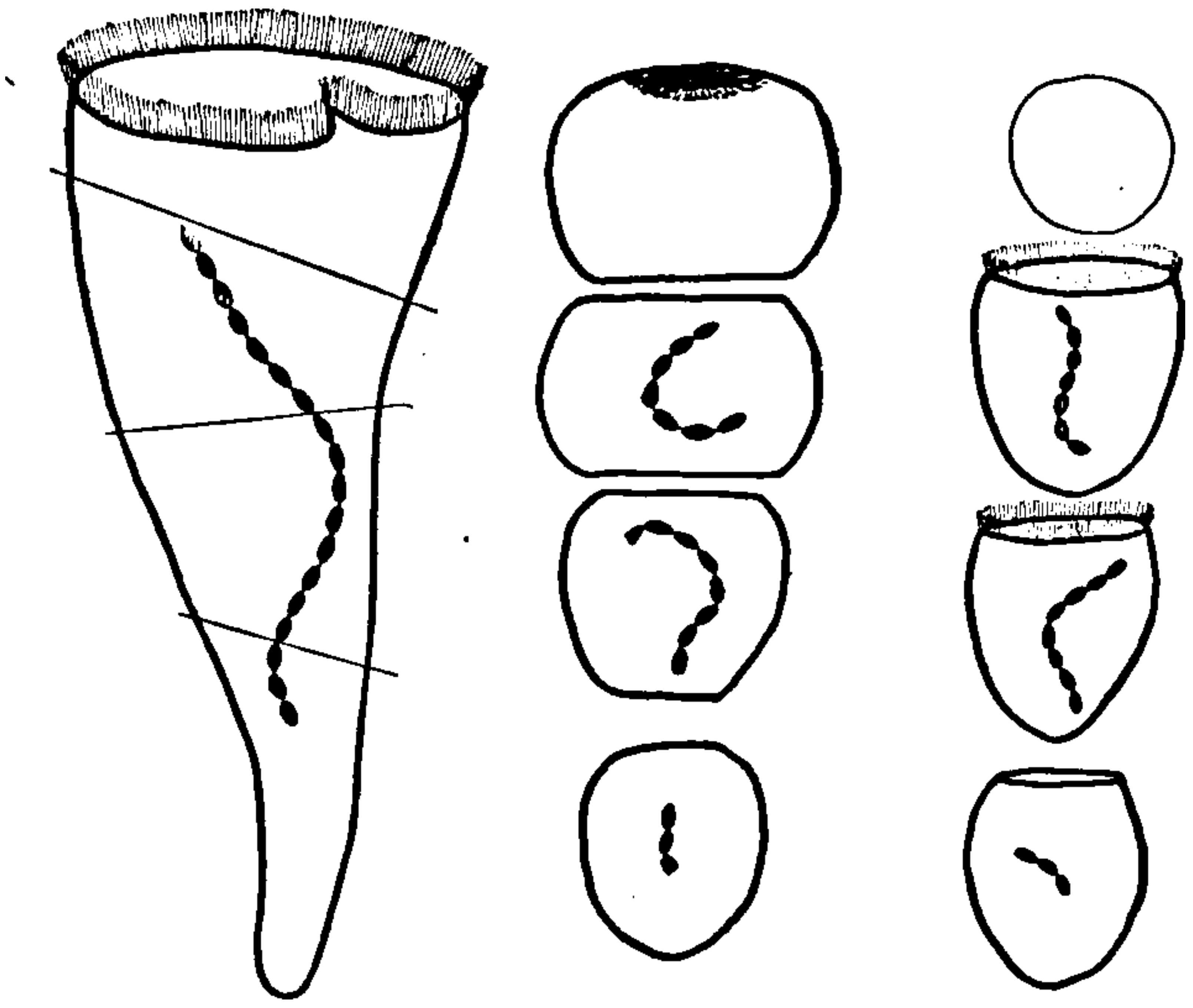


Fig. 33.—Diagram of regeneration in Stentor. The nucleus is a beaded chain, and if the animal is cut pieces of the body containing large portions of the nucleus regenerate rapidly; pieces containing less of the nucleus regenerate more slowly; and pieces containing none of the nucleus die and disintegrate without regenerating.

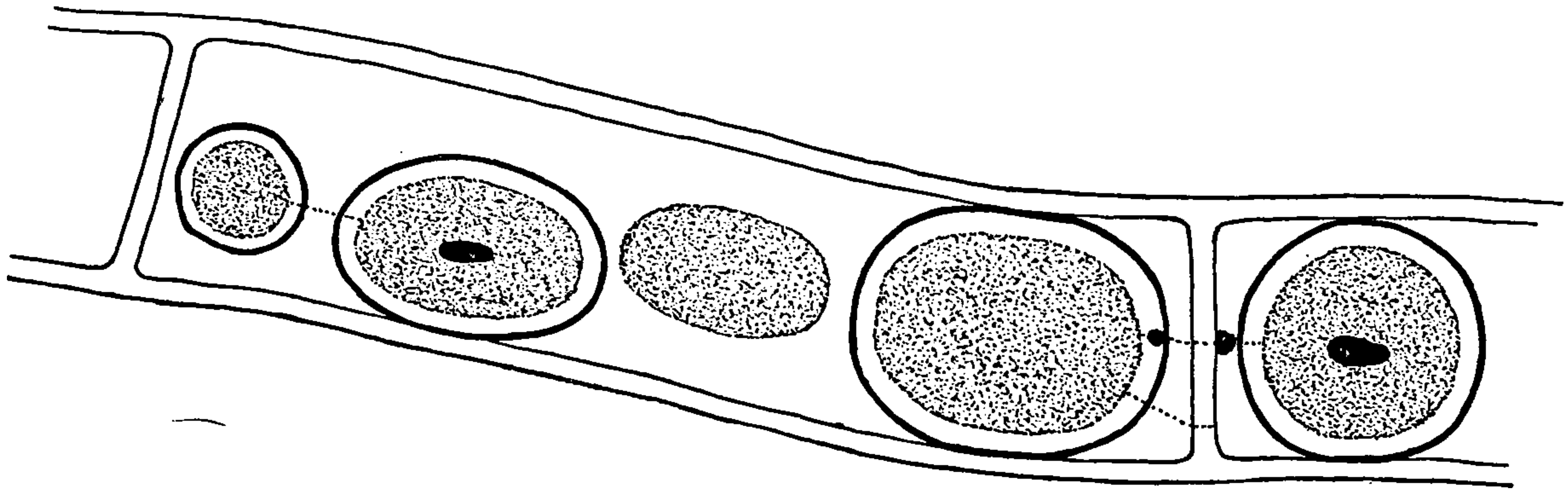


Fig. 34.—A plasmolyzed cell. On immersing the cell in a salt solution the protoplasm shrunk into several more or less distinct masses. Each mass containing a nucleus or connected by a fine filament of protoplasm with a nucleated mass produced about itself a cell membrane. Other masses remained naked. (*Modified from Townsend.*)

pieces, have lost the power of producing new membranes; and though they may continue to produce starch by photosynthesis, this starch cannot later be utilized.

Evidence From Position of Nucleus.—The position of the nucleus in cells that are physiologically very active also strongly suggests the constructive function of the nucleus. In plant cells in which the cell wall on one side is being thickened, the nucleus is usually found adjoining the thickening wall; and observations have shown that the nucleus proceeds to that position before the thickening of the wall begins. In cells which are producing root-hairs by the outgrowth of the wall, the nuclei are generally at or near the point of growth.

Summary and Inference.—In each of the cases of cell fragmentation mentioned above, the non-nucleated piece lacked some capacity for reconstruction. The missing parts of Oxytricha and Stentor could not be replaced; the shell of Polystomella was not repaired; digestion ceased in Amœba, probably owing to failure to produce the necessary enzymes. In plasmolyzed cells the non-nucleated portions do not produce a cell wall or membrane, nor the enzymes with which to utilize the starch which their chloroplasts manufacture. In highly active cells the nuclei are at the places of greatest activity. The conclusion is scarcely to be avoided that, while neutral or destructive processes, like movement, respiration, or excretion, may go on in the absence of a nucleus, the nucleus has some very fundamental control over the constructive processes of the cell. The influence of the nucleus may be exerted through its supposed effect in increasing oxidation, the rate of oxidation being too slow in the absence of a nucleus to permit of the syntheses mentioned.

There is abundant evidence from other sources that the portion of the nucleus which exercises this control is the chromatin. The minute accuracy of the behavior of the chromatin in cell division and the facts of development and heredity indicate that this substance is of unusual importance, but consideration of this evidence must be deferred to later chapters.

How the nucleus, or the chromatin in the nucleus, if that is the important substance, exercises this control over the activities of the cell is not known. Some have held that material particles of chromatin pass out from the nucleus into the cytoplasm at intervals, and thus bring about the regulation that the nucleus performs. In support of this view are observations on some of the Protozoa, preparations of which occasionally have the nuclear membrane ruptured and a mass of deeply staining granules near the point of rupture. Such an occurrence has even been reported for the many-celled animals by some observers, but other competent investigators of wide experience have been unable to verify the claim. It seems more likely, therefore, that the chemical reactions in which the chromatin is involved occur with the chromatin still in the nucleus. What soluble substances may pass back and forth between nucleus and cytoplasm is completely unknown. Chromatin is a very complex matter. There is evidence, which is briefly mentioned in the chapter on Genetics, that the chromatin of a single cell may comprise hundreds of different things. What these things are is a matter of speculation, but that they are responsible for as many different activities in the cells has been pretty well determined. Furthermore, there is a great variety of other substances in the nucleus and in the cytoplasm. The complexity of the protoplasmic mixture is great enough to account for the great number of activities that have been demonstrated in cells.

Deferred Subjects.—Numerous activities of cells reveal their full significance only in relation to the activities of cells around them, or to the processes going on in distant organs. Discussion of these must await the further development of the idea of complexity of structure in the succeeding chapters. Complexity of structure, resulting in complexity of function, is a consequence of the adherence of cells after division and their morphological differentiation. Cell division, which is itself one of the characteristic activities of living matter, is described in the next chapter, and differentiation in the one following.

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CHAPTER IV

CELL DIVISION

One of the most important biological questions in the several decades following the enunciation of the cell theory by Schleiden and Schwann in 1838 and 1839 had to do with the origin of cells. The founders of the theory believed that cells might arise either by a process of division of a preëxisting cell, or by "free cell formation." In the latter case, cells were thought to crystallize out, as it were, from a formative or nutritive substance, the "cytoblastema." The latter method was considered to be the usual one. By 1855, however, biologists had arrived at the conclusion that cells arose only from preëxisting cells and this doctrine was summed up in that year by Virchow, the famous pathologist, in the words, "*omnis cellula e cellula.*"

Discovery of Cell Division.—While the origin of cells from cells was thus early established, the mechanism by which cells originated from other cells was not known until in the seventies and eighties of the last century. This apparent slowness was probably due to the fact that investigators were concerned in verifying the cell theory. It was also due in part to the want of good lenses, in part to the fact that staining methods were in their infancy, and that no accurate method of section cutting had been devised. These early investigators of cell phenomena had frequently to improve methods or devise entirely new ones and to design new apparatus for their work. They labored under great difficulties. Remak in 1855 and 1858 proposed a scheme of cell division which much resembled the method described below under the head of amitosis. Remak's scheme was essentially as follows. The nucleolus divides, and there follows division of the nucleus into two parts, each containing a nucleolus. The division of the nucleus is in turn followed by a progressive constriction about the middle of the cell, which is thus pinched in two. This scheme was accepted as correct for some years, but investigators at times noted that the process was not quite so simple as Remak outlined it. Schneider in 1873, followed in quick succession by a number of others, made discoveries concerning cell division which showed that the division of the cell was usually a complicated process, but that there was also a less frequent method which did not differ greatly from Remak's scheme.

Nomenclature.—The complicated method has received several names which have come into general use, namely, *karyokinesis*, *mitosis*, and *indirect cell division.* The word karyokinesis is derived from two Greek words which mean nut or nucleus and change or movement. The word mitosis is from a Greek word meaning a thread. As will be seen in the description of indirect cell division, the word karyokinesis is more descriptive of the process than is the term mitosis, since the latter is descriptive only of a very brief stage of the process which in some cells may not occur at all. Nevertheless, the name mitosis, introduced by Flemming in 1879, is now more commonly used than karyokinesis, proposed by Schleicher in 1878.

GENERALIZED ACCOUNT OF MITOSIS

The scheme of mitosis here outlined deals with the process in animal cells in which a centrosome is present, and is applicable with certain modifications and reservations to most cases of indirect cell division in animal cells. The process involves a series of changes in the nucleus, the cytoplasm and the centrosome which are actually parallel or synchronous, but the description of the process cannot follow the precise chronological order and be made clear. For convenience in description and discussion the process may be divided into four stages or general phases which have no sharply defined limits. These stages are (1) the *prophases,* that is, the phases from the beginning which lead up to, but do not include, the splitting of the chromosomes, (2) the *metaphase,* involving the actual splitting of the chromosomes, the most important stage of all, (3) the *anaphases,* the phases in which the chromosomes are distributed, and (4) the *telophases,* involving the division of the body of the cell, the formation of daughter cells, and the reconstruction of the daughter nuclei.

The Prophases.—Prior to the beginning of mitosis the chromatin of the nucleus is arranged in the form of a network or as scattered granules supported by the linin network. This arrangement of chromatin is shown in Figs. 20 and 35. Occasionally where large fragments of the chromatin network cross each other rounded masses may be noted. These masses are called net-knots. As indicated in Chapter II, they are entirely distinct from nucleoli, as may be determined by the use of proper staining methods. On the approach of division the chromatin undergoes changes in form, and as indicated by its greater affinity for dyes it apparently also undergoes changes in its chemical constitution. It becomes condensed into a very fine thread which in some species seems to be continuous and in others discontinuous. This thread which is at first very fine and closely coiled is usually called a *close skein* or *close spireme* (Fig. 36) because the threads are near each other, giving a closely tangled appearance. Even at this early stage of division the chromatin stains more intensely than did the chromatin granules of the resting nucleus. As the process continues the thread thickens and shortens and the parts of the skein become further separated. In this condition the thread is called a *loose skein* or *loose spireme* (Fig. 37).

Meanwhile other changes in the cell have been taking place. The nuclear membrane has usually disappeared or is in process of disintegration. If a centrosome surrounded by a centrosphere was present in the cell it has already divided, and about each of the two resulting centrosomes a figure made up of radiating lines (the *aster*) has appeared. There have also appeared other lines arranged in the form of a *spindle* extending from the region of one centrosome to that of the other. The whole structure (spindle and asters) is called the *amphiaster*. Since

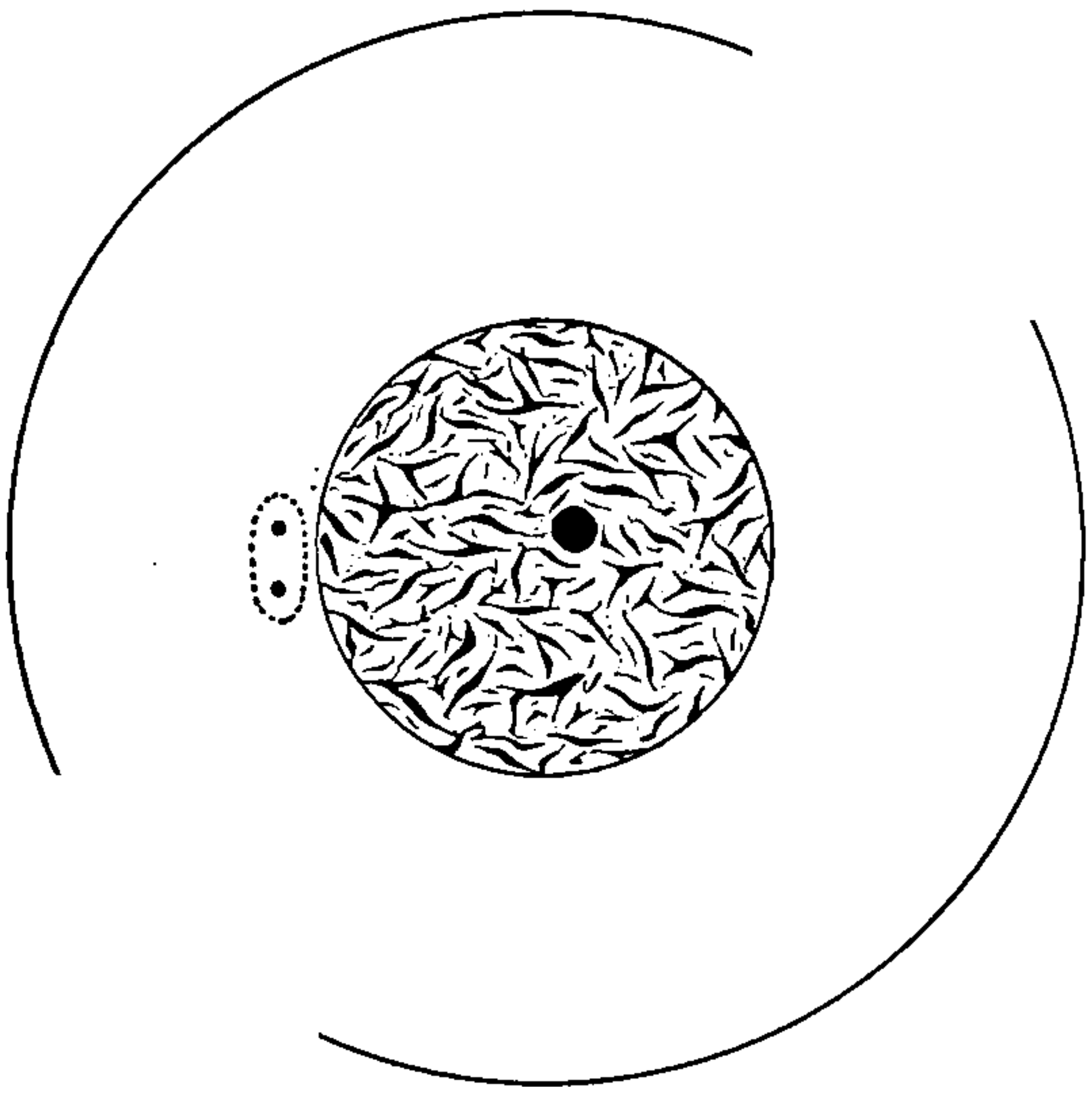

Fig. 35.—Resting cell. The centrosome has divided preparatory to mitosis, and the nucleolus is present.

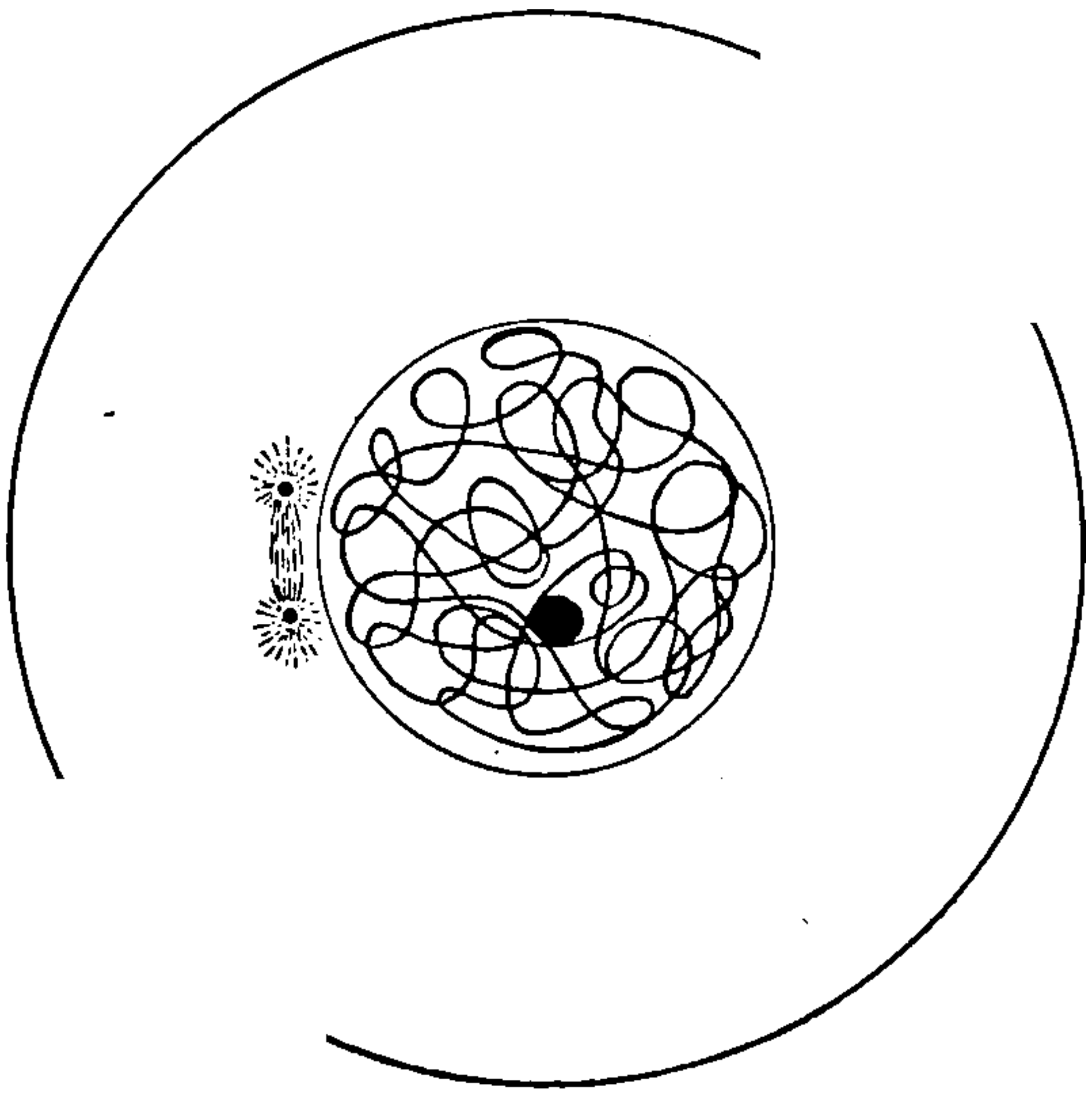

Fig. 36.—Formation of the close spireme and development of the amphiaster in a cell about to divide. Figures 36–40, inclusive, illustrate prophases.

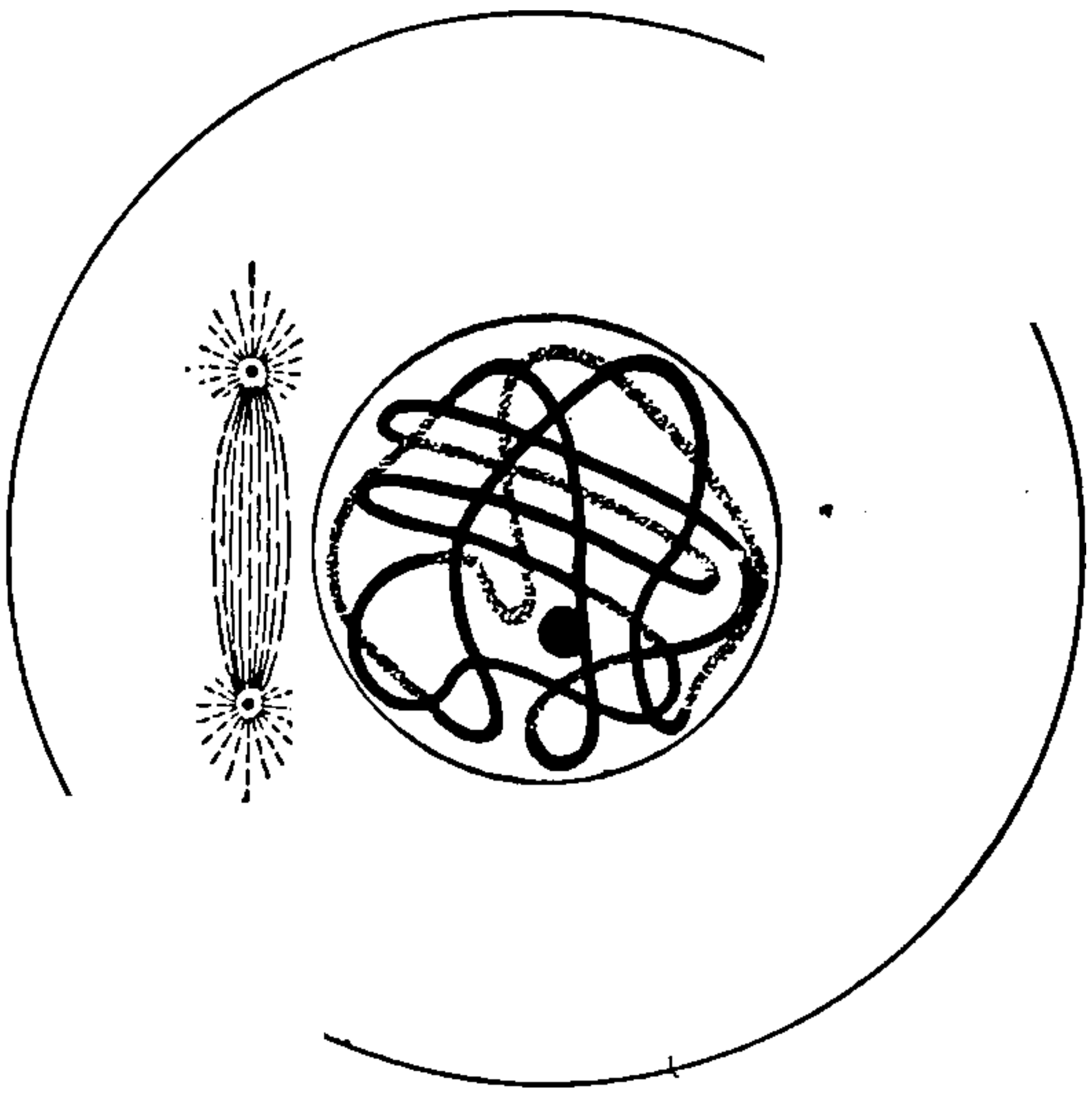

Fig. 37.—Loose spireme in a dividing cell. The spindle is enlarging.

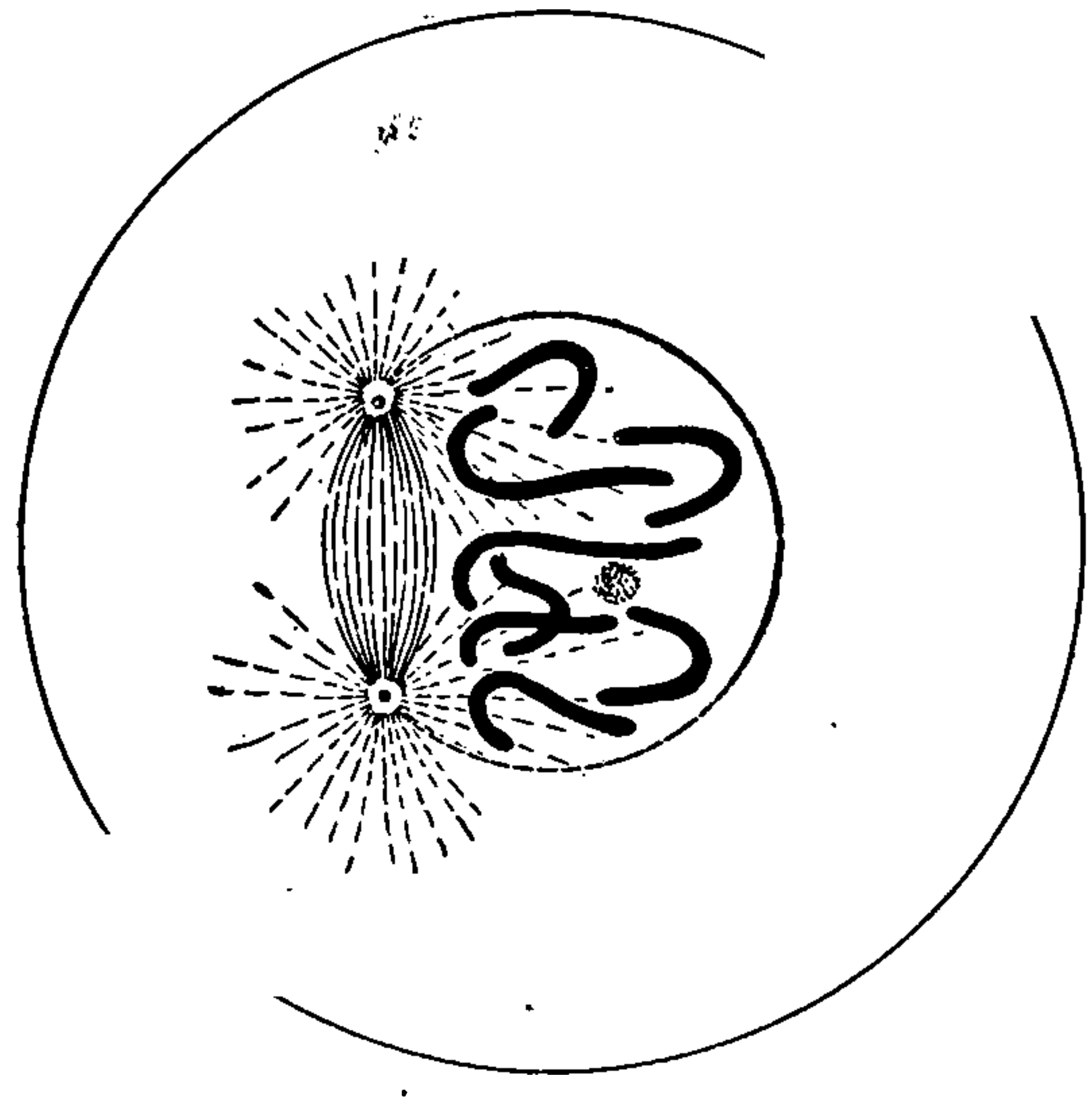

Fig. 38.—Dividing cell in which chromosomes have been formed by the segmentation of the spireme. The nuclear membrane and nucleolus are degenerating and the astral rays are entering the nucleus.

view the chromosomes form a figure which may resemble a star (Fig. 39). Viewed from the side the chromosomes appear to lie in a plane (Fig. 40). In this position the chromatic figure (the chromosomes) may be spoken of as an *equatorial plate.* The chromatic figure is now at the height of its affinity for stains, and from this point on its ability to take up stains decreases.

All of the stages from the beginning of the process of cell division to this point are included in the prophases.

The Metaphase.—In this phase each chromosome splits lengthwise into two equal portions. It is held that in general each chromosome is thus approximately halved in a quantitative fashion (Fig. 41). And since the chromomeres, which are supposed to contain the elements that control cell activities and heredity, are believed to be arranged in a series along the chromosomes an equal qualitative division of each chromosome is thought to occur at the time of splitting. The metaphase is a brief phase covering no more than the period of splitting of the chromosomes. In some species of animals the splitting of the chromosomes occurs before their arrangement in the equatorial plate.

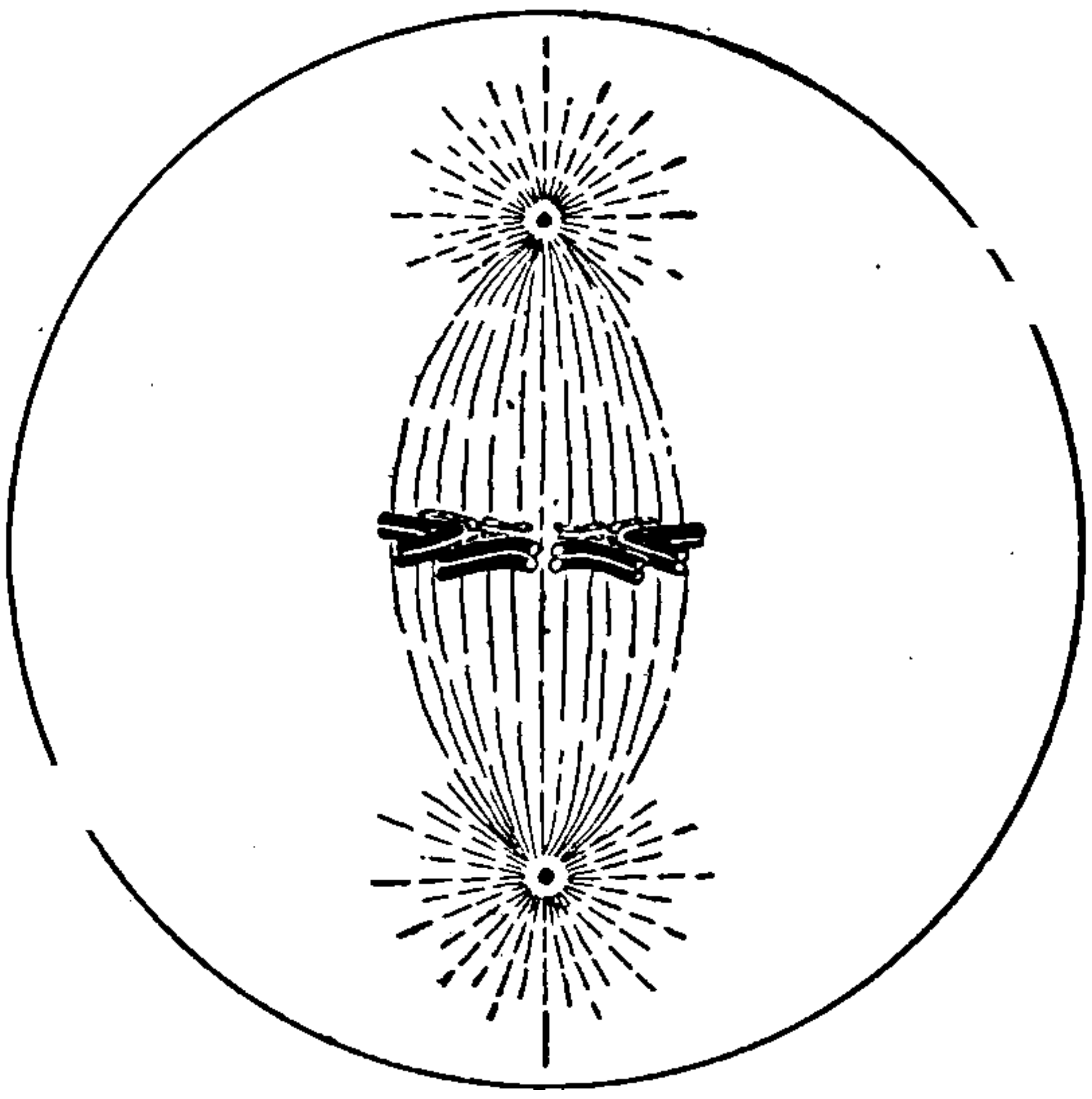

FIG. 41.—Metaphase of cell division. The chromosomes have split lengthwise.

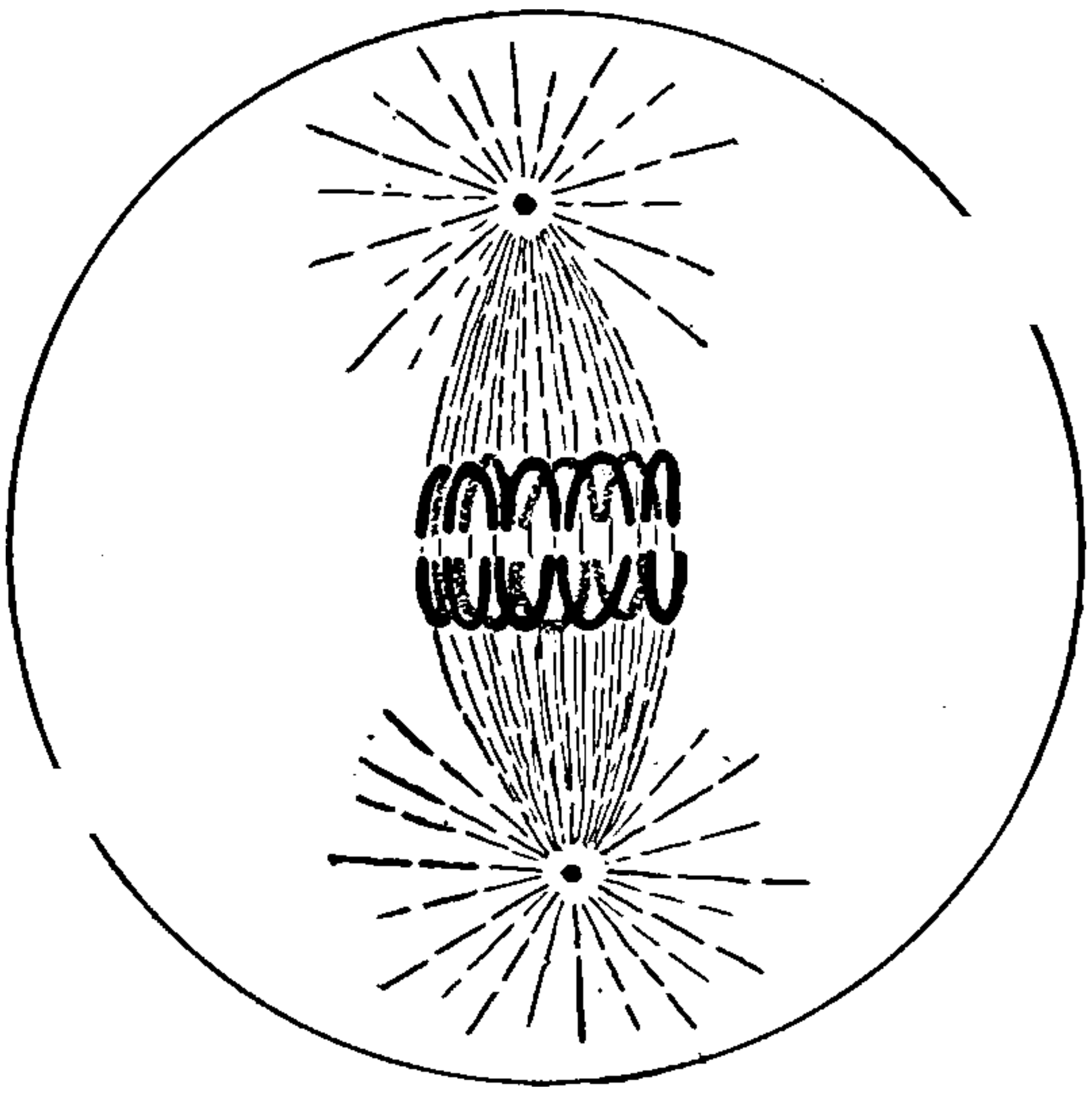

FIG. 42.—Early anaphase of cell division. The chromosomes are withdrawing toward the poles.

The Anaphases.—Almost immediately after the chromosomes have divided the two new chromosomes formed from each old one begin to draw apart, one going to one pole of the spindle and the other going to the opposite pole. This movement begins almost simultaneously for all the daughter chromosomes, and as a result they pass to the poles as two groups. In an examination of preparations which show many mitotic figures it is possible to find many anaphase stages from those in which the chromosome groups are just drawing apart, as in Fig. 42, to a condition in which the chromosomes are more or less densely massed about the ends of the spindle, as in Fig. 43. Thus the anaphases are concerned with the distribution of daughter chromosomes to the two new cells about to be formed, and the end of the phases is not definitely marked. In the late anaphase there may sometimes be found a slight indentation of the cell membrane on either side of the cell in the plane of the equator of the spindle. These indentations mark the beginnings of the division of the cytoplasm into two portions. At this time in some cells it may be possible to note small granules on the spindle fibers in the plane of the equator. The new cell membrane when formed passes through these granules. The division of the cell into two is completed by the gradual tightening of the constriction about the equator of the cell. In plant cells, a cell plate is usually formed at the plane of the equator of the spindle as the result of thickenings on the spindle fibers, and there is no constriction of the cell at its middle.

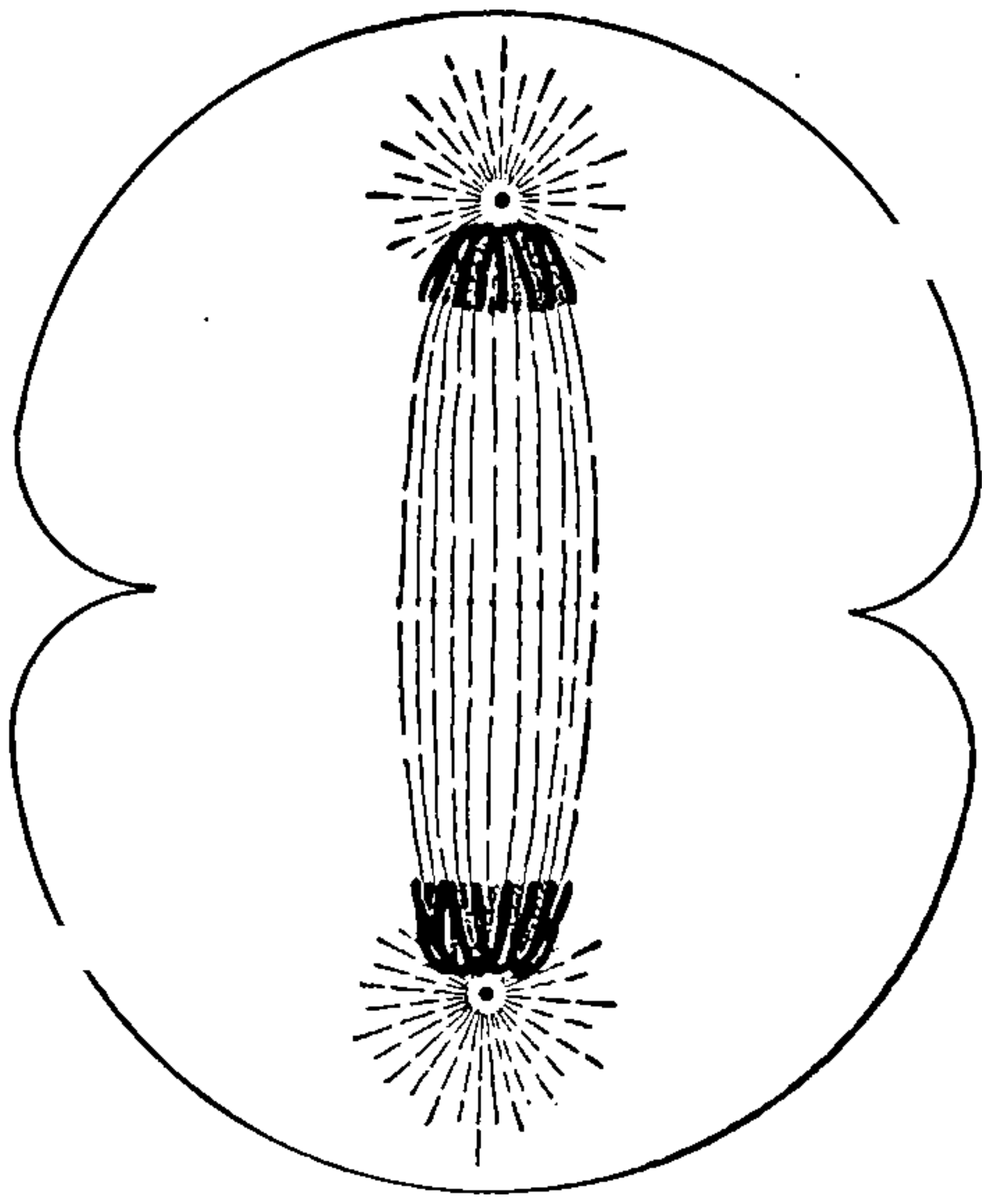

Fig. 43.

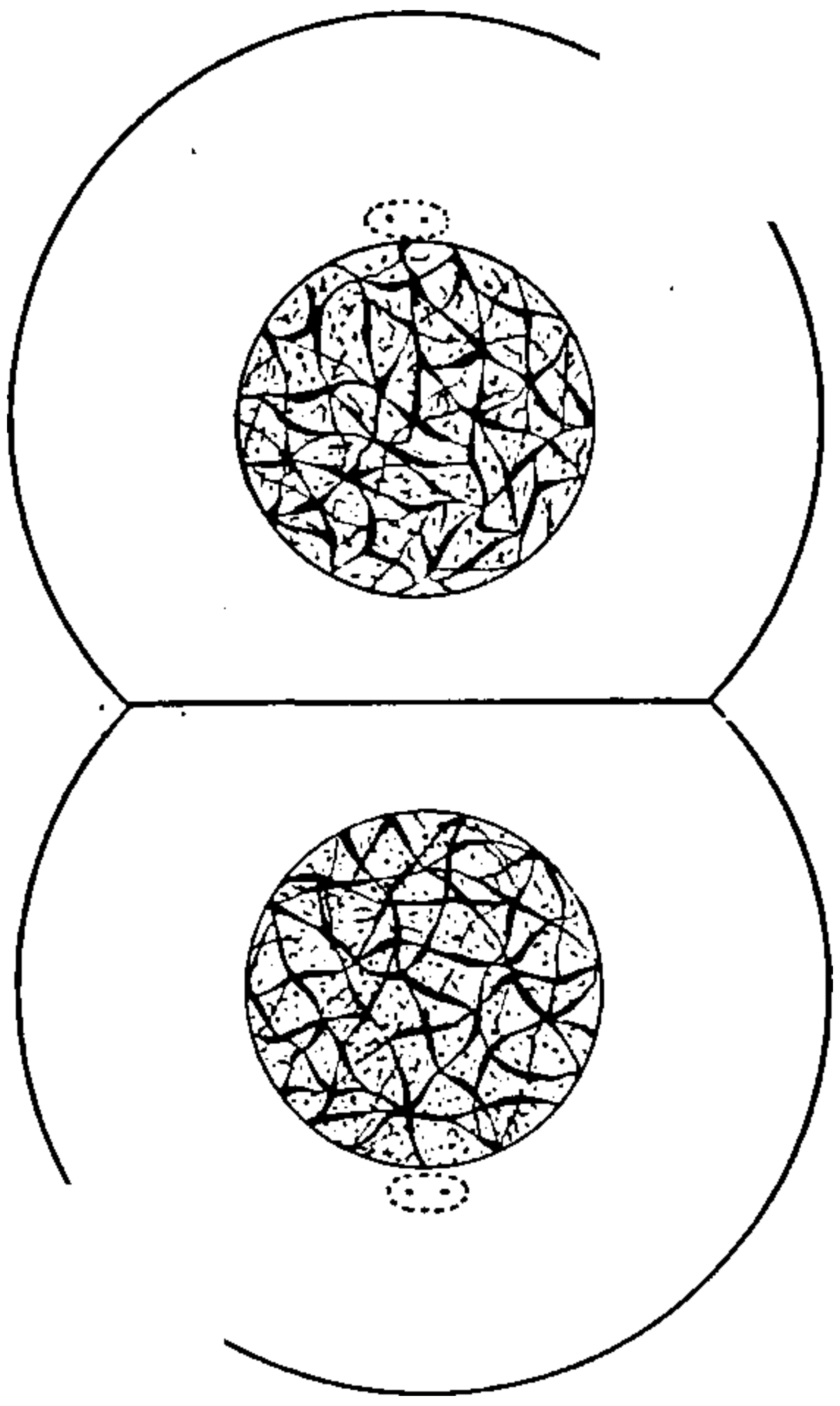

Fig. 44.

Fig. 43.—Dividing cell exhibiting a constriction of the cell membrane in the equatorial region and a massing of the chromosomes at the poles in late anaphase.

Fig. 44.—Late telophase, or the completion of cell division. The centrosomes have divided as if preparatory to the next division, and the nuclei are again in the resting condition.

The Telophases.—In these concluding phases (Fig. 44) occurs the reconstruction of the cells and nuclei after division. The new cell membrane in the plane of division is completed by a constriction of the membrane in the equator of the cell, whose beginning at the surface is shown in Fig. 43. The chromatin becomes diffuse; in some cells retracing the prophases, that is, undergoing changes in inverse order, often through an apparent loose and close spireme which finally assumes the condition of a network with net-knots. In other cells the chromosomes become inflated vesicles which fuse to form the nucleus. A nuclear membrane is formed but the source of the material of which it is formed is not known with surety. It is believed in some cases to be of the same material as linin. Sooner or later nucleoli appear. The achromatic figure begins to fade away. Traces of the spindle, however, may sometimes be seen connecting the two nuclei, but pinched together in the middle by the constriction of the cell membrane. The astral rays about the centrosomes disappear. The centrosome of each daughter cell may divide at this time in certain species or it may remain undivided until about the time of the next division of the cell. In some species it may entirely disappear only to reappear at the beginning of the next mitosis. In cells of the flowering plants a centrosome does not exist.

Reconstruction may now be said to be complete (Fig. 44). The daughter cells, however, are only half the size of the mother cell from which they arose. There succeeds a period of growth which is followed in turn by another division of the cell. The process of cell division is repeated most frequently in young and rapidly growing animals but it occurs at all times during the life of the individual.

VARIATIONS IN MITOSIS

In many cells of animals and plants mitosis differs in unessential features from the generalized process described above. These variations may concern the achromatic figure, the chromatic figure, the time relations of certain parts of the process, or the mode of division of the cytoplasm.

Achromatic Figure.—The centrosome is usually demonstrable in dividing animal cells if proper staining methods are employed, but painstaking research has now conclusively shown that cells of higher plants do not possess centrosomes. The difference is shown in Figs. 45 and 46 which illustrate animal cells with centrosomes, and Figs. 47 and 48 representing plant cells in mitosis without centrosomes. Centrosomes are remarkably well shown in the dividing germ cells of *Ascaris*. When the centrosome is present in the cell its division usually precedes the formation of a spireme. Sometimes, indeed, the division of the centrosome occurs during the telophase of one cell division in preparation for the next division. The movement of the centrosome to the opposite poles of the nucleus frequently occurs before rather than during the formation of the spireme.

The origin of the spindle is subject to some variation. In cells of some species, the salamander for example, the spindle originates outside of the nucleus and its fibers penetrate into the nucleus upon the dissolution of the nuclear membrane, while in other species the original spindle fibers of the amphiaster disintegrate and new ones arise from material within the nucleus, possibly from the linin fibers. In certain species of Protozoa (Fig. 49) and in some other animals, among them certain arthropods and rotifers, the spindle is formed inside the nuclear membrane.

Chromatic Figure.—The spireme is described for some species as a continuous thread. In other species there is no continuous thread for the chromatin forms in segments directly at the time of the condensation of the chromatin network. Even so important a feature as the splitting

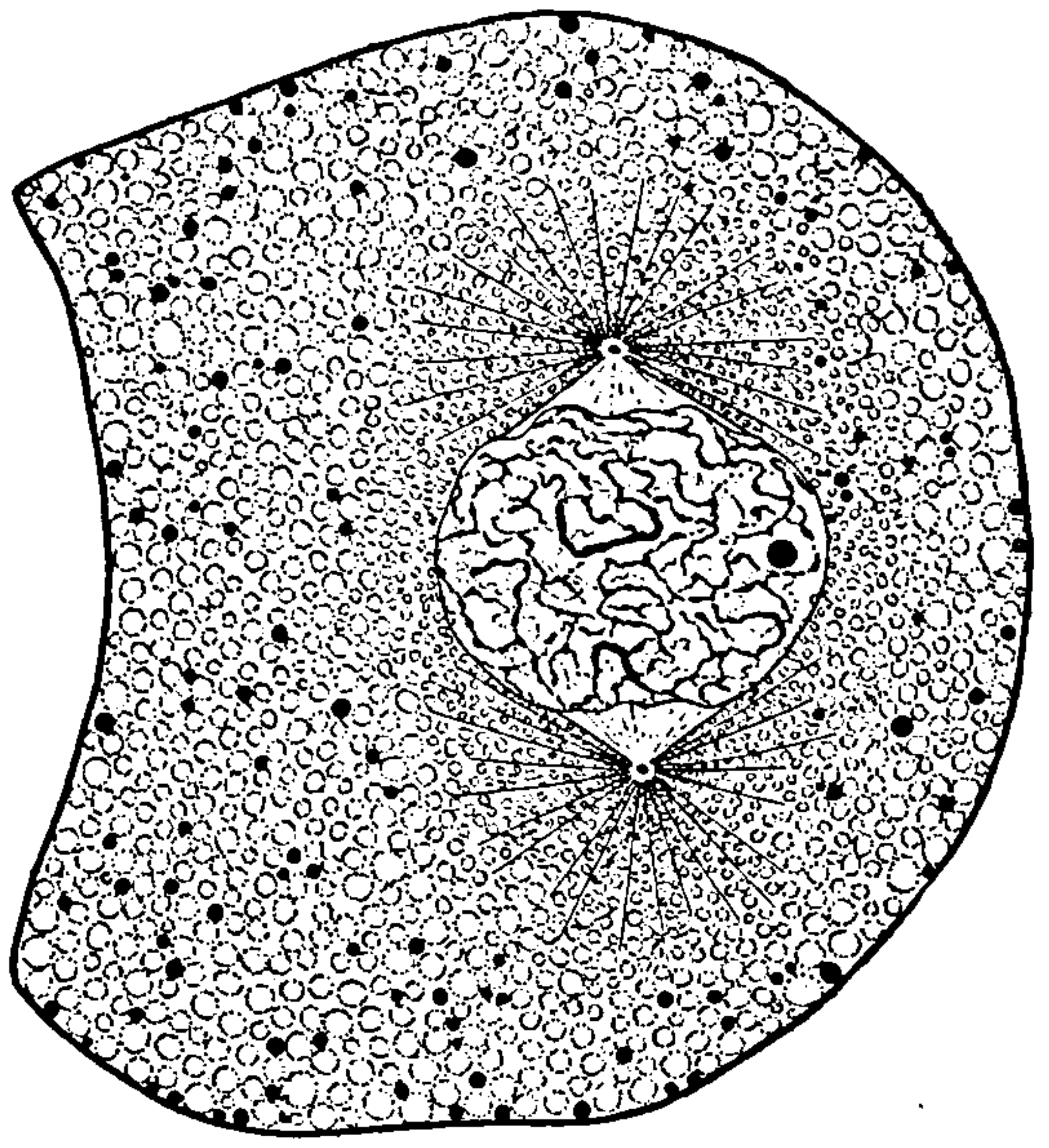

Fig. 45.

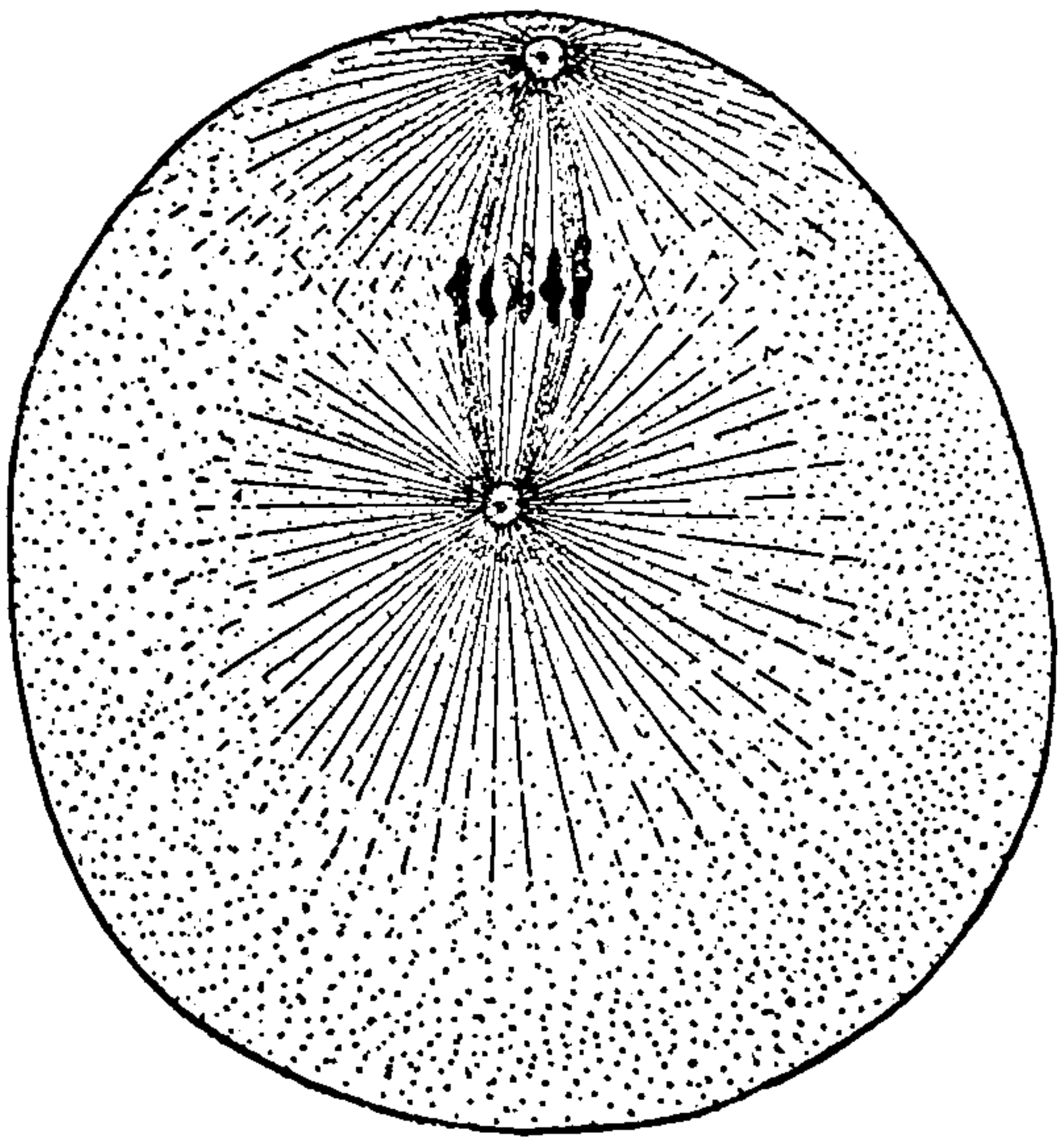

Fig. 46.

Fig. 45.—Mitosis involving centrosomes in a cell of the segmenting ovum of Unio. The spireme is irregular and the nuclear membrane is undergoing degeneration. (*From Dahlgren and Kepner's Principles of Animal Histology.*)

Fig. 46.—Mitosis involving centrosomes in the egg of the mollusk Diaulula. The equatorial plate is shown in side view. (*From Wilson's The Cell, after MacFarland.*)

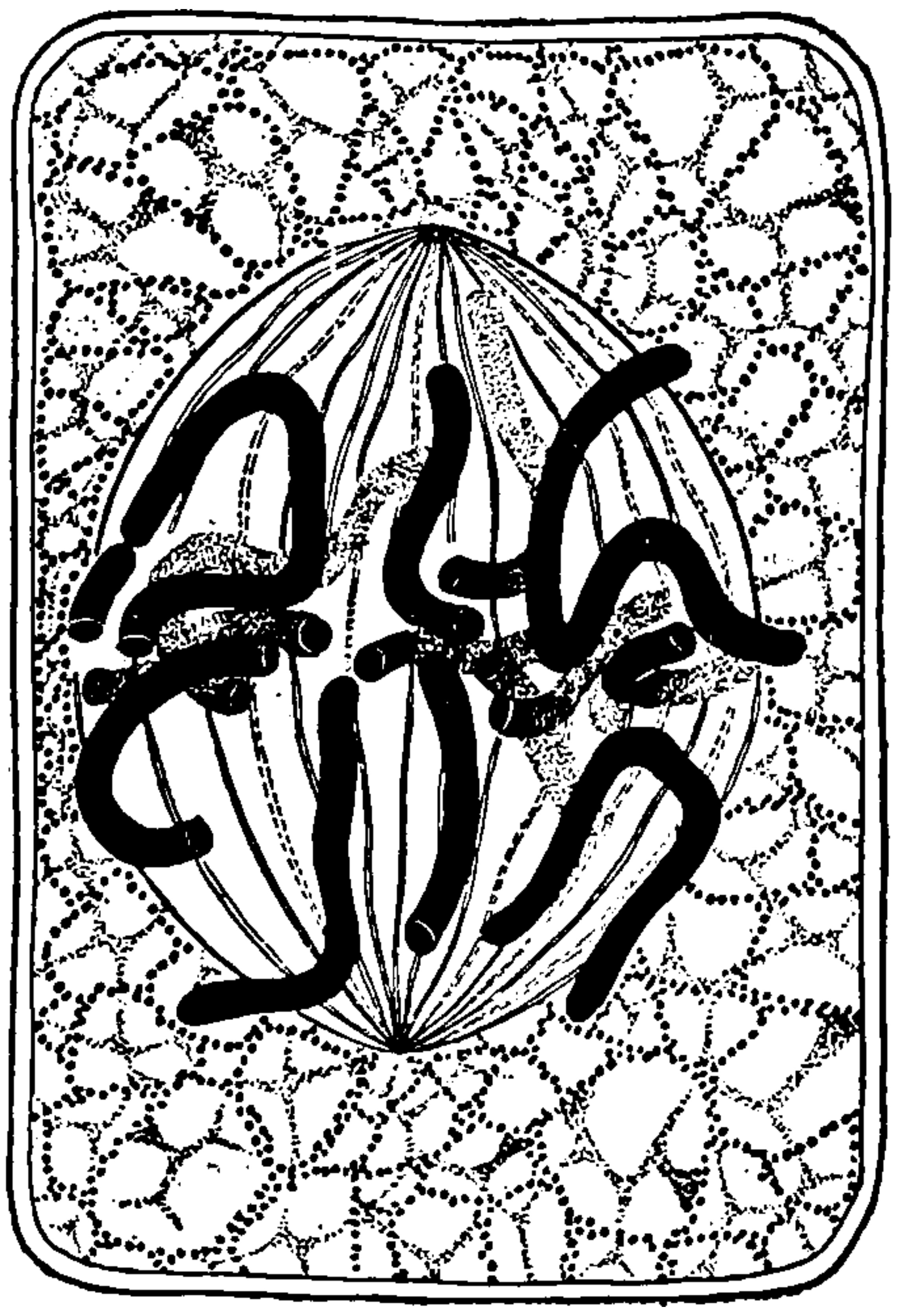

Fig. 47.

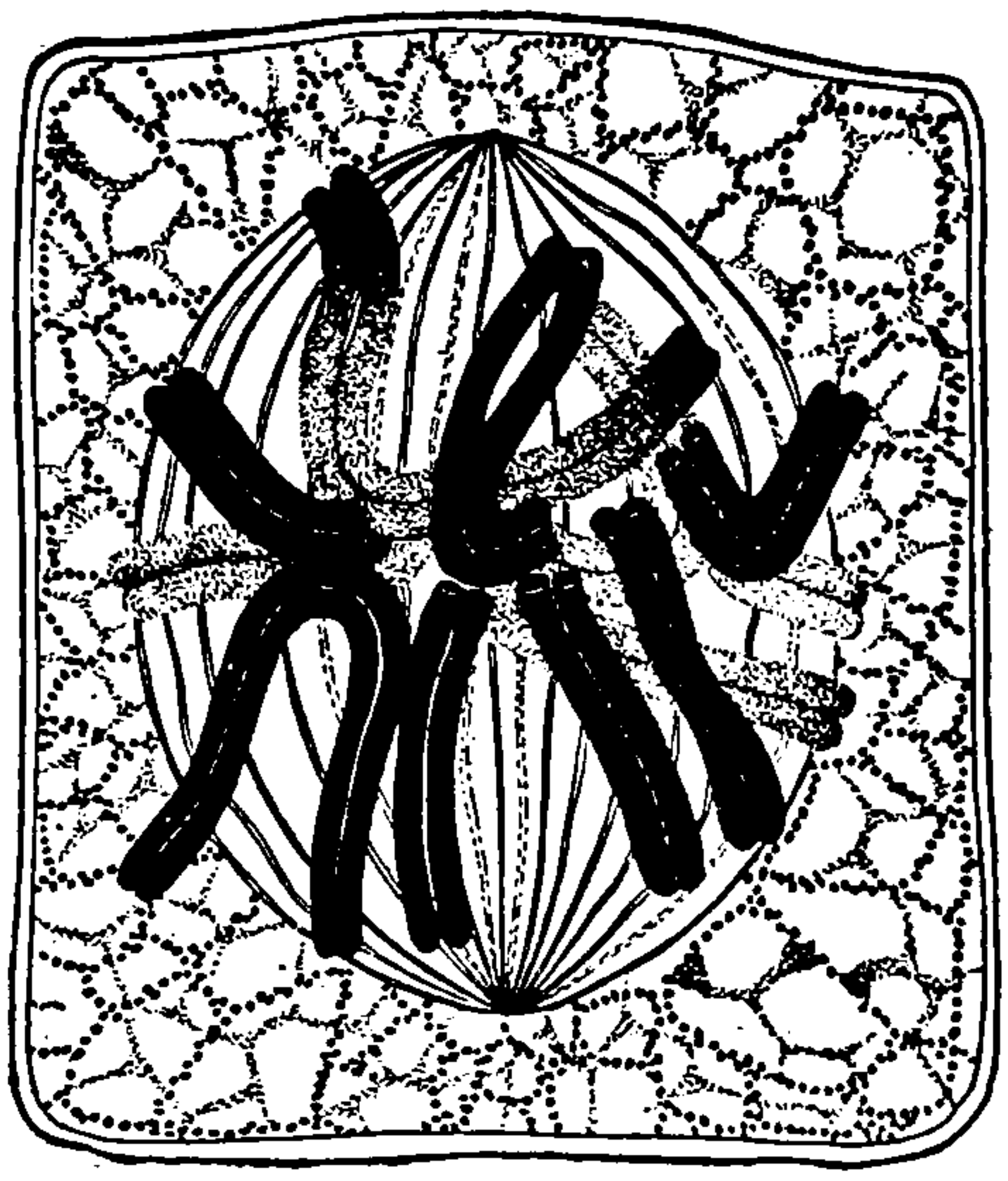

Fig. 48.

Fig. 47.—Mitosis in the absence of centrosomes in a cell of the root-tip of the hyacinth. The spireme has recently segmented into chromosomes. (*From Dahlgren and Kepner's Principles of Animal Histology.*)

Fig. 48.—Metaphase of cell division in the root-tip of the hyacinth (see also Fig. 47). The centrosomes are absent throughout the process. (*From Dahlgren and Kepner's Principles of Animal Histology.*)

of the chromosomes has its variations. While, as stated above, it typically occurs while the chromosomes are in the equatorial plate, there are many instances in which the chromosomes divide long before they assume an equatorial position. In some species this splitting occurs as early as the spireme stage.

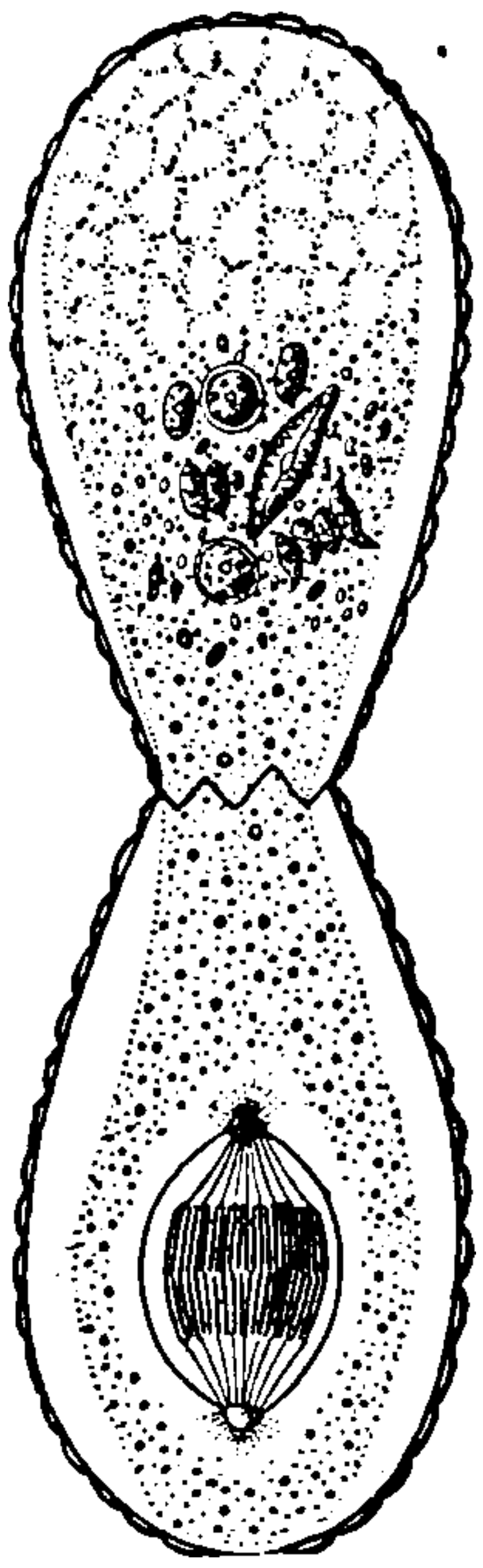

FIG. 49.—Intranuclear mitosis (anaphase) in the rhizopod protozoön Euglypha. (*From Wilson's The Cell, after Schewiakoff.*)

The chromosomes vary greatly in form. Frequently they are V-shaped. Short or long rods and spherical forms are also common, while some are hook-shaped. In the maturation of eggs and sperms chromosomes usually unite in pairs, and then the pair may assume ringlike and various other forms.

Division of Cytoplasm.—In the method of dividing the cytoplasm into two parts at the time of mitosis there is a difference between plant and animal cells. In most animal cells there occurs a constriction of the cell body in the equatorial region. This process of constriction continues until the cytoplasm is divided into two parts. In plant cells division of the cytoplasm is accomplished by the growth of a cell plate at the median points of the spindle fibers. The position of the cell plate is first marked by thickenings on the spindle fibers (Fig. 50). These thickenings increase in size and number during the telophases and eventually a new cell wall is laid down in the plane which they occupied.

Significance of Mitosis.—The significance of the mitotic method of cell division may be appreciated when one contemplates the fact that the process results in an approximately equal quantitative and qualitative division of the material of each chromosome. The equal *qualitative* division of the chromosomes is especially of great importance. It is the present day conception, supported by a considerable body of evidence derived from breeding experiments and observation, that many of the substances (of whatever sort they may be) which determine the activities of the cell and also those which determine hereditary qualities (the *genes*, Chapter XI), are distributed along the length of the chromosomes. It is also believed that the individual

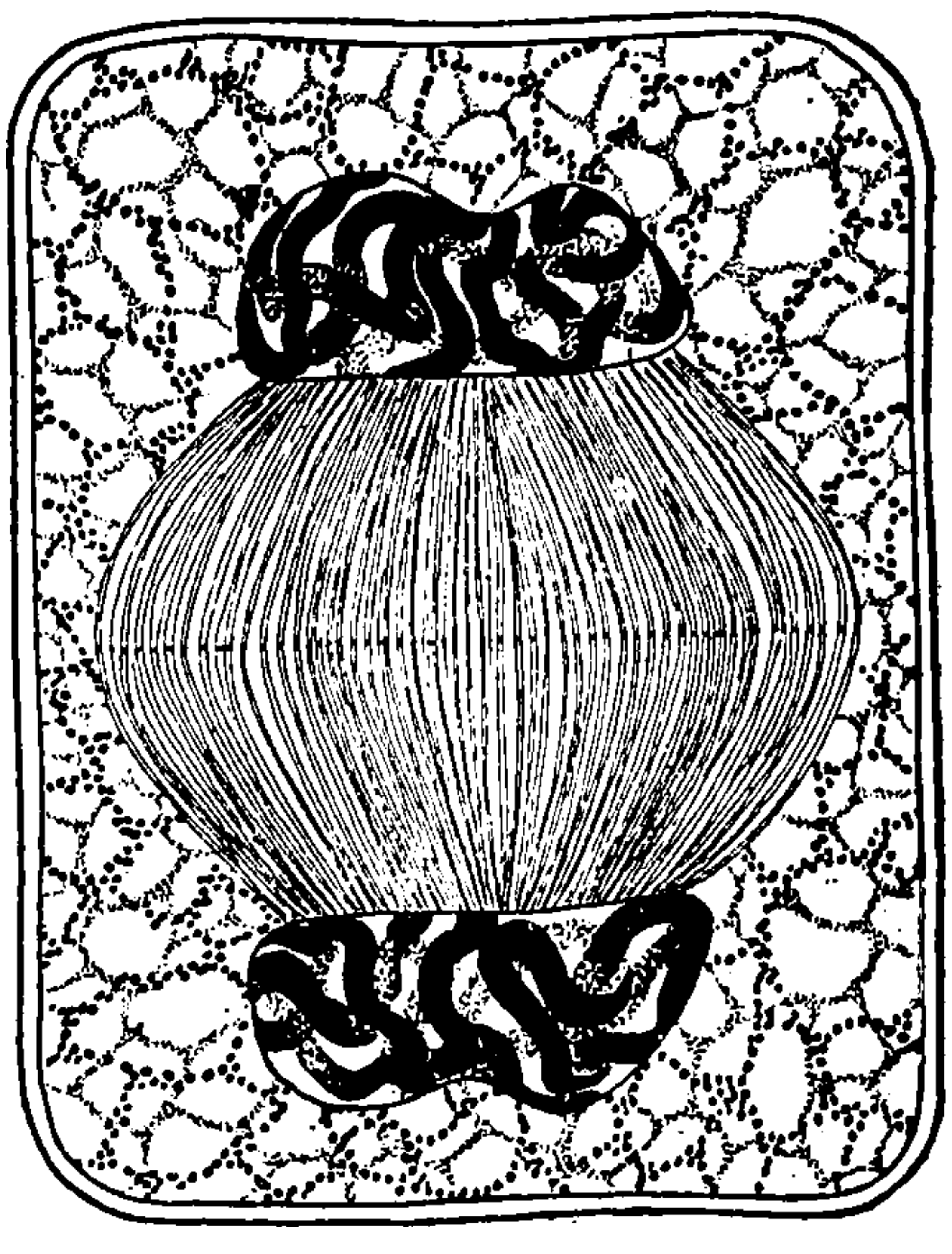

FIG. 50.—Formation of the cell plate in a dividing cell of the root tip of the hyacinth. The thickenings on the fibers of the spindle are the beginning of the process. (*From Dahlgren and Kepner's Principles of Animal Histology.*)

chromosomes retain their individuality even during the period when the chromatin is arranged in the form of a network, so that when the chromosomes are reformed during the prophases each chromosome contains the same chromomeres which it contained at the close of the anaphase. According to this view certain chromosomes or groups of chromosomes are responsible for certain hereditary characters and probably for certain physiological activities depending on the elements contained in their chromomeres. If this assumption be correct, the longitudinal splitting of the chromosomes with the resulting splitting of the longitudinally arranged chromomeres, is the only method by which the equal division of those substances which control cell activity and heredity may be assured. It is worthy of note in this connection, however, that while the exact halving of the chromosomes occurs in the division of the somatic or body cells of animals, it does not occur in the reduction mitoses of the germ cells, which are dealt with in detail in Chapters X and XI.

Excepting frequent differences between the sexes, the number of chromosomes is constant for each species. Thus there are four chromosomes in the nematode worm *Ascaris megalocephala*, eight in the fruitfly, *Drosophila melanogaster*, 22 in one of the bugs, and according to one investigator 47 in the male of the human species. 48

Mechanism of Mitosis.—The form of the mitotic figure in the late prophases, metaphase and the early anaphases, and particularly that portion of it made of achromatic material has led to its comparison with the lines of force revealed by the arrangement of iron filings in the field of a horseshoe magnet. Such a comparison furnishes an excellent illustration or model, but it offers little to the solution of the mechanism of mitosis. Nevertheless, it is not impossible that mitosis is an electromagnetic phenomenon.

One of the older views in regard to the forces operating in mitosis was that the astral rays and spindle fibers of the achromatic figure were protoplasmic threads which were capable of contraction. According to this view certain fibers were attached to the chromosomes and the movement of the chromosomes was due to pulling by these fibers. This conception is not without support at the present time. Originally evidenced only by observations on fixed and stained cells it has had within recent years some support from the experimental side. A long series of experiments in which dividing plant cells were subjected to solutions of various poisons has shown that these achromatic structures act as if the parts were made up of definite fibers which are thrown out of their normal position by the action of the poison. Certain investigators claim to have dissected out individual chromosomes from the dividing cells of salamander testes and occasionally to have found a chromosome to which was attached a minute protoplasmic thread which they considered to be a portion of the achromatic figure. What causes these fibers (if they are fibers) to behave in the definite and orderly fashion which may be observed in mitosis cannot be stated.

Active migration of the protoplasmic substances, due no doubt to their chemical reactions, has been appealed to to explain the movements of the chromosomes. Another view attributes these movements to the enlargement and collapse of multitudes of vesicles in the protoplasm. Further knowledge of the mechanism of mitosis probably awaits discoveries in the field of colloid chemistry.

It was once thought that the whole process of mitosis was under the control of the centrosome which was supposed to be present in every cell. When it became known that the centrosomes behaved in a different manner in various cells and that although they were non-existent in most plant cells mitosis proceeded in an orderly fashion in such cells, the idea of the importance of the centrosome was abandoned. The splitting of the chromosomes is probably to be accounted for by some form of protoplasmic movement. It is not impossible, also, that their movement in the anaphases of mitosis is due, at least in large part, to active migration of the chromosomes themselves.

AMITOSIS

In contrast to the exceedingly complicated method of cell division outlined above is the method of direct cell division to which the name *amitosis* is applied. The process is begun by an elongation of the nucleolus and a constriction of the nuclear membrane. The nucleolus finally separates into two portions and the constriction about the nucleus continues until the nucleus is cut in two, each part of the nucleus containing one of the halves of the nucleolus. Figure 51 illustrates this mode of division. Not infrequently a process occurs which resembles incomplete amitosis, but which may not be strictly related to cell division at all. Thus the nucleus may become and remain bilobed, but the cell not divide. In certain cases, for example in the follicle cells of the cricket's ovary, the nucleus completely divides in amitotic fashion, but the cytoplasm remains undivided. In this instance amitotic nuclear division does not result in cell division but in an increase of nuclear surface. Nuclear division of a similar type has been reported in developing muscle cells and is said to be common in stratified epithelial cells of higher vertebrates. According to some investigators cell multiplication is carried on by mitosis usually, but late in the series of cell generations nuclear amitosis occurs giving increased nuclear surface without division of the cell; while observations by at least one investigator have shown that in tissue cultures the nuclei may divide at first by amitosis and later by mitosis.

Limited Occurrence of Amitosis.—Amitosis as a mode of cell division seems to be of limited occurrence. It has been reported by numerous

DISCUSSION

The physiological causes of cell division are still problematic. One of the suggested causes of the initiation of the process is change in the surface tension of the cell. Evidence in support of this view is believed by some biologists to be found in the fact that unfertilized eggs of many aquatic animals may be caused to segment (divide) if they are subjected to certain chemical treatments. Such treatment reduces surface tension. If it were regularly true that this change in surface tension were localized, the phenomenon might offer an explanation of cell division. Another theory connects the initiation of cell division with the well-known capacity of colloidal substances, mentioned in the preceding chapter, for changing from the liquid to the semi-solid state and *vice versa*. A rhythmical change in the viscosity of the protoplasm of certain dividing eggs has been demonstrated, the protoplasm becoming more solid during the prophases and more liquid during the later stages; and when these changes in viscosity are artificially prevented, the division of the eggs is arrested. Whether the change in viscosity is a cause, either direct or indirect, of cell division, or is merely an effect of some other factor which causes division, is uncertain. A change in the rate of oxidation of substances in the protoplasm has likewise been proposed as an agency causing cell division, and it is not impossible that electrical phenomena are also concerned with the process. It is stated that cell division tends to preserve a certain relationship between the bulk of the protoplasm of the cell and the area of its surface, but this statement throws no light on the factors which initiate cell division and thus bring about the readjustment between the bulk and surface area of the cell.

Universality of Cell Division.—That cells originate only from preexisting cells was affirmed in an earlier part of this chapter. Evidence secured from the observations of an enormous number of investigators working with both plants and animals substantiate that statement. No trustworthy evidence has been secured to show that cells originate in any other way than from cells or by any other method than cell division. Biologists are thus forced to accept the idea of the continuity of protoplasm. Evidence for the continuity of certain specialized cell organs is also at hand. Plastids, such as chloroplasts, originate only from existing plastids by fission. Other cell organs besides chromosomes and plastids are known to divide and thus perpetuate themselves, but their maintenance and growth depend upon their relation to the cell. It is this division of the cell and its organs, and especially the equal qualitative division of the chromosomes, which furnishes the mechanism by which the two cells resulting from the division of a parent cell resemble each other. It is through the operation of this mechanism that hereditary qualities are transmitted from parent to offspring.

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CHAPTER V

CELL AGGREGATION, DIFFERENTIATION, AND DIVISION OF LABOR

Even a brief survey of living things reveals the fact that there is a great diversity in size and complexity of animals. At one extreme are animals so small as to require the aid of the microscope to see them and so simple in structure as to cause wonder that they are able to maintain their life processes, while at the other extreme are animals of great complexity and sometimes of enormous size. Examples of the first group are the Protozoa (one-celled animals); while insects, fish, birds, snakes, and such mammals as the mouse and the whale illustrate the second group. Between the extremes of simplicity and complexity many gradations occur, so that animals may be arranged in an ascending or descending scale of organization. In such a scale it is found that in certain species the individual consists of a single cell and that in species not widely differing from them the cells are grouped into some form of aggregation. Furthermore, some aggregations exhibit a slightly more complicated relationship of the cells to one another than do other aggregations in which the cells are very similar. That is, the scale at many places is a finely graded one, and the nature of the steps from one member of the series to the next may be various. These differences in the method of aggregation open wide possibilities for differences in physiological influence or dependence of cells upon each other. They also raise important questions regarding the origin and significance of the higher degrees of complexity. Changes in structure and changes of function of the cells or individuals during the evolutionary development of the complicated forms are strongly suggested, and speculation upon the nature of these changes is invited. Almost the only source of information regarding these questions is an examination of the different types of aggregation now found in animals and the probable relationships that exist among them.

From Single Cell to Colony.—The point of departure in seeking the facts in regard to cell aggregation is obviously the single cell as it exists in the majority of protozoan species. In these species the cell carries on the functions of the body. It takes in food, digests it, and assimilates the products of digestion. Within this one cell are carried on the processes of respiration, secretion, excretion, and locomotion. It responds to stimuli, and it produces other cells. Thus the cell in such protozoan species carries on all its life processes independently of its fellows. Its

tree-like colony. In this species the separation of the cells is complete and the cells rearrange themselves after division. Codosiga (Fig. 54) is a stalked form. After a cell divides the two new cells remain attached to the old stalk but each cell begins to secrete a new stalk. With successive divisions followed each time by stalk-formation a tree-like colony is produced. Anthophysa (Fig. 55) is a further example of a dendritic

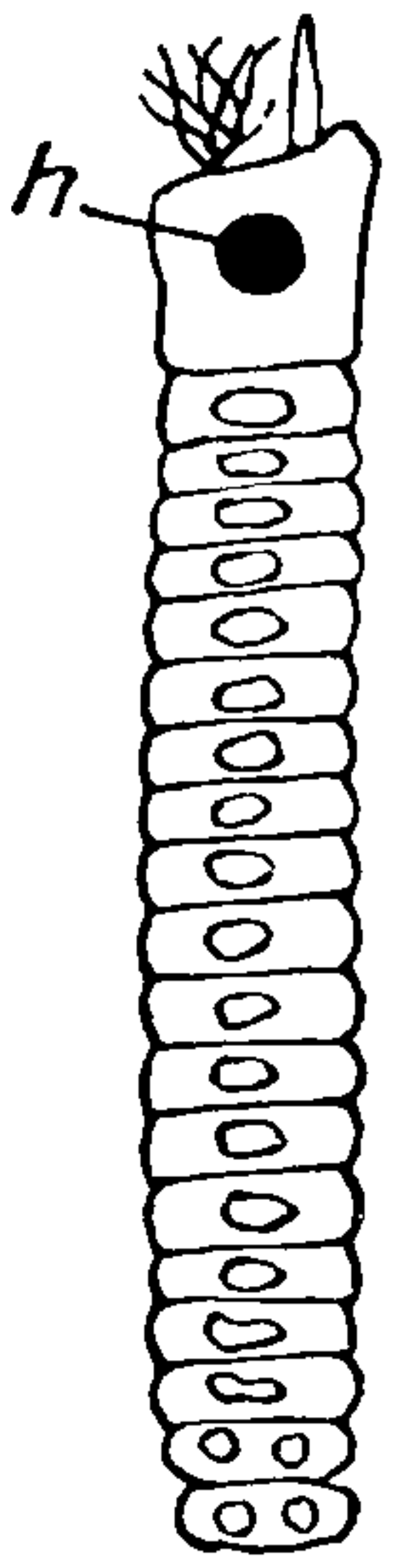

Fig. 52.—*Haplozoön lineare*, an example of a linear colony. *h*, somatic cell; other cells germinal. (*From Huxley after Dogiel.*)

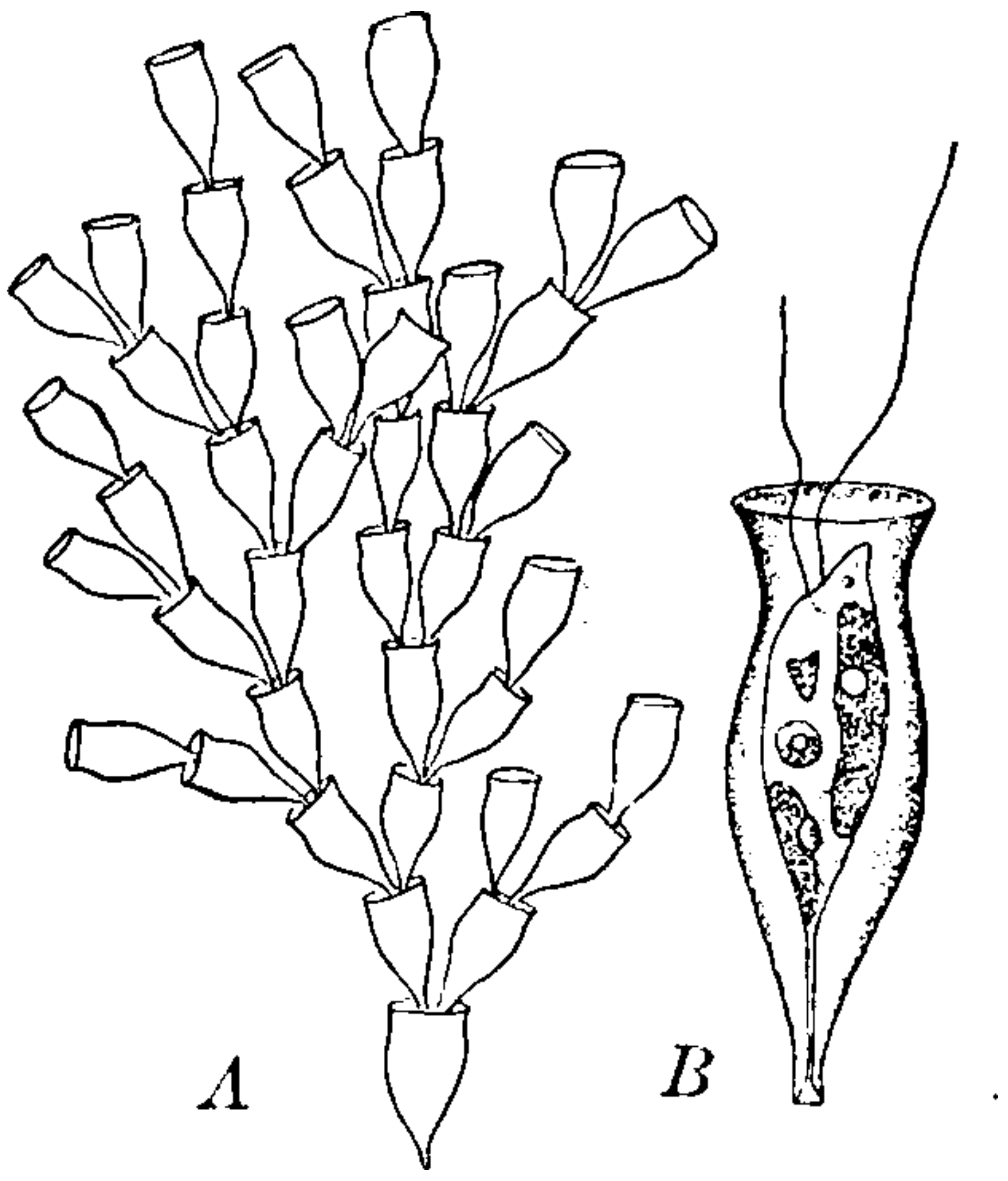

Fig. 53.—*Dinobryon sertularia* Ehrenberg. *A*, arrangement of cells in a tree-like colony; *B*, individual in its cup-like sheath. (*After Kent.*)

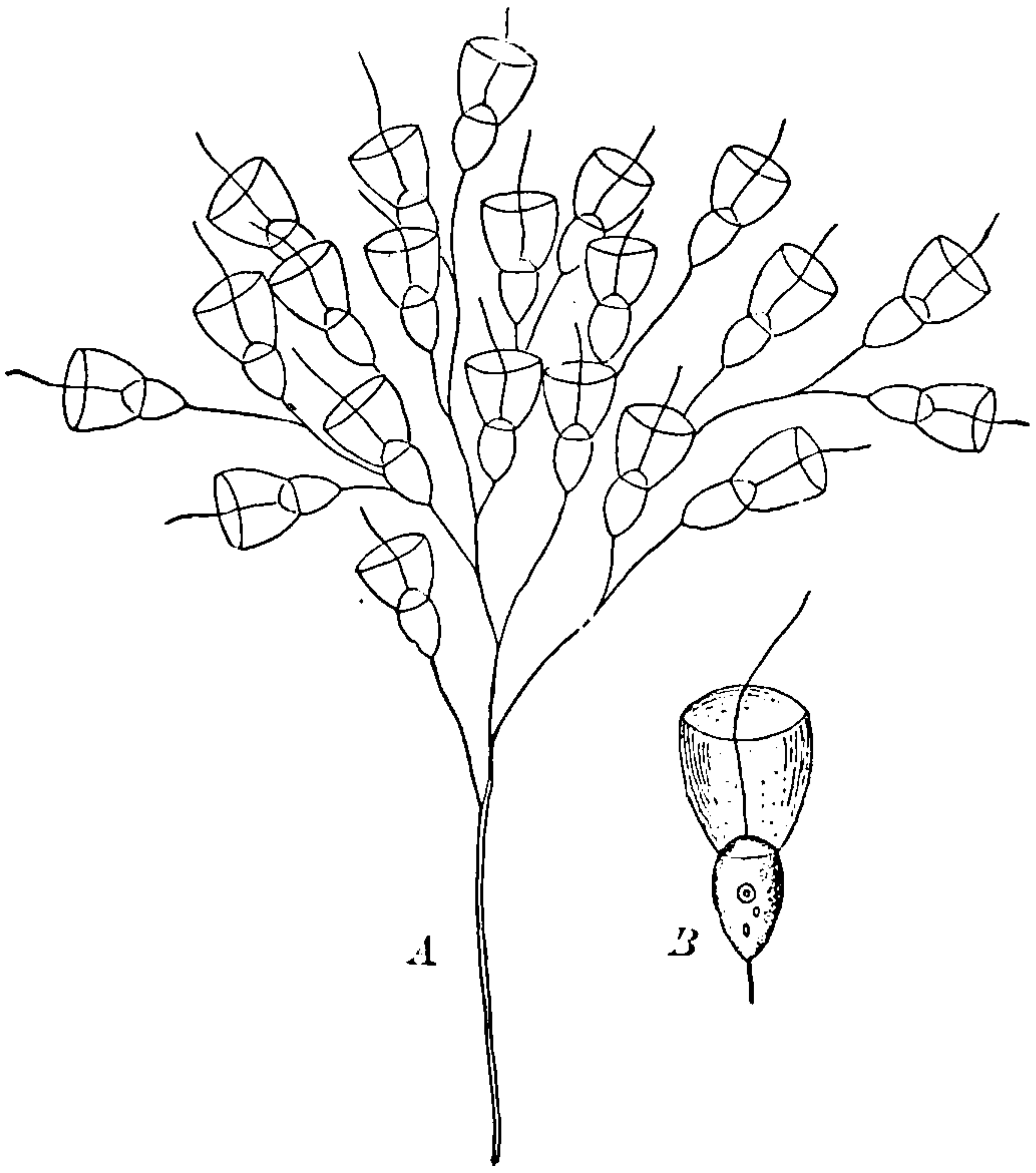

Fig. 54.—*Codosiga cymosa* Kent. *A*, treelike form of colony; *B*, individual cell in detail. (*After Kent.*)

colony. It is composed of groups of flagellated cells borne on the tips of a branched stalk.

A series of dendritic colonies beautifully graded in complexity is exhibited by species of Vorticella, Epistylis, Carchesium, and Zoöthamnium. Individuals belonging to species of Vorticella are unicellular and never form organic colonies. Each individual is provided with a contractile stalk. Cell division is followed by the complete separation of one or both cells from the old stalk. The free cells swim about and finally each attaches itself to some object by its aboral end and then produces a new stalk. The species of the other genera named above occur as more or less complex tree-like colonies. In some species of Epistylis there may be as few as two cells on a non-contractile stalk, but in *E. flavicans* there may be hundreds of individuals and many primary stalks with their branches imbedded in a mass of jelly of the size of a walnut or even of a baseball. Such a colony is a combination of the dendritic and spheroid types.

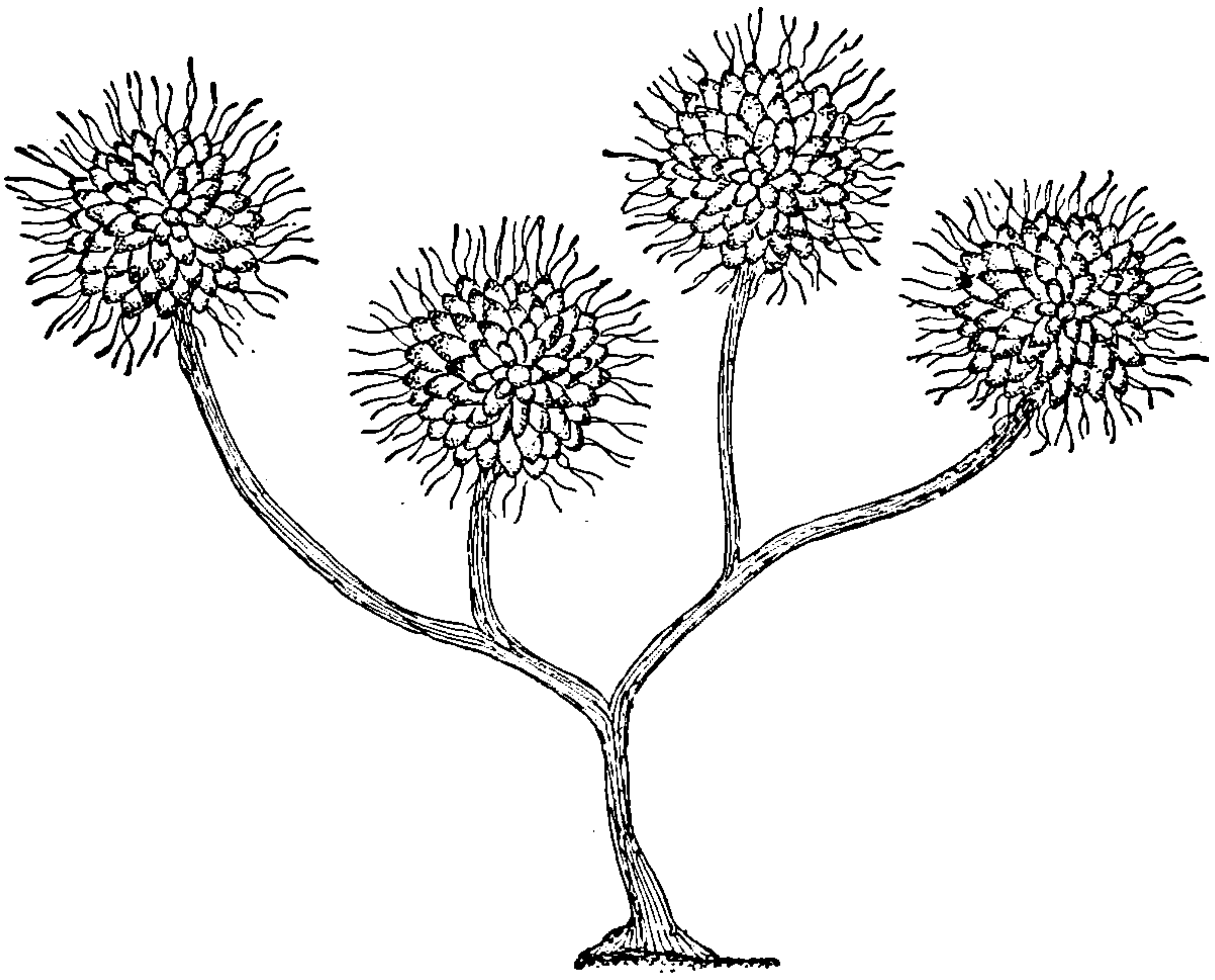

FIG. 55.—*Anthophysa vegetans* Müller. Spheroidal colonies arranged on a branching stalk, thus combining two types of colonies. The stalk is made up of many fibers. (*After Kent.*)

Spheroid colonies are somewhat spherical or ellipsoidal in form. Their cells usually form a superficial layer in a gelatinous mass (Fig. 56). Stalks may connect the cells with a common center, as in Synura or in some species of Uroglena, while in other genera there may be no stalks.

A beautiful series of spheroid aggregations illustrating development in complexity is found in the Volvocales. The genera comprising this series are Gonium, Pandorina, Eudorina, Pleodorina, and Volvox. The members of the series probably all took their origin from a form like Chlamydomonas, whose single cell is furnished with a nucleus, chloroplast, pyrenoid, stigma, vacuoles, two flagella, and a cell wall (Fig. 57).

With regard to differentiation the simplest colonial form of the series is Gonium, of which there are two species, *G. sociale* with only four cells and *G. pectorale* with 16 cells arranged in the form of a plate.

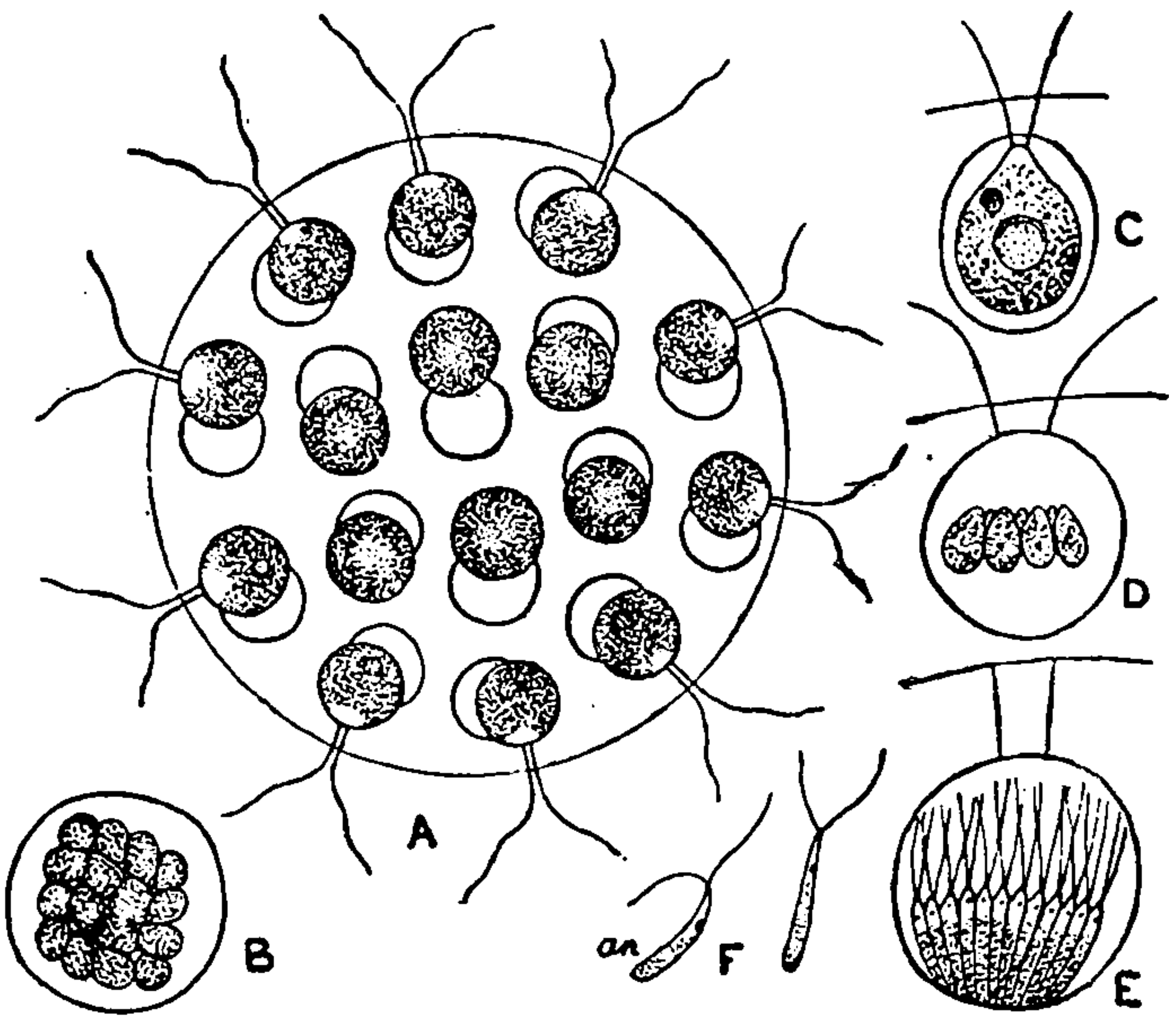

FIG. 56.—*Eudorina elegans* Ehrenberg. *A*, adult colony, × 475; *B*, daughter colony produced by division of one of the cells of *A*, × 730; *C–E*, development of spermatozoa from a mother cell; *F*, spermatozoa. (*From West after Goebel.*)

The cells of these species are so arranged that all their flagella protrude from the same side of the jelly mass. The inclusion of *Gonium pectorale*, a flat plate, among spheroid colonies would be open to question if it were not for the fact that the cells of the young colony are not arranged in a plate but in a rounded mass formed by division in three planes. By a subsequent rearrangement of the cells they come to lie in a plane. The adult colony of *Gonium pectorale* and *Gonium sociale* are shown in Fig. 58. *Pandorina morum* forms the next step in the series. A colony of Pandorina (Fig. 59) consists of a compact group of 8 to 32 cells, the usual number being 16, arranged in the form of a small sphere. The whole is embedded in a secreted jelly-mass to which each cell contributes. Since the cells are in contact their sides are flattened. Each cell resembles a little pyramid whose apex is at or near the center of the sphere. A slight step in advance of Pandorina is presented by *Eudorina elegans*. A colony of Eudorina (Fig. 56) consists of 32 cells situated rather far apart and near the surface of a nearly spherical mass of jelly. In each of these forms (Gonium, Pandorina, Eudorina) the cells of a colony are similar to one another.

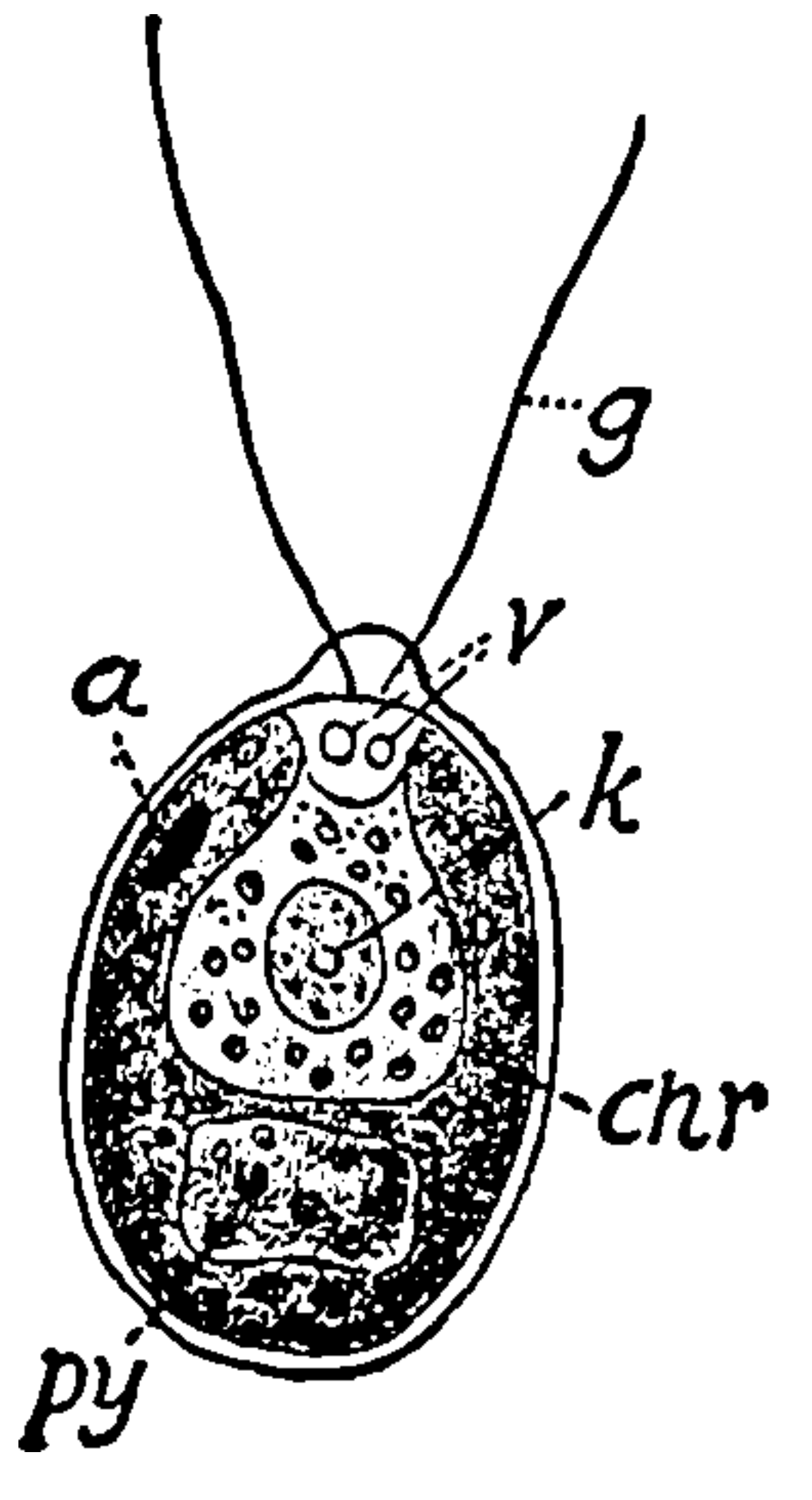

FIG. 57.—Chlamydomonas, a single vegetative cell. *a*, stigma; *chr*, chromatophore; *g*, flagellum; *k*, nucleus; *py*, pyrenoid; *v*, vacuoles. (*From Hegner after Oltmanns.*)

The series finds its culmination in the genus Volvox, the species of which show considerable range in size and complexity. The number of cells in the mass ranges from 200 to 2000 in the smallest species, *Volvox aureus*, and to more than 50,000 in *V. rousseletii*. In all the species the cells are arranged near the surface of a hollow sphere of a gelatinous or mucous material. In old specimens of *V. perglobator* the cells are widely scattered while in *V. rousseletii* they are compactly arranged. The cells of Volvox are of two sizes, the small cells being in great abundance.

New colonies of the species of Gonium, Pandorina and Eudorina are formed by the repeated division of each of the old cells of the parent colony. In this manner as many new colonies are formed as there were cells in the parent. In Pleodorina only the large cells are capable of producing new groups of cells by fission, the small cells having lost this power. In Volvox the function of reproducing asexually is possessed only by very large cells, the *parthenogonidia*. Since all the small cells have lost this function they resemble cells of the bodies of higher animals and hence are called *somatic* cells (from *soma*, body). The parthenogonidia are irregularly distributed among the somatic cells. Their number varies in different species. They are provided with chloroplasts and in young stages with two flagella. Numerous protoplasmic strands connect the parthenogonidia with the neighboring somatic cells, in the same manner as the somatic cells are connected with one another. When a parthenogonidium divides it produces a plate of cells which by subsequent movement of the cells becomes molded into a hollow sphere which for some time has an opening to the exterior. As the sphere increases in size it sinks into the cavity of the parent and finally comes to lie entirely within the parental cavity. After having attained considerable size, these small spheres, the young individuals, escape from the parent by a rupture in the wall of the latter. Sexual reproduction occurs in all the genera of the Volvox series by means of specialized cells, the gametes or mature germ cells, two of which fuse to form the oösperm. The oösperm then divides to form a new individual. The variations in the reproductive processes of this series cannot be described here, but when they are discussed in a later chapter it will be found that in its method of sexual reproduction as well as in its structure Volvox is more complex than the other members of the series.

This series shows increasing complexity in aggregation, a complexity which involves not only increase in the size of the aggregation as a whole, but also a modification in the size, form, and function of some of the component cells. These modifications may be traced as a series of steps, beginning with colonies of unmodified cells and extending to aggregations possessing three types of cells.

Differentiation.—Modification from the simple to the complex, like that which has apparently occurred in the development of Volvox, may be called *differentiation,* which means a becoming different. This term is also used concretely to denote the end result of the change. Differentiation always involves structural changes of some sort, such as changes in size, form or proportions, and also internal changes, some of which may be invisible. Differentiation, moreover, always involves *specialization,* and is always accompanied by *division of labor.* By specialization is meant limitation of function to one or a few processes; by division of labor, the parceling out of various functions among cells, structures, or individuals. The most obvious applications of the terms differentiation and division of labor are found in complex animals, but they may be properly employed for very simple cells. For instance, simple cells are not made up of a homogeneous material. Their protoplasm is differentiated into parts, as was pointed out in Chapter II. In Amœba there are relatively few parts, in Paramecium there are many more parts. In other words, differentiation has gone farther in the latter animal than in the former.

It is not sufficient, however, to regard differentiation as referring entirely to structural features since differentiation also involves function. Each differentiation of protoplasm as manifested in some structure of a cell is concerned with the performance of a certain function or at most with a limited group of functions. In Paramecium, for example, a certain part of the cell is concerned with locomotion, another with the expulsion of waste materials, another with movements incident to food-taking. Other portions secrete digestive enzymes. The micronucleus is concerned with sexual reproduction and perhaps with certain other functions. Thus even in single cells there is division of labor.

Division of labor is more apparent, but no more real, in some cell aggregations than in the single cell. In Volvox certain cells (the somatic cells) maintain the form of the body and care for the general functions of the entire group, such as locomotion, nutrition, and responses to stimuli; cells of another type (the parthenogonidia) are set apart for the multiplication of the species by asexual methods; and still other cells (the true germ cells) for the sexual method of reproduction. The somatic cells are incapable of functioning as germ cells. Each type of cell has a definite duty or circumscribed group of duties to perform. In a word each cell is a specialist in its work. Its structure is such that it can perform its function sufficiently well for the species to maintain itself and when each cell performs its functions properly all the needs of the aggregation are met. Division of labor is thus a type of coöperation accompanying differentiation in which the sum of the functions of the parts makes up the functions of the organism as a whole.

Organization.—With differentiation, specialization, and division of labor there is always *organization.* This is true of an animal or plant whether composed of only a single cell, or of many cells. In such a living thing the separate parts are organized into a whole. This whole is the *organism.* It may be simple or complex, small or large, but to be an organism it must be capable of maintaining itself. Its parts live and grow and even increase their kind while in connection with the whole, but these parts cannot maintain a separate existence.[1]

Analogy From Industrial Organization.—The relations of the parts of some animal organizations to the whole will be made clear by an analogy drawn from the field of industry. At the beginning of an enterprise a man usually carries on the whole business alone. In the conduct of the business he combines in one person the functions of producer, seller, buyer, and executive. As the volume of the business increases the individual associates with himself another who shares these duties. With the passage of time the business grows and the partnership becomes a company hiring many helpers, and finally it becomes a corporation the conduct of whose affairs requires the combined efforts of many people, each person performing a certain kind of work, perhaps at the forge, lathe, or saw, or as foreman, factory superintendent, sales manager, or clerk. There may, in fact, be whole groups of people, each group doing the same kind of work. All these form a complex organization of individuals all working not only as individuals with certain ideas regarding profit to themselves but as members of an association working toward the accomplishment of a common end. The groups in turn perform duties and create products which bear certain relations to the functions or business of the corporation. The output is therefore the result of the coördinated efforts of many individuals. The corporation is a complex organization for a community of effort. It is the sum of its parts, that is, executive force, sales force, factory, and so on. The executive cannot maintain the proper function of the corporation without the rest of the organization, nor can the individual laborer perform his function which may be a single operation, the shaping of a single piece, apart from the organization. Specialization and division of labor in such an organization has been carried to a high degree of perfection. Among men the development of any particular corporation is likely to proceed gradually as indicated above. Thus it is possible to find at any time industrial organizations in any stage of development from the stage of individual endeavor to the corporation or the trust. So, too, among animals grades of organization exist with their attendant differentiation into parts and varying degrees of division of labor.

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[1] Experiments have shown that this statement requires some qualifications which cannot be given here. See works of Loeb, Morgan and others on regeneration.

Organization in Simple Metazoa.—In the simpler metazoa organization has not gone as far as outlined above. In the sponges, for example, there is no differentiated nervous system (Fig. 32), but any of the exposed cells are capable of receiving stimuli and conducting impulses in addition to their other functions. In the sponge there are but few contractile cells. These occur singly or in very small groups, and their function is to close up the pores through which the water passes. The germ cells are scattered and do not form tissues. The cells which line the radiating canals and which are therefore widespread in the animal carry on digestion. There is no circulating medium which carries food in solution, but digested materials diffuse through the digestive cells into neighboring tissues. There is no tissue specialized for the respiratory function since all cells which come into contact with water carry on respiratory functions in addition to other functions, nor are there any special cells for the elimination of waste materials. From these few statements it is obvious that the cells of the sponge are but little removed from protozoan cells in their degree of specialization.

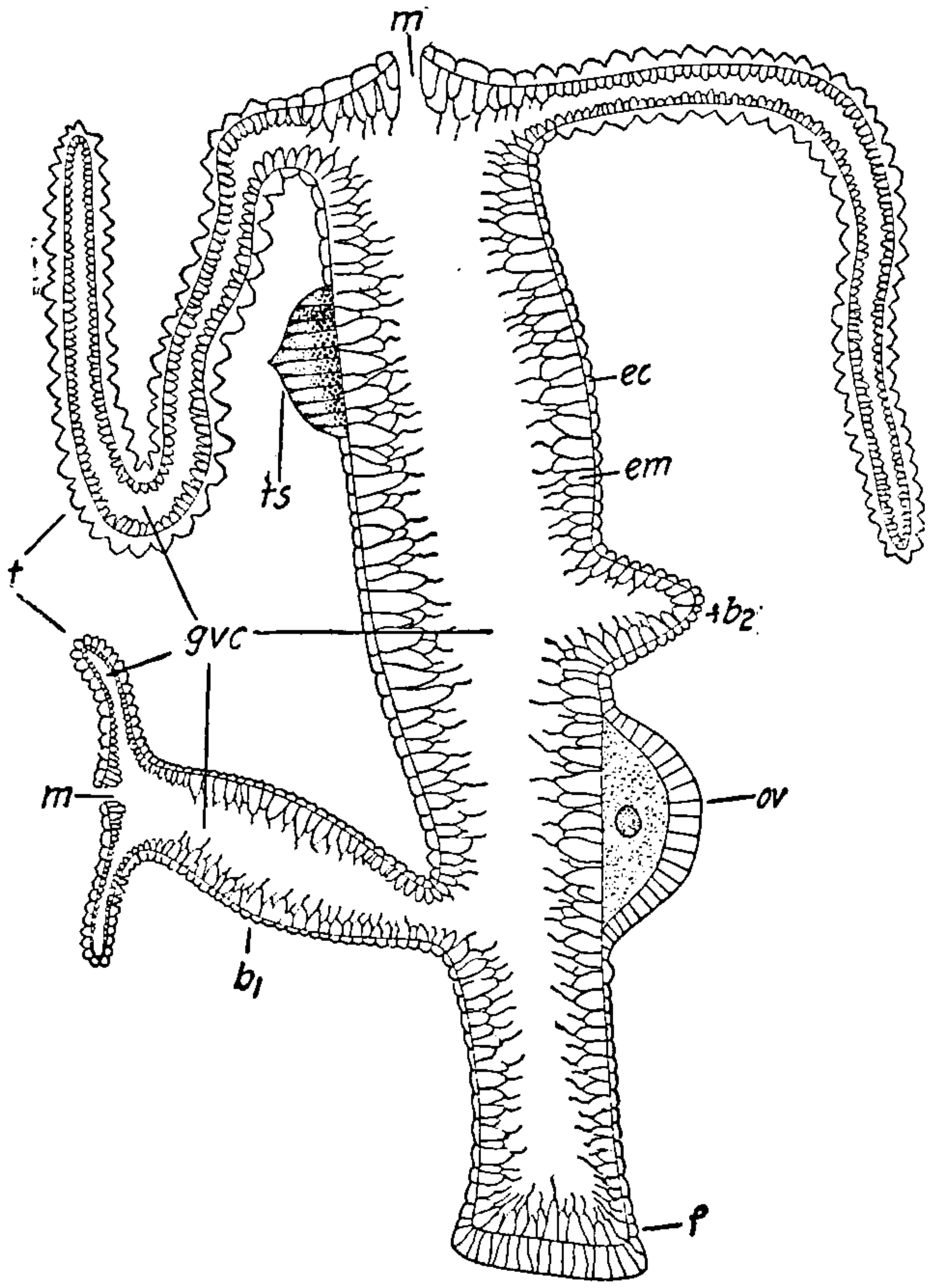

FIG. 60.—Hydra, diagrammatic representation of a sagittal section. *b*1, *b*2, buds in different stages of growth; *ec*, ectoderm; *em*, endoderm; *f*, foot; *gvc*, gastrovascular cavity or cœlenteron; *m*, mouth; *ov*, ovary; *t*, tentacle; *ts*, testis.

Hydra and its allies differ from the sponge in the greater development of cells capable of contraction and in the grouping of reproductive cells into spermaries or ovaries. The cells of the outermost layer (Fig. 60) serve several functions, such as contraction, conduction of stimuli, suppor and covering. Furthermore there are cells of this layer which by means of their thread-like stinging processes are able to serve as a means of protection or assist in the killing of prey. As in the sponge no set of cells is especially concerned with respiration, with the transfer of nutritive solutions, or with the control of the responses of the organism, for most or all of the cells share in these general functions. Thus in the sponge and Hydra there are tissues but their number is small.

Tissues, Organs, Systems.—In more highly organized metazoa the tissues are often grouped into *organs.* A few examples of organs will suffice to make clear the meaning of the term. In vertebrate animals (those with back-bones) the stomach is a highly developed organ. Its inner lining is composed of a single layer of columnar epithelial cells commonly called the *mucosa.* Portions of the mucosa are modified into gastric glands (complex secretory structures) by which is secreted the gastric juice which plays an important part in the digestion of proteins. Surrounding this epithelial tissue is a layer of tough spongy tissue, called connective tissue, which forms a good support for the delicate epithelial cells. About the connective tissue are two layers of muscle cells, the fibers of one layer running round the stomach and those of the other extending lengthwise. They strengthen the stomach wall and by their rhythmic contractions mix the contents of the stomach with the gastric secretion. About the stomach is a layer of closely fitted cells called the peritoneum which acts as a fine, tough, well-lubricated covering. Together these tissues make up the stomach. Such an organization of tissues into a structure which as a whole performs certain functions is called an organ. Other organs are the heart, liver, kidneys, brain, eye, tongue, etc.

Only a part of the general function of digestion is carried on by the stomach. Other organs which play important parts in the process of digestion are the small intestine, pancreas, liver and large intestine. These organs together with the organs for food taking and for the voiding of indigestible portions of the food comprise the *alimentary system.* The term *system* may be defined as an aggregation of organs which coöperate in the performance of one or more general functions. Very complex animals have several systems, among which are the respiratory, circulatory, excretory, genital, muscular, sustentative, and nervous systems.

The number and complexity of the systems possessed by an animal are to a certain extent an index of the degree of its organization. The lowest and simplest metazoa, as Hydra and the sponge, are made up of tissues and it is scarcely proper to use the term organ in referring to any of their structures. Higher metazoa, contrariwise, have many of their tissues incorporated into organs which may be grouped into systems. Higher animals usually have more systems than lower ones and their systems are more complex and the functioning of the systems more complicated. An account of the structure of tissues, organs and systems is deferred to the following chapter and the functions of organs to Chapter VII.

Colony Formation in Metazoa.—Among the metazoa as among the Protozoa certain methods of asexual reproduction, such as budding or fission, may give rise to aggregates or colonies of individuals. The term colony is strictly applicable only to groups of individuals with organic connections and is so used in this book.

An understanding of the nature of colonies will proceed more easily from a knowledge of similar animals in species which do not form colonies. Especially useful for this preliminary purpose, because its near relatives are mostly colonial, is the simple freshwater Hydra. Hydra (Fig. 60) reproduces by budding. As a bud increases in size it may give rise to another bud; and before the first bud becomes separated from the parent three or four buds may begin to grow at other points on the surface of the parent's body. The parent with its buds forms, in effect, a temporary colony. The association does not become permanent because the cells of the parent finally close the connection between the digestive cavity of parent and that of each of the buds and the buds are gradually pinched off. However, while colony formation never occurs in Hydra it is very common in the phylum Cœlenterata to which Hydra belongs, being especially common in the classes Hydrozoa and Anthozoa. The classical examples are the *hydroids*, or Hydra-like colonial members of the former class.

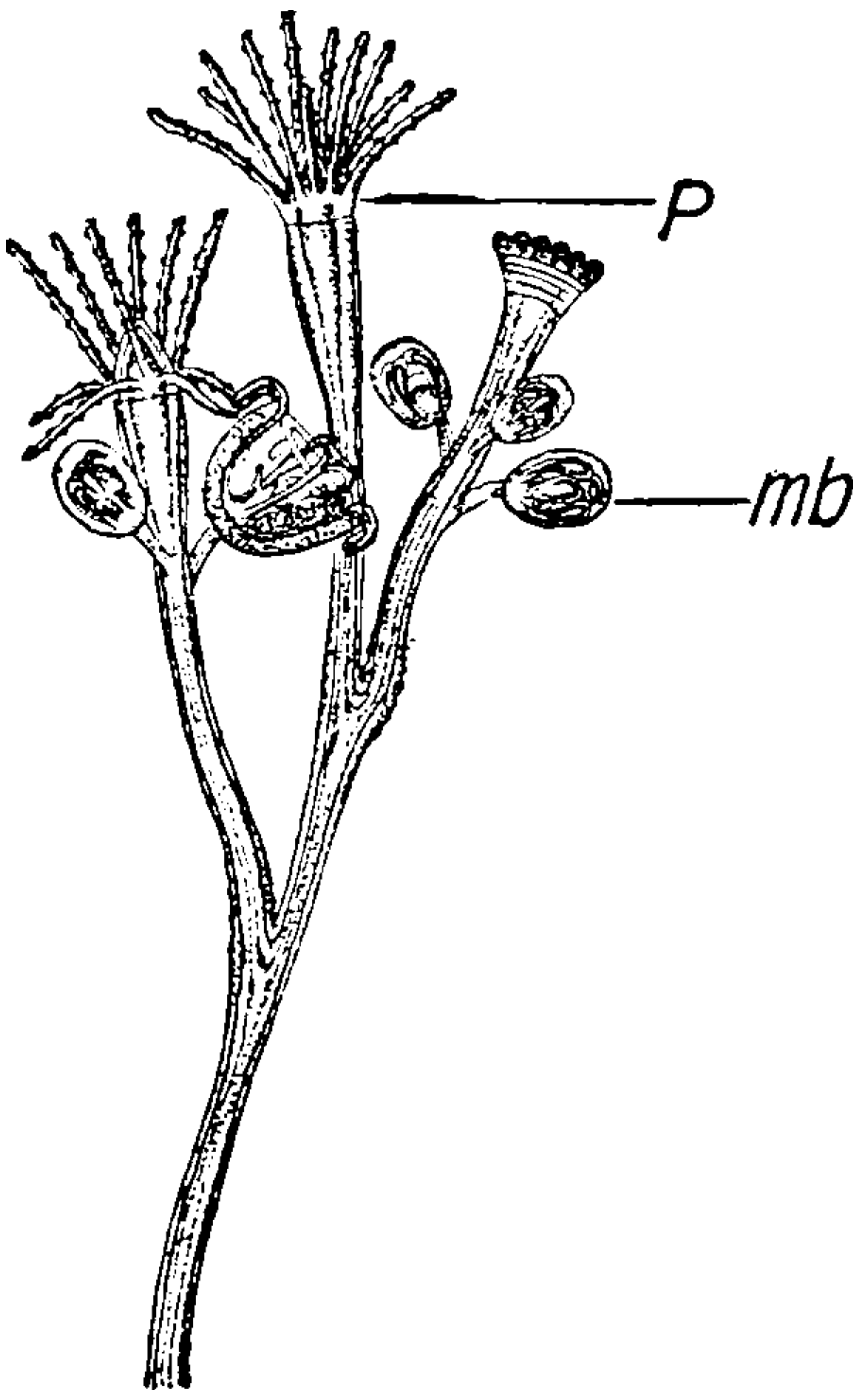

FIG. 61.—The hydroid, *Bougainvillea ramosa*, portion of a colony. *p*, polyp; *mb*, medusa bud. (*After Allman.*)

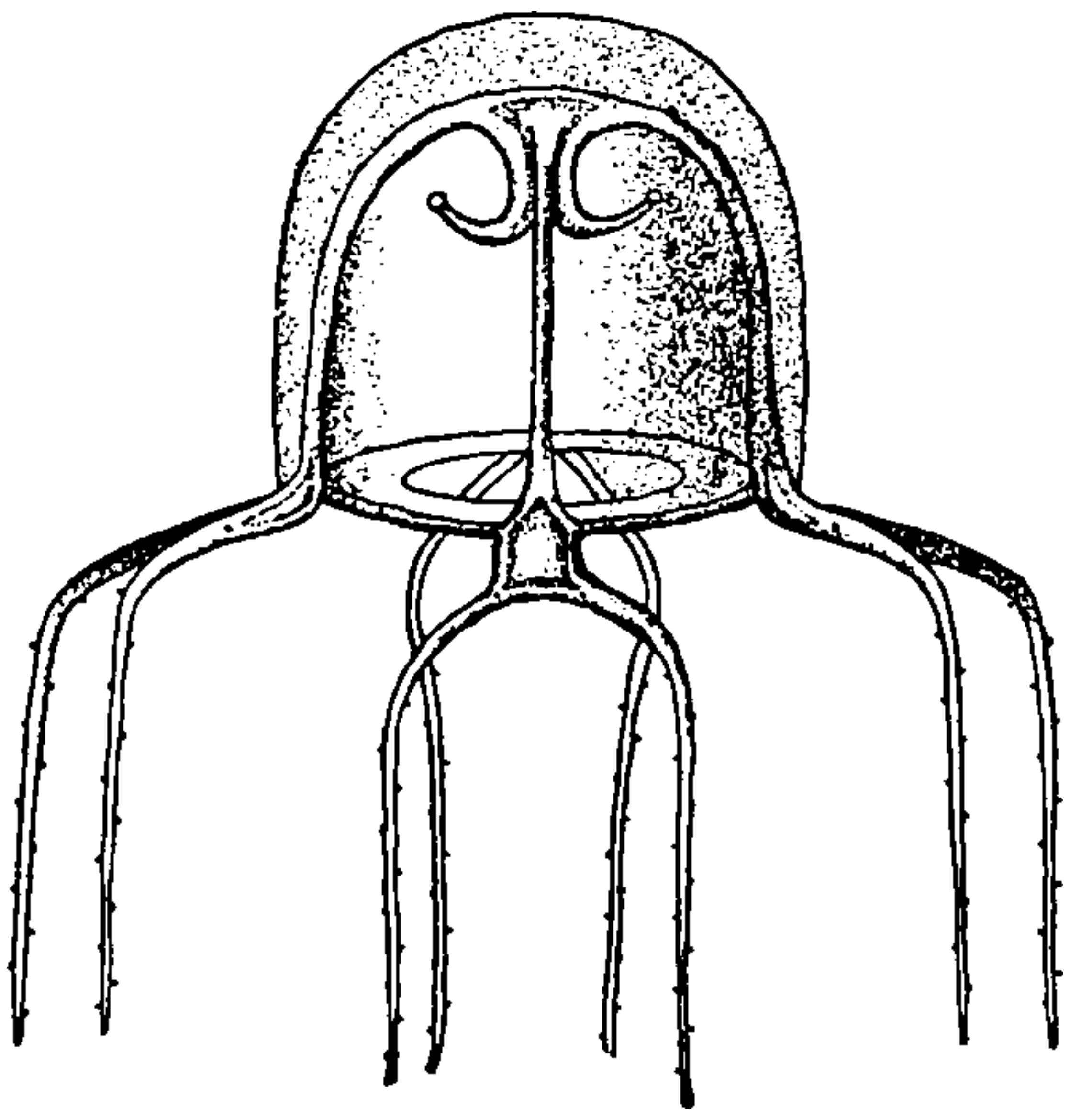

FIG. 62.—Medusa of *Bougainvillea ramosa* freed from the colony, enlarged more than Fig. 61. (*After Allman.*)

Colonies in Hydrozoa and Corals.—Excellent examples of colony formation may be found in the hydroid genera Bougainvillea, Obelia, and Hydractinia. *Bougainvillea ramosa* (Fig. 61) forms a colony with a

phism, meaning that within the same species individuals may have different forms.

The corals are fine examples of colony formation and their skeletons represent the results of the combined lime-secreting activities of the colony continuing through a considerable period of time. Most corals do not show differentiation into two or more types of individual but such differentiation occurs in Hydrocorallinæ.

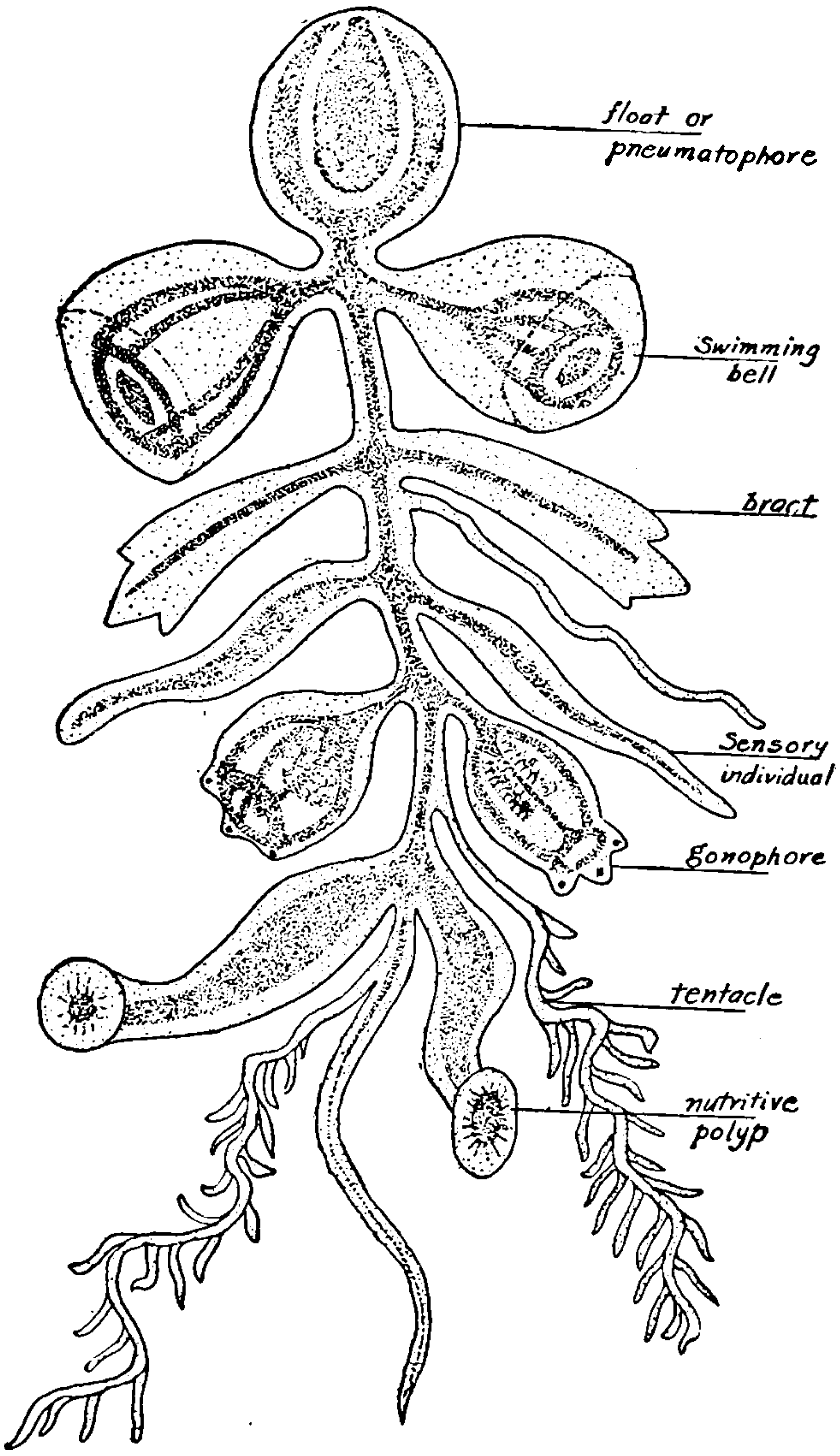

FIG. 64.—Diagram of a siphonophore colony composed of six kinds of individuals. (*Modified from Fleischmann.*)

Colony Formation in Siphonophora.—The most remarkable examples of colony formation and polymorphism accompanied by division of labor occur among the Siphonophora, one of the orders of Hydrozoa. These are free-swimming colonies of great complexity. Each siphonophore colony (Fig. 64) consists of a common tube of cœnosarc 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 cœnosarcal tube. It generally contains gas and serves to support the colony which hangs free in the water. Near the float is a group of swimming bells (*necto-calyces*) which resemble medusæ 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, 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 and Hydractinia and other Hydrozoa, it may be determined that each type of zooid which in a siphonophore resembles and functions as an organ is really a much modified individual,

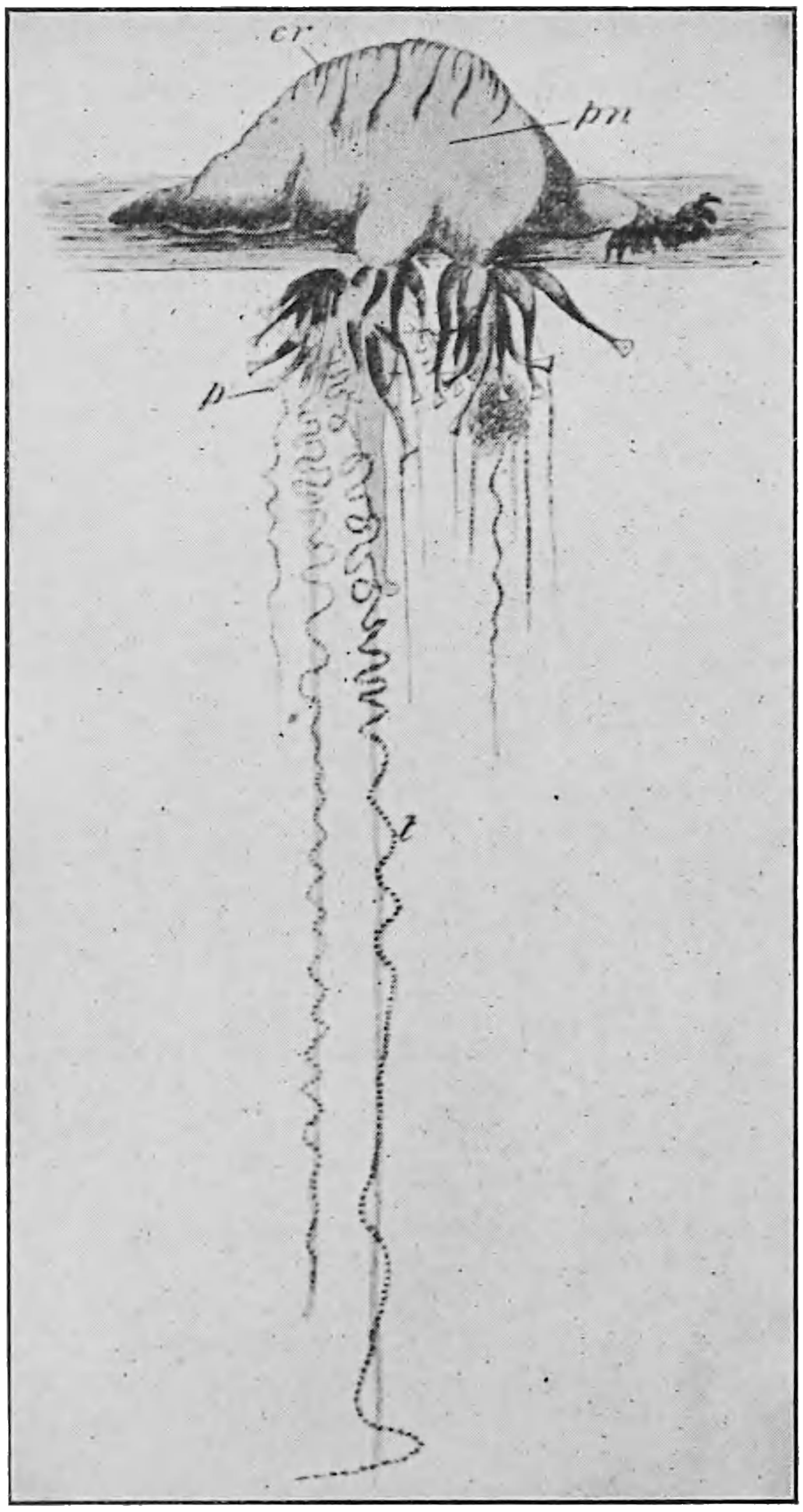

FIG. 65.—*Physalia*, the Portuguese man-of-war, drawn from live animal floating on the surface of the sea. *cr*, crest; *p*, polyp; *pn*, pneumatophore; *t*, tentacle. (*From Parker and Haswell's Textbook of Zoölogy, after Huxley.*)

either polyp or medusa. In certain species the bracts contain remains of *radial canals* which are characteristic of medusæ. The bracts, swimming bells and gonophores are constructed on a medusoid 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 medusæ in typical hydroids, but usually they remain attached.

The "Portuguese man-of-war," Physalia (Fig. 65), 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.

Colonies in Other Metazoa.—Colony formation occurs among a few other groups of animals, namely, the Porifera, the Bryozoa, Cestoda, Annelida (rarely), and Tunicata. Sponges (Porifera) are considered to form colonies but the fusion of the bodies of the individuals is so complete that it is difficult to distinguish their limits. The Bryozoa (moss animals) form dendritic, spheroid, or irregular colonies. Some of them, for example Bugula, also exhibit polymorphism. In a colony of Bugula the most common individual is the nutritive zooid provided with tentacles. Of the other members of the colony the *avicularia* (Fig. 66, *A*), a type of individual shaped like a bird's head and having a movable jaw-like structure, may serve as grasping devices, perhaps for defense; and *ovicells* are

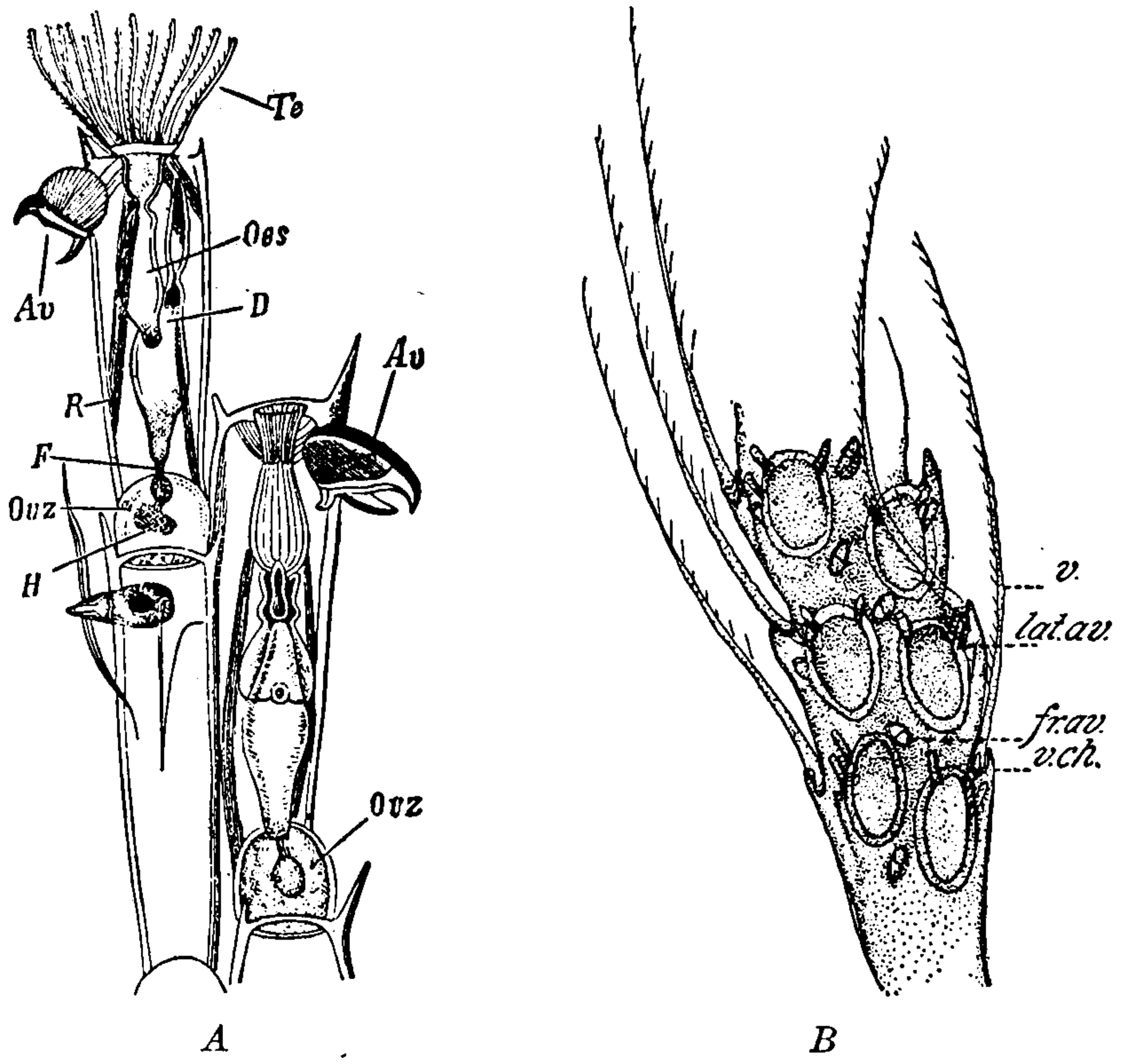

FIG. 66.—Structures of Bryozoa. *A*, *Bugula avicularia*, portion of a colony; *Av*, avicularia; *D*, alimentary canal; *F*, funiculus; *Oes*, esophagus; *Ovz*, ovicells; *R*, retractor muscle; *Te*, tentacles. (*From Sedgwick's Textbook of Zoology, after von Nordmann.*) *B*, *Caberea ellisi*, portion of a colony. *fr. av*, frontal avicularia; *lat. av*, lateral avicularia; *v*, vibracularia; *v. ch*, vibracular chamber. (*From Robertson in University of California Publications.*)

have an individual sheath. Whereas in the colonial cœlenterates there is a common digestive cavity, in the tunicates each individual has its own mouth opening and digestive cavity which discharges through a common *cloacal chamber.* Such a condition is well shown in Botryllus. In Pyrosoma (Fig. 70) the oral apertures open on the outer surface of the cylinder in which the individuals are embedded and the anal (cloacal) opening on the inner surface.

Among the metazoa the formation of colonies (as distinct from societies such as exist among ants, wasps, and bees) 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 or aggregates. Unlike the Protozoa, among which colonies are sometimes formed by rearrangement of cells following fission, among the metazoa colonies are never formed by a rearrangement of the individuals.

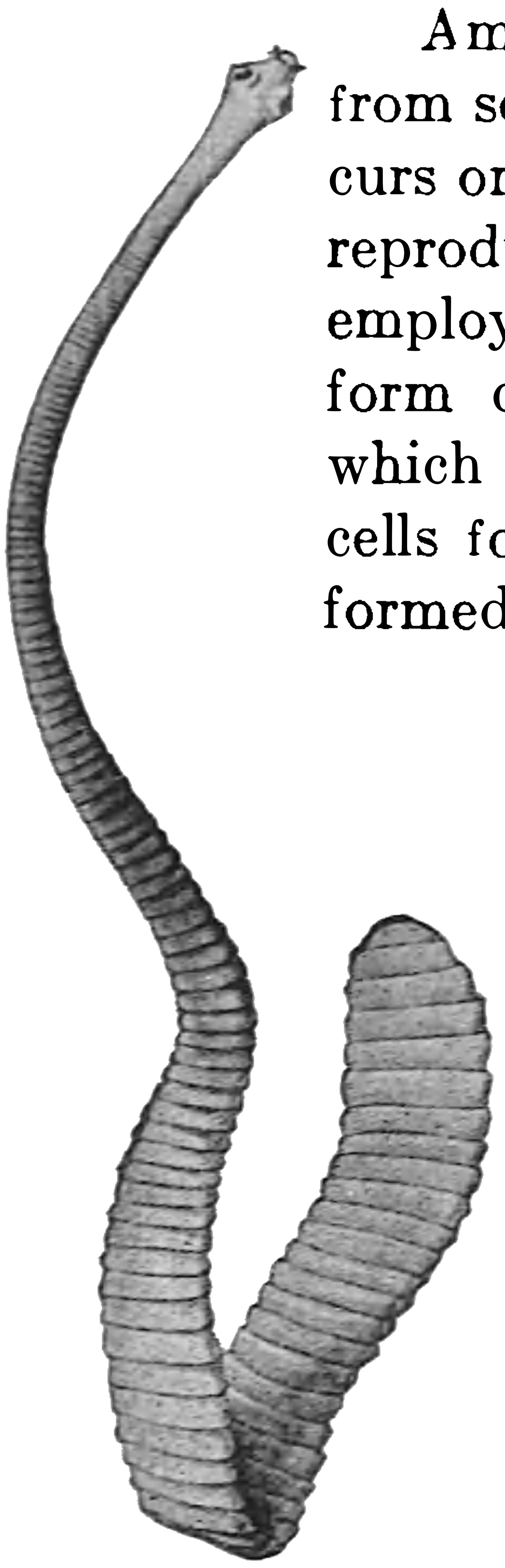

Fig. 68.

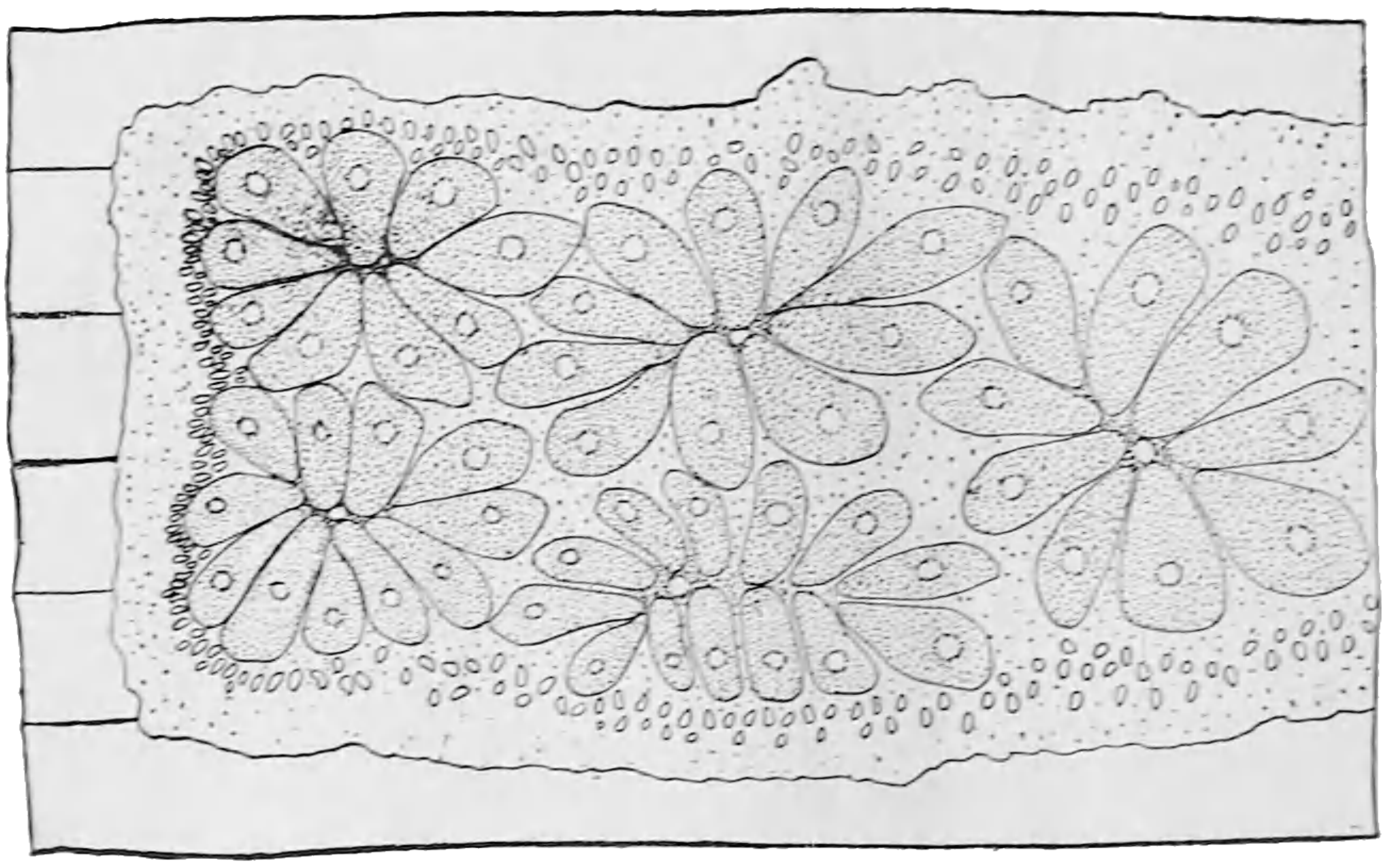

Fig. 69.

Fig. 68.—Tapeworm, *Hymenolepis murina*, from the intestine of the rat. At the upper end of the figure is the scolex or so-called head with suckers and hooks. The segments of the body are equivalent to individuals. (*From Hesse and Doflein.*)

Fig. 69.—*Botryllus gouldii*, portion of a colony attached to a piece of seaweed. Individuals are here arranged in the form of five rosettes, each rosette about a common cloacal aperture.

Origin of Colony Formation.—The colonies described above are organic colonies since each is an intimate union of individuals of the same species. Such colonies may consist of like individuals or there may be differentiation, polymorphism, and division of labor. Differentiation of individuals and division of labor exhibit their beginnings in the Protozoa but find their greatest development in the cells of the metazoan individual and the individuals of the metazoan colonies. Colony formation occurs chiefly among the less highly organized groups of animals and it is most frequent among attached forms. The formation of colonies may be of advantage to the species in that it permits members of the species to occupy as solid masses positions which are favorable to their life processes. This is true of the corals which by reason of their method of building solid skeletal structures as an activity of the whole colony are enabled to thrive in situations where single polyps could not do well. 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. Colony formation seems rather to have been more or less of an accident made possible because of the presence of an asexual reproductive method. It seems not improbable that its origin was due in some groups to a failure of the mechanism by which budding or fission is normally completed.

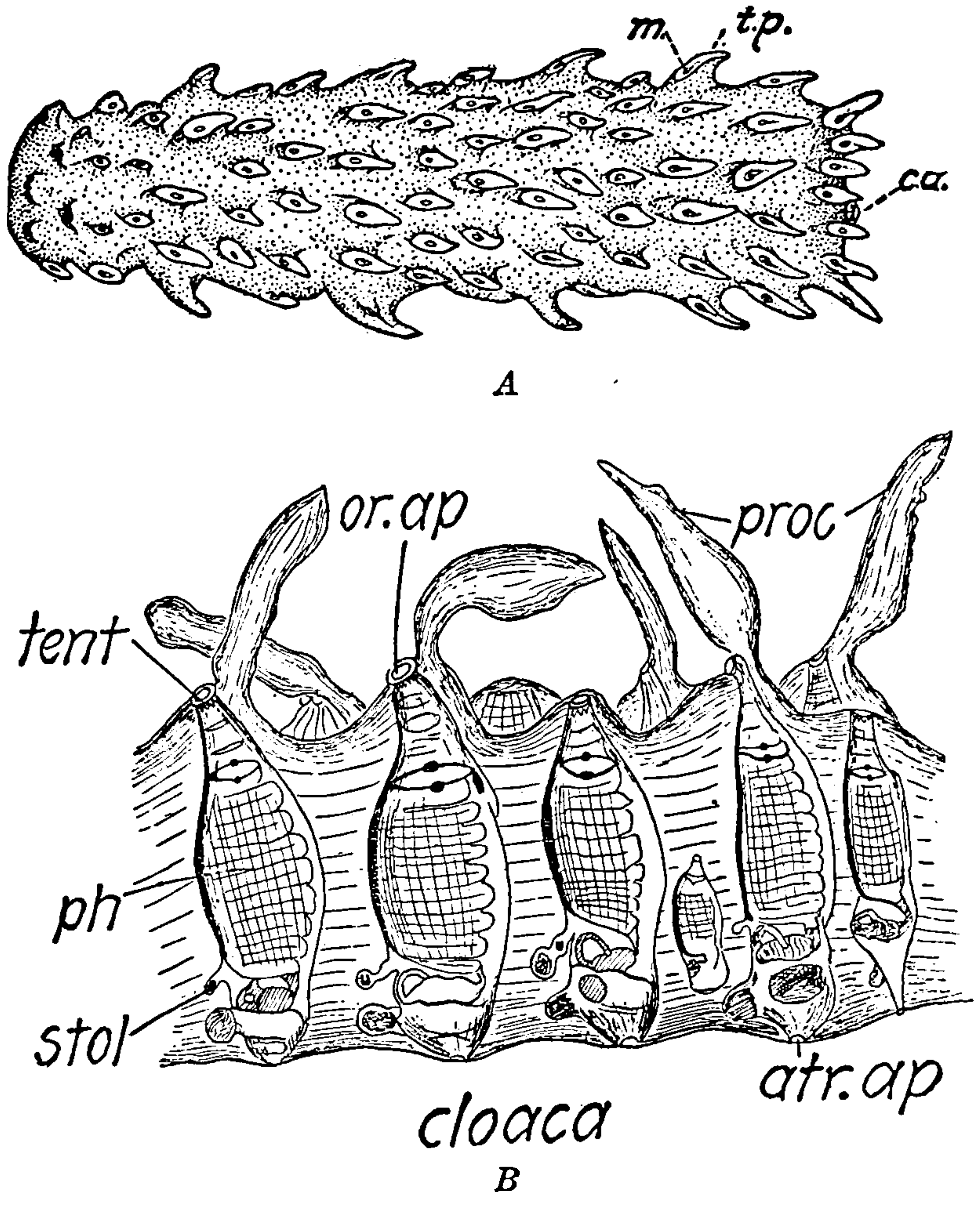

Fig. 70.—The colonial ascidian *Pyrosoma*. *A*, external view of the entire colony, diagrammatic. *ca*, colonial aperture; *m*, mouth of individual; *tp*, test process. (*From Metcalf and Hopkins, after Ritter.*) *B*, longitudinal section of a colony; *atr.ap*, atrial aperture; *or. ap*, oral aperture of individual; *ph*, pharynx; *proc*, process of test; *stol*, stolon from which buds arise; *tent*, tentacles. (*After Herdmann in Challenger Reports.*)

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amples of nearly cylindrical animals are to be found among the Cœlenterata, such as Hydra, jellyfishes, sea-anemones and most hydrozoan and coral polyps. A few of these are illustrated in Fig. 71. In all these animals, whether sessile or motile, the ends differ from each other. Hence a plane which divides the body into two mirrored halves must pass through the long axis of the body; but since the body is circular in cross-section and not differentiated into dorsal and ventral sides almost any plane which passes through the long axis of the body will cut it into mirrored halves. This type of symmetry is called *radial.* Ideally if an animal is to exhibit radial symmetry it must be possible to pass an infinite number of planes through the long axis, such that each plane cuts the body into mirrored halves. Actual examples of such perfect radial symmetry are unknown and in practice an animal is regarded as radially symmetrical if two or more planes of symmetry are present. Thus in jellyfishes, because of the radial canals and some other structures, there are only four planes of symmetry, and in Hydra (leaving out of account certain inconstant features) there are as many planes of symmetry as there are tentacles, yet these animals are regarded as radial. The starfish is sometimes used to illustrate external radial symmetry, the number of dividing planes being five if five arms are present. However, the starfish falls short of radial symmetry in that one of its organs, the madreporite, is not placed in the center but to one side.

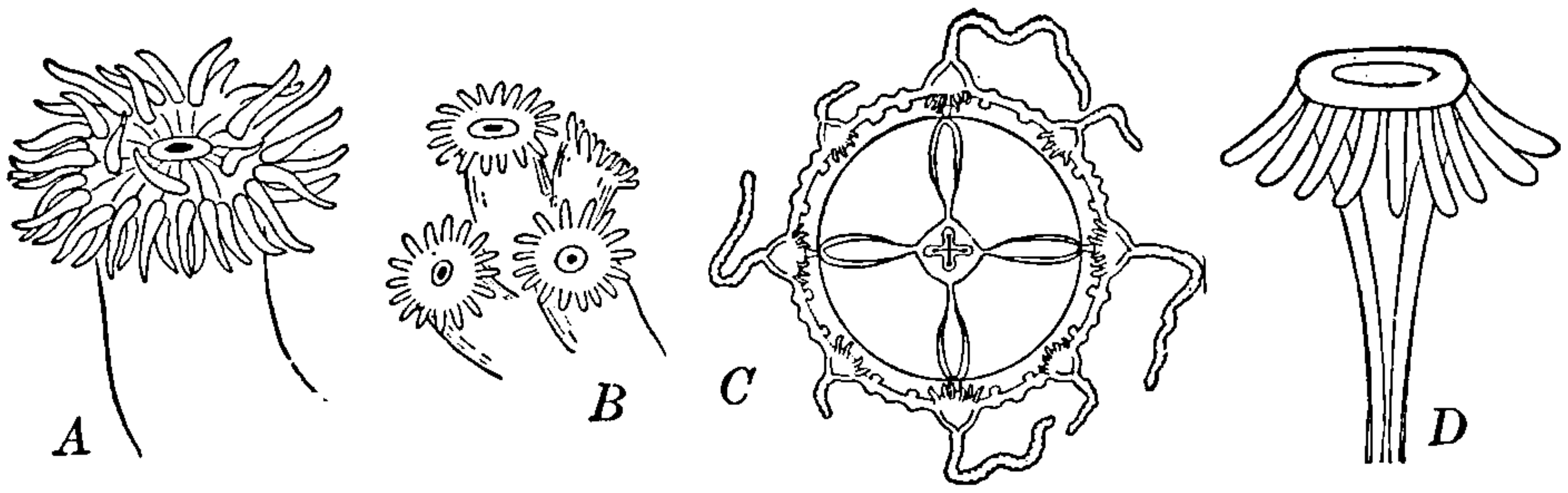

FIG. 71.—Various cœlenterates, showing their radial symmetry. *A*, sea anemone; *B*, group of coral polyps; *C*, the medusa, *Mitrocoma cirrata*, ventral view. *D*, polyp of the hydroid, *Perigonimus serpens*. (*A and B after Jordan, Kellogg and Heath*; *C after Mayer*; *D after Allman.*)

Universal Symmetry.—A few animals possess an approximate *universal* symmetry, but none show it perfectly. To exhibit universal symmetry it must be possible to pass planes through the body in any direction. Such planes must necessarily pass through a central point and the only geometrical solid which may be so cut is a sphere. Very few animals or aggregations of cells or individuals are truly spherical and most of those which are spherical exhibit polarity, that is, opposite sides are in some way differentiated, which makes their symmetry radial and not universal. Volvox comes as near universal symmetry as any animal which can be named, yet some species of Volvox exhibit a certain degree of polarity in that the germ cells tend to develop at one pole or on one side of the sphere.

Asymmetry.—Animals whose bodies cannot be cut by a plane into two mirrored halves are *asymmetrical*. Examples of asymmetrical Protozoa are Páramecium, Amœba (in most states of motion), and Stylonychia. The snail with its coiled shell is asymmetrical but the body is built on a bilaterally symmetrical plan which has been subsequently modified by twisting.

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. Cases in point are found in the heart, stomach, and in fact the major portion of the alimentary tract and the lobes of the liver in man, which are arranged asymmetrically.

Symmetry and Locomotion.—An examination of a large number of animals in regard to their symmetry and a consideration of the mode of life employed by each animal, whether sessile, or capable of slow movement or of rapid movement, reveals a certain relationship between the type of symmetry and the character of locomotion. It is found that most animals which move rapidly or are capable of well coördinated direct movement exhibit bilateral symmetry. Examples in support of this statement are such mammals as the dog and horse, the fishes, amphibians, reptiles, the arthropods, most mollusks and most worms. A large proportion of animals of very slow movement, and especially those which are sessile, show radial symmetry. Examples are the cœlenterates, sponges, and some echinoderms.[1] Universally symmetrical animals are aquatic, and progress by a rolling motion.

Asymmetrical animals which have retained their powers of locomotion are relatively rare except among the Protozoa. In many species whose individuals are apparently asymmetrical the asymmetry is due to modification of a fundamental plan of bilateral symmetry. The flatfishes, such as the halibut, flounder and sole, which have two eyes placed on one side of the head, are in their early stages bilaterally symmetrical, but one eye migrates through the head to its new position. Asymmetry in adult parasitic crustacea is fairly common and is the result of degeneracy. Those species of crustacea, including some parasitic species as well as free-living ones, which retain their powers of locomotion are bilaterally symmetrical. The individuals of many parasitic species which are asymmetrical in either the adult or larval periods are always bilaterally symmetrical in their free-swimming stages.

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[1] Frequent mention must be made, in this chapter, of the groups of animals. It is not important that the student be able to recognize these groups at the present time, but reference should be made to the synoptic table in Chapter XII to determine whether the groups stand low or high in the animal scale. Common names of members of the group may usually be found in the glossary.

Metamerism.—Animals exhibiting metamerism are composed of a linear series of body segments fundamentally alike in structure. These units are called *segments, somites,* or *metameres* and animals so constructed are said to be *segmented* or *metameric.* In simple metameric animals the somites closely resemble one another in size, form and in 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. 83 and 142) is a metameric animal.

It is composed of a series of ring-like 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 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. However, the primitive arrangement 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 adults of vertebrates, however, for in the mammals, for example, metamerism may be seen in the vertebræ, ribs, spinal nerves and ganglia and branches of the dorsal aorta (artery).

Metamerism is interpreted by some biologists as indicating an earlier colony formation, the somites representing the individuals of the colony. It is not improbable, however, that rhythmical processes occurring during development are responsible for the division of the body into similar parts, and that the ancestors of metameric animals were never colonial.

Internal Organization.—The organization of cells into tissues, tissues into organs and organs into systems has been described in the preceding chapter and repetition of this account is avoided as far as possible here. It is important, however, in relation to problems discussed later, to describe in more detail tissues, gland-formation, and the general morphology of the systems of organs as they exist in the more complex animals.

Tissues may be classified with reference to their general function into four types, *epithelial, sustentative, contractile,* and *nervous.* All animal tissues may be referred to one or another of these general types which are discussed briefly below with reference to their structure and functions.

Occurrence and Function of Epithelium.—This kind of tissue covers all outer and inner surfaces of the body. It is composed of simple cells

axis. The cells adhere after division and in this manner several layers of cells (Fig. 72, *H*) are built up and the epithelium is spoken of as *stratified.* The outer layers of cells in such epithelia become flattened until the outermost layer is composed of very thin flat cells which have the shape of polygonal tiles (Fig. 72, *D*) accurately fitted together. Stratified epithelium forms the lining of the mouth and rectum of mammals and some other vertebrates. The outer skin of adult vertebrates is also made up of stratified epithelium. In the frog and other amphibians and certain reptiles, as snakes, the hardened outermost layer of skin (*stratum corneum*) is shed as an extensive layer. In most terrestrial vertebrates these outer cells are shed in minute flakes.

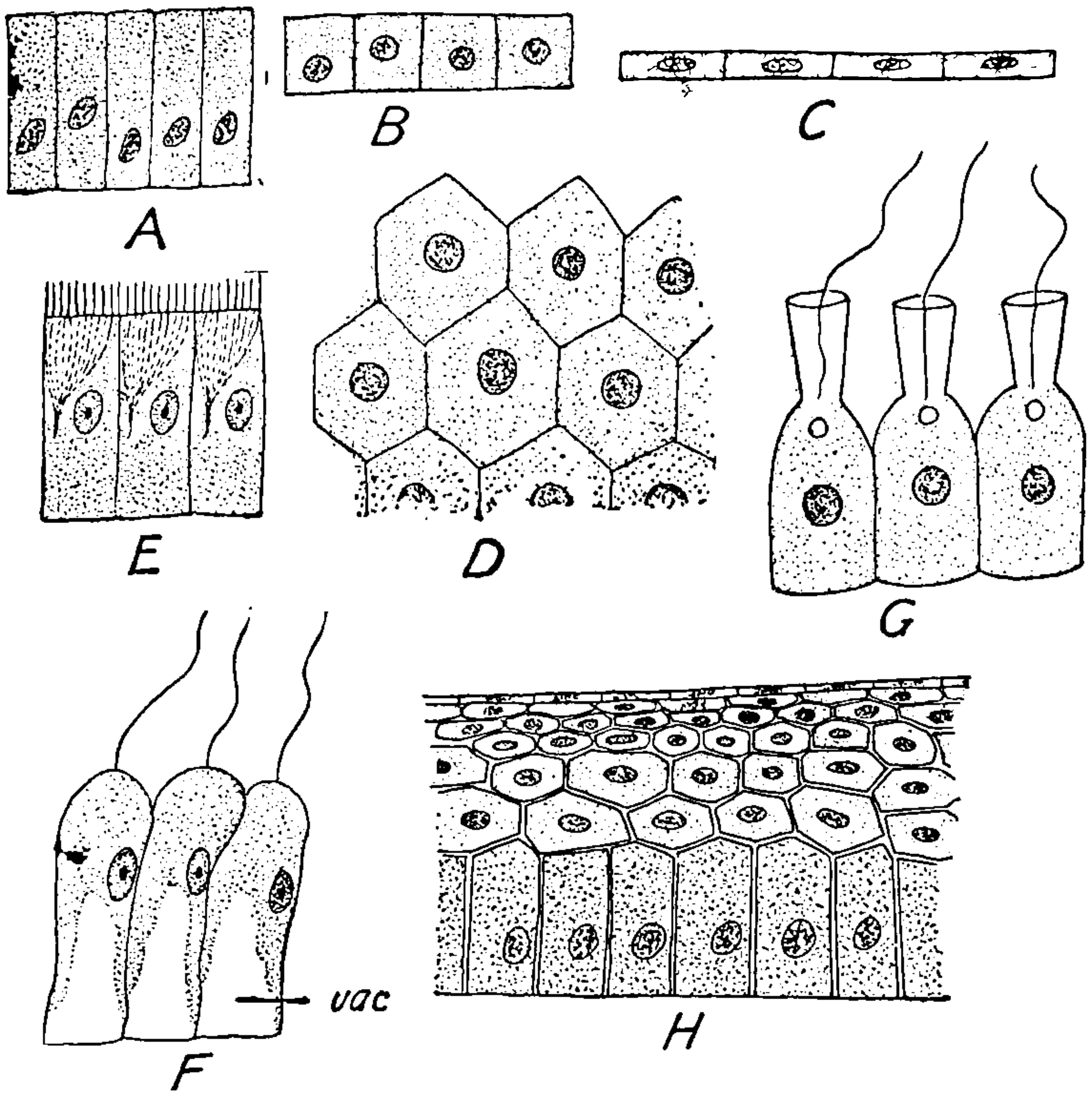


Fig. 72.—Types of epithelium. *A*, columnar; *B*, cubical; *C* and *D*, squamous (side and surface views, respectively); *E*, ciliated; *F*, flagellated; *G*, collared; *H*, stratified; *vac*, vacuole.

Glands.—Many epithelial surfaces are smooth or plain with all the cells lying in a single layer. In such a tissue scattered cells may be differentiated from the others for the production of a secretion. The substance produced may be *mucin,* from which mucus is derived, some digestive secretion, or any one of many other products. Such a layer of epithelium is shown in Fig. 73, *A*, and examples of it are found in the hypodermis of the earthworm or the intestinal epithelium of the frog. This is the simplest form which secreting surfaces take. In slightly modified secretory epithelia the bodies of some large secretory cells may drop below the general level, as in Fig. 73, *B*. Examples of such enlarged and displaced secreting cells may be found in the epithelia covering the tongue of the frog and the foot and mantle of freshwater mussels. In other instances the secreting cells may be grouped instead of isolated, in which case they form what may be called a surface gland, as in *C*. A greater secreting surface is secured when a group of secretory cells drops below the general surface as in *D*. This constitutes a *simple* gland, that is, one which consists of a single depression and is not branched. It is produced by a process of *invagination* or infolding and may be *tubular* (Fig. 73, *F*) or *alveolar* (*D* and *E*) depending on whether the channels are of uniform bore or are inflated. If the invagination is carried far below the general surface, a *neck* (*E*) may be produced through which the secretions are conducted to the surface. The neck is usually composed of non-secreting cells. Glands of this sort are common in the skin of amphibians.

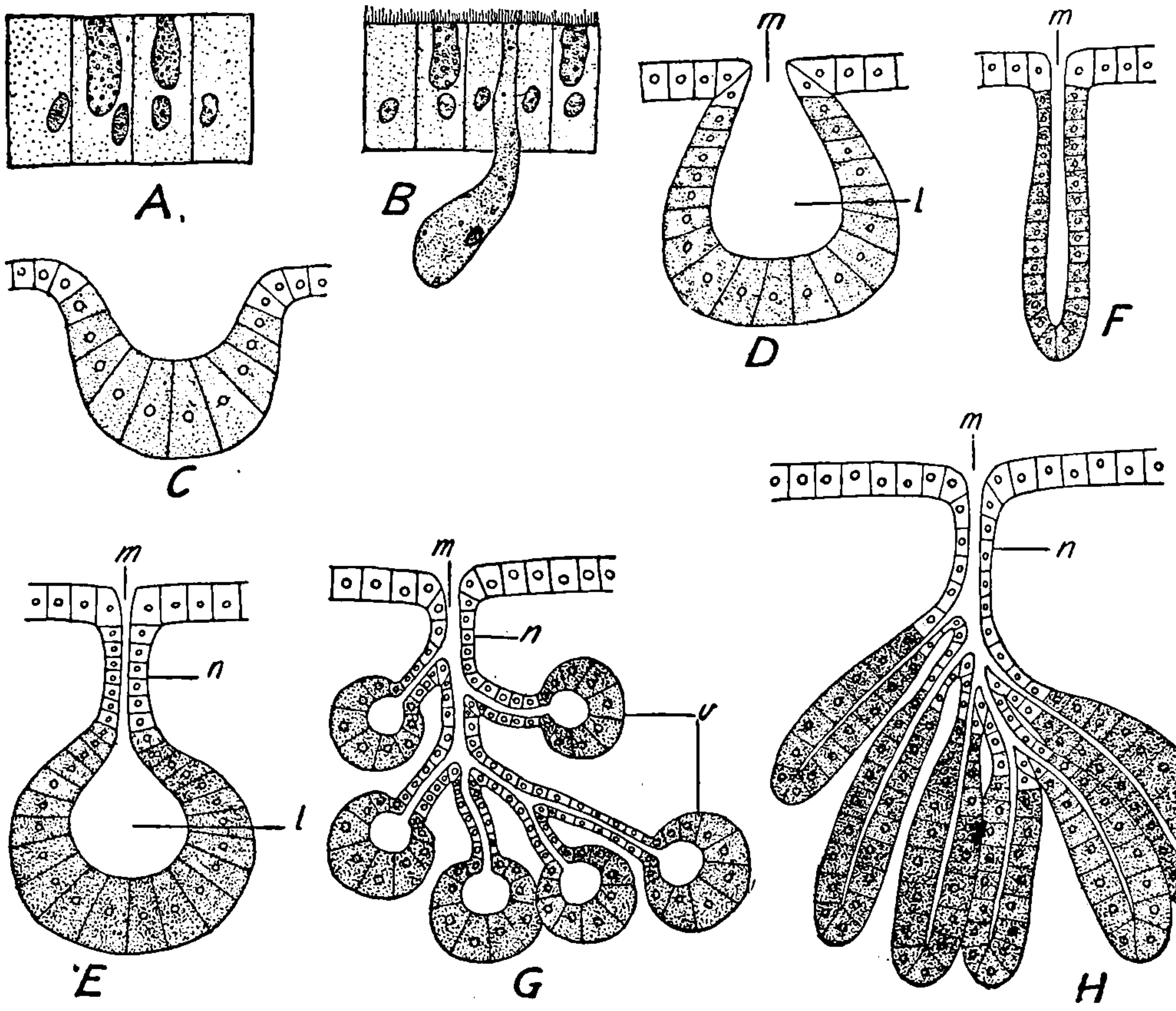


Fig. 73.—Types of secreting surfaces and glands. *A*, scattered gland cells (two goblet cells containing secretion in the darkly stippled *goblets*); *B*, gland cell enlarged and dropped below general level; *C*, group of secreting cells dropped slightly below the general level; *D*, a simple multicellular 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.

From a simple gland, as shown in Fig. 73, *E* or *F*, a *compound* gland may be formed, as in *G* or *H*, by secondary invaginations from the original invagination. Compound glands are common in the wall of the esophagus of mammals and certain amphibians. In the proventriculus (first division of stomach) of the chicken or pigeon are large compound glands.

It is not uncommon that glands produce two or more secretions. If so, there are usually as many kinds of cells as there are secretions produced. When stained the different types of cells can usually be distinguished by their form and appearance. Glands producing two secretions are to be found in the cardiac end of the frog's stomach, and the pancreas produces three secretions.

Glands may be of microscopic size or they may be large. Examples of large glands are the spleen, pancreas, kidneys and liver, the last of which is the largest gland of the body in vertebrates. The large size of these organs is not due, however, entirely to the amount of secreting tissue present, for most large glands as the liver and kidneys are composed of several kinds of tissue in addition to the epithelium. The additional portions include connective tissue, blood vessels and nerves. These tissues have only an accessory function, for in each case the secreting tissue is epithelium.

In view of the morphology of secreting organs, as described above, a gland may be defined as a structure which is derived from an epithelial surface and whose function is the production of a secretion or an excretion.

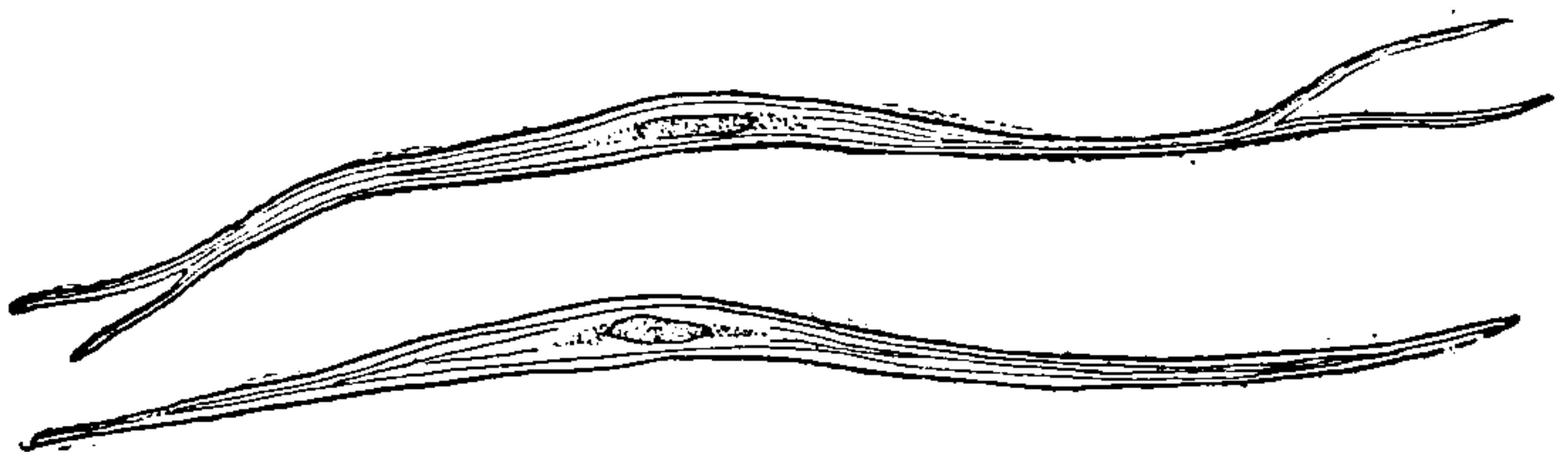


FIG. 74.—Smooth muscle cells.

Sustentative Tissues.—The sustentative tissues are all those which give support to the body and its parts, or connect and bind together cell layers, organs, and systems. They may take the form of rigid supporting tissues such as cartilage or bone; dense connective tissue such as tendons or ligaments; spongy, fibrous, or elastic connective tissues; or adipose tissue for storage of fat. In lower animals simpler types of rigid supporting tissues may be noted but they are omitted from this account. The sustentative tissues find their highest development among the vertebrates.

Contractile Tissues.—Under the term contractile tissues are included all tissues which by their contraction serve to produce motion of an organ or part, or locomotion of the animal as a whole. Among lower animals many individual cells, as the *porocytes* which control the size of the pores through which water enters a sponge, have the power of contraction. Such scattered cells do not form tissues.

Muscle.—In many invertebrates and in all vertebrates contractile cells are aggregated into sheets, layers or groups called *muscles.* Two general structural types of muscles may be recognized, namely, *smooth* and *striated.* Smooth muscle cells, Fig. 74, are somewhat spindle shaped with undivided or with branching ends, and possess one nucleus to

is not so controlled. In general, smooth muscle tissue is involuntary and striated muscle is voluntary, but this distinction fails in part, for the heart muscle of vertebrates is striated but not voluntary.

Nervous Tissues.—Nervous tissues are those which have as their chief function the reception of stimuli and transmission of impulses. These tissues include the perceptory cells of the *auditory, visual, olfactory* and *gustatory* organs and the cells by which the sensations of heat, cold, pressure and so on are perceived. They also include the *nerves, ganglionic masses,* and *central nervous system* which includes brain and spinal cord in the vertebrates and analogous organs in the invertebrates. As mentioned in the discussion of epithelial tissues, some epithelial cells receive stimuli and transmit impulses, and may therefore also be classed with the nervous tissues. The receptive cells of audition, vision, smell and taste are of this epithelial character. Examples of nerve cells are illustrated in Fig. 78.

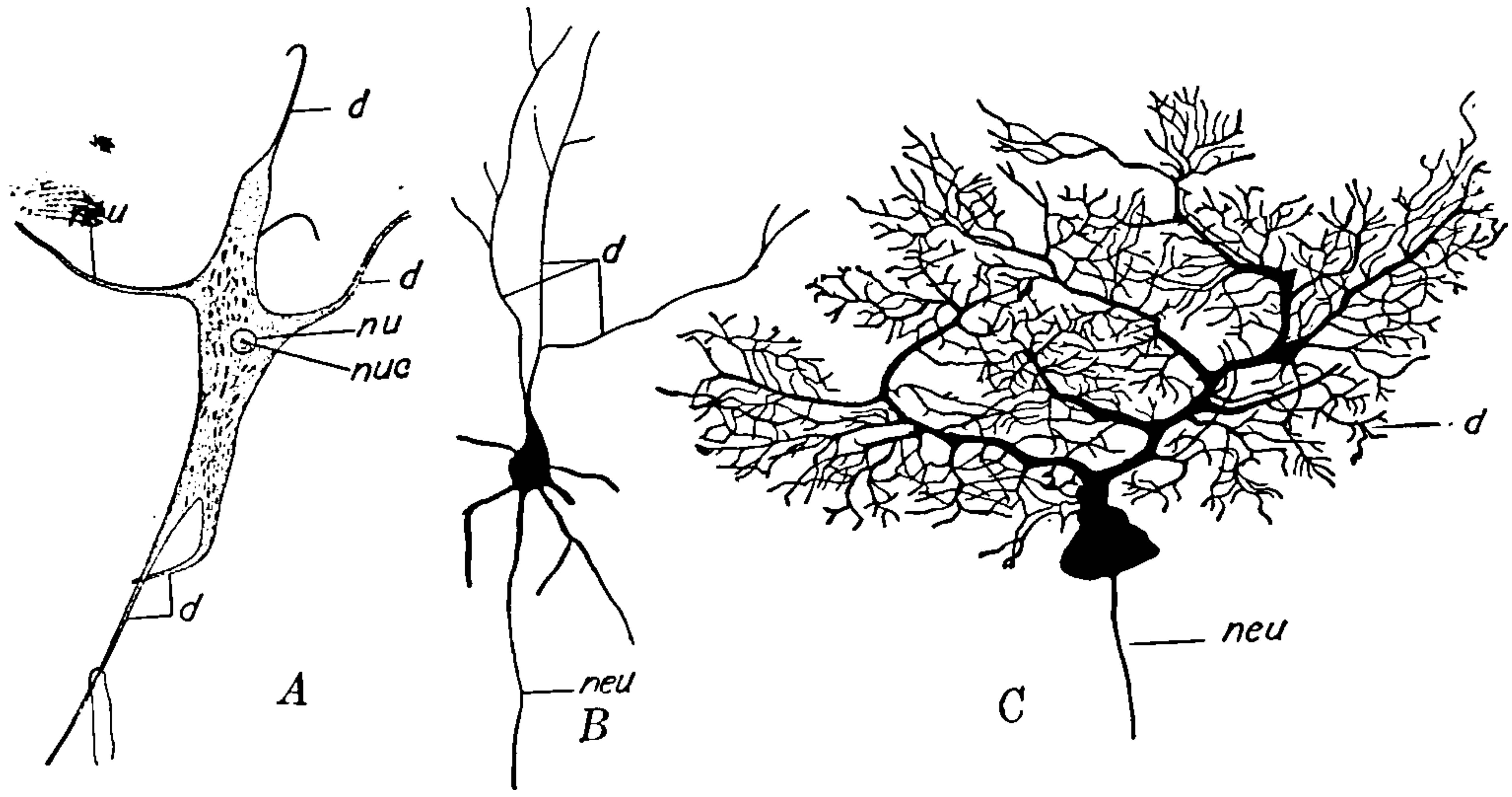


FIG. 78.—Three kinds of nerve cells. *A*, from ventral horn of spinal cord of an ox; *B*, from cortex of cerebrum of a cat; *C*, Purkinje cell from cerebellum of a cat; *d*, dendrite; *neu*, axon; *nu*, nucleus; *nuc*, nucleolus. (*B and C from Golgi preparations. Original.*)

ORGANOLOGY

Organology comprises the study of the organs of the body and their arrangement into systems. Under this head the great systems of organs of the bodies of higher invertebrates and vertebrates are considered in this chapter with special reference to certain chosen types. The digestive, respiratory, circulatory, excretory, sexual, locomotor, and nervous systems are discussed seriatim, and while structural aspects are especially considered it is not possible to ignore function. It should be borne in mind throughout the discussion that the various systems are intimately related and that no system can be properly discussed with respect either to its structure or to its function without involving one or more of the other systems. An understanding of the relations of these systems to one another requires a knowledge of certain fundamental cavities of the body, the *cœlenteron* of simple animals and the *cœlom* of more complex ones. To these cavities attention is first turned.

Cœlenteron.—In the Cœlenterata (Hydra and its allies) there is found within the body a single cavity (Fig. 60) which functions as a digestive and vascular cavity and is therefore sometimes called a *gastrovascular* cavity, but the name *cœlenteron* is more expressive of its structural relations.

Cœlom.—In many higher invertebrates and in the vertebrates there is a second body cavity bounded by peritoneum lying between the gut and the body wall. This second cavity, the cœlom, is well shown in a diagrammatic cross-section of a developing Amphioxus (Fig. 79). In the earthworm and in most other Annelida the arrangement of the body is clearly that of a tube within a tube. The wall of the outermost tube is the body wall while the alimentary tract forms the inner tube which is supported by circular partitions, the *septa*. The cavity (cœlom) between the walls of the two tubes is lined with the peritoneum, a layer of flattened epithelium. In the vertebrates the inner tube is suspended from the inner surface of the outer tube by means of dorsal mesenteries which are merely continuations of the peritoneum from the mid-dorsal line. The relation of cœlom to intestine is illustrated in Fig. 80. In that figure the line limiting the cœlom represents the peritoneum. Fig. 80 also clearly illustrates the fact that while the organs of the body really lie outside of the cœlom they are pushed down into it and are suspended by peritoneum. A true cœlom always bears the gonads on its walls and is lined with peritoneum. From the latter feature this cavity is frequently called the *peritoneal* cavity.

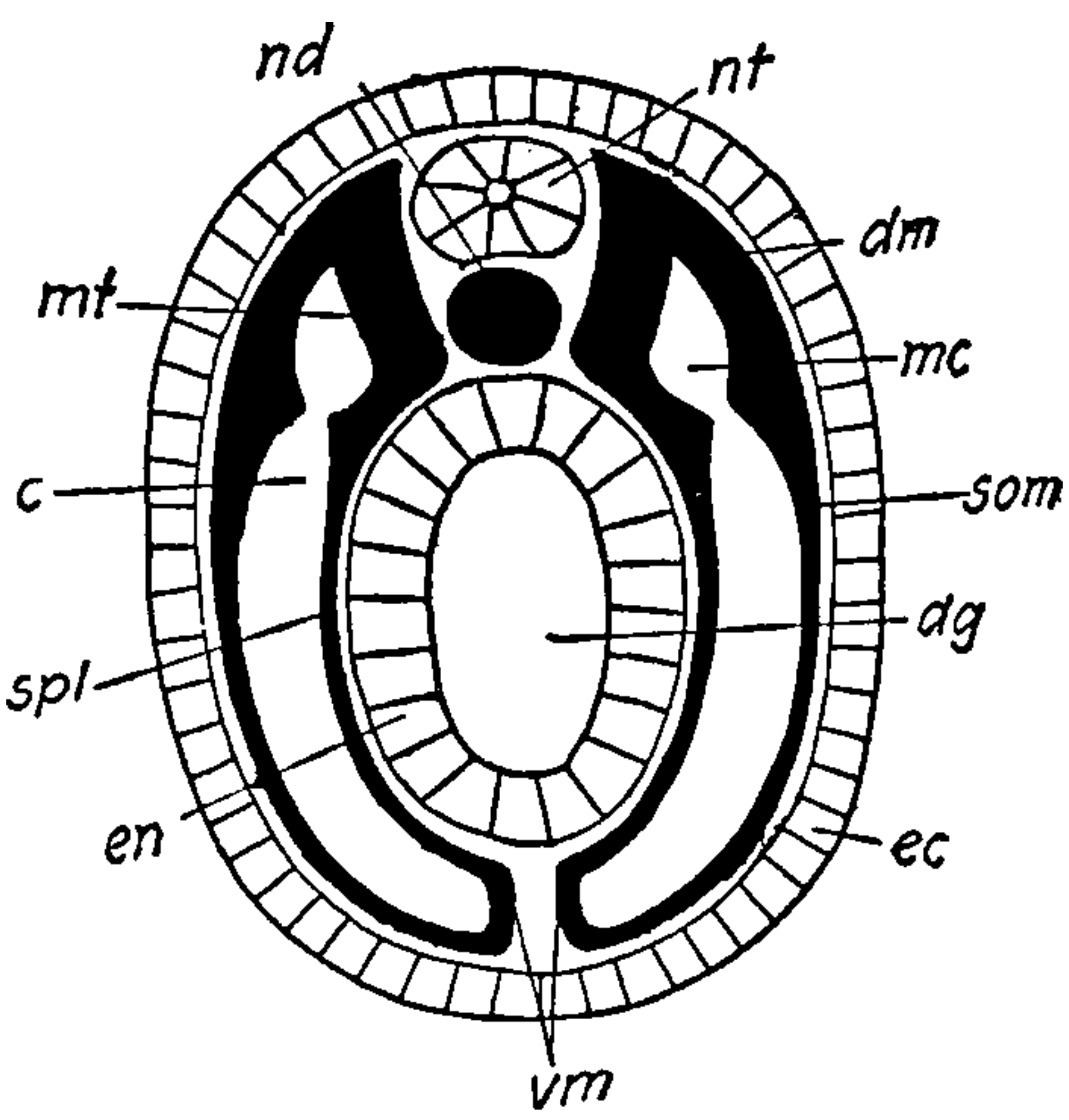


Fig. 79.—Cross-section of an embryo of Amphioxus, showing formation of cœlom. c, cœlom; *dg*, digestive tract; *dm*, dermatome; *ec*, ectoderm; *en*, endoderm; *mc*, myocœle; *mt*, myotome; *nd*, notochord; *nt*, neural tube; *som*, somatic layer of mesoderm; *spl*, splanchnic layer of mesoderm covering the digestive tract; *vm*, ventral mesentery.

In the roundworms, of which Ascaris may be taken as an example, a cavity exists between the alimentary tract and the body wall but since it is not bounded by peritoneum this cavity is not considered to be a true cœlom.

Simplest Digestive Apparatus.—Since in the Protozoa and sponges digestion is intracellular no digestive system or digestive organ can be said to exist. The most primitive multicellular digestive organ occurs in the simple cœlenterates. The gastrovascular cavity of Hydra may be taken as an example. In this animal (Fig. 60) the digestive organ consists of a simple bag whose wall is composed of flagellated epithelial cells. Branches of the bag extend out into the tentacles and into the buds if the latter are present. A single opening, the *mouth,* leads into this cavity. The cœlenterates in general have a digestive organ of this type and few modifications are shown. In none of them is there a second opening, the *anus,* through which indigestible materials may be voided to the exterior. The digestive apparatus of the cœlenterates thus consists of a single organ, and can hardly be called a system.

Digestive Systems in the Invertebrates.—Among the flatworms (Platyhelminthes) a true digestive system may be found. In the rhabdocœle turbellarians (Fig. 81) it consists of a mouth, a short *pharynx,* and a sac-like *intestine.* In the triclad turbellarians the intestine (Fig. 82) is branched into three main parts of which one extends forward and two backward to the extremities of the body. These main branches have secondary branches which extend laterally toward the periphery. In the roundworms (Nemathelminthes) the digestive system consists of a straight tube which extends through the length of the body from the mouth to a posterior opening, the anus, through which undigested material is voided. In some species tooth-like structures may be developed in the mouth cavity and muscular swellings may be present in the walls of

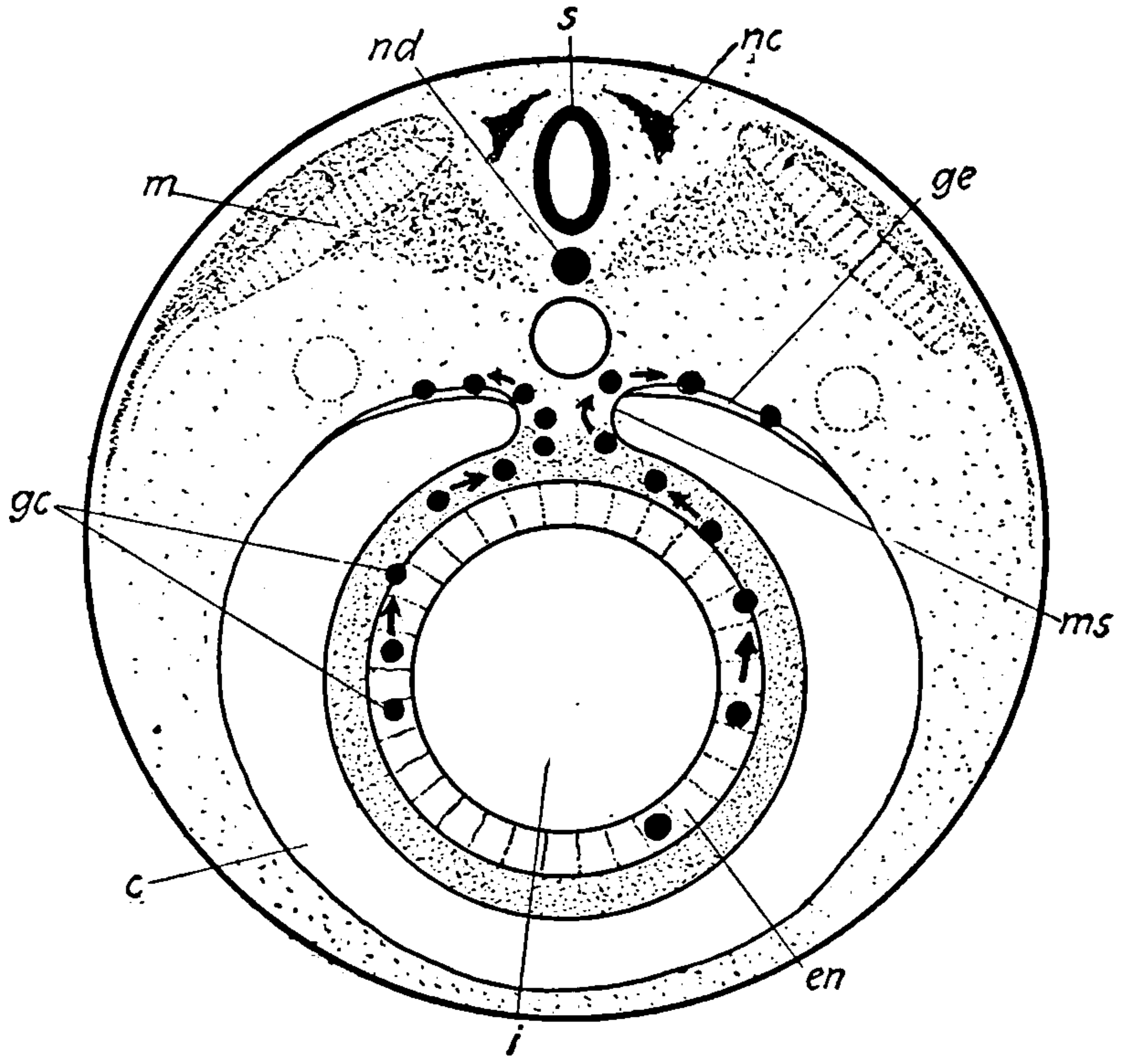


FIG. 80.—Diagram of cross section of a vertebrate animal to show cœlom. c, cœlom; *en,* endoderm of intestine; *gc,* germ cells; *ge,* germinal epithelium which later covers the gonads and from which the germ cells issue; *i,* cavity of intestine; *m,* myotome, or muscle segment; *ms,* mesentery; *nc,* neural crest, from which nerves and ganglia develop; *nd,* notochord, forerunner of the backbone; *s,* spinal cord.

These regions as a rule merge imperceptibly into each other, 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

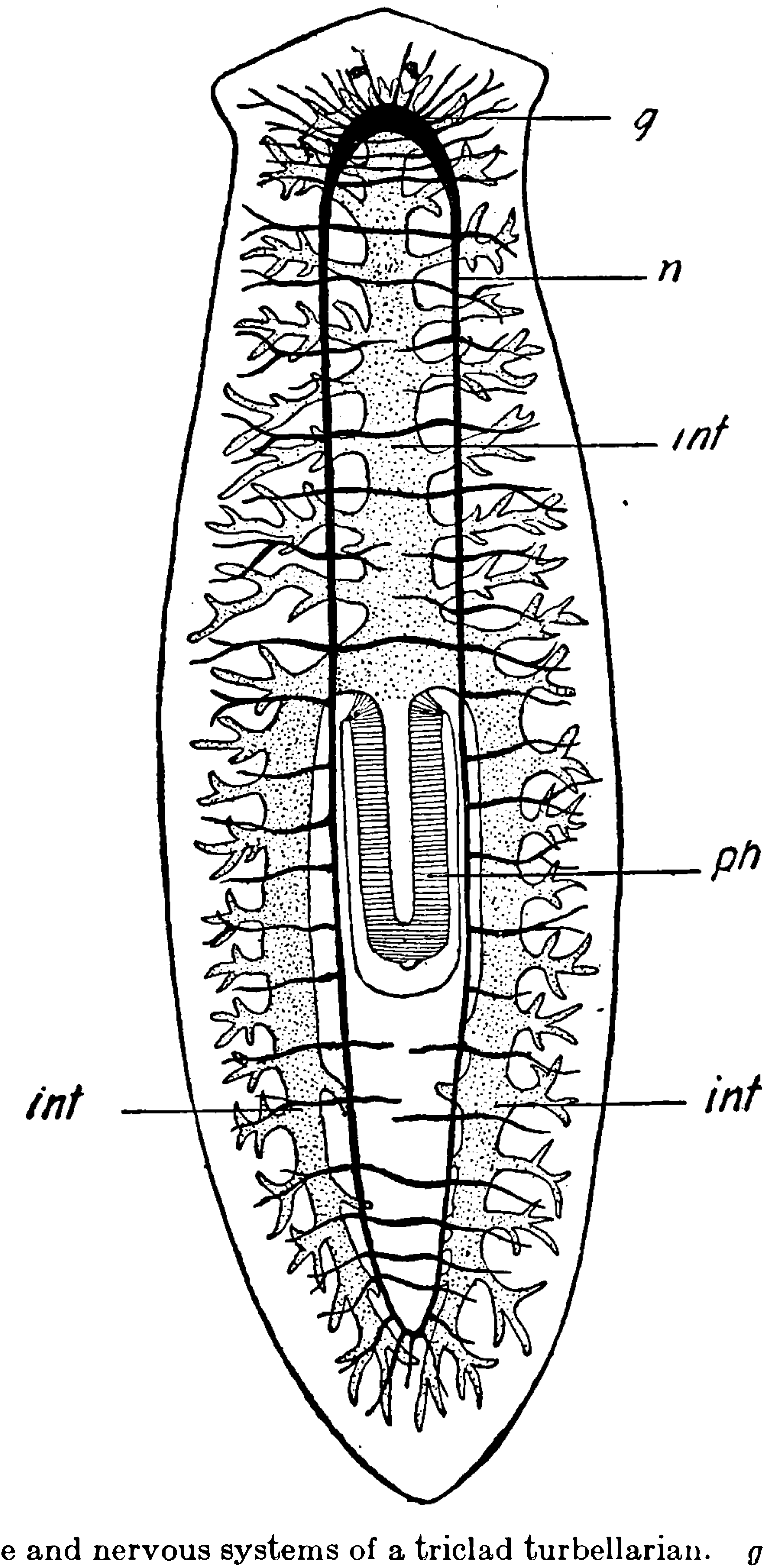


FIG. 82.—Digestive and nervous systems of a triclad turbellarian. *g*, ganglionic mass; *int*, intestine; *n*, nerve; *ph*, pharynx. (*After Lang.*)

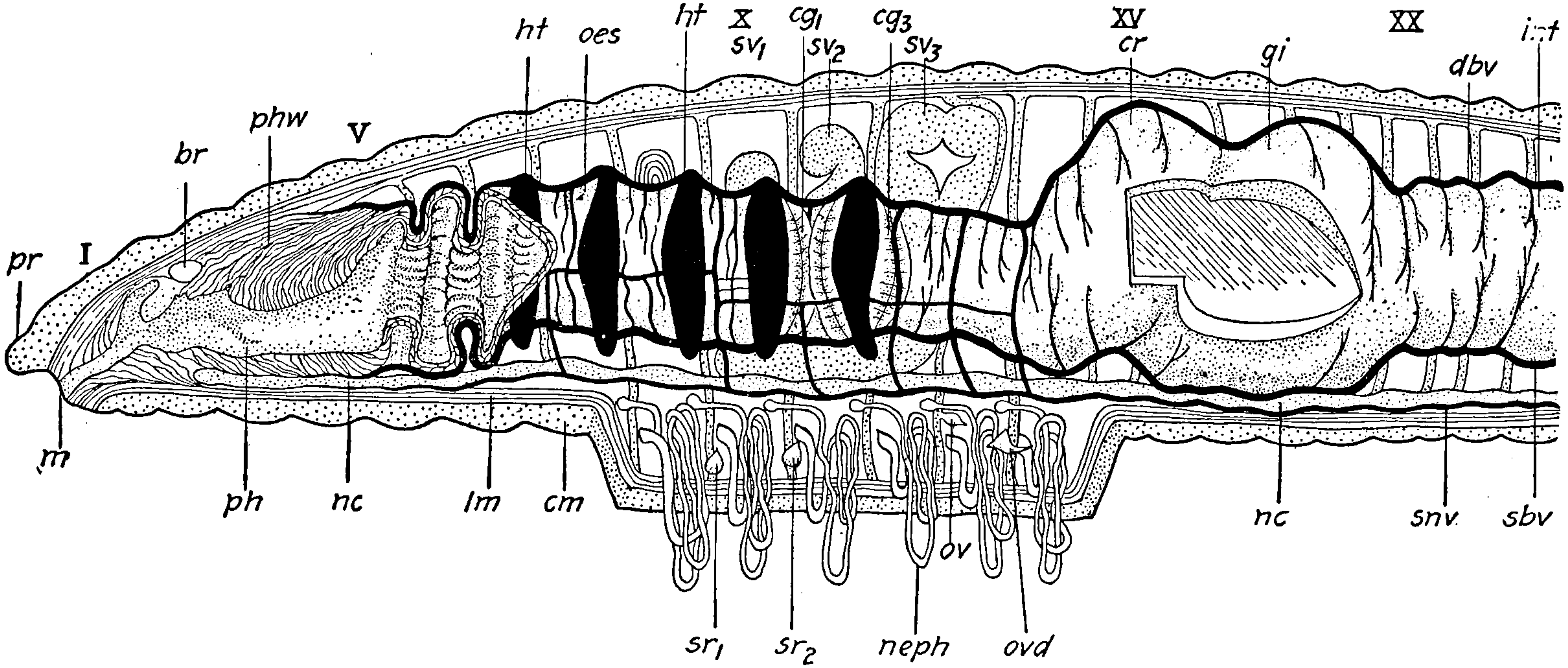


FIG. 83.—Dissection of the earthworm, *Lumbricus terrestris*, side view, showing various systems of organs. I, V, X, XV, XX, number of somite. Digestive system includes mouth (*m*), overhung by prostomium (*pr*), pharynx (*ph*), with thick muscular wall (*phw*), esophagus (*oes*), calciferous glands (*cg*1-*cg*3), crop (*cr*), gizzard (*gi*), intestine (*int*), anus not shown. Circulatory system includes hearts (*ht*), dorsal blood vessel (*dbv*), sub-intestinal vessel (*sbv*), sub-neural vessel (*snv*), and certain other vessels not here named. Excretory system includes nephridia (*neph*). Muscular system includes circular muscles (*cm*), longitudinal muscles (*lm*). Nervous system includes brain or supraesophageal ganglion (*br*), ventral nerve cord (*nc*), nerves not shown. Female reproductive system includes ovary (*ov*), oviduct (*ovd*), seminal receptacles (*sr*1, *sr*2). Male reproductive system includes seminal vesicles (*sv*1, *sv*2, *sv*3), which enclose testes not shown, vasa deferentia not shown. For more complete diagram of reproductive system see Fig. 95. (*Modified from Linville and Kelly.*)

intestine which is used as a common passage for undigested materials from the 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*.

Conditions Necessitating Respiratory System.—Special organs for respiration apparently arose much later than organs of digestion since they do not occur in the cœlenterates, rotifers, flatworms or roundworms, while digestive organs are present in these groups. Most Annelida (true worms) have no special respiratory system, nor do they require one since the moist mucous surfaces of their bodies serve the purpose of a membrane through which gaseous exchange may take place. In general it may be said that a respiratory system has developed *pari passu* with the development of a circulatory system. In many small animals living in water or in moist environments, respiration may be carried on through the general body surface, and in such animals the diffusion and osmosis of oxygen and digested food through the tissues is sufficient to care for the needs of the cells farthest from the sources of these substances. With increased mass of body, however, and with the decrease of surface in

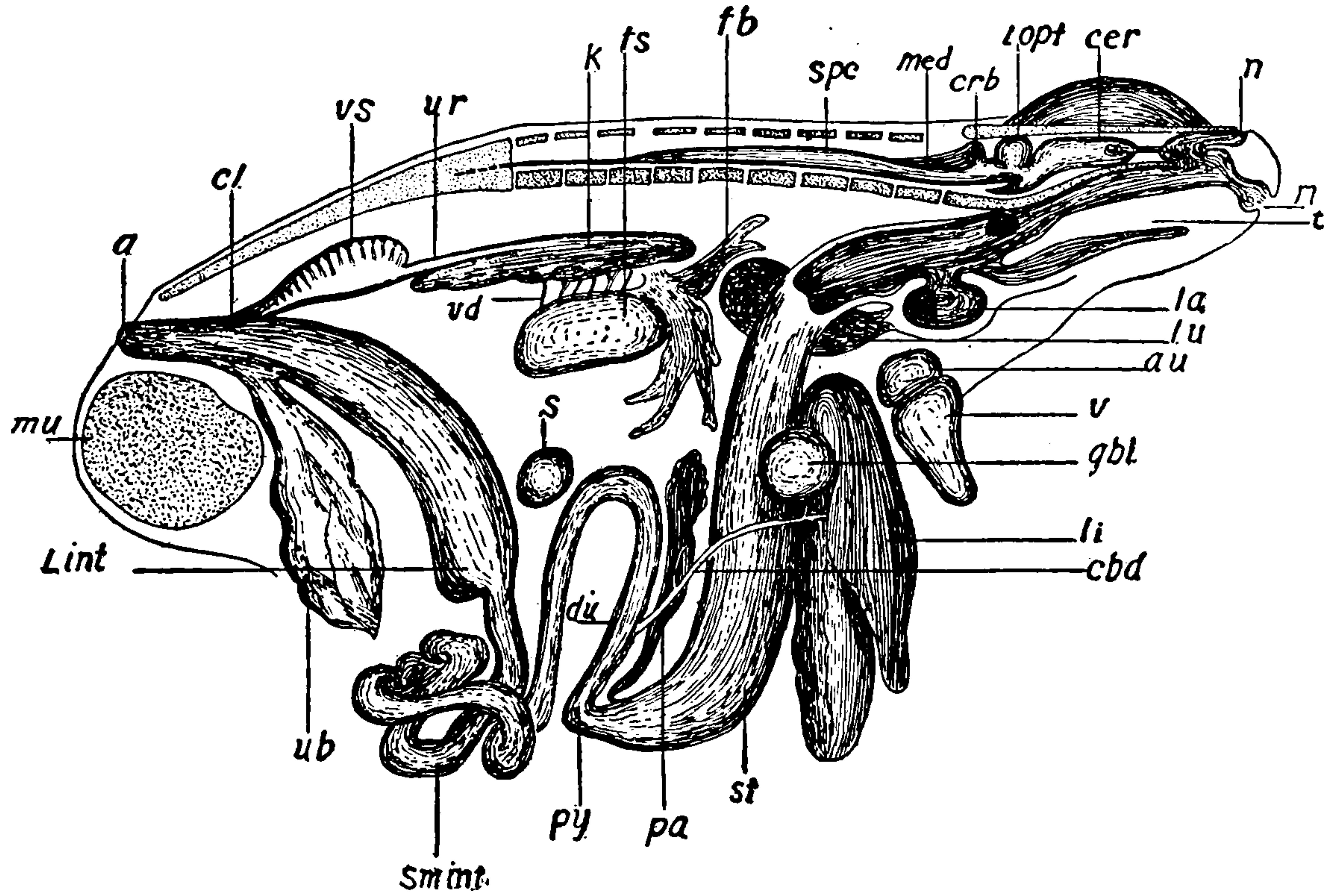


FIG. 84.—Dissection of the frog, side view. *a*, anus; *au*, auricle of heart; *cbd*, common bile duct; *cer*, cerebrum; *cl*, cloaca; *crb*, cerebellum; *du*, duodenum; *fb*, fat bodies; *gbl*, gall bladder; *k*, kidney; *la*, larynx; *li*, liver; *l. int*, large intestine; *l.opt*, optic lobe; *lu*, lung; *m*, mouth; *med*, medulla oblongata; *mu*, muscle; *n*, nasal aperture; *pa*, pancreas; *py*, pylorus; *s*, spleen; *sm. int*, small intestine; *spc*, spinal cord; *st*, stomach; *t*, tongue; *ts*, testis; *ub*, urinary bladder; *ur*, ureter; *v*, ventricle of heart; *vd*, vasa efferentia; *vs*, vesicula seminalis. (*Modified from Parker and Haswell's Textbook of Zoölogy, after Marshall.*)

arches through which water taken in at the mouth flows out over the gills. These arches and slits, in the embryo, are diagrammatically shown in Fig. 182. In fishes and some amphibians a covering, the *operculum*, conceals and protects the gills, but in other amphibians, as Necturus and some other salamanders, the gills are external and are not covered. A diagram showing the structure of external gills is shown in Fig. 86.

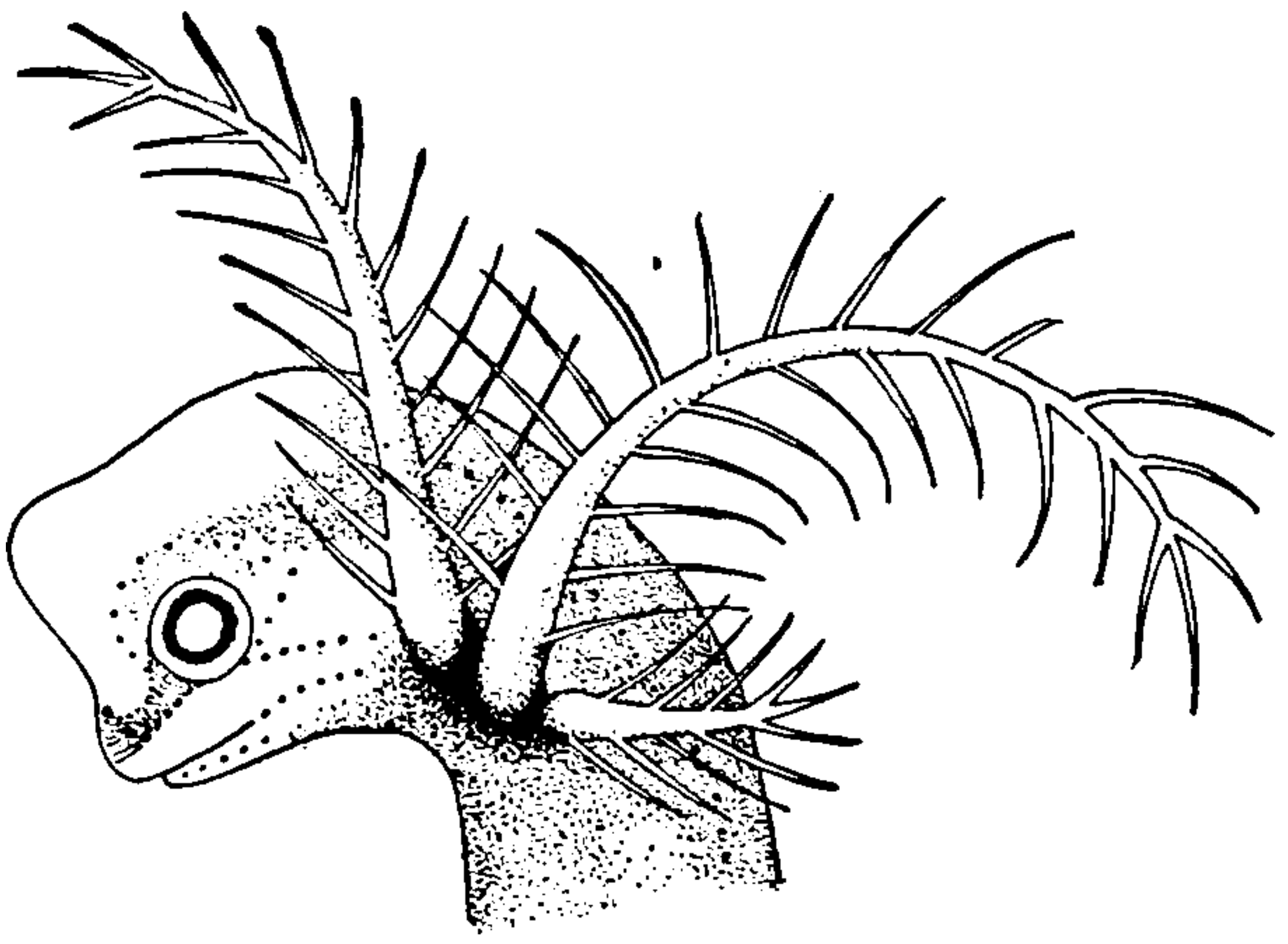


FIG. 86.—External gills of the amphibian, *Epicrium glutinosum*. (*From Wiedersheim, after Sarasin.*)

LUNGS. Lungs are organs developed in the embryo of vertebrates as evaginations from the anterior end of the alimentary tract as described in Chapter X. By means of accessory organs of respiration air is brought into the lungs where it comes Into contact with mucous membranes richly supplied with blood vessels. Here exchange of gases takes place. In case of either lungs or gills the successful operation of the respiratory mechanism is absolutely dependent upon the continual changing of the blood in contact with the moist mucous surfaces. A halt in the flow of blood stops respiration very promptly, and unless the flow of blood can be quickly resumed death results.

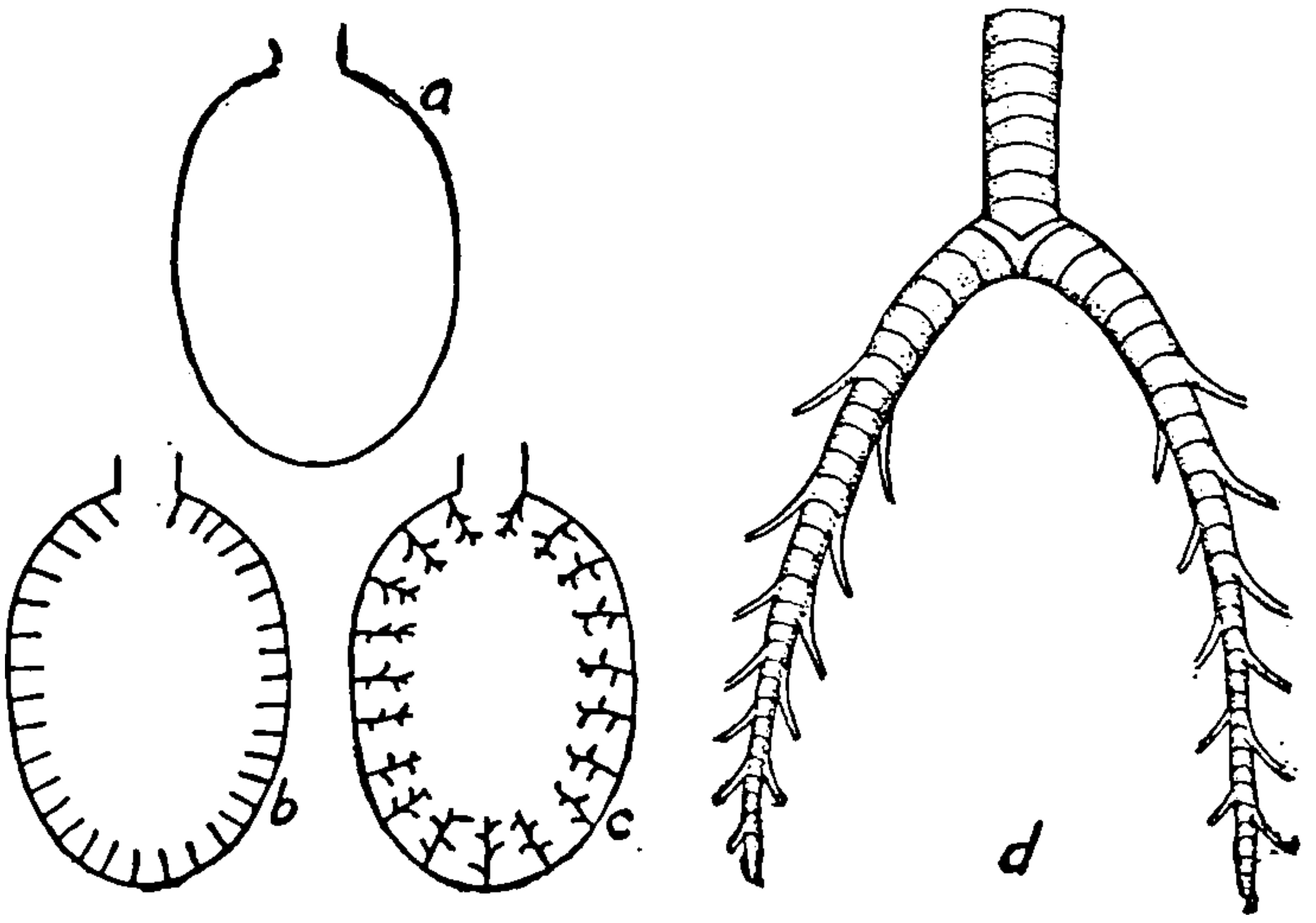


FIG. 87.—Diagrams of types of lungs. *a*, amphibian lung with plain surface; *b*, amphibian lung with low folds making simple alveoli; *c*, amphibian lung with higher folds which are themselves folded making more numerous alveoli; *d*, trachea and bronchial tree of a mammal.

The lung in lower amphibians is a bag-like organ with a large central cavity (Fig. 87); but in higher amphibians it becomes more complex since its inner surface is thrown up into corrugations which with cross corrugations form box-like spaces. These corrugations increase the respiratory surface. In higher vertebrates the lung is entirely subdivided into minute air spaces which are in direct connection with one another through large branching tubes, the *bronchi.* In this way there is an enormous increase of the inner surface of the lung. 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 slit-like *glottis.*

Accessory Respiratory Organs.—Since in all vertebrates the mouth serves as a chamber for passage of water or air to gills or lungs, respectively, it may be considered a portion of the respiratory apparatus. For the same reason the olfactory passages of forms possessing lungs should also be included as a part of the respiratory apparatus. Located in the trachea or between the lungs and glottis is an organ of sound-production, the *larynx.* This is a box-like structure in which are stretched two membranes, the *vocal cords.*

Relation to Circulation.—Since the essential part of the respiratory apparatus of animals with gills or lungs is the system of blood vessels with which it is richly supplied, and since the exchange of gases takes place directly through the walls of the blood vessels, the respiratory system is really subsidiary to the circulatory system.

Circulatory System.—The circulatory system is not present below the annelid and nemertean worms and mollusks. In the flatworms, for example, there are irregular spaces in the parenchyma, the tissue of the interior, filled with a liquid which sometimes contains granules and globules. This fluid shifts back and forth with movements of the body, but there is no true circulation and no true circulatory system. The essential feature of a circulatory system is a set of tubes which branch extensively so as to bring all parts of the body in contact with the circulating medium, *blood* or *lymph.* There is usually a contractile organ, the *heart,* or paired organs which by their rhythmic contractions serve to maintain a flow of the blood or lymph. The main distributing vessels are called *arteries,* the main collecting vessels *veins,* and the minute tubes leading from arteries to veins *capillaries.* In its course through the body the blood comes into intimate contact with the walls of the digestive organs where it secures dissolved food. It also comes in contact with the membranes of the gills or lungs where it takes up a supply of oxygen. The blood then carries this nutriment and oxygen out to all the tissues of the body and from them brings back to the lungs and the excretory organs carbon dioxide, urea, and other waste materials. In animals which have air tubes (tracheæ) the blood is a carrier primarily of nutriment and waste materials.

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. 88. This diagram indicates that the blood of animals with gills and a two-chambered heart passes from the heart through the gills, and then out through the *dorsal aorta* to the organs of the body, where it passes through capillaries (not shown) and returns to the heart by means of the veins. The blood thus passes over a single course from the heart back to the heart again.

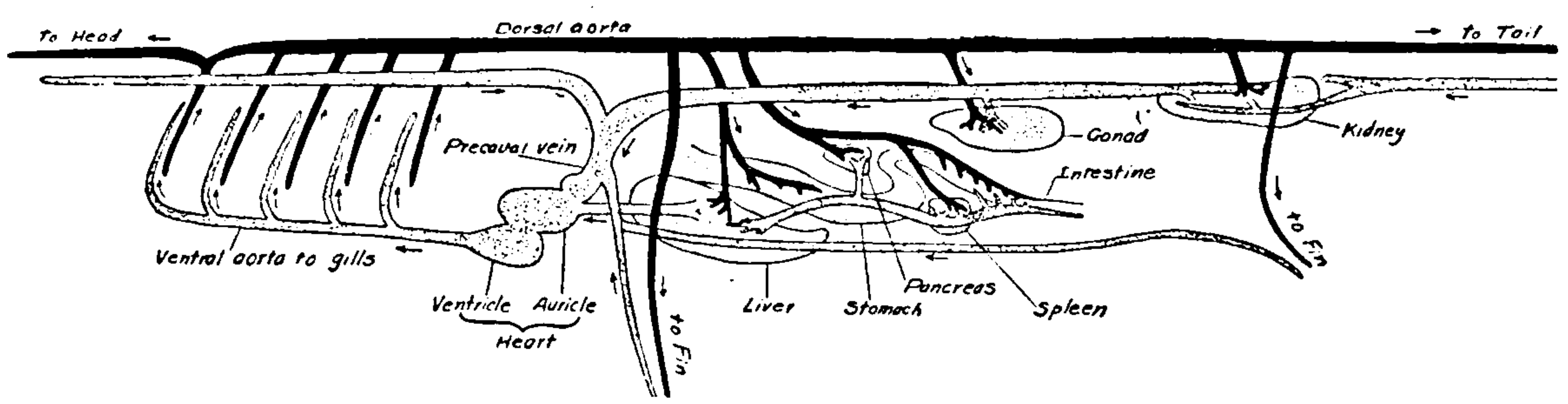


FIG. 88.—Diagram of the circulatory system in the dog-fish. The capillaries and finer arteries and veins are omitted. (*Modified from Parker and Haswell's Textbook of Zoölogy.*)

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. 88), 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 b[illegible] [illegible]ere 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. 89, which also suggests the path of the blood.

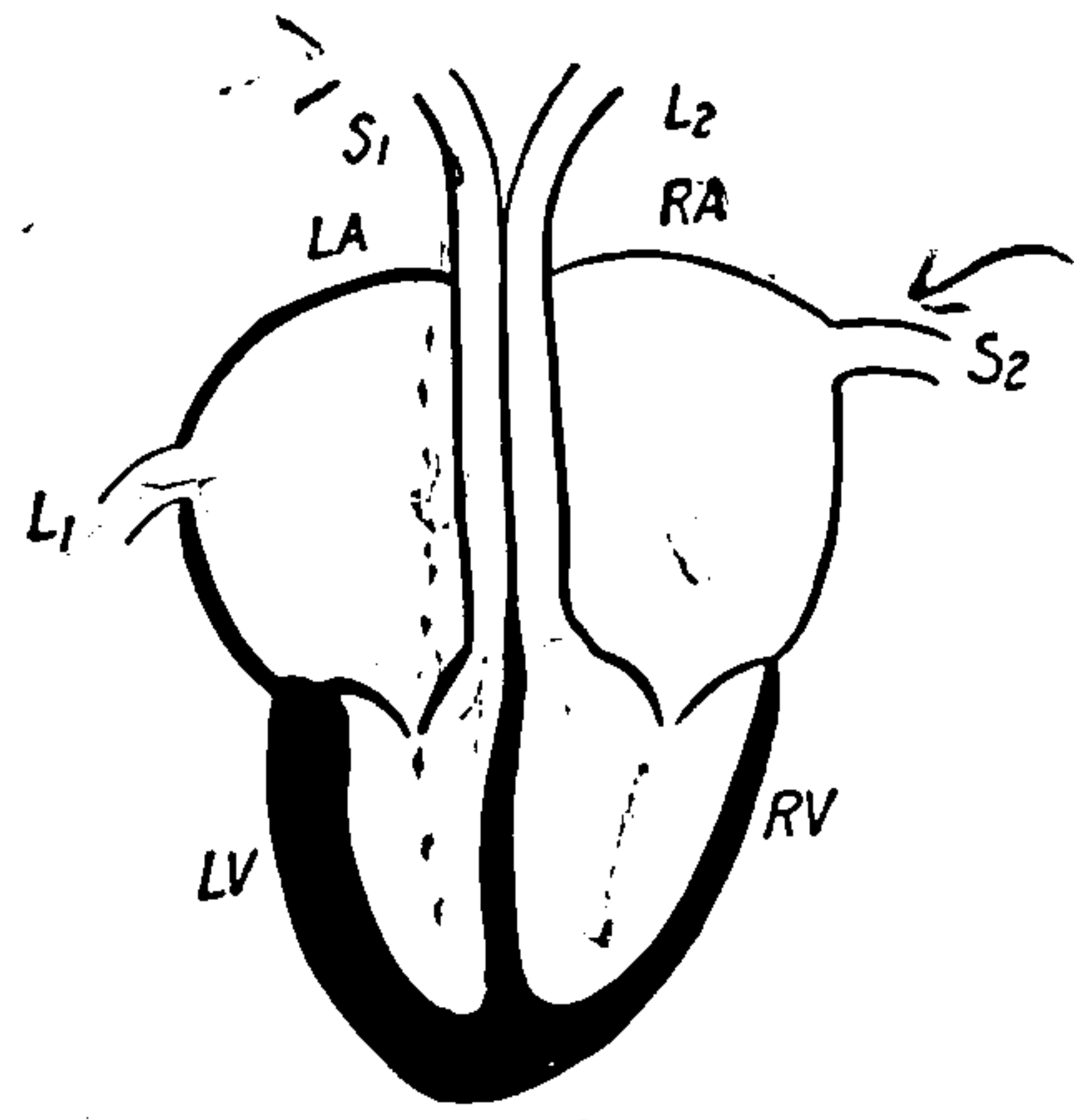


FIG. 89.—Diagram of a four-chambered heart. *LA*, left auricle; *RA*, right auricle; *LV*, left ventricle; *RV*, right ventricle; *L1*, vessel from lungs; *L2*, vessel to lungs; *S1*, vessel to system; *S2*, vessel from system.

The blood of such an animal, after having made a circuit through the *systemic circulation* (through the body) is returned to the right auricle, whence upon contraction of the auricle it passes through a valve to the right ventricle. Upon contraction of the right ventricle the blood is sent through the pulmonary arteries to the lungs. Having completed the circulation of the lungs (*pulmonary circulation*) the blood returns to the left auricle through the pulmonary veins and from this auricle passes through the opening to the left ventricle. Upon contraction of the left

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. 90, and the structure of a flame cell in Fig. 91. 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 funnel-shaped ciliated opening, the *nephrostome,* which projects through the septum into the cavity of the somite ahead. There it opens directly into the body cavity or cœlom. The other end of the coiled tube is connected to the body wall where it has an opening to the exterior. The body of the nephridium in the earthworm, shown diagrammatically in Fig. 92, is composed of coiled tubes arranged in three distinct loops. The nephrostome sweeps in liquid and small solid particles by the action of its cilia. A portion of the tube is also provided with cilia which assist in propelling liquids through the nephridium to the exterior Other portions of the nephridium are composed of cells which have a secretory function.

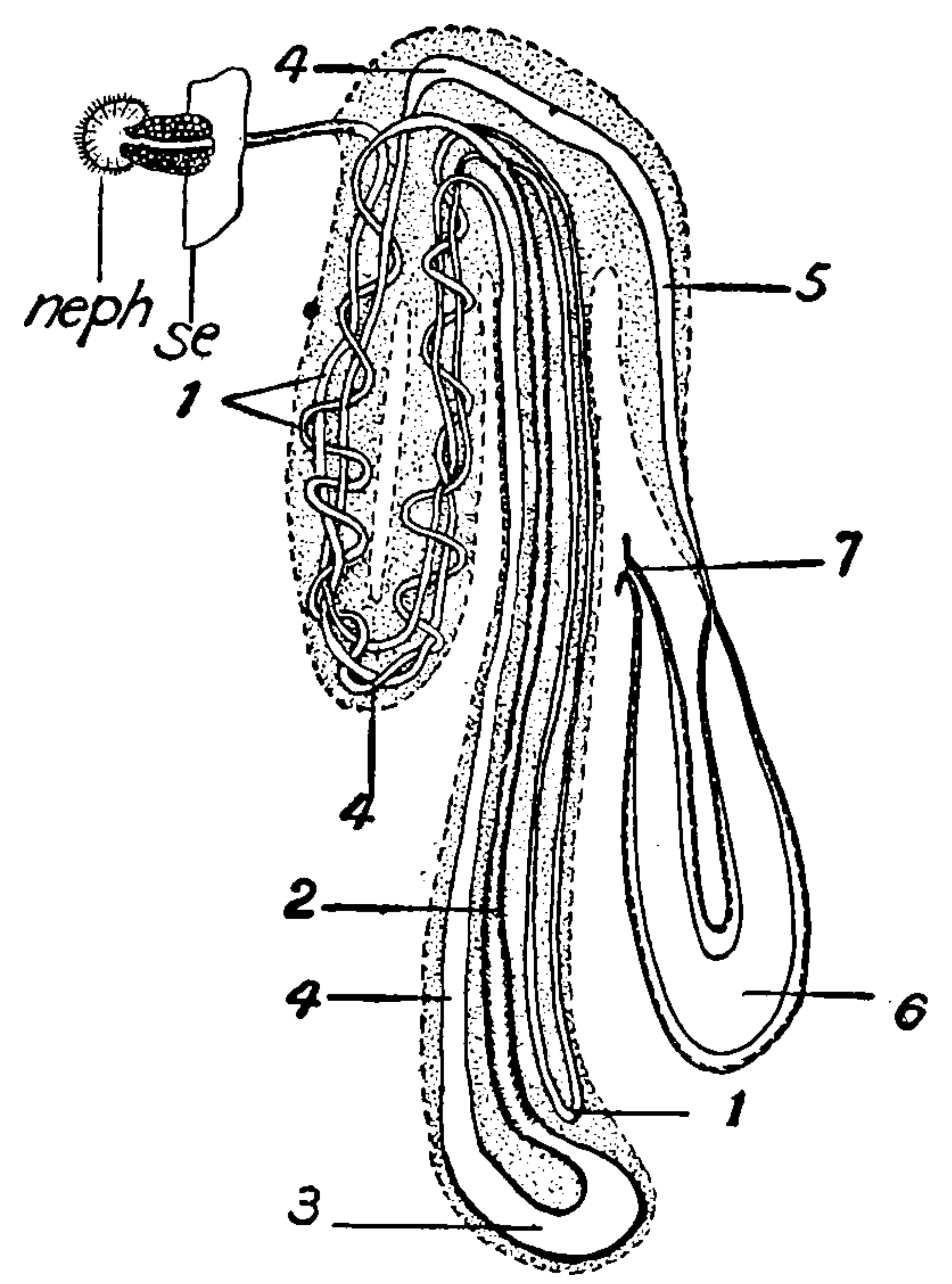


FIG. 92.—Nephridium of earthworm, schematic. *neph,* nephrostome; *se,* portion of septum; 1–6, portions of tubule of the nephridium; 7, opening to exterior. (*From Hesse and Doflein after Maziarski.*)

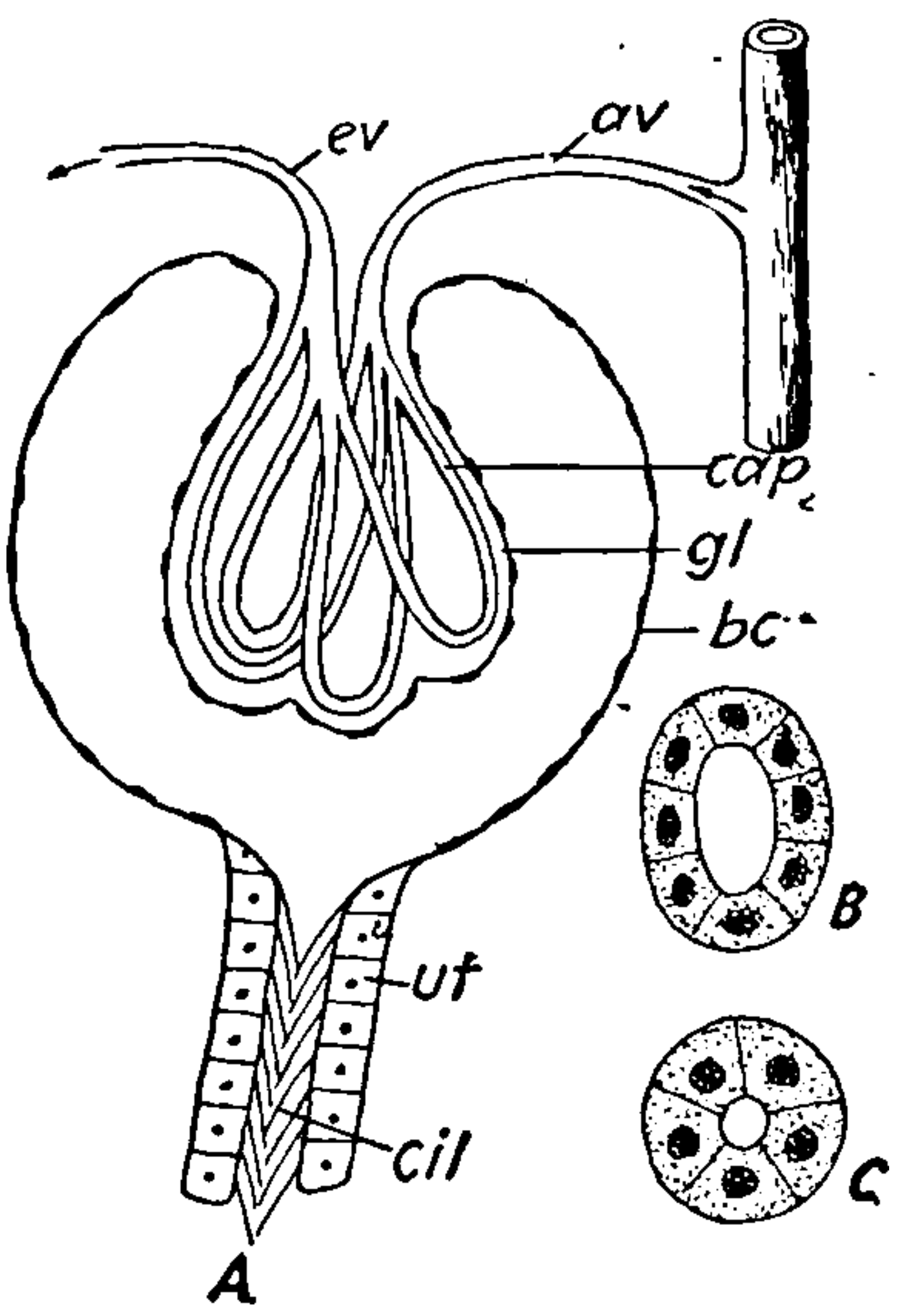


FIG. 93.—Structures from vertebrate kidney, diagrammatic. *A,* Malpighian corpuscle; *B* and *C,* cross-sections of uriniferous tubules at different levels; *av,* afferent vessel; *bc,* Bowman's capsule; *cap,* capillary; *cil,* cilia; *ev,* efferent vessel; *gl,* glomerulus; *ut,* uriniferous tubule.

Kidneys.—The excretory organs of vertebrate animals consist o large compact glands, the *kidneys,* which are made up of convolute tubules (called *uriniferous tubules*) beginning in globular swellings, the *Malpighian corpuscles* (Fig. 93). The Malpighian corpuscle is composed of two parts, the glomerulus and Bowman's capsule. The glomerulus consists of a group of blood capillaries. Surrounding the group of capillaries is Bowman's capsule which is the expanded and invaginated end of one of the uriniferous tubules forming a double-walled cup. Each tubule consists of a single layer of secreting epithelium lying throughout its course in intimate contact with a rich supply of capillaries from the circulatory system. In some of the lower vertebrates, as the lamprey and the frog, there are ciliated funnels or *nephrostomes* (Fig. 94) situated on the ventral surface of the kidney and opening into the body cavity. In the larvæ of these species the nephrostomes connect the body cavity with the uriniferous tubules but in adult frogs the nephrostomes are connected with the blood vessels instead of with the tubules. A diagram of the structures found in the kidney of the frog is shown in Fig. 94.

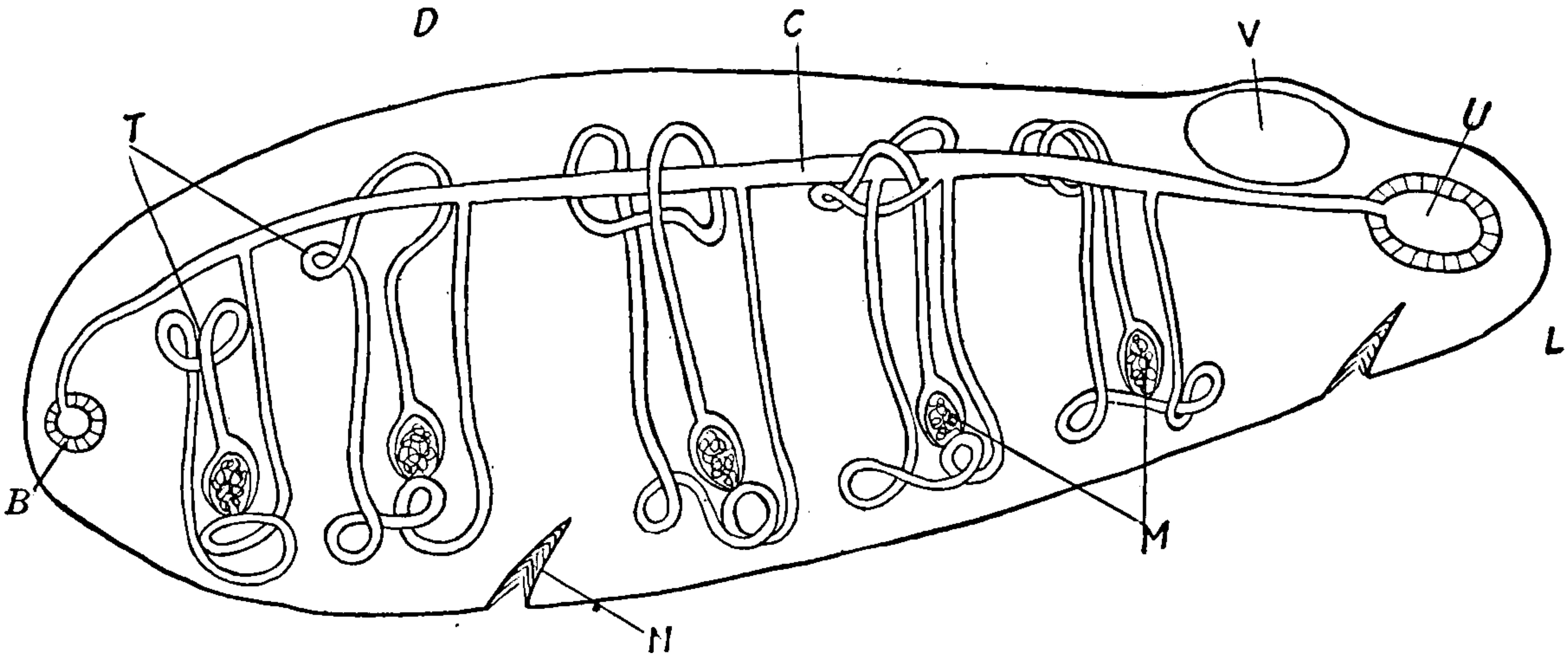


FIG. 94.—Diagrammatic representation of a cross-section of the kidney of a frog. *B*, Bidder's canal. *C*, collecting tubule; *D*, dorsal; *L*, lateral margin of kidney; *M*, Malpighian corpuscles; *N*, nephrostome; *T*, uriniferous tubule; *U*, ureter; *V*, renal portal vein. (*Modified from Holmes's Biology of the Frog.*)

The kidneys discharge into *ureters* which in turn discharge into the *cloaca* in lower vertebrates, as the frog, or into the urinary bladder in mammals. In the frog the urinary bladder is located on the ventral side of the cloaca but the ureters are not directly connected with it. Urine discharged into the cloaca by the ureters collects in the bladder and thence is discharged at times through the cloaca. The urinogenital apparatus of a male frog is shown diagrammatically in Figs. 84 and 98. In mammals, except the few which have a cloaca, the urinary bladder is connected with the exterior by means of the *urethra*.

Sexual or Genital System.—The sexual or genital system has for its primary function the production of the *germ cells*. The transportation of the germ cells, their storage before and after fertilization, and the protection or nutrition of embryos developing from the germ cells are secondary sexual functions. The essential feature of any genital system, therefore, is one or more *gonads*, the glands or organs which produce eggs or sperms. Those gonads which produce eggs (or *ova*) are the *ovaries*, and those which produce sperms the *spermaries*, or *testes*. All other parts of the reproductive system are accessory to the gonads. The complexity of these accessory genital organs bears a close relation to the mode of life of the animal, its breeding habits, and the place where fertilization occurs, that is, whether external or internal. In the simpler cœlenterates (Fig. 60) the sperms are discharged from the spermaries directly into the water, and to fertilize the ova they must penetrate the ovary. In others the sperms are discharged into the gastrovascular cavity whence they escape through the mouth into the water. In this group there are no tubes, or *gonoducts*, for the transfer of germ cells from the gonads to the exterior but the germ cells must break through the body wall. In certain polychæte worms also the germ cells are shed into the water by the bursting of the body wall in certain somites of the body.

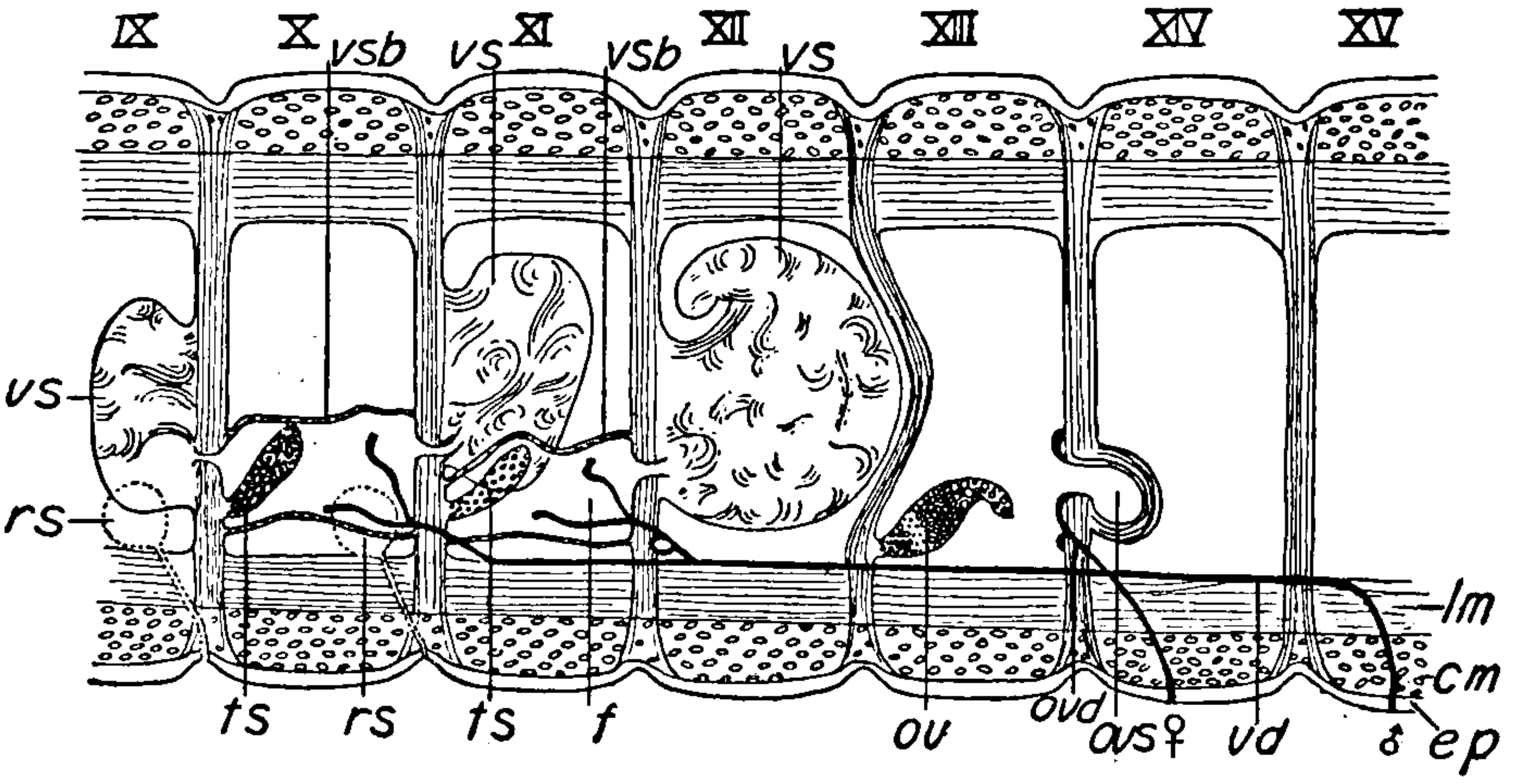


FIG. 95.—Reproductive organs of the earthworm, schematic representation of the side view. *IX–XV*, numbers of somites; *cm*, circular muscles; *ep*, epithelium; *f*, funnel of vas deferens; *lm*, longitudinal muscles; *ov*, ovary; *ovd*, oviduct; *ovs*, ovisac; *rs*, receptaculum seminis; *ts*, testis; *vd*, vas deferens; *vs*, vesicula seminalis; *vsb*, base of vesicula seminalis; ♀, opening of oviduct; ♂, opening of vas deferens. (*Modified from Hesse.*)

Systems with Accessories.—In the oligochæte worms, represented by the earthworm, a much more complicated group of organs serve the reproductive functions. The male organs are two pairs of *testes*, three pairs of *seminal vesicles* and one pair of *vasa deferentia*. The testes (Fig. 95) are imbedded in the bases of larger organs, the seminal vesicles, in which the sperms undergo the later stages of their development and await the time of copulation. Delicate tubes, the vasa deferentia, which originate in funnels in the base of the seminal vesicles and which open to the surface in the common earthworm on somite 15 conduct the sperms to the exterior. 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 *receptacula seminis*. The eggs are discharged from the ovaries

entia. At the other end the vas deferens is connected to an evertible copulating organ, the *cirrus* or *penis*, which lies, when not everted, within a *penial pouch.* The principal female organs are the bilobed *ovary*, the so-called *vitelline glands*, *uterus*, and the ducts which connect these organs with each other and with the exterior. Of these ducts the copulation passage, or *vagina*, opens to the exterior beside the cirrus through a common genital chamber. The vagina extends inward and backward and then expands into a *receptaculum seminis* in which the sperms are stored, and thence proceeds backward to join the *oviduct* which takes its origin from the mid-piece of the bilobed ovary. From the junction of the oviduct and vagina, a continuation of the oviduct which serves as a fertilization passage discharges into the *oötype.* The oötype receives also the *vitelline duct* which may be traced to the vitelline glands, so called because they were once believed to furnish the yolk for the eggs. Into the oötype the oviduct discharges fertilized ova while the vitelline duct discharges cells from the vitelline glands. In the oötype each ovum and a group of vitelline cells are converted into what is commonly called the egg, which is covered with membranes. These eggs are conducted through a uterine passage to the uterus where they and their developing embryos are stored. The uterus is at first a straight tube without branches, but as the proglottis (segment of the tapeworm) becomes older the uterine walls put out hollow lateral branches which become filled with eggs. In this tapeworm there is no definite opening of the uterus to the exterior but finally the ventral wall of the proglottis splits lengthwise opening up the uterus and discharging the eggs.

Urinogenital Systems.—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. In both sexes of the frog the gonads develop ventrally to the kidneys and here they hang suspended in loops of peritoneum. This relation is most plainly seen in the male and in young females whose ovaries have not yet become voluminous.

Lying dorsally to the ovaries in the female frog and extending into both ends of the body cavity are coils of the oviduct (Fig. 97). Each duct takes its origin in a ciliated funnel which lies just dorsal to the heart and at the extreme anterior end of the cœlomic 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 currents caused by general body movements, assisted by pressure of the fore arms of the clasping male. The cilia of the funnels of the oviduct create currents which 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. 98) 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 also open. Spermatozoa in the frog must therefore pass through the vasa efferentia, Bidder's canal, the collecting tubules, the ureter and 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 sperms are stored until they are emitted at the time of breeding.

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

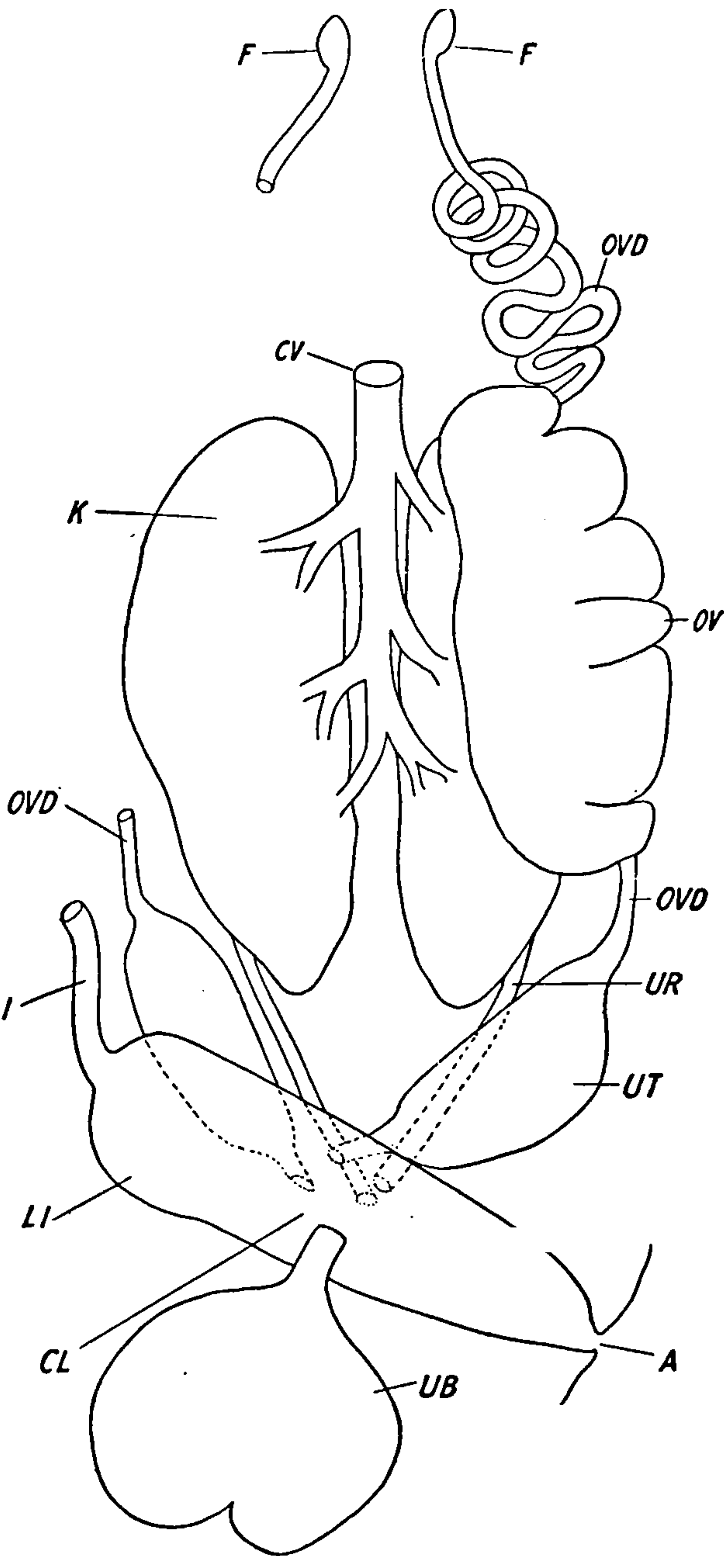


FIG. 97.—Urinogenital system of female frog, diagrammatic. *A*, anus; *CL*, cloaca; *CV*, postcaval vein; *F*, funnel of oviduct; *K*, kidney; *LI*, large intestine; *OV*, ovary; *OVD*, oviduct; *SI*, small intestine; *UB*, urinary bladder; *UR*, ureter; *UT*, uterus.

In most mammals, the two systems open to the exterior through a common opening which is separate from the opening of the digestive system. In the female, the funnel of the oviduct is very near 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. 99 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 some mammals there are accessory glands in connection with the female urinogenital system. In the male,

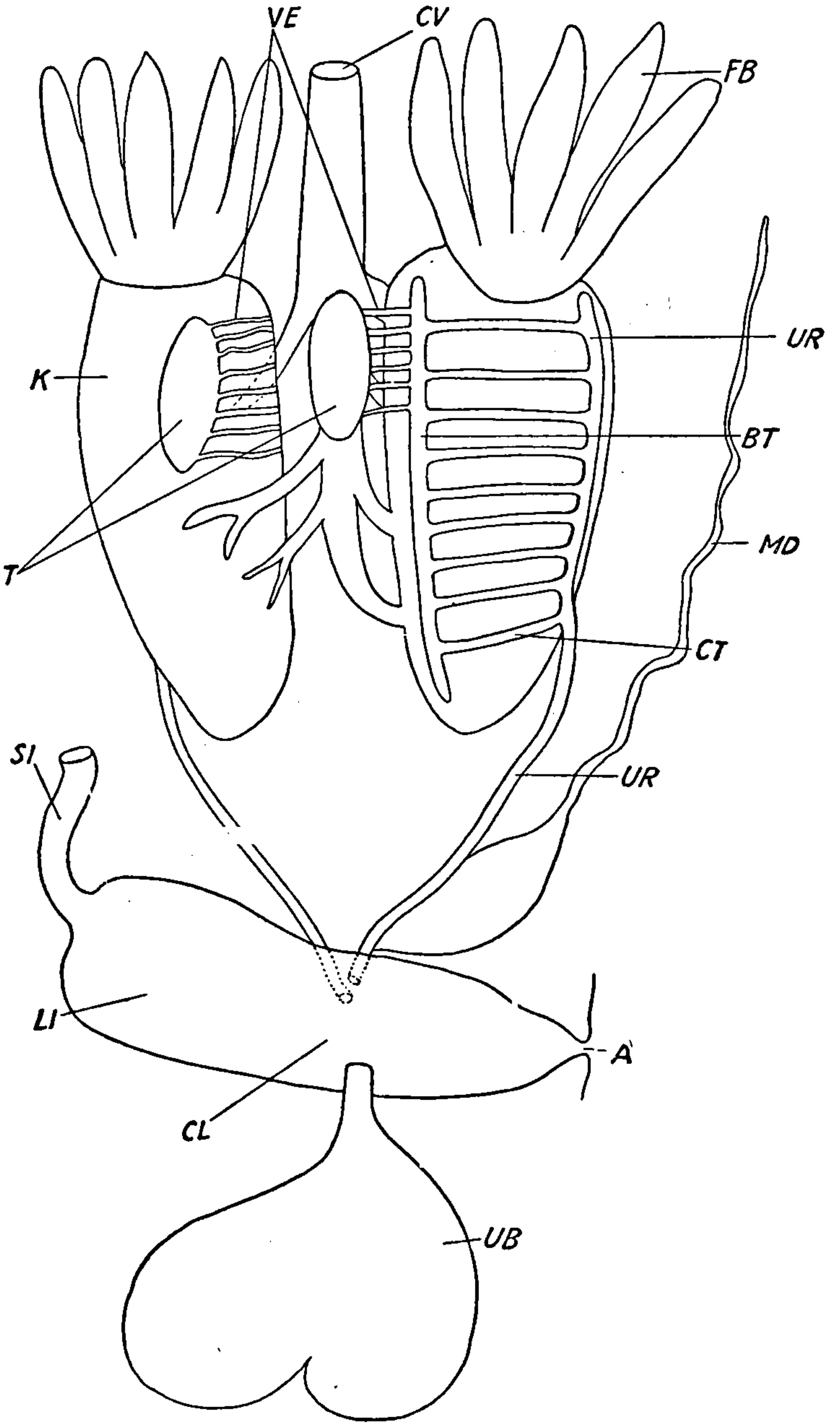


Fig. 98.—Urinogenital system of male frog, diagrammatic. The kidney at the left is in surface view, at the right in diagrammatic optical section. *A*, anus; *BT*, Bidder's tube; *CL*, cloaca; *CT*, connecting tubule; *CV*, postcaval vein; *FB*, fat bodies; *K*, kidney; *LI*, large intestine; *MD*, Muellerian duct; *SI*, small intestine; *T*, testes; *UB*, urinary bladder; *UR*, ureter; *VE*, vasa efferentia.

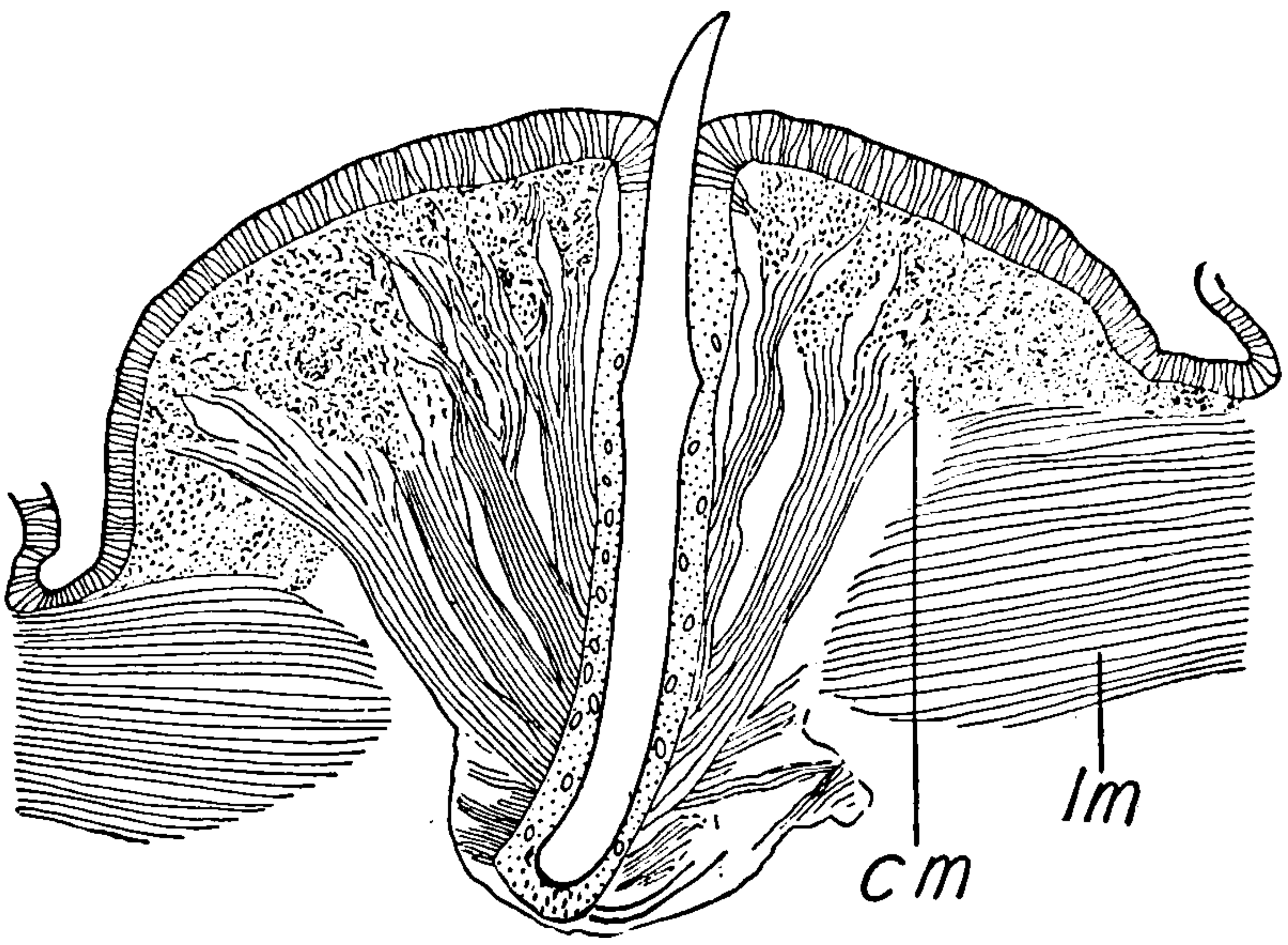


FIG. 100.—Seta and muscles in the earthworm, drawn from a longitudinal section anterior to the clitellum. *cm*, circular muscles; *lm*, longitudinal muscles. (*Original.*)

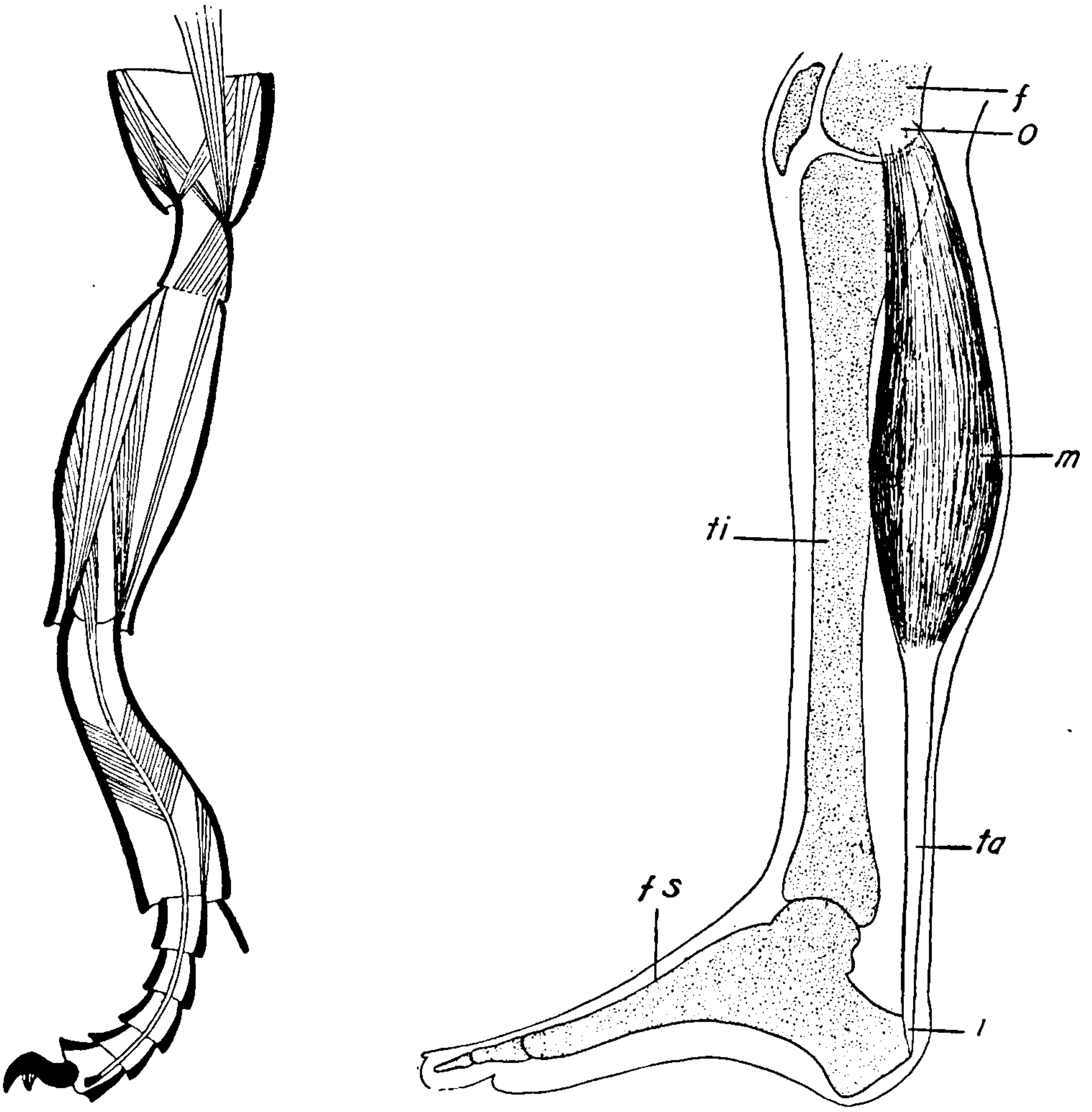


FIG. 101.—Relation of muscle to hard parts in appendages of insect and man. *A*, leg of insect; *B*, leg of man; *f*, femur; *fs*, skeleton of foot; *i*, insertion of muscle; *m*, muscle; *o*, origin of muscle; *ta*, tendo-Achilles; *ti*, tibia. (*A after Berlese· B after Hesse and Doflein.*)

whose outer ends project slightly from the body. These setæ are pivoted in the body wall and their inner ends are moved by the contractions of muscles (Fig. 100). The setæ play an important part in the locomotion of the earthworm because after the body is extended they catch on the soil and hold fast until the contraction of the longitudinal muscles shortens the body and brings up the rear. Since they are pivoted and are provided with muscles their angle with the surface can be changed. With the angle of the setæ changed the contraction and relaxation of the circular and longitudinal muscles move the worm in the opposite direction

In the Arthropoda (including shrimps, crayfish, crabs, insects, and spiders) the locomotor organs likewise consist of sets of levers moved by the contraction of muscles regardless of whether the form of locomotion be swimming, creeping, walking, or flying. The hard parts are outside and the muscles inside, as shown in (Fig. 101, *A*). This relation of levers and muscles is reversed in the vertebrate leg (Fig. 101, *B*), in which the bones are beneath the muscles.

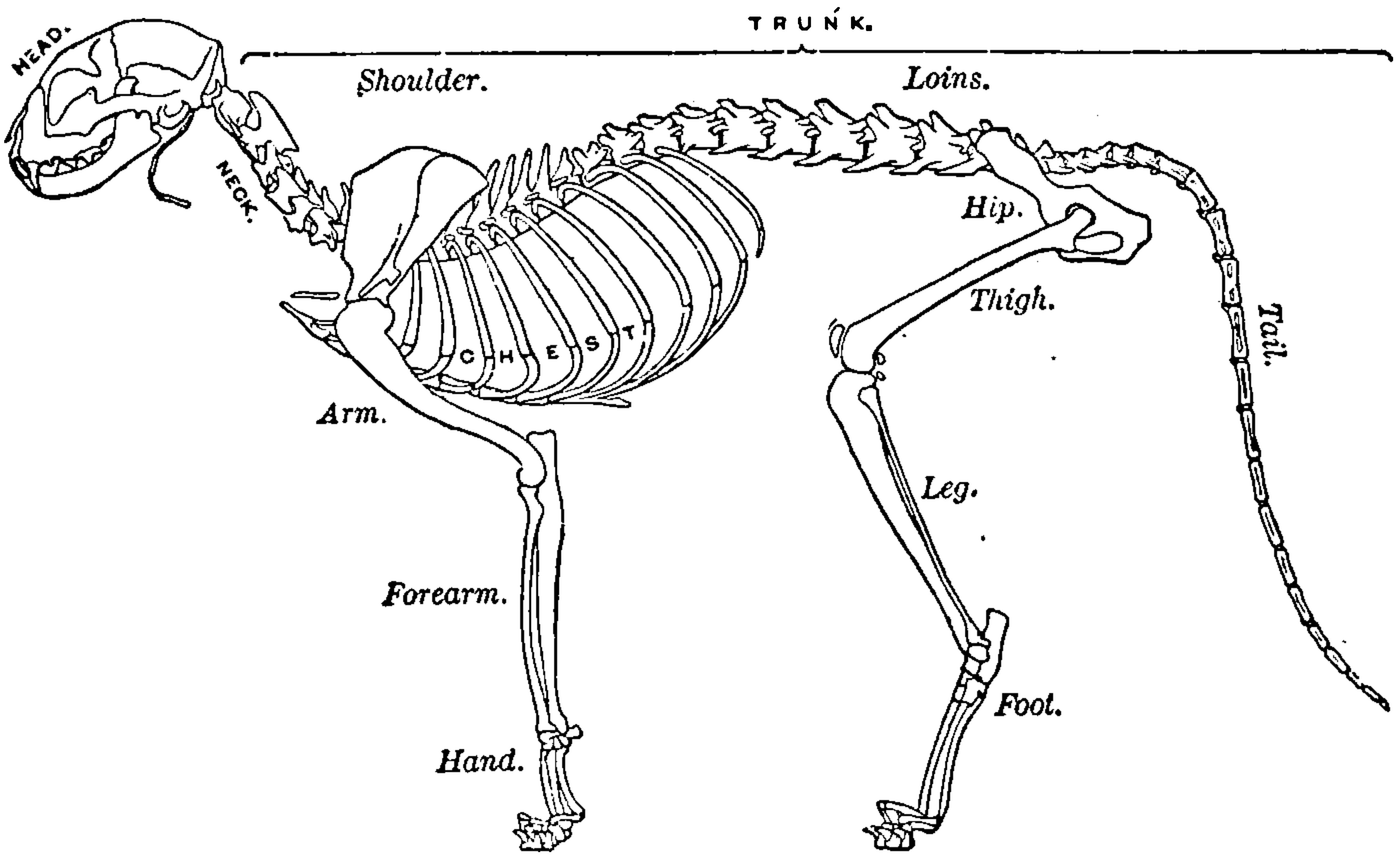


FIG. 102.—Regions of the vertebrate skeleton (cat). (*From Jayne's Mammalian Anatomy.*)

Skeleton of Vertebrates.—The vertebrate skeleton largely determines the form of the body and serves as attachment for muscles and other tissues. It is composed of bones and cartilages united partly by ligaments, is covered 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. 102. On more fundamental anatomical grounds it is also subdivided into the *axial* and the *appendicular* skeleton.

AXIAL SKELETON. The axial skeleton (Fig. 103) 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 vertebræ 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, *cervical, thoracic, lumbar, sacral,* and *caudal* regions (Fig. 103). The plan of a vertebra is shown in Fig. 104. 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 *neural spine.* One pair of articular processes or *zygapophyses* project 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 vertebræ are made clear in Fig. 105.

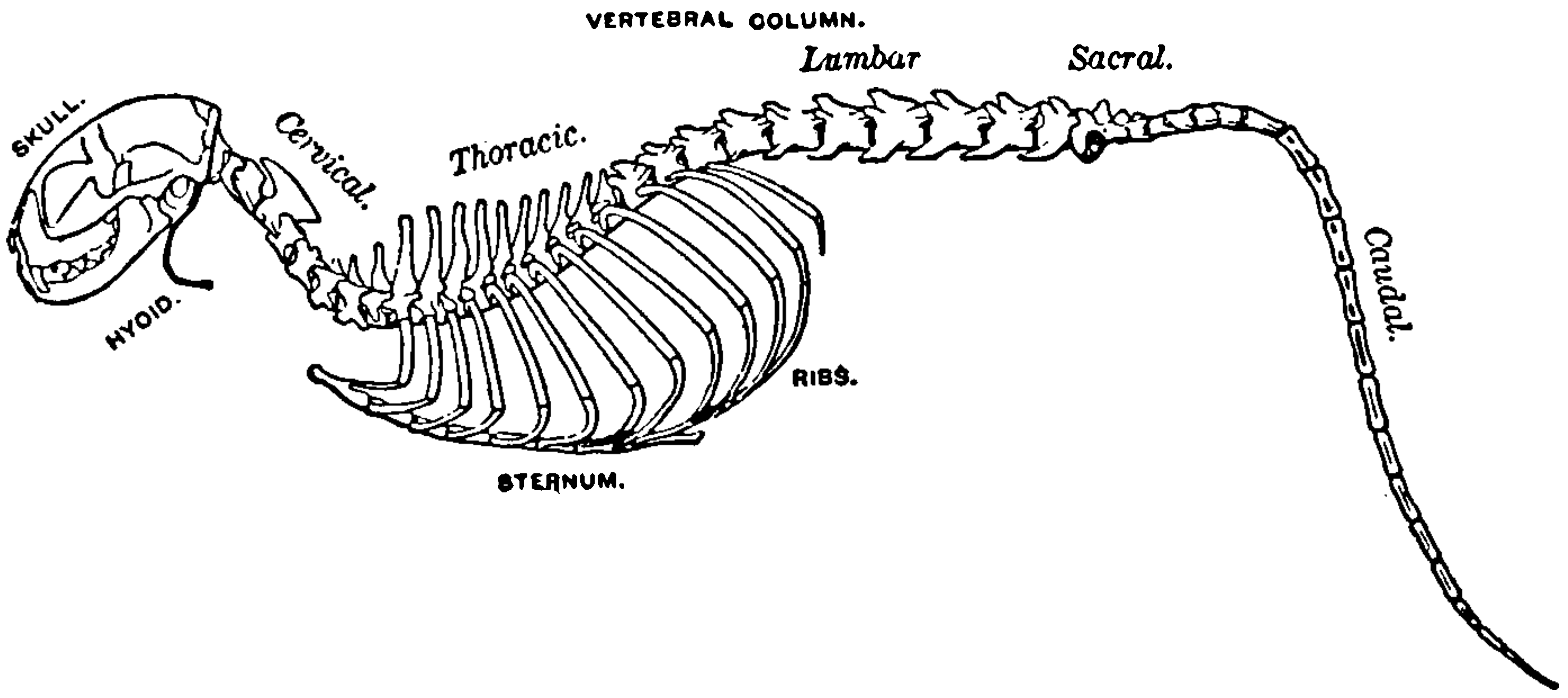


FIG. 103.—Axial skeleton of the cat. (*From Jayne's Mammalian Anatomy.*)

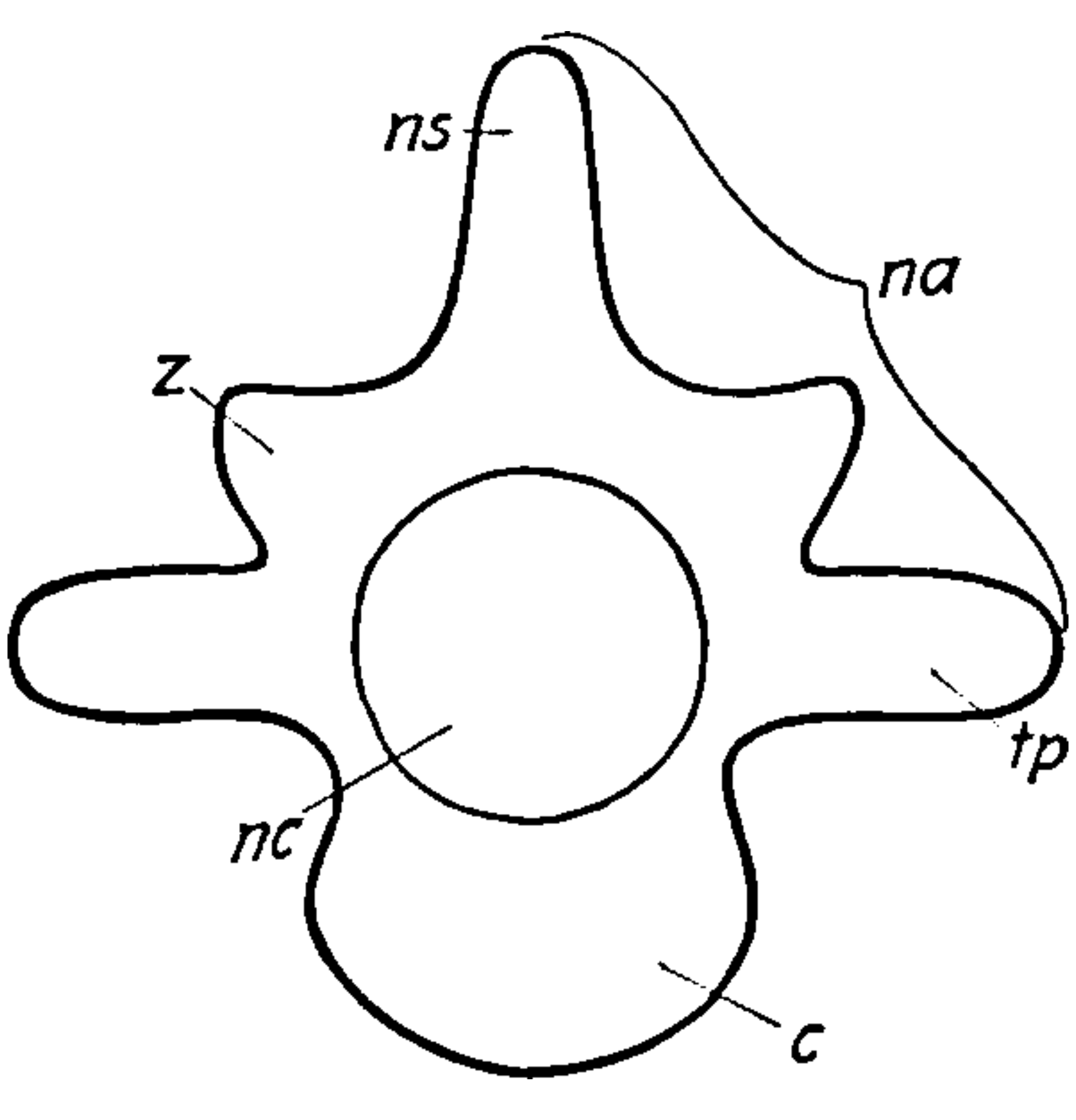


FIG. 104.—Diagram of a typical vertebra viewed from in front or from behind. *c,* centrum; *na,* neural arch; *nc,* neural canal; *ns,* neural spine; *tp,* transverse process; *z,* zygapophysis.

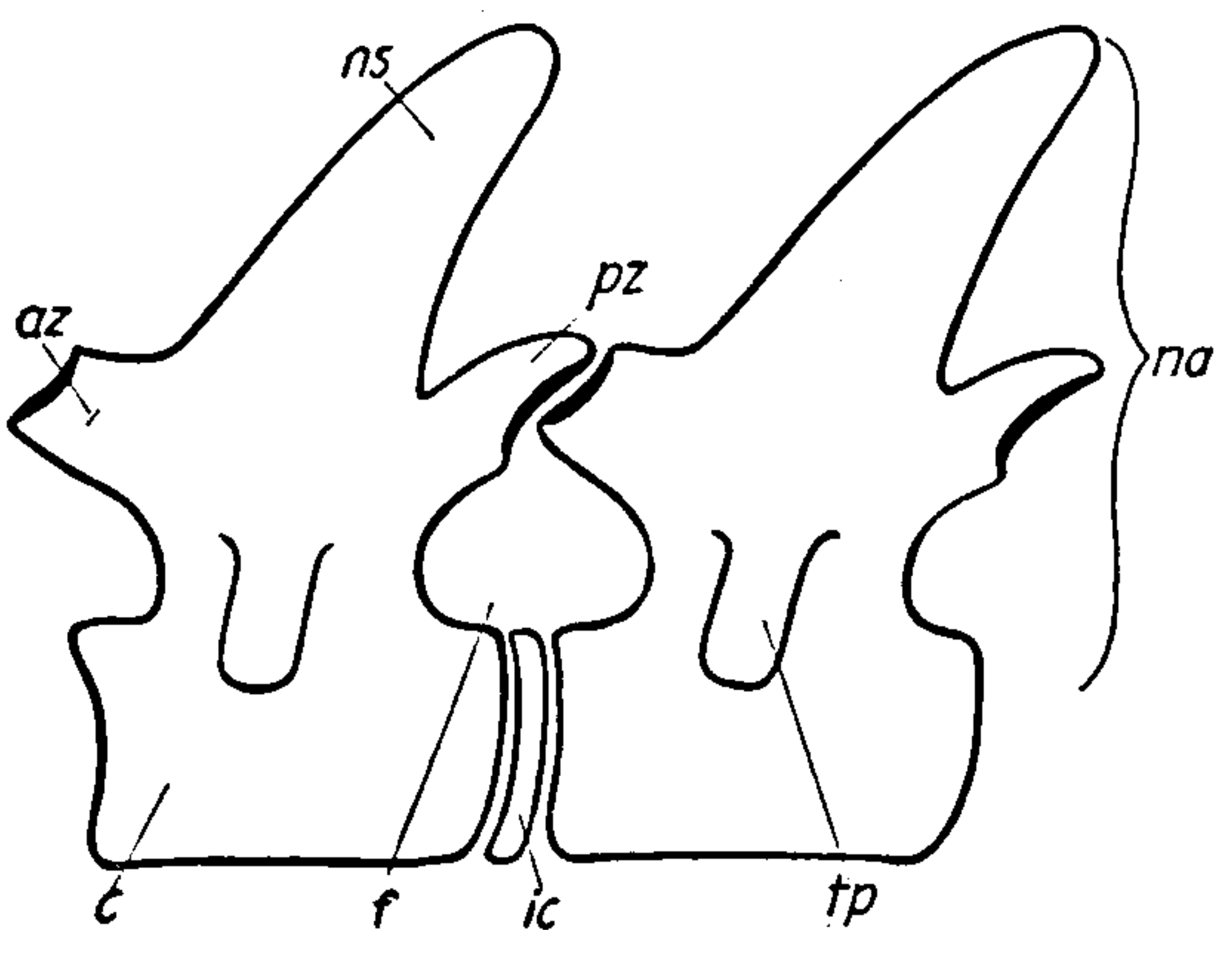


FIG. 105.—Diagram of two typical vertebræ viewed from the side, with anterior end at the left. *az,* anterior zygapophysis; *c,* centrum; *f,* intervertebral foramen through which nerves and bloodvessels pass; *ic,* intervertebral cartilage; *na,* neural arch; *ns,* neural spine; *pz,* posterior zygapophysis; *tp,* transverse process.

of the clavicle. A cavity, the *glenoid fossa*, located at the junction of scapula and coracoid serves as the point of attachment of the fore-limb.

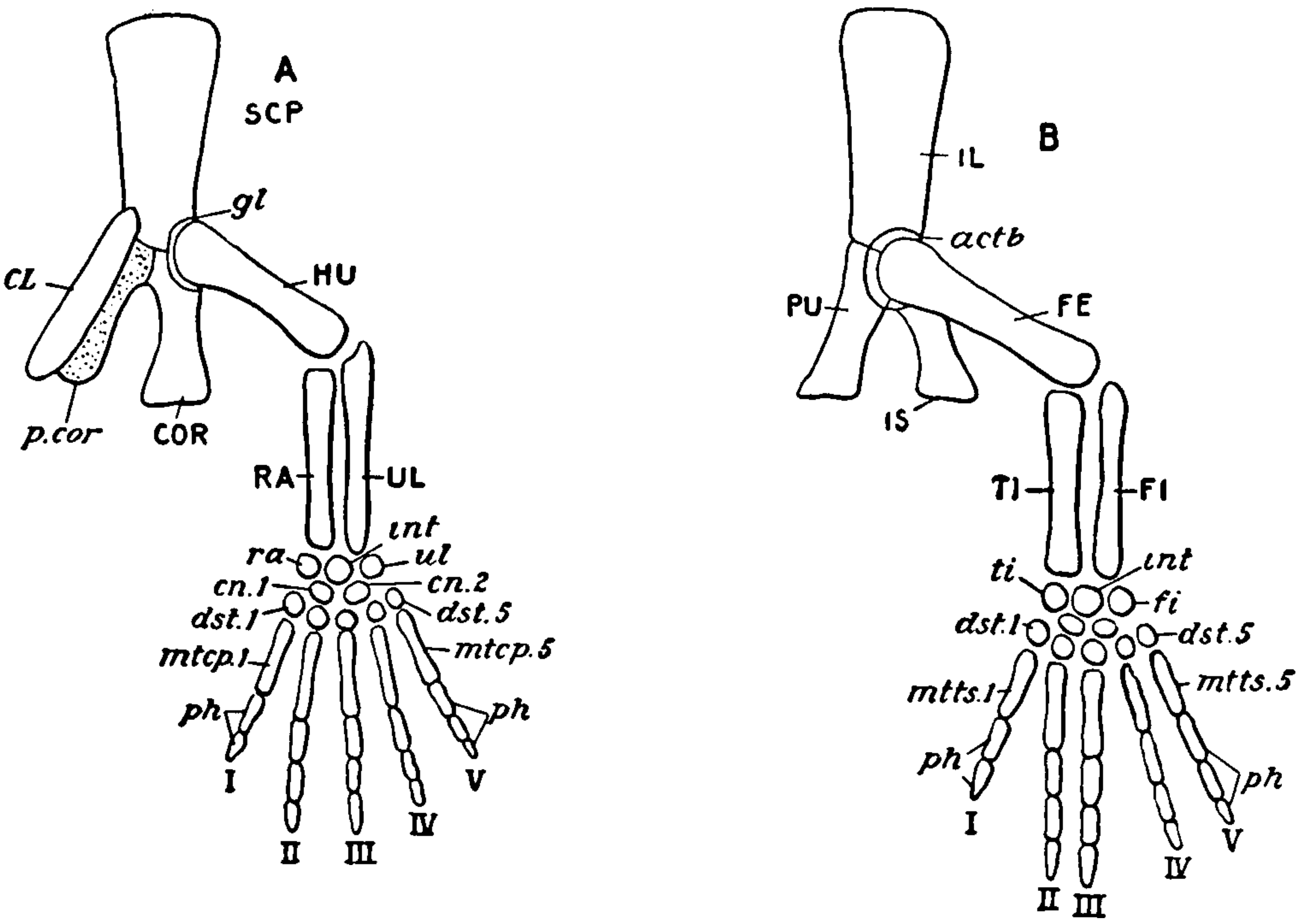
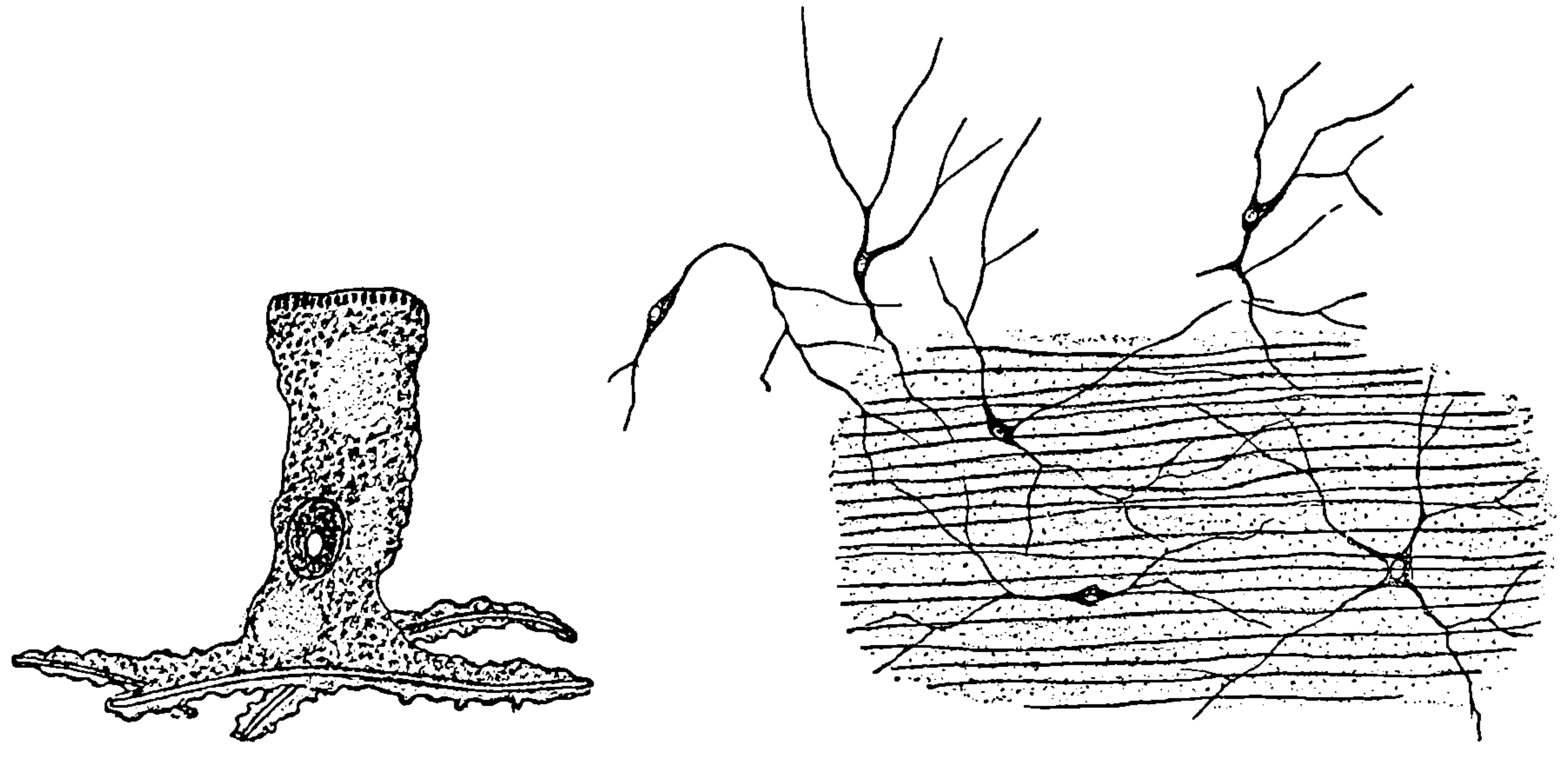


Fig. 107.—Diagrams of generalized fore (*A*) and hind (*B*) limbs with limb girdles. *actb*, acetabulum; *CL*, clavicle; *cn.* 1, *cn.* 2, centralia; *COR*, coracoid; *dst.* 1–5, distal row of carpals and tarsals; *FE*, femur; *FI*, fibula; *fi*, fibulare; *gl*, glenoid fossa; *I-V*, digits; *IL*, ilium; *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's Textbook of Zoölogy.*)



A *B*

Fig. 108.—Nervous mechanism of Hydra. *A*, neuromuscular cell from ectoderm; *B*, ectodermal nerve plexus. The long fibrils in the background are the contractile parts of neuromuscular cells. They lie in the mesoglœa. (*From Schneider.*)

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 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.

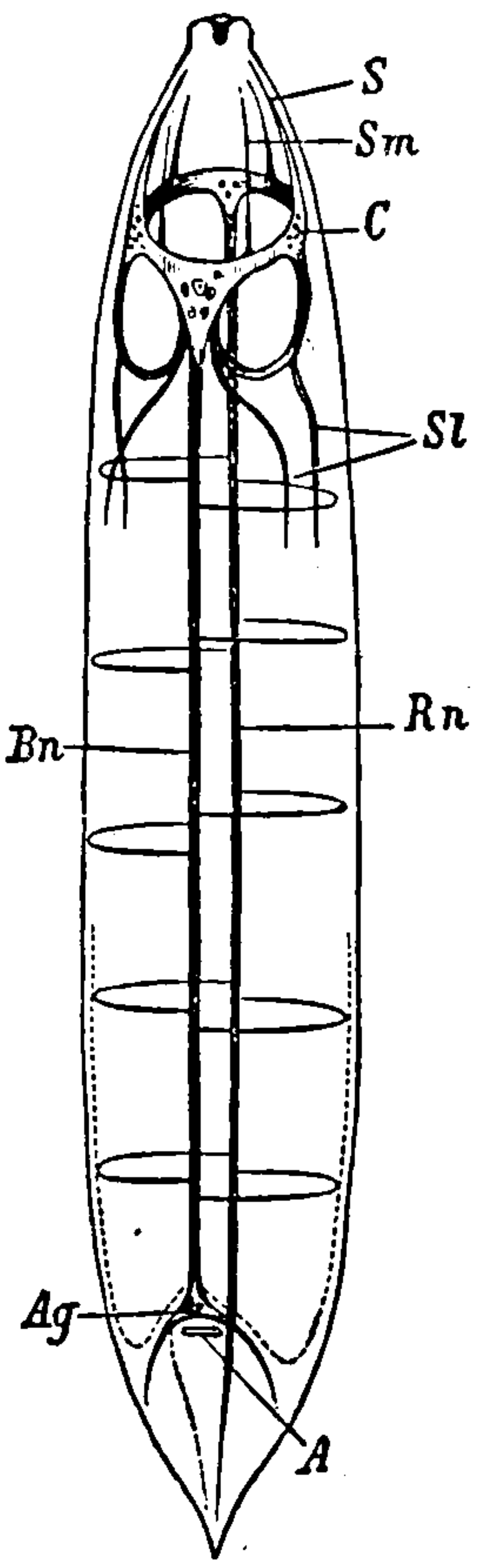


Fig. 109.—Nervous system of a roundworm, diagrammatically represented. *A*, anus; *Ag*, anal ganglion; *Bn*, ventral nerve; *C*, lateral ganglion of nerve ring; *Rn*, dorsal nerve; *S*, anterior lateral nerve; *Sl*, sub-lateral nerve; *Sm*, sub-median nerve. (*From Sedgwick's Student's Textbook of Zoölogy, after Bütchli.*)

Nervous System.—The function of the nervous system is to receive stimuli and transmit impulses. Not present in the Protozoa and Porifera, nervous tissue is first found in the Cœlenterata. In the hydroid polyps there is little specialized nervous tissue, but many ectodermal cells (Fig. 108) have elongated processes at their bases which serve the dual function of contraction and transmission of stimuli and are therefore properly called *neuromuscular* cells. Connected with these cells are sometimes other cells with long processes which serve as nerves for transmission of impulses.

Degrees of Centralization in Nervous Systems.—In jellyfishes, a ring of nervous tissues encircles the rim of the umbrella. ✓ Nerve cells of the ring are connected with a network of nerve cells in the umbrella, making a diffuse nervous system. This type of nervous system is the lowest in the animal scale. A more centralized nervous system is found in the flatworms and roundworms. In the flatworms, for example in the rhabdocœle and triclad Turbellaria, there is a single *ganglion* or thickened mass of nervous tissue in the anterior end of the worm. From this ganglion (Figs. 81 and 82) two main nerve trunks extend to the posterior region of the body. Branches from the ganglion and from the nerve trunks extend forward and to the lateral regions of the body. In the roundworms (Fig. 109) a ganglionic mass, the *nerve ring,* surrounds the esophagus and from this mass a dorsal and a ventral nerve trunk extend backwards. These are connected at intervals by *commissures.* From the nerve ring, branches extend forward and for a short distance backward.

In the Annelida (segmented worms) the nervous system is more highly developed but it is not highly centralized. It consists of a chain of ganglionic masses extending ventral to the alimentary tract from near the anterior end to the posterior end of the worm. In the anterior end the nerve cord divides, the two halves together encircling the pharynx and uniting above it, at the juncture of the pharynx and buccal pouch, to form the so-called *brain,* which in reality is no more than a pair of ganglia. From the brain, branches extend forward to the prostomium and to the other organs of the first few somites. There is a ganglionic mass in each somite, from which paired nerves extend out to the body wall and there branch out to all parts of the somite.

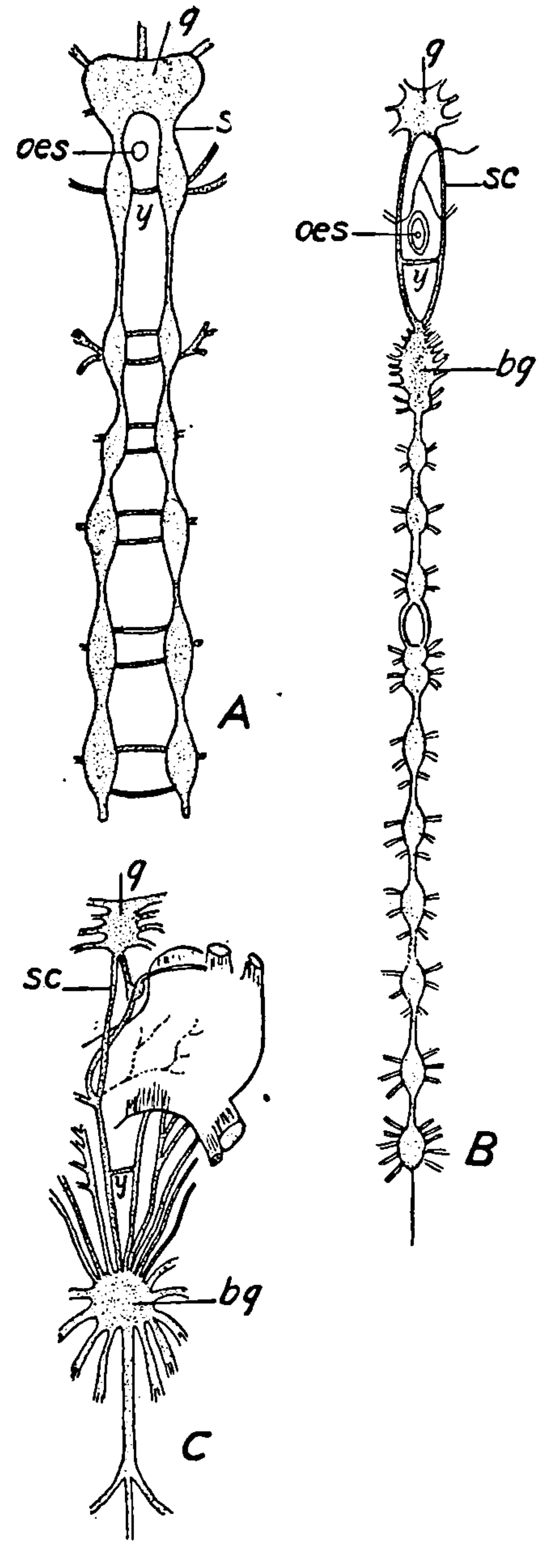


FIG. 110.—Nervous systems of arthropods, showing advance in centralization. *A*, ladder-like nervous system of *Limnadia*, anterior portion only (*after Klunzinger*); *B*, *Astacus fluviatilis* (*after Vogt and Yung*); *C*, *Maia squinado* (*after Milne-Edwards*); *bg*, subesophageal ganglion; *g*, brain or supraesophageal ganglion; *oes*, esophagus; *sc*, esophageal commissure; *y*, postesophageal commissure. (*From Sedgwick's Student's Textbook of Zoölogy, after Lang.*)

The nervous system of the Arthropoda has certain points in common with that of the Annelida. It lies ventral to the digestive system, which it encircles at the anterior end, and is composed of ganglia from which nerves arise. Whereas in the annelids the paired ganglia of each somite are fused into one ganglionic mass, in some Arthropoda they have a ladder-like arrangement as in Fig. 110, *A*, and in others the ganglia are fused into a chain (Fig. 110, *B*) like that seen in the earthworm. A more advanced type of nervous system in which the ganglia of the chain are fused into larger ganglionic masses from which nerves arise may be seen in Fig. 110, *C*. In this type centralization has gone further than in the preceding forms.

Concentrated System of Vertebrates.—Concentration of the main masses of the nervous system into organs of limited extent is carried farther in the Vertebrata where the nervous system is highly organized. Even within the group of the Vertebrata, the nervous system shows a considerable increase in complexity and in the degree of centralization from the condition in the lower vertebrates to that in man. The central nervous system of the frog (Fig. 111) consists

and innervate the organs of the head and neck and many organs of the trunk. The distribution of these nerves is practically the same in all the craniate vertebrates (those possessing crania or skulls). From the spinal cord paired nerves originate, corresponding to the somites of the body as indicated by the vertebræ. Each spinal nerve originates by two roots, dorsal and ventral (Fig. 112). The dorsal root just median to its union with the ventral root expands into a ganglion which is composed of nerve cells whose processes make up much of the nerve. Originating in the brain (Fig. 111) and extending down on either side of the spinal cord are two strands of nervous tissue which are connected by nerves with the dorsal root ganglia. These strands with their branches and ganglia, which may be widely separated from the strands, comprise the *sympathetic nervous system.*

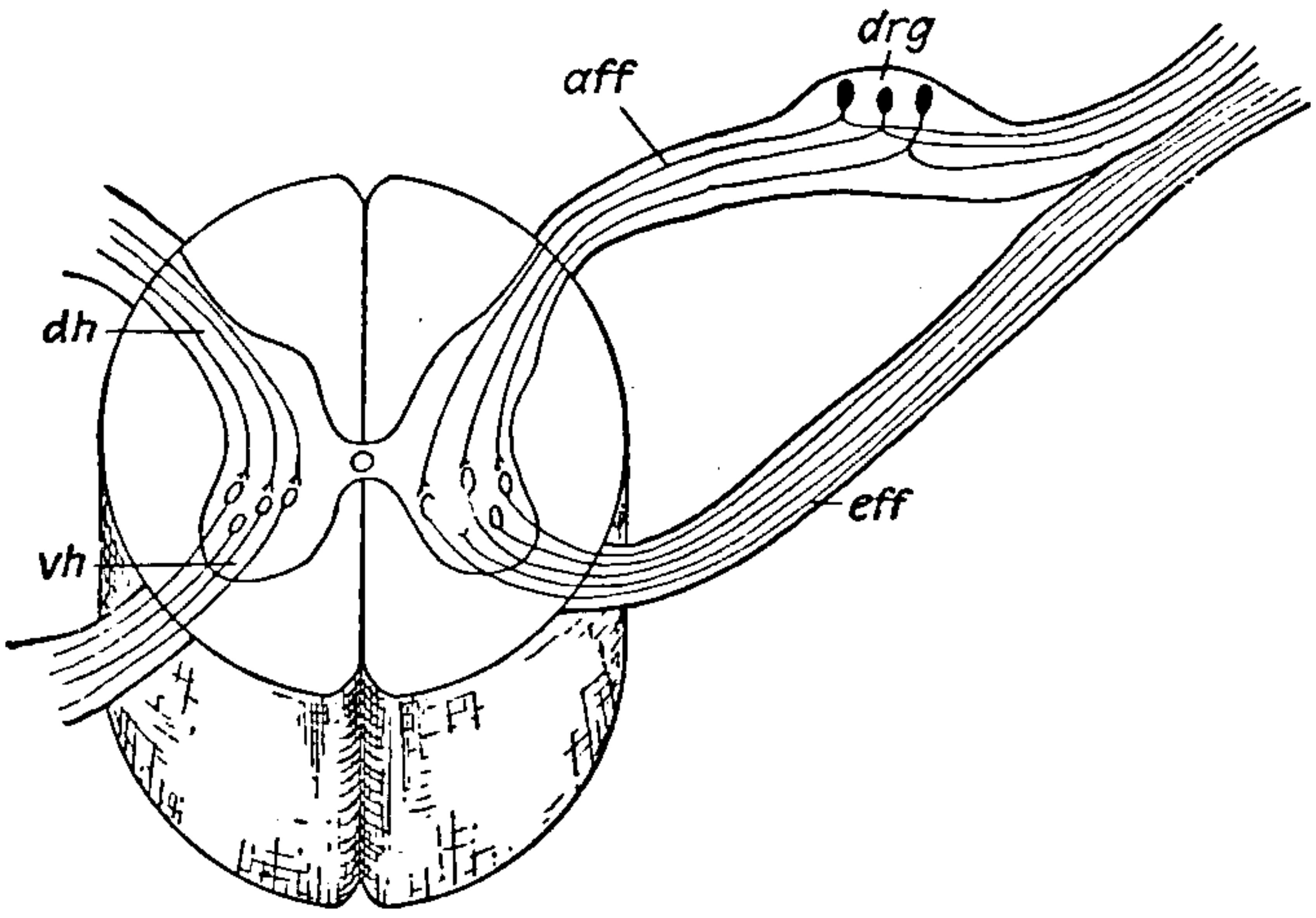


FIG. 112.—Diagram showing origin of spinal nerve by two roots. *aff*, afferent fibers; *dh*, dorsal horn of the gray matter of the spinal cord; *drg*, dorsal root ganglion; *eff*, efferent fibers; *vh*, ventral horn of the gray matter of the cord.

Neurons.—The unit of structure of the nervous system is the *neuron* or nerve cell. These cells are of various shapes and sizes, a few of which are illustrated in Fig. 78. The neuron consists of a cell body from which commonly arise short branching processes, the *dendrites*, and a single unbranched process, the *axon*. The latter is often very long and may be surrounded by a sheath (Fig. 119). Neurons are brought into relation with other neurons by means of their dendrites and axons, which may come directly in contact with the bodies of other neurons or indirectly through their dendrites. The ends of the processes may be in contact with tissues.

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KINGSLEY, J. S. Textbook of Vertebrate Zoloögy, Part I.
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CHAPTER VII

PHYSIOLOGY OF ORGANS

The organization of the bodies of higher animals into organs and systems obviously makes possible a degree of interrelationship of function not found in the physiological processes of simpler organisms.

Organ Physiology Rests Upon Cell Physiology.—The basis of organ physiology is the physiology of the cell, for obviously the function of an organ is, in a sense, the sum of the functions of its component cells. The cells do not share equally, however, in determining the function of the whole organ, for certain cells *directly* perform the service to which the organ is devoted, while others are only accessory to the main function. For example, in the stomach the functions of the cells of the mucous layer are of far greater immediate importance than are the functions of any other cells of that organ, although the other cells are indirectly indispensable. The physiology of an organ is more, however, than the functions of its cells, since in coöperating the cells modify the performance of one another, and there results a function of the organ as a whole, which rests upon the functions of its parts. In like manner, though an organ has a recognizable function, that function cannot be isolated from the functions of other organs, for few organs occur singly. Usually they form part of some system, and the functions of the system are the functions of the organs of which it is composed, plus certain activities which depend on the close mutual relations of the included organs. In the account of these functions duplication of the descriptons of functions which were necessary in connection with the account of the morphology of organs in Chapter VI cannot be wholly avoided, and reference should be made to that chapter for some of the facts of physiology and for further details as to the structure of the organs and systems involved.

Digestion in Man.—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 capable of transforming starch to sugar. This is not accomplished instantly, but the operation is much more rapid on cooked than on raw starches. The ptyalin first splits starch into *erythrodextrin* and *maltose*, one of the sugars. If time is allowed for the reaction the erythrodextrin is further acted upon, yielding maltose and another dextrin. This dextrin is broken down with somewhat similar results, and the final result of the action of ptyalin is that all of the starch is converted into maltose. 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. The maltose remaining from salivary digestion is acted upon by inverting enzymes in the small intestine and associated organs, to which reference is made below. In the salivary secretion there is also some *albumen* and *mucin.* The latter is changed to mucus which acts as a lubricant for the particles of food.

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 mucous layer of the stomach. The movement of the muscles of the stomach mixes the food with the gastric secretion, which contains *hydrochloric acid,* two important enzymes, *pepsin* and *rennin,* and perhaps a third enzyme of less importance, the gastric *lipase.* The hydrochloric acid affords a suitable medium for the action of the enzymes (except the lipase), 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 rendered active (converted into pepsin) by the hydrochloric acid, which is secreted in a concentration of about 0.4 to 0.5 per cent. The acidity of the gastric juice is usually estimated at about 0.3 per cent. Pepsin acts only on proteins converting them to peptones and proteoses. The process of absorption of the products of digestion through the gastric mucosa is not very active. Water and some sugar and peptones are absorbed, particularly if the solution be strong. Ordinary fats are not acted upon in the stomach, but emulsified fats (cream) are said by some investigators to be digested by the gastric lipase. A statement of the results of digestion of fats is deferred, however, to a later paragraph.

Secretin.—When the acid stomach contents are ejected through the pylorus, the acid acts upon a substance in the mucosa of the duodenum and changes this substance to *secretin.* The secretin is absorbed by the blood and is carried to the pancreas which is thereby stimulated to secrete its fluids. Since secretin is not affected by heat nor by alcohol it is not considered to be an enzyme, but is classified in a group of activators called *hormones.* That the stimulation of the pancreas is not by means of nerves is proved by the fact that the pancreas functions properly after the branches of the vagus and splanchnic nerves with which it is innervated are cut.

The Pancreatic Juice.—The pancreas produces a thin watery secretion which amounts in quantity to about 500 cc. to 800 cc. per day, or about 1 to 1¾ pints. This secretion contains three enzymes, which act

of a biliary fistula 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, sometimes called the *succus entericus*, is produced in small tubular glands which are local invaginations of the mucosa of the intestine. This secretion consists of *enterokinase*, *erepsin*, several inverting enzymes, and *secretin*. Enterokinase, as stated above, converts inactive trypsinogen into active trypsin. Erepsin is a protein-splitting enzyme which acts particularly on peptones and deutero-albumoses, reducing them to amino-acids and supplementing the action of trypsin. The inverting enzymes are three in number. These are *maltase*, *invertase*, and *lactase*. Maltase converts into dextrose the maltose and dextrins resulting from the operation of ptyalin and amylopsin upon starches. Invertase changes cane sugar to dextrose and levulose. Lactase converts milk sugar to dextrose and galactose.

Secretin, as indicated above in connection with the stimulation of the pancreas, is not an enzyme but a hormone. It exists in the mucosa 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 enzymes. 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 rapidly removed.

Assimilation.—After foods have been converted into simple substances and rendered soluble they are absorbed. These substances are then resynthesized into more complex substances, that is, proteins, carbohydrates, or fats; or perhaps portions of them without being recombined are oxidized with the liberation of energy. The method of synthesis is unknown but it is presumed that enzymes play an important part in the process.

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 unchanged, or possibly it is synthesized first in the endodermal cells, in which case the proteins, fats and carbohydrates must again be broken down into diffusible substances before they are passed on to the other cells. In animals with a circulatory system, the simpler substances pass through the absorbing cells directly into the blood stream, or into the lymphatic system and then into the blood stream. The principles of osmosis, diffusion and imbibition are usually invoked to explain absorption through the walls of the alimentary tract. Numerous experiments, however, conclusively show that absorption is often greatly modified by the activity of the absorbing cells.

Synthesis of Absorbed Substances.—During passage through the absorbing cells some of the simpler substances may be synthesized into more complex ones. This is certainly true of fats which are absorbed as glycerol and fatty acids, for these latter substances are not found as such in the blood stream nor in the lymphatics. Globules of fat can be demonstrated by proper staining methods in the epithelial cells of the intestine during the process of digestion, and after a meal the branches of the lymphatics which arise in the intestinal walls are white from the emulsified fat contained in the lymph.

There is still considerable discussion regarding the history of the amino-acids after absorption. Recent investigations show that they are absorbed as such and that they occur in small quantities in the blood. It seems probable that they circulate in the blood stream and are selected as needed by the various organs for the synthesis of the particular proteins found in these organs. It is believed that some of the amino-acids not used in the tissues are deaminized, that is, their NH_2 groups are removed, and the nitrogen is eliminated as urea, while the organic compound remaining may be oxidized yielding energy.

The carbohydrates absorbed as dextrose or levulose are collected in the liver where they are transformed into glycogen, $(C_6H_{10}O_5)_x$, a substance having the same empirical formula as starch. This transformation is accomplished by means of enzymes. From time to time glycogen is released into the circulation as dextrose which is carried to the muscles and other tissues of the body where it is reconverted to glycogen and is finally used as a source of energy. In animals glycogen may be synthesized from the products of protein hydrolysis and also from fats, especially from the glycerol portion of the fat molecule.

Whether, in animals, fats and carbohydrates can be utilized in the synthesis of protein is not certain, but plants are capable of synthesis of this type. In animals the use of fats and carbohydrates effects a saving of proteins. Reserve fats are stored in special fat-storing organs as the fat-bodies (*corpora adiposa*) of frogs and toads; in connective tissues between the skin and muscles, or between muscles; or about the abdominal viscera along the mesenteries. A small quantity of fat can be demonstrated in all the tissue cells where it occurs in minute globules.

The utilization of reserve foods requires the use of enzymes which occur in all the tissues of the body. These are proteolytic, amylolytic, and lipolytic enzymes, that is, protein-, carbohydrate- and fat-splitting enzymes respectively. How food reserves are built up into protoplasm is not known but it is supposed that enzymes are concerned in the process.

Respiration.—The oxygen requirement of living things is met by securing uncombined oxygen from the air or from solution in water. In most animals of any size and complexity tracheæ, gills, or lungs (described in Chapter VI) serve as respiratory organs. These organs present a surface large enough and of such a character that an ample supply of oxygen enters the tissues. In animals not so highly differentiated, or in some of those living in situations favorable to the maintenance of a moist external surface, the highly vascularized skin itself may function as a surface for gaseous exchange. This is particularly true of many of the annelid worms in which there are no gills, and of the frog and other amphibians in which the skin is an important organ of respiration.

Respiratory Movements Not Respiration.—Any movements of the body or of its parts which tend to bring fresh air or fresh oxygen-laden water to these external or internal respiratory surfaces may be called *respiratory movements.* These movements are ordinarily termed breathing in terrestrial animals. Respiratory movements also include the movements of the mouth and the gill covers of fish by which fresh water is circulated over the gills, and the movements of portions of the bodies of certain small aquatic annelid worms (Tubifex) which raise the posterior third or half of the body above the mud and wave it about in order to bring the skin in contact with more oxygen. Respiratory movements are accessory to the act of respiration, but they do not constitute respiration.

Mechanism of Oxygen Collection and Transportation.—In insects the circulatory system has little or nothing to do with the transportation of oxygen. Air enters the tracheal system through breathing pores (spiracles) on the sides of the body and is carried into the ramifications of the system by means of respiratory movements of the body. Oxygen in the minute tracheal vessels diffuses through the delicate membranes into the plasma with which the tissue cells are bathed and thence into the tissue cells. In most higher invertebrates and in the vertebrates, oxygen is transported by means of the blood contained in the circulatory system from the respiratory surfaces to the tissues of the body. Gills or lungs present a large surface for gaseous exchange. The internal surface of the human lungs has been estimated at more than 100 square yards, or many times the area of the body. Coming in intimate contact with the delicate membrane of the lungs or gills is the blood which is continually making a circuit through the circulatory system, as described in Chapter VI. The efficiency of the mechanism for oxygen absorption depends largely upon the properties of the protein *hemoglobin* which in vertebrates resides in the red blood corpuscles but which in most of the invertebrates having red blood is diffused throughout the blood

It is estimated that in man the hemoglobin which reaches the capillaries out in the tissues is nearly saturated with oxygen, while the tissues and the lymph in which the cells are bathed are practically devoid of oxygen. Expressed in the usual way the tension of oxygen in the hemoglobin as it arrives in the capillaries is estimated at about 75 to 80 mm. of mercury while in the tissues the tension of the oxygen is practically zero. Hence the oxygen rapidly diffuses from the blood plasma and the hemoglobin into the lymph and thence into the tissue cells where it is used in metabolism. The passage of the blood through the capillaries is estimated to require about one second; yet in this brief period of time the tension of oxygen in the hemoglobin is reduced from about 75 or 80 mm. of mercury to about 37.6 mm., a loss in pressure equal or about 50 per cent. The blood plasma gives up practically all of its oxygen.

External and Internal Respiration.—From the above account it may be seen that respiration in animals that use a circulating medium for the transportation of oxygen to the cells resolves itself into two parts, namely, the passage of the oxygen from the outside medium (air or water) into the blood, and the passage of oxygen from the blood into the tissue cells. These parts have been designated *external* and *internal* respiration, respectively. Internal respiration may be compared to respiration in Amœba, Paramecium or Hydra. This is true respiration. External respiration is merely an accessory operation, loading oxygen upon the transportation system. The oxygen conveyed to the cells is consumed in the oxidation of carbohydrates, fats, and proteins, a process which is accompanied by the release of energy, and the production of materials which cannot be used in the body.

Excretion.—The materials which result from the oxidation of fats, carbohydrates, or proteins, are wastes or excretions. They are largely carbon dioxide and water. The oxidation of proteins also gives rise to nitrogen compounds as well as carbon dioxide and water and certain sulphates and phosphates. The methods of elimination of these substances are described seriatim.

Carbon Dioxide Elimination.—A very small proportion of the carbon dioxide produced by the metabolic activities is discharged, in the mammals, through the skin in the secretion of the sweat glands; but in the frog a large proportion (in some species as much as 74 per cent.) of the carbon dioxide may be eliminated through the skin. A small quantity is eliminated through the kidneys, but in mammals and most other air breathing vertebrates the lungs are the most important organs for the elimination of carbon dioxide. The relative efficiency of gills and skin in aquatic forms with respect to carbon dioxide elimination is apparently not well established. The mechanism employed in carbon dioxide elimination from the tissues and through the lungs is about the same as that of the oxygen intake. The operation of the mechanism depends upon diffusion of gases. The tension of carbon dioxide in the tissue cells is greater than in the blood of the capillaries. This tension has been found by experiment in man to be about 50 to 70 mm. of mercury in the tissues and about 35 mm. in the arterial blood. Under these conditions the carbon dioxide diffuses from the cells into the lymph and from the lymph through the capillary walls into the blood stream. Here some of the carbon dioxide goes into solution in the plasma, some enters into chemical combination with sodium and potassium salts in the plasma and in the corpuscles, and some into chemical combination with the hemoglobin. The tension of carbon dioxide in the alveolar air of the lungs of man has been determined to be equal to 35 mm. of mercury while that in the venous blood is 42.6 mm. As a result of this difference in tension the carbon dioxide diffuses through the membrane into the alveoli of the lungs. From the alveoli it is carried to the exterior with the exhaled air. The method of elimination of carbon dioxide from gills does not differ in its essential features from the method outlined above. The quantities, however, are proportionately smaller.

Elimination of Water.—Water is eliminated from the lungs, skin and kidneys, but the relative importance of these organs varies widely in different species. In the frog the elimination of water through the skin may be very great especially if the frog is in dry air. Under such circumstances the loss of water from the skin may be sufficient to kill the frog in a few hours. In the dog very little water is eliminated through the skin, while in other mammals which perspire the elimination of water through the skin may be considerable. In man the quantity of sweat may amount to 2 or 3 liters per day, but the quantity is very variable. Sweat is secreted by the sweat glands, of which there are about two millions in the human skin. The lungs of man eliminate an appreciable quantity of water as water vapor but this quantity varies within narrow limits. In the dog, which eliminates very little water through the skin, the quantity of water eliminated by the lungs varies considerably being much greater when, because of heat or exertion, the dog pants. The kidneys are the most important organ for elimination of water. The quantity of water eliminated through them in man varies inversely with the quantity eliminated through the skin.

Nitrogen Elimination.—Normal digestion of proteins in the alimentary canal gives rise to amino-acids and some ammonia. Probably the hydrolysis of proteins in the protoplasm yields the same nitrogenous compounds. Some of the ammonia is eliminated in the form of ammonium salts and some of the amino-acids in the free or combined form. The larger proportion of each substance, however, is first converted into *urea.* It has been established that urea is not formed in the kidneys, which eliminate it, but is formed in the liver and perhaps also in the tissues whence it is carried to the kidneys by the blood. Other sources of urea may be ignored in this account.

Relation of the Structure of the Kidney to Excretion.—From the preceding account of excretion it may be inferred that the kidney is the chief organ for the elimination of soluble wastes from the body. The kidney contains a large number of *Malpighian corpuscles* (Fig. 113) each located at the end of a much coiled *uriniferous tubule,* which discharges through a *collecting tubule* into the *ureter.* The Malpighian corpuscle consists of a *glomerulus* (a knot of minute blood vessels) surrounded by two layers of a very delicate membrane (Bowman's capsule) which is the expanded and invaginated end of the uriniferous tubule. The vessels of the glomerulus take their origin in an afferent arterial blood vessel and discharge into an efferent arterial vessel. The uriniferous tubules (Fig. 113) are composed of more or less cubical or pyramidal cells which have a granular protoplasm. Near the Malpighian corpuscle the cells of the tubules, in lower vertebrates at least, are ciliated. The tubule may vary considerably in size in different parts of its length.

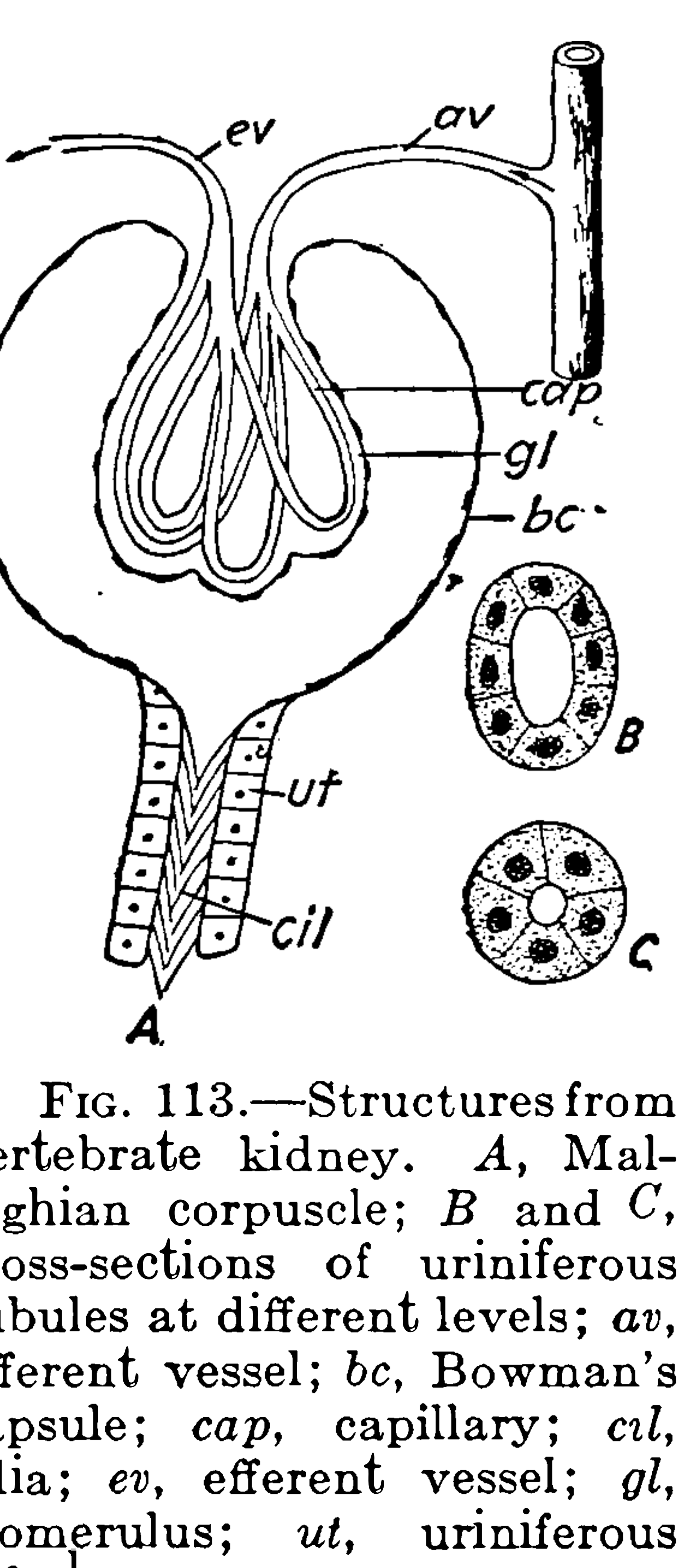

Fig. 113.—Structures from vertebrate kidney. *A*, Malpighian corpuscle; *B* and *C*, cross-sections of uriniferous tubules at different levels; *av*, afferent vessel; *bc*, Bowman's capsule; *cap*, capillary; *cil*, cilia; *ev*, efferent vessel; *gl*, glomerulus; *ut*, uriniferous tubule.

In addition to the blood vessels which form the glomeruli there are very numerous minute blood vessels in intimate contact with other parts of the uriniferous tubule. It is probable that there is no other organ in the body which is more richly supplied with blood than this organ. It has been estimated that under the influence of diuretics (substances which cause increased flow of urine) the amount of blood flow to the kidney may in one minute equal the weight of those organs. This is said to be 4 to 19 times the average relative blood supply of other organs of the body.

Theories of Urine Elimination.—There are two principal theories as to the action of the parts of the kidney in elimination of urine. The earliest and simplest one of these theories, that proposed by Ludwig, is known as the *mechanical theory.* According to it urine elimination is explained by the *filtration* of water and dissolved substances, as salts, urea, etc., from the blood through the thin membranes of the glomerulus and the capsule. The urine according to this theory is dilute as it enters the tubules but is modified during its passage through the tubule by diffusion. The other theory, developed by Bowman and Heidenhain, asserts that water and certain salts are eliminated from the blood through the membranes of the glomerulus by an act of *secretion,* and that the urea and other organic compounds found in the urine are secreted by the cells of the tubules. Many experiments have been performed to test

retained in a dilatation of the lumen of the gland until the secretion is required. When the gland is stimulated in the appropriate manner the secretion is poured out as a result of contraction of the muscles of the gland. In many other glands the secretions are retained within the cells and are not discharged until the gland is stimulated. Stimuli which rouse glands to activity are of various sorts, the chief of them being nervous and chemical (by means of hormones). The action of a hormone has been cited in the account of the stimulation of the pancreas by secretin. This substance is produced from a material in the cells of the duodenum by the action of the acid chyme. The secretin is absorbed by the blood and is carried to the pancreas where it stimulates the cells to discharge their secretions. Control by the nervous system is discussed below.[1]

Glands of Internal Secretion.—Glands which have no ducts and whose secretions must diffuse (or are emptied) into the lymph and blood are called glands of *internal secretion.* In this category may be included the pituitary, thymus, thyroid, and adrenal glands. Some of the glands provided with ducts also produce one or more secretions that are absorbed by the blood and so these glands must be regarded as glands of internal secretion. These are the pancreas, liver, and sexual glands. The last mentioned glands maintain the germ cells, but they also produce some secretions which are absorbed by the blood and have a most profound influence upon physical and mental processes. The functions of some of these glands of internal secretion are coming to be known through experiments with removal of the glands and with feeding the extracts of glands. Some of their secretions influence blood pressure; others affect muscular contraction and muscular tonus; others control the growth of skeletal parts and of tissues, the growth of primary and accessory sexual organs and development of secondary sexual characters; and some influence nutrition and other metabolic activities. A study of internal secretions figures largely in the training of the medical investigator, but a further discussion of them would be too involved for this book.

Diversity of Glandular Secretions.—A considerable number of secretions have already been named and something of their functions pointed out, but they form only a beginning of the list that might be given. Among the secretions that may not immediately occur to the student as belonging to this class of substances are the sebaceous materials which make the hair and skin oily, milk for nourishment of young, wax such as beeswax, poisons like those of snakes and certain insects, acids such as formic, sulphuric, and hydrochloric, gas as in the swim bladder of fishes and the float of the Portuguese man-of-war, the ink-like sepia which is thrown out to cover up the escape of the cuttlefish, silk of silkworms and other insects and of spiders, the odors of insects by which they attract

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[1] Reference should here be made to the description of the morphology of glands in the preceding chapter, where many facts regarding function are also given.

the members of the opposite sex, and the disagreeable odors of certain insects and mammals by means of which they repel other animals. Uncommon instances of glandular activity are the production by glands in certain fish of an electric current sufficient to cause a decided shock, and, in other animals, of secretions which by oxidation produce light.

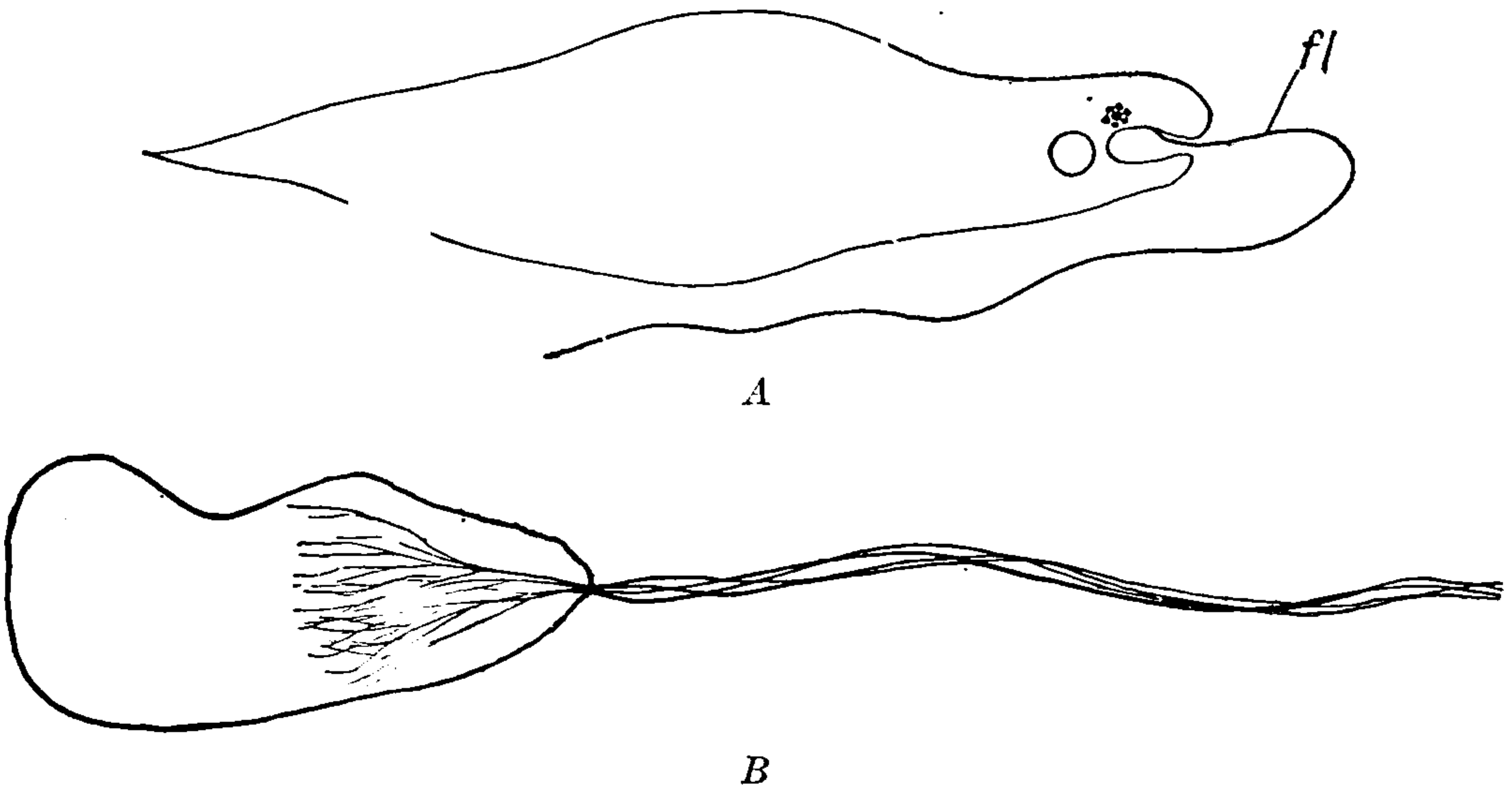

Fig. 114.—Euglena. *A*, individual showing flagellum (*fl*); *B*, fibrils in flagellum. (*A original*; *B after Dellinger in Journal of Morphology*.)

Muscular Contraction.—Protoplasm is contractile, but vigorous contractions are possible only when the protoplasm has developed within it specialized contractile structures. These are of a fibrillar nature. In Protozoa possessing structures capable of strong contraction these fibrils are known as *myonemes*. Myonemes may be found in the flagellum of such animals as Euglena and Peranema and in the stalk of Vorticella, as mentioned in Chapter III. The flagellum of Euglena (Fig. 114) or Peranema is constructed of an external layer of elastic substance enclosing a number of myonemes which extend from the tip of the flagellum into the cytoplasm of the cell. The myonemes are twisted in the form of a loose spiral. Contraction of the myonemes or of certain of them bends the flagellum. The stalk of Vorticella is likewise composed of a sheath of elastic material enclosing a core made of myonemes (Fig. 115). Contraction of the myonemes causes the stalk to assume the form of a closely wound spiral. The spiral form is due to the fact that the myonemes

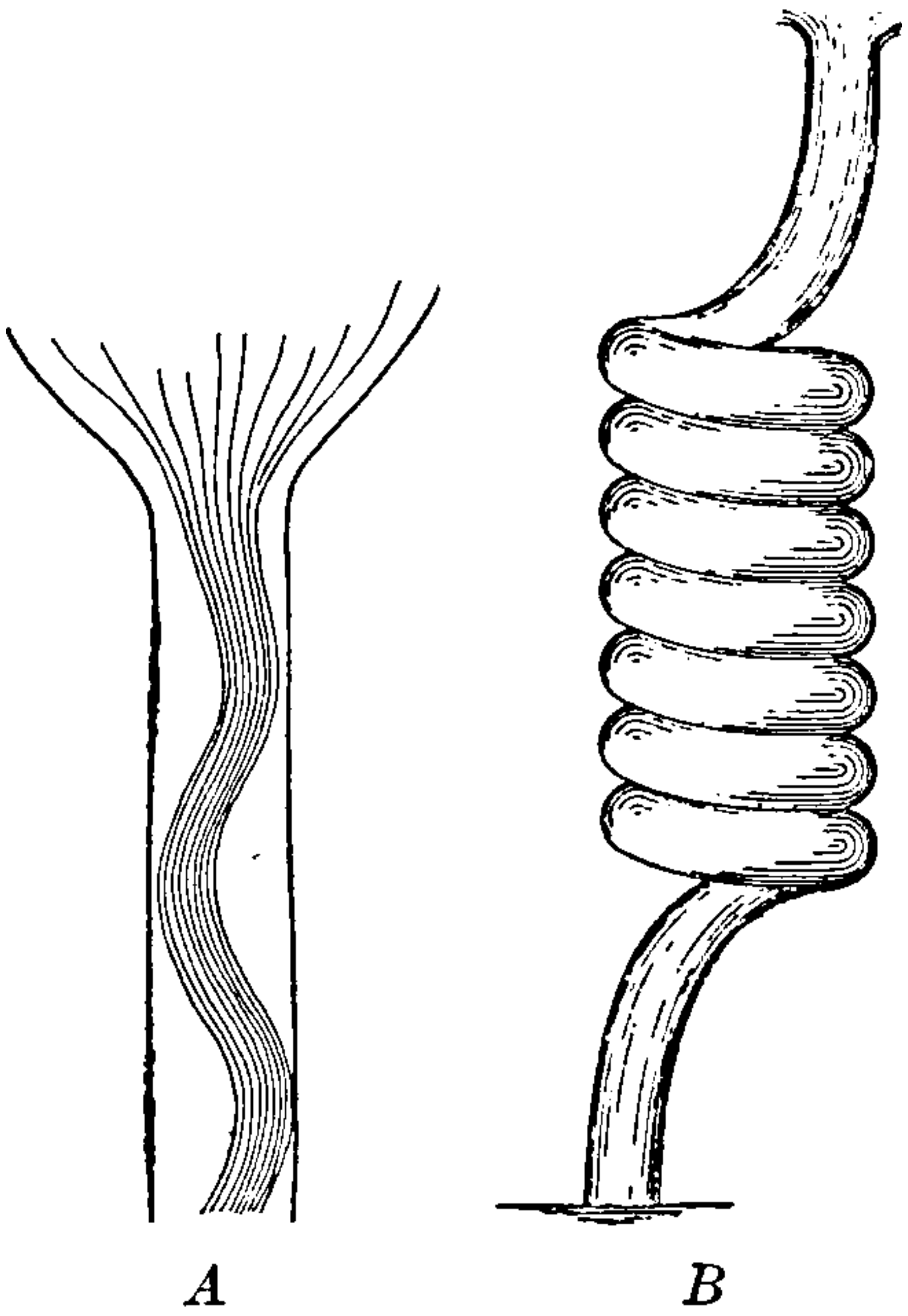

Fig. 115.—The stalk of Vorticella. *A*, arrangement of myonemes within the elastic sheath; *L*, stalk contracted.

occupy the form of a loose spiral in the sheath and perhaps to other peculiarities in the shape of the myonemes. Relaxation of the myonemes permits the elastic stalk to extend to its full length.

Muscle.—In multicellular animals, while a large proportion of the cells are capable of slight contraction, certain cells are highly developed for purposes of contraction. As in the Protozoa, cells of metazoa which function for strong contraction have developed within themselves fibrillar structures capable of great contractility. Cells containing such structures are *muscle cells.* Muscle cells rarely occur singly in organs or tissues but usually as plates or bundles. These groups of muscle cells are called *muscles.* Two types of muscle cells have been developed. Cells of one of these kinds are simple in structure, capable of only relatively slow contraction; those of the other kind are complex and are capable of rapid contraction. The former are known as *smooth* muscle cells and the latter as *striated.*

Smooth muscle is composed of cells each of which is provided with a nucleus. The cytoplasm contains well marked longitudinal fibrils. These cells (Fig. 116) have the form of slender spindles with unbranched tips or in certain organs the tips may be branched. They are capable of strong but relatively slow contraction and relaxation. In higher animals they occur in organs in which rapid contraction is not required, for example in the walls of the digestive tract, urinary bladder, gall bladder, arteries and veins, and in certain glands and their ducts. Often these cells are arranged in layers which are applied to the organs in different directions, as transversely and lengthwise, respectively, giving rise to *circular* and *longitudinal* muscles. Smooth muscle is under the control of lower nervous centers and is therefore not directly subject to the will. For this reason it is sometimes called *involuntary* muscle. Striated muscle, except heart muscle, is under the control of higher nervous centers, and since its contraction may be initiated by an act of the will it is called *voluntary* muscle.

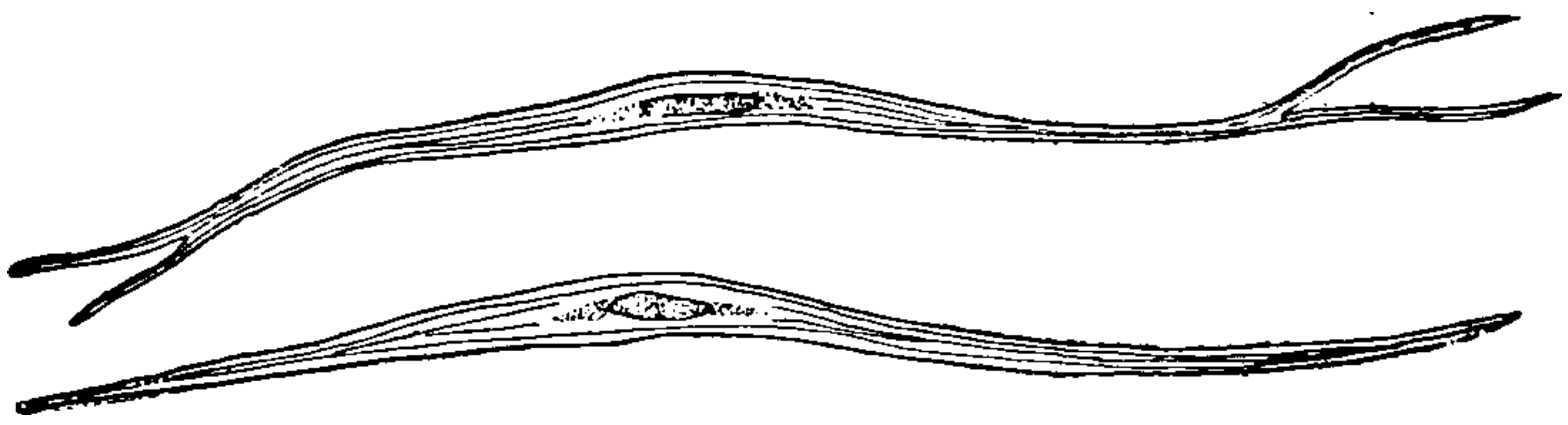

FIG. 116.—Smooth muscle cells.

Striated muscle differs from smooth muscle in the character of its fibrillæ which are striated and in respect to the number of nuclei within the cell. Striated muscle, except the heart muscle of the vertebrates, is composed of much elongated parallel cells each containing numerous nuclei which are scattered among the fibrillæ. Striated muscle cells originate embryologically from cells each of which has a single nu-

gate somewhat and become thicker, while the light bands shorten or are covered up by the dark bands. These changes are usually studied in stained preparations in which it is difficult to interpret appearances. They may also be studied in living muscles composed of but few sarcostyles. Such muscles have been studied in the legs of some of the smaller aquatic insects and in certain aquatic mites parasitic in the gills and mantle of freshwater mussels. Here the changing length and appearance of the dark and light bands can be readily studied because of the transparency of the thin cuticle which covers the muscle and because movement is slow.

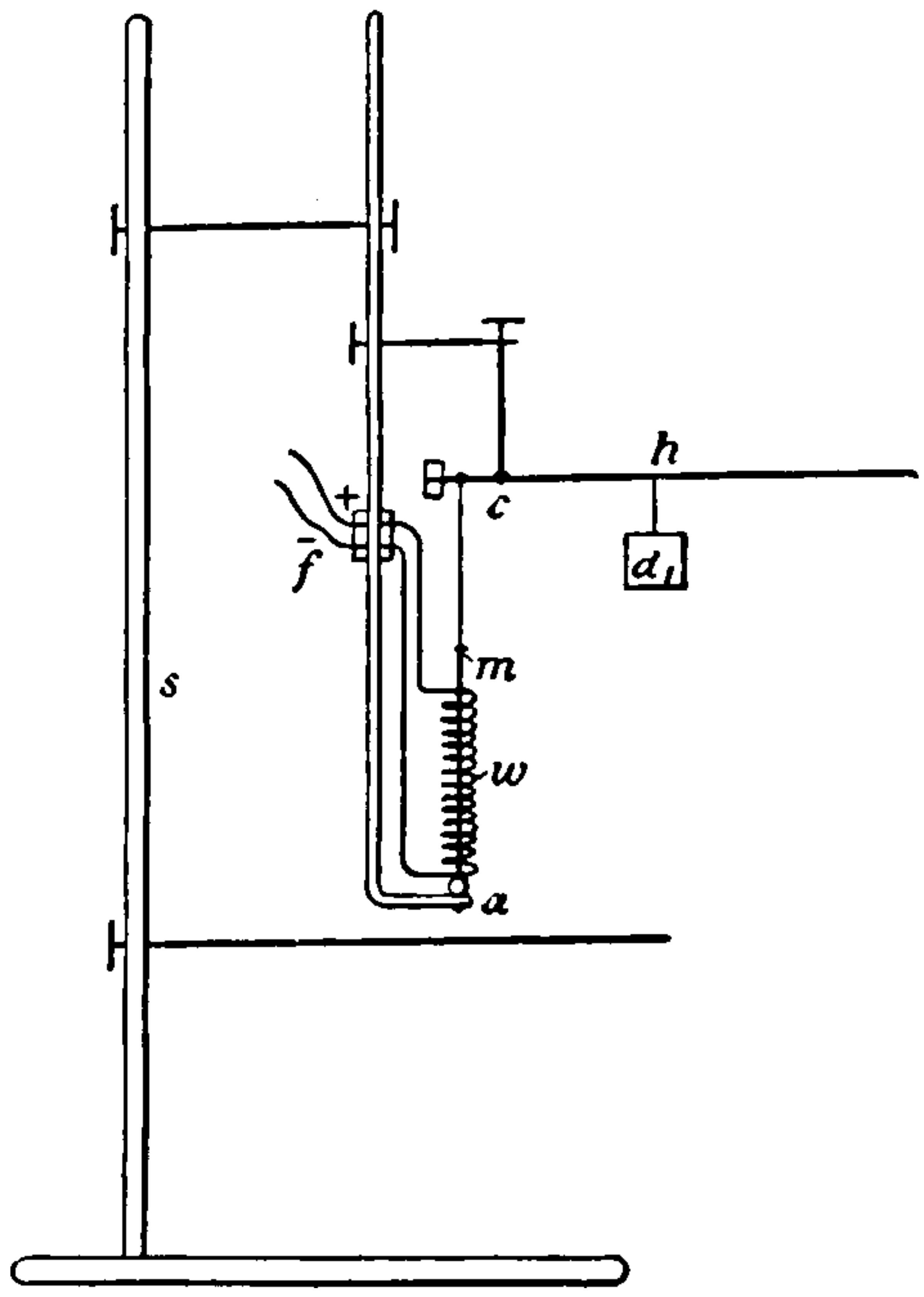

FIG. 118.—Engelmann's apparatus for simulating muscle contraction. *c*, fulcrum of lever; *h*, lever; *m*, catgut; *w*, coil of platinum wire. (*From Howell's Textbook of Physiology, after Engelmann.*)

When the fibrillæ are viewed by polarized light, it is found that the dark stripe of striated muscle is doubly refractive and the light stripe singly refractive. Engelmann, the eminent physiologist, explained muscular contraction by saying that upon stimulation the material of the dark stripes absorbed the material of the light stripes and that since the dark stripe was long and narrow it tended to become spherical when it imbibed material from the light stripe. The thickening of all the dark stripes in all the sarcostyles of a muscle would account for its increased girth upon contraction. By the imbibition of material from the light stripe the dark stripes are brought closer together. This accounts for the shortening of the muscle. How can a stimulus bring these changes about? Engelmann answered this question by saying that the stimulus initiates chemical changes in the protoplasm surrounding the sarcostyles of such a nature that reserve materials as glycogen are oxidized with release of heat and the formation of lactic acid and carbon dioxide. The heat, according to Engelmann's theory, causes the dark stripe to absorb liquid. As a demonstration he arranged an apparatus in which a piece of violin string, which is made from the dried smooth muscles of the intestine of the sheep, was substituted for a live muscle. The violin string contains doubly refractive particles. The string was first soaked in water and attached to the writing lever of a kymograph. About the muscle was placed a coil of platinum wire connected to a source of electricity. The water around the violin string was warmed to about 55° to 60°C. and then an electric current was sent through the coil of wire for a brief time. This heated the coil and the violin string was observed to contract. Upon cooling again it relaxed. The curve which the lever made on the smoked drum of the kymograph agreed in all essentials with that made by a fresh smooth muscle. The explanation of the contraction of this violin string is that the sudden heating of the string caused by the heated coil of wire caused the doubly refractive particles to absorb more water and to change their shape from linear or prismatic to spherical. A diagram of Engelmann's apparatus is shown in Fig. 118.

While Engelmann's theory of muscular contraction may not be correct, it at least visualizes the process, and properly appeals to chemical or physical processes for an explanation.

Nervous Control.—There are three means of controlling the mass of cells of which a metazoön is composed. These are (1) the tissues which bind the organs together and the skin which encloses the whole, (2) hormones and other substances which act by virtue of their chemical nature, and (3) the nervous system. The first of these modes is largely mechanical, but it is not unimportant for without the mechanical effect of the connective and muscular tissues there could be no unification of the various parts into an individual. The second method of unification and control (by means of hormones or other chemical substances) has already been illustrated in an earlier part of the chapter. It is exemplified by the discharge of pancreatic secretions in response to stimulation of the pancreas by secretin. This mode of control is automatic, that is the various events or circumstances leading to the end result stand in the mutual relation of links in a chain. Control by hormones is involuntary, not under control of the will. By this chemical means of regulation many of the metabolic activities of the body are wholly or partly directed. The nervous system plays a rôle in certain instances of hormone control; but this system also directs a large number of activities with which the organs of internal secretion and their products have nothing to do. The nervous system not only coördinates the activities of many of the internal organs but also controls the reactions of the individual to conditions of the environment. Much of this control is performed automatically, that is, without involving thought on the part of the individual.

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. 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.* Which direction the impulse travels, and hence which processes are dendrites or axons, is determined by the manner in which the given neuron is connected with other neurons. Figure 119 represents a typical neuron.

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.

The functions of the nervous system depend largely upon the manner in which the neurons are connected into neuronic systems and upon the character and positions of the terminations of the the axons and dendrites. These systems are of varying degrees of complexity.

The Reflex Arc.—A simple reflex arc is composed of one *sensory* neuron and one *motor* (activator) neuron. Such an arc is diagrammatically represented in Fig. 120. The example chosen involves the spinal cord and a spinal nerve. The dendrites of the sensory neuron branch out between the cells of the skin. The body of the neuron lies in a ganglion, and its axon passes into the dorsal horn of the gray matter of the spinal cord where its terminal branches come in contact with the dendrites of the motor neuron. The body of the motor neuron lies in the ventral horn of the gray matter and its axon emerges from the ventral side of the cord, passes by the ganglion, and then runs for some distance in the same bundle (nerve) with the dendrite of the sensory neuron. The axon of the motor neuron terminates in a muscle in the example chosen. In other similar reflex arcs it may end in a gland. Stimulation of the sensory endings in the skin causes an impulse to pass along the dendrite and axon of the sensory neuron to the motor cell

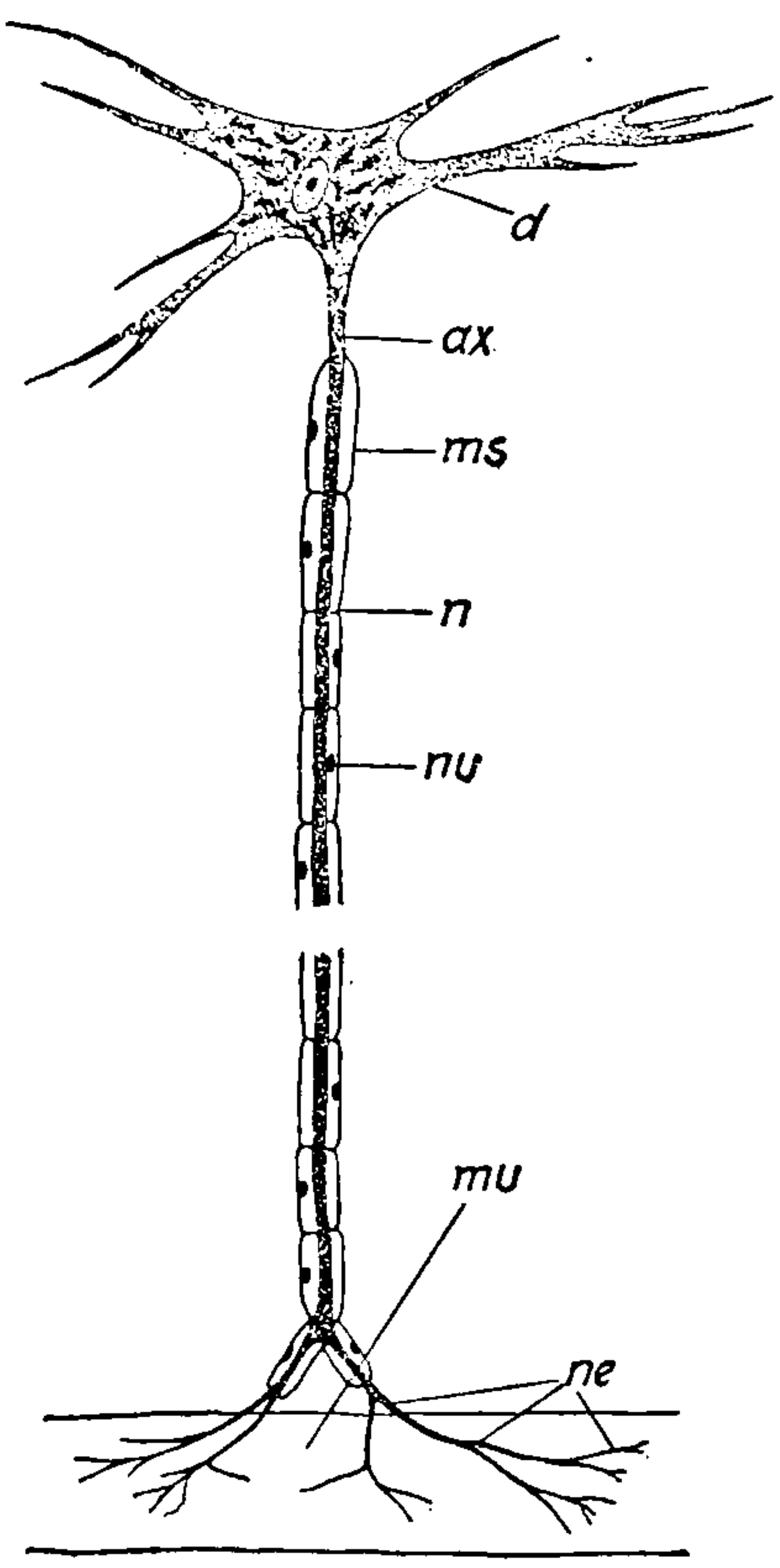

FIG. 119.—Diagram of a typical neuron. *ax*, axon; *d*, dendrite; *ms*, medullary sheath; *mu*, muscle; *n*, node; *ne*, nerve endings; *nu*, nucleus of cell of medullary sheath.

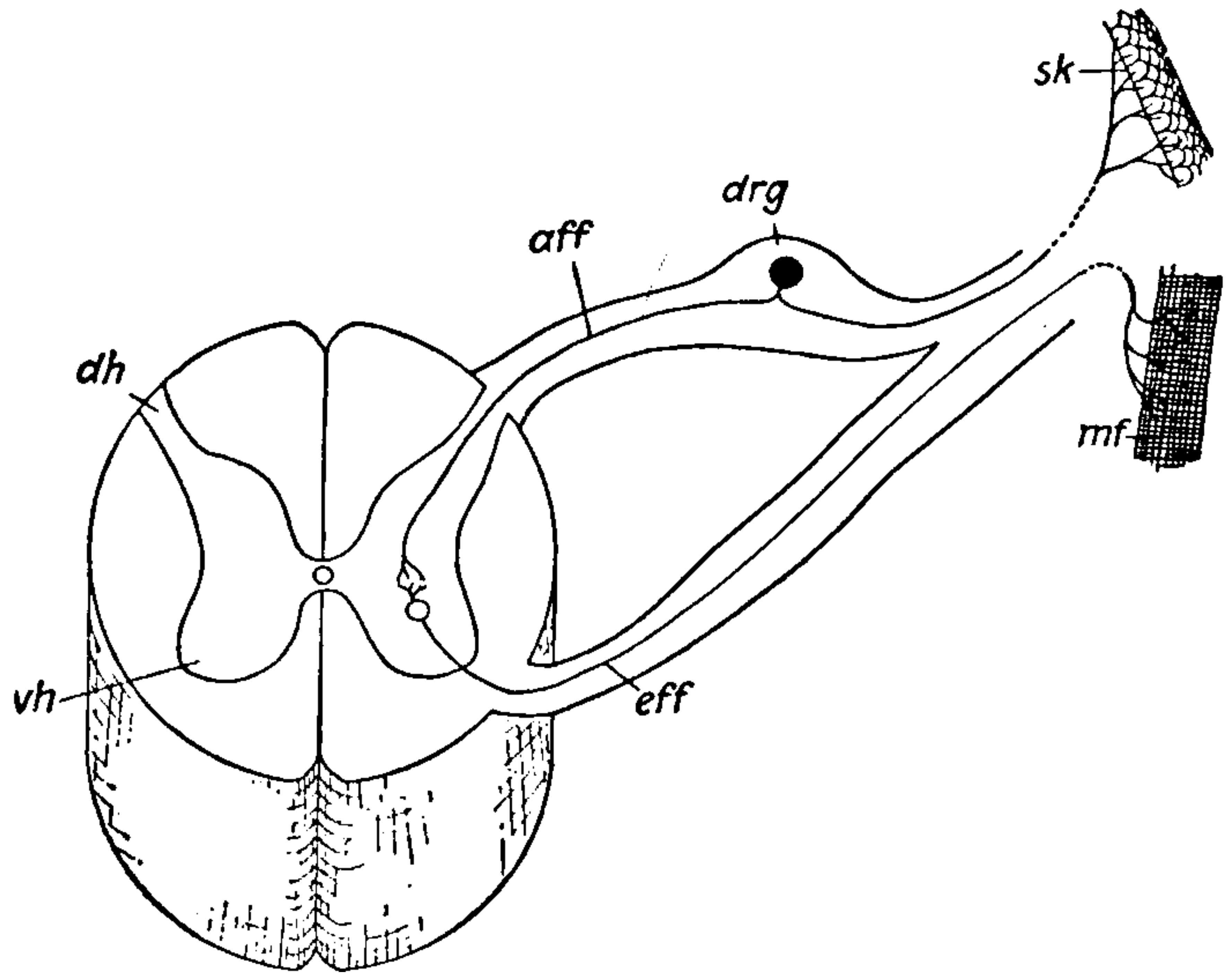

FIG. 120.—Diagram of a simple reflex arc involving the spinal cord. *aff*, afferent fiber; *dh*, dorsal horn of spinal cord; *drg*, dorsal root ganglion; *eff*, efferent fiber; *sk*, skin; *mf*, muscle fiber; *vh*, ventral horn of spinal cord.

secutively, but all related to one another. The reflex mechanism is sufficiently complicated to care for two or more complex series of reflex actions at the same time. For instance one may swim and talk, or play the piano and sing. In some of these instances part of the action may be voluntary, the remainder involuntary.

Functions of the Spinal Cord.—The spinal cord acts as a system of reflex centers which control the activities of various glands, visceral organs, and skeletal muscles. In addition to this function it serves as a pathway to and from the brain. In man more than half a million neurons enter the cord through the dorsal roots of the spinal nerves. These bring in afferent impulses from the peripheral endings of sensory cells. By means of neurons which lie in the white portion of the cord and which end in the brain, impulses may be carried upward to the brain while a multitude of other neurons which originate in the brain form the pathway of impulses from the brain to the ventral roots of the spinal nerves. In terms of a telephone system the spinal cord may be likened to a series of centrals for the handling of local messages and to a great trunk line which transmits long distance messages arising at any point on the periphery of the system or at the great central station, the brain. Unlike the telephone system, however, messages (impulses) can pass only in a certain direction on the line (neurons). Hence in every reflex arc there is a neuron for carrying in the impulse initiated by the stimulus and another neuron for carrying out the impulse from the controlling center to the organ which executes the appropriate action.

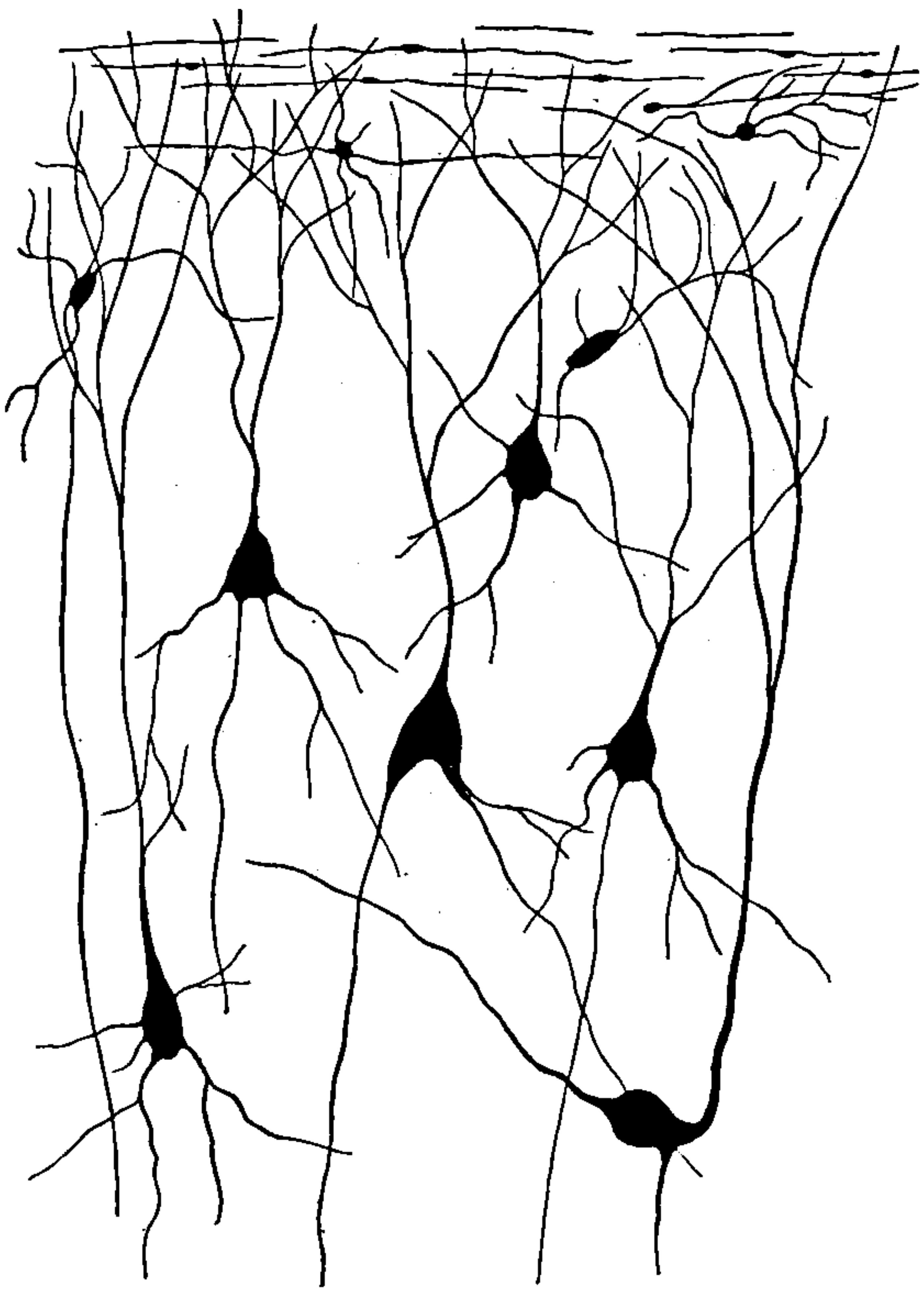

Fig. 121.—Cells of the cortex of the cerebrum of a cat as shown in a Golgi preparation.

Functions of the Cerebrum.—The cortex of the cerebrum, that is, the layer of gray substance which covers the organ and dips down into the furrows, is the seat of intelligence and of conscious sensations. It is the organ of memory associations. In higher animals it controls voluntary motions. In the cerebrum the neurons of one side (right, for instance) give rise to axons which cross to the other side (left) as they extend down to lower centers, and there terminate around cells whose axons in turn go to the muscles (left). Hence the movements of the muscles of one side of the body are controlled by neurons located in the opposite side of the cerebrum. This statement is not entirely true since certain muscles are connected to neurons in both sides of the brain.

The cells of the cortex are mostly of the type illustrated in Fig. 121.

Functions of the Cerebellum.—Although great progress has been made in the study of the cerebellum there still exists much difference of opinion regarding its function. In some manner it regulates the mechanism of automatic movements. It has the effect of coördinating voluntary movements, especially the complex movements of equilibrium and locomotion. It is not believed that the cerebellum is responsible for a high degree of consciousness, if any. Unlike the relations of the cerebrum to muscles, each half of the cerebellum is connected with the organs on the same side of the body with itself. The cells of the cerebellum are of several types and the arrangement of fibers is very complex.

Functions of the Medulla Oblongata.—This portion of the brain includes centers which control the activity of the organs of circulation and respiration. Through the vagus (tenth cranial) nerve it has an inhibitory effect on the heart. It also controls the movements and secretions of the alimentary canal.

Important Nerves Not Discussed.—To name the twelve pairs of cranial nerves and state their distribution to the organs of the head and trunk would lead beyond the limits of this book. For these and many other facts in regard to the nervous system reference should be made to textbooks on anatomy, physiology, and psychology.

Functions of the Sympathetic or Autonomic Nervous System.—Neurons from this system supply the smooth muscle of the viscera, the cardiac muscles, and the erector muscles of the hair. Blood vessels and glands are also supplied by nerves of this system. Impulses carried by its cells originate in the central nervous system in centers lower than the cerebral cortex. These impulses are involuntary.

Sensory Nerve Endings.—The dendrites of the afferent neurons originate in the skin and in the tissues of the body, especially in epithelium, muscle and connective tissues, and in organs of special sense. Each neuron when stimulated at its peripheral ending conveys an impulse to the central nervous system where it usually gives rise to an impulse that finds expression in the contraction of muscle or discharge of a glandular secretion. Besides initiating this reflex action the stimulus may cause an impulse to be carried over an appropriate path to a higher nervous center where it enters the consciousness of the subject producing a sensation of some sort. The particular kind of sensation aroused by the stimulation depends not so much upon the character of the stimulus as it does upon the kind of sense organ involved and the nature of the central connections. The classes of sensations which originate from stimulation of body surfaces and tissues other than the organs of special sense are those of pressure, warmth, cold, pain, strain sensation from muscle and tendon, and various organic sensations. For the mediation of each of these sensations there must be appropriate sensory endings and nerve cells. The types of endings responsible for the mediation of the different classes of sensations cannot be distinguished on the grounds of histological structure but only by experiment. Figure 122 illustrates the termination of an afferent fiber in the skin of the salamander.

Organs of Special Sense.—The sensations of light, sound, taste and smell are not perceived through scattered sensory cells but through the grouped sensory cells of the organs of special sense, the eyes, ears, taste buds and olfactory epithelium respectively. Although the structure of these organs is very different the sensitive cells of each may be considered to be modified ectodermal epithelial cells connected in some manner with the central nervous system. The sensory cells of the ear and of the retina of the eye and of the taste buds are connected with the central nervous system by means of nerve cells whose peripheral branches are in contact with the bodies of the sensory cells and whose inner branches terminate in the central nervous system. The cells of the olfactory epithelium, on the contrary, have no intercommunicating cells between them and the central nervous system but each cell has a fine process which extends from the base of the cell to the central nervous system.

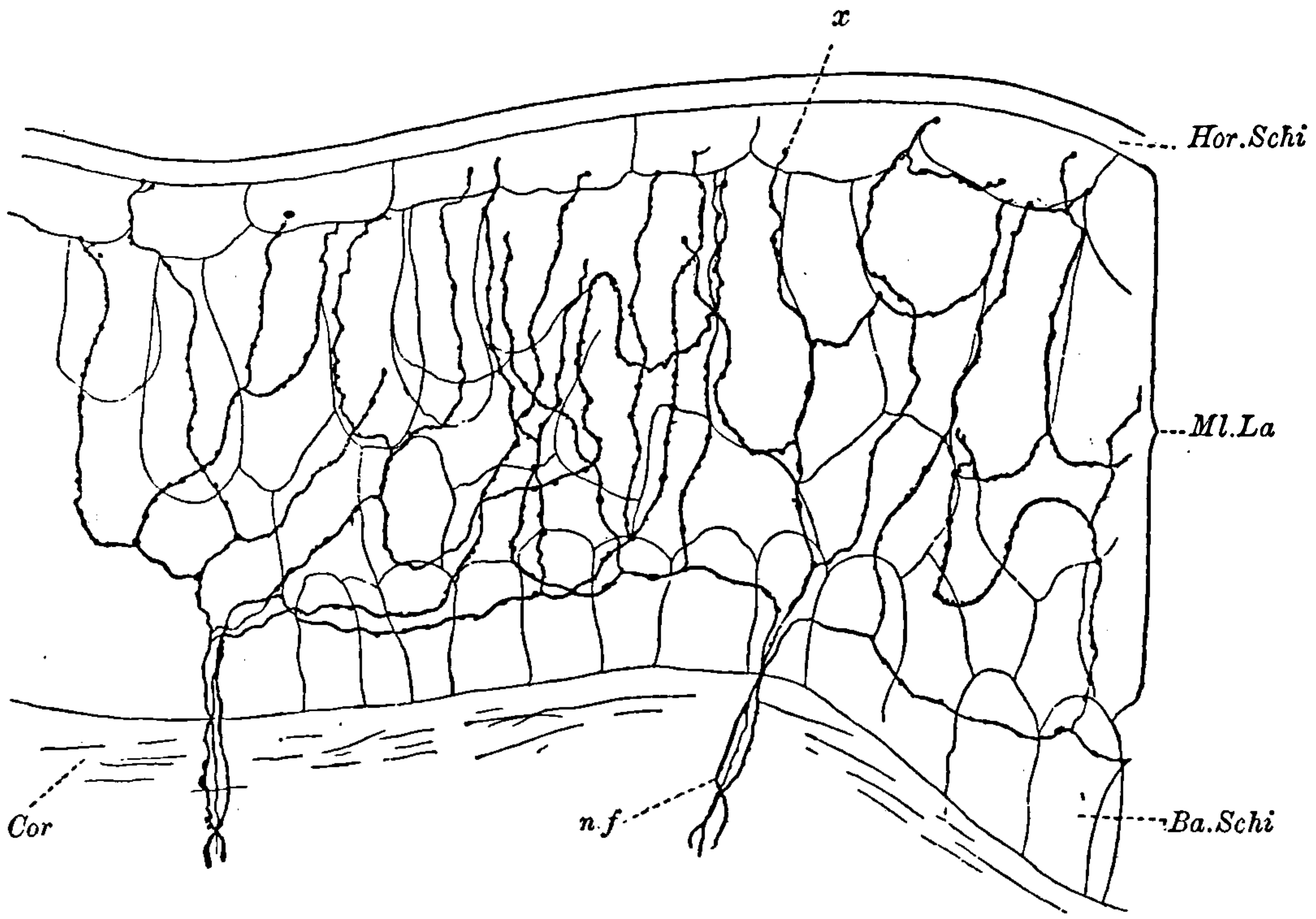

FIG. 122.—Termination of afferent fibers in the skin of the salamander, *Salamandra maculosa*. *Ba. Schi*, basal layer of skin; *Cor*, corium; *Hor. Schi*, stratum corneum; *Ml. La*, middle layer; *nf*, nerve fibers; *x*, end of a terminal. (*From Schneider after Retzius.*)

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were few men fitted by reason of their learning and temperament to observe carefully and to plan and execute critical experiments by which these ideas might be tested. Authority ruled. Eventually, however, there arose among men a spirit of inquiry which impelled them to question authority and to demand verification by means of observation and experiment. One skeptical inquirer was the Italian Redi (Fig. 123).

Experiments Discrediting Spontaneous Generation.—Previously to Redi's time people accepted apparently without question the idea that maggots were generated spontaneously in meat. Redi, as a result of his observations on the actions of flies about meat, conceived the idea that there might be some connection between the flies and the maggots. To test the new idea he devised some experiments. He put some meat in a jar and covered it with parchment. The meat putrefied but there were no maggots. When he substituted a fine gauze cover for the parchment the flies perceived the odor of meat about the dish, but since they could not reach the meat they laid their eggs on the gauze where the eggs hatched. By a series of experiments of this sort Redi showed how organisms might arise in a variety of situations without appealing to the idea of spontaneous generation.

By the introduction, early in the 17th century, of the microscope as a means of study opportunity was given to investigate a whole new world of living things whose existence could only have been suspected. Leeuwenhoek (Fig. 6) discovered bacteria and Protozoa about 1683. Many investigators believed that these minute things were the beginnings of more complex organisms which were in process of originating *de novo.* These ideas were retained with considerable tenacity for a hundred years or more, until experiments were performed which rendered them untenable.

Spallanzani, 1777, objected to the methods employed in making the cultures of microörganisms used in support of the theory of spontaneous generation. He filled flasks with culture solutions in which bacteria and other low organisms were supposed to originate, boiled the contents and hermetically sealed the flasks. These flasks were then subjected to conditions thought to be favorable to the formation of new living things, but no organisms appeared. When, in response to criticisms of his method, Spallanzani tapped the glass making a slight fracture in order to let in the air, organisms always appeared. No more critical experiments seem to have been performed until about 1836 when Schultze perfected a method for admitting air to the culture medium. He drew the air through a series of tubes containing acids or strong alkalies which he believed would kill any organisms in the air. Schwann in 1837 and others used still other methods of removing possible organisms from the air before allowing it to come in contact with the culture medium. Cotton wool was used by some to plug up the containers. Pasteur (Fig. 124) in 1861 devised a flask (Fig. 125) with a tube fused in the side. The tube was so bent (down, then up, then down) that no particle of dust could pass the curve in which a droplet of water was left by condensation after boiling. When the flask had been partly filled with putrescible material and then sterilized its contents remained without putrefaction. Pasteur's experiments were so carefully carried on and were so extensive that the idea of spontaneous generation in its old form was generally abandoned. Careful experiments by the physicist Tyndall and the work of Lord Lister who made application of the results of Pasteur to surgery did much by confirming Pasteur's teachings to overthrow the idea of spontaneous generation.

Pasteur's investigations and teaching resulted in the origin of a whole new field of biological investigation, namely, bacteriology. The investigations of the bacteriologists show beyond a doubt that bacteria are not now originating *de novo* in cultures. Bacteria originate only from preëxisting bacteria. If a bacteriologist finds in a culture a bacterium which he did not put there he ascribes its presence to contamination through air currents or instruments, or to faulty sterilization. The old idea of spontaneous generation is now recognized as untenable, and present-day organisms are known to arise only from previously existing organisms through some form of reproduction.

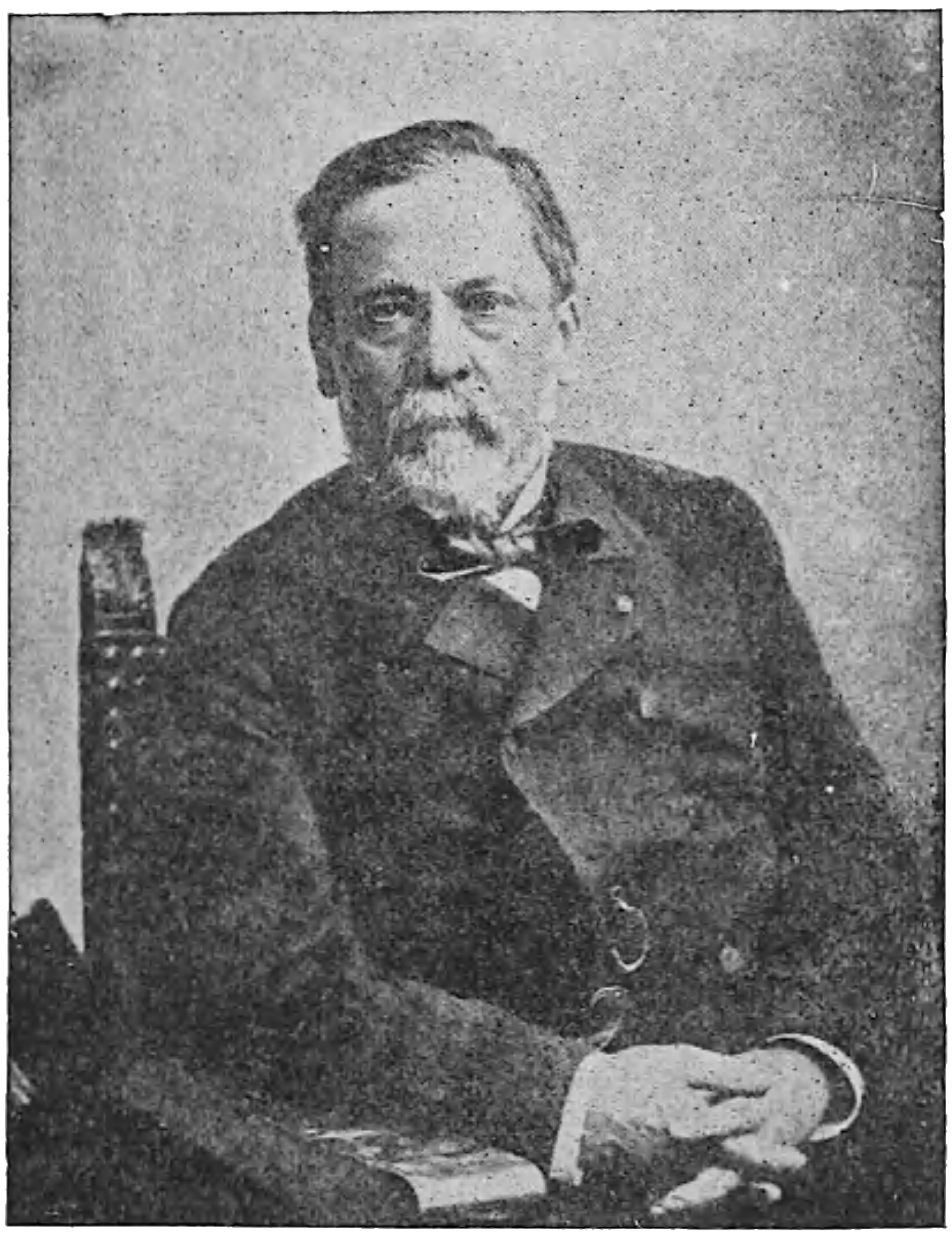


FIG. 124.

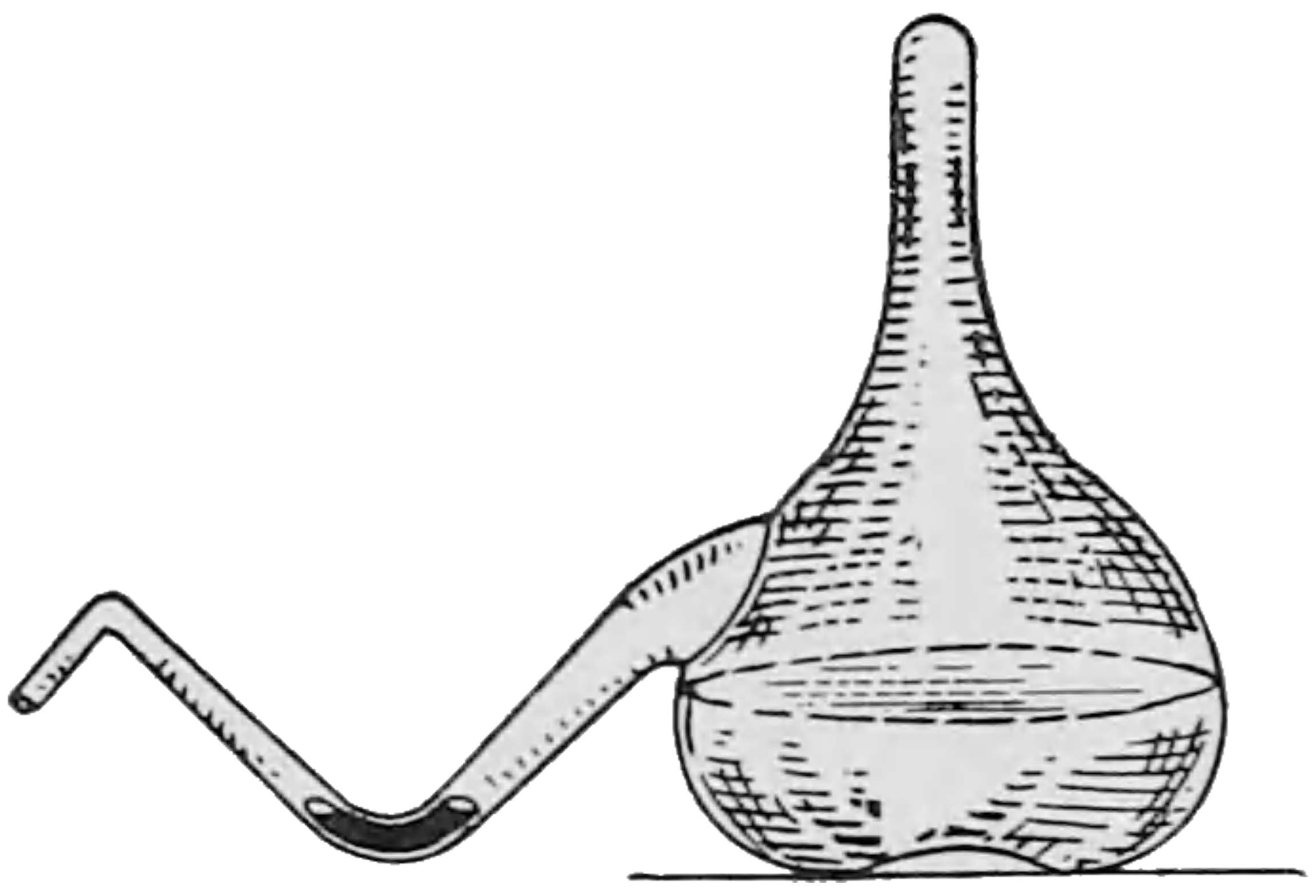


FIG. 125.

FIG. 124.—Louis Pasteur, 1822–1895. (*From Garrison's History of Medicine, W. B. Saunders Co.*)

FIG. 125.—Flask used by Pasteur in experiments upon spontaneous generation. The open top was sealed after the flask was filled with a nutrient solution. After boiling, water vapor condensed and filled the low curve in the side tube thus preventing access of organisms borne by the air. (*After MacFarland.*)

Modern Idea of Spontaneous Generation.—Many biologists believe that while living things are not originating under present conditions, life at some time in the past originated by a combination of the proper elements when conditions were other than at present. This belief is sometimes designated as the modern theory of spontaneous generation.

Some investigators still hope that a simple living substance may be synthesized under special conditions of temperature, moisture, and pressure by the combination of the elements carbon, nitrogen, oxygen, hydrogen, phosphorus, iron, etc., usually found in protoplasm. This hope, which has not been widely entertained, has so far been disappointed, and, although chemists have been able to synthesize many organic compounds once thought to be incapable of production by other means than the activities of cells, the manufacture of the complex mixture called protoplasm is still beyond their reach.

The modern conception of spontaneous generation differs from the ancient view in that it does not propose to account for the origin of organisms of the kind we now know. It therefore has no relation to ideas regarding reproduction, and further discussion of it is omitted.

Reproduction.—Since no living thing can maintain itself for an unlimited period of time the ability of the members of a species to produce other individuals is most important from the standpoint of the welfare of the species. Living organisms provide for increase of numbers of individuals by a variety of reproductive methods which fall into two general categories, namely, *asexual* reproduction and *sexual* reproduction.

Asexual or non-sexual reproduction includes all those methods of reproduction which require but a single parent for the production of offspring and do not involve germ cells. Sexual reproduction as a rule involves two parents and the production of two kinds of germ cells, the eggs and sperms. It is usually brought about by the union of a sperm cell with an egg, or less commonly by the development of the egg without union with a sperm.

Asexual Reproduction: Budding.—A simple and common mode of asexual reproduction is that of *budding.* The bud starts as a protrusion of protoplasm in a small area of the surface of a protozoan cell or as a localized proliferation of cells in a multicellular animal. The protuberance grows until it assumes the form and perhaps the size of the parent. It 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.

Nearly all sponges bud. Among the Cœlenterata, the common Hydra shows the process well and is a good example of an animal whose buds separate from the parent. Other budding members of the same group are Hydractinia (Fig. 63), Obelia, Bougainvillea (Fig. 61) and other Hydrozoa, also the corals, and the Siphonophora (Fig. 64). Some of these have been described in Chapter V. These forms all demonstrate lateral budding or budding from the side of the parent, and some of them produce tree-like colonies by the failure of the buds to separate from the parent. Among the worms the most usual form of budding is terminal

the mesoglœa (gelatinous material) of the sponge. These cells are enclosed within a dense layer of material in which spicules of peculiar types may be imbedded. Gemmules are usually produced in abundance during summer and fall. When the body of the sponge disintegrates the gemmules (Fig. 127) are left clinging to the log or stone to which the sponge was attached. They may remain here or they may be transported considerable distances by water currents or perhaps on the feet or beaks of water birds. With the return of favorable conditions the bud enclosed within the outer coating of the gemmule begins to develop. In some manner it removes the plug which closes the aperture of the covering

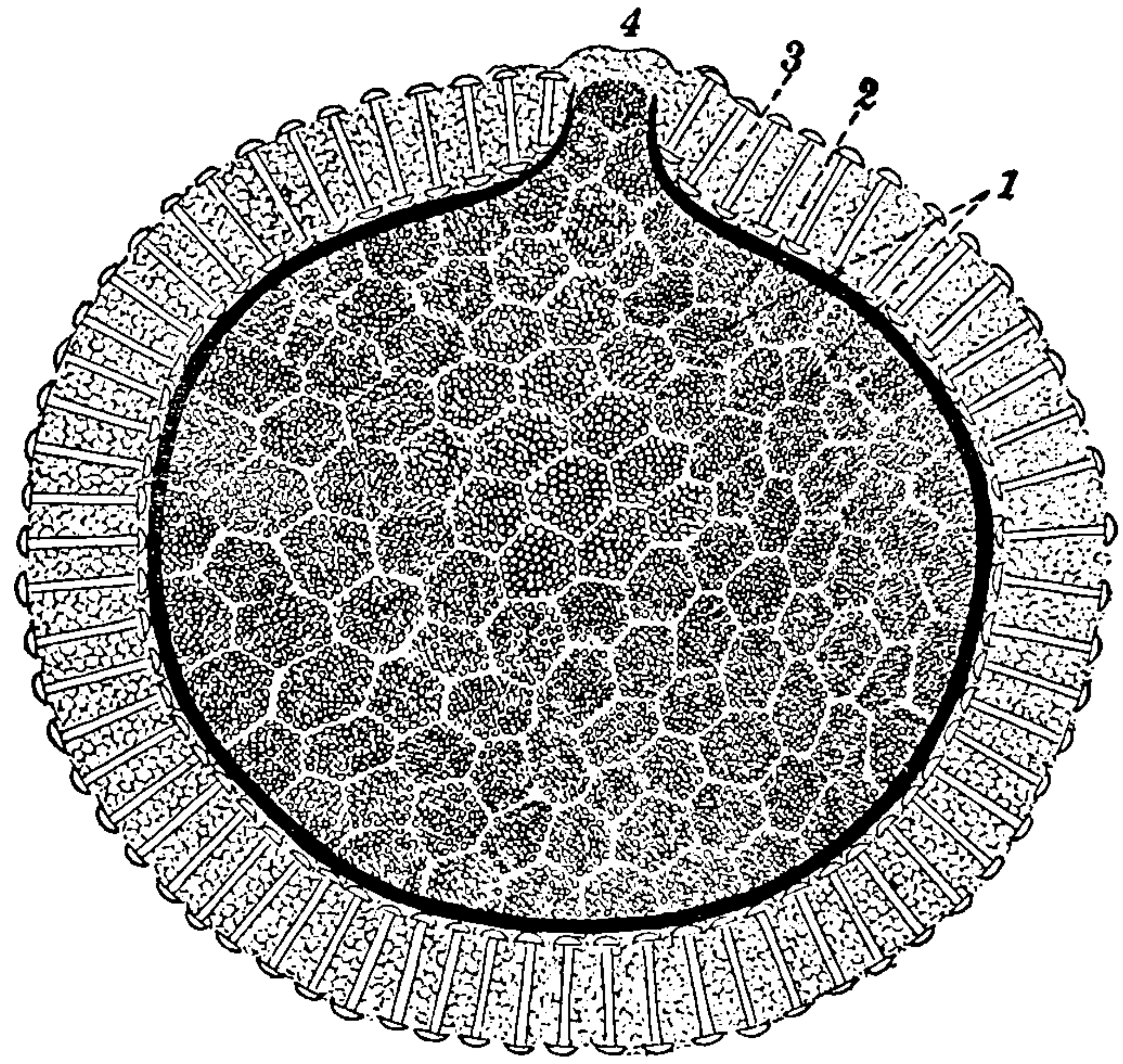


Fig. 127.—Gemmule of the freshwater sponge Ephydatia, in schematic cross-section. 1, cells; 2, chitinous case; 3, shell with amphidisc spicules; 4, foraminal aperture. (*From Hesse and Doflein.*)

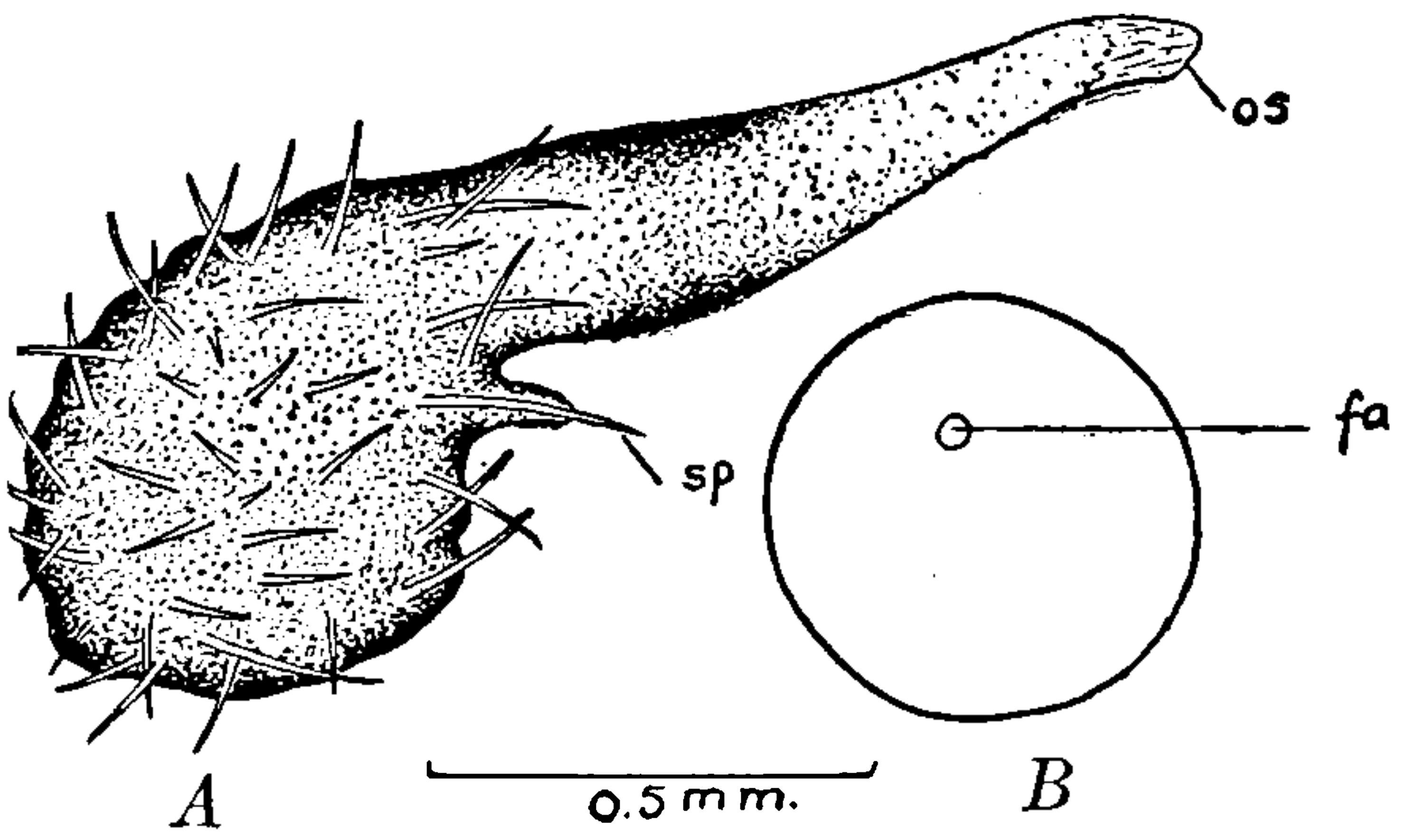


Fig. 128.—Origin of sponge by asexual reproduction. *A*, young freshwater sponge recently emerged from a gemmule; *B*, outline sketch of the gemmule of the same species; *fa*, foraminal aperture; *os*, osculum; *sp*, spicule. The scale beside the figures indicates their size.

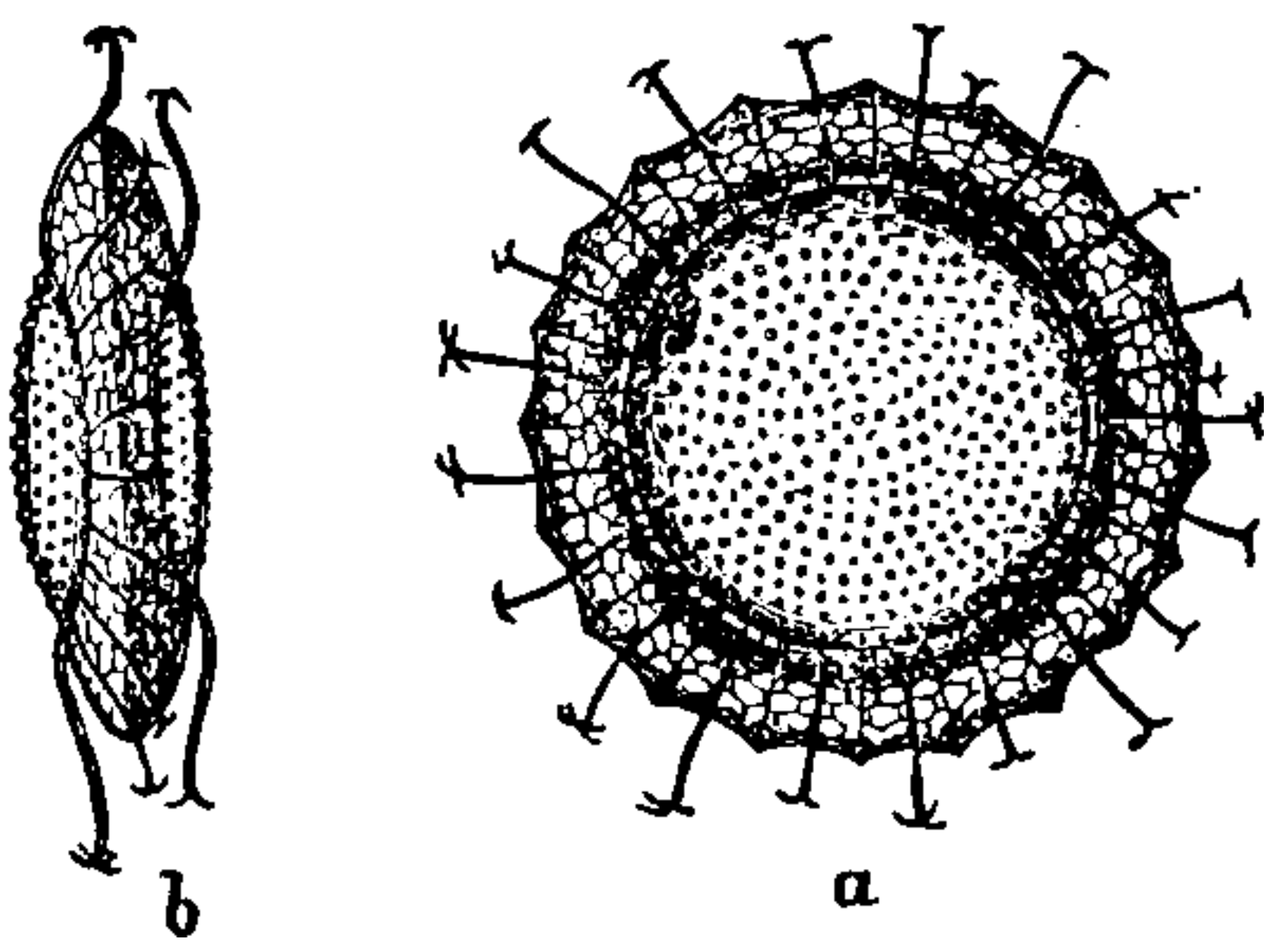


Fig. 129.—Statoblasts of *Cristatella mucedo*. *a*, surface view; *b*, side view. (*From Sedgwick, after Allman. Courtesy of Macmillan Co.*)

and the minute sponge emerges either by amœboid movement or as a result of growth. It soon assumes the form and appearance of a minute sponge (Fig. 128) which by growth and external budding becomes the large sponge as it is found during the summer and fall. The gemmule of the sponge is, therefore, not only a medium for multiplying the number of individuals, but also a means of dispersal of the species and a means of surviving the vicissitudes of winter.

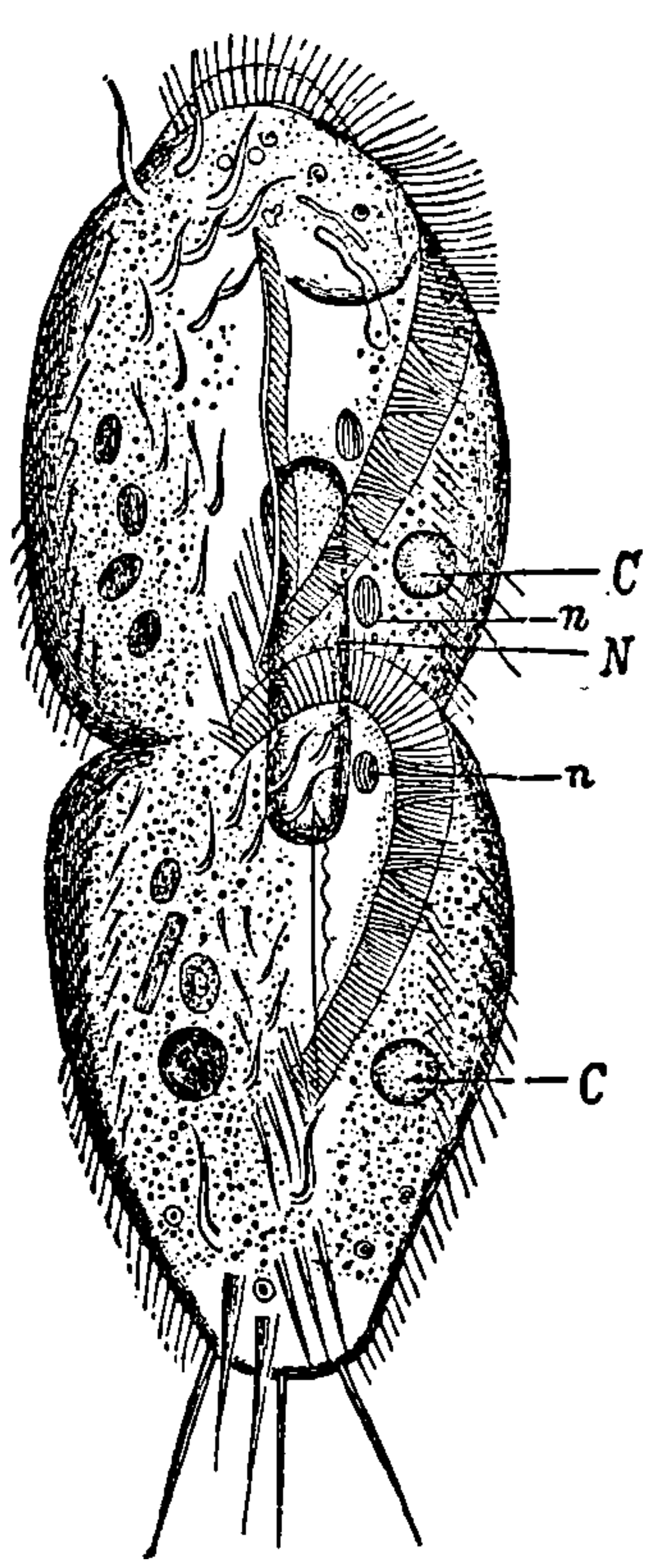


FIG. 130.—*Stylonychia mytilus* dividing. *C*, contractile vacuole; *N*, macronucleus; *n*, micronuclei. (*From Sedgwick, after Stein. Courtesy of Macmillan Co.*)

The Bryozoa (moss animals) living in fresh water also produce internal buds which when enclosed in a dense protective covering are called *statoblasts*. A statoblast of *Cristatella mucedo* is shown in Fig. 129. In some lakes and ponds where there are many Bryozoa statoblasts are produced in such numbers that they float up on the shore in quantities sufficient to blacken the beach or cloud the water in which they float. Statoblasts persist over winter and give rise in the spring to new colonies. Since most Bryozoa are attached organisms or have only limited locomotor powers the statoblasts serve as a means of dispersal.

Fission.—Fission is a more common reproductive method among Protozoa than budding. Fission differs from budding in that the body of the parent is about equally divided into two parts which come to resemble the parent after a period of growth and regeneration of missing parts. In fission, especially among the Protozoa, the parent disappears as an individual and two new individuals take its place. The plane of fission may be longitudinal or transverse. Transverse fission, that is, division perpendicular to the long axis, is the more common. It is illustrated in Fig. 130 which shows Stylonychia in division. Even in forms like Vorticella (Fig. 131), in which fission appears to be longitudinal, the division is really transverse, since the ciliated disk which seems to be the end of the cell is morphologically its ventral surface.

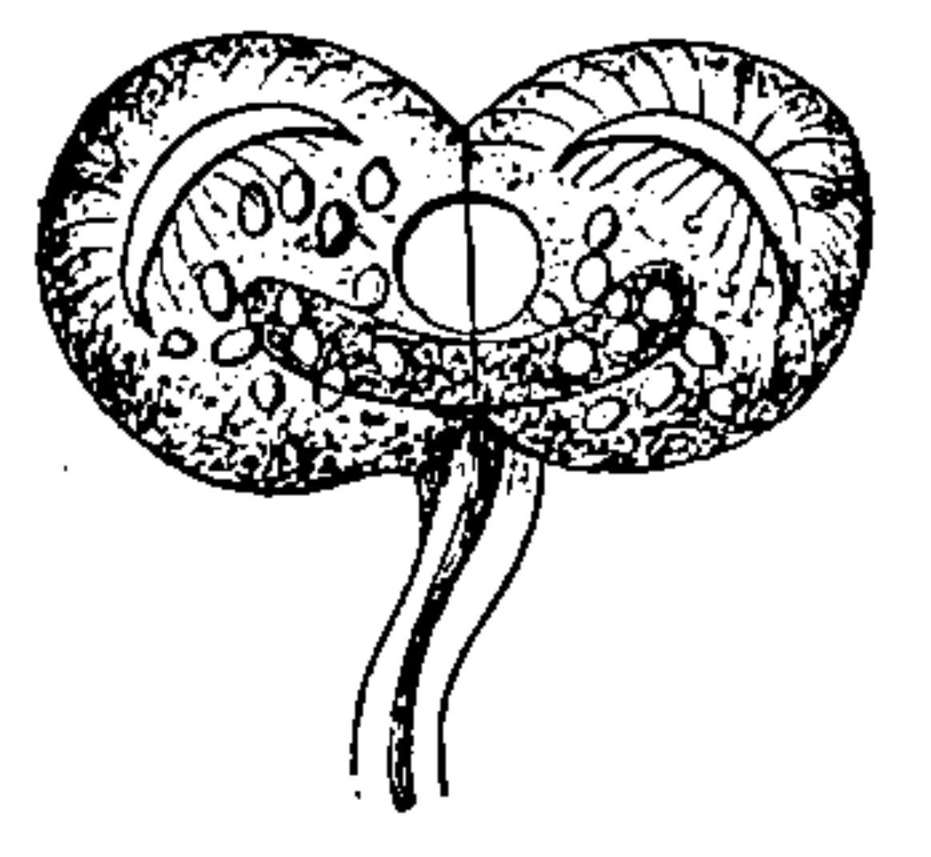


FIG. 131.—Vorticella in division. (*From Kent after Greef.*)

Fission involves the nucleus as well as the cytoplasm. Structures which extend across the plane of fission are halved 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 species 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. In Stylonychia and many other forms the ciliary apparatus is developed afresh, sometimes before fission is completed. 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. In the protozoan parasite *Opalina ranarum* division of the nucleus proceeds until many nuclei, even as many as a hundred or more, are produced, then the cytoplasm divides by successive binary fissions to form as many little cells as there were nuclei. Encystment of the small individuals frequently follows these divisions. In Paramecium, when well fed, fission occurs once in about 16 to 24 hours.

As a method of reproduction fission occurs in certain of the worms, as the triclad Turbellaria and some species of nemerteans.

Sporulation.—Many species of Protozoa produce large numbers of minute individuals by a process of internal or external budding or by multiple fission. This process is commonly called *sporulation.* This is one of the methods of reproduction in the Sporozoa, a class of Protozoa parasitic in the cells, tissues and cavities of many of the metazoa. Examples are the gregarines, coccidians and malarial organisms. The gregarine Monocystis is rarely absent from the seminal vesicles of the earthworm. Other gregarines occur in the cells and lumen of the intestine of insects and their allies, the arthropods. Coccidians occur in the cells and lumen of the intestine and other organs of arthropods, other invertebrates, and vertebrates.

The method of sporulation as it occurs in *Coccidium schubergi* is illustrated in Fig. 132, *IV–VII.* This parasite occurs in the intestine of *Lithobius forficatus,* a centipede. A part of the life cycle (*II–VII, XIa–XIc* and *XIIa–XIIc*) occurs within the cells of the intestine, part of it (*XIId–XIX*) free in the intestine of Lithobius and part of it (in a resting condition) outside the body of the host. When the oöcyst (*XX*) is swallowed by Lithobius the cyst opens and minute *sporozoites* emerge. They enter cells of the intestine (*II*) where they grow (*III, IV*) and finally by multiple division of the nucleus and fragmentation of the cytoplasm (*V, VI, VII*) a large number of minute motile individuals (*VIII, IX,* X) are formed. These minute individuals may be called *merozoites.* This latter part of the life history (*II–VII*) is wholly asexual and is sporulation, the rest of it has to do with the formation of gametes (sexual individuals).

Limits of Asexual Reproduction.—Asexual reproduction occurs only among the lower forms of animal life. It never occurs among vertebrate animals, although it does occur among the ascidians which are placed in the phylum to which vertebrates are also assigned. It also does not occur in the following phyla of invertebrates: the Nemathelminthes (roundworms), the Rotifera (rotifers), Echinodermata (starfishes, sea-urchins,

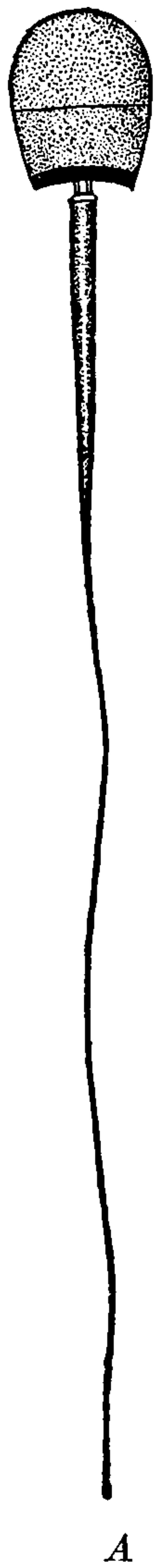
In general terms the basis of sexual reproduction is the union of two cells to form a single cell, the *zygote*, which by its subsequent divisions produces a new individual if the uniting cells are of metazoan origin, or a new series of individuals if they are of protozoan origin. Not all cells are capable of uniting in this way, and cells which are capable of this act are called *gametes*, or, in the metazoa, *germ cells*. Certain gametes are relatively large, contain a considerable amount of nutritive material, and are non-motile. Such gametes are named *macrogametes*, *ova* (singular, *ovum*), or *eggs*. Other gametes are minute, often a mere fraction of the size of the macrogamete of the same species. These are poorly supplied with nutritive material, have little cytoplasm, and usually are motile; they are known as *microgametes*, *spermatozoa* (singular, *spermatozoön*), *sperms*, or *sperm cells*. The terms macro- and microgamete are usually reserved for use in speaking of the gametes of Protozoa. They indicate size relations, or they are very general terms, while ovum or egg and sperm or spermatozoön are the names used for gametes of metazoan animals. The individuals in which eggs develop are known as females, and those in which sperms develop as males.

Sexual Reproduction in Metazoa.—In metazoa the germ cells, ova and sperms, are the direct descendants of the primordial (first) germ cells. They retain their power of uniting to initiate the development of a new metazoan individual. All other cells have completely lost this power. In a sense the germ cells are primitive cells, resembling the Protozoa in respect to their potentialities. They are stored in the metazoan body where they live at the expense of the somatic cells but without taking part in the general body functions. As the time for sexual reproduction draws near the germ cells undergo a certain process of development or of preparation for the sexual act. This preparatory process, known as *maturation*, is discussed in detail in Chapter X but its essentials may be stated here. Maturation of the ovum consists in the main of two mitoses 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 non-functional. Maturation of the sperm cell does not differ essentially from maturation of the ovum, except that the process 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. 133.

When matured sperms and eggs of the same or closely related species are brought together, the actively motile sperms meet and penetrate the eggs. Usually but one sperm can enter an egg. After the entrance of the sperm, either by a change in the surface of the egg or by some other mechanism, other sperms are excluded. The sperm nucleus and egg nucleus arrange themselves side by side; their chromatin undergoes changes in arrangement, assuming the form of a spireme and then of chromosomes; a spindle is formed and the zygote divides by mitosis. This sequence of events indicates that the egg is induced to divide because of some stimulus given to it by the sperm. The nature of fertilization is discussed in the later pages of this chapter.

Sexual reproduction is concerned with the initiation of the long process of development which results in the formation of the individual. It is not concerned with the multiplication of the cells of the animal body. The processes which follow fertilization in metazoa, as well as the late history of the germ cells, are treated in Chapter X under the general title Embryology.

Sexual Reproduction in Protozoa.—In the Rhizopoda (Amœba and others having pseudopodia), so far as sexual reproduction is known, union between *similar* individuals is the rule. In many of the species where it has been observed it apparently occurs only at rare intervals.



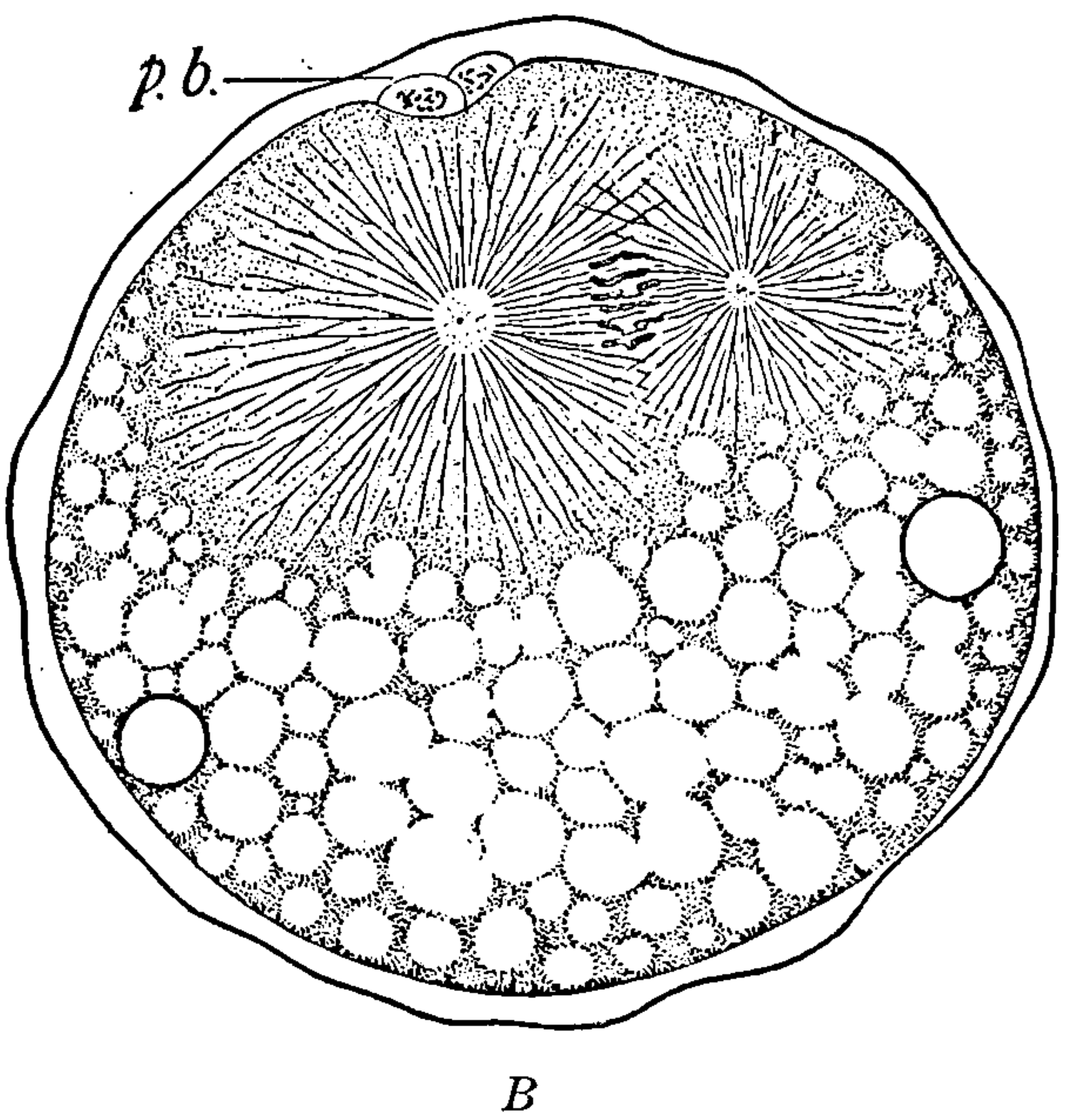


FIG. 133.—Sperm cell and ovum. *A*, spermatozoön of badger; *B*, fertilized ovum of Nereis with two polar bodies, *pb*. (*A from Dahlgren and Kepner's Principles of Animal Histology; B from Wilson's The Cell. Courtesy of Macmillan Co.*)

The Mastigophora (flagellate Protozoa) produce gametes which may be of the same size or of different sizes. If the gametes are of the same size they are said to be *isogametes*. In this case, however, the gametes are perhaps alike only in size, since it is conceivable that there are internal differences which are not visible. The gametes may both be motile or the smaller only may be motile. In *Gonium pectorale* the gametes are of the same size. They are produced by the division of any cell of the colony into 8 small cells of equal size. Two gametes fuse to form the zygote. In this instance both gametes are much smaller than the vegetative cells. In *Heteromita lens* (Fig. 134) and in some other species the isogametes are of the same size as the vegetative cells. In *Pandorina morum* (Fig. 135) there are gametes of two sizes, and two combinations are possible: two small gametes, or one small and one large, may fuse but not two large ones.

Eudorina elegans (Fig. 136) shows well marked differentiation into macro- and microgametes and union always takes place between a large and a small gamete. Union of unlike gametes is known as *anisogamy* in contrast to *isogamy* (union of like gametes). The macrogamete of Eudorina is not only large but is well supplied with nutritive material. It is unlike the ovum of the metazoa in that it is motile. The microgamete is small, has little stored nutritive material and has motor organs. Pleodorina and Volvox have similar reproductive methods. The macrogamete of Volvox may be properly called an ovum, since the cell has no motor organs (at least in its later stages), and something comparable to maturation appears to occur. The microgametes of Eudorina, Pleodorina, and Volvox are similar in their general features.

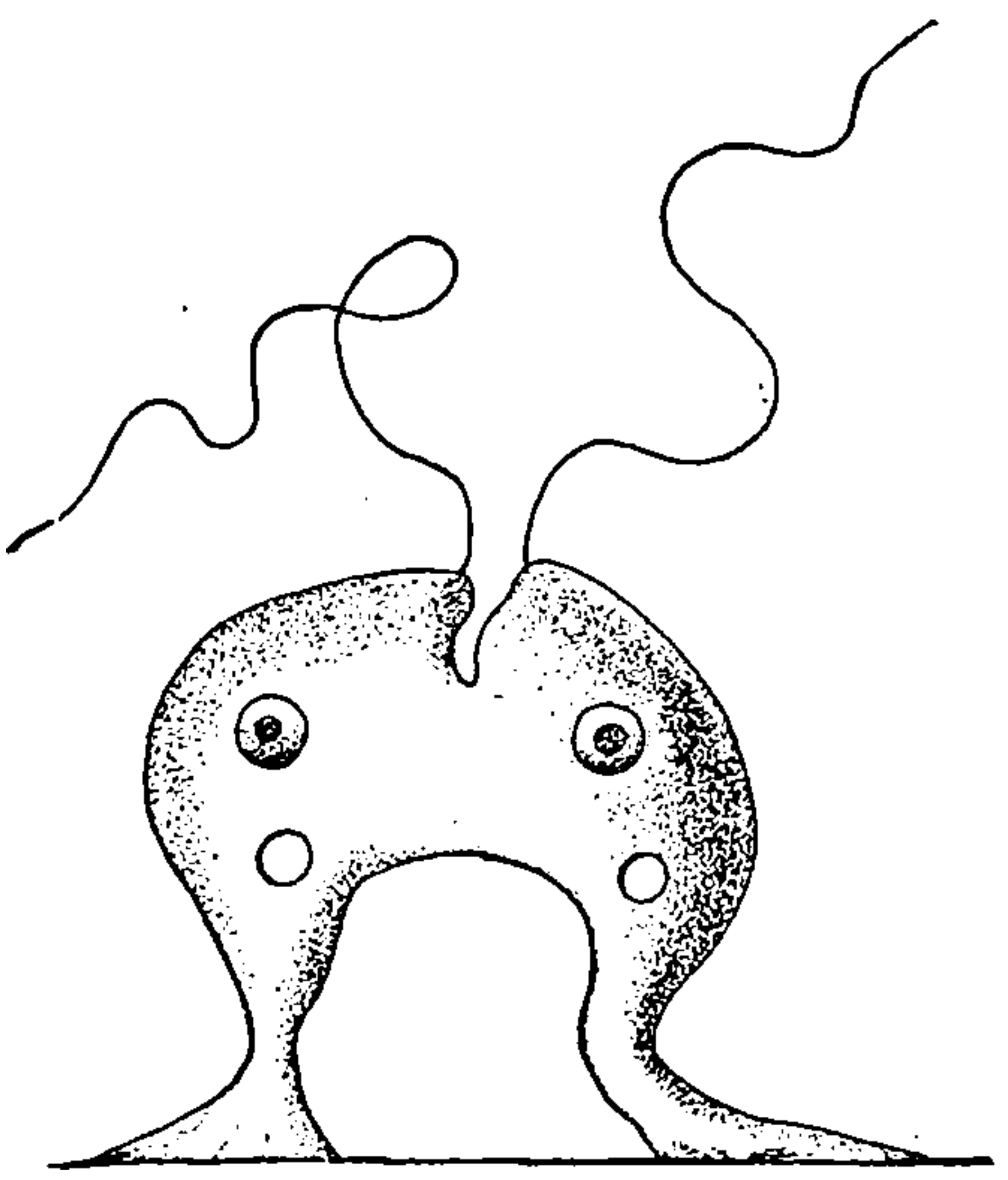


Fig. 134.

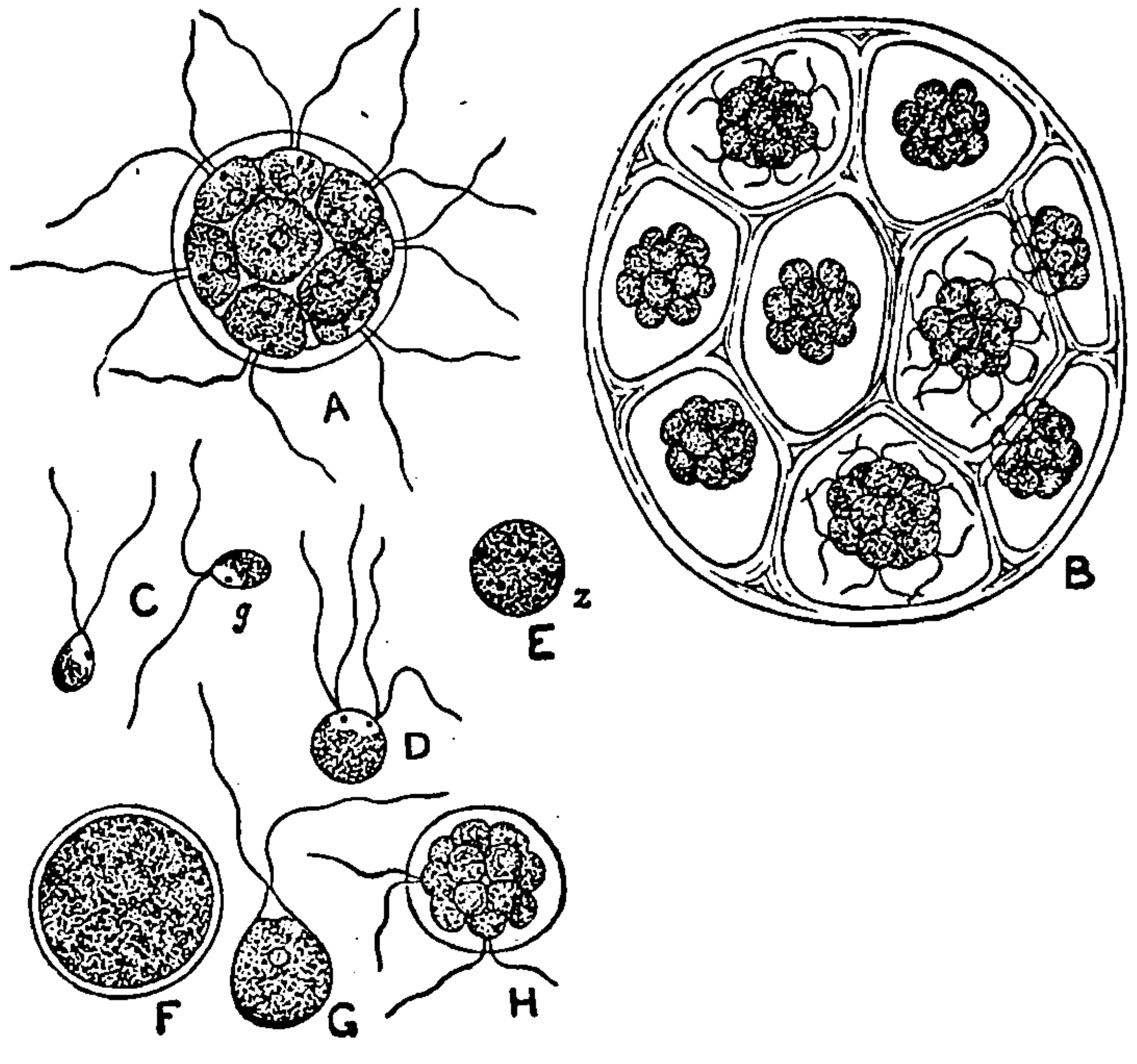


Fig. 135

Fig. 134.—Isogamy in *Heteromita lens.* (*After Kent.*)

Fig. 135.—Reproduction in *Pandorina morum* Borg. *A*, normal colony; *B*, daughter colonies arising by division of mother cells within old colony, ×475; *C–H*, gametes (*g*), formation of zygospore (*z*) and its development. (*From West after Pringsheim.*)

In the Sporozoa differentiation of gametes into micro- and macrogametes is well marked. In *Coccidium schubergi* (Fig. 132) the microgametes are formed by repeated divisions of a large cell (*XIIb–XIId.*) The microgametes are minute, possessing little cytoplasm. With their

unions simply as fusion. The process of conjugation is here described and illustrated as it occurs in Paramecium.

✓ At the time of conjugation, Fig. 138, *A*, two individuals of Paramecium 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 a process of modified or primitive mitosis, and then each half divides again. Thus each micronucleus gives rise to 4 micronuclei (Fig. 138, *C*). Of these micronuclei, three undergo degeneration, and the one remaining in each Paramecium divides again into two parts, usually of unequal size (*D* and *E*). The smaller micronucleus of each individual now passes over into the other individual (*F*) while the larger one is retained. The two pieces, one derived from each individual, now fuse to make the fusion micronucleus (*G*). During these stages of the process the macronucleus has been undergoing fragmentation and sooner or later its parts degenerate completely. The parts, however, may linger for a considerable time and thus render difficult the interpretation of subsequent stages. 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 ex-conjugants are essentially as follows. The fusion micronucleus divides

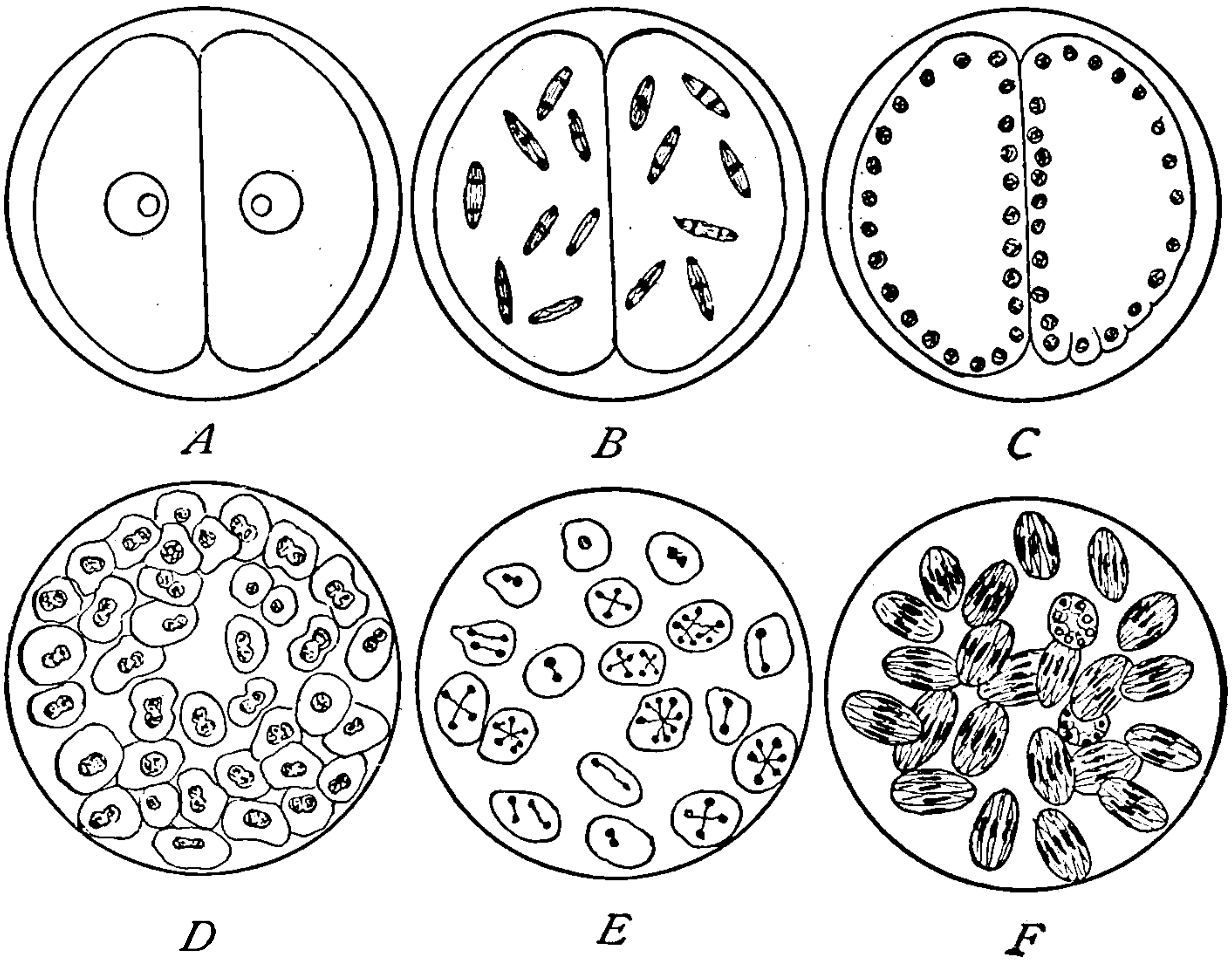


FIG. 137.—Scheme of spore formation in gregarines. *A*, two individuals united in a common cyst; *B* and *C*, gametes of similar size in process of formation; *D*, union of amœboid gametes; *E* and *F*, formation of sporozoites within the spores. (*From Calkins's Protozoa. Courtesy of Macmillan Co.*)

three times (Fig. 138, *H–J*), resulting in the formation of eight micronuclei. Of these, four are segregated and become macronuclei, three of the remainder degenerate, and one continues as a micronucleus which soon divides. The ex-conjugant which now has four macronuclei and two micronuclei then divides (*M*, *N*), each new individual receiving one micronucleus and two macronuclei. After a brief growth period the micronucleus again divides and another division of the cell takes place, thus leaving each cell with one macro- and one micronucleus. After another growth period each cell divides by fission, 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

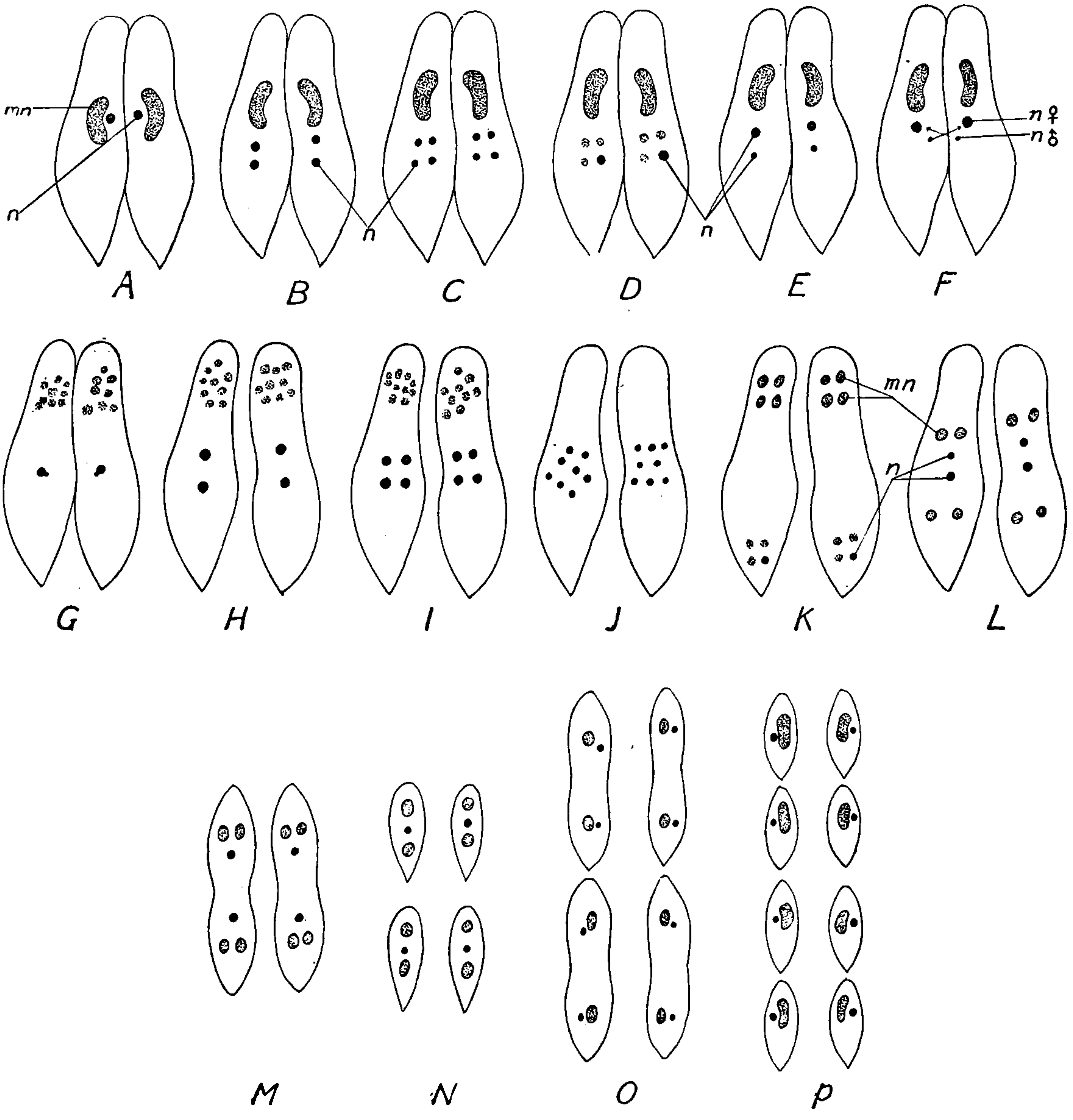


FIG. 138.—Diagram showing sequence of nuclear changes during and following conjugation in Paramecium. *A–P*, successive stages. The dotted bodies represent degenerating nuclei; *mn*, macronuclei; *n*, micronuclei; *n* ♀, portion of micronucleus which remains in same individual; *n* ♂, portion of micronucleus which migrates to the other individual and fuses with *n* ♀. During stages *A–G* the conjugating paramecia remain in contact; after those stages they are separate.

exchange of micronuclei and the formation of a new nucleus from the two parts. The repeated divisions of the cells following conjugation are to be likened to segmentation of the fertilized ovum of the metazoa.

In Vorticella and its allies there is a series of nuclear changes somewhat like that in Paramecium, but there is complete fusion of a smaller with a larger individual.

Possible Maturation in Protozoa.—In most Protozoa there is no process which can be considered analogous to the process of maturation of the ovum and sperm of the metazoa. The chromosomes in the Protozoa are so small and their number is so great that it is not possible to count them to determine whether reduction in number has taken place. In a few species of Rhizopoda and Sporozoa a portion of the nucleus of each individual is known to be cast out into the cytoplasm where it degenerates. A number of phenomena once interpreted as reduction are now regarded as indicating degeneration. In Paramecium and other Infusoria there is a loss of nuclear material, but it has not been shown conclusively that there has been a reduction in the number of chromosomes.

Significance of Fertilization in Protozoa.—Because of the diversity of conditions under which sexual reproduction in the Protozoa occurs, and the variety of arrangements for its accomplishment, the function of fertilization[1] in this group has been variously interpreted. When it occurs regularly and involves specialized gametes, it may appear to be of fundamental importance; but when it occurs only at rare intervals fertilization seems unessential. The view has long been held that fertilization in Protozoa, as in metazoa, results in rejuvenation, or a renewal of vigor. This view has been seriously questioned, however, in the light of evidence which on the one hand appears to indicate that sexual reproduction in certain Protozoa is not indispensable and on the other hand shows that it does not necessarily result in reinvigoration. Further discussion of a question so much in doubt would scarcely be profitable here.

Parthenogenesis.—In an earlier part of this chapter the statement was made that sexual reproduction involves two parents and the fusion of two germ cells. Nevertheless it is not uncommon to find species of invertebrates among which, for considerable periods of time, no males can be found. Eggs, however, are produced by the females, and these develop into new individuals like the parent, although fertilization does not occur, since no males are present. By their origin and maturation the cells giving rise to new individuals are ova, hence the method is ob-

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[1] The term *fertilization* is properly used only to designate the union of egg and sperm among higher organisms; but to emphasize the analogy between similar processes in complex and simple animals, it is applied here to the union of gametes in the Protozoa.

reproduce by means of parthenogenetic ova. The liver fluke, *Fasciola hepatica*, is an excellent example whose life history has been thoroughly studied. This life history, illustrated in Fig. 140, is essentially as follows. From the fertilized egg produced by the adult emerges a ciliated larva, the *miracidium* (Fig. 140, *a*, *b*), which must live in water. The miracidium finds a snail of the genus Lymnæa, bores its way into the snail and develops into a bag-like individual, the *sporocyst*. The sporocyst (*c*) produces within its cavity a number of parthenogenetic ova which develop into individuals very different from the sporocyst. These are *rediæ*. The rediæ (*d*) are provided with a short digestive canal, some ear-like appendages and a birth pore. They emerge from the sporocyst but remain within the snail. The rediæ produce parthenogenetic ova which may develop into more rediæ or into a tailed form, the *cercaria*. In the event that further generations of rediæ are produced by parthenogenetic means, cercariæ are nevertheless finally produced. The cercaria (*e*) is the larval form from which by growth and certain changes the adult liver fluke (*g*) arises. In this species there are thus always two or more generations of a larval type which produce parthenogenetic ova and only one generation producing fertilized ova. The origin of parthenogenetic ova in the redia of another species and a much magnified ovum which has undergone maturation are shown in Fig. 141, *A* and *B*. The polar bodies are plainly indicated and give evidence that these cells are true ova.

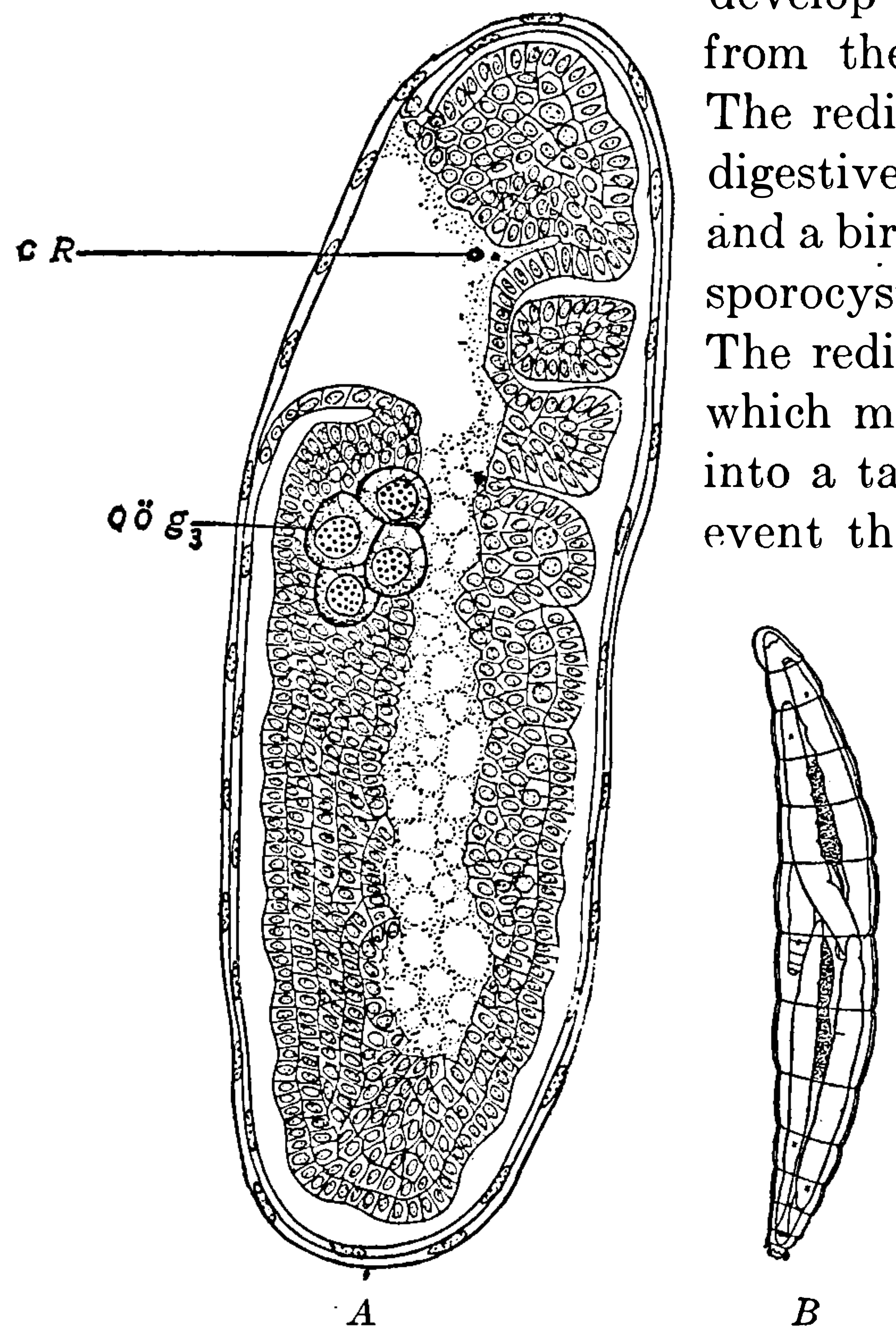

FIG. 139.—Pædogenesis in the fly Miastor. *A*, sagittal section (greatly enlarged) through an embryo of *Miastor americana*, showing four oögonia (*oög*3); *B*, mother larva of Miastor with young pædogenetic larvæ. (*A from Hegner's Germ Cell Cycle, Macmillan Co.; B from Folsom after Pagenstecher.*)

In the succeeding instances pædogenesis of the bisexual type occurs. The ctenophore *Bolina hydatina* while still in the larval condition becomes sexually mature and its gonads (reproductive organs) produce eggs or sperms. Fertilized eggs develop in the usual manner. The larva eventually assumes the adult condition and the gonads, which had degenerated, again attain sexual maturity and produce eggs and sperms.

Among vertebrates the famed axolotl, *Ambystoma tigrinum* or tiger salamander, under certain conditions attains sexual maturity and breeds while it is still in the larval form. In some of the Mexican lakes this is said to be the usual occurrence. In Kansas and Nebraska this method of reproduction in *Ambystoma tigrinum* has been observed but rarely, while in many localities it probably does not occur at all.

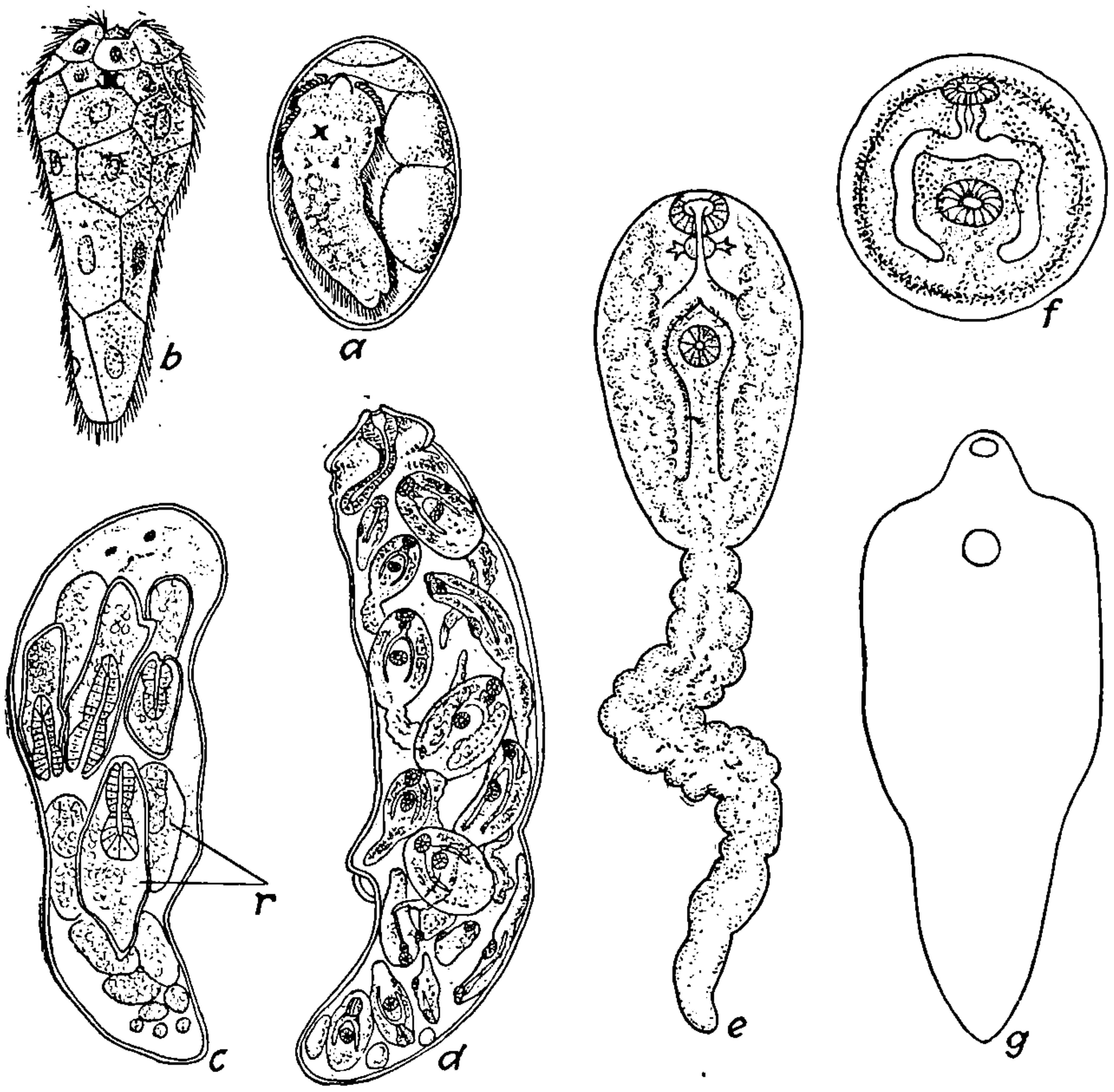

FIG. 140.—Stages in the life history of the liver fluke, *Fasciola hepatica*. The scale of enlargement is not the same for the several figures. *a*, egg with the ciliated larva (miracidium); *b*, miracidium or ciliated larva emerged from egg; *c*, sporocyst producing rediæ (*r*) within itself; *d*, a redia producing cercariæ; *e*, cercaria emerged from redia; *f*, cercaria which has lost its tail and has encysted; *g*, adult liver fluke (outline only). (*From Leuckart-Nitsche Wall Chart.*)

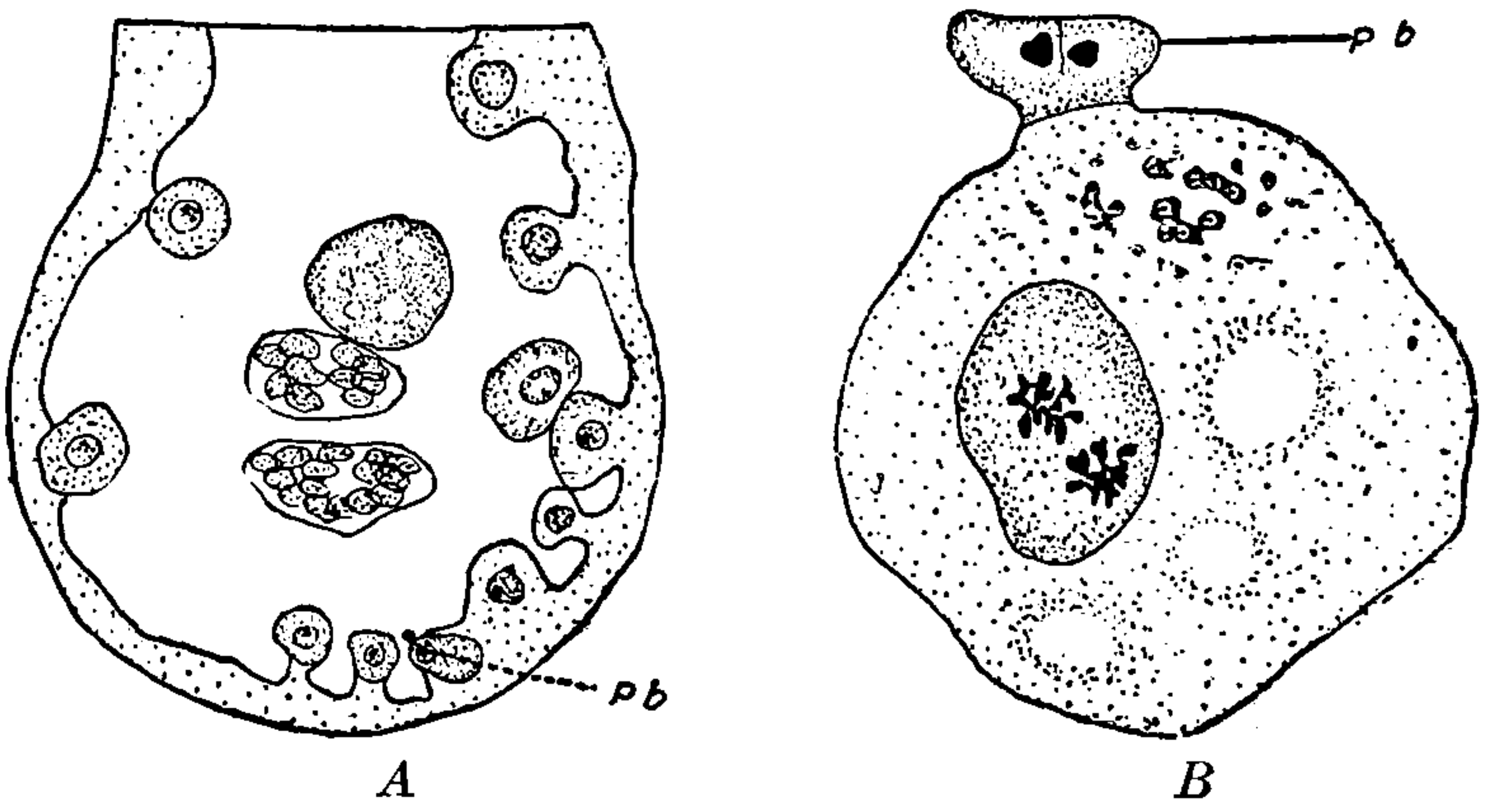

FIG. 141.—The origin of parthenogenetic ova in the redia of *Cercaria flabelliformis*. *A*, lower end of redia with developing parthenogenetic ova, some in process of maturation; *B*, much magnified parthenogenetic ovum with polar body, ovum and polar body preparing to divide; *pb*, polar body. (*From Faust in University of Illinois Biological Monographs.*)

Hermaphroditism.—Most animals possess either male or female organs of reproduction but not both. This is the condition in the great majority of species of the metazoa. Species which have separate sexes are said to be *diœcious* (living in two houses) while those species whose individuals produce both eggs and sperms are called *monœcious* (living in one house). Individuals with both male and female organs are known as *hermaphrodites* and they exhibit the phenomenon called *hermaphroditism.* True hermaphroditism is rare among vertebrates but traces of it are found in certain cyclostomes and commonly among Amphibia. The invertebrates present many cases of true hermaphroditism. *Hydra viridissima* and *H. vulgaris* are common laboratory examples. Most species of flatworms including the turbellarians, cestodes or tapeworms, and trematodes or flukes, are hermaphroditic. A few species of nematodes or roundworms and most snails are also hermaphroditic. In many 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 is assured. In the earthworm, eggs and sperms are produced in the same individual and at the same time. Cross-fertilization is assured in this case by the arrangement of the generative organs and by the method of mating.

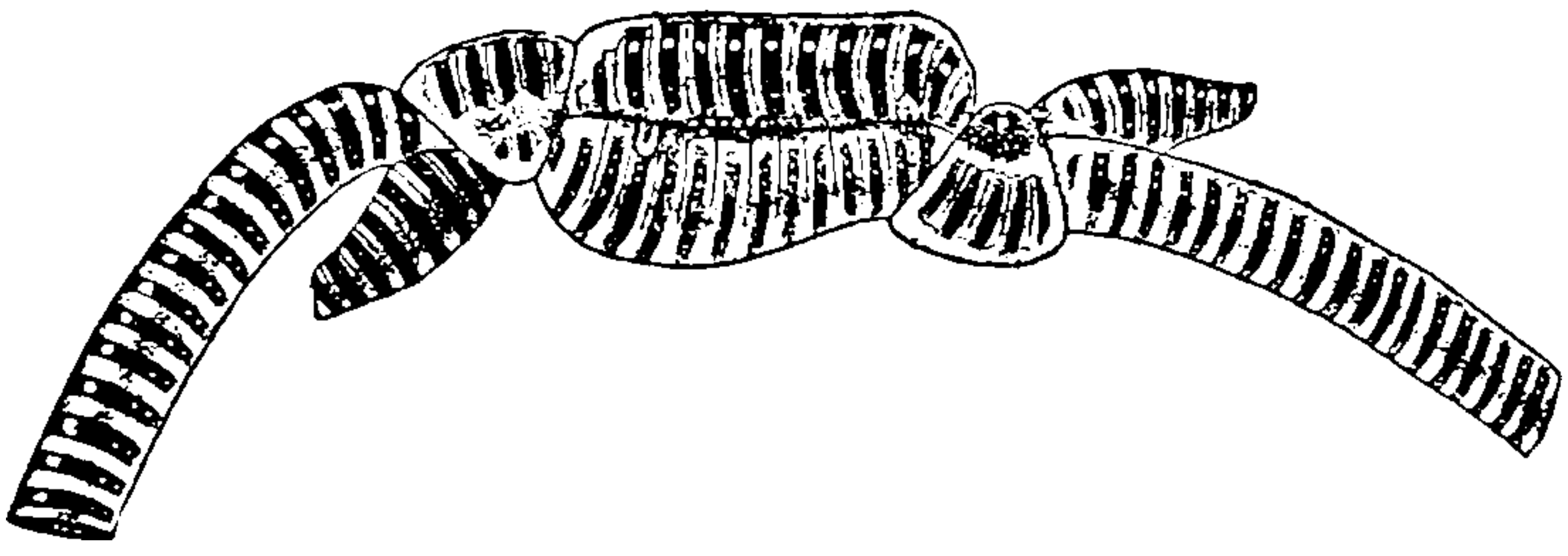

FIG. 142.—Earthworms, *Helodrilus fœtidus* (Savigny), copulating. (*After Foot.*)

Mating in the earthworms may occur under the surface of the soil, or in a compost heap as in the case of *Helodrilus fœtidus* (the manure worm), or above the soil as in *Lumbricus terrestris,* the large worm generally used for laboratory dissection. In these species the bodies of the 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 other worm (Fig. 142). In this position each worm secretes a *slime tube* which encircles its body from about segment 8 to segment 33 or even as far back as 39. In some instances, at least, the slime tubes of the two worms seem to be independent of each other. In the region of the clitellum of each worm thickened rings of the slime tube encircle both worms and bind them closely together. The sperms are discharged from the *spermaducal pores* into the space bounded by the slime tube and the body of the worm. Here the sperms form into irregular masses or *spermatophores* which are carried backward

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 (the cestodes and trematodes) both cross- and self-fertilization have been observed. Indeed, in some species of tapeworms which possess two sets each of male and female organs in each proglottis, every conceivable form of cross- and self-fertilization has been observed.

Combined Types of Reproduction.—In the foregoing pages enough has been stated in regard to the reproductive processes to show that many animals reproduce by more than one general method. In many (probably most) life histories which include budding, fission, or sporulation there is always at some time also sexual reproduction. Likewise in most animals which employ parthenogenesis there is at times a period of bisexual reproduction as illustrated by the life history of many species of aphids. In some instances there is no known regularity in the recurrence of the sexual act, and in many cases there is no striking difference in the structure of the asexual and sexual individuals. In the type of life cycle known as *metagenesis,* however, there is a regular alternation between asexual and sexual reproduction accompanied by definite changes in the form of the individual. The Hydrozoa, of which Obelia and Bougainvillea are examples, illustrate this kind of life history. In Obelia the colony arises from a single polyp by a method of budding (asexual). Two types of buds are produced, the *hydranth* or nutritive polyp, and the *blastostyle* which together with the enveloping sheath forms the *gonangium.* By budding the blastostyle produces individuals of a third type, the *medusæ,* which upon maturity are released to swim freely in the water. The medusæ which are similar to those of Bougainvillea (Fig. 62) are sexual individuals producing eggs or sperms. Upon fertilization the egg develops into a ciliated embryo, the *planula,* which soon attaches itself and develops into a polyp from which by budding a colony arises. The polyps are incapable of sexual reproduction and the medusæ of most species are incapable of asexual reproduction. The sexual and asexual forms are unlike in structure. Metagenesis is rare outside the Cœlenterata but what appears to be metagenesis has been reported in a few species of marine annelid worms and in some other groups. In the worms, however, the difference in structure between sexual individuals and the vegetative individuals is not so great as in the Hydrozoa.

Artificial Parthenogenesis.—The exact nature of sexual reproduction has been a matter of speculation and in recent years a matter of painstaking research. The researches of Loeb and others upon artificial stimulation of development of the egg have thrown considerable light upon the effect of the sperm upon the egg. Development of the egg induced by artificial means is called *artificial parthenogenesis.*

Loeb found that if the unfertilized eggs of a sea urchin be placed for about two hours in sea-water whose osmotic pressure has been increased a definite amount by increasing the proportion of salts to water, and then replaced in normal sea water, the eggs segment and develop into swimming larvæ. Other methods were employed for the initiation of development of eggs of other animals, as starfish, mollusks and annelids. Some of the parthenogenetic agents used are the fatty acids, saponin, solanin, bile salts, the solvents of lipoids (as benzol, toluol, amylene, chloroform, aldehyde, ether, alcohols, etc.), bases, salts, hypertonicity and hypotonicity of solutions, and rise in temperature. Serum extracts of cells or of sperms of unrelated species or even contact with living foreign sperms as those of the shark, fish or fowl sometimes cause eggs to segment. Shaking the eggs of certain marine animals, stroking the eggs of moths, and pricking the egg of a frog with a fine needle have also been shown to cause development. In most of these instances development does not proceed very far, but the problem of fertilization is in part concerned with the mere initiation of development.

The immediate cause of development of an artificially parthenogenetic egg is uncertain. In normal fertilization of an egg by a sperm, it has been shown that the rate of oxidation of the egg increases about 400 to 600 per cent., and there is much to indicate that the agents inducing artificial parthenogenesis also increase oxidation. Even if the increase of oxidation is not the real cause of development, that cause is almost certainly some chemical or physical phenomenon. It is known in some cases that the agents which artificially cause segmentation of the ovum alter the colloidal state of the protoplasm. The protoplasm becomes stiffer (more viscous), and this change is followed by segmentation. Toward the close of each division the protoplasm becomes more liquid, but more viscous again at the beginning of the succeeding division. Similar changes occur at the time of normal fertilization by a sperm, suggesting that the artificial agents operate in the same way as does the sperm.

Nature of Fertilization.—Hertwig's definition of fertilization as the fusion of sperm and egg nuclei is not wholly satisfactory since in artificial parthenogenesis there can be no union of two nuclei; nevertheless, the egg is fertilized, that is, it is stimulated to develop. Moreover, occasionally the sperm and egg nuclei do not fuse before the egg segments; indeed, these nuclei may retain their identity for many cell generations in the dividing egg. A comparison of the results of the work on artificial parthenogenesis with normal fertilization shows that one effect of the sperm is the initiation of development and that this initiation is due to the presence and action of substances introduced by the sperm which produce certain chemico-physical effects. The sperm nucleus also brings in, as pointed out in Chapter XI, material bearing hereditary qualities.

Thus it may be assumed that the sperm in ordinary fertilization plays a dual rôle. It brings in a substance or substances which initiate development and in its nucleus it brings chromosomes which participate in the control of heredity.

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be brought together. The general act of bringing the germ cells or their equivalents together has often been termed *copulation.* Under this broad interpretation of the term copulation, the simplest method is that of some unicellular animals, such as Vorticella, *Heteromita lens* and many other Protozoa where two individuals meet and their bodies completely fuse. A somewhat more complex reproductive method is shown by Paramecium in which two individuals meet and interchange portions of their micronuclei, the portion received by each being subsequently fused with the portion retained within the body. As pointed out in the preceding chapter the uniting animals may be apparently similar (Paramecium, *Heteromita lens,* and Gonium), or they may be dissimilar, as in Vorticella, Eudorina and Volvox. The end result is virtually the same, whether the individuals are like or unlike in size, or whether there is complete fusion of the bodies of the individuals or only an interchange of nuclear material. The term copulation, however, is not usually applied to the Protozoa, since these simple animals do not possess germ cells, as distinct from somatic cells. The word copulation is in practice used only for the metazoa, in which true germ cells are formed, leaving the union of Protozoa for nuclear exchange to be designated by the term conjugation, or fusion if there is complete union of their bodies. Furthermore, while frequently used in a general sense to designate the act of bringing the germ cells together, the word copulation is more accurately used when restricted to the act of introducing the male elements into the body of the female in those forms which have internal fertilization. The act of clasping while the eggs are being fertilized outside of the body or while the male is depositing spermatozoa to be later secured by the female is specifically known as *amplexus.* As will be shown later not all animals have copulatory habits but when these occur they are known as fusion, conjugation, amplexus or copulation depending upon the nature of the union.

Fertilization in Hermaphroditic Animals.—In metazoa special sexual cells (eggs and sperms) are developed. A relatively small number of forms, among them some sponges, Hydra and a few of its relatives, worms and snails, are *hermaphroditic* (Fig. 145). Among these hermaphroditic forms, as in many sponges, the production of ova usually predominates in some individuals, the production of spermatozoa in others. In many hermaphroditic species the male and female elements are produced at different times, a condition known as *dichogamy.* When, as in most tunicates, the hermaphroditic animals are regularly female at first and later male, they are said to be *protogynous.* Others, like the mollusk Crepidula, are first male and then female and are said to be *protandrous.* Regarding hermaphroditism in general it may be said that it is more common among the invertebrates than among the vertebrates; that it is the normal condition in tunicates and a few fishes; that it is occasional in other fishes and in the amphibians; and that it occurs as an abnormal condition in reptiles, birds and mammals. In most of the cases of hermaphroditism in the higher animals the individuals do not, however, function as both sexes. They may be so abnormal as not to function as either sex. Concerning such forms, of course, there can be no discussion of methods of insuring fertilization.

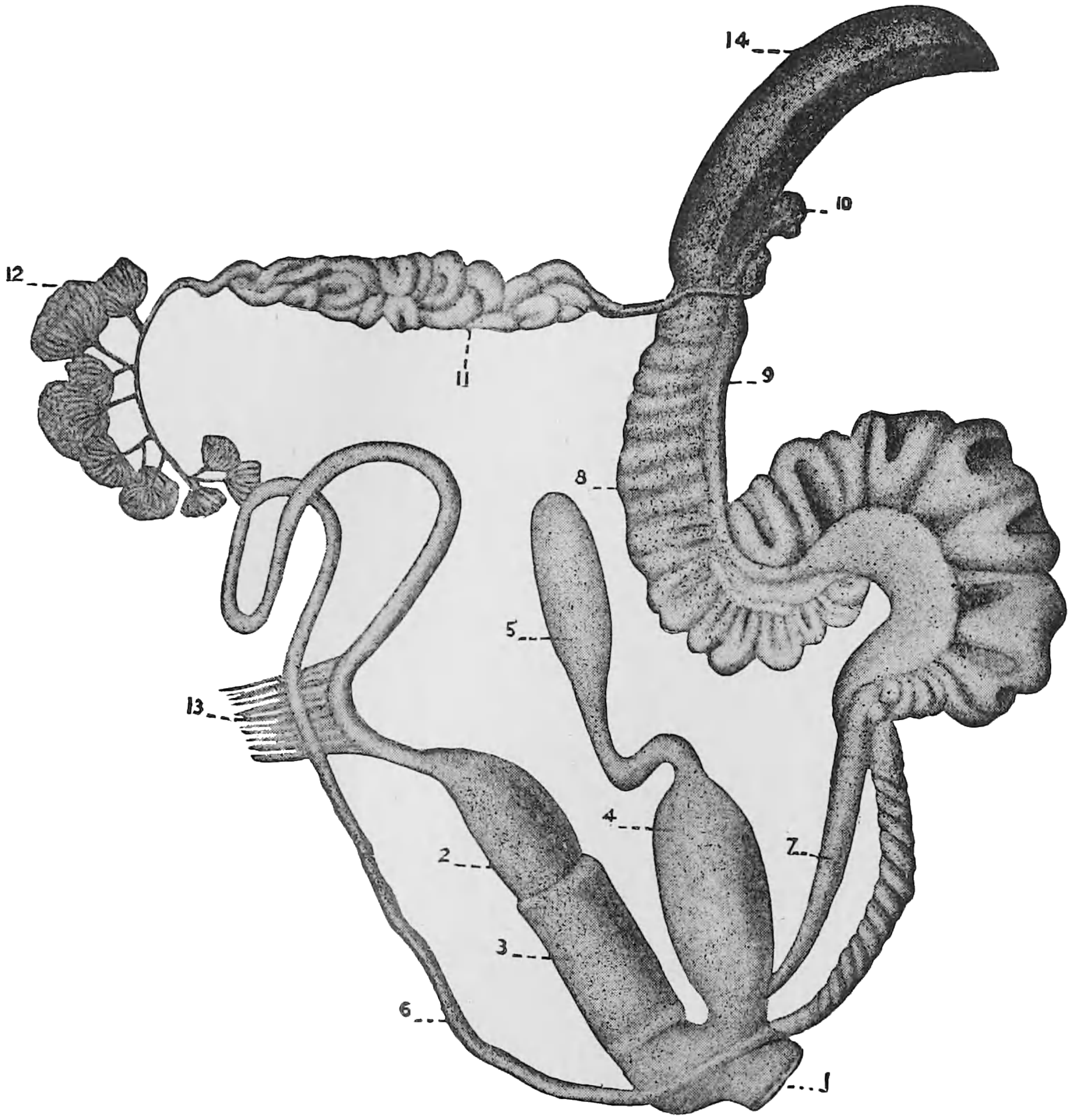

FIG. 145.—Genital organs of a hermaphrodite animal, a common land snail *Polygyra albolabris* (Say). Note that some of the organs are characteristic of a male, others of a female. 1, atrium; 2, penis; 3, prepuce; 4, vagina; 5, spermatheca; 6, vas deferens; 7, free oviduct; 8, uterus; 9, spermatic duct; 10, talon; 11, hermaphroditic duct; 12, hermaphroditic gland; 13, penis retractor; 14, albumen gland.

Only a few of the hermaphroditic animals, for example some nematode worms and the parasite Sacculina, are self-fertilizing. In self-fertilizing forms the eggs are usually fertilized within the body and there is no act of copulation. In hermaphrodites that are not self-fertilizing the eggs are in some cases fertilized within, in other cases outside of the body, and various methods of insuring fertilization are to be observed. In hermaphroditic hydras the spermatozoa are shed into the water and find the ova, still within the body, largely by chance, perhaps assisted by chemical attraction. In the earthworm, on the contrary, there is an elaborate copulatory process and capsule-formation, as described in the preceding chapter.

Fertilization in Diœcious Species.—In many aquatic animals 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 happen to meet the eggs, which are retained in the ovary of the female; in the starfishes and sea-urchins both eggs and spermatozoa are poured into the water, where they may or may not chance to come in contact. In other animals there is congregation of the sexes at the breeding time and the eggs and sperms are liberated in proximity. This congregation makes it more likely that the germ cells will meet, but chance still plays an important rôle. The giant salamander Cryptobranchus is a form that congregates with its fellows at the breeding season. In certain other salamanders, those of the genus Ambystoma, 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. 146). The mass of spermatozoa at its top is subsequently nipped off by the female with the lips of the cloaca, and the eggs are fertilized within her body. There is no copulation nor amplexus among any of the forms just mentioned. Copulatory habits are to be found, however, among some forms in which fertilization does not take place until after the eggs are laid, as well as among those in which the eggs are fertilized within the body of the mother. Furthermore, the eggs may or may not be fertilized at the time of copulation or amplexus. In the tailless amphibians (the frogs and toads) and some fishes the sexes congregate during the breeding season, the male clasps the female, and the seminal fluid is poured over the eggs as they are emitted (Fig. 147). Here the fertilization occurs during or just after amplexus. In the crayfishes, however, the spermatozoa transferred during copulation are stored in a seminal receptacle in the abdomen of the female, from which they are presumably emitted to fertilize the eggs as these are laid several months later. In some of the salamanders in which the male deposits spermatophores amplexus also occurs. In this respect these species differ from Ambystoma, mentioned above, in which there is no amplexus. Thus, in *Notophthalmus viridescens* the males clasp the females and deposit the spermatophores afterwards,

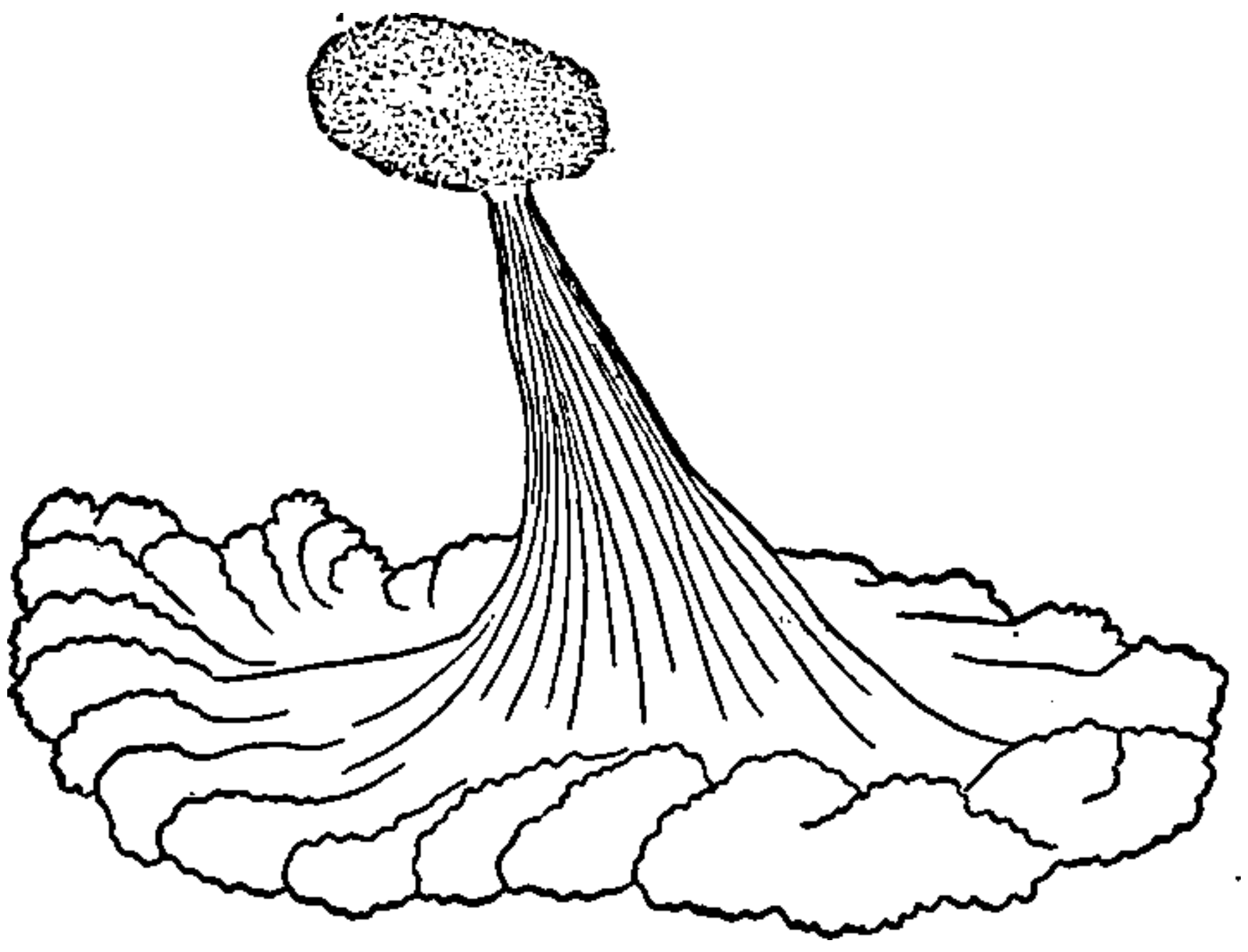

FIG. 146.—Spermatophore of *Notophthalmus viridescens viridescens* (Raf.), the common newt of eastern North America. The stalk is a clear gelatinous substance; the apical mass (dotted in the figure) is a snowy-white mass of seminal fluid containing spermatozoa. The mass of spermatozoa is taken up by the cloaca of the female. (*After B. G. Smith.*)

lation) or are deposited by the male during or just after amplexus. In the latter case the female secures them immediately or after an interval.

Do the Methods of Insuring Fertilization Exhibit an Evolutionary Series?—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. Thus, as pointed out above, the last of the four types of habit recognized, which involves more specialized behavior than any of the others, is employed by some parasitic worms, some snails, and the insects, which stand low or intermediate in the animal series, and by reptiles, birds and mammals which belong to the highest phylum. Furthermore, most of the fishes and amphibia use the second and third of these methods while some members of each of these groups follow the fourth method. 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. If, therefore, breeding habits are the result of an evolutionary process that process has small relation to the evolution of structure.

It is worthy of note, however, that among aquatic or amphibious forms the habit prevails of depositing the sperms and eggs freely in the water or in immediate proximity to each other, or depositing the sperms 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 at least the fertilized eggs can endure the water for a prolonged period.

Place of Development.—From the description of the methods of insuring 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. It is now to be pointed out that 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 of 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. Much more commonly, however, if the eggs undergo any development at all 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. Such animals are not said to lay their eggs, since it is well advanced larvæ or embryos that are discharged.

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 of 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. 148), 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. 99. The blood vessels of the embryo, running through the umbilical cord and expanding in a highly vascular tissue known as the *placenta,* are brought into very close contact with the maternal blood vessels in the wall of the uterus (Fig. 149). While no blood cells pass from the vessels of the mother to those of the embryo, nutritive materials and oxygen in solution readily diffuse into the blood of the latter. Forms in which the embryo is connected with the maternal uterus by a placenta are spoken of as truly viviparous. Viviparity is found in some insects, as in the plant lice, but it is not likely that the mother furnishes any nutrition. The eggs are small, but there is nothing comparable to a placenta. Hydra and jellyfishes exhibit something like

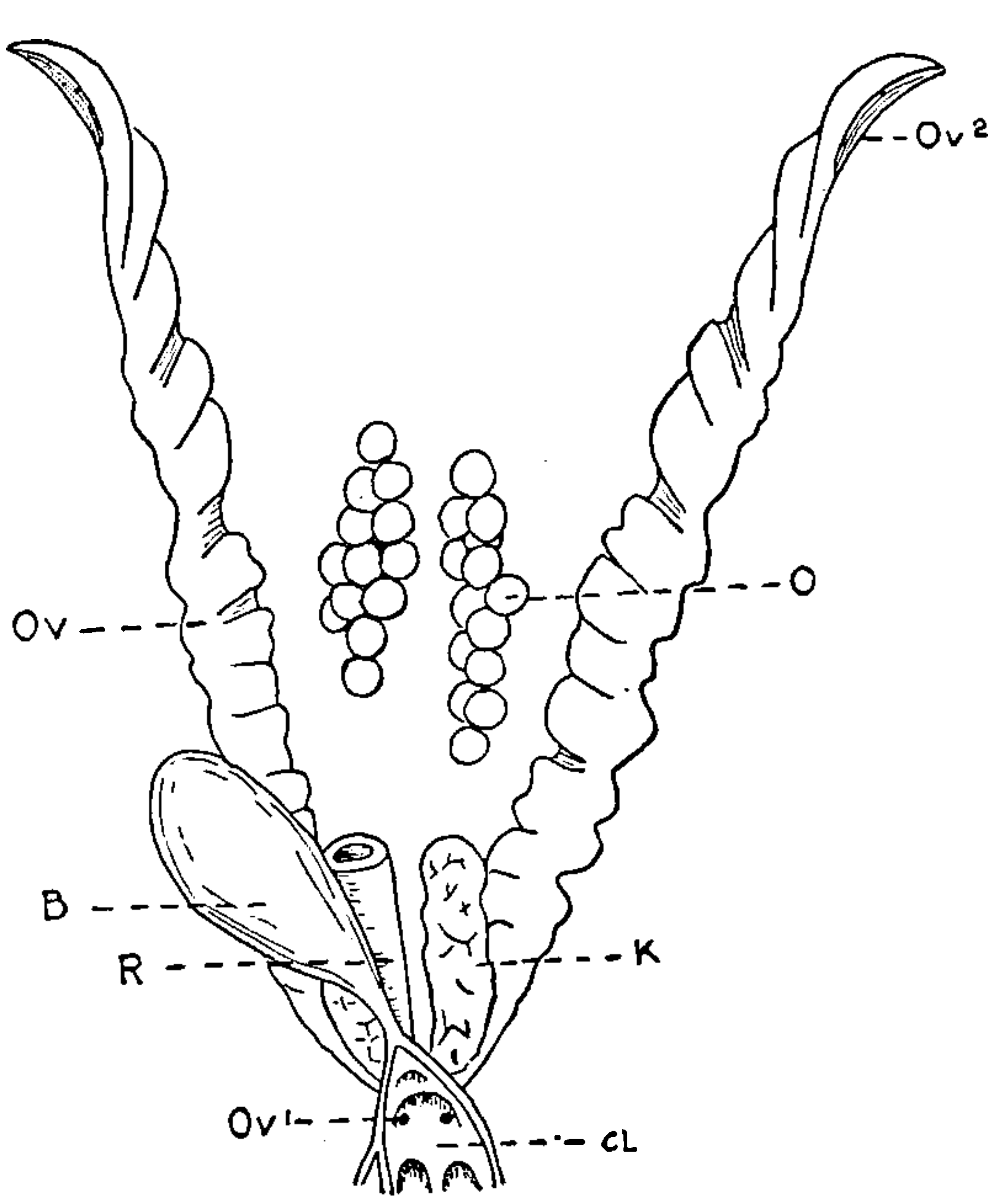

FIG. 148.—Urinogenital system of a lizard. *B*, bladder; *Cl*, cloaca; *K*, kidney; *O*, ovary; *Ov*, oviduct; *Ov*^{1}, cloacal opening of oviduct; *Ov*^{2}, abdominal opening of oviducts; *R*, rectum. The lizards are oviparous or ovoviviparous. In ovoviviparous forms, those in which the young reach an independent stage before birth and are not attached to the mother, the development of the fertilized eggs takes place in the oviducts.

viviparity, since only the spermatozoa are shed into the water. The sperms 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 all 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. 150) exemplify this intermediate condition.

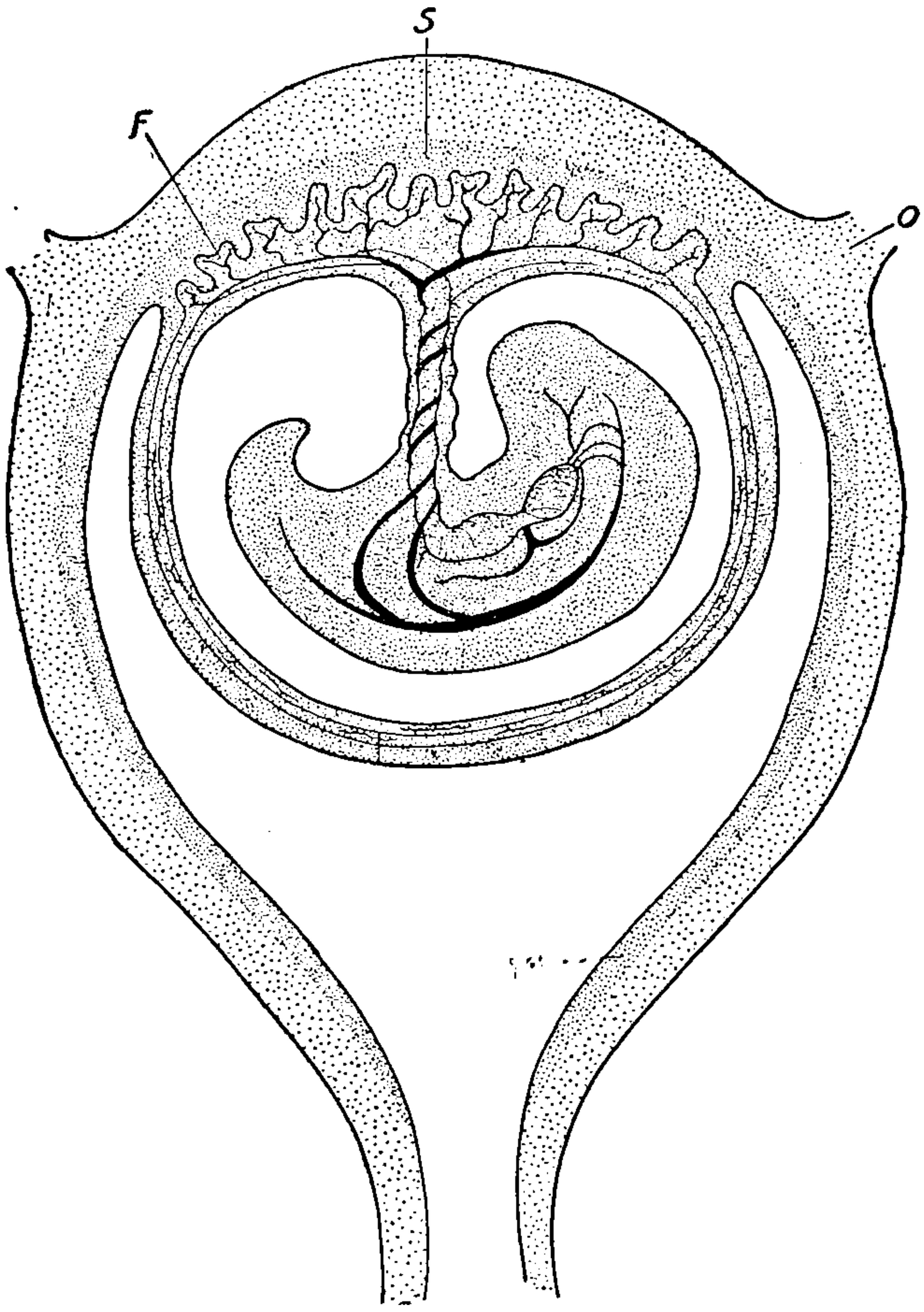

FIG. 149.—Uterus of mammal and contained embryo. The embryo is attached to the uterine wall by an umbilical cord in which blood vessels belonging to the embryo extend. These vessels do not connect with any vessels of the mother, but the capillaries of the two systems approach one another very closely. *F*, fetal placenta; *O*, opening of oviduct; *S*, maternal placenta. (*From Kingsley's Vertebrate Zoölogy, Courtesy of Henry Holt and Co.*)

Summary of Locus and Nutrition of Embryo.—The variations in the breeding habits of animals, with respect to the place of development of the egg and the source of nutrition of the embryo, may be summarized as follows:

OVIPARITY

(*a*) Eggs fertilized after being laid.

(*b*) Eggs fertilized before being laid.

VIVIPARITY

(*a*) Eggs retained until the young are capable of independent exist-

of insuring fertilization so there is apparently none in the method of bearing the young. Oviparity and viviparity are found in the vertebrates and the invertebrates. Certain conditions of the reproduction itself, however, make one generalization possible. It is to be noted that the forms in which the eggs are fertilized outside the body of the mother are necessarily oviparous. Also, it is only among forms with internal fertilization that viviparity, ovoviviparity and the laying of fertilized eggs can occur. It results that viviparity, ovoviviparity and the laying of fertilized eggs prevail among land forms, where protection against evaporation of the eggs is necessary, and that 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. There are many animals which give no care whatever to the eggs. This is particularly true of aquatic species which pour the eggs and sperms freely into the water to come together by chance. The starfishes and sea-urchins and many other marine animals exhibit this lack of any 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. The aquatic turtles come to land to lay the eggs in the warm sand which hastens their development. The digger wasps, ichneumon flies and certain other insects deposit their eggs in various places and provision them with living or dead animal food. One group of birds, the Megapodes, lay the eggs in a pile of decaying vegetation, the decomposition of which liberates heat that aids in development (Fig. 151). 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 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 insure *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. 152). 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 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, both among 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. Freshwater mussels keep their eggs in the chambers of the gills of the

Fig. 151.—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. The nests are commonly about six feet high and ten or twelve feet in diameter and constructed for the use of one pair of birds, but much larger ones are found which are said to be used by several breeding pairs. (*Photo by E. R. Sanborn, loaned by the New York Zoölogical Society.*)

female, where they are furnished oxygen by the water that is constantly passing through the gills. In spiders, the silken egg case mentioned above is often carried about by the mother. Certain frogs (Fig. 153) 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

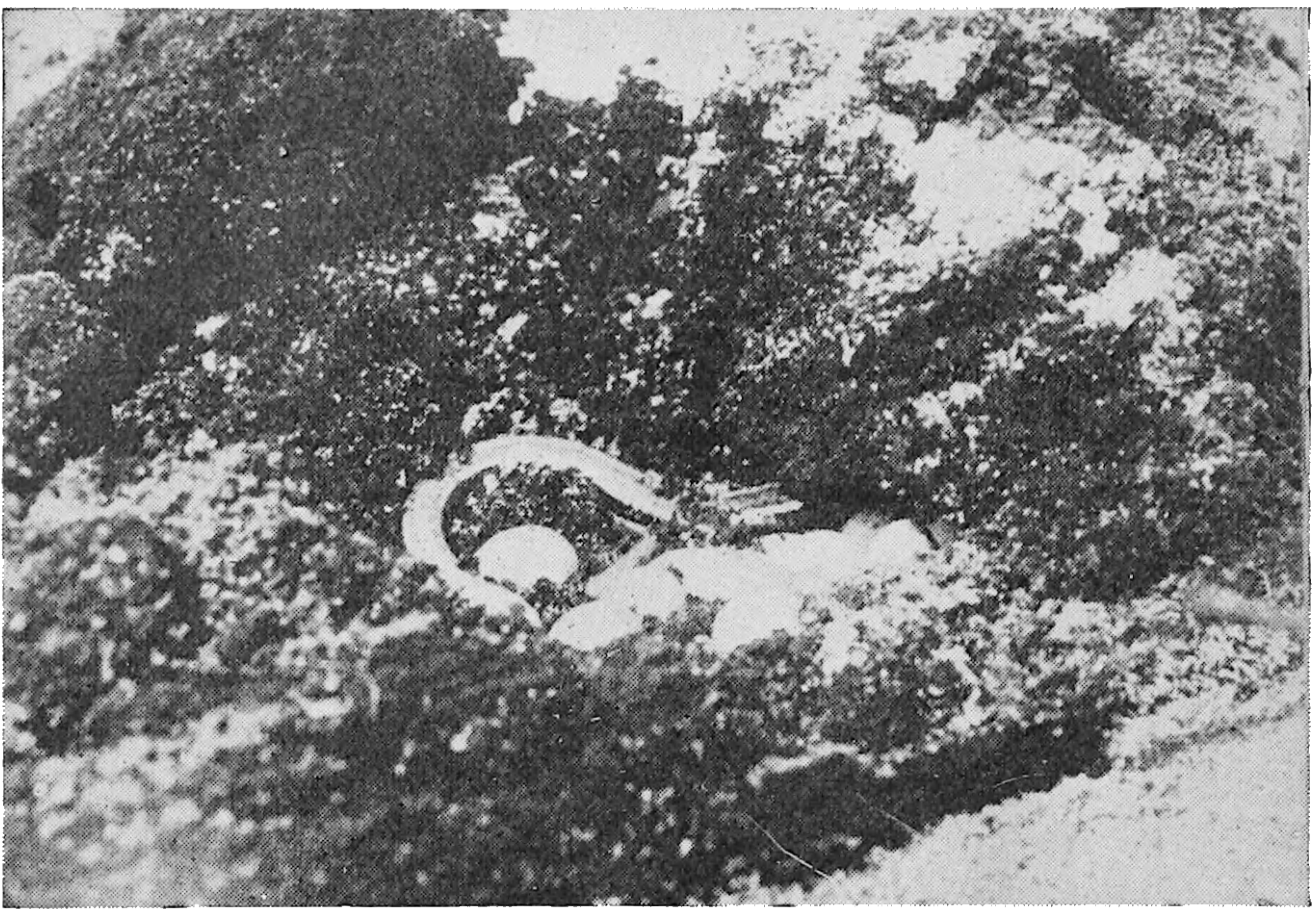

FIG. 152.—Blue-tailed skink, *Plestiodon fasciatus* (Linnæus), with eggs. This lizard buries its eggs (the white mass in the middle foreground) in decaying wood and stays with them until hatched. Probably the incubation of the eggs is not assisted by the presence of the parent. The curved white streak 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. (*Photo by A. G. Ruthven.*)

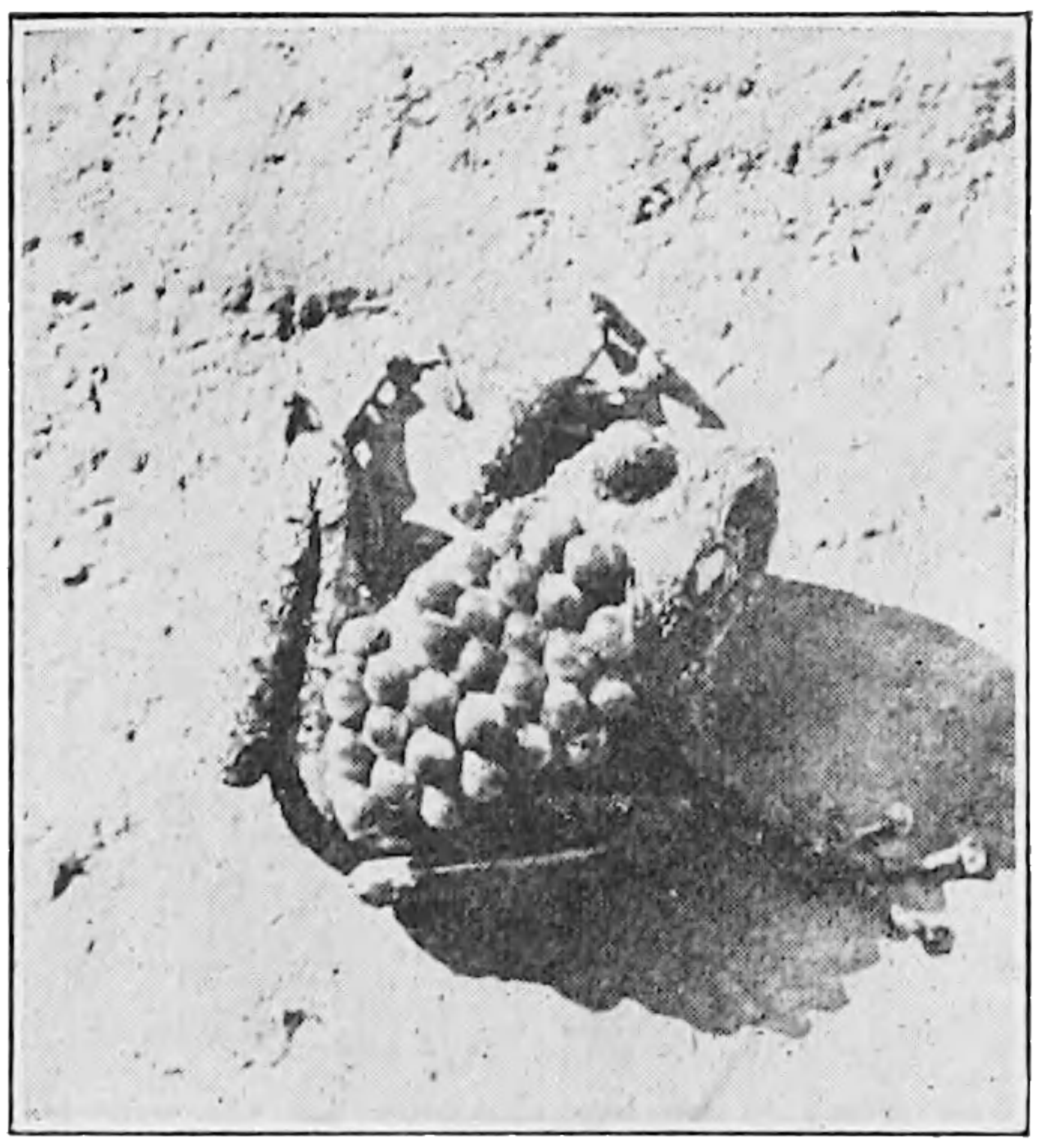

FIG. 153.

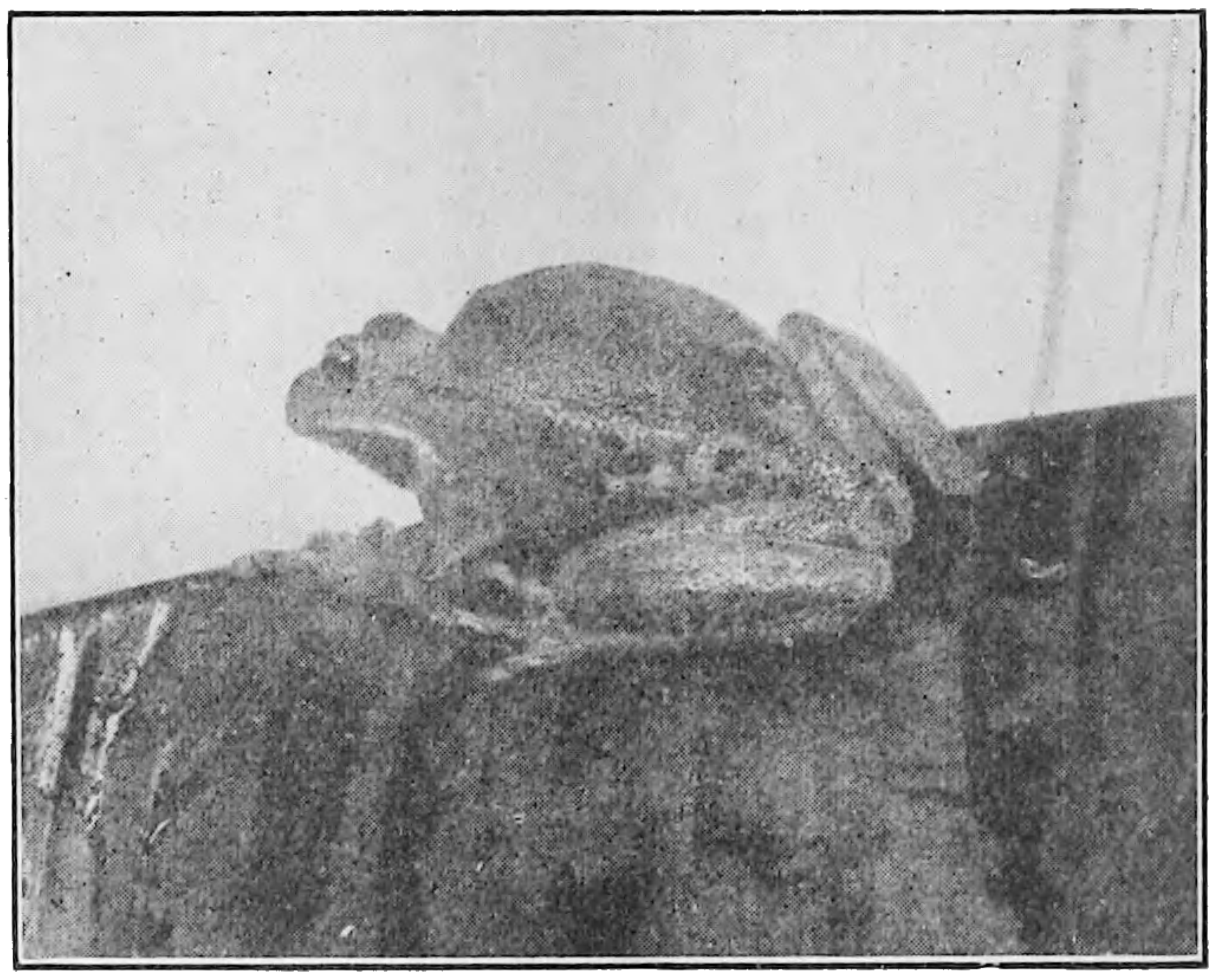

FIG. 154.

FIG. 153.—*Hyla fuhrmanni* Peracca, a South American tree-frog which has the habit of carrying the eggs on the back. The female carries the eggs, and the larval (tadpole) stage is passed in the egg, the young emerging from the egg membrane in the adult stage. (*Photo by A. G. Ruthven.*)

FIG. 154.—A marsupial frog, *Gastrotheca monticola* Barbour and Noble, from Peru. The female carries the eggs in a large pouch on the back. The opening of the pouch and a protruding egg may be seen in the lumbar region. (*Photo by G. K. Noble.*)

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 *larvæ.* The offspring of jellyfishes emerge from the ovary of the mother, where as stated above 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. 158) and marine worms are

FIG. 156.—The black swamp-wallaby. This is a marsupial, or pouched mammal, found in Australia. The young are born in a very immature stage and are carried in a pouch (marsupium) on the ventral side of the mother. For some time the young is attached to the nipple in the marsupium, the nipple forming a bulb in the back part of the mouth. Even after it is weaned and has attained a considerable size, the young when alarmed seeks the pouch for protection (*Photo loaned by the New York Zoological Society.*)

also capable of free-swimming existence at a very early stage. In the frogs and toads, the tadpole is a larval form (Fig. 159), but it hatches at a much later developmental stage than do the larvæ of the several preceding examples.

Larval development may be direct or indirect. In direct development the larva develops directly toward the sexually mature condition, the organs being outlined and developed one after the other. In indirect 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. 159) 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

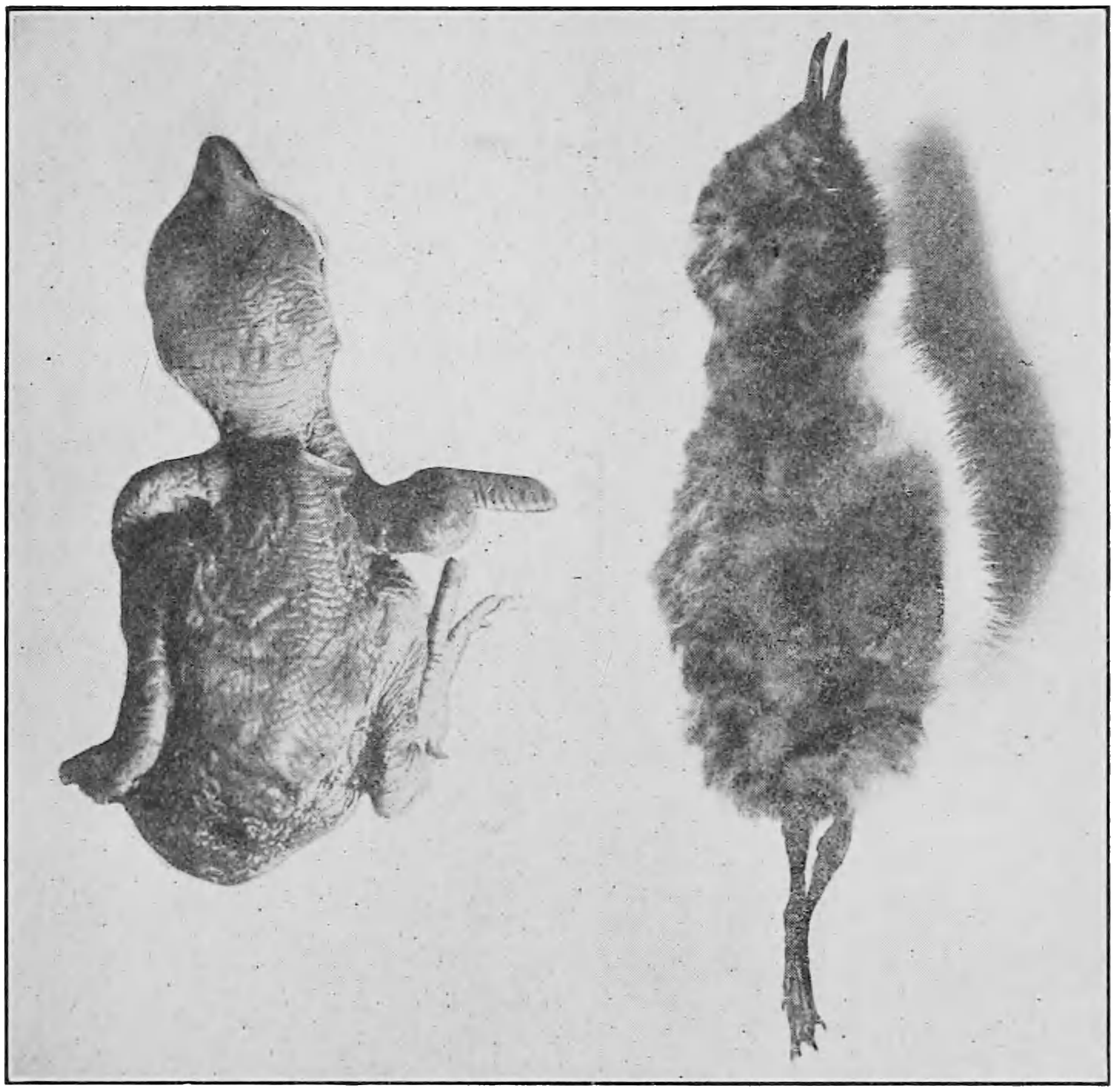

FIG. 157.—Recently hatched young of the chimney swift, *Chætura pelagica* (Linnæus) (left), and spotted sandpiper, *Actitus macularia* (Linnæus) (right). These are examples, respectively, of altricial and precocial birds. The chimney swift is blind and naked when hatched (altricial); the sandpiper is covered with down and the eyes are functional (precocial).

larval organs the more pronounced the metamorphosis becomes. This phenomenon is further described in Chapter X.

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 as a group that the stage of development at birth determines the amount of parental care necessary, for many of the lower invertebrates with incomplete larvæ 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 post-embryonic 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.

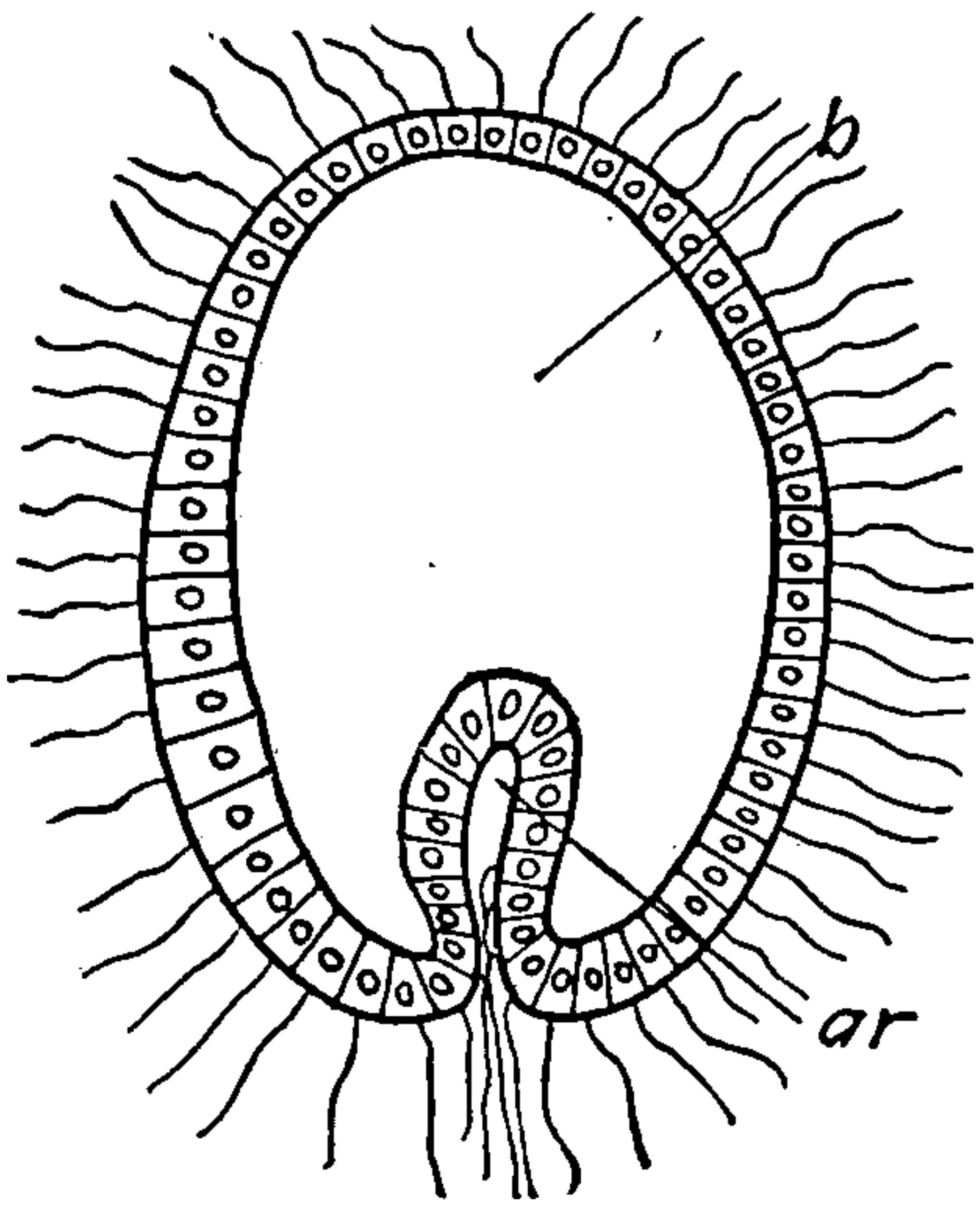

FIG. 158.—Free-swimming larva of the holothurian Synapta, leading an active independent existence at a very early stage of embryonic development. (*From drawing by P. O. Okkelberg.*)

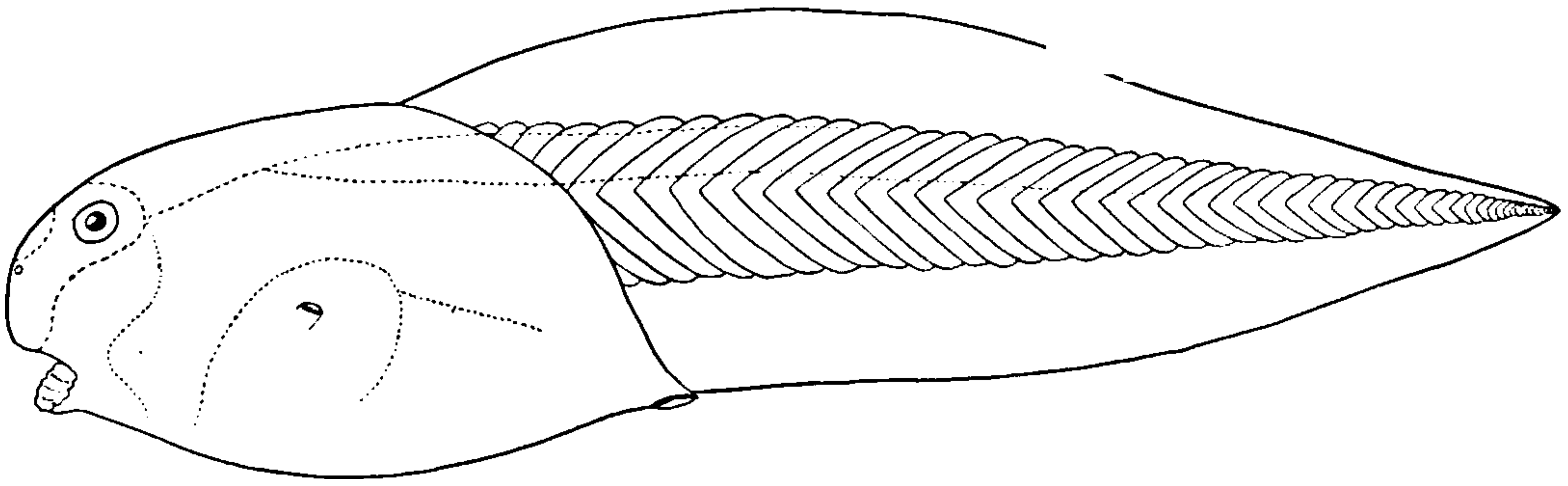

FIG. 159.—Tadpole of frog, illustrating a larval form. Organs are present which are lacking in the adult, and some organs are missing which the adult possesses.

Conclusion.—The brief analysis just given shows that the breeding habits of animals are very varied, that they bear some relation to the mode of life, and that there is no general evolutionary sequence in the

CHAPTER X

EMBRYOLOGY

Although knowledge of the habits by which animals insure the occurrence of reproductive processes and the maintenance of their young during critical periods is much of it comparatively new, the principal steps by which the fertilized egg is transformed into an animal in the form of the adult have long been known. The field of embryology has been diligently explored, and knowledge of embryonic development is correspondingly definite.

An *embryo*, strictly speaking, is an undeveloped animal while still in the egg membrane, in the case of oviparous or ovoviviparous species, or while attached to the maternal uterus, in viviparous animals. One might expect, therefore, that *embryology* would deal only with that part of development taking place after the fertilization of the egg and prior to birth or hatching. In practice, however, embryology is more inclusive. It has been pointed out in the preceding chapter that animals may be hatched or born in very immature stages. In some of them certain organs characteristic of the adult are not yet present at the time of hatching, or the young animal may have organs which the adult does not possess. Such immature animals are spoken of as larvæ. The transformation of a larva into the adult form, a phenomenon known as *metamorphosis*, is usually included in embryology.

The germ cells, moreover, undergo a characteristic development before they are capable of union in fertilization, and hence before any embryo is produced. This process of development in the germ cells is independent of the special breeding habits of the animal, and is reckoned as a part of embryology. In the term embryology, therefore, is comprehended the entire development of the germ cells, and of the embryo which they produce, up to the time of birth or hatching, or until such later time as the organs of the adult are laid down and any temporary larval organs are lost.

Early Origin of Germ Cells.—The differentiation of cells into two general classes, *somatic* cells which are sterile, and *germ* cells capable of reproduction, has been described in Chapter V. It was shown that a difference between sterile and reproductive cells is found in aggregations which are otherwise very simple in structure, such as Pleodorina, whereas differentiations other than that between somatic and germ cells appear only in more complex aggregations, like Hydra. The occurrence of this distinction between reproductive and non-reproductive cells in very simple aggregations of cells probably indicates that, in the evolution of animal forms, germ cells arose at an early time. As if a reminder of the historically early origin of germ cells in the evolution of the metazoa, the reproductive cells appear at very early stages in the development of individual animals today. Development has not proceeded very far until, in most animals, the germ cells are easily recognizable. Furthermore, there is evidence to show that certain cells may actually be destined to become germ cells from a time much earlier than their visible differentiation. How early their fate is sealed is known in the case of only very few animals; but it is not improbable that in most species germ cells exist as definite germ cells, although not recognizable, almost from the earliest stages of embryonic development.

Origin of Germ Cells in the Invertebrates.—The early origin of germ cells in the embryo has been demonstrated in Sagitta, the arrow-worm.

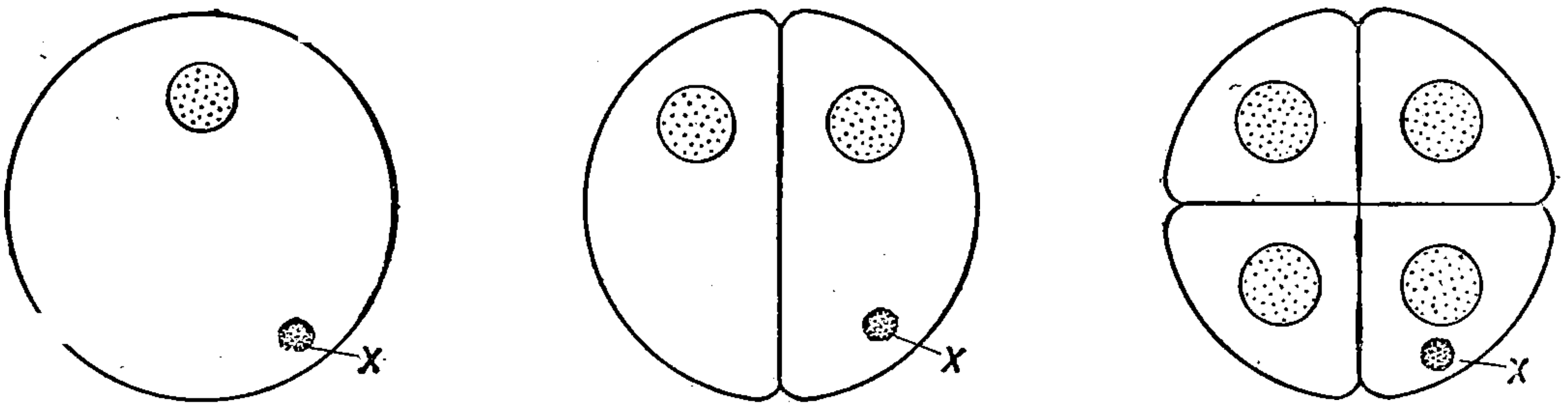

FIG. 160.—Diagram illustrating the early recognition of the germ cells of the arrow-worm Sagitta. At each of the early divisions the X-body (x) passes to only one cell; and that cell gives rise eventually to all the definitive germ cells. (*From original diagram by P. O. Okkelberg.*)

In the egg of this animal a structure in the cytoplasm known as the *x-body,* is present while the egg is still unsegmented (Fig. 160). When the egg divides, the x-body passes to only one of the cells. At the second division it again passes undivided to one of the cells, the other three lacking such a structure. In each of the next four divisions its behavior is the same, so that of the 64 cells present at the end of that time only one contains the x-body. In the seventh division, however, this body divides and passes to the two daughter cells. From these two cells, out of a total of 128, come the germ cells of the worm that is to develop from the embryo. The question whether the x-body causes the cells that contain it to become germ cells need not be debated; but that it distinguishes them as germ cells is certain.

In *Ascaris megalocephala,* a roundworm parasitic in the intestine of the horse, the germ cells are early recognizable from the behavior of their chromosomes in cell division. When the first two cells derived from the fertilized egg divide to form four cells, the chromosomes of one cell remain intact, while in the other the thickened ends of the chromosomes are separated off and cast out into the cytoplasm (Fig. 161), leaving only the middle portion of the chromosomes to participate in mitosis. All of the germ cells of the future worm are derived from that one of the first two cells which retains all of its chromatin. Not all of the cells, however, which descend from that cell are germ cells, for at each of the next four or five mitoses some of the cells repeat the fragmentation of their chromosomes and thereby give rise to somatic cells. After about the sixth division the elimination of chromatin ceases, and the cells that have kept their entire chromosomes produce only germ cells.

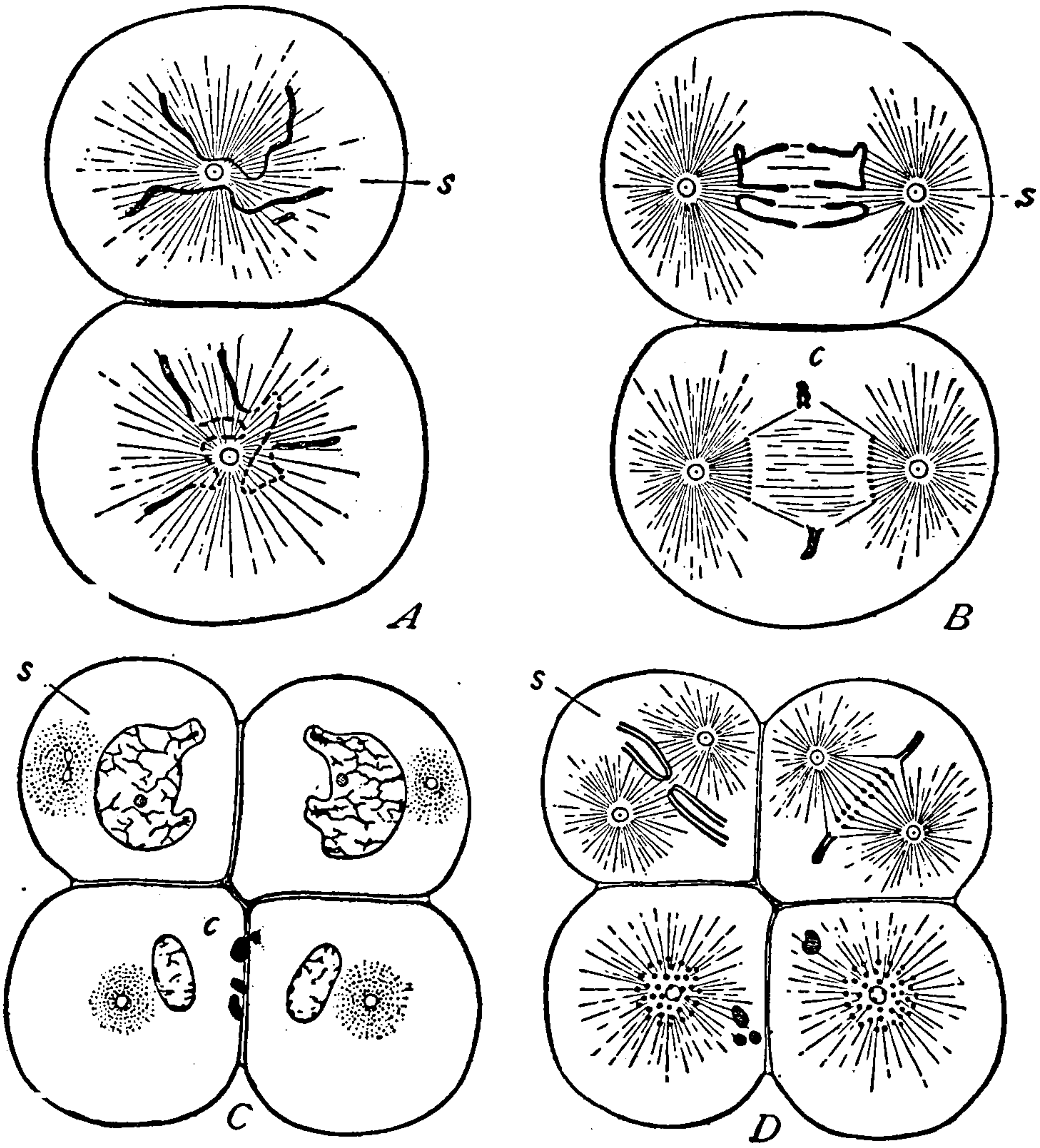

Fig. 161.—Early cleavage of the egg of Ascaris, showing the origin of the germ cells. *A*, two-cell stage, with the cells preparing for another division; the chromosomes of one cell remain intact, those in the other cell become fragmented; *B*, the same cells later, showing the ends of the chromosomes in the lower cell being eliminated into the cytoplasm; *C*, the four cells resulting from the preceding division; the lower cells contain masses of eliminated chromatin, and their nuclei are smaller; *D*, division of the preceding four cells, showing a repetition of the fragmentation of the chromosomes in one of the upper cells; *s*, stem cell, from which germ cells are derived; c, chromatin eliminated into the cytoplasm. (*From Wilson, after Boveri. Courtesy of Macmillan Co.*)

In insects also it has been found that the germ cells are recognizable at an early stage in cleavage, either by their size or by certain granules or bodies that they contain (Fig. 162). When these cells are destroyed the embryo may go on and develop, but contains no reproductive cells.

Spermatogenesis.—This name is given to the maturation of the male germ cells. 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, and are ready to initiate the changes included in maturation, 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. Now, 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, whether somatic or immature germ cell, may therefore be designated paternal, the other half maternal. These chromosomes may look precisely alike, and may in fact be exactly alike; the terms paternal and maternal refer only to their source, not to their nature.

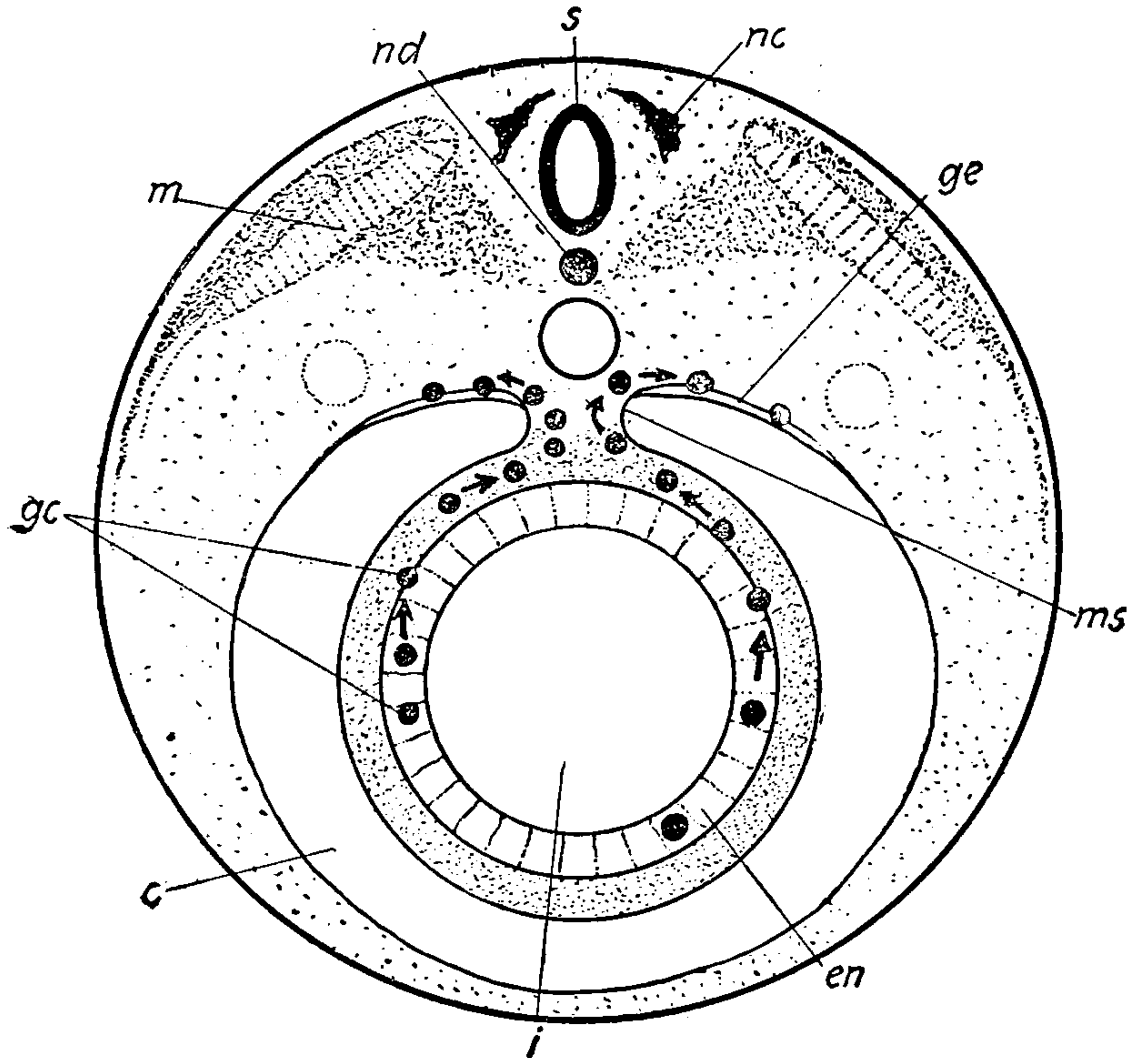

FIG. 163.—Origin of the germ cells of a vertebrate animal. Diagram of a cross section of the body of the embryo, showing the germ cells originating in the endoderm of the intestine and migrating as shown by the arrows to the later position of the reproductive bodies. *c*, cœlom; *en*, endoderm of intestine; *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.

In the early stages of maturation, the spermatocytes grow considerably in volume. In these stages also the chromosomes come together in pairs. Each pair is composed of one paternal and one maternal chromosome.

Furthermore, the pairing is not a purely fortuitous occurrence, for each paternal chromosome meets with 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.

Tetrads.—The pairs of chromosomes often do not appear as double bodies; for while the chromosomes have been coming together they may also have divided. Each pair thus consists 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. In the two maturation divisions the tetrads are divided, in two planes, first into double bodies called *dyads*, next into their single components.

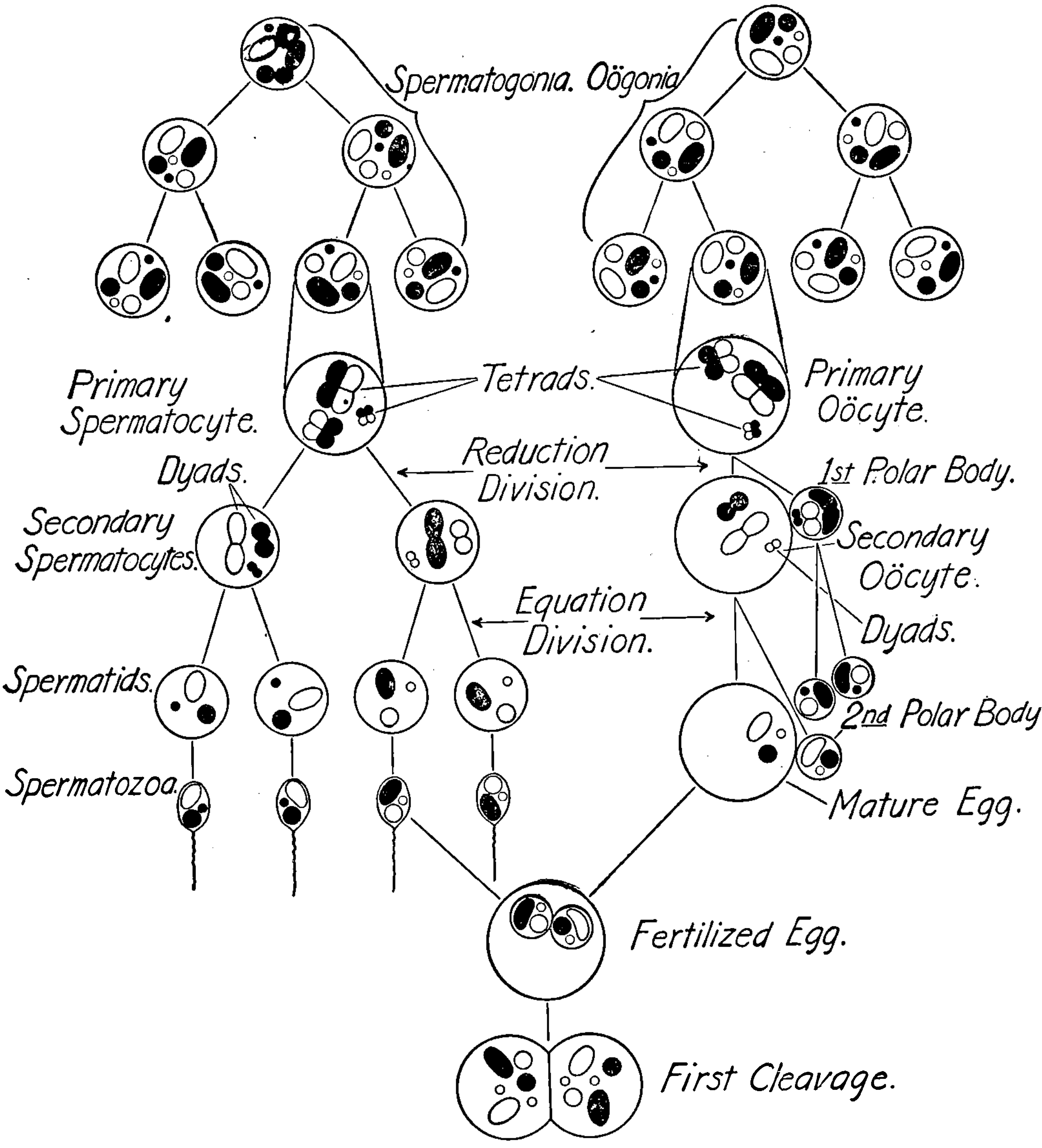

FIG. 164.—Maturation of the germ cells, diagrammatically represented for both sexes. The black chromosomes may be assumed to be of paternal origin, the white ones maternal.

First Maturation Division.—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 part, this position appears to be fixed and always the same in the same species. In the illustration (Fig. 164), they are represented as having been so placed that the maternal half of the tetrad is 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 of the paternal dyads go into one cell and all of 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.*

It is worthy of note that in the division just described, no chromosomes have 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; it never occurs in cell divisions except in maturation, and in only one of the maturation divisions.

Second Maturation Division.—The secondary spermatocytes divide very shortly by a mitosis in which the dyads are separated 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.

By a transformation in shape, the spermatid becomes a mature *spermatozoön.* This cell consists usually of a head, which may be rounded or long and slender, and a whip-like tail. The chromosomes are all contained in the head, the tail being merely a motile organ.

Oögenesis—The maturation of the female germ cells is in most respects similar to that of the male. The early germ cells undergo a period of multiplication in which they divide by ordinary mitosis. During this time they are called *oögonia* (singular, *oögonium*). Eventually this ordinary division ceases, and the cells are ready to initiate the maturation process. At this time they are known as *primary oöcytes.* These oöcytes grow rapidly to many times their original volume, the growth being much greater than in the male.

Tetrads.—During growth the chromosomes meet in pairs, each pair, as in the male, being composed of one maternal and one paternal chromosome. Each chromosome divides as they come together, so that each pair presents a quadruple body, the tetrad. These tetrads are divided in the two maturation divisions, first into dyads, next into their single components, in a manner strictly comparable to the divisions in the male.

First Maturation Division.—When a spindle is formed for the first division, it appears, not in the center, but near the surface; and it is placed approximately perpendicular to the surface. The tetrads take their place on this spindle. If the animal is one in which, as illustrated in Fig. 164, the first division is the reduction division, the tetrads are placed so that the paternal half is toward one end of the spindle, the maternal half toward the other. The resulting cells therefore contain

the oviparous and ovoviviparous vertebrates (reptiles, birds), on the contrary, the eggs are very large. The yolk material is also very differently distributed in the eggs of different species. With respect to the distribution of yolk there are recognized three classes of eggs which are of course connected by all gradations. They are as follows:

1. *Homolecithal* eggs are those in which the yolk is nearly uniformly scattered through the cytoplasm. Usually the amount of yolk is not very great. The echinoderms (sea-urchins, starfishes), marine worms and mammals produce eggs of this kind (Fig. 165).

2. In *telolecithal* eggs the yolk is massed toward one side, the vegetative pole, leaving the bulk of protoplasm at the opposite side, the animal pole. The yolk is abundant in such cases. The eggs of fishes, reptiles, and birds are strongly telolecithal, while those of the frog are mildly so (Fig. 166).

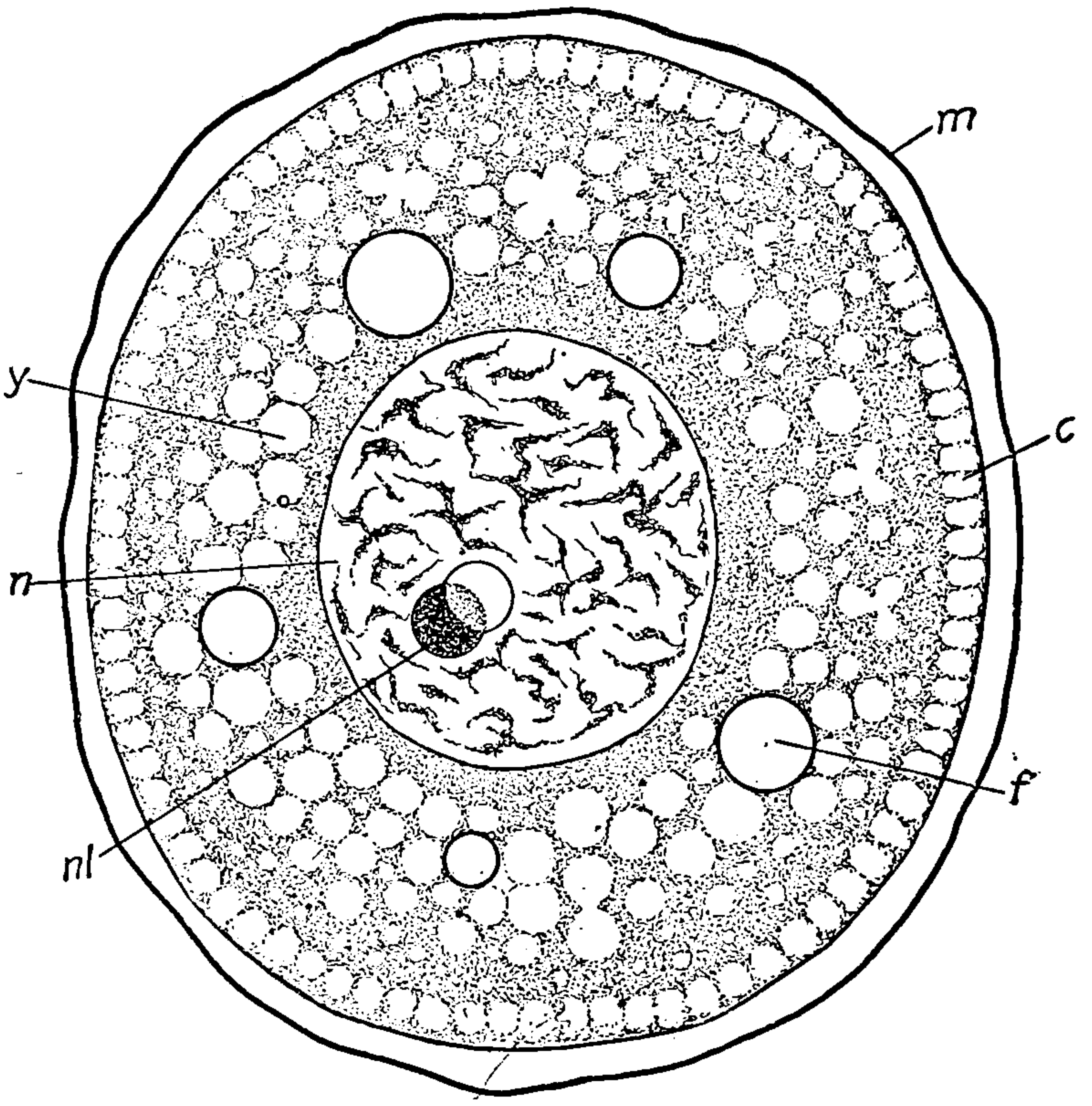

FIG. 165.—Homolecithal egg of the sandworm Nereis. *c*, cytoplasm; *f*, fat droplets; *m*, egg membrane; *n*, nucleus; *nl*, nucleolus; *y*, yolk spheres. (*After Wilson, courtesy of Macmillan Co.*)

3. *Centrolecithal* eggs have the yolk occupying the central portion, while the greater part of the cytoplasm is in a layer at the periphery. There is usually also an island of cytoplasm in the middle of the yolk mass, in which the nucleus of the cell is located. Insect eggs are regularly of this type (Fig. 167).

Eggs are very often enclosed in a membrane or shell, particularly among species that lay their eggs on land where evaporation must be largely prevented. 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 calcareous particles with conical faces pointing inward. These particles do not fit closely, and air may pass between them. Outside of this layer is a compact sheet of calcareous strands which also permits the 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, a provision necessary in eggs laid in air, and yet it permits the passage of gases necessary for the respiration of the 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.

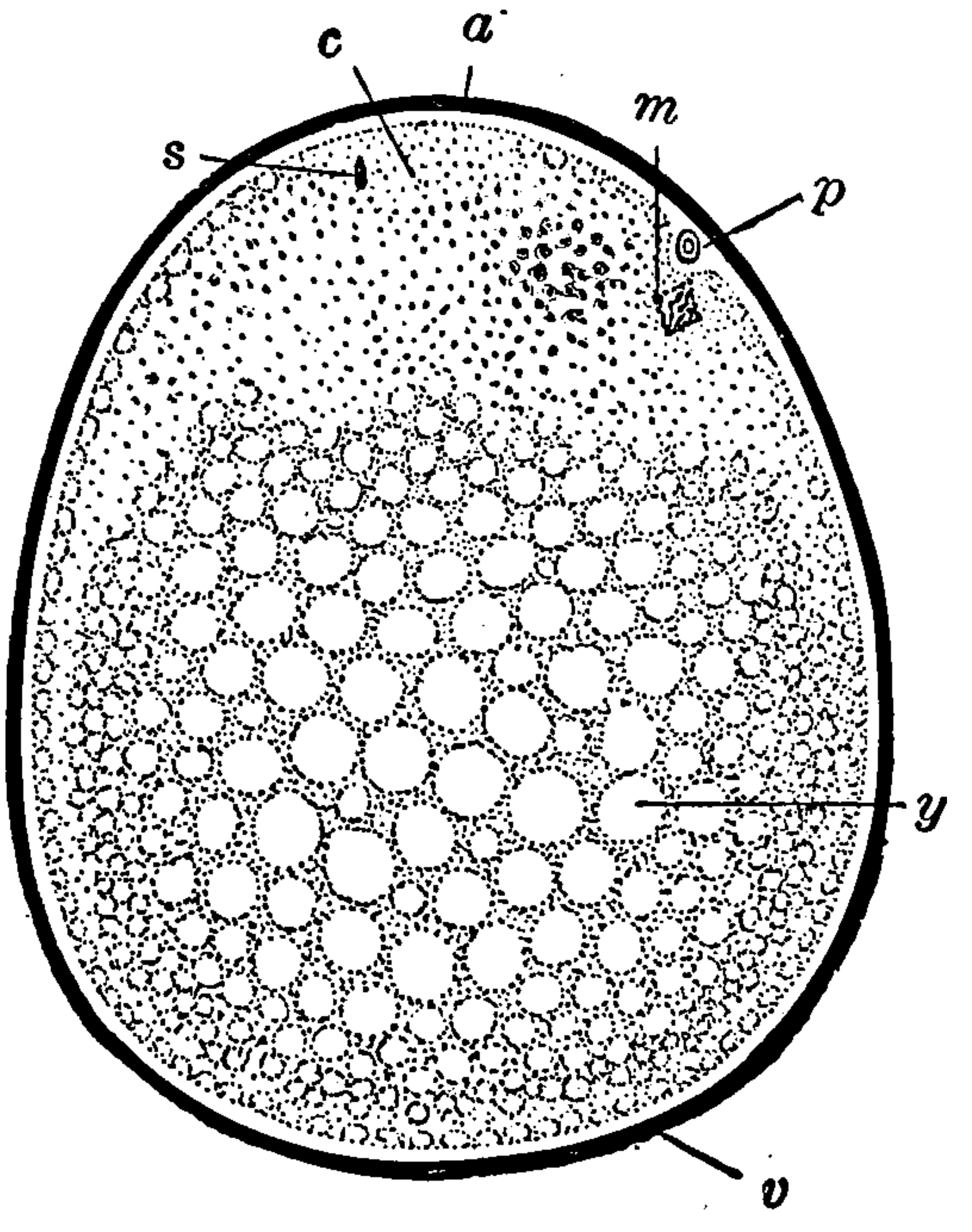

FIG. 166.—Telolecithal egg in generalized form. *a*, animal pole; *c*, cytoplasm; *m*, second maturation spindle; *p*, first polar body; *s*, spermatozoön; *v*, vegetative pole; *y*, yolk crowded toward vegetative pole. (*Modified from original drawing by P. O. Okkelberg.*)

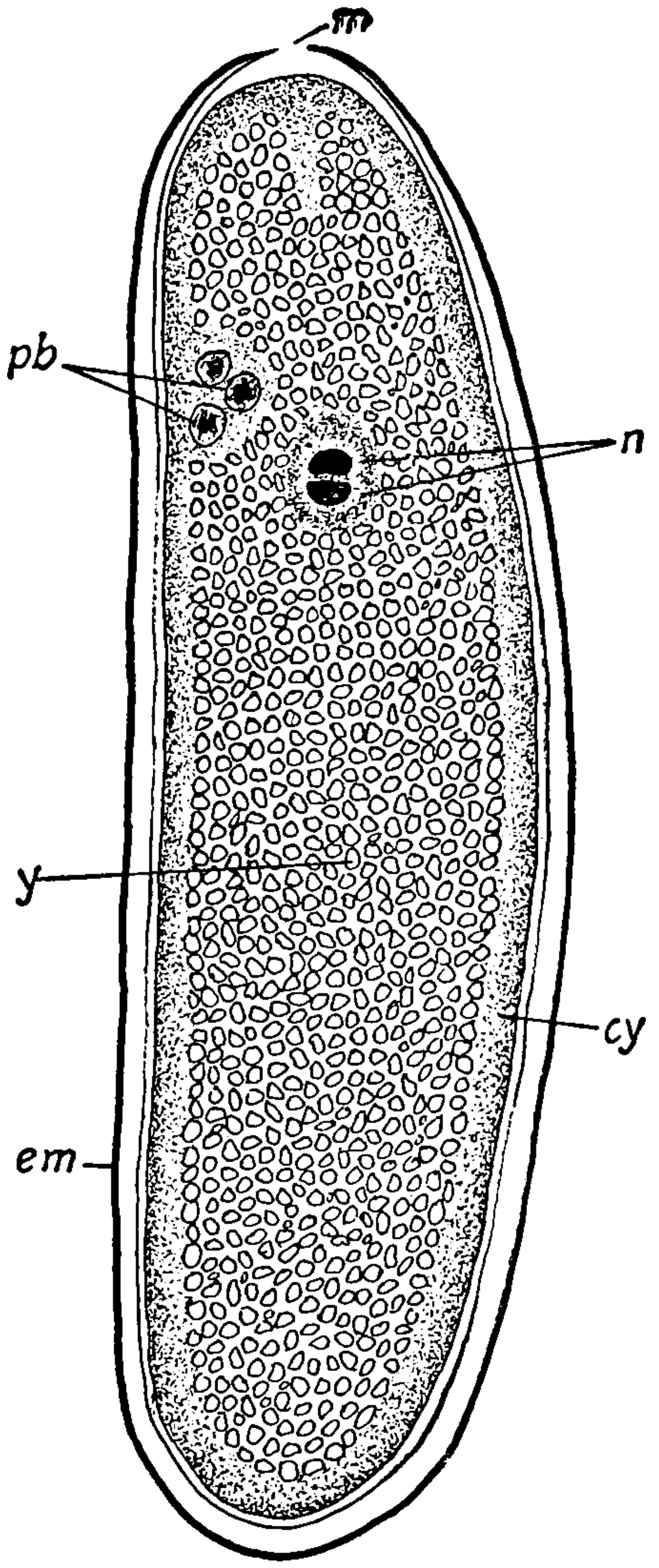

FIG. 167.—Centrolecithal egg of the fly Musca, in longitudinal section. *cy*, cytoplasm; *em*, egg membrane; *m*, micropyle; *n*, egg and sperm nuclei; *pb*, three polar bodies; *y*, yolk. (*From Korscheit and Heiaer, after Henking and Blockmann, courtesy of Macmillan Co.*)

The Spermatozoa.—Spermatozoa exhibit much greater variety of form than eggs. Typically they consist of an enlarged anterior *head*, in which the nucleus is contained; a minute body, the *mid-piece*, behind the head, from which in some animals a centrosome is known to develop in the fertilized egg; and a whip-like *tail* used as a motile organ. Most of the higher animals produce spermatozoa of this kind, but in a variety of shapes as shown in Fig. 168 (*A–E*). In other animals the form may be wholly different (*F–J*).

Fertilization.—The dual function of the union of egg and sperm has been pointed out in Chapter VIII, and some of the methods of insuring that the two cells are brought together are described in Chapter IX. It was shown in the latter chapter that the time of fertilization, relative to the location of the egg, is variable; that is, the egg may be fertilized while still in the body of the female, or not until the egg is laid. In those that are fertilized within the body of the female, fertilization occurs in the oviduct in the vertebrates, or as in some invertebrates while the egg is still in the ovary. It is now possible also to relate the time of fertilization to the stage of maturation which the egg or oöcyte has reached when the sperm enters.

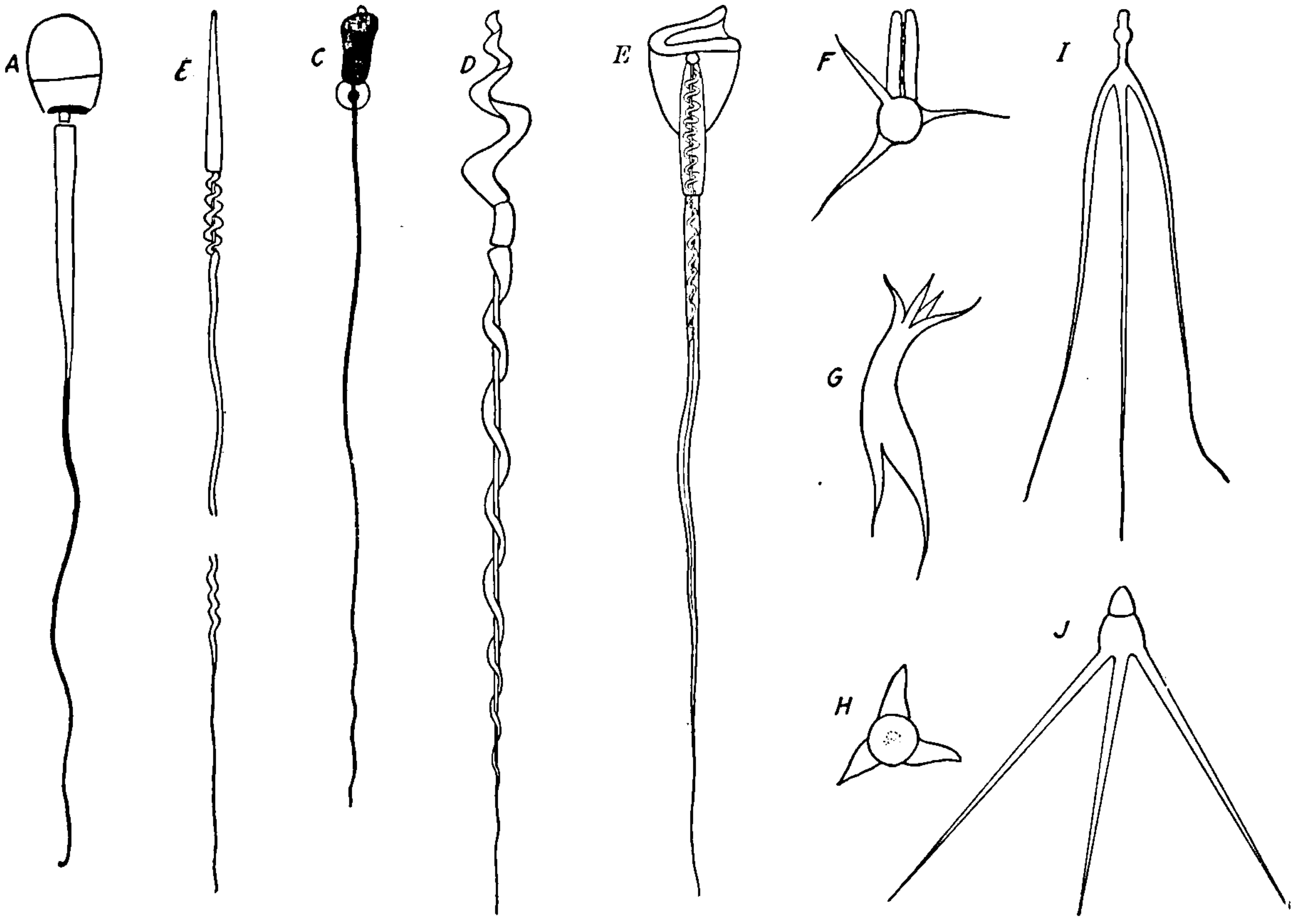

Fig. 168.—Different forms of spermatozoa. *A*, badger; *B*, sheldrake Tadorna; *C*, sturgeon; *D*, flycatcher Muscicapa; *E*, opossum; *F*, lobster; *G*, crustacean Polyphemus; *H*, crab Dromia; *I*, crab Porcellana; *J*, crustacean Ethusa; (*A–D after Ballowitz; F after Herrick; G after Zacharias; H–J after Grobben. From Wilson's The Cell in Development and Inheritance, courtesy of Macmillan Co.*)

In *Ascaris megalocephala*, parasitic in the horse, the sperm enters the cytoplasm of the primary oöcyte about the time of the formation of

good example. 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. Often, especially when a distinct amount of yolk is present, the third cleavage plane is slightly above the equator, so that the upper four cells are smaller than the lower quartet.

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 a homolecithal egg, the divisions usually take place at the same time in all the cells. Irregularities occur later, some cells dividing 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.

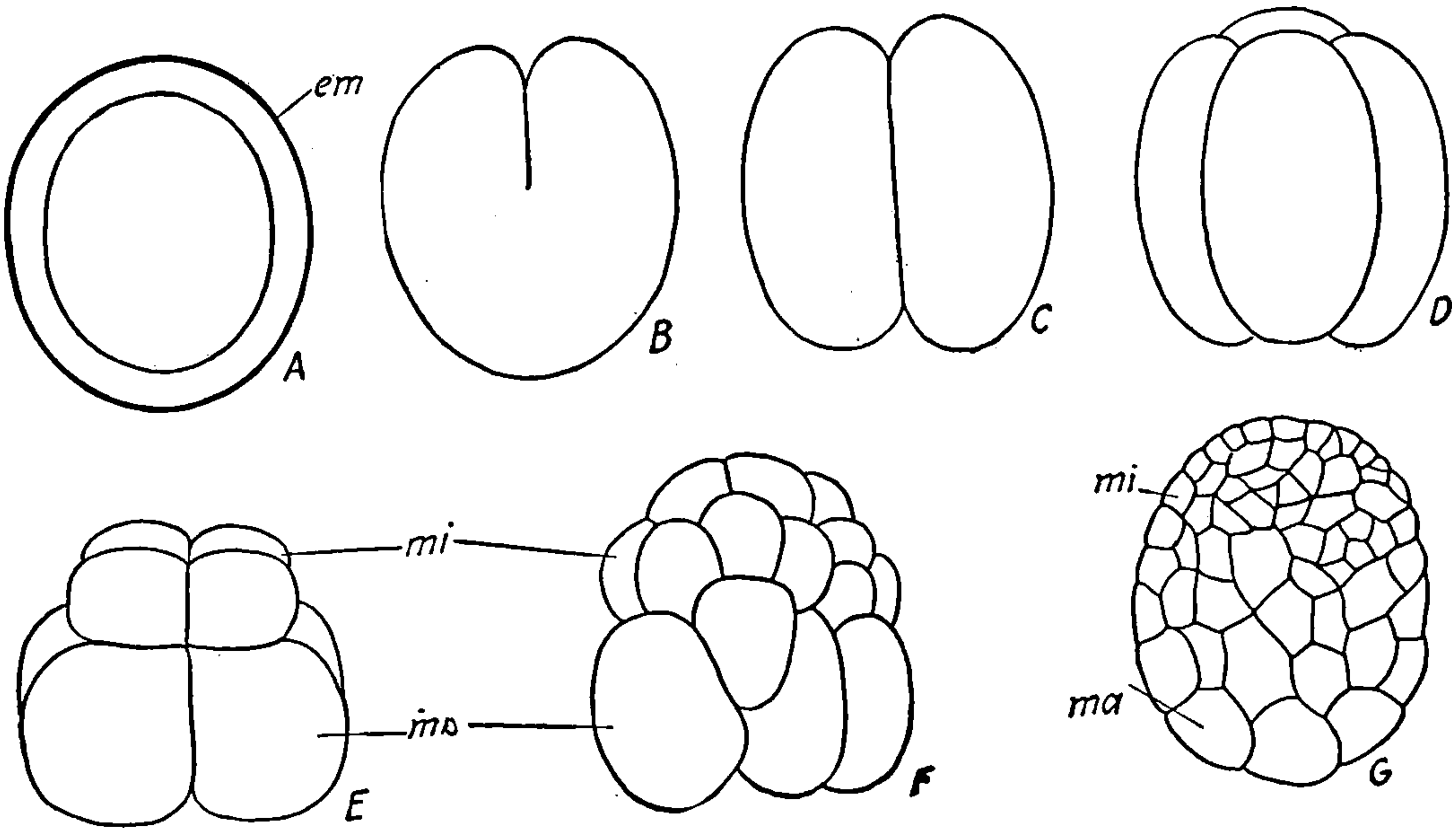

FIG. 170.—Cleavage in the telolecithal egg of the lamprey. The third cleavage (*E*) is distinctly above the equator, and the later cells (*F*, *G*) are very unequal in size. *em*, egg membrane; *ma*, macromeres; *mi*, micromeres (*Modified from original drawings by P. O. Okkelberg.*)

At the point to which the process of cleavage has been followed in the preceding paragraphs, the egg, now more correctly called an embryo, is a hollow ball of cells. Often the cells are arranged in a single layer at the surface, sometimes in a few layers, and there is a cavity in the center filled with liquid. The whole embryo is now designated a *blastula*, the cavity within it the *blastocœle*. The blastocœle appears at a very early stage. Even in the four-cell stage, the inner corners of the cells are rounded off, as in Fig. 169, leaving a space. This space is continually present through later cleavages, and becomes larger as segmentation proceeds. The term blastocœle may properly be applied to it in any of these stages.

Cleavage in Telolecithal Eggs.—The extent to which, in the presence of much yolk, cleavage departs from the regular method described for homolecithal eggs, appears to depend on how much yolk is present, and how sharply it is separated from the protoplasm of the egg. In the lamprey, which may be described as "mildly" telolecithal, the egg is divided much as in Synapta, except that the third cleavage plane is far from equatorial (see Fig. 170). The upper quartet of cells in the eight-cell stage is much smaller than the lower. Also, in the lamprey, the irregularities of division occur much earlier and are much more obvious. A blastula is formed, but the blastocœle is eccentric in position (see Fig. 171). The wall of cells is much thicker and is composed of much larger cells at the vegetative pole than at the animal pole. Cleavage in the frog's egg is very similar to that of the lamprey.

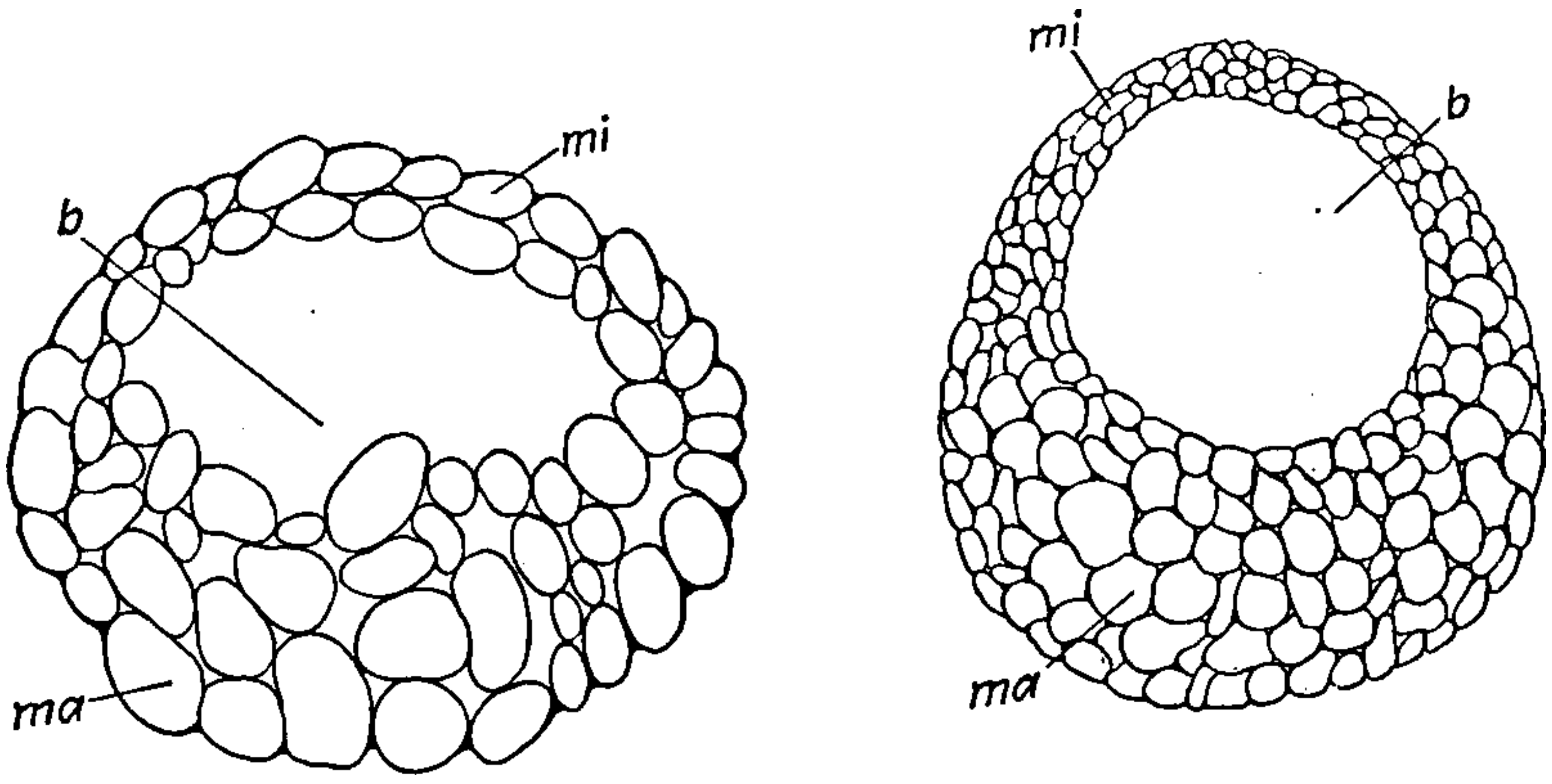

Fig. 171.—Blastula of the lamprey, two stages, in section. The cells are very unequal in size, and the blastocœle is eccentric in position. *b*, blastocœle; *ma*, macromeres; *mi*, micromeres.

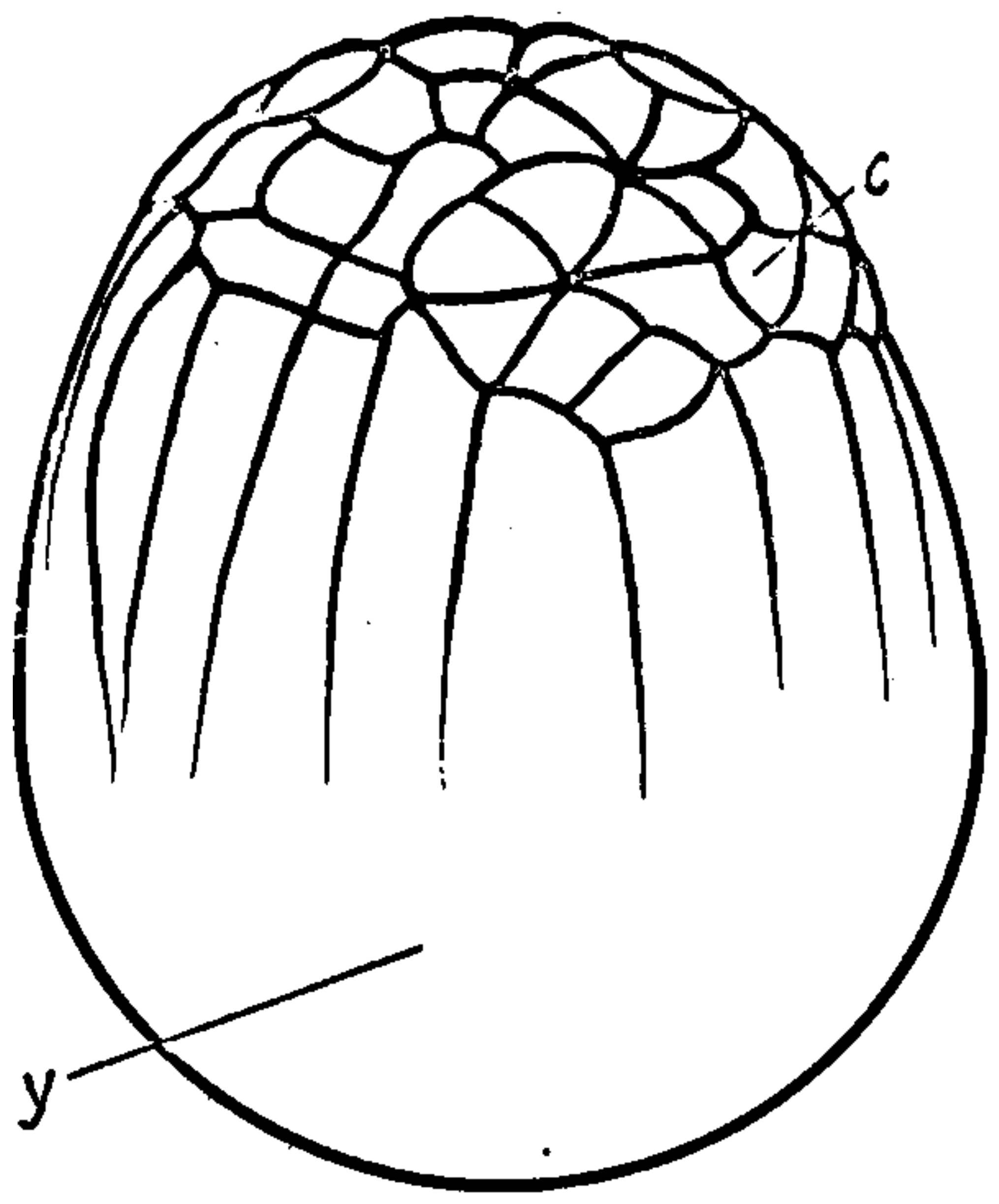

Fig. 172.—Cleavage of the telolecithal egg of the gar-pike, *Lepidosteus osseus*, about 5 hrs. after fertilization. The yolk-laden vegetative half of the egg remains undivided. (*After Eycleshymer, courtesy of Gustav Fischer.*)

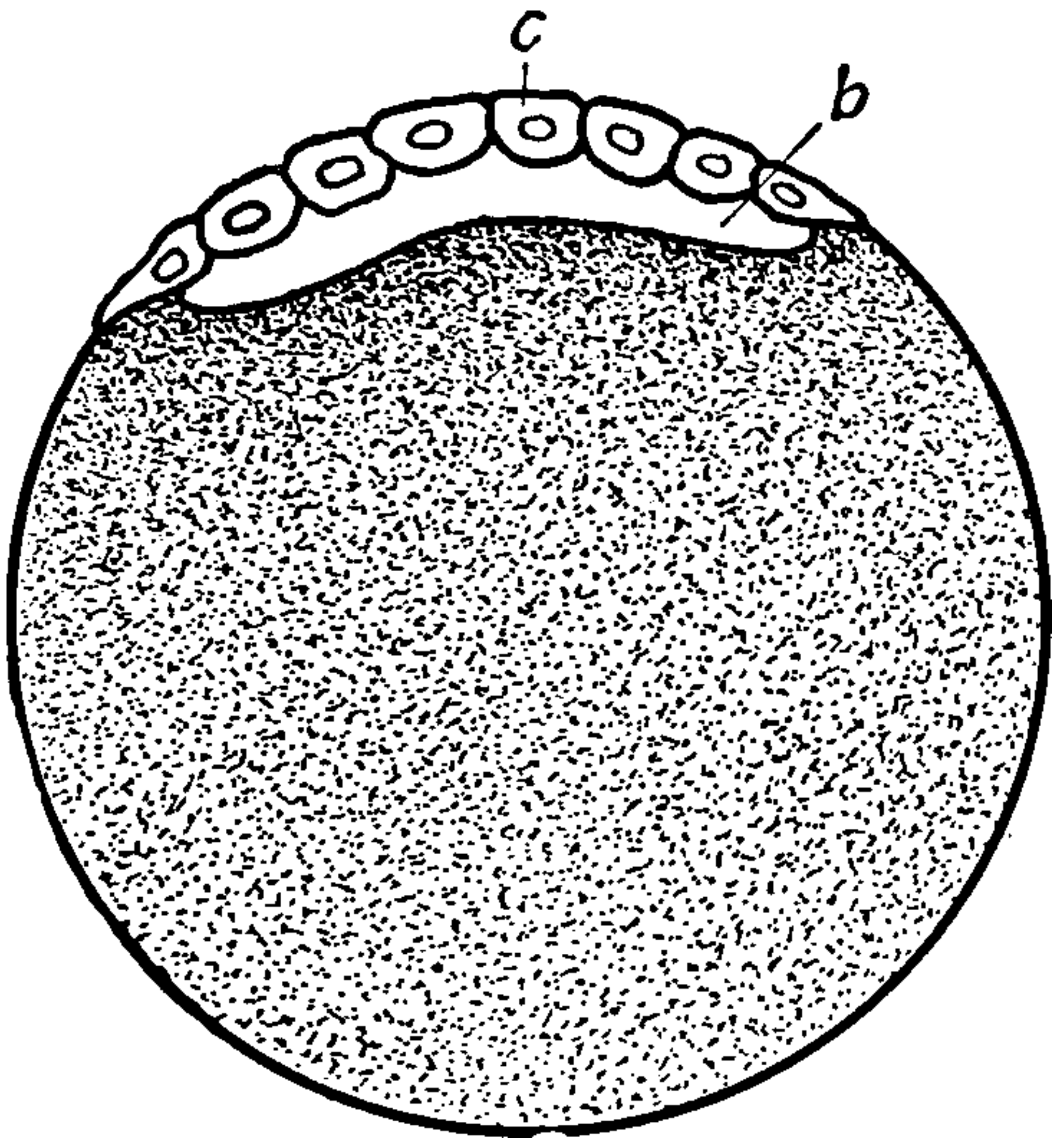

Fig. 173.—Blastula of telolecithal egg, diagrammatically represented in vertical section. *b*, blastocœle; *c*, cleavage cells.

In the eggs of fishes the yolk and protoplasm are almost completely separated; the protoplasm is a convex disc resting on top of the yolk mass. In such eggs the cleavage is limited to the protoplasmic portion, as shown in Fig. 172. The yolk is never divided at any stage. Cleavage does not follow such a regular scheme as in homolecithal eggs. A blastula is formed, but the blastocœle is only a narrow space between the disc of cells above and the undivided yolk below (Fig. 173). Scattered cells may, however, rest upon the yolk at the bottom of this cavity.

Like the cleavage of the fish egg is that of the birds and reptiles, whose eggs are also strongly telolecithal.

Cleavage in Centrolecithal Eggs.—Cleavage in the eggs of insects and others of the same type is at first limited to division of the nucleus. The nucleus, ordinarily situated in a small mass of cytoplasm in the middle of the egg, divides repeatedly while the cytoplasm is everywhere unsegmented. The daughter nuclei migrate toward the periphery of the egg, accompanied by small portions of the central mass of cytoplasm, and arrange themselves in a layer at the surface. Then division of the cytoplasm takes place between the nuclei (see Fig. 162). For a long time, however, the cytoplasmic divisions do not pass entirely around their respective nuclei, so that the inner ends of the "cells" at the periphery are continuous with the mass of the egg.

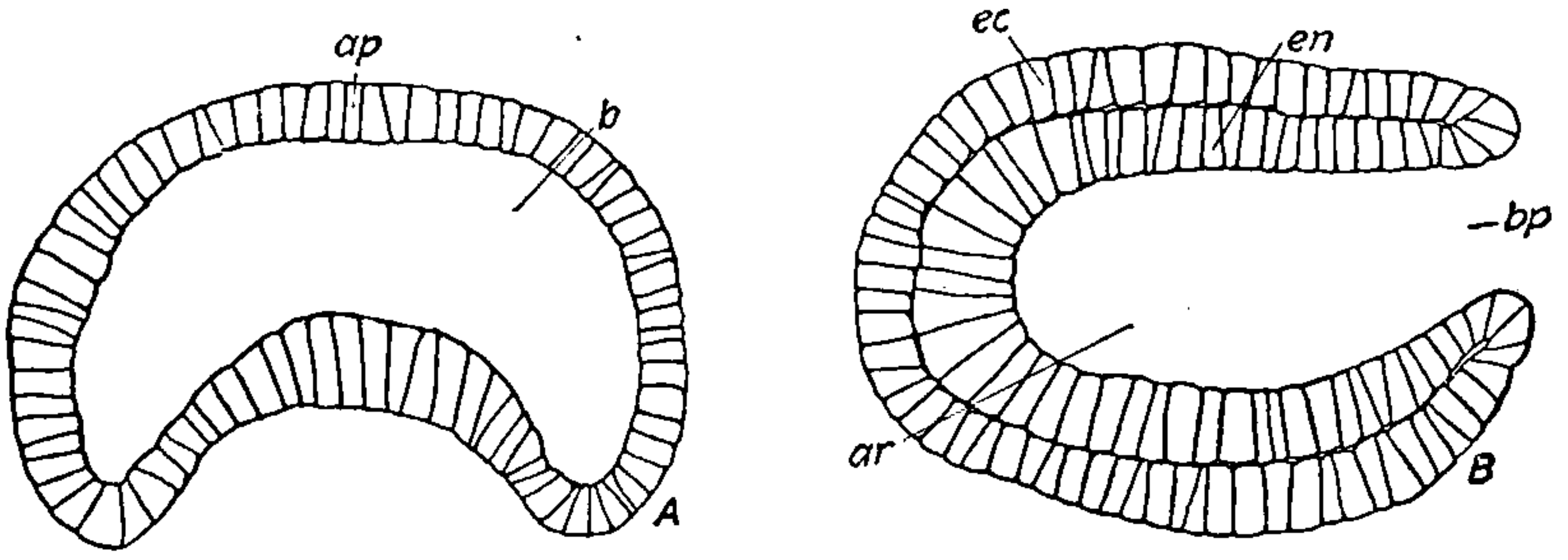

FIG. 174.—Gastrulation in Amphioxus, early (*A*) and late (*B*) stages. *ap*, animal pole; *ar*, archenteron; *b*, blastocœle; *bp*, blastopore; *ec*, ectoderm; *en*, endoderm.

Gastrulation.—When the blastula is well formed the wall of cells on one side of it begins to be turned in, gradually obliterating the blastocœle. This inturning, or invagination, of the wall of the blastula is styled *gastrulation*, and the end product a *gastrula*. The process differs in blastulas of different forms.

Gastrulation in Homolecithal Embryos.—The simplest form of invagination takes place in those animals whose eggs have a small amount of yolk evenly distributed. The fish-like Amphioxus and the holothurian Synapta are classical examples (Figs. 174 and 175). The vegetative pole of the blastula becomes flattened, and then turned inward, much as a hollow rubber ball might be indented on one side by pressure. The invagination proceeds until the inturned cells are in contact with those of the opposite side. The blastocœle is thus completely obliterated. The two-layered embryo thus formed is called a *gastrula*. The outer layer

The method of formation of the mesoderm differs in different animals. In Amphioxus the upper lateral portions of the endoderm (Fig. 177) are turned outward in the form of grooves, shown in cross-section in the figure. The edges of each groove meet and fuse, and the groove now in the form of a tube is completely separated from the endoderm. The two tubes thus formed are the mesoderm, and the slender openings in them constitute the body cavity, or *cœlom*. In later stages of development the tubes

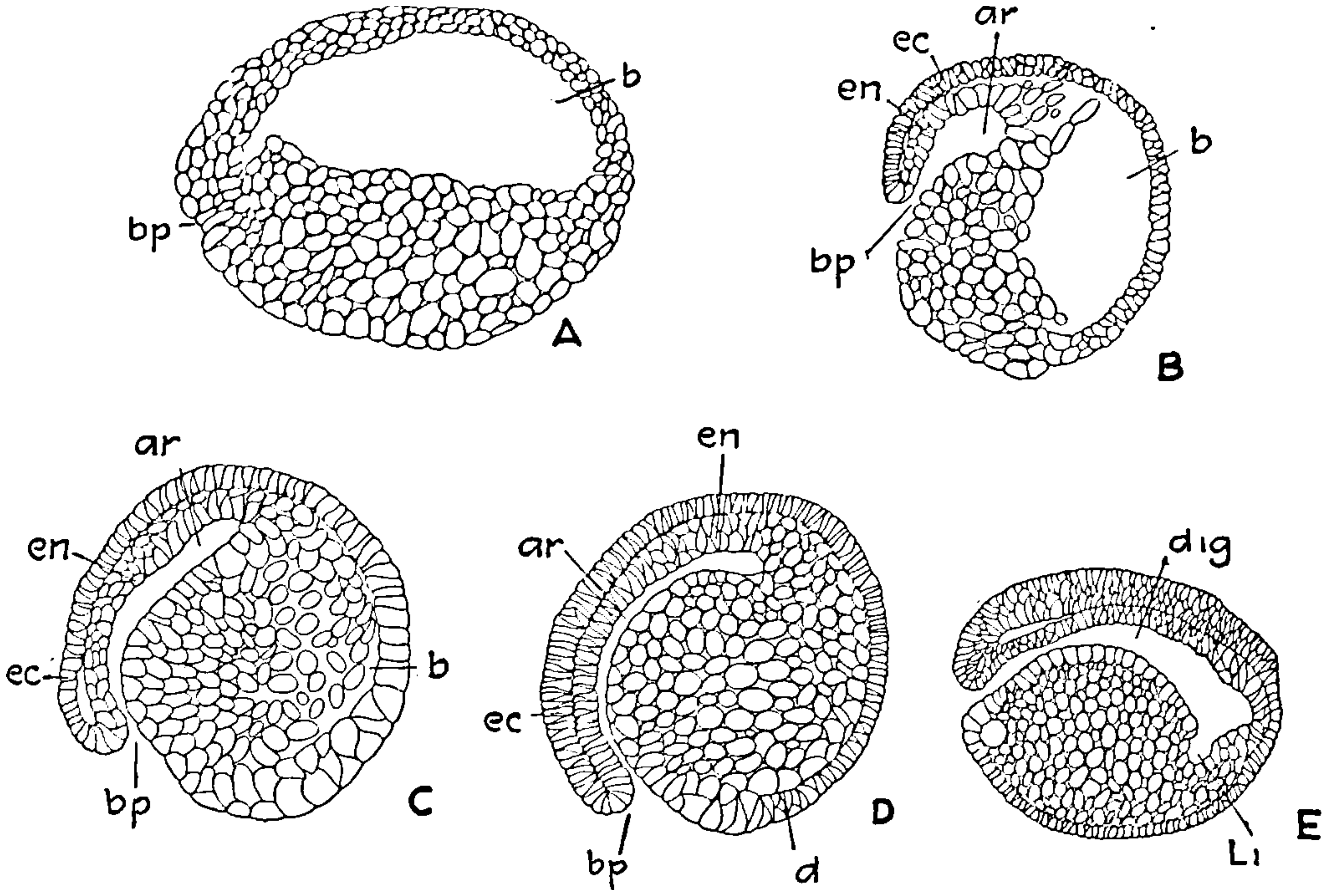

FIG. 176.—Gastrulation in the telolecithal embryo of the lamprey. *A, B, C, D, E,* successive stages; *ar,* archenteron; *b,* blastocœle; *bp,* blastopore; *d,* line of delamination; *dig,* digestive tract; *ec,* ectoderm; *en,* endoderm; *Li,* liver. (*After Glaesner, courtesy of Gustav Fisher.*)

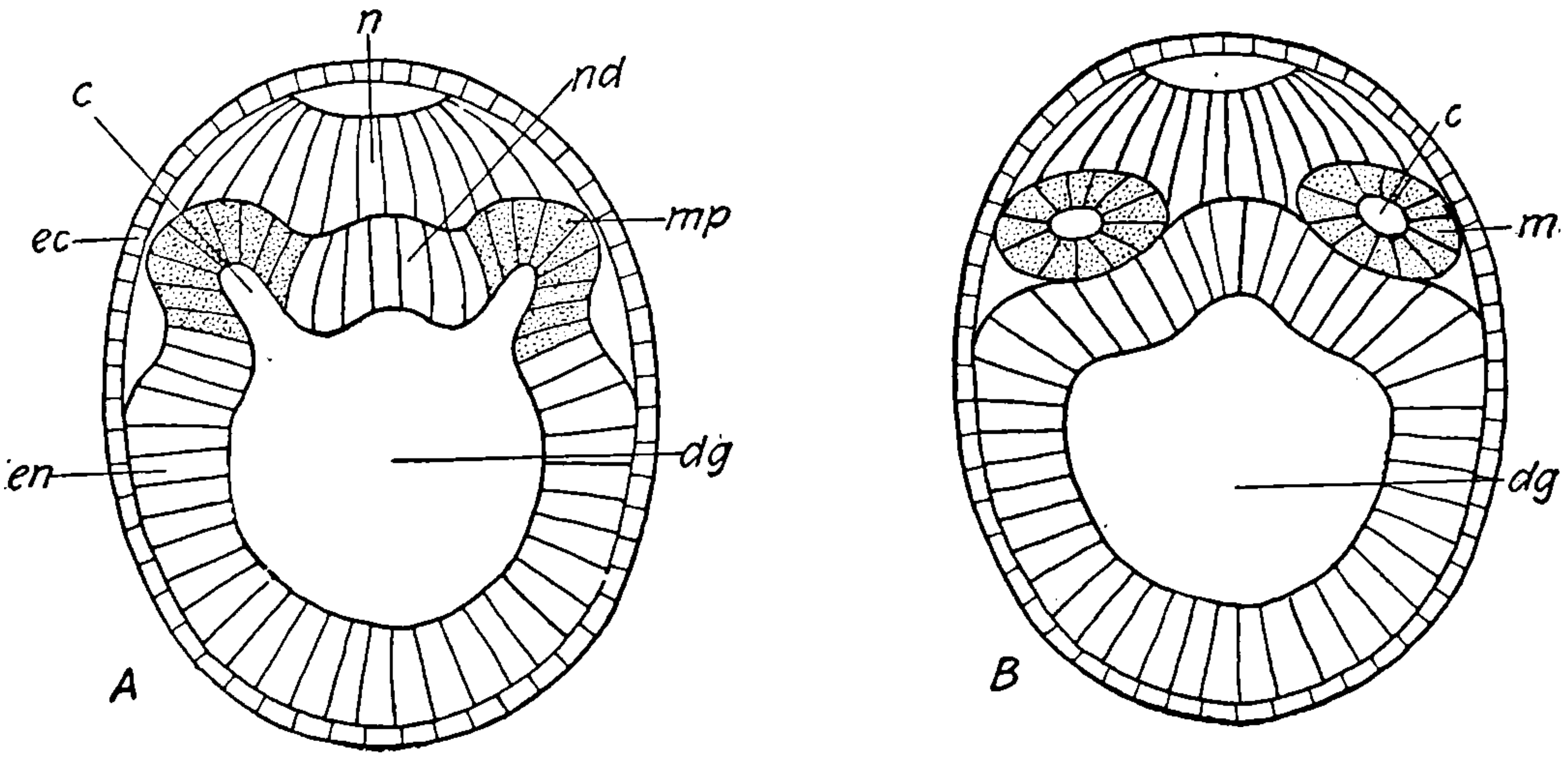

FIG. 177.—Mesoderm formation in Amphioxus. *A,* evagination of the upper lateral portions of the endoderm; *B,* separation of the mesodermal pouches from the endoderm; *c,* cœlom; *dg,* digestive tract; *ec,* ectoderm; *en,* endoderm; *m,* mesoderm; *mp,* mesodermal pouch; *n,* neural tube; *nd,* notochord. (*After Hatschek.*)

expand, as in Fig. 178. One side becomes a thin layer of cells applied to the digestive tract, while the other side lines the inside of the ectoderm.

In telolecithal embryos like that of the frog and the lamprey, the endoderm is so thick that folded grooves like those of Amphioxus could hardly be formed. In such cases the mesoderm may be simply split off from the outside of the endoderm. In Fig. 179, which represents a cross-section of the gastrula of the lamprey, the slit (*d*) above the archenteron represents the beginning of this delamination.

In the higher vertebrates the formation of mesoderm is often a very complicated or obscure process.

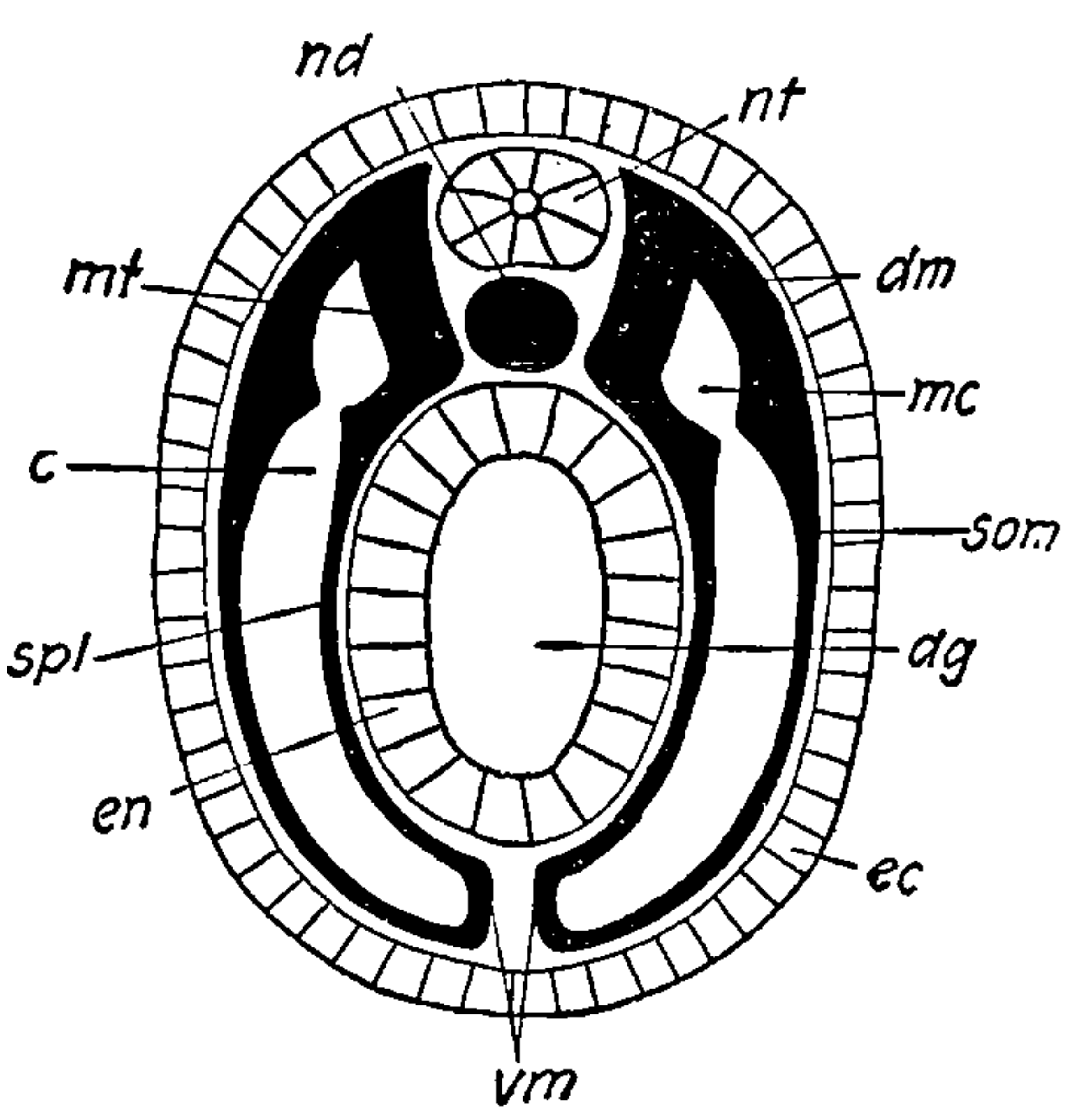

FIG. 178.—Cross section of embryo of Amphioxus, showing expansion of the mesoderm between ectoderm and digestive tract. *c*, cœlom; *dg*, digestive tract; *dm*, dermatome; *ec*, ectoderm; *en*, endoderm; *mc*, myocœle; *mt*, myotome; *nd*, notochord; *nt*, spinal cord; *som*, somatic layer of mesoderm; *spl*, splanchnic layer of mesoderm covering the digestive tract; *vm*, ventral mesentery.

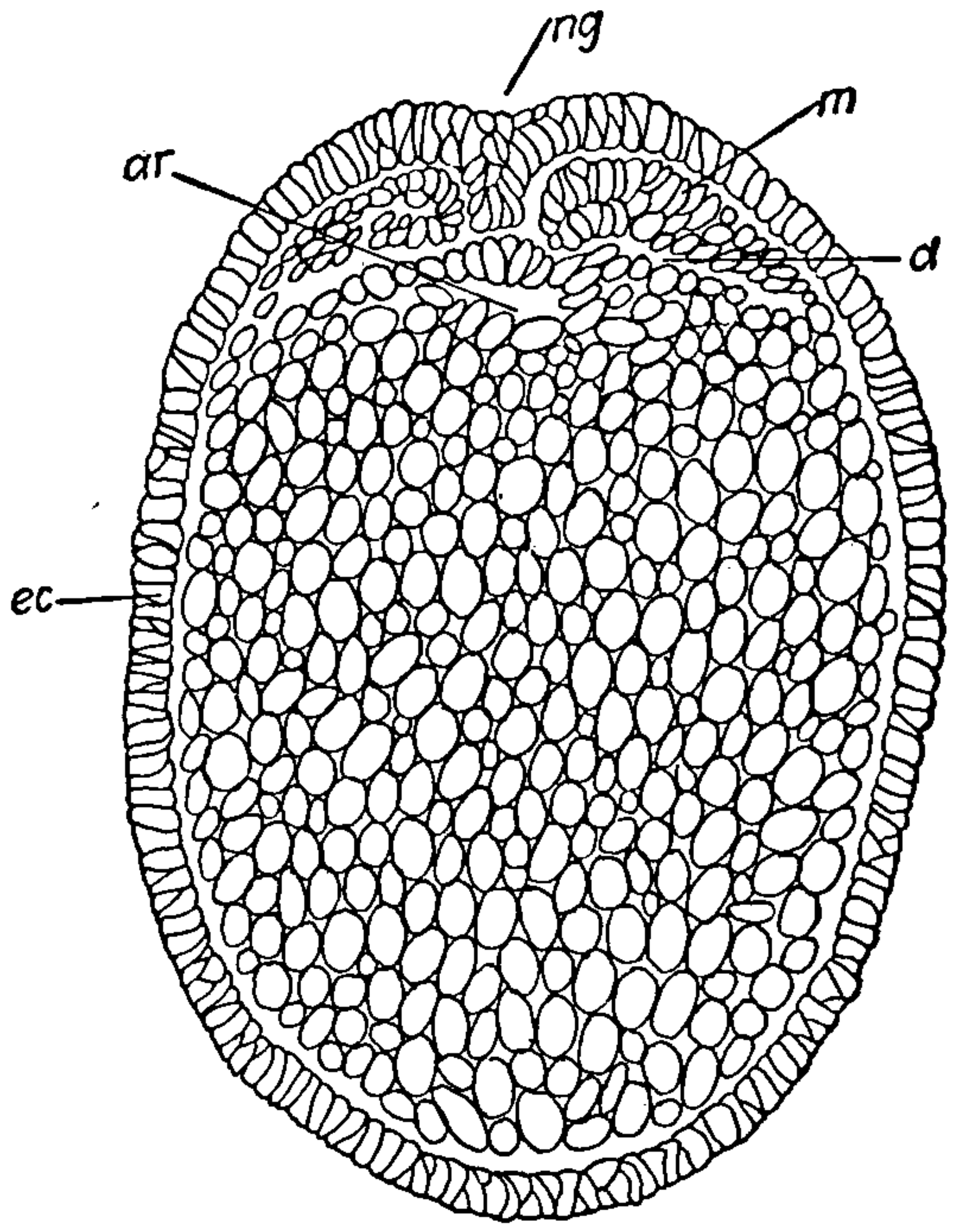

FIG. 179.—Mesoderm formation by delamination in the lamprey. The mesoderm is simply split off the endoderm. *ar*, archenteron; *d*, line of delamination; *ec*, ectoderm; *m*, mesoderm; *ng*, neural groove. (*After Goette, courtesy of Leopold Voss.*)

ORGANOGENY IN THE VERTEBRATES

The three layers of cells, ectoderm, endoderm, and mesoderm, are often called the *germ layers*. They are so designated because certain organs are derived from each one, so that the layers may be thought of as containing the germs of those organs. Thus, from the ectoderm come the nervous system, important parts of the sense organs, the outer layer of the skin, and some others; from the endoderm the lining of most of the digestive tract, and of such out-growths of the digestive tube as the liver, pancreas, and lungs; and from the mesoderm the muscles, bones, blood system, kidneys, etc. If all the facts were known it might be possible to point out the specific cells, even in stages prior to gastrulation, which will become certain organs of the embryo, just as in some animals the germ cells can be early distinguished. If that were possible, the earliest recognizable cells whose ultimate fate were known would be regarded as the germs of those organs. In the absence of such knowledge, the three layers ectoderm, endoderm, and mesoderm exhibit the first general division of the embryo into parts whose destiny can be predicted —hence the name germ layers.

The development of the organs from these layers is termed *organogeny.* In very large measure the production of organs consists of the rolling, or folding, or protrusion of portions of various layers of cells. When a layer of cells is bent inward, into a cavity enclosed by that layer, the bending is termed *invagination.* If the layer of cells is bent or folded outward, the protrusion is called *evagination.* Invagination and evagination may occur in long and narrow areas, resulting in the formation of furrows or ridges. Or the bending may occur in a very limited region, producing pits or knobs.

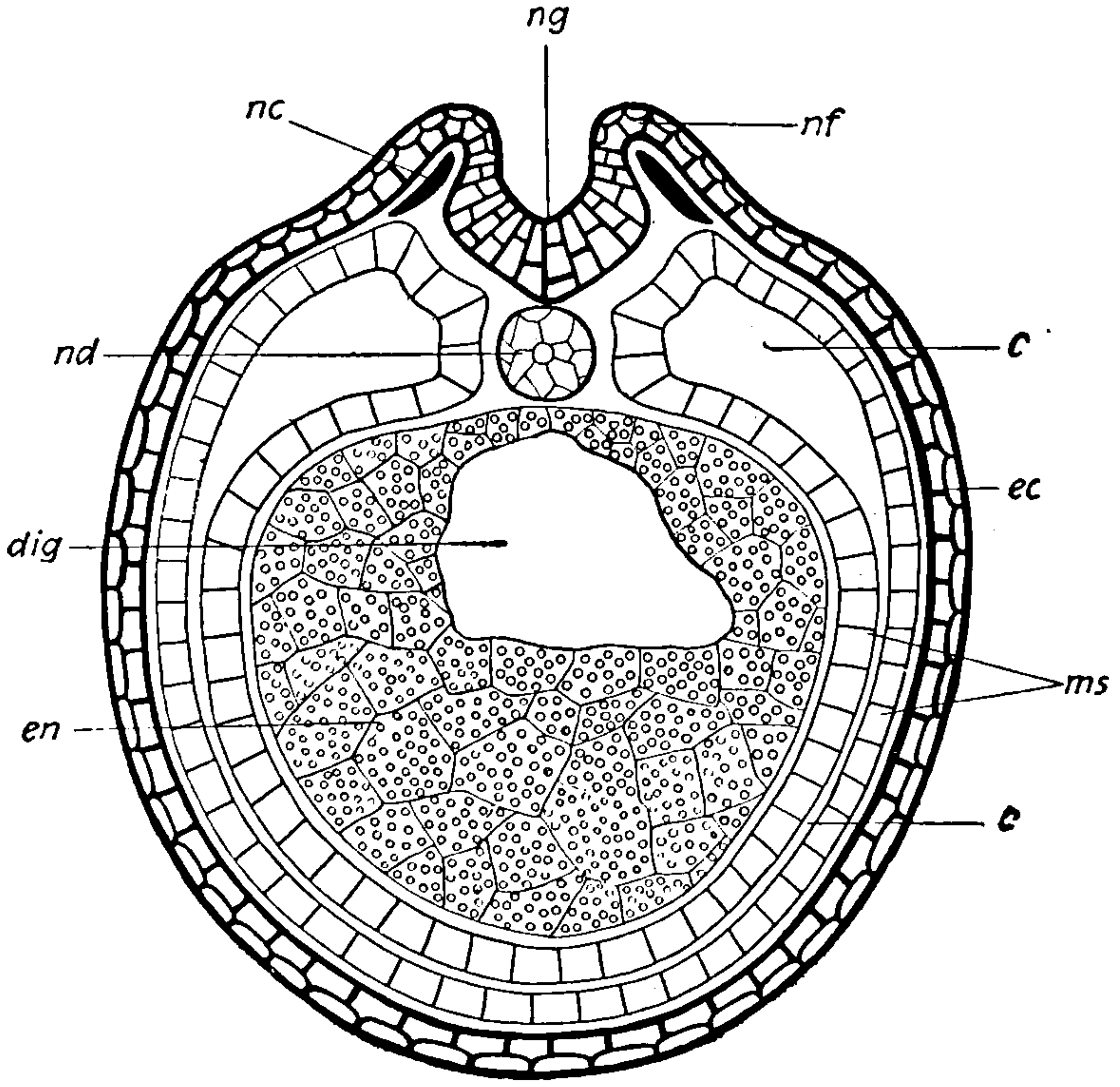

FIG. 180.—Cross-section of the early embryo of a frog, diagrammatic. *c*, cœlom; *dig*, digestive tract; *ec*, ectoderm; *en*, endoderm; *ms*, mesoderm; *nc*, neural crest; *nd*, notochord; *nf*, neural fold; *ng*, neural groove.

Owing to the great diversity of organs found in various groups of animals, and to the fact that many of these organs have no counterpart in other groups, it seems wise to confine the account of the early development of organs to those of the vertebrates. Even within this one group a complete list of organs cannot be mentioned. Some of the more important ones will be described, to illustrate the kind of processes involved in organ formation.

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. 163) which later suspends the digestive tract in a sack of peritoneum. In the longitudinal section, Fig. 181, 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.

Digestive Tract and Its Derivatives.—From the invaginated vegetative side of the embryo, which forms the endoderm, is formed most of the lining of the digestive tract, and the lining of organs which branch off from the digestive tract, such as the gill pouches, the liver, lungs, pancreas, and some others.

Gill Pouches.—The *gill pouches,* represented as seen from above in Fig. 182, are evaginations from 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 Fig. 182, *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 are developed upon the tissue (*gill bars*) between the gill clefts. The gills are organs for the absorption of oxygen. In the production of certain types of gill the endoderm of the gill pouches has a share.

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 nonfunctional organs. Thus, the first pouch becomes, as is pointed out below, part of the Eustachian tube and middle ear. Others share in the production of the tonsils, the thymus, and the parathyroid glands.

Mouth.—The *mouth* starts as an invagination of the ectoderm from the outside, as in Fig. 183, *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 (Fig. 184), 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.

Liver.—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. 181, *li*). An early indication of the liver is also shown in Fig. 183, *li*. This pouch grows in extent and soon becomes branched, as in Fig. 184, *li*. 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, of course, 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.

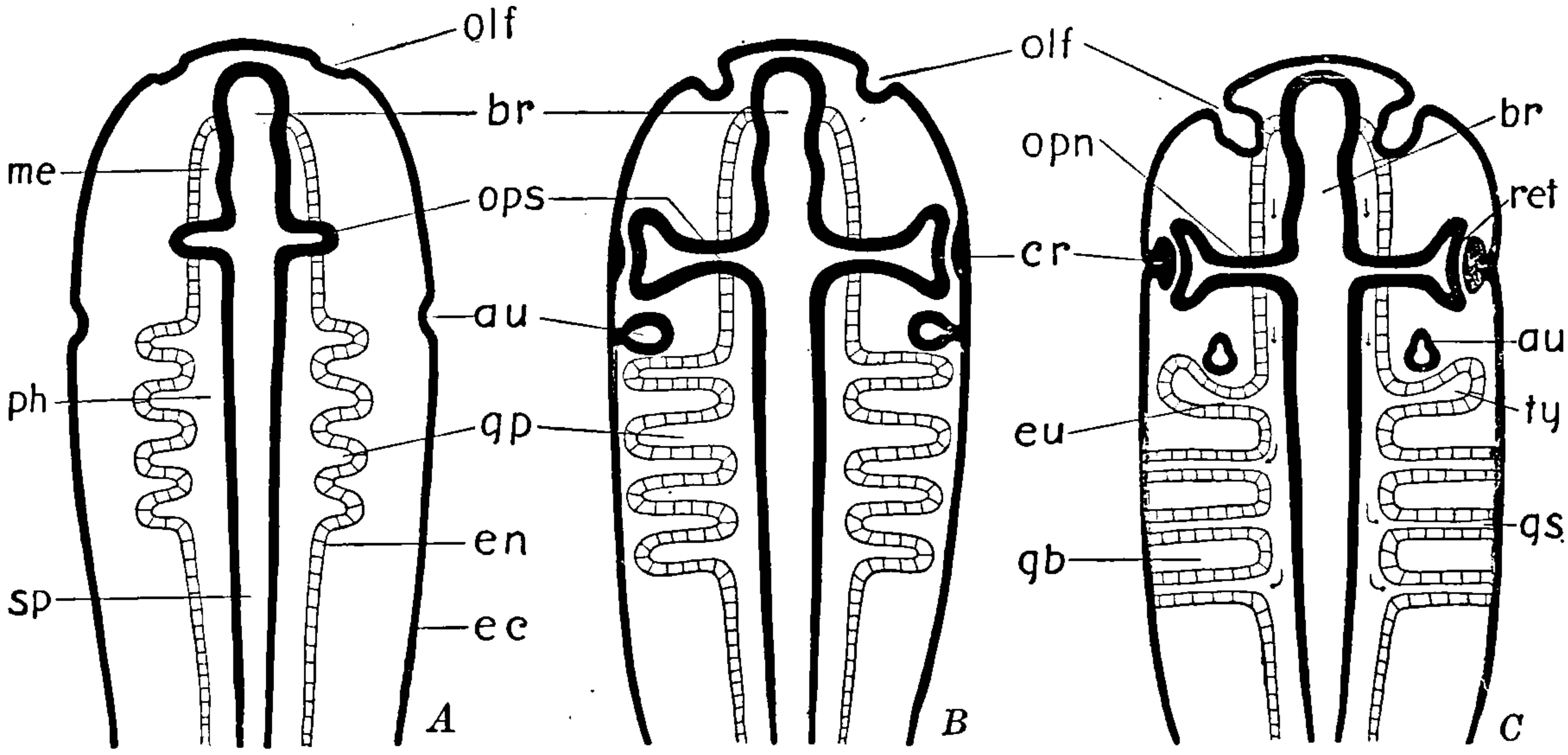

FIG. 182.—Diagrams showing the early development of some of the organs of vertebrate animals, as seen in section from above. The stages here shown are not contemporaneous in all cases. *A*, *B*, *C*, successive stages; *au*, auditory vesicle; *br*, brain; *cr*, crystalline lens; *ec*, ectoderm; *en*, endoderm; *eu*, Eustachian tube; *gb*, gill bar; *gp*, gill pouch; *gs*, gill slit; *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.

Pancreas.—The *pancreas* originates from two pouches evaginated from the intestine, as in Fig. 184. One arises from the dorsal side of the intestine nearly opposite the liver (*dp*); the other springs from the angle between the liver and the intestine (*vp*). The latter pouch turns dorsalward, to one side of the intestine, where it unites with the dorsal rudiment. Their further development which in many respects is similar to that of the liver need not be traced.

Lungs.—The *lungs* take their origin from a protrusion from the ventral side of the gut some distance in front of the stomach, as in Fig. 184, *lg*. This pouch is at first single, as shown in Fig. 185, *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 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.

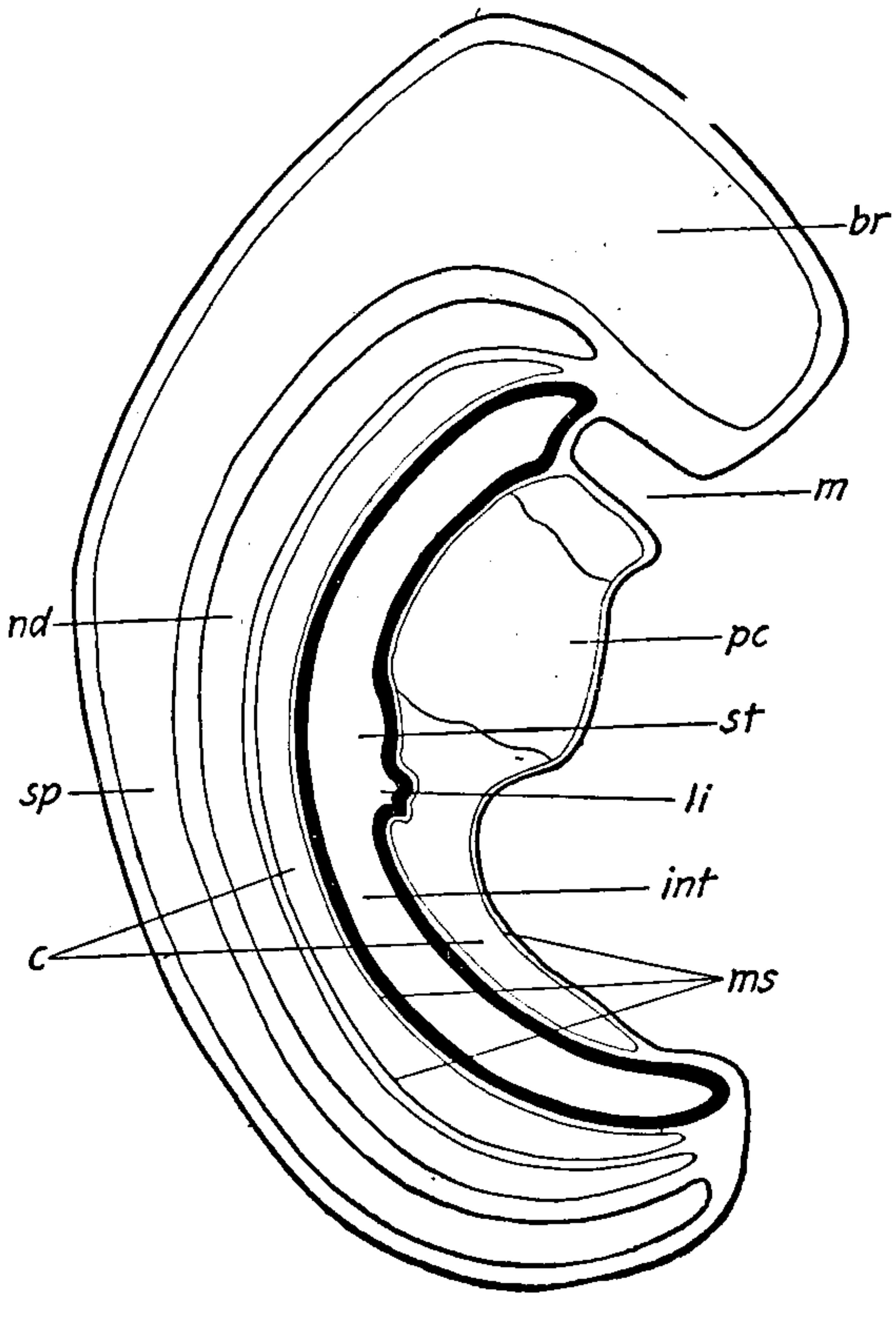

FIG. 183.

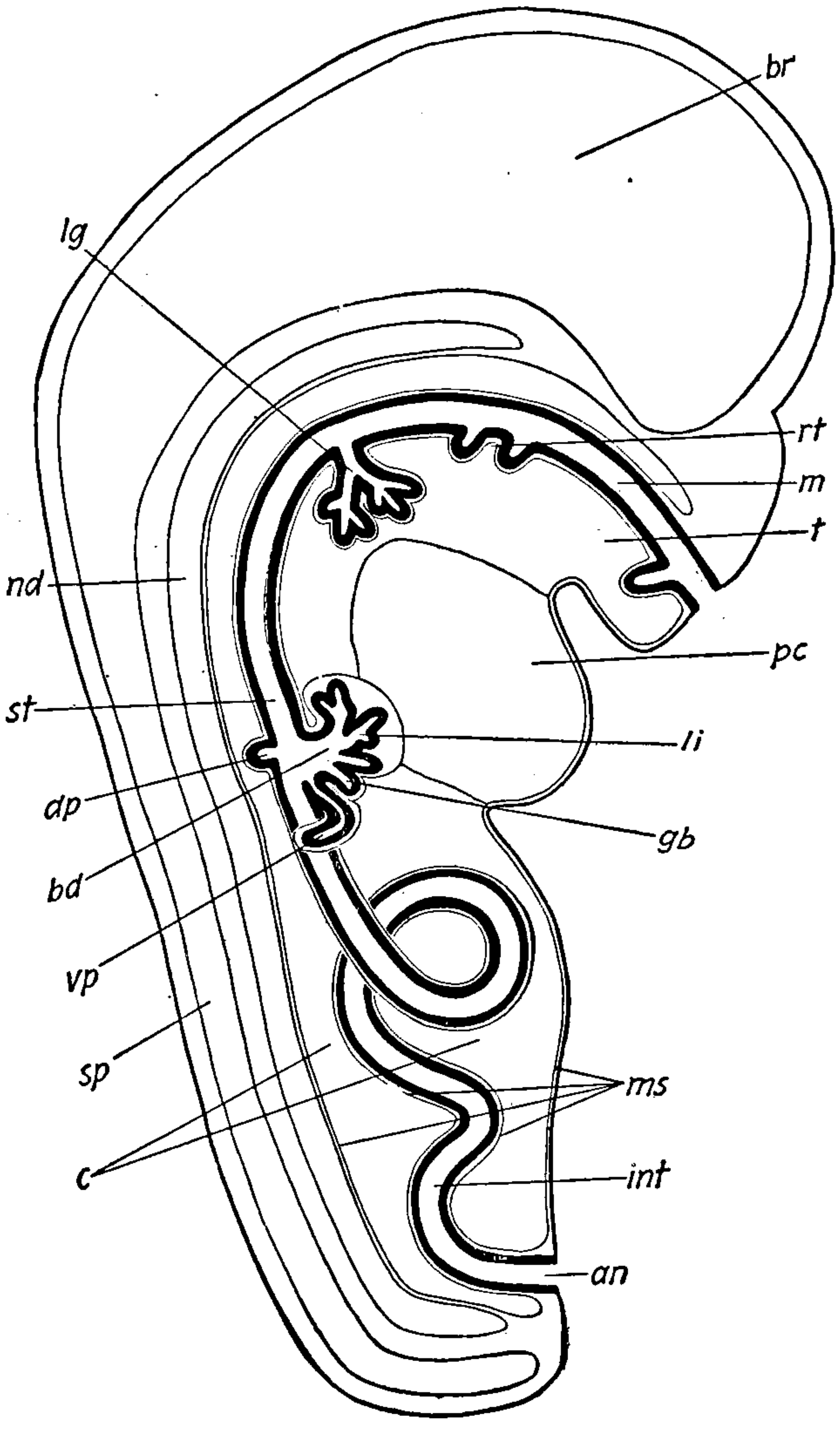

FIG. 184.

FIG. 183.—Diagram illustrating the development of some of the organs of a vertebrate animal as viewed from the side. The section is taken a trifle to one side of the median plane. The stages shown are not all contemporaneous. *br*, brain; *c*, cœlom; *int*, intestine; *li*, liver; *m*, mouth; *ms*, mesoderm; *nd*, notochord; *pc*, pericardial chamber; *sp*, spinal cord; *st*, stomach.

FIG. 184.—Diagram representing the development of some of the organs of vertebrate animals, at a later stage than in Fig. 183. The figure is a trifle to one side of the median plane. The stages shown are not necessarily contemporaneous. *an*, anus; *bd*, bile duct; *br*, brain; *c*, cœlom; *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.

Minor Features of Digestive Tract.—The *tongue* begins in a group of elevations from the floor and sides of the mouth. Two of these elevations are represented in Fig. 184.

The *anus* develops, in a few animals, directly from the blastopore, and in them is never closed. In other animals, in which the blastopore

This 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 neural crest toward the periphery of the body forming the sensory part of the spinal nerve. The ventral motor root of the nerve grows out from the ventral part of the spinal cord, and joins 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.

The development of some of the cranial nerves (those extending from the brain) is in many respects similar to that of the spinal nerves.

The Eye.—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 system, or by a combination of these two modes of origin. The *eye* begins as an evagination from the side of the brain (Fig. 182, *A*). This protrusion elongates, and at the same time expands at its outer end into a hollow bulb. The bulb-like expansion flattens on its outer side, and is then invaginated to form a double walled cup resembling a gastrula (Fig. 182, *B* and *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 in contact with the ectoderm, the latter thickens and later invaginates, finally pinching off a rounded mass of cells (*B* and *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.—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. 182, *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 semi-circular canals and the (sometimes) coiled body of the inner division of the ear. Only certain groups of cells in this vesicle acquire sensory functions; these groups are joined to the brain by processes of nerve cells growing out from the ganglion of the eighth (auditory) nerve which, as in the spinal nerves, is derived from one of the neural crests.

The middle ear, which contains the bones of the ear, is derived at least in part from the first gill pouch (Fig. 182, *A*, *B*, *C*). In some vertebrates this pouch never perforates to the exterior, in others it opens for a time and then closes again. Its distal end comes to lie beside the vesicle which is derived from the ectoderm, and in this portion the ear bones are much later developed out of mesoderm. The connection of this first pouch with the digestive system either remains open or after closing re-opens again, in either case forming the *Eustachian tube* which connects the middle ear with the pharynx.

The outer ear develops first as an invagination from the outside. The pit or canal thus formed approaches the middle ear, but always remains separated from it by a membrane, the *ear drum.* The shell-like external ears of animals that possess them are erected out of mesoderm with, of course, an ectodermal covering in the epidermis of the skin. The outer ear is not shown in the illustrations (Fig. 182).

Olfactory Organ.—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. 182, *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. The nasal chamber in many vertebrates becomes curiously altered in form, and receives the ducts of various glands.

The development of the few organs described in the foregoing pages will suffice to illustrate the kinds of processes involved in organogeny, especially in structures arising from the outer and inner germ layers. Organs and tissues derived from the mesoderm, such as muscles, bones, heart, blood vessels, kidneys and their ducts, are as a rule much less sharply defined in their early stages than are those of the ectoderm and endoderm. A description of their early development is therefore omitted.

Metamorphosis.—Besides the usual course of development, which is in large measure the same for different members of the same group of animals, as described above for a few organs of the vertebrates, some members of a group may undergo an unusual series of changes. *Metamorphosis* is one such series of developmental processes. Animals that metamorphose are born or hatched with one, or several, or many organs which they will not possess as adults, and they may retain these organs for a considerable period after birth or hatching. Or the young animal may lack organs that will be developed before it becomes adult. The process of losing the larval organs and of gaining the missing adult organs is called metamorphosis.

Metamorphosis in Invertebrates.—Metamorphosis is common among insects, in many groups of which the young stages are wholly unlike the adult. In butterflies, beetles, bees and flies, the egg hatches into a caterpillar or grub or maggot, from which a person ignorant of the life history could not possibly predict the adult (see Fig. 186). After growth, these larvæ become quiescent *pupæ*, enclosing themselves in a chitinous case and taking no food. They may undergo squirming movements, but are incapable of locomotion. However, in some of them remarkable changes are going on in the interior during this quiescent period. Many of the cells of the larva disappear entirely, being dissolved and devoured by certain wandering cells. Whole organs may appear thus to degenerate into a milky pulpy mass. But some cells always remain, and out of these the organs of the adult take their origin. Doubtless the material derived from the degeneration of the lost organs is used as nutrition for the development of the adult organs, but there is much uncertainty as to just what happens during that process. This destruction of the larval organs, and the formation of new organs out of their remains, constitutes for these insects the process of metamorphosis.

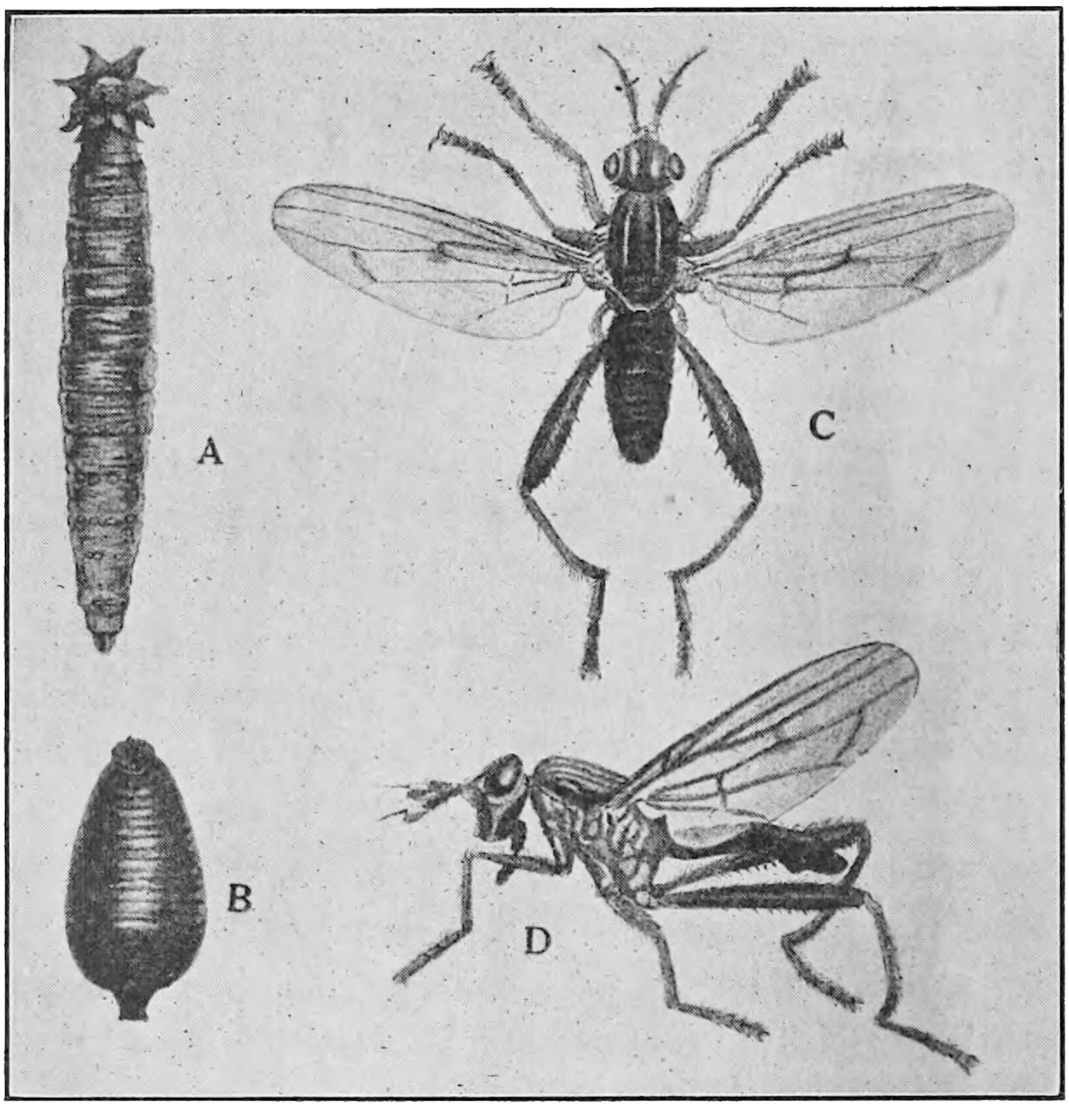

Fig. 186.—Metamorphosis of the swale-fly *Sepedon fuscipennis*. *A*, larva; *B*, pupa; *C*, adult from above; *D*, adult, side view. (*From Needham.*)

Metamorphosis in Vertebrates.—In some of the higher groups, metamorphosis, where it occurs at all, is shrouded in much less mystery. In the vertebrates, the transformation of a tadpole into a frog 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. Besides these changes

Origin of Homology.—Homology is no accident. The discussion in the chapters on taxonomy and evolution may be anticipated by the statement that homology results from the inheritance of a common ancestral condition. All animals now possessing homologous organs must have descended from a common ancestral form. The organs of the present-day descendants of that ancestor arise in the same way in the embryo, because in some fundamental respect the organs of the ancestor arose in that manner. If homology is not an inheritance from a common ancestor, it can hardly have any significance at all.

If this view is correct, the vertebrates are all related to one another through common ancestry. Birds, and reptiles, and mammals, and fishes, and frogs are all actually distant cousins of one another. As pointed out in Chapter XII, homology is for this reason the chief basis of classification of animals.

Biogenetic Law.—The evident dependence of homology upon a common descent led, a few decades back, 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, the embryonic stages of animals of today represent the condition of successive ancestors of these animals. That is, early embryonic 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 its individual development. In some cases, this simple procedure is almost feasible. A series of fossil cephalopods (allies of the cuttlefishes), described in Chapter XV, 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. 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.

In most animals, however, embryonic development has undergone a good many changes, so that steps in embryology 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 plainly correct is in the development of gill pouches in all of the vertebrates. Gills are never developed in the reptiles, birds, and mammals; but gill pouches are formed, 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 (frogs, toads, etc.). 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 with much certainty to the conclusion that the ancestor was a fish-like animal—fish-like at least to the extent of being aquatic and respiring by means of gills.

MECHANISM OF DEVELOPMENT

The practical identity of the steps of development in all members of the same species of animal creates the problem of the mechanism of this development. What insures that, at a given stage in cleavage, the vegetative half of an embryo shall be invaginated within the animal half? What causes the neural folds to arise always in the same way, and at the same relative time in development? Why does an eye always begin as an evagination at the side of the brain? Why does the vesicle of the inner ear originate behind the eye, instead of in front of it, or in some other location? What causes the protrusion of the endoderm just behind the early stomach, and the subsequent branching of this outgrowth to form a liver?

Explanations.—Most of these changes can be explained as due to inequalities of growth in cells and layers of cells. A layer of ectoderm must bend or fold if at some point one surface of it grows more rapidly than the other. Increase in the size of one cell displaces the cells adjoining it. Actual migration of cells may also be appealed to in the explanation of certain developmental changes.

These explanations are not, however, very far-reaching, for they omit the factors that cause the migration or inequalities in growth of cells. Physiological processes are at the basis of all embryonic development, but the nature of these processes is obscure. It has been suggested that cells react to stimuli, just as organisms react to stimuli. Many animals appear to act in purely mechanical ways in response to changes in their environment, and it is not unlikely that cells of embryos have a similar behavior. The stimuli to which they respond in their growth may be chemical substances diffusing from the cells around them. Or mere pressure of neighboring cells may act as a stimulus to specific kinds of development. It cannot be too strongly emphasized, however, that a statement of the cause of development must be largely conjectural.

Independence of the Germ Cells.—A knowledge of the embryonic development of animals leads to a conception of the relation of the germ cells to the somatic cells that is very useful in the study of genetics and evolution. Although an anatomical examination of the body of one of the metazoa would indicate merely that the *gonad* (ovary or testis) is an organ among a host of other organs, there are reasons for not regarding these organs as being of equal rank. Referring only to the germ cells themselves, and not to the surrounding connective tissue or epithelia whose cells can never have reproductive functions, the gonads must be thought of as occupying a position of superiority. The body is not merely a collection of organs, all of which have come from a common source, the fertilized egg. The fertilized egg is rather a detached representative of the groups of germ cells of the parents, from which a soma (body) has been produced. Viewed in this light, the germ cells are a reserve supply out of which in each generation a soma is erected.

Immortality of Germ Cells.—Germ cells possess a potential immortality. That is, each oögonium or spermatogonium has a chance of producing other germ cells through an indefinite number of cell divisions. There is no necessity of death for any particular germ cell, nor for any specific one of its descendants. It is true, germ cells do die in great numbers. Many eggs are never fertilized, and perish. Eggs and spermatozoa are more often than not liberated at times when they have no chance of surviving in new individuals. Gonads always contain some germ cells when the body in which they are located dies, or when the reproductive function of the individual ceases. These remaining cells of course perish. But in each of these cases there is nothing inherent in the germ cells as germ cells which determines that particular cells shall be lost. Each cell has the capacity for escaping from association with its fellows, a chance of uniting with another germ cell in fertilization, an opportunity of giving rise to a new individual in which descendants of the germ cell shall live on and have a chance of surviving. Although some germ cells are inevitably lost each individual cell has the possibility of avoiding that fate and of being permanent in the form of germ cells descendent from it. The germ cells are potentially immortal.

Contrasted with the possible permanence of germ cells is the necessary mortality of the somatic cells. No metazoan body is capable of endless existence. Body cells or their descendants may live on in uninterrupted series for hundreds of years in some animals, but they eventually die. No final physiological reason can be assigned for the necessity of death, but experience indicates that there is no escape from it. While the individual is said to have descendants, it is only through the germ cells that these are made possible. Strictly speaking, it is only the germ cells that have descendants, and the somatic cells of the next generation are some of those descendants.

Germ Cells a Reserve Supply.—The germ cells may in a sense be regarded as being the animal. They constitute a series that may be

cells may and do produce body cells, but except perhaps in very low metazoa it is improbable that body cells ever produce germ cells.[1]

This independence of the germ cells need not be insisted on in most ordinary relations of animals. Indeed, in a physiological sense it may tend to obscure certain fundamental facts, such as the dependence of the germ cells upon the body for nutrition. The body is the environment of the germ cells. But in some phases of genetics and evolution the distinctness of germ and body cells is a useful conception.

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[1] Much of the conception of the independence and distinctness of the germ cells and somatic cells is inapplicable to plants, in which germ cells are not formed until late in the life of the individual, and in which germ cells may, under suitable circumstances, originate from many parts of the body.

CHAPTER XI

GENETICS

In the preceding three chapters have been examined the various methods by which new individuals are brought into existence, the habits which insure reproduction and the early care of the young individuals, and the developmental processes which these young individuals undergo in becoming adult. The last of these topics (embryology) was discussed in a general way, with reference only to the major features of animals, those in which not only are all the members of one species alike, but in which members of one large group of animals often closely resemble the members of distantly related groups. However, development results in the production of many details in which individuals may differ, but which are just as definitely represented in the fertilized egg as are the nervous system, the digestive tract, or even the gastrula. The production of these minor features and the laws that govern their occurrence are the subject matter of the science of genetics.

Scope of Genetics.—The word genetics means literally the origins of things. Specifically, however, it is applied only to such origins as are implied in heredity, variation, determination of sex, and their applications. Genetics is sometimes defined very broadly to include the origins of the larger groups of animals from other groups; and in this sense it is nearly synonymous with evolution. But such definitions have met with opposition from those who study evolution by other than the experimental method, with the result that the narrower use of the term is most common. A more exact definition than the one implied in this paragraph is not necessary for an elementary discussion, and would, in fact, be difficult to formulate before the account of the facts and mechanism of heredity in the following pages.

The present day knowledge of heredity was gained through painstaking experiments upon hundreds of animals and plants, and from a study of the cytology of the germ cells and the processes of embryonic development. Out of the facts gleaned from these studies there has come a knowledge of the mechanism by means of which a trait belonging to the parents is so often reproduced in the offspring. A more perfect knowledge of this mechanism is the principal immediate goal of the majority of investigators of heredity, and it is being sought through the medium of experiment and microscopic examination of the structures involved. For the purpose of this chapter, however, the order of discussion may be reversed. The results of breeding experiments will be more readily understood if the mechanism of heredity, so far as it is now known, is described first.

The Genes or Factors.—Each inherited character of an animal or plant may be regarded as being produced by a definite something in the undivided germ. This "something" has been given various names, of which *gene* and *factor* are the most commonly used. A fertilized egg contains two genes for each inherited character of the adult that will develop from it; that is, two for color of hair, two for length of stem, two for shape of comb, and so on. These statements would need some qualification in an extended study of heredity, but for the present purpose

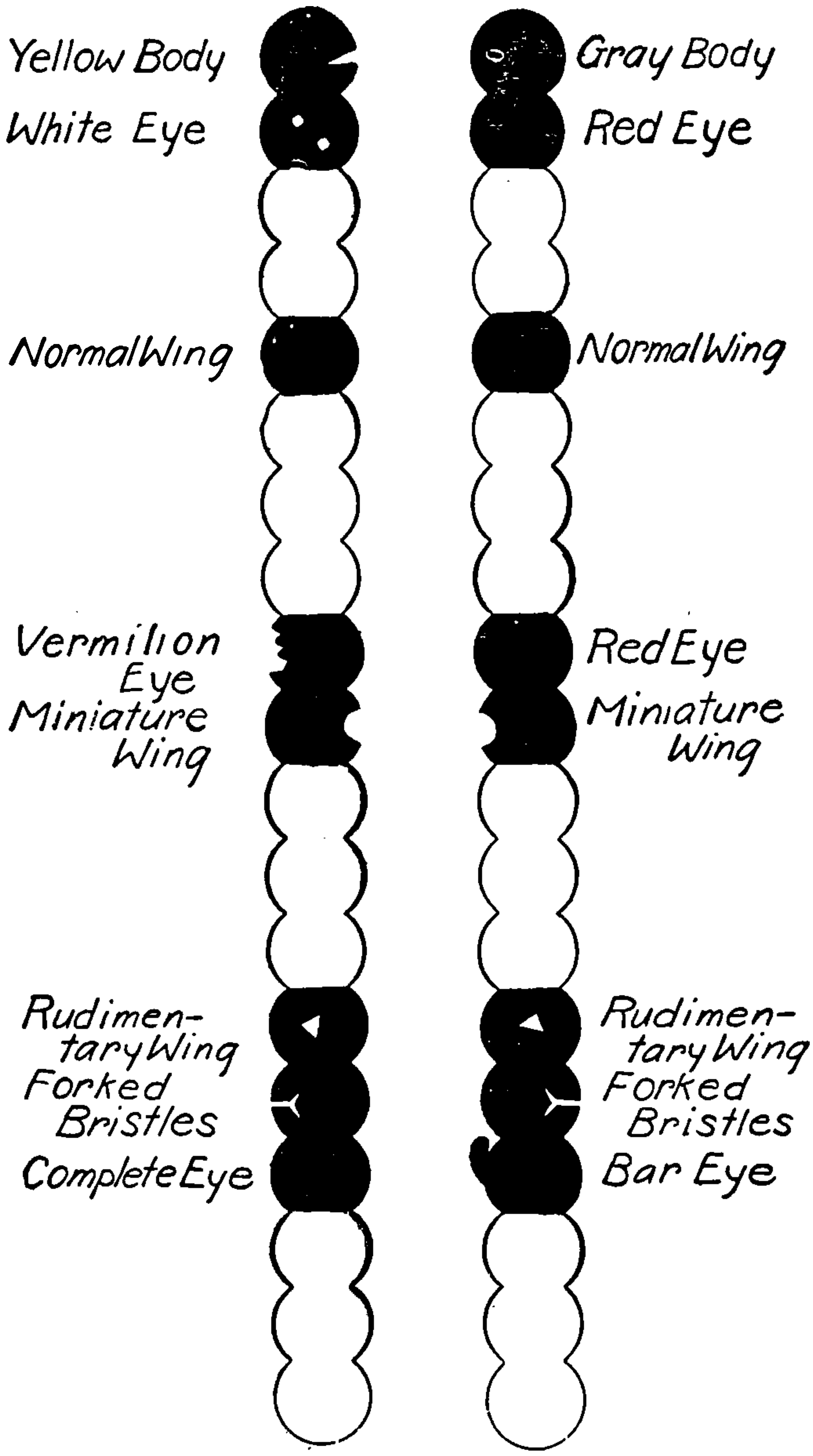

FIG. 189.—Diagrams of two homologous chromosomes of the fruitfly Drosophila. Some of the genes are represented, and are in their proper order through the length of the chromosome. Corresponding genes are located at the same level of the two chromosomes.

the two maturation divisions[1] (the first in some animals, the second in others), the chromosomes do not split as in ordinary mitosis, but the chromosomes that have come together merely separate again. Each daughter cell receives one of the chromosomes of each pair, not halves of both of them. The number of chromosomes in each daughter cell is thereby reduced to one-half. In the fruitfly Drosophila, whereas the somatic cells and the oögonia and spermatogonia have eight chromosomes, the mature germ cells have only four.

Moreover, as a result of this reduction division in maturation the germ cells may be different from one another. If the two chromosomes of a pair are precisely alike in all their genes, then all the mature germ cells will be precisely alike with respect to those genes. If, however, the chromosomes are unlike in some of their genes, the mature germ cells will be unlike. Thus, if an individual contained the two chromosomes represented in Fig. 189, the mature eggs produced by it would all be alike with respect to their genes for size and shape of wings and genes for shape of bristles, but would be of two different kinds with respect to their genes for body color, eye color, and extent of eye. The fact that the different mature germ cells of one and the same animal may carry different genes is of capital importance in heredity.

Terminology.—The distribution of different genes to different germ cells is called *segregation,* and it results from the phenomenon of *reduction* (the separation of homologous chromosomes without division) in one of the maturation divisions. The hereditary constitution of an animal (with certain exceptions) involves two genes for each kind of character; the hereditary constitution of a germ cell includes but one gene for each kind of character. The formula of an individual is thus a double one, that of the germ cells a single one. Thus, since genes are usually symbolized by letters, if the formula of an animal with respect to any character were *AA,* the formula of its germ cells would be *A.* If the formula of an animal were *Aa,* the genes for one kind of character being unlike, the germ cells would be of two kinds, some with the formula *A,* others with the formula *a.* An animal in which the two genes for a given kind of character are alike (*AA* or *aa*) is called a *homozygote,* and is said to be *homozygous.* If the two genes of the pair are different (*Aa*), the animal is a *heterozygote,* or is said to be *heterozygous.* A given animal may be homozygous for some characters, heterozygous for others. A fly containing the chromosomes of Fig. 189 would be homozygous for four characters, heterozygous for four others.

With the foregoing facts concerning the germ cells and their chromosomes in mind, it is possible to analyze the results of breeding experiments. The better known cases rest, as is shown below, upon a very simple foundation.

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[1] This statement would have to be altered to be applicable to plants, since the time of reduction of the chromosomes varies.

Color in Guinea-pigs.—Among the well known animals, the guinea-pigs furnish excellent material for the study of heredity. There are many color varieties of these animals, which *breed true;* that is, whenever one member of a pure breed is mated to another like itself, the offspring are all like their parents. Uniformly black animals constitute such a true-breeding variety (Fig. 190). Albinos form another such variety (Fig. 191). Albinos are animals in which the usual pigments of the skin, hair and eyes are wanting. As a result the body is entirely white, and the iris of the eye pink. Two albinos mated together always produce albino children.

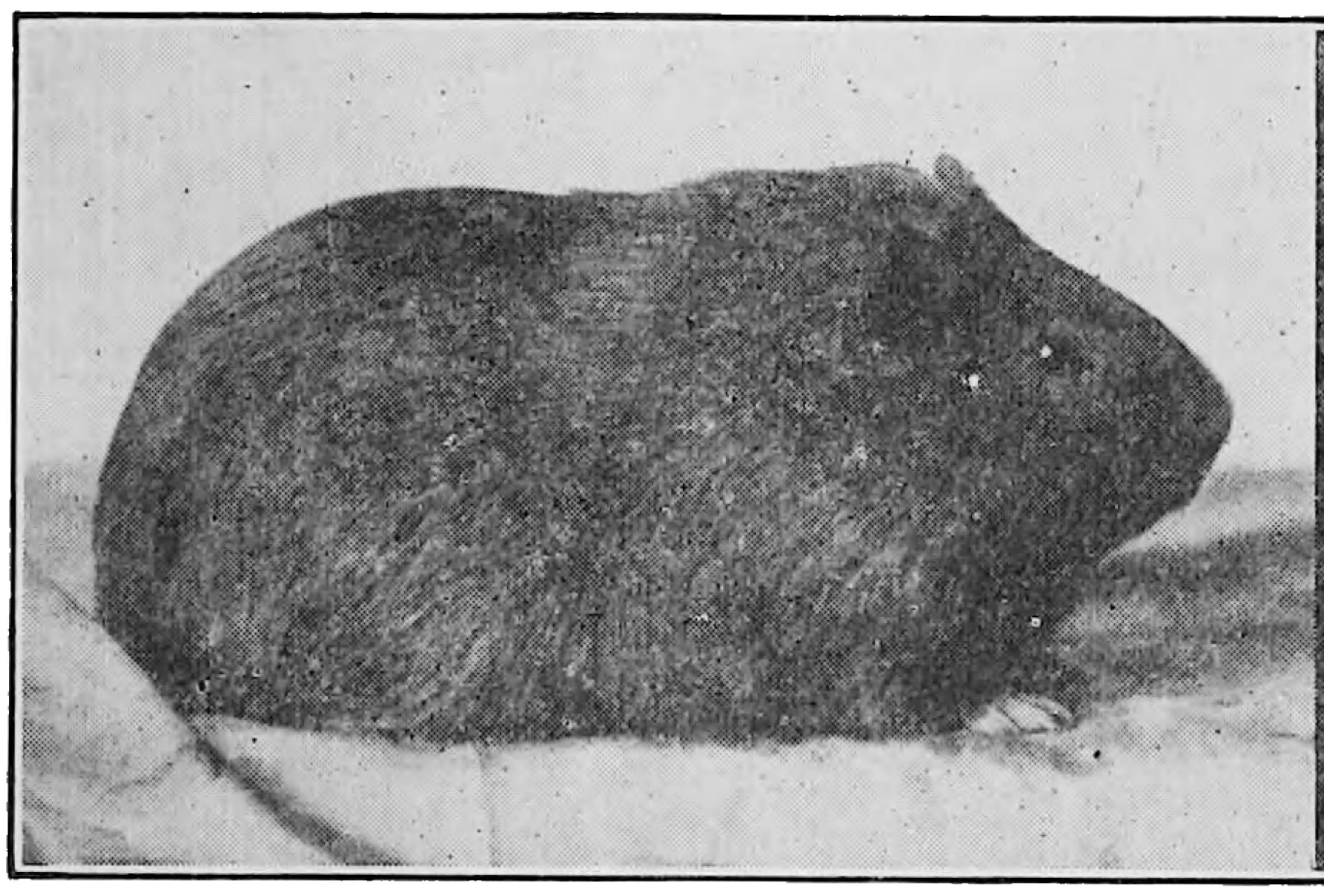

Fig. 190.

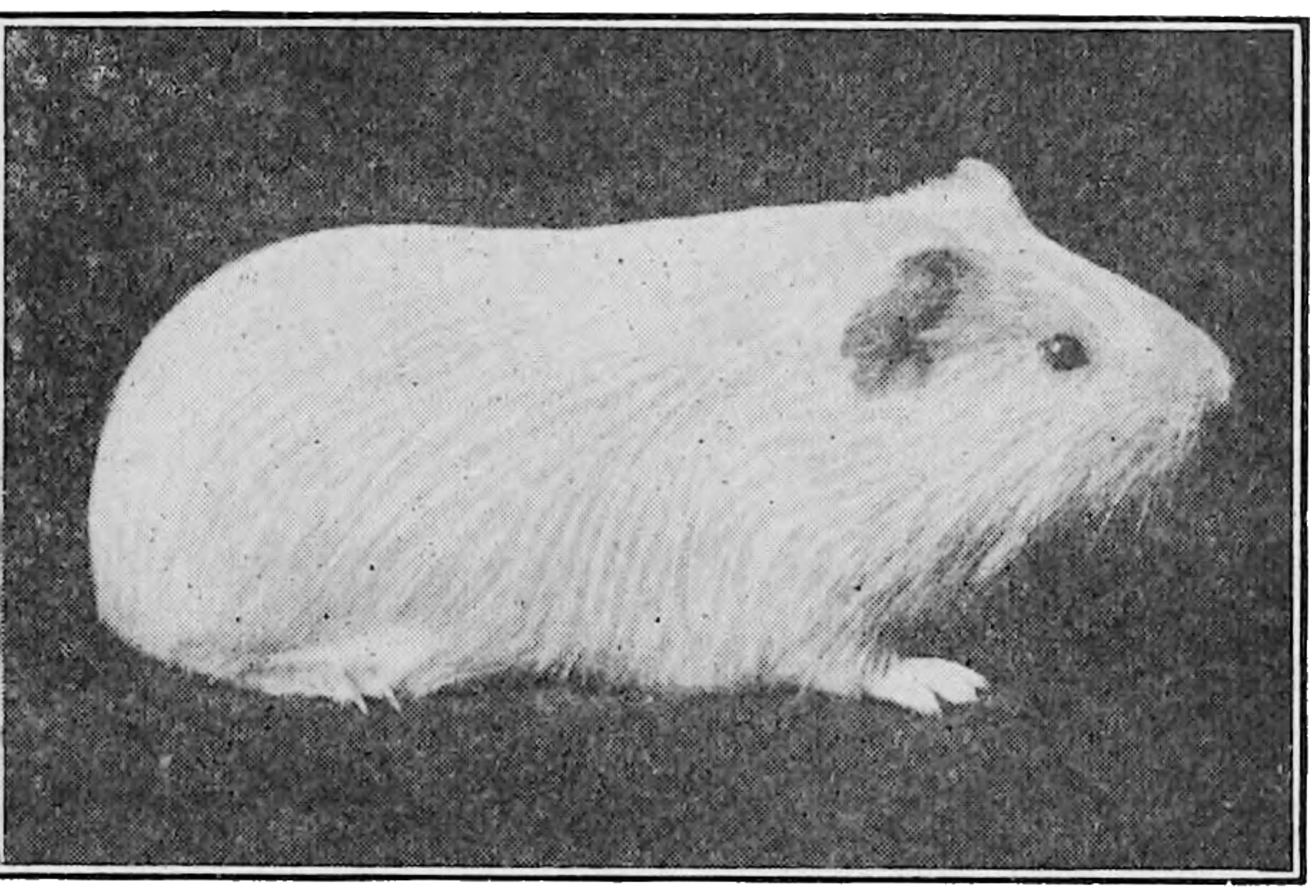

Fig. 191.

Fig. 190.—A black, smooth-coated guinea-pig.
Fig. 191.—An albino smooth-coated guinea-pig. (*Both figures by courtesy of Professor W. E. Castle and the Harvard University Press.*)

If, now, a black guinea-pig of a pure breed is mated with an albino guinea-pig, the offspring will all be black. Ordinarily the black offspring are indistinguishable from the black parent. But when these hybrid blacks are mated together, the two original colors reappear. Some of the members of the second hybrid generation are black, others are albino. Roughly the blacks constitute three-fourths of the total, the albinos one-fourth.

Generation	Nature of individuals
P_1	Black × Albino
F_1	All black
F_2	¾ Black, ¼ Albino

Fig. 192.—Diagram showing the results, through two hybrid generations, of mating a pure black and an albino guinea-pig.

These results are stated in tabular form in Fig. 192, in which the parents are referred to as P_1, their offspring as F_1 (meaning *first filial* generation), and the second hybrid generation as F_2 (*second filial* generation). Albinism disappears in the F_1 generation, a fact which is expressed by saying that the black coat is *dominant*, or that albinism is *recessive*. Its disappearance, however, does not indicate its absence, for albinism reappears in the F_2 generation.

Explanation of the Experimental Results.—The explanation of these results is fairly simple. The genes are in practice designated by letters. When two characters are contrasted, both are commonly designated by the initial letter of the dominant character. (Some geneticists, however, employ the initial letter of the more recent character, whether it is dominant or not.) The dominant character is represented by a capital letter, the recessive character by a small letter. Thus, in the case of color in the guinea-pig, when black is contrasted with albino, black may be represented by *B*, albino by *b*.

The hereditary formulas may now be written for the guinea-pigs whose color inheritance was described. The formula of the P_1 black pig was *BB*, the formula being double because the animal had two parents. In similar manner the formula of the albino parent is to be written *bb*. When these animals produce germ cells, however, the two genes separate from one another, due to the separation of homologous chromosomes in one of the maturation divisions as explained above, so that each germ cell has only one gene. All the germ cells of the black parent have the formula *B*, those of the albino parent the formula *b*.

When these germ cells unite in making the cross, the genes *B* and *b* are brought together, and the formula of all the F_1 individuals is *Bb*. One gene *B* is capable, however, of producing enough black pigment to render the F_1 pigs indistinguishable from the P_1 black. That is the reason for the dominance of black over albinism. If one *B* could produce only a fraction of the amount of pigment produced by two *B*'s, so that the F_1 pigs were lighter in color than their black parent, the character black would be only partially dominant over albinism. Cases of partial dominance are not uncommon in other organisms. If one *B* alone were incapable of producing any pigment at all, all F_1's would then be albinos, and albinism would be the dominant character, black pigment would be recessive. In that case, also, three-fourths of the F_2 would be albino, one-fourth black, and one would probably have selected some other symbols than *B* and *b* to represent the genes.

When the F_1 individuals, whose formulas are all *Bb*, produce germ cells, the phenomenon of segregation occurs just as in the germ cells of their parents. This time, however, since the genes that segregate from one another are unlike, some of the germ cells receive the one gene *B*, others receive the one gene *b*. The F_1 pigs thus produce two kinds of germ cells, which, if all cells survive, are present in equal numbers. Half the eggs of each female contain *B*, half contain *b*. Half the spermatozoa

generation of Fig. 193. Or the F_2 parents might both be *Bb*, so that the F_3 generation would be of three kinds, just like the F_2 generation in Fig. 193.

The other two possible matings between F_2 individuals are *Bb* × *bb*, and *BB* × *Bb*. Crosses of these two types are often made between F_1 animals and their two parent varieties, and are then spoken of as *back crosses*. The results of the former cross, that of a heterozygous black with an albino, are shown in Fig. 194.

Formulas of parents (F_2)	*Bb*	*bb*
Formulas of germ cells of black F_2 parent	*B* and *b*	
Formula of germ cells of albino F_2 parent	*b*	
Formulas of F_3 individuals	½*Bb*,	½*bb*

FIG. 194.—Diagram showing the result of mating a heterozygous black guinea-pig with an albino. This result is one of the possibilities in the production of an F_3 generation.

The first formula in F_3 is of course that of a heterozygous black, the second that of an albino.

The other remaining possible mating in F_2 for the production of an F_3 generation is that between a homozygous black (*BB*) and a heterozygous black (*Bb*). The nature of the F_3 in such a case may be determined from Fig. 195.

All of the F_3 animals in that diagram are black, but half of them are homozygous, half of them are heterozygous.

Formulas of parents (F_2)	*BB*	*Bb*
Formula of germ cells of homozygous black parent	*B*	
Formulas of germ cells of heterozygous black parent	*B* and *b*	
Formulas of F_3 individuals	½*BB*,	½*Bb*

FIG 195.—Diagram showing the result of mating a homozygous black and a heterozygous black guinea-pig. This result is one of the possibilities in the production of an F_3 generation.

It is not desirable to carry this account beyond the F_3 generation. The nature of the F_4 and succeeding generations would depend on principles illustrated in the production of the F_3. No new matings are possible.

The actual results described in this account are not in themselves important. But it is important that the student should be able, in the case of any two parents whose hereditary formulas for a single character are known, to predict the nature and formulas of all of their progeny.

Thorough familiarity with the principles involved in the guinea-pig matings described above should insure this ability.

Accuracy of the Ratios.—In describing the offspring of various matings it has seemed advisable to start from the formulas in many cases and state the result that is expected on theoretical grounds. When an F'_2 was described as being composed of 75 per cent. of black individuals and 25 per cent. of albinos, no particular experiment was in mind. The proportion stated is the one theoretically expected. In a large number of individuals, if there are no disturbing circumstances, such as a greater death rate in one of the classes than in the other, the actual observed numbers are rather close to the theoretical ones. One actual experiment which should theoretically have resulted in an F_2 of two classes, of 75 per cent. and 25 per cent. respectively, did actually result in 72 per cent. and 28 per cent. respectively. How nearly observed results approach the theoretical may be determined by the student, without the labor of a breeding experiment, by tossing pennies. If two coins of regular form, with edges perpendicular to the flat surfaces and with sharp corners, be tossed upon a hard smooth surface, heads and tails should turn up in the following proportions: in one-fourth of the throws both heads, in one-fourth both tails, in one-half one head and one tail. The mathematician can compute how far observed results may diverge from the theoretical without indicating any defect in the theory, but for most persons the trial by pennies is more convincing.

Simultaneous Inheritance of Two Pairs of Characters—In many cases it is important to trace the inheritance of two pairs of contrasted characters at the same time. This is not a needless complication of what is otherwise a simple matter, for some of the most important advances in our knowledge of heredity have followed from such simultaneous tests. An example in guinea-pigs will make clear the usual relation between two independent pairs of characters.

In most guinea-pigs the hair on the back all slopes in one general direction, producing a smooth coat. The animals in Figs. 190 and 191 both have smooth coats. In some, however, the hair is arranged in whorls, sloping away from a central point in each whorl. The occurrence of several such whorls on the back gives an animal a very unkempt appearance, and it is said to have a rough coat (Fig. 196). Rough coat is found to be dominant over smooth, and all of the numerical results obtained with black and albino colors, in F_2 and F_3, can readily be duplicated with rough and smooth coat.

When these two pairs of characters are studied in the same animals, they behave independently of one another. If a smooth black pig, homozygous for both these characters, be mated with a homozygous rough albino animal, all the offspring will be black and rough (see Fig. 197, F_1). The one dominant character is contributed by the one parent, the other

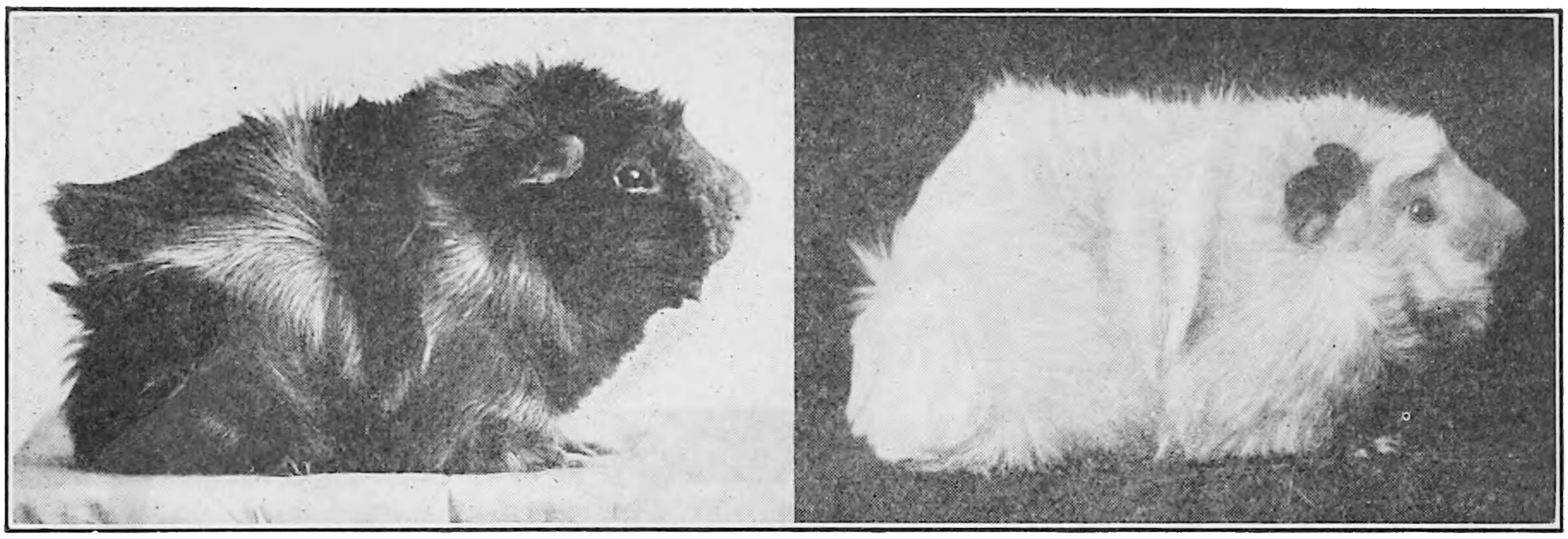

FIG. 196.—Two guinea-pigs with rough coats. The hairs are in many places arranged in whorls, sloping away from a central point. Rough coat is dominant over the smooth coat of Figs. 190 and 191. *(Courtesy of Professor W. E. Castle and the Harvard University Press.)*

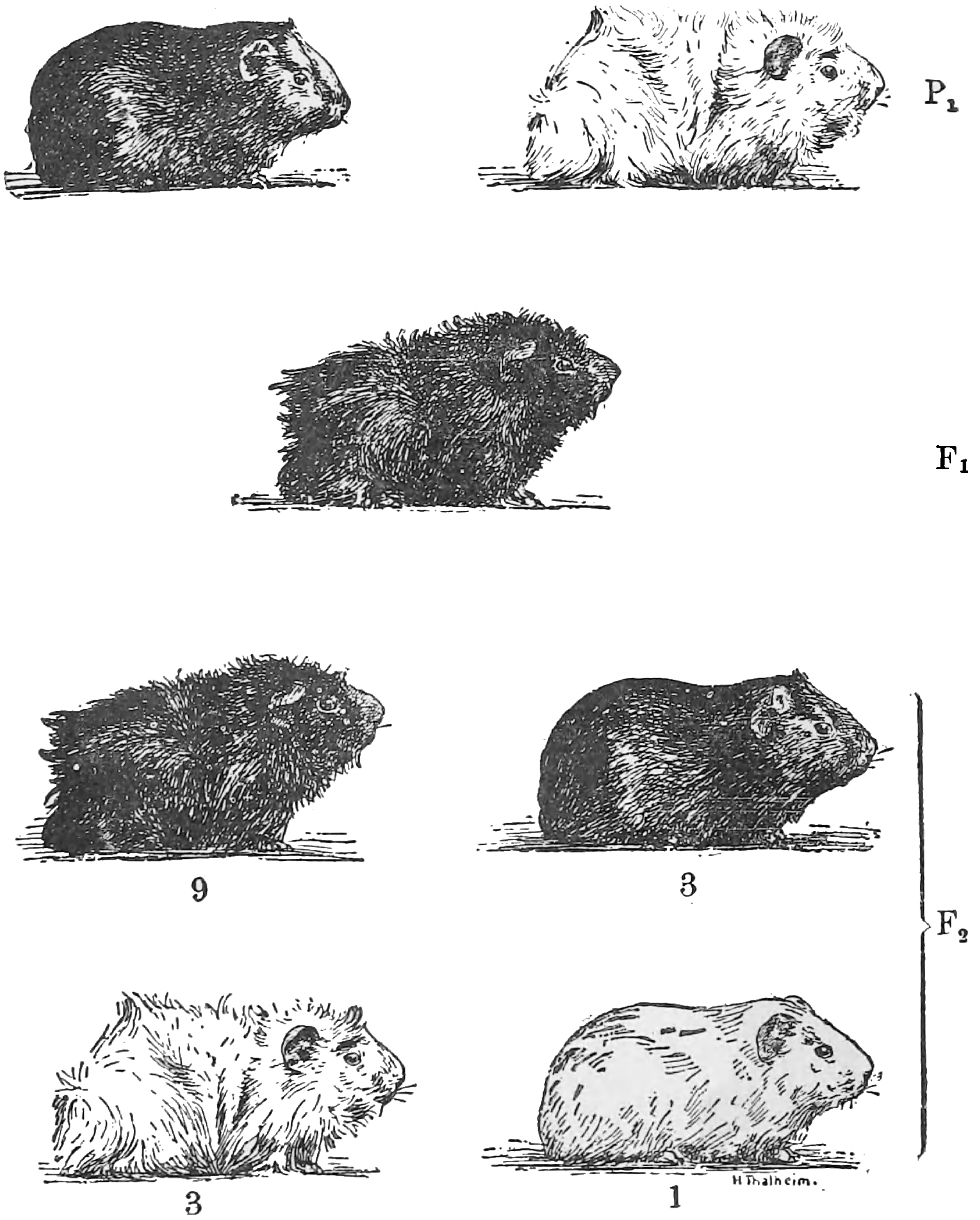

FIG. 197.—Illustration of the simultaneous inheritance of two pairs of contrasted characters. The parents are black smooth, and white rough, respectively. Black and rough are dominant. The F_2 generation consists of four visibly different types, in the ratio of 9 black rough: 3 black smooth : 3 white rough : 1 white smooth. *(From Babcock and Clausen, after Baur.)*

four times in a *vertical* row, placing the formula of the spermatozoön under the formula of the egg. The result follows (Fig. 199).

Egg of F_1	BR	BR	BR	BR
Sperm of F_1	BR	Br	bR	br
Nature of F_2	Black, rough	Black, rough	Black, rough	Black, rough
Egg of F_1	Br	Br	Br	Br
Sperm of F_1	BR	Br	bR	br
Nature of F_2	Black, rough	Black, smooth	Black, rough	Black, smooth
Egg of F_1	bR	bR	bR	bR
Sperm of F_1	BR	Br	bR	br
Nature of F_2	Black, rough	Black, rough	Albino, rough	Albino, rough
Egg of F_1	br	br	br	br
Sperm of F_1	BR	Br	bR	br
Nature of F_2	Black, rough	Black, smooth	Albino, rough	Albino, smooth

FIG. 199.—Diagram showing the sixteen possible combinations of F_1 eggs and spermatozoa, hence the sixteen possible kinds of F_2 individuals, in crosses where two independent pairs of characters are involved.

The four letters in each group are the hereditary formula of one kind of F_2 animal. Whenever at least one B and at least one R are included in this formula, the animal is black and rough. There are nine of these out of each sixteen. When at least one B is present, with two r's (hence no R), the animal is black and smooth. There are three of these in each sixteen. When at least one R is present, with two b's (hence no B), the animal is albino and rough. There are three of these in each sixteen. When neither B nor R is included in the formula (that is, when two b's and two r's are present), the animal is albino and smooth. There is one such animal in each sixteen. The ratio 9 : 3 : 3 : 1 is the characteristic ratio in F_2, when two independent pairs of characters are studied simultaneously. While this ratio, and the proportions stated above, are given with mathematical precision, it is nowhere intended to imply that every sixteen animals will be divided exactly this way. One class might easily be wanting entirely in so small a number. Actual results of breeding experiments, however, accord as nearly with the expected proportions as the laws of chance require.

Linkage.—The two characters studied simultaneously in the foregoing case were said to be independent. That is, in its hereditary behavior, neither character influenced the other in any way. Such is not always the case, however. Occasionally two characters go together much more frequently than would be expected if they were independent. Such characters are said to be linked. Usually, in an F_1 individual which is heterozygous for two characters (like the $BbRr$ in the above example), if linkage occurs, the genes that were together in the parents go together more frequently than do the other combinations of genes. Thus, as shown in Fig. 198 the genes in the parental germ cells were in one parent *Br*, in the other parent *bR*. If linkage occurred between the color of the animal and the direction of its hair, the four kinds of germ cells formulated in the last line of the figure would not be equally numerous. *Br* and *bR* would be more numerous than *BR* and *br*. A corresponding change in the ratio of F_1 individuals would result. The ratio would no longer be 9 : 3 : 3 : 1.

Linkage is almost certainly due to the fact that the genes for the linked characters are in the same chromosome. The eight characters whose genes are represented in Fig. 189 are thus linked. If the chromosomes always remained intact, all characters whose genes are in the same chromosome would be absolutely bound together. But such appears not to be the case. Very often, perhaps usually, the chromosomes separate into fragments of greater or less size and these fragments recombine in other ways, so that the association between any two genes in a chromosome may be broken. Further discussion of linkage would, however, be unprofitable here.

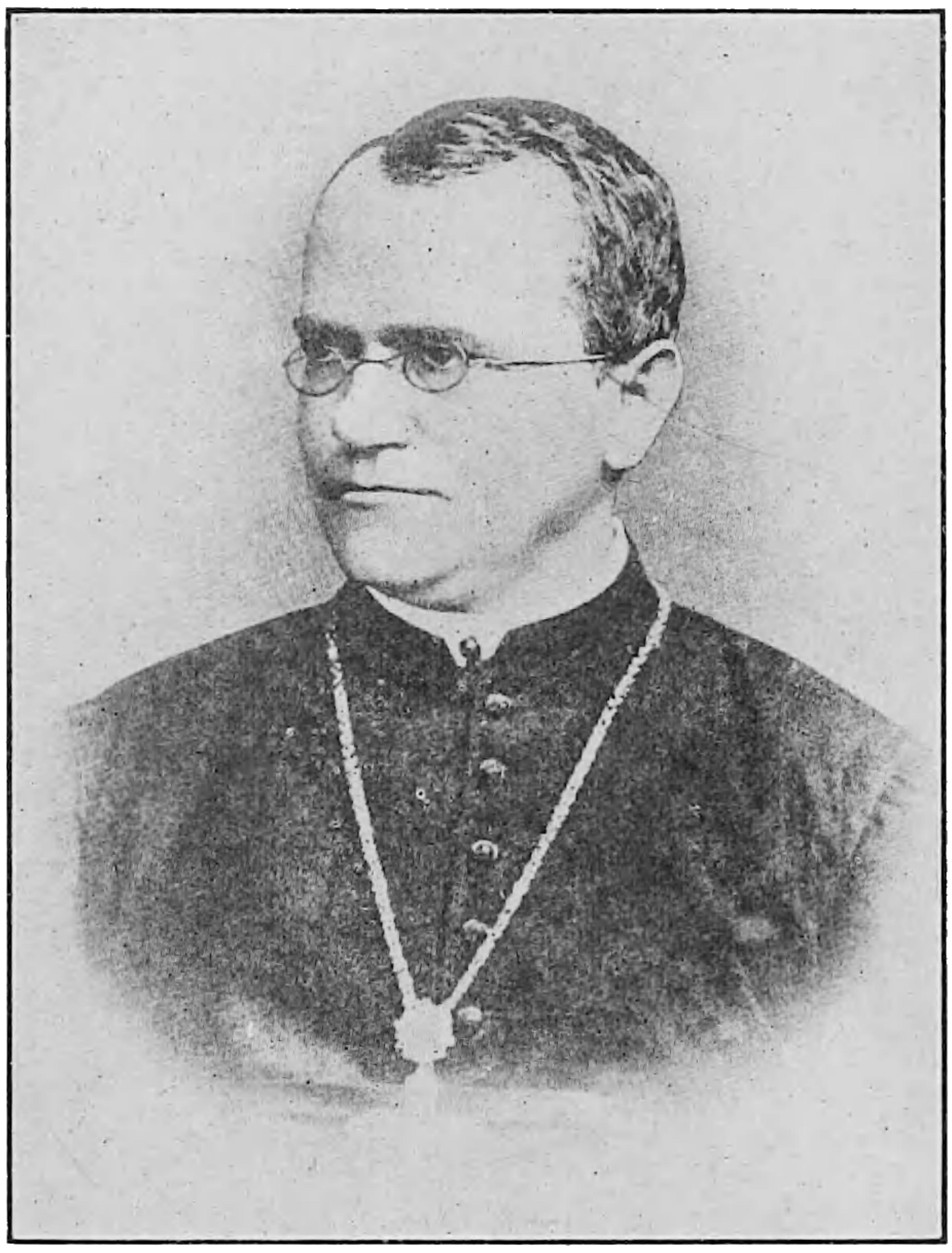

FIG. 200.—Gregor Johann Mendel, 1822–1884, to whom is due much of the present activity in the study of genetics. (*Reproduced from the report of the Royal Horticultural Society Conference on Genetics,* 1906. *By permission of the President and Council.*)

Gregor Mendel.—The simple operations of heredity described in the foregoing paragraphs are in accordance with what is known as Mendel's Law. An Augustinian monk, Gregor Mendel (Fig. 200), who labored in the monastery at Brünn, in Austria, in the latter half of the last century, found time to experiment with garden peas on the monastery grounds. He knew a number of varieties which differed from one another in the height of their stems, the form and color of the seeds, the shape and color of the pods, and the position of the flowers. From crosses between these varieties Mendel derived the simple law of heredity which bears his name. He published the results of his experiments in 1865 and 1866, but they attracted no attention. Probably because biologists were engrossed with Darwin's theory of Natural Selection, which had been announced a few years before, Mendel's work lay unnoticed for a third of a century. Then, in 1900, three European biologists, working independently, rediscovered the principle which Mendel had published. At the same time Mendel's paper was brought to light, and his three successors in this field generously gave him the credit that was his due. Since 1900 Mendel's Law has been abundantly verified. Although his scheme of inheritance has been elaborated since that time, the fundamental feature of it is now generally recognized as applicable to the bulk of the known facts regarding heredity.

Mendel's Law.—The fundamental feature of Mendelian heredity is the segregation of the genes in the production of the germ cells. The two genes concerned with a given character separate from one another, going to different germ cells. Different pairs of genes segregate, at least frequently, independently of each other, so that genes may be brought together in the germ cells in combinations that never existed before. The fertilization of eggs by sperms may introduce further variety into the combinations, for in the fertilized egg the variety among the ova is multiplied by that of the sperms. As a result, the inherited characters of animals may be grouped in ever new combinations. Because such inherited traits as color of hair, color of eye, length of ear, length of hair, and direction of hair can be combined in new ways in hybrid individuals, they have sometimes been called *unit characters*. That these characters behave as units is due to the segregation, resulting in new combinations, of genes in the germ cells. This is the essential feature of Mendel's Law. That law does not require dominance, for there are cases in which dominance is lacking but all other phenomena are typical. No particular ratios, such as 3 : 1, are necessary, since many things may conspire to alter these ratios. Mendel's Law refers to the segregation and recombination of the genes.

Determination of Sex.—Closely related to heredity are the phenomena of sex-determination. What causes some embryos to develop the organs characteristic of a male, while other embryos that look precisely like them in early stages develop female organs? The answer to this question is not the same for all animals, and for many of them the question is still unanswered. One explanation, however, is applicable to a large number

are produced. A spore develops asexually into a thread-like structure (*protonema*) on which a number of moss plants grow. All the moss plants from a single protonema are, in certain species, of the same sex. The spore evidently contains something which determines the sex of the plants growing from its protonema. What that something is has not been determined. There is no evidence that sex is associated, in these mosses, with the number or kind of chromosomes, although such an association has lately been discovered in another plant.

Sex-linkage.—In many animals in which sex is dependent upon the number of certain chromosomes present, there is linkage of sex with certain other inherited characters. As a result, in certain crosses the males and females inherit the body characters unequally. A case of this kind is found in the eye color of the fruitfly Drosophila. These flies are normally red-eyed, but white-eyed individuals are known. When a white-eyed male is mated with a red-eyed female, the F_1 are all red-eyed. In F_2, however, though there are three reds to one white, the two sexes do not share equally in the two colors. The F_2 females are all red-eyed, while half of the males are red-eyed, half white-eyed. Plumage characters in fowls are not infrequently linked with sex in similar manner. A detailed explanation of sex-linkage would be out of place here. It is enough to say that it results from the fact that the genes for the sex-linked characters (eye color in flies, plumage characters in fowls) are located in the chromosomes which determine sex. All the characters whose genes are represented in Fig. 189 are sex-linked, since these chromosomes are the sex-chromosomes.

Mechanism of Heredity: a Retrospect.—In the foregoing discussions it has twice been asserted dogmatically that the genes are in the chromosomes. The evidence for this statement is abundant, but only a small part of it can be advanced here. In sea-urchin eggs, certain chromosomes have been lost in the course of experiments, and with them were lost some of the characters of the larval skeleton. Still better evidence is found in the fact that the chromosomes behave, in maturation, in such a way as to furnish an explanation for many of the fundamental facts of heredity, if only the assumption be made that the genes are in the chromosomes. Some of these fundamental facts may be referred to.

First, the segregation of the genes in the germ cells is accounted for if the genes are in the chromosomes. It has been shown that, in maturation, the chromosomes come together in pairs. Presumably the two genes for a given kind of character are in these two chromosomes. In a heterozygous black guinea-pig (*Bb*) the gene *B* is assumed to be in one chromosome, *b* in another. These two chromosomes pair with each other. In a heterozygous rough guinea-pig (*Rr*), *R* is in one chromosome, *r* in another, and these chromosomes pair early in maturation. Likewise in a homozygous organism (*BB* or *rr*), the two genes that produce the same character are in different chromosomes, and these chromosomes meet in a pair in maturation. It has also been shown that in one of the maturation divisions the tetrad that is formed by a pair of chromosomes is divided in such a way that the original chromosomes are separated from one another. In this separation is the mechanism by which the genes are segregated—if only the genes are in the chromosomes.

Secondly, the phenomena of linkage can be explained if the genes are in the chromosomes. Characters that hang together in their distribution to the germ cells, to a greater degree than would be expected on the theory of chance, are assumed to be represented by genes in the same chromosome. The argument from linkage has been elaborated by a long series of important discoveries in the last decade to such a degree that it now amounts almost to proof that the chromosomes contain the genes. For this evidence, however, the student should consult works on genetics.

What the genes are is largely a matter of conjecture. Since the chromosomes are presumably composed of very complex proteins, it is not unnatural to suppose that the genes are proteins. Some have held that they might be, not distinct substances, but merely the side-chains of protein molecules in the chromosomes. Others have suggested that they are enzymes. But there is little evidence on which to base a theory of the nature of the genes, and further discussion of the matter would be chiefly speculation.

How the genes produce the characters they represent is likewise little understood. It is evident that they influence a long series of chemical reactions (metabolic processes) in the development of the organism. Since the cytoplasm must participate in many of these reactions, objections have occasionally been raised against the view that the genes determine the characters. However, with the exception of the plastids the cytoplasm appears not to exercise any specific influence[1] in producing the characters of the adult; it is merely a medium in which the genes act, and material out of which the genes produce their characters. Although the cytoplasm exercises no specific influence on the genes, it is probable that interactions among the genes themselves regularly occur. A gene by itself, even if it were in the usual kind of cytoplasm, would doubtless produce nothing. The absence of only one or two of the genes ordinarily present is known, in many cases, to change entirely the characters produced by those that remain. The genes are perhaps, then, not as distinct and independent as the student was led to suppose from the somewhat mathematical accounts of the phenomena of heredity given earlier in the chapter, but are members of a highly organized system.

[1] There is room to debate the influence of the cytoplasm in heredity, but such a debate would introduce a whole new group of phenomena many of which are not clear. It seems unwise to discuss these phenomena here.

Definition of Heredity.—Following the account of the mechanism of inheritance the term heredity may be defined with greater precision than was possible at the beginning of the chapter. Heredity is the occurrence, in the offspring, of the same genes that were in the parents. Definitions which involve a likeness between parents and offspring have always been objectionable because environmental conditions may intervene to destroy such likeness. Thus, the offspring of a red-flowered Chinese primula will, if reared under ordinary conditions, also produce red flowers. But if these offspring are reared at a high temperature their flowers are white. Heredity has not been destroyed, however, for if the plants are returned to normal temperature they soon begin to produce red flowers again. A definition that involved likeness of parent and offspring would imply the absence of heredity in the case of the primulas. The definition requiring likeness of genes in parents and offspring permits such environmental effects.

Variation.—All the knowledge of heredity which we now possess has been made possible through the fact that animals differ from one another in discernible features. It is a commonplace to say that, had such differences been wanting, little of the operations of heredity could have been discovered. Characters might have been transmitted in precisely the way they are known to be, but without individual differences the mode of transmission would have remained unknown. Perhaps no curiosity concerning it would ever have existed. Variation is therefore one of the cornerstones of genetics.

Variation is due to several causes, prominent among them hybridization. It has been shown that, in an F_2 generation, members of the same family differ from one another merely because they contain different genes. When the grandparents differ in only one character, there are only two "varieties" in F_2; when the grandparents differ in two characters, the F_2 generation includes four visibly different combinations, as was seen in the case of rough, smooth, black, albino in guinea-pigs. When many differences between the grandparents are involved, the F_2 presents exceedingly numerous possibilities.

The differences involved in such cases must, however, have had an origin. If it is true that animals have reached their present condition by a process of evolution, a thesis that is developed in the last several chapters of this book, it is inconceivable that this change has been brought about merely by the recombination of genes in different ways. It is inconceivable that the earliest organisms, whatever they were like, contained genes for all the characters that are now possessed by their descendants, only waiting to be shaken and thrown like dice to produce the combinations now known. Changes must have been introduced in some other way. There is, moreover, abundant evidence that changes of this kind have been recognized in specific cases. A number of years

Genetics and Race.—It is a corollary of the foregoing discussion that races of men are dependent for their existence as races solely upon the inheritance of their distinguishing features. The blue-eyed fair-skinned race inhabiting the Scandinavian countries has been blue-eyed and fair for centuries, and will doubtless continue to be so in the future, because these traits are inherited. The dark people of southern Italy and Spain are dark because their ancestors were, not because of geographical location. The long skulls and round skulls of northern and central Europe, respectively, owe their distribution to inheritance. Mental and moral features of different races are equally fixed by heredity. The dogged determination of one race, the emotionalism and idealism of another, the arrogance, the love of gain, the irresponsibility, the deception, the sturdy honesty of other races, are all inherited traits. It is only because of this fact that one may speak of racial characteristics at all.

Along with the heredity of these characteristics goes a certain amount of geographical isolation. Races do not wander rapidly nor uniformly. They tend to go in groups when they do wander, and even when they mingle with other races free intermarriage may be long postponed. Were it not for this geographical separation, or avoidance of intermarriage, it would be but a short time until there would be no races. All the racial attributes would still exist and be transmitted as before, but they would no longer be combined in individuals as they now are. Even at present there is a good deal of intermingling of races, with intermarriage, and race distinctions have to a considerable extent broken down. The use of the words English and French, for example, to refer to races is vitiated by this intermingling for it is certain that both of these nations are mixtures of originally distinct races. It is difficult now to place the inhabitants of these countries into one or another of the contributing races, for intermarriage has occurred, and there are numerous intergradations between the racial types.

As a result partly of migration, without intermarriage, political boundaries do not coincide with racial boundaries. This is a fact of capital importance in history. Few nations possess racial unity. Since race implies mental and moral attributes as well as physical, most nations are working at cross purposes. The chief weakness of the former empire of Austria-Hungary lay in its eight or nine more or less distinct races. The difference in ideals is not a temporary condition. Although racial ideals and ambitions are in part traditional, they are largely the result of inheritance, and are for that reason likely to be rather permanent. Propinquity of races may sometime enforce a cosmopolitanism that is desirable, but so long as political lines of cleavage ignore racial distinctions, there is danger that the nation will be a house divided against itself.

Practical Applications of Genetics.—Although genetics as a science is comparatively young, it has already yielded results in the development of domesticated animals and plants that are of economic value. These results have been more simple and clear in the case of plants than in that of animals, though the end products have been scarcely more valuable. Inheritance in animals is very complex in nearly all characteristics which are of commercial worth, and the practice of the breeder is still very largely the method of cut and try. But even by this empirical method the milk-production of cattle, the egg-laying qualities of poultry, the wool-clip of sheep, the productivity of the silk-worm and many other economic features of animals have been marvelously improved. In plants the economically important features are more often inherited in simple fashion, and it is possible to apply promptly the principles of heredity which have been elaborated since 1900. By these means the productivity of wheat and other grains, and of hay, has been appreciably increased. It has been possible to combine in one variety of wheat, for example, such desirable qualities as high yield, stiff straw, winter hardiness, and resistance to rust; in oats, high yield with the absence of hulls; in tobacco, high number and desirable shape of leaves with proper texture and "grain." And the end is not yet. The prospects for further valuable improvements are bright.

In human beings the application of the knowledge of heredity has scarcely begun. Progress has been slow for the reason that such application must either be voluntary, which requires much education of the public, or must be enforced by legislation, which always meets with objections from those to whom "personal liberty" is dear. Furthermore, less is definitely known of heredity in man than in domestic animals, because knowledge can only come from family histories, not experiments, and family records can seldom be traced for many generations. While much that is known could well be applied voluntarily by intelligent people, legislation should limit itself for the present to those characters which are of the greatest social importance and whose heredity is best known. Feeble-mindedness is such a characteristic, and radical steps looking toward its eradication would be justified even in the present state of knowledge.

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CHAPTER XII

TAXONOMY

Taxonomy (from the Greek *taxis* = arrangement and *nomos* = law) is literally an orderly arrangement. As applied to living things it refers to the classification of animals and plants on the basis of fundamental similarities. The taxonomy of animals, with which this chapter deals, is wholly distinct, except in principle, from that of plants, though the simplest members of the plant and animal kingdoms are not readily distinguishable from one another. Zoölogical taxonomy is often called *systematic zoölogy.*

Conceptions of Taxonomy.—An orderly arrangement of objects or facts presupposes a system of classification, and the same objects or facts can usually be classified in different ways by the use of different characters, qualities or relations as a basis. Moreover, different systems of classification may be adopted to suit particular purposes or to satisfy particular bents of mind. Thus because it is possible to classify animals in different ways, taxonomy has often been considered a mere cataloging of animal forms, and it has been assumed that the purpose of taxonomy is merely to find a way in which the forms may be *conveniently* arranged, described and cataloged. This conception is erroneous, but to state wherein lies the error requires that the aims of those who propose the various systems be compared. Much of this comparison must await the historical account below. It may be pointed out here, however, 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 cataloged and perhaps cross-cataloged. So long as prevention of confusion was the chief aim, it made little difference whether the shelves were numbered in vertical columns or in horizontal rows. Every classification which sought nothing more than convenience might therefore be artificial and arbitrary, and one person's classification might be quite as good as another's. 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 grown up largely since the general acceptance of the evolution doctrine, according to which

1735 and 1768 and, after his death, in a thirteenth, edited by Gmelin. In this work Linnæus 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. Linnæus also had the courage to defy prejudice in such details as removing the whales from the group of fishes, and placing them with the terrestrial hairy animals called mammals. For in the Linnæan classification structural characters, rather than habits or external forms, were used as a basis. Six categories or *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 the same nominal rank. Thus, a Linnæan 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. However, since Linnæus did not hold any evolutionary views, such discrepancies did not trouble him.

Later Temporary Systems of Classification.—Following Linnæus, many naturalists concerned themselves with systematic zoölogy. Some of them adopted the Linnæan 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 groups, called branches, which he divided into classes, nineteen in number; and some parts of his classification remained in vogue in his own country for three-quarters of a century. Superior to Cuvier in his conceptions was de Blainville (1777–1850) who 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. Mention may also be made of the systematic work of Pierre Latreille (1762–1833), Johannes Müller (1801–1858), and Louis Agassiz (1807–1873). Then there was a host of minor systematists the value of whose labors has been 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.[1]

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 zoölogy would have imposed upon them. The system of Linnæus, 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 Linnæan System.—That the Linnæan system was rapidly adopted and is now universally employed by zoölogists is doubtless due largely to the fact that it introduced a sharply defined grouping, a definite terminology, and brief, clear diagnoses; that it permitted early naturalists to group those forms that resembled each other; and that it equally well permitted the classification of forms according to their relationships. As stated above Linnæus 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 the others are used for some groups or by some naturalists. The rank of recognized categories may be expressed as follows:

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[1] For many of the facts regarding these old attempts at classification we are indebted to Theodore N. Gill, Annual Report of the Smithsonian Institution for 1907.

- **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 squirrel-like rodents)
            - **Family.** Example, *Sciuridae* (the flying-squirrels, marmots, squirrels and chipmunks)
              - **Subfamily.** Example, *Sciurinae* (the marmots, squirrels and 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 Linnæan 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 rhombifer* 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*. The term variety is usually considered synonymous with sub-species in taxonomy, but it may be used to indicate divisions smaller than sub-species, and in one group, the ants (family Formicidæ), 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. Linnæus seems to have appreciated the necessity for rules and to have proposed a set. These rules were not sufficient, and several other codes were proposed, the more important of which were the *British Association Code*, the *American Ornithological Union Code*, the *Code of the German Zoölogical Society*, and the *Code of the International Zoölogical Congress.*

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 in general correct. However, since evolution has probably not proceeded at the same rate at all periods, nor 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. 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, nevertheless, the groups of higher rank have sprung from ancestry more remote than that of the groups of lower rank.

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, the evidential value of 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; and there are certain lizards (Amphisbænidæ) which closely resemble certain snakes (Typhlopidæ) in being blind, limbless, and having a short tail. The early systematists were very liable to bring together in their classification *analogous* forms, that is, those which are functionally similar; or animals which are only superficially similar. In contrast with the early practice, the aim of taxonomists at the present time is to group forms according to homology (see Chapter X), which is considered an indication of actual relationship. Since a genetic classification must take into consideration the entire animal, the search for affinities becomes an attempt to evaluate the results of all morphological knowledge, and it is also becoming evident that other things besides structure may throw light upon relationships. The fossil records, geographical distribution, ecology and experimental breeding may all assist in establishing affinities.

The Method of Taxonomy.—It is evident that before the relationships of animals can be determined the forms must be known, for unknown forms constitute breaks in the pedigrees of the groups to which they belong. Moreover, as pointed out above, the structural characters, variation and distribution must be known before a form can be placed in the proper place in a genetic system. For these reasons an important part of systematic work is the description of forms and an analysis of their differences. After the Linnæan system was adopted zoölogists attacked this virgin field and for many years "species making" predominated. Even at the present time when other aspects of zoölogy have come to receive relatively more attention it is an interesting fact that the analytical method prevails in systematic studies, and taxonomy suffers from, and in part merits, the criticism that it is a mere cataloging of forms and ignores the higher goal of investigation, namely, the discovery of the course of evolution. Many systematists, however, recognize that the ultimate purpose of taxonomic work is to discover the relationships as well as the differences between the described forms in order that the course of evolution may be determined. In other words, it is appreciated that while analytical studies are necessary they are only preliminary, and that upon their results must be built synthetic studies, if taxonomy is to fulfill its purpose.

The Difficulties of Taxonomy.—One of the greatest obstacles to a genetic classification of animals is the incomplete fossil record of extinct forms. The comparative poverty of records makes it necessary to determine the breaks in the chain as well as possible until such a time as they shall be closed by additions to the data of paleontology. A further difficulty lies in the nature of the material. The structure of animals is so complex and variable, and the distribution and ecology are so complicated, that the task of making analyses which will permit a satisfactory grouping is a laborious one. The enormous number of forms is another difficulty. So many forms have been discovered and so many apparently await discovery, study, and description, that systematic zoölogists must generally limit their work to some one or two orders and in some cases to a single family. To distinguish the workers on the different groups of animals different names have been applied. Thus, one who is engaged with the Protozoa is a *protozoölogist;* the student of worms is a *helminthologist;* of the mollusks, a *conchologist;* an *entomologist* deals with insects, a *herpetologist* with reptiles or Amphibia or both, an *ornithologist* with birds, and a *mammalogist* with mammals. These names do not, however, imply an interest in classification alone, since an entomologist may be concerned with ecology and a conchologist with geographical distribution, etc.

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 zoögeographer, as will be apparent in Chapter XIV, 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.

TABULAR VIEW OF THE CLASSIFICATION OF ANIMALS AS FAR AS ORDERS

The complete classification of animals includes, of course, extinct and living forms, and there are differences of opinion as to the position and composition of many groups. The following classification, including the living and a few fossil forms, now in use in the Zoölogical Laboratory of the University of Michigan, has been compiled from many sources.

PHYLUM I. PROTOZOA

- **Class I. Rhizopoda**
  - Order 1. Lobosa
  - Order 2. Heliozoa
  - Order 3. Radiolaria
  - Order 4. Foraminifera
- **Class II. Mastigophora**
  - Order 1. Flagellata
  - Order 2. Choanoflagellata
  - Order 3. Dinoflagellata
  - Order 4. Cystoflagellata
- **Class III. Sporozoa**
  - Subclass I. Telosporidia
    - Order 1. Gregarinida
    - Order 2. Coccidiidea
    - Order 3. Hæmosporidia
  - Subclass II. Neosporidia
    - Order 1. Myxosporidia
    - Order 2. Sarcosporidia
- **Class IV. Infusoria**
  - Subclass I. Ciliata
    - Order 1. Holotricha
    - Order 2. Heterotricha
    - Order 3. Hypotricha
    - Order 4. Peritricha
  - Subclass II. Suctoria

PHYLUM X. ARTHROPODA

- **Class I. Crustacea**
  - 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**
- **Class III. Myriapoda**
  - Order 1. Pauropoda
  - Order 2. Diplopoda
  - Order 3. Chilopoda
  - Order 4. Symphyla
- **Class IV. Insecta**
  - 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**
  - Order 1. Araneida
  - Order 2. Scorpionidea
  - Order 3. Phalangidea
  - Order 4. Acarina
  - Order 5. Pedipalpi
  - Order 6. Palpigradi
  - Order 7. Solifugæ
  - Order 8. Chernetidia
  - Order 9. Xiphosura
  - Order 10. Eurypterida

GROUPS OF INVERTEBRATES OF MORE OR LESS UNCERTAIN SYSTEMATIC POSITION

- Group 1. Mesozoa
- Group 2. Nemertinea
- Group 3. Nematomorpha
- Group 4. Acanthocephala
- Group 5. Chætognatha
- Group 6. Rotifera
- Group 7. Bryozoa
- Group 8. Phoronidea
- Group 9. Brachiopoda
- Group 10. Gephyrea

PHYLUM XI. CHORDATA

- SUBPHYLUM I. ENTEROPNEUSTA
  - Order 1. Balanoglossida
  - Order 2. Cephalodiscida
- SUBPHYLUM II. TUNICATA
  - Order 1. Ascidiacea
  - Order 2. Thaliacea
  - Order 3. Larvacea
- SUBPHYLUM III. CEPHALOCHORDA
- SUBPHYLUM IV. VERTEBRATA
- **Class I. Cyclostomata**
  - SUBCLASS I. MYXINOIDEA
  - SUBCLASS II. PETROMYZONTIA
- **Class II. Elasmobranchii**
  - SUBCLASS I. SELACHII
    - Order 1. Squali
    - Order 2. Raji
  - SUBCLASS II. HOLOCEPHALI
- **Class III. Pisces**
  - SUBCLASS I. TELEOSTOMI
    - Order 1. Crossopterygii
    - Order 2. Chondrostei
    - Order 3. Holostei
    - Order 4. Teleostei
  - SUBCLASS II. DIPNOI

PHYLUM XI. CHORDATA (*Continued*)

- **Class IV. Amphibia**
  - Order 1. Apoda
  - Order 2. Caudata
  - Order 3. Salientia
- **Class V. Reptilia**
  - Order 1. Testudinata
  - Order 2. Rhynchocephalia
  - Order 3. Crocodilini
  - Order 4. Squamata
- **Class VI. Aves**
  - SUBCLASS I. ARCHÆORNITHES
  - SUBCLASS II. NEORNITHES
    - Order 1. Hesperornithiformes
    - Order 2. Ichthyornithiformes
    - Order 3. Struthioniformes
    - Order 4. Rheiformes
    - Order 5. Casuariiformes
    - Order 6. Crypturiformes
    - Order 7. Dinornithiformes
    - Order 8. Æpyornithiformes
    - Order 9. Apterygiformes
    - Order 10. Sphenisciformes
    - Order 11. Colymbiformes
    - Order 12. Procellariiformes
    - Order 13. Ciconiiformes
    - Order 14. Anseriformes
    - Order 15. Falconiformes
    - Order 16. Galliformes
    - Order 17. Gruiformes
    - Order 18. Charadriiformes
    - Order 19. Cuculiformes
    - Order 20. Coraciiformes
    - Order 21. Passeriformes
- **Class VII. Mammalia**
  - SUBCLASS I. PROTOTHERIA
    - Order 1. Monotremata
  - SUBCLASS II. EUTHERIA
    - *Division I. Didelphia*
      - Order 1. Marsupialia
    - *Division II. Monodelphia*
      - *Section A. Unguiculata*
        - Order 1. Insectivora
        - Order 2. Dermoptera
        - Order 3. Chiroptera
        - Order 4. Carnivora
        - Order 5. Rodentia
        - Order 6. Edentata
        - Order 7. Pholidota
        - Order 8. Tubulidentata
      - *Section B. Primates*
        - Order 9. Primates
      - *Section C. Ungulata*
        - Order 10. Artiodactyla
        - Order 11. Perissodactyla
        - Order 12. Proboscidea
        - Order 13. Sirenia
        - Order 14. Hyracoidea
      - *Section D. Cetacea*
        - Order 15. Odontoceti
        - Order 16. Mystacoceti

BRIEF CHARACTERIZATIONS OF THE MAJOR GROUPS OF ANIMALS

The principal groups of animals are given below with brief diagnoses which may serve as definitions. It must be understood that the characters given will often not be sufficient to distinguish all the forms in a group, for there is much variation within the groups. They are intended to give the student a general conception of the phyla, subphyla and classes.

Phylum PROTOZOA. Single celled animals without true organs or true tissues. If colonial, the cells are all potentially alike.

Class RHIZOPODA. Protozoa with changeable protoplasmic processes (pseudopodia). Amœba. (Figs. 17, 26, 28.)

Class MASTIGOPHORA. Protozoa with one or more vibratile processes (flagella) which serve for locomotion and for taking food. Euglena. (Figs. 31, 53, 54, 55.)

Class SPOROZOA. Parasitic Protozoa, usually without motile organs or mouth, reproducing by spores. (Figs. 132, 137.)

Class INFUSORIA. Protozoa having numerous slender vibratile processes (cilia), a cuticle, and fixed openings for the ingestion of food and the extrusion of indigestible matter. Paramecium. (Figs. 18, 33, 130, 131, 138.)

Phylum PORIFERA. Diploblastic, radially symmetrical animals with body wall penetrated by numerous pores. Body usually supported by a skeleton of spicules or spongin. Sponges.

Class CALCAREA. Sponges with spicules composed of calcium carbonate, monaxon or tetraxon in form. (Figs. 127, 128.)

Class HEXACTINELLIDA. Sponges with spicules composed of silicon, triaxon in form.

Class DEMOSPONGIÆ. Sponges with spicules composed of silicon, not triaxon in form, or skeleton composed of spongin, or with skeleton of both spicules and spongin.

Phylum CŒLENTERATA. Diploblastic, radially symmetrical animals with tentacles, stinging cells, single gastrovascular cavity, no anus. Two body forms are prevalent, the hydroid and the medusa. Jellyfishes, polyps and corals.

Class HYDROZOA. Cœlenterates without stomodæum and mesenteries; sexual cells discharged to the exterior; hydroid and medusa forms in the life history of same species, or only the medusa, the latter having a velum. Polyps (including Hydra), a few corals, small jellyfishes. (Figs. 60–65, 212, 216.)

Class SCYPHOZOA. Cœlenterates with only the medusoid, not hydroid form; velum lacking; notches at margin of umbrella. Larger jellyfishes.

Class ANTHOZOA. Cœlenterates without medusoid forms, with well developed stomodæum and mesenteries. Sea anemones, most corals. Fig. 71, part.

Phylum CTENOPHORA. Triploblastic animals; symmetry partly radial, partly bilateral; eight rows of vibratile plates radially arranged. Sea walnuts or comb jellies.

Phylum PLATYHELMINTHES. Triploblastic, bilaterally symmetrical animals with body flattened, with a single gastrovascular cavity (sometimes wanting) and no anus. Flatworms.

Class TURBELLARIA. Free-living flatworms with ciliated epidermis. Planaria. (Figs. 81, 82.)

Class TREMATODA. Parasitic flatworms without cilia but with a hardened ectoderm, usually parasitic and with attaching suckers. Flukes. (Fig. 140.)

Class CESTODA. Parasitic flatworms with the body differentiated into a head (scolex) and a chain of similar joints (proglottides), the whole being usually regarded as a colony. Tapeworms. (Figs. 68, 96.)

Phylum NEMATHELMINTHES. Bilaterally symmetrical, triploblastic animals with an elongated cylindrical body covered with a cuticle, with a true body cavity, and a digestive tract with both mouth and anus. Roundworms.

Phylum ECHINODERMATA. Radially symmetrical (with minor exceptions), triploblastic animals with well developed cœlom, and usually with five antimeres, spiny skeleton of calcareous plates, and organs of locomotion known as "tube feet" operated by a water-vascular system. Starfishes, sea urchins, sea cucumbers.

Class ASTEROIDEA. Free-living, typically pentamerous echinoderms with wide arms not sharply marked off from disc and with ambulacral grooves. Starfishes.

Class OPHIUROIDEA. Free-living, typically pentamerous echinoderms with slender arms sharply marked off from disc and no ambulacral grooves. Brittle stars.

Class ECHINOIDEA. Free-living, pentamerous echinoderms without arms; test composed of calcareous plates bearing movable spines. Sea urchins, sand dollars.

Class HOLOTHURIOIDEA. Free-living, elongated, soft-bodied echinoderms with muscular body wall and tentacles around mouth. Sea cucumbers.

Class 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 ANNELIDA. Triploblastic, bilaterally symmetrical elongated animals with external and internal segmentation; cœlom usually present; setæ common. True worms. (Figs. 67, 83, 95, 142, 143, 144.)

Subclass DIPNOI. Fishes with a skeleton of cartilage and bone, and air bladder functioning as a lung. Lungfishes.

Class 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. 84, 97, 98, 147, 153, 154, 159.)

Class REPTILIA. Cold-blooded vertebrates usually covered with scales, breathing throughout life by means of lungs. Lizards, snakes, crocodilians, turtles. (Figs. 152, 228–231.)

Class AVES. Warm-blooded vertebrates with the body covered with feathers, with the fore limbs usually modified as wings, and a heart of four chambers. Birds. (Figs. 157, 245.)

Class MAMMALIA. Warm-blooded animals which are covered with hair at some stage and suckle the young, and have a diaphragm between thorax and abdomen. (Figs. 156, 190, 191, 196, 211, 232.)

Subclass PROTOTHERIA. Egg-laying mammals. Monotremes.

Subclass EUTHERIA. Viviparous mammals. True mammals.

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 thread-like 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.

Chætognatha. Marine invertebrates with a distinct cœlom, alimentary canal, nervous system and two eyes.

Rotifera. Invertebrates with a head provided with cilia, usually a cylindrical or conical body often with a shell-like covering, and a bifurcated tail or foot provided with a cement gland.

Bryozoa. Mostly colonial invertebrates resembling hydroids in form, with distinct cœlom, and with digestive tract bent in the form of a letter U. (Figs. 66, 129.)

Phoronidea. A single genus of worm-like 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.

Gephyrea. Worm-like animals of doubtful affinities.

CHAPTER XIII

ECOLOGY

Ecology embraces the study of the relations of animals and plants to the conditions in which they live. The discussion in this book has special reference to the ecological relations of animals. It has long been recognized that animals are dependent upon certain physical conditions, such as food and water, and that different forms require somewhat different conditions, for example that fishes require an aqueous medium, that some animals require plant food, and others animal food, etc. But the extent to which the peculiar combinations and intensities of the various physical and biological conditions existing in nature are necessary to the maintenance of the individuals of particular species, and to what extent the absence of these combinations and intensities may cause the destruction of the animals or influence their distribution, has but recently attracted the attention of zoölogists.

Several terms have been applied to the study of environmental relations, such as Hexiology (erroneously spelled hexicology by Mivart); Physiology of Organisms (Semper), as opposed to special physiology or physiology of organs; Bionomics (Lankester); and Oecology (Haeckel). These terms have been differently defined by different authors, but *Ecology* is now in general use and the conception that it comprises the study of all the relations of the animal to the environment seems to prevail.

Scope of Ecology.—Defined as the relation between the animal and the environment, ecology is a very broad subject and encroaches to some extent upon other fields. As so defined, it includes the relations of individuals or species to each other, such as colony formation, society formation, parasitism, slavery, symbiosis; and the relation of enemy and prey; and their relations to the physical environment, such as the effect of the chemical content and the temperature of the water, and the effect of the nature of the soil, temperature and moisture on land.

Structural Adaptations.—The relations of animals to the environment may be classified as structural and physiological. Characters whether structural or physiological which fit an animal for life under given conditions are commonly referred to as adaptations. The most conspicuous adaptations are those of structure, including color. Thus, to take a simple example, a fish is adapted to life in the water by having fins and gills which permit it to swim and respire in that medium, while terrestrial mammals are adapted to life on land by having legs and lungs.

Not all animals in the same environment are adapted in the same way to the conditions of that environment. Thus the manatee, whales and porpoises, all of them aquatic mammals, do not have the fins of fishes, and they breathe by means of lungs; and many terrestrial animals do not have legs. The fact remains, however, that animals living in different conditions are often structurally different, and these differences in structure may fit them for life in their respective environments. This does not mean that all differences in structure are adaptive, for such universal adaptation has not been established; but it is reasonably clear that animals are often structurally adapted to particular conditions, and are probably never found in conditions to which their structural characters are seriously ill-adapted. As more detailed examples of structural adaptations may be mentioned the suctorial disks on the toes of the tree-inhabiting frogs, the webbed or lobate feet of ducks and other aquatic birds, the tuberculate teeth of browsing animals like the elk, and the teeth with flat grinding surfaces in grazing animals like the bison.

Animals may also be apparently adapted to particular environments by their coloration. Whatever the explanation may be, many forms in a particular environment have a coloration which tends to conceal them by making them look like something in the environment. However, the dependence of forms so colored upon their resemblance to specific things in the environment has not been shown, and the resemblance may be much less adaptive than commonly supposed.

Physiological Adaptation.—The general physiological dependence of animals upon the physical conditions which surround them has also long been recognized, but the extent of this dependence and the difference in the effect of the same conditions upon different forms is only now coming to be appreciated. It is generally known for example that most of the marine animals cannot live in fresh water, nor freshwater species in salt water; that many northern animals are adversely affected by the higher temperatures of the tropics, while many tropical animals cannot be acclimated to temperatures which prevail in northern latitudes; that species which thrive in regions of moist conditions many times cannot live in desert areas; and so on. It is not, however, so generally known that the dependence upon certain conditions is so close as to cause differences in the local occurrence of a form in a very limited region and in the purely local distribution of nearly related species. The data show that the physiology of the animal is affected by many conditions of the environment, and that variations in any of the conditions may be measured from an optimum (most favorable condition) which may be quite different for different species. Thus water containing 6 cc. of oxygen per liter is said to be suitable for the brook trout while the Mackinaw trout requires less and is found in water with but 1 cc. of oxygen per liter. In one family of freshwater fishes the acidity of the water preferred

Colonies.—Colony formation has been considered in the chapter on cell aggregation, and it is not necessary to go into detail here. An animal colony is a union of numerous individual animals by an organic body connection. True colony formation results, as pointed out in Chapter V, only from the adherence of individuals produced by fission or budding. It is not accomplished by the coalescence of originally separate individuals; the fusion of separate cells of the slime-molds (Myxomycetes) into a multinucleate streaming mass (the plasmodium), and the secondary union of two individuals of a metazoön, *Diplozoön paradoxum*, in a permanent copulation, are not to be thought of as producing colonies. The marine hydroids and corals are examples of colony formation by incomplete division and budding. The colonies formed by budding may consist of thousands of individuals which have sprung from a sexually produced ancestor. Frequently in such colonies there is polymorphism, permitting the functions of the entire aggregation to be distributed among the individuals, so that there are reproductive units, units which capture and digest food, protective and sensitive units, etc.

Societies.—In social animals the reciprocal dependence of the individuals is much less than in colonial forms in that there is communal life but no organic connection. It is probable that the sexual impulse plays an important part in the formation of animal societies. It is known that under the influence of the sexual impulse many animals are drawn together temporarily; for example, sea urchins, many fishes and snakes congregate in numbers during the breeding season. Other forms are drawn together into loose but more persistent groups apparently principally because of the reproductive impulse and for the protection of the young; herds of gregarious mammals, like the bison and deer, are examples.

Finally there are very elaborate societies among insects, in which there is pronounced division of labor and polymorphism and thus reciprocal dependence. Many of the ants and bees live in complex communities composed of males and females (drones and queens) and others with degenerate female sexual organs (workers). The sexual forms give rise to the next generation, while the workers care for the home, provide the food, and serve for defence. Sometimes the workers are also divided into castes with a division of labor, a common division being that between true workers and soldiers, the defence of the colony being delegated to the latter.

Parasitism.—Individuals of different species often stand in close relation to each other because of advantages which they derive from one another or because of something which one furnishes to another. Where one form attaches itself to another and derives all the benefit, the association is called *parasitism*. A *parasite* is an animal which finds its dwelling-place upon or in the body of another animal, the *host*, and obtains nourishment from it. Parasitic forms have thus come into a more or less dependent condition and many of them have undergone such extensive changes in their organization as to make them incapable of life elsewhere than on or in the host. The following statement of the degeneration associated with internal parasitism, taken from Hertwig's Manual of Zoölogy, p. 168, will make this clear.

> "The degree to which a parasite has become dependent upon its host varies in the different species; it is determined by the extent to which the parasite has adapted itself to the organization of its host. Therefore it is necessary when speaking of parasitism to consider the changes of form which the parasitic mode of life has caused in the structure of animals. These concern most immediately the organs of locomotion and nutrition. Since a parasite needs to fix itself as firmly as possible to the host, the locomotor apparatus more or less completely disappears and an apparatus for fixation to the host becomes necessary; parasites of different groups are provided with hooks, claspers, sucking disks, etc. The blood, tissue-fluids, or liquid food of the host furnishes nourishment to the parasite; these are substances in solution which scarcely need digestion. Usually, therefore, the digestive canal is simplified or quite disappears; among the parasites there are gutless worms as well as gutless Crustacea. The mode of life of a parasite is also simplified, since it is no longer compelled to seek its food; in all parasites the nervous system and sense organs undergo a high degree of degeneration; the former becomes limited usually to the most indispensable portion; the latter, except those of touch, may entirely disappear."

There are two classes of parasites, those living within the host, *entoparasites*, and those living on the outside of the body, *ectoparasites*. Examples of entoparasites are tapeworms, which live in the alimentary canal, and liver-flukes, which occur in the liver; and among the ectoparasites may be mentioned lice, fleas and mites.

Symbiosis.—If the individuals of different species stand in close reciprocal relation the association is known as *symbiosis* and the associated animals are called *symbiotes*. Symbiosis is rare among animals, a classic example being that of the hermit crab, *Eupagurus pubescens*, and an actinian, *Epizoanthus americanus*.

> "Like every species of hermit crab this also inhabits a snail shell, from the opening of which only his fore legs and pincers are protruded. Upon this shell an Epizoanthus becomes attached and by budding soon covers it with a colony of polyps. 'After thus covering the shell it is not only capable of extending the aperture by its own growth, but also has the power of entirely dissolving and absorbing the substance of the shell so that no trace of it can be found, though the form is perfectly preserved by the somewhat rigid membrane of the polyp. The advantage which the actinian derives from this symbiosis is clear; it gains a share of the food which the crab obtains. It is less clear what the crab gains by the association; however, the polyp is perhaps a protection to him, by means of its batteries of nettle cells, while by growth it increases the size of the house occupied by the hermit, and thus saves him from periodic changes of abode." (Hertwig, Manual of Zoölogy, p. 170.)

Slavery.—Closely related to symbiosis is slavery. Social animals frequently not only hold other animals in bondage, but also protect and serve them. Certain ants, for example, use the secretion of plant lice, and some of the species protect the plant lice in various ways. Because of the mutual advantages in the relation of ants and plant lice, this relation is often called symbiosis rather than slavery. Some ants enslave ants of other species which gather food or even feed their captors. The dependence in the latter case may be very close, some of the slave-makers not being able to feed themselves.

Predaceous Habit.—Many animals are entirely carnivorous and many which have herbivorous habits are also flesh-eaters. Flesh-eating forms are frequently restricted in their diet, or at least feed principally upon a limited variety of animals. Thus there are *insectivores*, or insect-eaters (for example, many lizards which feed largely or exclusively upon insects); true *carnivores*, or flesh-eaters (as the dogs, which feed upon vertebrates); *piscivores*, or fish-eaters (the fishes whose main diet is fish); and so on. There is much variation in the diet of such predators, but the fact that many forms live exclusively upon animals and that many others must have animal food of a certain kind as well as plant food is an ecological relation of importance.

Mimicry.—A highly questionable kind of relation based upon the interrelation of animals of different species has been termed *mimicry*. It has been noted that in the same region with certain animals, known or supposed to have exceptional means of defence, are other forms without such means of defence which resemble them very closely. For example, in southern United States the venomous coral snake occurs in the same region as a harmless snake, *Cemophora coccinea*, which resembles it so closely that the two species cannot be distinguished at a little distance, unless it is known that in the color pattern of alternating rings of red, black and yellow there is a different sequence of colors in the two forms. Other examples are syrphid flies which mimic wasps, and numerous cases among the butterflies. The resemblance is often very close, and may involve both form and color. In each case one of the two forms has, or is supposed to have, some repellent or dangerous property which saves it from attack. The repellent form is regarded as the *model*, the harmless or defenceless species as the *mimic*.

It has been held that this resemblance is advantageous to the mimicking forms, on the assumption that they are avoided by their enemies because the latter mistake them for the repellent species, in which case a certain dependence might be claimed. It may fairly be said, however, that an advantage has not been established in any instance. Furthermore, the fact that the mimicking form may occur alone, and that in some cases two noxious forms resemble one another very closely, seems to show that the resemblance is fortuitous.

and so on. In those cases in which two or more species form galls on the same species of plant, or in which galls are produced on plants used in some other way by another species of animal, the gall-producing habit leads to the formation of animal communities.

Highly Specialized Relations of Animals to Plants.—A few instances of the relations between animals and the plants that serve as their food and perhaps protection are so intimate and mutually so advantageous as to require special mention. These relations are quite as close, in the examples to be described, as is the relation called symbiosis; but the term symbiosis is ordinarily applied only to relations between animals or between plants. The interdependence in these cases is, indeed, so specialized that it does not lead to the formation of animal associations, for in each instance only one species is thus related to a given plant.

MOTHS AND YUCCA. Moths of the species *Pronuba yuccasella* live upon the developing seeds of common Yuccas, and the success of the moths depends on a plentiful supply of these seeds. Now, seeds in plants develop only when the stigmas of the flowers are pollinated. The moths appear deliberately to collect the pollen from the flowers and apply it copiously to the stigmas, insuring the production of the maximum number of seeds. At the same time they lay eggs in the ovaries of the plant where the seeds later develop. There are always more seeds than are required as food for the moth larvæ, so that subsequent generations of the food plant are provided. Since the adult moth does not itself use for food the pollen which it collects, the habit of gathering it and placing it upon the stigmas has reference only to the success of the offspring. Since one cannot ascribe forethought to the adult moths in this case, their behavior is said to be instinctive; but the psychology of such remarkable behavior has never been satisfactorily explained.

INSECTS AND FIGS. A fig is a thick-walled hollow receptacle on the inner surface of which numerous minute flowers are produced. The fig does not attain its maximum size or best flavor unless these flowers are pollinated so that seeds are produced, and pollination is wholly dependent upon an insect, the fig-wasp Blastophaga. These insects enter the fig at a minute opening in the end, for the purpose of laying their eggs, and incidentally they carry pollen from some fig previously visited. The cultivated Smyrna fig is so constructed that the eggs of Blastophaga cannot be laid in it, but the insects visit it in search of a suitable place, so that the Smyrna fig receives the benefit of pollination without offering much in return. The insects must come from inferior wild figs in which their eggs can be laid, and it is the practice of fig-growers to hang wild figs containing Blastophaga ready to emerge in the Smyrna fig-trees when the flowers of the latter are ready for pollination.

Relations of Animals to the Physical Environment.—That various conditions in the environment participate in bringing about animal associations is obvious. It may be said in general that many physical conditions are effective, such as light, temperature, soil, and depth of water, and that intensities of the conditions are grouped in a very general way in nature. Thus in lakes there are different conditions of temperature, gases, bottom, light, etc., at different depths; and on land the soil conditions, temperature, moisture, and other factors are different in swamps, grass-land areas and forests. A study of the conditions in any one place soon reveals that there are not only freshwater, marine and terrestrial animals but that these general habitats may be divided. Thus there are lake, pond and stream forms, prairie and forest animals. Furthermore, detailed investigations show that each one of these groups or associations may be divided into numerous subdivisions, because certain forms prefer specific depths, temperatures, or chemical conditions in the water, or temperature, moisture, and soil conditions on the land. Along with these forms occur other more tolerant species which live in two or more associations, but these are not so numerous as to obscure the smaller groups. The following list of the animal communities of the streams and forests of a region on the south shore of Lake Michigan, adapted from Shelford, will illustrate the associations into which the animals of a region may be grouped according to physical conditions. The associations are named either from the nature of the habitat, or from the dominant plants.

- I. **Stream Communities.**
  - 1. *Intermittent stream communities.*
    - (*a*) Intermittent rapids associations.
    - (*b*) Intermittent pool associations.
    - (*c*) Permanent pool associations.
  - 2. *Permanent stream communities.*
    - (*a*) Spring dominated stages.
      - (1) Spring associations.
      - (2) Spring brook associations.
    - (*b*) *Creek and river communities.*
      - (1) Pelagic associations.
      - (2) Rapids associations.
      - (3) Sand or gravel-bottom associations.
      - (4) Sandy-bottomed stream associations.
      - (5) Silt or sluggish-stream communities.
        - (1) Sluggish-creek associations.
        - (2) Pelagic associations.
        - (3) Silt-bottom associations.
        - (4) Vegetation associations.
- II. **Forest Communities.**
  - 1. *Elm-ash series.*
    - (*a*) Low prairie associations.
    - (*b*) Marsh-margin thicket associations.
    - (c) Elm-ash association.
  - 2. *Tamarack or floating bog series.*
    - (*a*) Low prairie or floating bog associations.
    - (*b*) Marsh-margin thicket associations.
    - (*c*) Tamarack forest associations.

3. *Flood-plain series.*
    (*a*) Terrigenous river-margin associations.
    (*b*) Stream-margin thicket associations.
    (c) Elm and river maple associations.
4. *Clay series.*
    (*a*) Bare clay association.
    (*b*) Sweet clover association.
    (c) High forest-margin associations.
5. *Rock series.*
    (*a*) Bare rock associations.
    (*b*) Thicket association.
6. *Sand series.*
    (*a*) Lake-margin association.
    (*b*) Cottonwood association.
    (c) Pine association.
    (*d*) Black oak association.
7. *Climatic forest formation of the deciduous forest climate.*
    (*a*) Birch-maple association of the tamarack-forest series.
    (*b*) Oak-elm-basswood association.
    (c) Black oak, red oak association.
    (*d*) Red oak, hickory association.
    (*e*) Beech-maple association.

It is not to be inferred that physiological dependence upon or preference for certain physical conditions is the only relation which has brought about the above listed associations, for some animals are there because others are, or because of the presence of certain plants. However, the fact that the associations correspond in distribution to the physical conditions indicates that the relations between the animals and the physical conditions are in considerable part responsible for them. It has been demonstrated by physiologists that animals react differently to different stimuli, that a variation from the optimum in any one of the physical conditions essential to life constitutes a stimulus, and that the optimum may differ with different species. This has led to the conclusion that organisms differ in the nature of their protoplasm as well as in their structure and gives a basis for the interpretation of the phenomena of animal associations. The power of spontaneous movement makes it possible within certain limits for a species to find preferred conditions; animals with the same general physiological requirements drift together; and an animal community, based at least in part upon physiological dependence upon the physical environmental conditions, results.

Animal Reactions and Habitat.—The reference made in the preceding paragraph to preferred conditions and physiological requirements, as factors in the choice of habitats, and hence in the formation of animal associations, may easily prove misleading unless restricted in its application. In higher animals, those with some degree of intelligence, there may be such things as preferred conditions. Such animals may actually seek places where their physiological requirements may be met,

of Fasten's account of *Lernæopoda edwardsii*, a copepod parasitic on the gills of the brook trout, *Salvelinus fontinalis*, in Wisconsin and elsewhere. This parasitic copepod hatches from the egg as a free-swimming larval form which immediately by swimming with a darting spiral motion begins a search (?) for a proper host. Its body has a high specific gravity, hence it tends to settle to the bottom when the animal is not actively swimming. In strong light, sunlight or artificial, the copepod swims near the surface of the water or toward the light, because it is positively heliotropic. To weak light its reaction is less marked, and if the light is very weak, as at night, the copepod gives no reaction at all and because of its high specific gravity it sinks to the bottom. Its behavior to light is not interfered with by most of the chemical substances used in experiments; but if into a dish containing larval copepods, the freshly excised gills of the brook trout are placed, the copepods dart about as if they sensed something in the water. If they come in contact with the gills they attach themselves at once. If in place of the gills of brook trout, gills of rainbow trout are substituted the copepods do not attach. The latter effect is also obtained if gills of German-brown trout are used. Evidently something diffuses from the gills of the brook trout which does not come from the other species of trout mentioned. This must be a chemical substance. Observations on fish from the ponds show that only brook trout are infested by this parasite while the two other species of trout mentioned, as well as suckers and perch, are immune. The copepod gives a positive chemotactic response to the gills of the brook trout and not to the other fish.

Now, in the ponds during the day time the parasitic copepod swims near the surface in response to light; so also do the young trout, probably in response to light stimulus but also because of the presence of food organisms which likewise are positively heliotropic. At night the trout seek the bottom; and the parasite, because it does not respond to weak light and because of its specific gravity, likewise goes to the bottom. Again parasite and host are brought into close quarters. While this proximity of parasite and host is advantageous to the parasite, it is not deliberately sought. It is the animals' responses to certain stimuli which bring this parasite into relation with its animal environment.

Numerous other examples in support of the general conclusion that responses to stimuli determine the habitat or immediate environment of animals might readily be found. Sometimes these responses lead the animal to an advantageous situation, and may then be described as adaptive. Often, on the contrary, the reaction appears to be of no benefit whatever. The response cannot, however, lead to very harmful conditions, for the animals would then perish. Probably, in the evolution of animals, such ill-designed reactions have repeatedly originated; but if they did, their possessors perished, and we have left today only those whose reactions are useful, or neutral, or at most only slightly detrimental.

The Environment as a Whole.—The relations of animals to each other and to the physical environment have been considered separately, but it should be pointed out that it is the sum total of the physical and biological conditions affecting the life of an animal which make up the environment as a whole. The specific complex preferred by a species constitutes its habitat, and a change in any detail may determine the existence, abundance, and distribution of the form. The physical conditions, the plants, and the associated animals comprise a complex of environmental conditions so closely interrelated that variations in any feature may disturb the balance and render difficult or impossible the existence of a particular form. In this connection it should be stated that the physical conditions everywhere are changing and that the environments are thus unstable. Modern geography teaches that streams change with age in respect to the nature of the bottom, swiftness, etc., that the lakes tend to become converted into dry land, and that land may be elevated and subsequently lowered by erosion with consequent changes in soil, climatic conditions, etc. The geographical changes bring about changes in animal life; and since they are orderly a rather definite succession of associations can be shown to accompany them. For example, under normal conditions the associations in lakes come to be supplanted by those of ponds, the pond associations give place to those of marshes, and the marsh associations yield to land associations. The animal communities change in this order because this is the geographical sequence which leads to the disappearance of freshwater lakes.

Methods and Aims of Ecology.—The work of the ecologist may be defined as the determination of the animal associations and the relations of the members of each association to the environment, for the purpose of discovering the principles in accordance with which the associations are formed. In the gathering of data two groups of students have become at least partially differentiated: first, those who place chief emphasis upon the determination of associations and, second, those who pursue studies of a physiological nature, experimenting upon animals to determine the effects of varying intensities of the physical conditions which are found in the natural habitat. The differentiation among zoölogists is not as pronounced as it is in the field of plant ecology. There seems to be a growing understanding among zoölogists that while a knowledge of the associations is necessary, their composition is an end result of the reactions of the inhabitants to the features of the environment, and that the subject to yield results must concern itself with these reactions.

Ecology can hardly be considered a science comparable to morphology and embryology. It has a number of points of contact with other sciences, but it is apparently essentially intermediate between physiology and zoögeography. In so far as it concerns itself with the determination of the nature of the interrelations it is physiology, and the term physiological ecology has been used to designate this work. The results of these studies as well as the determination of the composition of the associations provide the data upon which zoögeographical studies must be based, if the latter phase of zoölogy is to be concerned with causes. The more important questions of geographical distribution of animals, which involves to a large extent the ecological relations, are reserved for the following chapter.

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taxonomic position as the genus. Thus the ranges of the species of the American genus Scaphiopus, the spade-foot toads, are given in a recent check-list as follows: *Scaphiopus couchii,* Texas to Arizona, northern states of Mexico, Lower California; *Scaphiopus hammondii,* western and southwestern states from Montana to Texas and Mexico, and westward to the Pacific states; *Scaphiopus holbrookii holbrookii,* eastern states, Massachusetts to Florida, west to Louisiana, Texas to Arkansas; *Scaphiopus holbrookii albus,* Florida Keys and possibly the extreme southern part of the peninsula of Florida; *Scaphiopus hurterii,* Texas.

Differences in Size of Range.—Just as there are great differences in the geographical position, so there are wide differences in the size of the range occupied by different forms. The ranges of the larger taxonomic groups (families, genera) are of course more extensive than those of their subdivisions (species, varieties), when they have more than one division, because of the wide differences in the position of the ranges of the lesser groups. Thus, the range of *Gopherus polyphemus,* one of the gopher turtles, is the coast of the United States from southern South Carolina to Florida and the Mississippi River and north into southern Arkansas; the range of *Gopherus agassizii* is in the deserts of southwestern Arizona, southern Nevada and southeastern California; and *Gopherus berlandieri* occurs in the southwestern corner of Texas and northeastern Mexico. Therefore the genus Gopherus which includes these three species has a range extending, with interruptions, from the Atlantic to the Pacific. Furthermore, the family Testudinidæ, which includes the genus Gopherus and a number of other genera, is cosmopolitan in the temperate and tropical regions except Australia and Papuasia.

There are, moreover, very great differences in the extent of the ranges of groups of the same rank, and great differences in the physical conditions inhabited by different forms. It has been stated above that the family Testudinidæ is cosmopolitan except in Australia and Papuasia. In contrast to this extensive range the family Carettochelydidæ (also turtles) is confined to the island of New Guinea, and the family Dermatemydidæ to Central America. The genus Camponotus (the carpenter ants) is found everywhere in North America (also on other continents) from the tops of the highest mountains to the lowest desert basin, from the Atlantic to the Pacific, and from the tundras of the north polar region to the tropical region along the gulf; while another genus of ants, Sympheidole, has been found only in the Garden of the Gods in Colorado.

Differences in the size of range of species may be illustrated by some of the North American species of the genus Hyla (the tree frogs). *Hyla versicolor* is found from southern Canada to the gulf states and from the Atlantic coast to Minnesota, Iowa, Arkansas and central Texas; *Hyla squirella* from Virginia to Florida, west to Texas, and northward up the

Mississippi basin to Indiana; *Hyla gratiosa* from South Carolina to Florida and Mississippi; *Hyla evittata* only along the Potomac and York rivers in Virginia and in New Jersey.

Differences in Continuity of Range.—It has long been noted that certain forms occupy a continuous area while others occur in two or more areas that may be distant from one another. Among the many examples which might be given, the following have been selected. Among the living genera in the family Camelidæ (the camels) one, Camelus (the camel and dromedary), occurs in central Asia and northern Africa; and another, Auchenia (the llama and vicuna), is found in western South America. The genus Alligator (the alligators) is composed of two species, one to be found in central China, the other in southeastern United States. These are groups comprising only a few species in each case, yet there are wide gaps in their known ranges. Perhaps more striking is the discontinuity sometimes found in the spread of a single species. Thus, the skink *Leiolopisma laterale* is found in the southeastern United States and in China and certain of the southern islands of the Japanese archipelago. The Central American and Mexican frog, *Leptodactylus albilabris*, occurs in the West Indies (on the Virgin Islands, Vieques and Porto Rico) as well as on the mainland.

It is well established that discontinuous distribution occurs more frequently and is more pronounced in the larger taxonomic categories, that is, it is more common and the gaps are wider in genera than in species, in families than in genera, in orders than in families, etc. Indeed it is so rare in species as to make it a matter of doubt in most instances whether discontinuity of a species range may not be due to convergent development; that is, it may be that the forms in widely separated areas which look so much alike that they are regarded as the same species are not really so closely related, but have come to resemble one another by an independent evolution towards the same goal. Discontinuity in the range of a species may also be due to transportation by man, or to accidental dispersion by nature, such as transportation to islands by means of floating vegetation.

A fact in regard to discontinuous distribution that is constantly receiving confirmation, particularly from paleontology, is that groups now interrupted in distribution were at one time continuous. Thus the presence of fossils shows that the camels, now in two or three regions separated by thousands of miles, formerly occurred more widely in Asia and also in North America; that tapirs have occurred in Europe, Asia and North America, although now found only in the Malay Archipelago and tropical America; and that a near relative of the alligators formerly ranged widely in North America and Europe. So much evidence of this kind has been obtained that it is now generally concluded that the distribution of groups with interrupted distribution was at one time continuous, except where accidental dispersal across barriers or dissemination by man has taken place.

Difference in Physical Conditions in Different Ranges.—The range of certain animals is in a general way coincident with areas characterized by certain general physical conditions. In North America, the open, treeless areas of the west comprise the principal range of the prong-horn antelope, bison, ground squirrels, and many other forms. The eastern deciduous forest areas are inhabited by many forms that are mostly restricted to them, as the opossum, grey fox, fox squirrel, cardinal bird, Carolina wren, and yellow-breasted chat. The coniferous forests of the north are the home of many species which extend little if any beyond them, such as the snow-shoe rabbit, pine martin, northern jumping mouse, three-toed woodpecker, and spruce grouse.

The fact that within areas characterized by certain physical conditions are found animals and plants which do not extend far beyond their limits has led to the recognition of major environments (Fig. 203), which may be divided into smaller environments (Fig. 204). The conspicuous plant associations of these environments afford a convenient means of designation, and coniferous forest areas, deciduous forest areas, bunch-grass areas, etc., are recognized. The environments are not sharply separated but intergrade on their common boundaries. Often this intergradation takes the form of interdigitation; that is, the regions dove-tail together. The interdigitation of the plains areas of the United States with the eastern deciduous forest regions is described by Ruthven as follows:

> "It has been shown elsewhere that the prairie region cannot be merged with the forest regions of the states east of Illinois, but that neither, on the other hand, can it be classed with the arid plains. The environic conditions differ from those of the eastern forest region in being more arid and principally characterized by grass associations, and from the arid plains in being less arid and supporting a greater tree growth. Furthermore and in harmony with these conditions the terrestrial vertebrate fauna consists almost entirely of a mixture of eastern and western forms. In view of these conditions the region must be considered as a transition area.
>
> "This point will not be discussed further, but it should be noted that the different elements in the fauna of northwestern Iowa occupy, as a rule, different habitats—the prairie forms being western and the marginal forest forms eastern types, while in general it is those associated with the aquatic conditions that occur in both regions. For instance, it is in the marginal forests along the shores of the streams and lakes (also now in the groves) that one finds the blue jay, Baltimore oriole, red-headed woodpecker and many other forms characteristic of the forests of eastern North America; it is on the prairie that one finds the prairie hare, thirteen-lined spermophile, Franklin spermophile, western meadow lark, grasshopper sparrow, prairie chicken, burrowing owl and many other distinctly arid forms; while it is in the aquatic habitats that one finds the generally widely distributed water birds and amphibious mammals."

From this description it appears that the prairies are intermediate between the forest regions and the plains in the same way as a checkerboard is intermediate between a plain white board and a black one. The checkerboard is not gray, but a patchwork. While on a map of

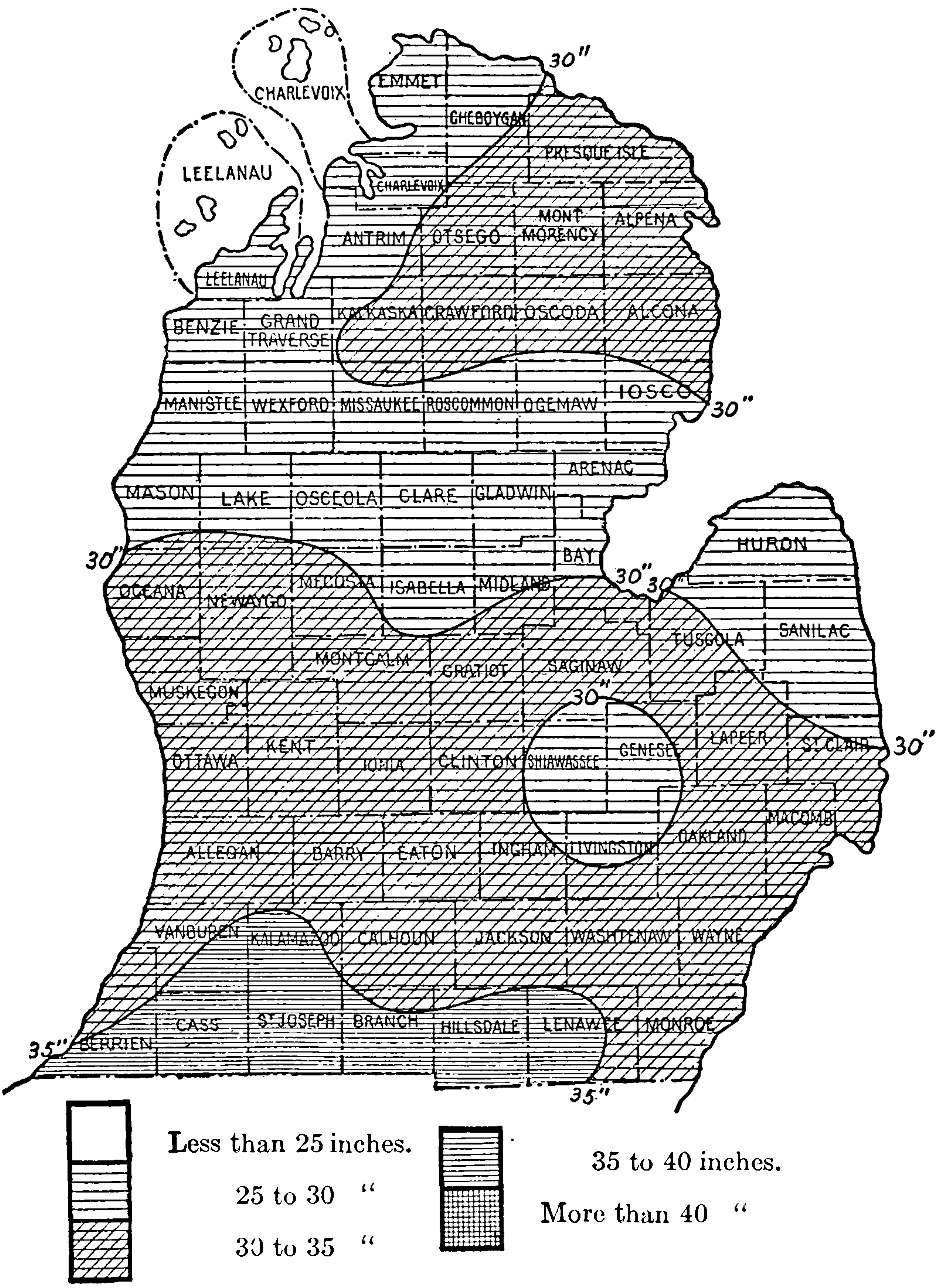

FIG. 205.—Annual rainfall in the lower part of the state of Michigan. This illustrates the differences in physical conditions which may prevail even in relatively small areas. (*After C. F. Schneider, Pub. 9, Mich. Geol. and Biol. Surv.*)

distribution typical plains animals and typical forest animals would occur together and so appear to indicate intermediate conditions, these forms tend to be distributed as an inlay or mosaic.

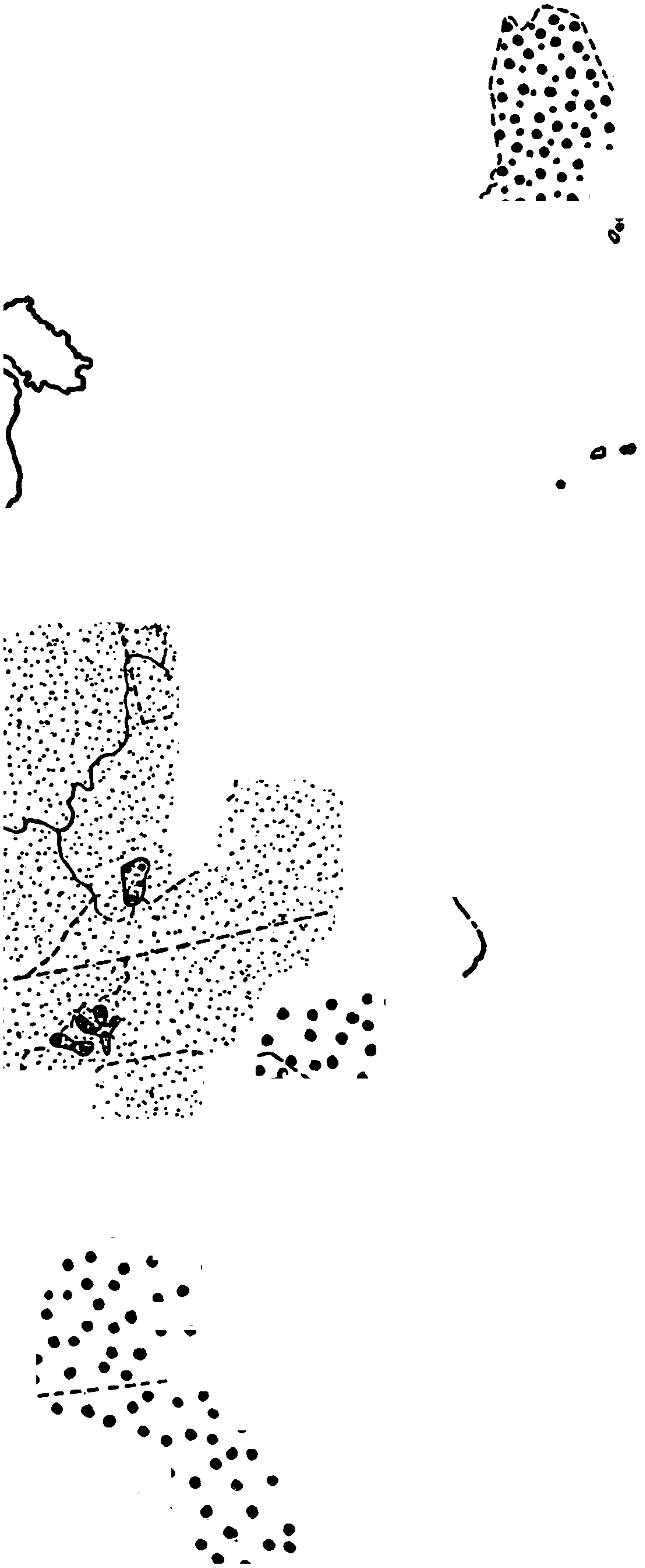

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FIG. 207.—R his sauritus
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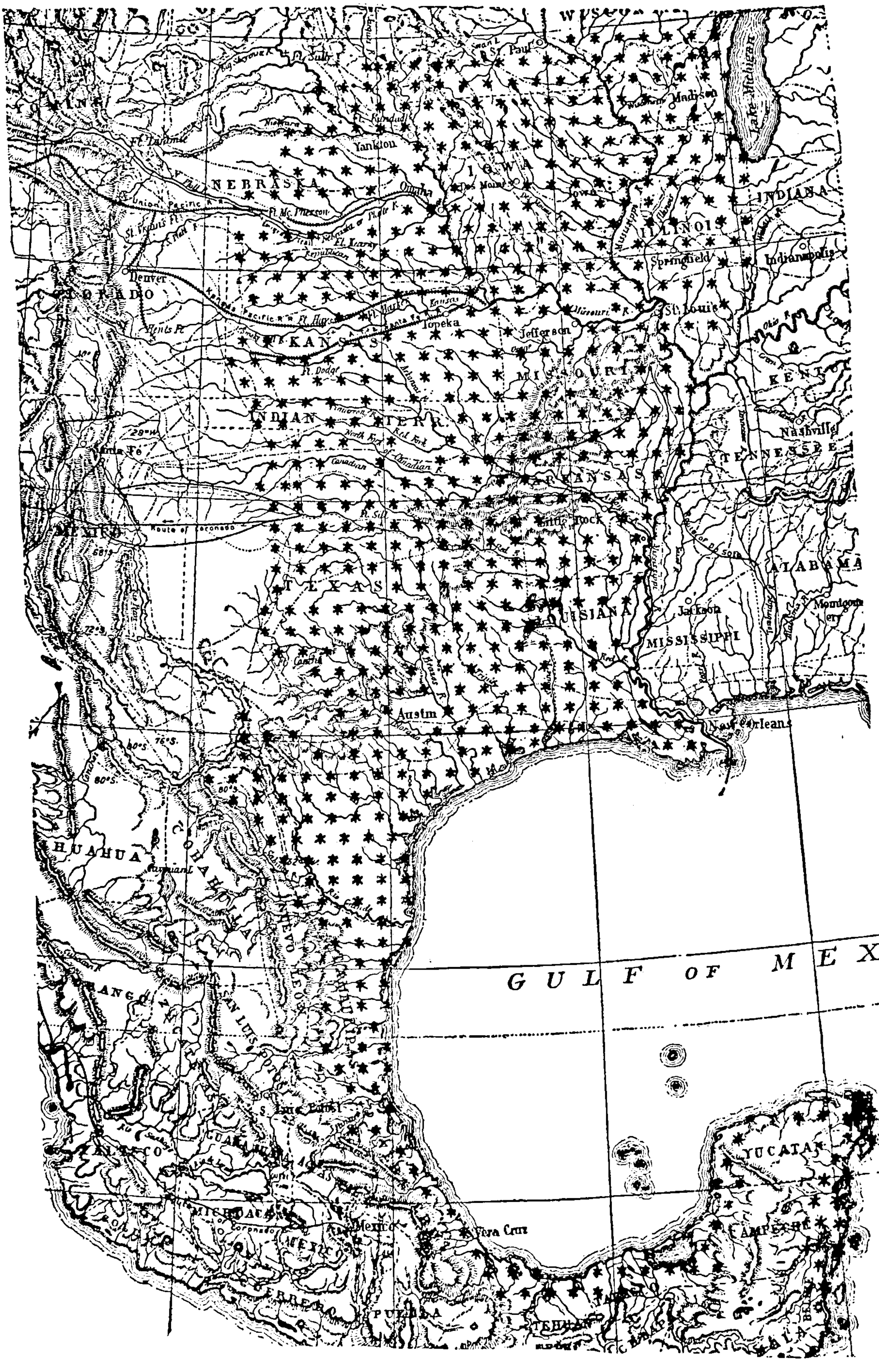

FIG. 207.—Range of *Thamnophis sauritus proximus* (Say), the western ribbon snake. (*After Ruthven.*)

short of the regional boundaries in certain directions. Many species may even have an extensive range in two or more areas. Thus *Rana pipiens*, the common leopard frog, occurs in general over all of North America east of the Sierra Nevada Range; and the raccoon, *Procyon lotor*, frequents the deciduous forests of eastern United States and the prairie-plains region as well. If all animals showed as little relation to natural vegetation areas as do these two, the major environments mentioned above would probably never have been recognized. Without pursuing this unconformity any further it may be said that there are two classes of animals which frequently ignore the major environments; first, terrestrial forms which are tolerant of a wide range of conditions, and, second, more or less aquatic forms. The leopard frog probably owes its general distribution mostly to its semi-aquatic habits, and the raccoon to its tolerance.

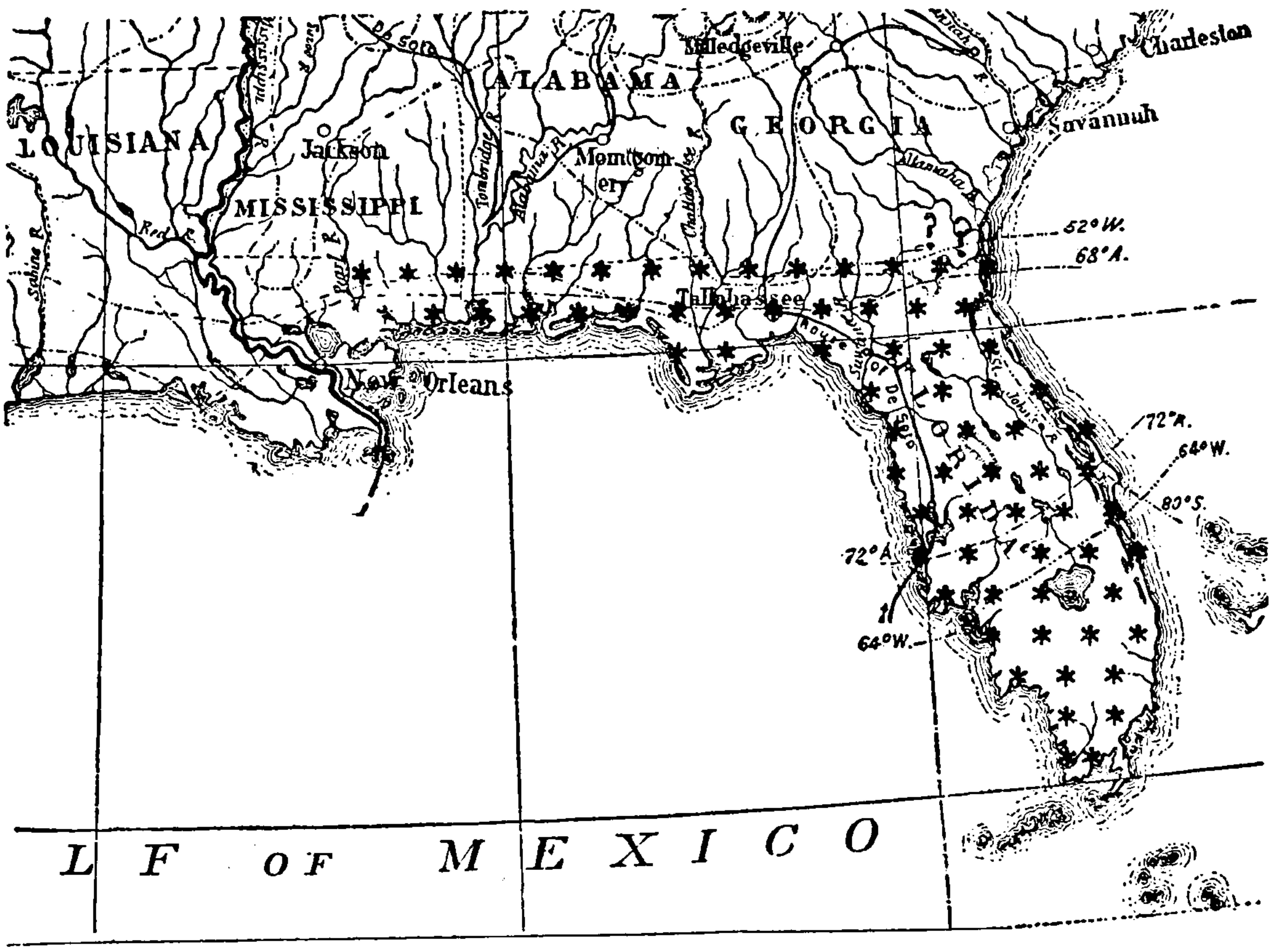

FIG. 208.—Range of *Thamnophis saurítus sackeni* (Kenn.), the southeastern ribbon snake. (*After Ruthven.*)

In view of the facts (1) that the apparent major environments are occupied to a different extent by different animals, (2) that many species which are chiefly confined to them transcend their limits, and (3) that many species occur over a large part of two or more regions, it may be concluded that these areas, when regarded as animal regions, are more apparent than real. They are the ranges of conspicuous plants with which are associated in certain parts some animals and plants which find there congenial conditions. These areas are not units in their biotas (animals and plants), since they mark the limits only for some of the included species, not for others. A line so drawn as to separate evergreen from deciduous trees, or two species of mammals from one another, may not separate any other two groups of organisms. However, it is often convenient to recognize these major environments, because a genus may be divided into its component species by the regional boundaries, or the range of a species may stop on or near their limits. The range of the North American flying squirrels (Fig. 206) illustrates this correspondence with the vegetation areas. Thus the range of *Glaucomys volans* is in general the deciduous forest region and is limited to the west by the great plains, and to the north by the coniferous forests, while the range of *Glaucomys sabrinus* closely approximates that of the coniferous forests of the north and the mountainous regions of the west.

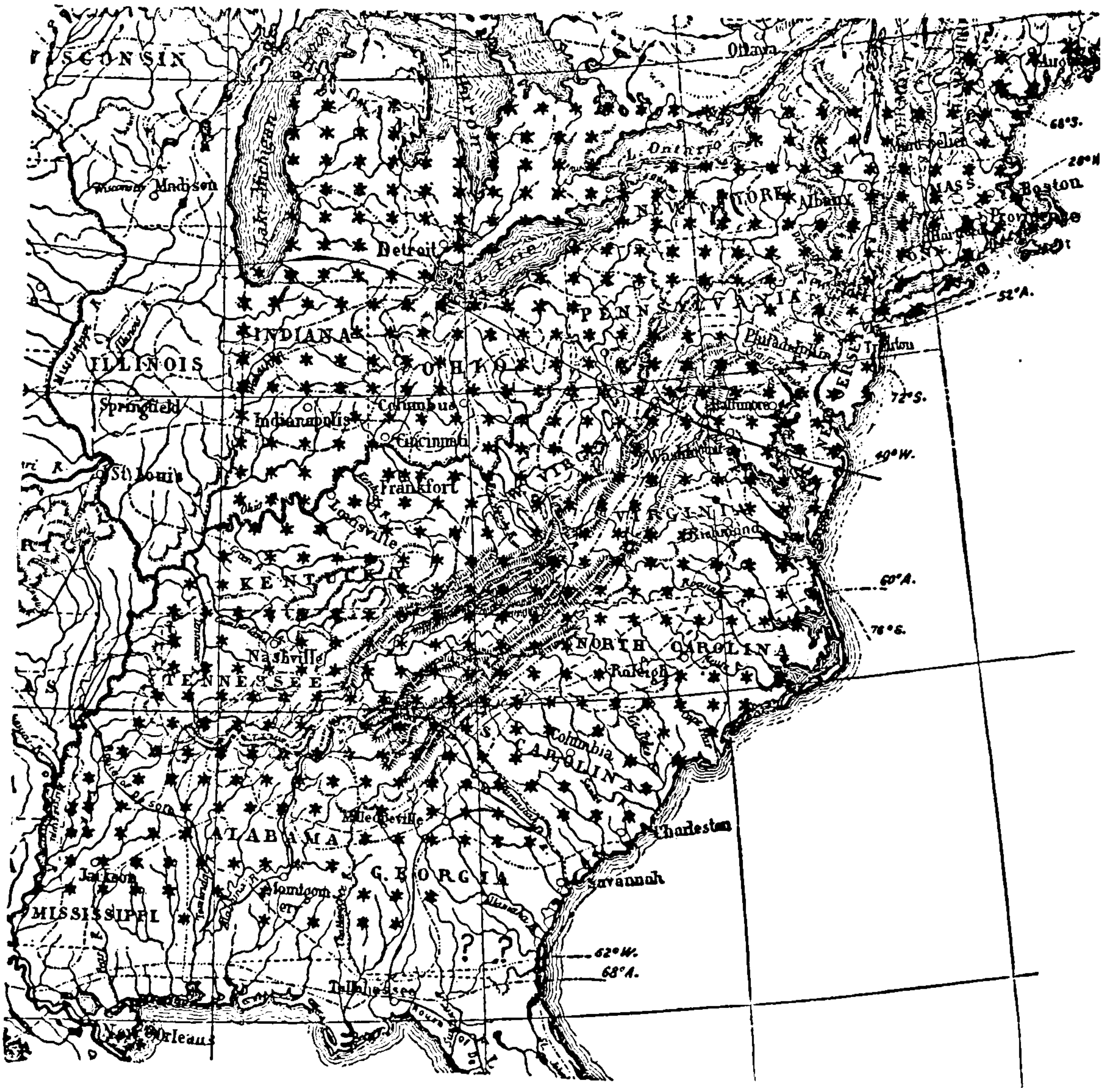

Fig. 209.—Range of *Thamnophis sauritus* (Linnæus), the eastern ribbon snake. (*After Ruthven.*)

Migration.—An important factor in geography is the wanderings of animals. Migration in some form or other is a fundamental attribute of animals. There are several kinds of migration, which may be termed periodic, sporadic, and normal.

Periodic Migration.—Certain forms 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 freshwater 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. This kind of migration may be called *periodic*, and it is doubtful whether it is effective in extending the range.

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 mammal related to the rats and mice. 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 the Pallas 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. A good example is the mouse plague of 1907–1908 in the Humboldt Valley, Nevada. This irruption has been described[1] as follows:

> "Always present in Humboldt Valley, these mice (*Microtus montanus*) attract little attention when in small numbers. Usually they are not uniformly abundant in the district; in fact in many of the fields they may not be present at all. They live in scattered colonies in swampy places; along the borders of sloughs and irrigation ditches; in salt grass patches and in similar damp areas. When in normal numbers a little damage may be noticeable about the borders of fields or along ditches where plants have been killed during winter and spring. Ordinarily the mice are very prolific, each pair producing 4 to 6 litters of about 6 young each during the long breeding season, which extends from March to November; and probably the young born early in the season breed before fall. Occasionally conditions favor excessive multiplication, and under such circumstances damage soon becomes evident, and in a single season may increase locally to the serious injury of fields. Extending from such centers during the next breeding season, and increasing not only by reproduction but by joining with other colonies, a vast army of mice is formed. Because of overcrowding and the limitation of food, such armies invade adjoining districts, and this progress becomes more rapid with the disappearance of green food in the fall. Through the combination of several such armies, entire districts are overrun.
>
> "Damage by field mice attracted the attention of the ranchmen in the lower part of the Humboldt Valley early in the spring of 1906 and became severe during the following summer. In the fall and winter of 1906–1907, damage had increased until fields here and there in the valley were seriously injured. Extensive ravages first occurred above and about Lovelocks. In May, 1907, fields on the Rodgers ranch, 5 miles below Lovelocks, were invaded from the lands farther up the valley, the progress of the mice being plainly marked, as the fields above the Rodgers ranch suffered first. The movement of this great body of mice, it should be noted, was a gradual, scattering progression, first by a few and later by increasing numbers, until the greater part had moved to fresh fields. Numbers, however, finding conditions improved, remained as stragglers in the fields deserted by the main body.
>
> "By October, 1907, a large part of the cultivated lands in this district had been overrun by vast numbers of mice. The yield of hay had been reduced by one-third; potatoes and root crops were largely destroyed; many alfalfa fields were ruined by the mice eating the roots of the plants; and the complete destruction of this, the chief crop of the valley, was threatened.
>
> "The height of abundance was reached in November, when it was estimated that on many large ranches there were from 8000 to 12,000 mice to each acre. The fields were riddled by their holes, which were scarcely a step apart, and over large areas averaged 150 to 175 to the square rod. Ditch embankments were honeycombed, and the scene was one of devastation. Serious losses in hay and root crops during the summer proved but a slight forerunner of the damage which began in the fall with the disappearance of green food. Burrowing down

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[1] U. S. Dept. of Agriculture, Farmers' Bulletin 352.

> about the plants, and extending their underground runs from root to root, they either killed or seriously injured the alfalfa. By November they had destroyed so large a percentage of the plants that many fields were plowed up as hopelessly ruined. They attacked also the roots of trees, seriously injuring or quite destroying orchards. They killed most of the young shade trees planted along ditches, and so completely girdled large Lombardy and silver poplars that in some cases they caused the death of even such hardy trees.
>
> "By January, 1908, in fields where the mice had existed by thousands the previous summer and fall, comparatively few, possibly 200 to 500 to each acre, remained. The border of the destroyed district was about 6 miles below Lovelocks, and the mice were gradually moving farther down the valley. In the area below this mice were somewhat in excess of normal numbers and in several centers of abundance had seriously injured fields. Even where most abundant, along the lower border of the affected area, they did not exceed 1500 to the acre. In the winter they attacked every available food supply. Small willows and even greasewood bushes about the borders of fields were stripped of all the bark within reach, and horse and cattle droppings were gnawed to pieces for the food they contained. Alfalfa roots, however, were the food supply on which the mice were chiefly dependent."

Apparently *sporadic migration*, as these irruptive movements may be termed, does not usually result in an extension of range, for the species are not in the cases observed able to maintain themselves in the invaded regions. However, it is at least not impossible 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 sporadic migration.

Normal Migration.—In addition to the above types of migration, and some variations of them, every species has a kind of movement which may be called *normal migration.* This is best seen in free-moving terrestrial forms. Among the individuals of such forms there is constant movement; and either as individuals or as flocks they wander about over a larger or smaller area, according to their powers of locomotion, to seek food, escape enemies or find mates. After the young are born they also begin to wander about in search of food, with the additional incentive of finding a new home. The individuals on the outskirts of the range thus constantly tend to invade new territory, and where not delimited by unfavorable conditions the form gradually spreads. In the absence of physical barriers the individuals of a species are held together by breeding instincts, so that each individual does not tend to wander far away from its fellows, or if it does it dies without progeny. It is for this reason that the spreading from the periphery of the range is relatively gradual. When the powers of migration and propagation are great the movement becomes more rapid. An illustration of the rapid spreading of a species

Again if a human family moved gypsy fashion, only on one day of each week, and not more than three miles, then it would wander about 156 miles each year, and the Mongolians, crossing Behring Strait might have, at this rate, reached the Straits of Magellan in about fifty years. It is thus believed by zoögeographers that normal migration is at once the general and most effective method of extending the range and that it is sufficient to account for the size of the range of most animals.

Accidental Dispersal.—Reference to accidental dispersal has been made in the discussion of discontinuous ranges. 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, which may be called *accidental,* is efficacious in extending the range, but the claim has very little supporting evidence. The possibility that islands may have received certain forms by accident is not to be ignored; but there are many difficulties in accounting for the entire faunas of islands in this way. Some of these difficulties are the inability of some forms to survive a long sea voyage, the fact that many island forms, such as the giant tortoises, could not possibly be carried on rafts or blown by the winds, 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. A conservative view is that it may operate at rare intervals and for certain forms, and most often over short distances.

Distribution by Man.—Human agency is responsible for the introduction of animals and plants to new regions in a few cases that are well known, and probably in numerous cases of which we are ignorant. Introduction may have been designed, or accidental. Sometimes the forms thus introduced have flourished exceedingly in the new range, witness the rabbit in Australia, the cotton boll weevil in southern United States, and the English sparrow in America. These instances lend color to the view that many species, living with moderate success or with difficulty in regions now occupied by them, require only to be transported to other places to multiply with rapidity or even to become dominant forms. It is not improbable that species that appear to be on the road to extinction owe the reduction in their numbers either to changes in their environment or to changes in themselves, and that removal to a habitat not ordinarily accessible to them would spell the difference between destruction and rehabilitation.

Dependence Upon Environmental Conditions.—Another factor of distribution is the dependence of each kind of animal upon certain conditions. This is discussed in the chapter on ecology, but it should be pointed out here that since animals are physiologically and often morphologically dependent upon certain conditions, the absence of these conditions will limit the range of the species in nature; or, as is often said, conditions other than those to which the animal is adjusted constitute a barrier to migration.

Barriers to migration are of two kinds: first, barriers that cannot be passed by means of the powers of locomotion of the animal, and second, uninhabitable areas. An expanse of salt water, such as intervenes between islands and the mainland, is a barrier to many land animals because they cannot swim across it, while a plains area is a barrier to typical forest forms, such as flying squirrels, not because they cannot move about on the plains but because the conditions of life are so unfavorable for existence that the forms cannot spread across them. The nature and effectiveness of barriers can easily be shown to depend upon the nature of the animal. Conditions which serve as a barrier to some animals will not act as a barrier to others. Furthermore, any feature of the environment, whether temperature, moisture, size of area, soil, absence of food, vegetation, other animals, or any other condition, may be the specific cause of unfavorableness if the animal is closely dependent upon some quality or degree of that feature.

Diversity and Mutability of Environment.—Closely related to migration as a factor of distribution and to the physiological and morphological dependence of animals on specific conditions is the diversity and changeableness of the earth's surface. It is common knowledge that there are great differences in temperature between the equatorial regions on the one hand and the polar regions on the other; that there are great differences in temperature between places in the same latitudes, depending upon altitude and upon the presence of large bodies of water, ocean currents, etc.; that the amount of rainfall varies enormously, being in some places as high as 100 inches annually and in others as little as a trace for years at a time; that there are great differences in soil; that some regions have only a very scanty desert flora, others are open grass lands, and still others are covered with forests which vary in density and the species which compose them; and that the waters vary in chemical composition, depth, size, etc., in addition to temperature. In fact there are no two areas that are exactly the same in the conditions which may affect animals, and no single area, if at all extensive, is the same throughout.

The data of geology also reveal that the physical conditions on the surface of the earth are constantly being altered, and that the changes which have taken place in the past are very great (Figs. 243 and 244).

Continents have been broken apart and united, islands have appeared and disappeared or been connected with and severed from the mainland, and climates have changed. Even at the present time it is evident that mountains are being destroyed, lakes filled in by débris, and the chemical nature of the water is being changed in many places. Moreover, with the constant modification which the surface of the earth has undergone and is undergoing the vegetation also has changed and is changing, as is evidenced either by a displacement of one association by another, such as a forest by a prairie, or by an alteration in the composition of the plant associations.

From what has been said concerning migration and dependence upon environments it will be readily perceived that the earth provides a multitude of environments, each of which may serve in turn as a barrier to a form in a neighboring region. A region which it has been impossible for an animal to enter may undergo such a change in some one or more of its physical or biological features that it no longer serves as a barrier. Thus the range of the potato beetle as stated above was, previously to 1850, apparently restricted on the east by the absence of a suitable food plant in the adjoining territory, but when a food plant was introduced migration in this direction began at once. Another instance, on a small scale, has recently been noted. Previously to 1907, the fox squirrel, a forest animal, was in northwestern Iowa confined to the timber along the larger streams. Since that date, owing to the number and size of the trees planted on the prairies by the residents, the squirrel has spread over large parts of the prairie areas. That changes on a much greater scale have in the past resulted in extensive changes of range seems to be shown by paleontology. Thus there is reason to believe from the relations of the faunas that Madagascar was at one time connected with Africa, South America has been joined to Australia and New Zealand, and North America and Asia have been united. Extensive migrations of animals have apparently occurred between these countries and then been halted by a breaking of the connections. Similarly the great changes in climate which occurred in North America and Europe during the Pleistocene epoch, from somewhat more equable and milder conditions than prevail at present, to polar conditions, brought the musk-ox, caribou, reindeer and similar forms into the United States and Europe far south of their present ranges.

Extinction.—Complete annihilation of a species in any region is also to be regarded as a factor of distribution, though in a sense somewhat different from that in which the preceding agencies are factors of distribution. Extinction does not affect the process of distribution, but it does help determine the range occupied. Extinction of itself neither helps nor hinders the spread of animals to new regions; but the destruction of the form in some part of the area occupied by it changes the range.

directions it is limited by unfavorable conditions either throughout its life or for some time. In other directions it extends its range. Anywhere within its range new types of individuals may arise through the process of evolution. These new types may be fitted to occupy new regions, and if they are formed near the limits of the range they may find opportunity to spread into areas which are inaccessible to the unaltered members of the species. Thus may arise recognizably distinct forms coincident in range with certain environmental conditions. If particular forms, or the individuals of a single form, are accidentally (or possibly by sporadic migration) transferred across barriers the distribution of the group becomes discontinuous. If these processes have been going on for a long time, that is, if the common ancestors of a group of forms existed long ago, the range may have had time to become very extensive, or its discontinuity very marked. If, contrariwise, the ancestors were comparatively recent, the range is likely to be much smaller. For this reason, groups that have diverged far enough to have attained the rank of families are on the whole more widespread than those so nearly allied as to be considered genera. Should the environment become altered within a given range, the occupying form might be driven from it or destroyed. If the environment in a region adjoining a range should change in a favorable manner, the range might be extended at that point without any alteration on the part of the animals.

The distribution of animals is inferred to be in harmony with this method, which involves, it will be noted, the factors of migration, evolution, physiological and morphological dependence upon the environment, the diversity and changeableness of the earth's surface, and extinction; and in this manner are explained the differences in geographical position, differences in size of range, differences in the continuity of range and the fact that ranges are at first continuous, differences in physical and biological conditions which characterize the ranges of different forms, and the geographical proximity of apparently related forms.

Methods and Aims of Zoögeography.—The principal data of zoögeography are museum specimens and published records of the occurrence of the forms. Modern museums endeavor to preserve specimens with detailed locality data and to obtain material from every part of the range of each species. From the museum specimens and records (and the student must usually obtain them from as many museums as possible) the ranges are described or mapped. The descriptions are usually brief summaries in which the localities on the outskirts of the known range are given. For example Stejneger and Barbour give the range of the frog *Pseudacris ornata* as "South Carolina to Florida, west to Texas," and that of *Pseudacris feriarum* as "Eastern United States, west to Illinois." When the distribution is mapped this is usually done by plotting the known localities or by connecting the outermost locality records and covering the enclosed area with symbols or shading. At present an increasing number of museums are endeavoring to preserve ecological data, and in time it should be possible to describe the range in terms of the environmental conditions; for example Stejneger and Barbour describe the range of the small blind snake *Siagonodon humilis* as "Deserts of Arizona, southern California, Lower California and northwestern Mexico." An advantage of this method is that it permits the student to judge of the possible completeness of the data, for if the principal range of a form as indicated by the records lies within a particular environment it is more liable to occur in parts of this environment which have not been explored than in adjacent areas having different conditions.

Many of the generalizations in zoögeography have been concerned with attempts to discover and delimit so-called natural regions. The fact that several species of animals are apparently limited in range by one factor in the environment, such as particular temperatures, and that conspicuous species of plants may have the same limitations of range has led students to attempt the delineation of areas on the basis of certain features and aggregations of forms. Thus the world has been divided into *major regions* or *realms* and the continents into smaller *provinces* or *life zones*. A critical study of these regions shows that they are principally based upon one or a few groups, for example, mammals, or mammals and birds; that students of different groups fail to agree on the extent of the regions; and that, as far as the inhabitants are concerned, they are based upon averages. In other words, neither different groups nor different forms in the same group respond equally to any one feature in the environment. This is what we are led to expect from the data of ecology. It would seem to follow that since each kind of animal is adapted to certain specific conditions, though there may be certain general regions for particular groups, the search for faunal regions applicable to several groups and based on one or a few environmental factors is hopeless. Progress in interpreting the distribution of animals can be made only by working out the geographical history of each group separately, and attempting to discover the several factors which have influenced its wanderings.

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Scharff, R. F. Origin and Distribution of Life in America.
Scharff, R. F. The History of the European Fauna.

CHAPTER XV

PALEONTOLOGY

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. When concerned with animals only, it is sometimes called paleozoölogy as distinguished from paleobotany. Anything having to do with animals not now living, and of which we have no knowledge except that derived from their remains, is part of paleontology. The paleontologist may study structure and classification only, or he may be interested in distribution, or in modes of life and relation to environment, or in the evolution of past animals. Thus for nearly every feature of the zoölogy of modern animals there is a corresponding branch of paleontology. Many facts concerning organisms of the past can only be inferred, and there is no way in which experiment may be applied to extinct forms; but in some other respects the paleontologist has sources of information far superior to any possessed by the student of modern life.

Nature of Fossils.—A *fossil* is, literally, something dug up. As ordinarily used, the term includes any trace of prehistoric life. Fossils are usually petrifactions of parts of the animals or plants themselves, but may be any other signs of the existence of such life. The term usually implies that the parts or traces of organisms have been buried, though this feature should probably not be insisted upon. In rare instances animals have been preserved in the flesh, almost as successfully as if immersed in spirits in a museum. Large mammals have been removed from peat bogs in various parts of the world, still in a good state of preservation. Mammoths (elephant-like animals) have been buried in frozen soil in Siberia and elsewhere for thousands of years, and then recovered practically intact (Fig. 211). Oil-bearing soils in central Europe have yielded a rhinoceros and a mammoth with some of the flesh still in place. Small animals, such as insects and even lizards have been found entire in deposits of amber. This substance is of resinous nature and of uncertain origin, being perhaps derived from pine trees. At first liquid, it flowed over and embedded the small bodies without injury to them, and then hardened. Some of the most beautiful of fossil insects are of this kind.

histological details, such as the structure of the kidney and of striated muscle are observable in fossils.

The remnants which we call fossils may represent the original animals in very different ways. In some, the original structures are practically unchanged; in others they are completely replaced with minerals; and between these extremes there are various degrees of replacement. The animals, or parts of them, were buried in deposits of silt at the bottom of bodies of water, or under wind-blown material. Bones buried in dry sand in an arid region may be practically the same bones today. But bones buried in silt, which later hardened into layers of rock now far beneath the surface of the land, have been constantly subjected to the action of percolating ground-water. Particle by particle they have been dissolved away, and bit by bit replaced by deposits of minerals carried in solution in the water. This replacement by minerals is known as *petrifaction*. The petrified object is not converted into minerals, it is merely replaced by minerals. In one fossil this replacement may have gone to completion, the original substance being entirely absent, in another the original material may be interspersed with islands of mineral deposits. In general, the older the fossil the more nearly complete is its petrifaction.

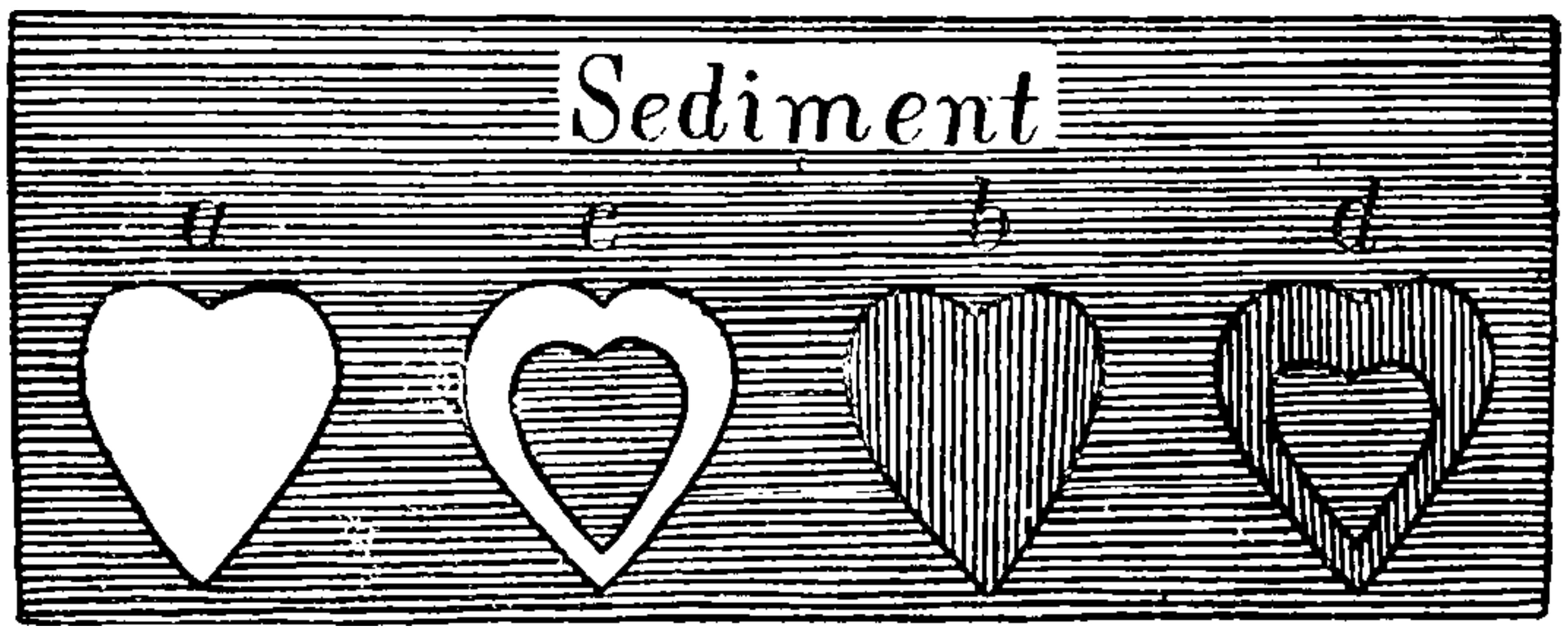

Fig. 213.—Diagram illustrating molds and casts. Horizontal shading represents sedimentary deposits, vertical shading the material subsequently filled in. *a*, mold of a shell which has been dissolved away by ground water; *b*, cast formed by subsequent filling in of the cavity of *a*; *c*, mold of a shell whose interior was filled with sediment; the shell itself was subsequently removed in solution; *d*, cast produced by filling the mold represented in c. (*From Schuchert's Historical Geology. Courtesy of John Wiley and Sons.*)

Molds are produced when the hard substance of a buried animal is dissolved away, but is not replaced by minerals. A cavity in the rock is thus formed, showing the external form of the original. This mold may be subsequently filled, forming a *cast;* but since the original was not replaced particle by particle the internal structure is not preserved. Figure 213 illustrates the relation of molds and casts to the original object. Casts may also be formed in the cavities of natural objects, such as snail shells; but here also the internal structure of the animal is not shown. Molds and casts are regarded as fossils, though no part of the original object is represented.

Animal *tracks* may also be fossilized by being filled in with later deposits of sediment. When the deposits solidify into rock, and are split apart, the lower stratum contains a mold, the upper one a cast, of the animal's foot. Figure 214 represents such a foot-print. The marks of raindrops in clay have been preserved in a similar manner (Fig. 215), but since they are not animal remains it is questionable whether they should be called fossils at all. Plant impressions are likewise very common, a

Fig. 214.—Footprints of two dinosaurs (one large and one small) and rain-marks preserved in a slab of Triassic sandstone. (*From Schuchert's Historical Geology. Courtesy of John Wiley and Sons.*)

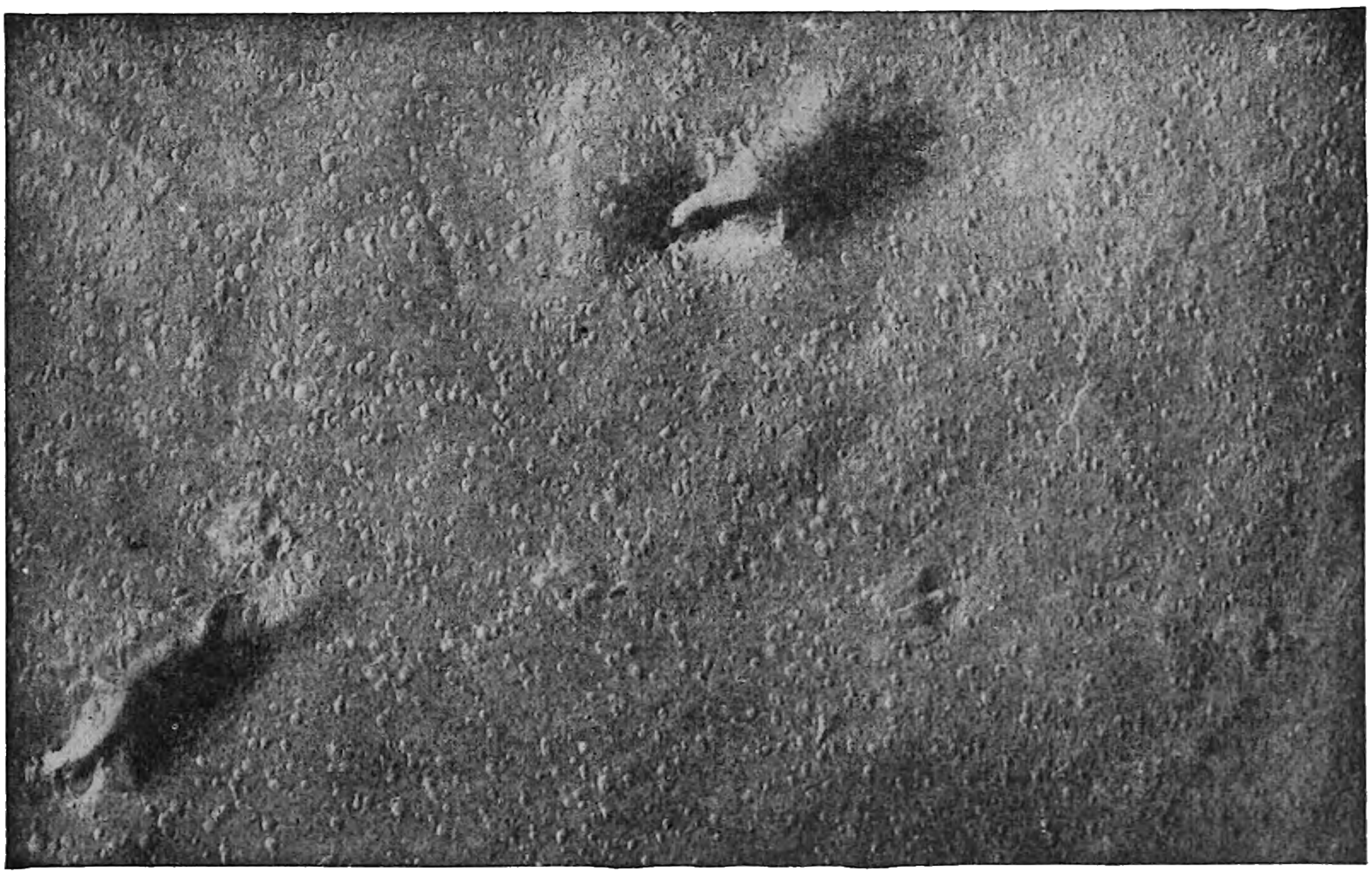

Fig. 215.—Natural casts of rain imprints and dinosaur tracks. (*From Schuchert's Historical Geology. Courtesy of John Wiley and Sons.*)

considerable proportion of fossil plant life consisting of molds and casts.

Subsequent Fate of Fossils.—Once a fossil is formed it is subject to physical agencies that may destroy it completely or considerably distort it. Formed under water, the rock strata in which fossils are now being discovered were elevated and drained. In this process of elevation, folding and breaking of the rocks, many fossils were injured or destroyed. Circulating ground water may redissolve the material of which the fossils are composed; and if the material is replaced the internal structure of the animal is likely to be lost. Erosion lays bare numerous fossils, which may be weather-worn, or washed away; and if the fossils were in fragments the parts are scattered beyond recovery. Pressure in the rock strata, due in part to the weight of rock above, but perhaps more largely to shrinkage of the sediment in drying-out, crushes many fossils, so that the latter are often in fragments and far from representative of the original form of the animals.

Discovery of Fossils.—Fossils are not found everywhere, and it is seldom that the paleontologist sets out to find them without some clue. Natural erosion may lay bare deposits of great value, in which the fossils are accidentally discovered by travelers or exploring parties. Excavations for buildings, drainage canals and ditches, railroad cuts, mines and quarries are prolific sources of first discoveries. Particularly valuable leads are often followed up by scientific expeditions sent out by museums and universities. Most of the valuable collections have been brought together by this concentrated, directed effort, not by casual discoveries.

Change in Species During Geological Time.—The primary fact of paleontology, which makes the study of fossils both fascinating and important, is that the animals of the past were very often unlike the animals of today. There are, it is true, many instances in which there is little or no difference between extinct and living animals, especially in late geological periods. Even in early periods some forms existed which were very similar to animals of today. Lingula, one of the brachiopods still living in marine waters, is almost identical with certain very ancient fossil brachiopods. But among the older forms of life similarity to recent forms is exceptional.

Moreover, the living beings of one past age differed from those that preceded or followed them. Examination of successively deeper and deeper strata of rock reveals differences in the animals which lived when those rocks were deposited. Animals which are abundant in the lower (older) strata are wanting in those above, while new forms take their place in the more recent rocks. So characteristic are these changes from one stratum to another that geological time may be measured, or at least divided, with reference to the fossils contained in the rocks.

In order to be able to speak of the successive rock deposits geologists

The interpretations to be put upon the differences in the animals of successive periods of time are manifold. The same group of facts may often be made to bear upon a variety of questions.

Change of Environment.—Probably nothing will appeal more forcibly to a person who knows something of living animals and the habitats in which they are found, than to discover in his excursions afield the fossil of an animal in a region where it could not possibly exist under present conditions. In Michigan, for example, some of the finest of extinct corals are found (Figs. 212 and 216). Corals are today exclusively marine animals, and presumably were marine in earlier times. Yet Michigan is now in mid-continent, hundreds of miles from the nearest salt water. The environment has changed. This is not an isolated instance, it is but one of many similar cases. Continents and shore lines have changed often and greatly, as the fossils of land and marine animals testify.


Fig. 216.—Fossil of cup coral found in Michigan, demonstrating that Michigan was once covered with marine waters. (*From specimen in the Museum of Geology, University of Michigan.*)

The same spot on the earth's surface has been repeatedly dry land and under water. Fossils indicate that swamps have changed to plains, forests to grass-lands and finally to deserts. Climatic changes have been frequent. Tropical temperatures, as indicated by luxuriant plant growth and attendant animals, changed to winter severity, which was later ameliorated. Humid regions have become arid in many places. No other assumptions will explain the fossils found at different levels in the same region.

Migrations of Animals.—The changes in the nature of the earth's surface in the past necessitated the migration or extinction of most if not all of the animals inhabiting the changing regions. Some of these earth changes were radical. As Michigan, for example, changed from sea-bottom to dry land by the elevation of the earth's crust, marine animals necessarily either followed the sea as it receded, or became modified so as to be capable of life under new conditions. Probably no animals emerged from the sea, during these changes, to live on land, for alterations to suit land conditions would have involved in most cases both structural and physiological changes, some of them fundamental in nature. Possibly a few could endure brackish, or eventually even fresh water, and remained in streams or inlets, but the majority almost certainly could not tolerate the new conditions, and followed the retreating ocean. If they did not migrate, they perished.

Smaller changes in the environment, especially those occurring on land such as a slight change of climate or of vegetation, probably presented less rigorous alternatives. As was pointed out in the preceding chapter, individual animals of today may become slightly altered structurally or physiologically so as to be capable of living in a habitat from which their unmodified relatives are barred. If these changed individuals live near the margin of their range they may migrate into some adjoining area where the other members of their species cannot follow them. Thus a new species, occupying a contiguous region, may arise. The same principle may have operated in the past, permitting migration to occur. Such modifications in animals as would fit them for slightly different environments may occasionally, where the environment itself was being altered, also have operated in a different manner and made migration unnecessary. There are some instances of ancient terrestrial animals which appear to have become modified almost simultaneously with changes in their environment. If while a region was being slowly altered as to climate, soil, vegetation or other features, certain individual animals within the region were modified in a way which happened to fit them for the new conditions, the changed individuals could remain while the unaltered members of their species might be forced to migrate or might perish. Some biologists hold that, in case of a simultaneous change in the environment and in the animals, the change of environment caused the change in the animals. But there is much in favor of the view that the two changes were wholly independent of one another in origin. In the cases of parallel alteration of animals and environment, the two changes happened to fit each other. We are ignorant of those (perhaps much more numerous) cases in which the changes of animals and environment did not suit each other, for the animals must have perished or migrated early in the period of modification.

Migration of animals has also been helped or hindered by the formation or destruction of land bridges connecting continents, etc. Reference to these geological changes was made in the preceding chapter to explain peculiarities of the present geographical distribution of animals. Paleontology also affords evidence of such changes. Fossils of horses in Europe and America indicate a former connection between those continents. North and South America were connected up to middle Eocene time (Fig. 217,*A*) and were then separated (*B*) until late in the Miocene epoch or later when, as indicated by fossils of mastodons, deer, horses, etc., migration between the two continents again became possible.

Migration of the Environment.—In the alteration of climate, topography, etc., a given kind of environment is believed to have traveled, in some instances, across a continent during the passage of time. Case has described what he suggests to be an instance of migration of the environment from Pennsylvania and West Virginia on the east to Texas, Oklahoma and New Mexico on the west. The "red beds" in the region indicated owe their color to the oxidation of iron under certain climatic

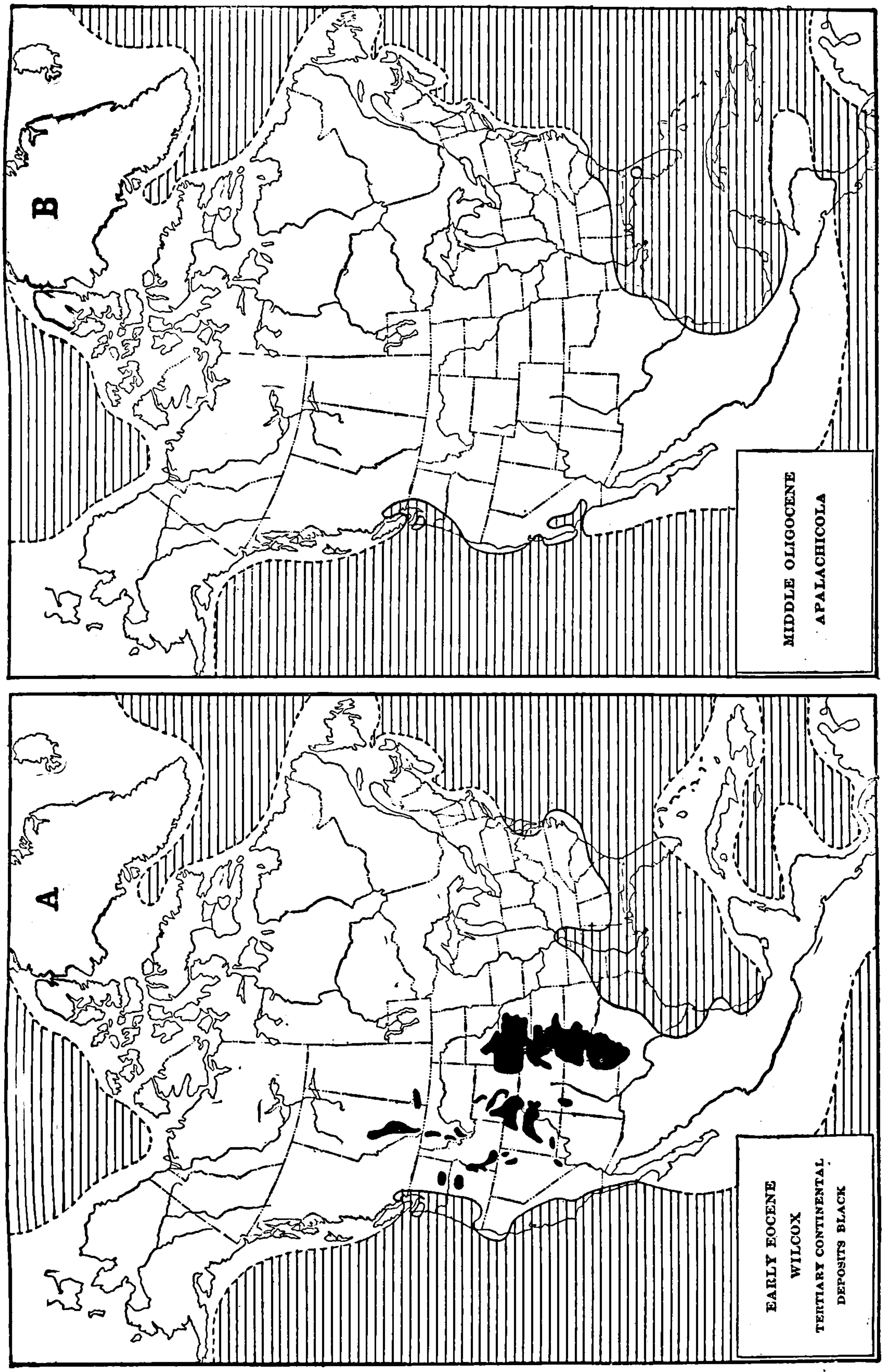

FIG. 217.—Geography of the American continents in Tertiary time. *A*, early Eocene showing connection of North and South America, and incorporation of West Indies with the mainland; *B*, middle Oligocene, showing severance of the two continents and submergence of the islands. (*From Schuchert's Historical Geology. Courtesy of John Wiley and Sons.*)

America; *Mastodon* from the Pliocene and Pleistocene of North America, Europe and Asia; *Stegodon* from the Pliocene of southern Asia; and *Elephas* from the Pleistocene of the Americas, Europe and Asia, as well as the living elephants of Asia and Africa. A study of Fig. 218 in connection with the following account will disclose the more striking steps of evolution. These forms differed from one another in a number of features, but the differences between any member of the series and the one that precedes or that which follows were so small that the series is obviously a continuous one. Mœritherium was very different from the modern elephant, but the intermediate forms completely bridge the gap. The series exhibits an enormous increase in size of body, changes in the form and size of the teeth, a reduction in the number of teeth, an alteration in the method of tooth succession, the enlargement of certain teeth to become tusks, the elongation and subsequent shortening of the lower jaw, the development of the upper lip and nose into a proboscis, and an increase in the height of the skull through the development of large cavities in the substance of the bone. These features are described in the several forms seriatim.

Mœritherium.—The earliest animal recognized as belonging to the elephant series, Mœritherium by name, was recovered from the late Eocene and early Oligocene deposits of northern Egypt. It was slightly over three feet in height. The features suggesting elephantine affinities are the high posterior portion of the skull (Fig. 218,*F′*) composed of somewhat 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 (Fig. 218,*F*); and the position of the nasal openings some distance back of the tip of the upper jaw, indicating probably a prehensile upper lip. There were 24 teeth, and the neck was long enough to enable the animal to put its head to the ground. It probably fed upon tender shoots and swamp vegetation.

Palæomastodon.—This form also lived in Egypt, but has recently been found in India. It dates from early Oligocene time. Palæomastodon was of somewhat larger size than the preceding form, the posterior part of the skull was distinctly higher (Fig. 218,*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 and bore a band of enamel on their front surfaces. The lower second incisors were present, but not enlarged. All other incisors and the canines had disappeared. The molar teeth (*E*) resembled those of Mœritherium but were larger. The lower jaw was considerably elongated, and the total number of teeth was still high (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.—Trilophodon, a great migrant and consequently widespread over several continents as stated above, exhibited in several respects a striking advance over Palæomastodon; but this advance was in the main in the same direction as was indicated by the change from Mœritherium to Palæomastodon. Trilophodon was a huge animal, nearly as large as modern Indian elephants. The tusks were considerably longer (Fig. 218,*D′*), and still bore a band of enamel. The molar

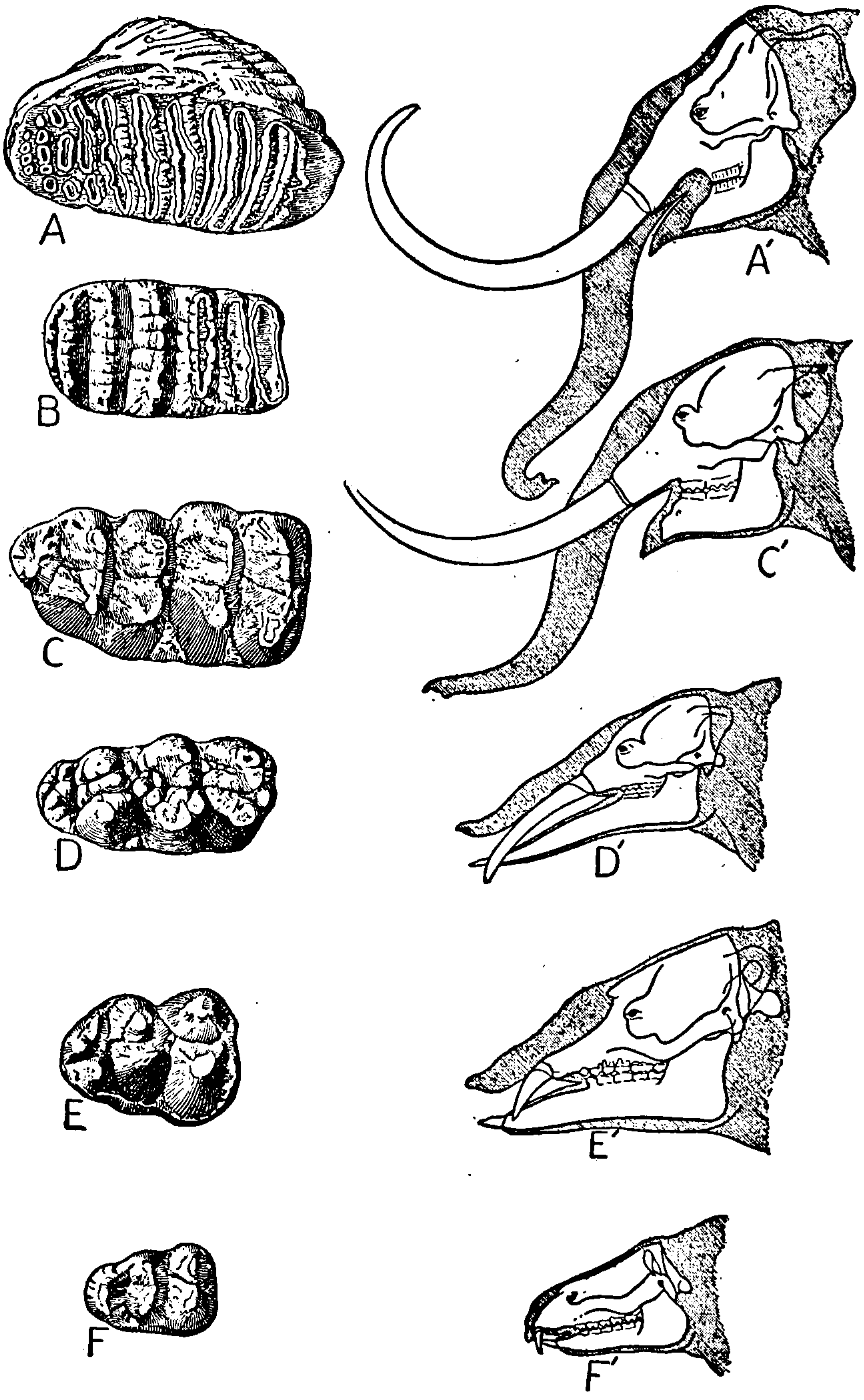

Fig. 218.—Evolution of the head and molar teeth of the mastodons and elephants. The skulls on the right are enclosed in the flesh in the form the latter is supposed to have had. *A*, *A′*, Elephas, Pleistocene; *B*, Stegodon, Pliocene; *C*, *C′*, Mastodon, Pleistocene; *D*, *D′*, Trilophodon, Miocene; *E*, *E′*, Palæomastodon, Oligocene; *F*, *F′*, Mœritherium, Eocene. (*From Lull's Organic Evolution, courtesy of Macmillan Co.*)

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 (Fig. 218,*D*) than were present in the earlier forms. The lower jaw was enormously elongated, so that it projected as far forward as the tusks. The great weight of the lower jaw and tusks was associated with a considerable development of cancellate bone in the skull, to which the supporting muscles of the neck were attached. Presumably there was a proboscis which extended to or beyond the tips of the tusks and lower jaw.

Mastodon.—The mastodons on the whole represent a line of development which became extinct; but in their incipient stages they appear to have given rise to the succeeding forms leading to the elephants. The body was somewhat larger than that of 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 (Fig. 218, *C*, and Fig. 219) were scarcely more complex than earlier forms, and numbered two on each side of each jaw. 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.

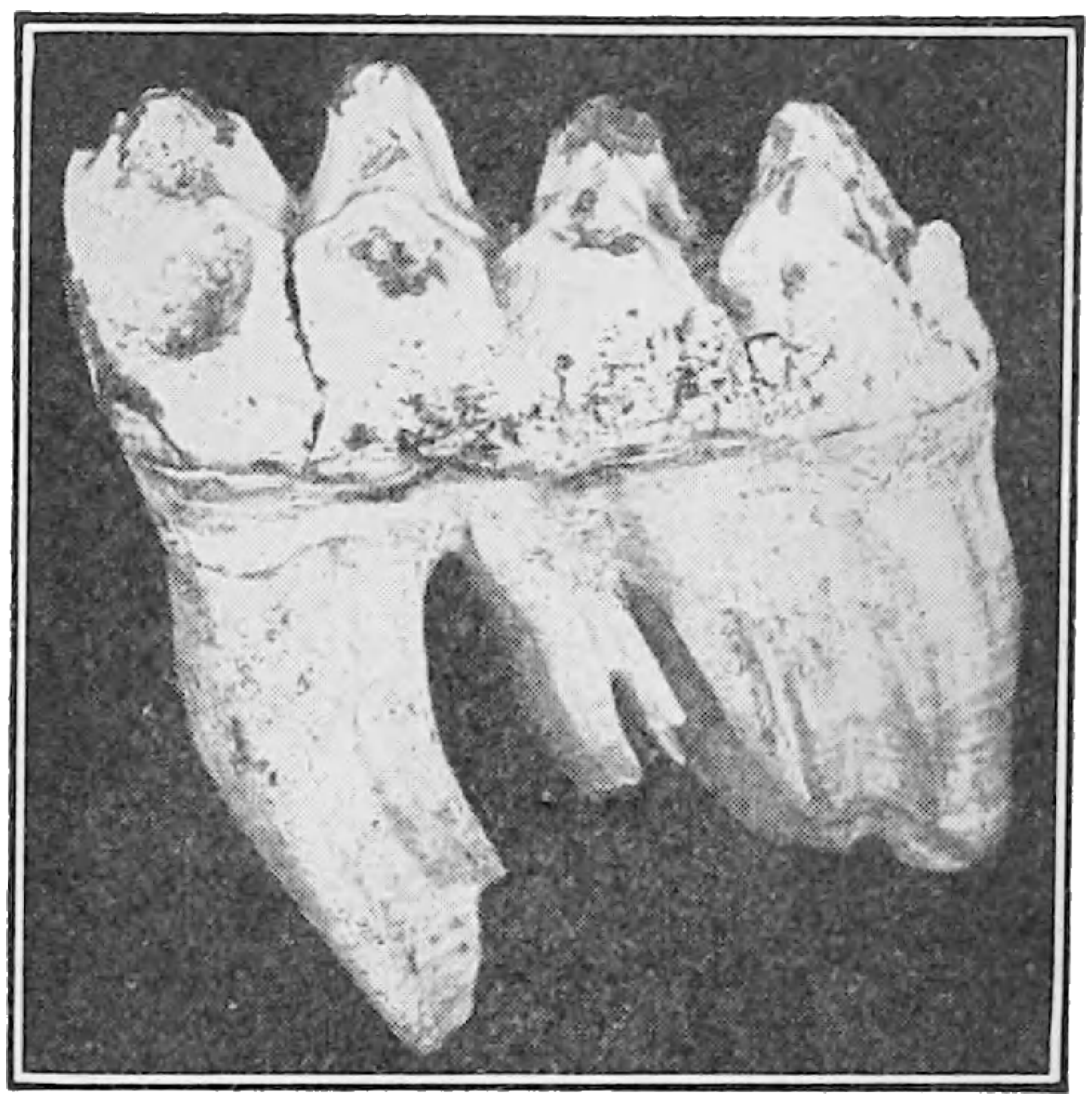

FIG. 219.—Mastodon tooth, showing the enormous cusps on the upper surface. (*From a California specimen in the Museum of Geology, University of Michigan.*)

Stegodon.—This animal is of interest chiefly because the molar teeth bore five or six well-defined transverse ridges (Fig. 218,*B*). These ridges were due to plates of *enamel* extending up through the tooth, and enclosing a substance known as *dentine*. Over the enamel in an unworn tooth was a thin coat of a third substance called *cement*, but there was not much of this substance between the ridges. In the latter respect Stegodon differed, as is pointed out below, from the elephants and mammoths (see Fig. 220 for the tooth of a mammoth). On the whole, Stegodon was intermediate between the mastodons and elephants.

and chewing habits. Whereas the ancestral forms whose molars bore prominent elevations lived on twigs and tender herbage which they *crushed* in mastication, 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. In this respect modern elephants are like the mammoths.

In the changes described above is found one of the most beautiful and best established evolutionary series with which the paleontologist is acquainted. Only a few others equal or approach it in clearness and completeness.

Evolution of the Horse.—An excellent evolutionary series is that of horse-like forms of America and the Old World. Practically the oldest recognizable equine animal is *Eohippus* of Eocene time in western North America, though Europe had a very slightly simpler animal of the same general period. Most of the development of the line of descent from Eohippus took place in North America, where, to select only some of the forms that seem to be in the direct line, there appeared *Mesohippus* in the lower Oligocene, *Merychippus* in the Miocene, *Pliohippus* of Pliocene time, and *Equus* which includes a number of Pliocene and Pleistocene fossil forms, as well as the living horses. These animals underwent changes in the feet from a three- or four-toed condition to the modern one-toed animal; the teeth, in the early forms short-crowned and capped with conical prominences on the upper surfaces, became high-crowned and wore down as they grew so as to have flat grinding surfaces; the skull changed in proportions and in certain features of the orbit of the eye; and the body as a whole increased greatly in size.

Eohippus.—Eohippus stood about twelve inches high, and had a short head and neck. The forefoot bore four well-developed toes, but the skeleton shows a splint bone on the inner side of the hand which indicates a five-toed ancestry (Fig. 221). The hind foot has three toes with a splint-bone representing a fourth, and in one specimen another small splint-bone remaining from a fifth toe. If the ancestors of Eohippus had five toes, as the splint-bones seem to show, the hind foot lost its toes more rapidly than did the fore foot. It is also worthy of note that, as shown by the size of the splint-bones, the inner digit of each foot was the first to disappear, the outer toe next in succession. The inner digit of vertebrate animals is customarily designated the first, and the others in order outward. Thus as portrayed in Fig. 221, the first digit in the horse was the first to be lost, the fifth digit next. As is pointed out below, in later members of the horse series, the second toe degenerated next, followed soon by the fourth. 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. 222). The skull (Fig. 223) was small, the lower jaw comparatively short, and the orbit was placed well over the teeth, making the face relatively short.

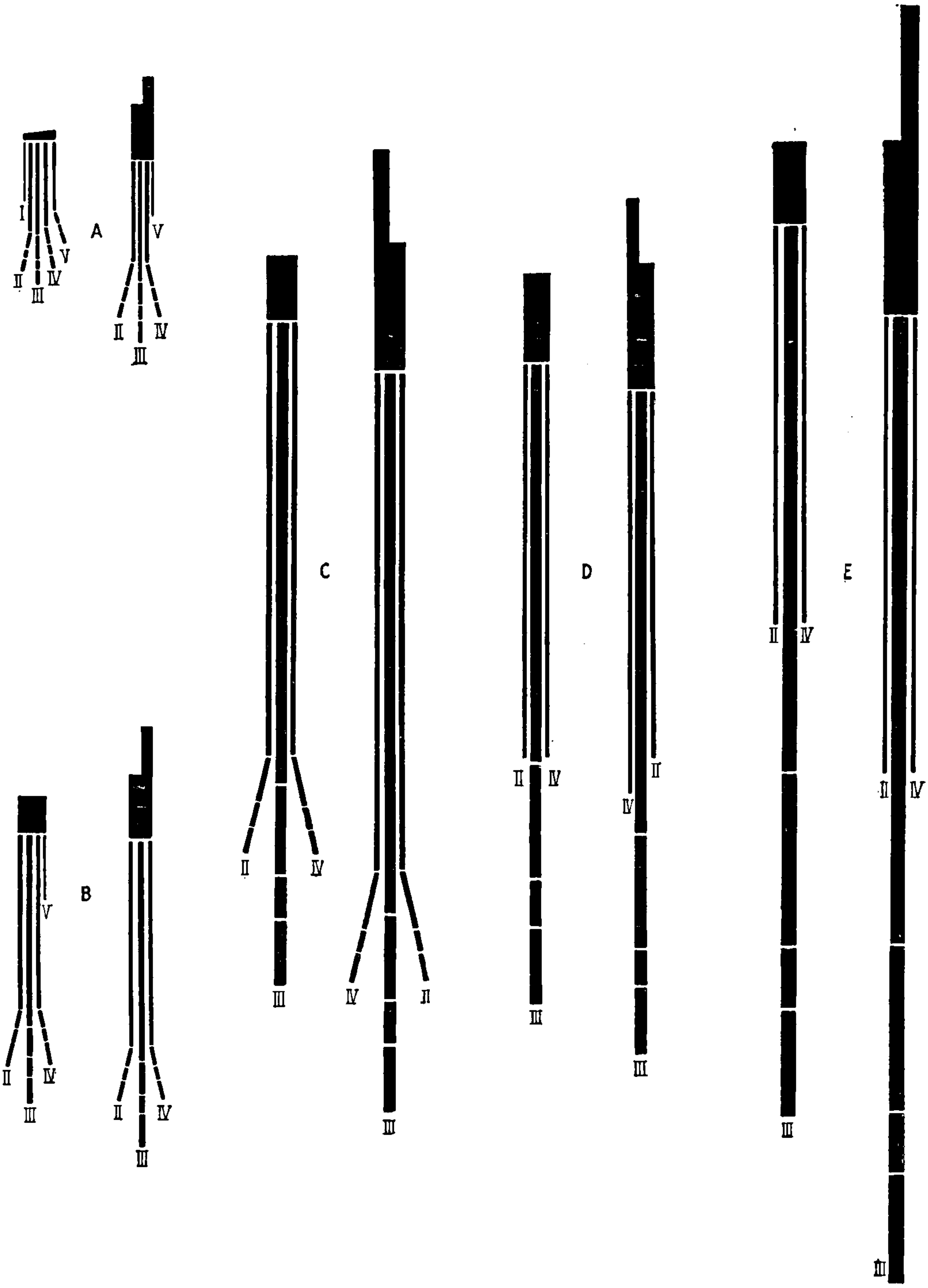

FIG. 221.—Diagrams of the feet of members of the horse series. The carpal and tarsal bones are not separately represented. The Roman numerals indicate the numbers of digits, the inner digit being designated I. *A*, fore and hind feet of Eohippus, lower Eocene; *B*, fore and hind feet of Mesohippus, lower Oligocene; *C*, fore and hind feet of Merychippus, Miocene; *D*, fore and hind feet of Pliohippus, Pliocene; *E*, fore and hind feet of Equus, Pleistocene and recent.

Mesohippus.—This animal was about 18 inches high. It had only three digits on each foot, but on the outer side of the fore foot was a splint bone representing an extra toe (the fifth). Figure 221 represents the feet diagrammatically. Of the three well developed toes, the middle one (third) was in each foot distinctly larger than the others. The skull (Fig. 224), except for its increase in size, had not changed strikingly. The crowns of the molar teeth were still low (Fig. 222) and were tuberculate, that is, provided with cusps on the upper surface, but the cusps were more distinctly united into ridges or crests.

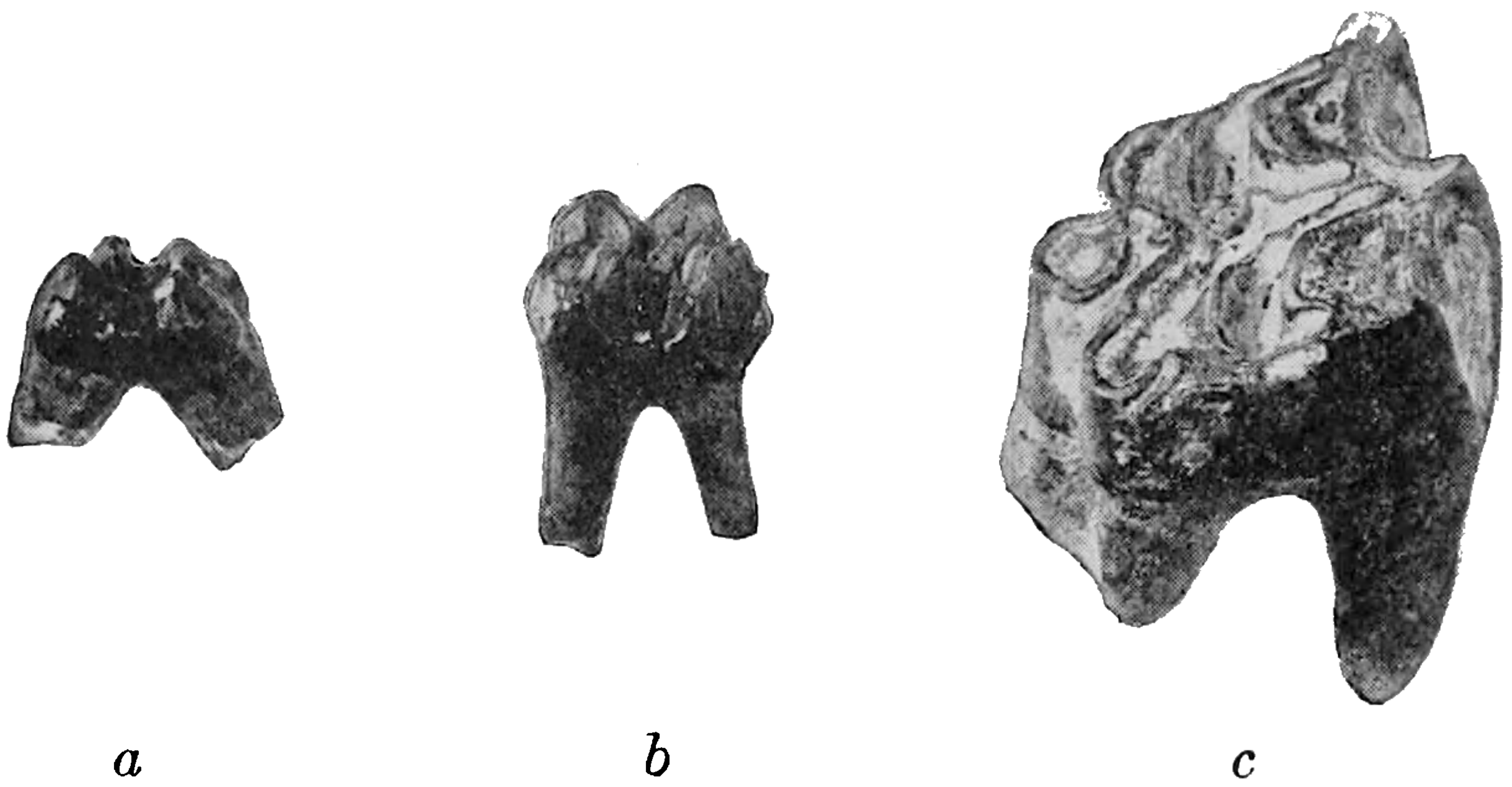

Fig. 222.—Fossil teeth of ancient horse-like animals. *a*, tooth of Eohippus with the roots broken; *b*, tooth of Mesohippus; c, tooth of Merychippus. (*Photographed from specimens in the Zoölogical Laboratory of the University of Michigan.*)

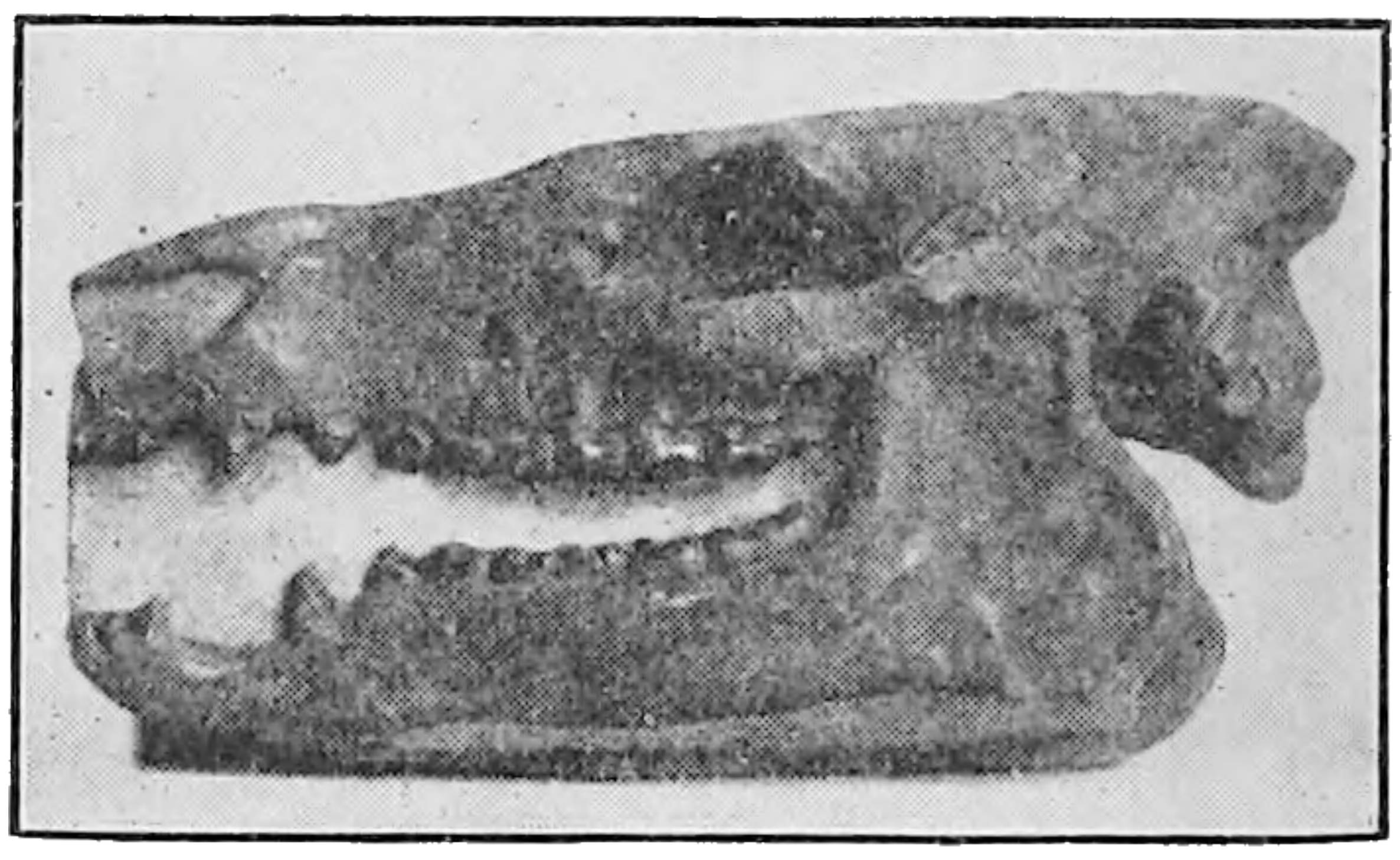

Fig. 223.—Skull of Eohippus, about 3/10 natural size. (*From model prepared by Ward's Natural Science Establishment.*)

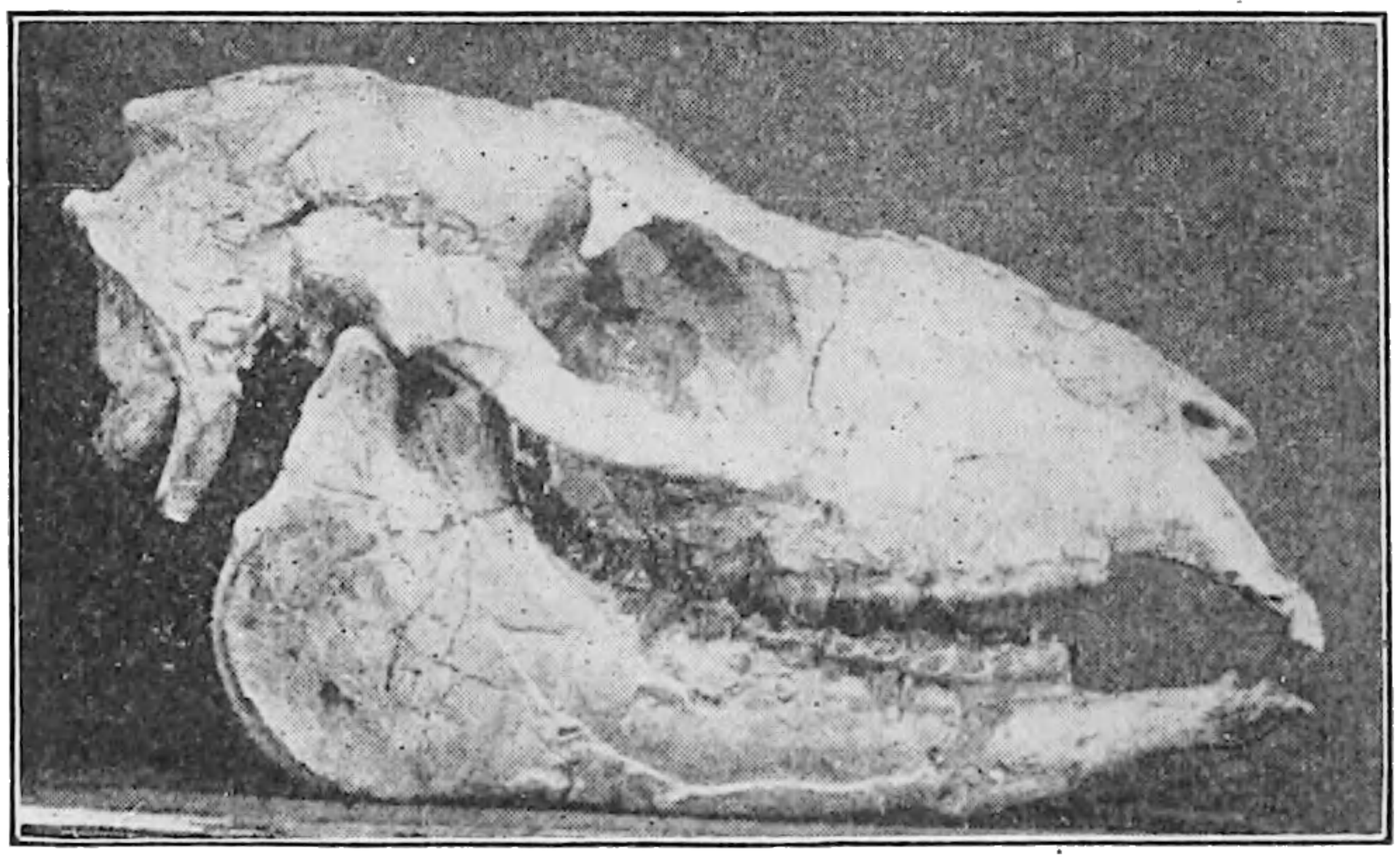

Fig. 224.—Skull of Mesohippus, about 3/10 natural size. (*From photograph of specimen in Museum of Geology, University of Michigan.*)

Merychippus.—The feet of Merychippus were all three-toed (Fig. 221), vestiges of the fifth toe being present in some specimens and wanting in others. The lateral toes, however, were high above the ground,

the foot diagrammatically. Of the three well developed toes, the middle one (third) was in each foot distinctly larger than the others. The skull

FIG. 222.—Fossil teeth of ancient horse-like animals. a, tooth of Eohippus with the roots broken, b, tooth of Mesohippus, c tooth of specimens in the Zoological Laboratory of the University

(Fig. 224), except for its increase in size, had not changed strikingly. The crowns of the molar teeth were still low (Fig. 222) and were tuberculate, that is, provided with cusps on the upper surface. the were more distinctly united into ridges or crests.

FIG. 223.—Skull of Eohippus, about ½ natural size. (From model prepared by Ward's Natural Science Establishment.)

224. Skull of Merychippus, about 1/6 natural size. (From photograph in Museum of Geology, University of Michigan.)

Merychippus.—The feet of Merychippus were all three-to 221), vestiges of the fifth toe being present in some specimens an in others. The lateral toes, however, were high above th thus marking a distinct advance from the condition in Mesohippus. The entire weight of the body was borne upon the middle (third) Quite as important as this reduction of the lateral toes was the chan the teeth. The permanent molar teeth had moderately high and the upper surface was worn down to a flat grinding surface by sharp ridges of enamel set among dentine and cement (Fig Merychippus was evidently a grazing animal, whereas its predec must have fed upon succulent herbage which was crushed, not groun The milk molars of Merychippus, unlike the permanent ones, were sho crowned and had little cement. The two sets of teeth thus showed the lifetime of one individual changes of the same kind as were takin

Fig. 225.—Skull of Merychippus about 1/6 natural size. (From model prepared Ward's Natural Science Establishment.)

place in the race of horses and recall the so-called Biogenetic Law (Chapter X) according to which the development of an individual repeats the evolutionary stages of the race to which the individual belongs. The skull was enlarged (Fig. 225), 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 relatively 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 three or four feet.

Pliohippus.—This animal was not appreciably larger than the preceding member of the series, but differed from it in at least one striking feature. The two lateral toes had disappeared (Fig. 221), 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.

Equus.—The fossil horses of Pleistocene time were so nearly like the living forms as to be included with the latter in the same genus. The recent animals are 60 inches or more in height, and weigh many hundreds of pounds. Each foot has but one toe (Fig. 221), on the tip of which the animal stands like a ballet-dancer. Two lateral toes are evidenced by splint bones, and in rare cases a reversionary horse is born with externally visible digits articulated with one of these splints on each fore foot. 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. Late in life growth of the teeth practically ceases, and then the teeth may become quite short. The skull is enlarged, particularly the front portion of it, probably in relation to the battery of large teeth which it contains. 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.

Relation to the Environment.—During Eocene time, when Eohippus lived, North America is believed to have had a moist climate with an abundance of soft or marshy ground. On such ground an animal with four-toed or three-toed feet, especially if it rested partially on the soles of these feet, could have walked more successfully than could an animal with but one toe on each foot, particularly if it stood on the tips of these toes. Later the climate became more arid, streams and lakes dried up, and the hard plains lands were developed. One-toed horses could occupy these plains successfully, and the lightening of the lower part of the legs was in the interest of speed. If, as is not improbable, the vegetation of the earlier periods was tender or succulent, while later the harsh grasses and sedges became prominent, the change in the teeth of the horse-like animals from crushing structures to grinders also served to fit the animals for the environment in which they lived. Whether the increase in size is to be regarded as an advantage is uncertain.

While the changes described above have in the main fitted the horses to live in the environment which they occupy, it is not to be assumed that the features of the environment caused the animals to change in this way. The causes of such evolutionary modifications are discussed in the following chapter.

Evolution of the Camel.—The camel family underwent most of its evolution in North America. The earliest genus recognized as ancestral

merely a mass of fat varying in size with the state of nutrition of the animal, and is not correlated with any peculiarity of the skeleton.

Evolution of the Cephalopods.—An excellent fossil record among the invertebrates has been established for the tetrabranchiate (four-gilled) Cephalopoda (Mollusca). This branch of the cephalopods is represented today by Nautilus, which lives in a coiled shell, externally resembling a snail shell. However, 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. These partitions, or septa, represent the positions occupied by the animal earlier in its life. As the body grows, it moves periodically forward into the wider part of the shell and secretes a partition behind itself each time it moves.

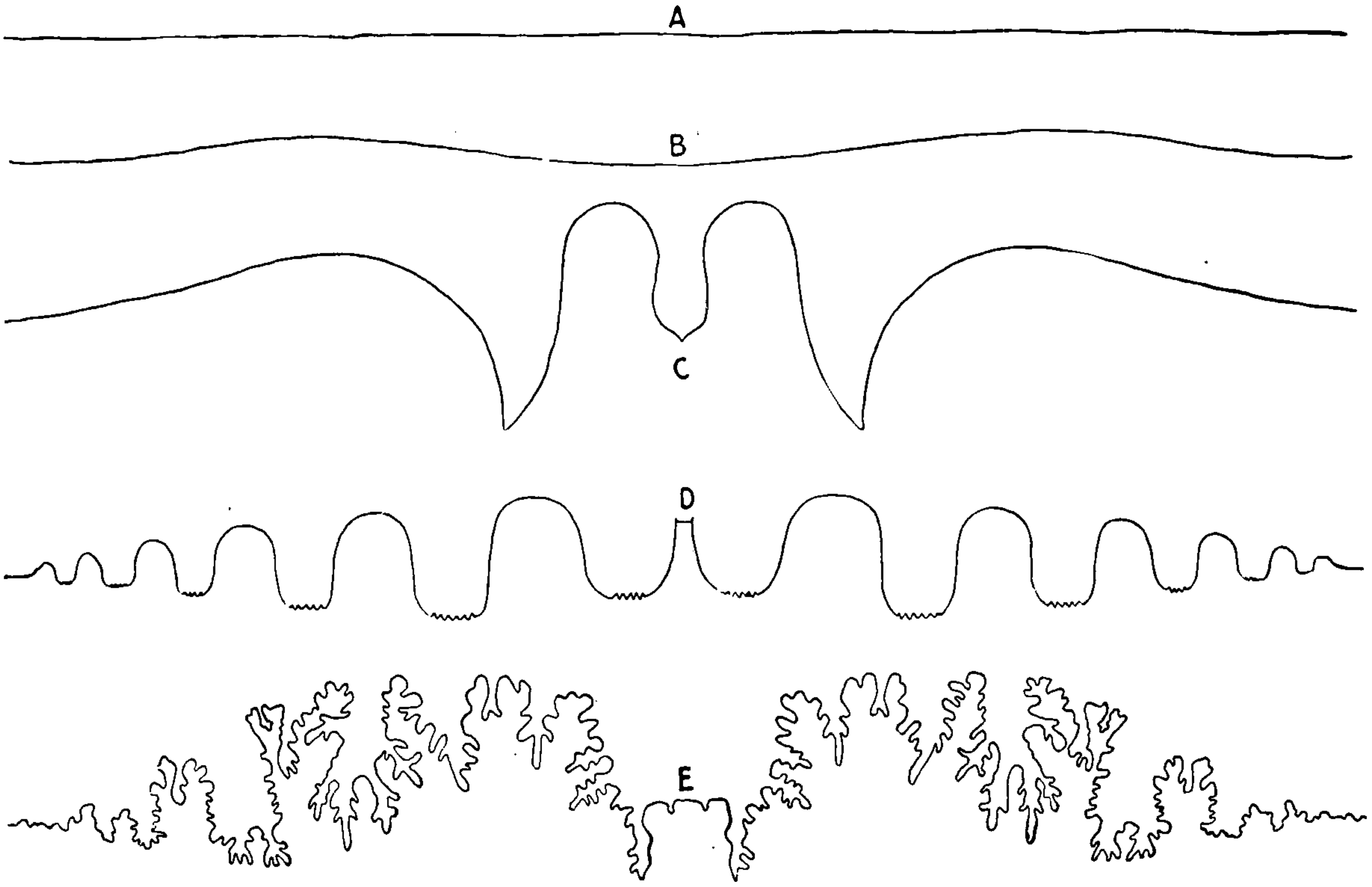

FIG. 227.—Diagrams of sutures of cephalopods, represented as spread out with the ventral point in the middle. *A*, orthocone; *B*, nautiloid; *C*, goniatite; *D*, ceratite; *E*, ammonite.

Tetrabranchiate cephalopods have been found, as fossils, in Cambrian rocks. They became fairly abundant in the 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. Fossils of cephalopods are found in the strata of all periods from the Ordovician to the Cretaceous, and as stated above a few members of the group are still living.

The course of evolution was as follows. The shell soon began to bend, and in many forms became closely coiled in flat spiral form 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. 227). 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 saw-teeth, 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 most exquisite foliaceous patterns. The ammonites were 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, angular, crooked, and finely lobed.

Relationships of Living Animals.—The existence of fossil records demonstrating step by step the origin of animals now living from more primitive ancestors can hardly escape throwing light upon obscure relationships of modern groups. Even when series as complete as the ones described above are lacking, fossils of animals intermediate between two living groups may create the presumption that both groups have sprung from a common stem. Thus the reptiles may be traced to an amphibian ancestry through the Stegocephali, huge armored Amphibia of the past. Birds are assigned a reptilian origin through Archæopteryx (Jurassic), a reptile-like animal which, however, had feathers. Mammals have been derived from reptiles, as indicated not only by fossils but also by the facts of structure and embryonic development. The paleontologist is not called upon to decide only the relationships of the major groups of animals. He is most successful, it is true, in establishing the connections between phyla, classes, and orders; but attempts to relate families by means of fossils are not uncommon, and problems of generic and specific rank are essayed with as little hesitation as in the case of living animals.

Extinction of Groups.—Everywhere in the rise of the animal groups of today there have been tragedies more thrilling than the memorable catastrophes of historical times among men. Races have come into being, have passed through a series of changes, and then perished. Sometimes what may be regarded as the main line of development was preserved, while only the offshoots were lost. At least, in those cases, the modern animals represent as complex an attainment as the lateral lines which disappeared. In other cases, the climax of the series was extinguished while all that now remains is from the primitive early members of the stock. In the horse series, we have left today the most highly modified member, while its less specialized ancestors and several less specialized lateral branches have been lost. In the elephants and camels, also, the greatest amount of modification of which we gain any knowledge from fossils is preserved in the modern animals, while only the forebears and several sister lines of less complexity have met extinction. In the cephalopods, however, the maximum development was lost. The forms with bent, crooked, and foliaceous sutures are known only as fossils, while the living forms of today are almost identical with the nautiloids, whose sutures were only gently curved. If, as is naturally assumed, the Nautilus of today is the practically unaltered direct descendant of the nautiloids of Silurian time, relatively primitive forms have been preserved while the highly specialized have perished.

Among the reptiles, too, the paths of glory led but to the grave. The reptiles rose to a mighty station in the Mesozoic era, which is known as the Age of Reptiles. They spread over most of the earth, and North America was an important scene of their development. Some were small animals, others as large as the largest whales. Their skeletons show the largest ones to be 60 to 80 feet in length; such animals in the flesh must have weighed many tons. But they did not specialize in size alone; they exhibited a variety of structure. Some were lizard-like and evidently ran low upon the ground, while others stood high on their legs. Some bore their weight on all fours; others, as indicated by two-footed tracks and the size of the bones, ran upon their hind legs. The forelimbs of the latter were used only for grasping. Necks and tails were long and slender in some, short and stout in others. Many of them were armored in striking fashions. Curious armatures had arisen before Mesozoic time, for Edaphosaurus (Figs. 228 and 229), a Paleozoic form, had long spines on its back joined together like a fin. It was in the dinosaurs of the Mesozoic era, however, that bizarre external structures attained their greatest diversity, as exemplified in the rows of flat plates of Stegosaurus (Fig. 230), and the curious horns on the head of Triceratops (Fig. 231).

The group of dinosaurs, dominant among the reptiles, of multitudinous form and high specialization, took its rise in the Triassic period; underwent its evolution in early and middle Mesozoic time; reached the extreme specialization described above in the Cretaceous period; and then perished! The reptiles of today are all much less specialized. The nearest modern reptilian relatives of the dinosaurs appear to be the crocodiles, of which there are but few species and none of them are highly specialized. In this case, as in the cephalopods, the most highly specialized branches of the group were extinguished, while the more primitive survived.

The cause of the extinction of whole groups of animals is unknown.

fitness for the environment came about through changes in the animals themselves, rather than through changes in the environment. The fantastic forms and the huge size which the dinosaurs, for example, assumed can hardly have been responses to factors in the environment. The evolution of these reptiles was probably started and directed by forces within the animals, independently of external conditions. What these

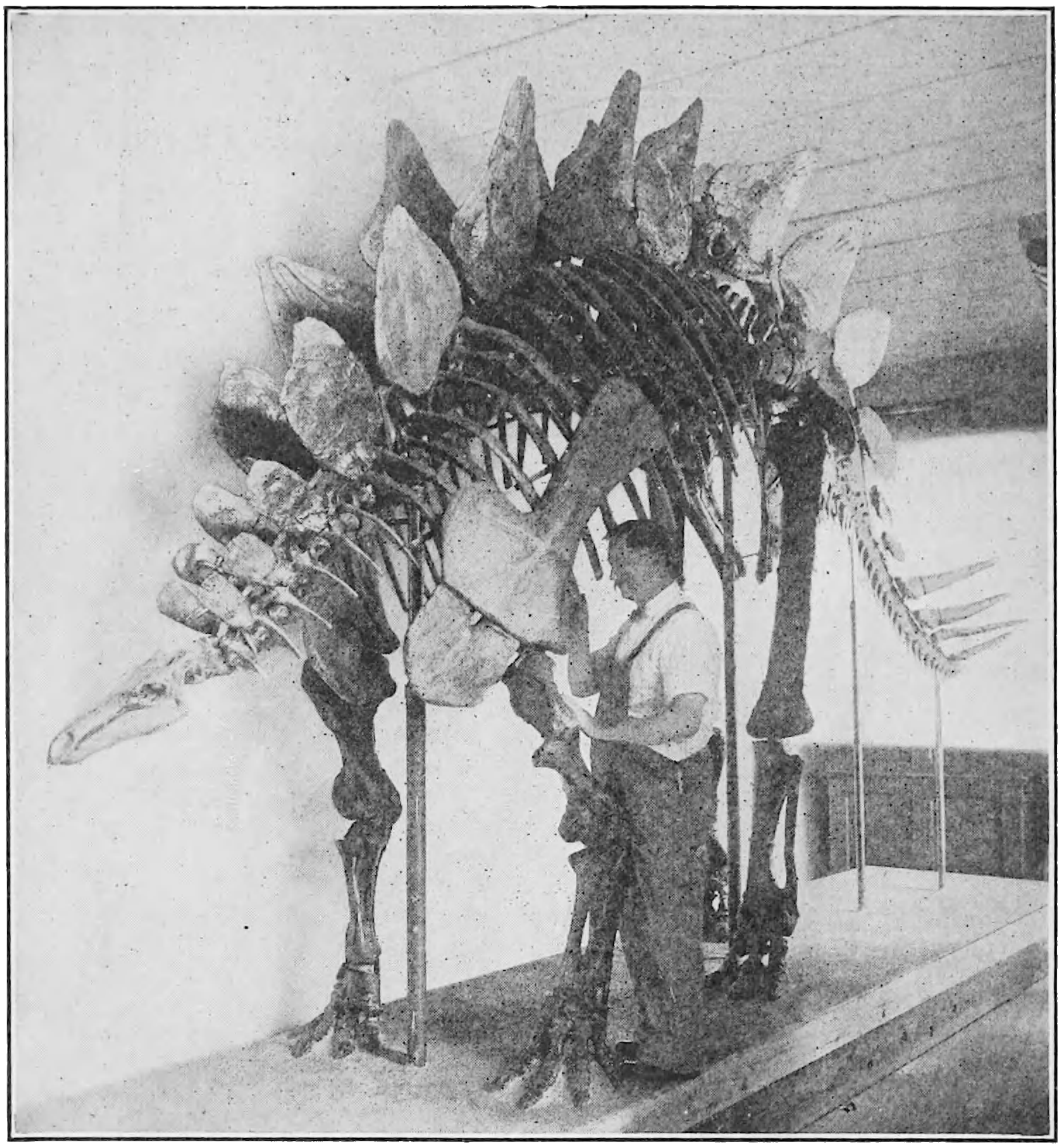

FIG. 230.—Skeleton of the armored dinosaur Stegosaurus. (*From Lull's Organic Evolution. Courtesy of Macmillan Co.*)

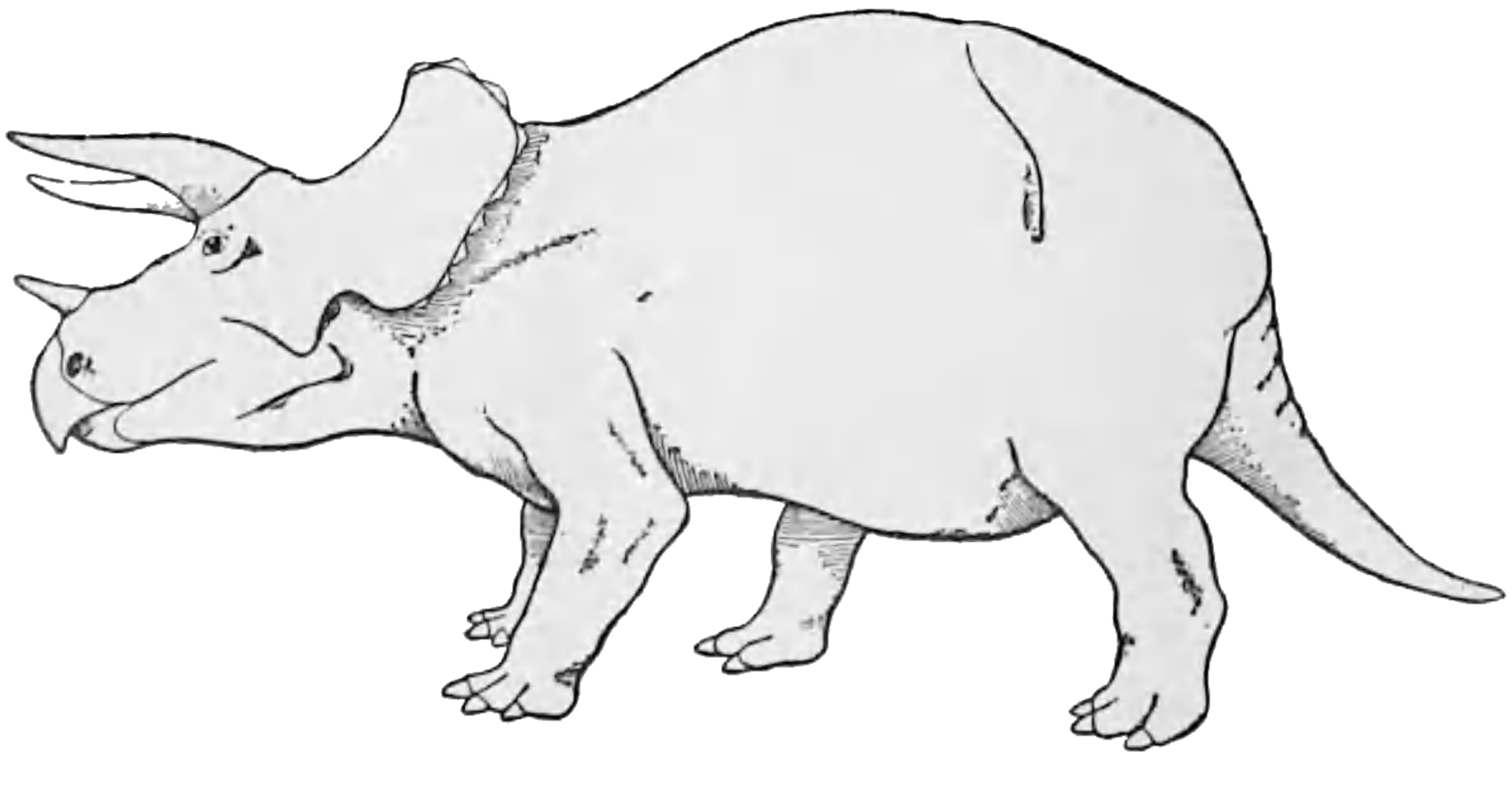

FIG. 231.—Restoration of horned dinosaur Triceratops. (*After Lull, from Schuchert's Historical Geology, John Wiley and Sons.*)

internal forces may have been can only be conjectured, but some possibilities are pointed out in the following chapter. If the evolution of fins and tails and plates and horns and ponderous size was due to internal causes, these causes may have effected still further evolution, until animals were produced that were unable to cope with the environment, whether that environment changed or not. Undoubtedly the environment did change during late Cretaceous time, as it is always changing; but there is nothing to indicate that this environmental change was responsible for the extinction of the dinosaurs.

Some one has wittily expressed the view that the extinction of groups was occasioned by factors within the animals by saying that they "died of evolution."

It may be pointed out that nations of men have also risen to prominence in the world, have been leaders for a period, and then sunk into oblivion, to be succeeded by other nations. However, the origin and extinction of animal races and the rise and fall of nations may have nothing in common, except the fact that no one knows the cause of either phenomenon.

Prehistoric Man.—The difficulty in an attempt to relate the rise and fall of nations of men to the evolutionary cycles of other animals is that nations are usually not biological units. They are political units, often held together by common language or by force, and with few exceptions do not represent racial unity. Abandoning, however, the artificial classification of men into peoples, and regarding the human race as a unit, we may find in man the same progressive development as in any of the other great groups of animals which once held a dominant place in the world. Man has had his rise, as did the reptiles, and before them the Amphibia and fishes. Whether he is also to experience a decline and extinction remains for the future to reveal.

Structurally man plainly belongs to the Primates, an order of mammals including the monkeys, marmosets, baboons, gorillas, and the like. To some of these animals he bears much more resemblance than to others. Thus, there is no question that the anthropoid apes stand much nearer to man, structurally, than do the other primates. Were one to look for evidences of genetic relationship of man to the other mammals, structure would point to these apes as furnishing the nearest living connection.

Actual establishment of this connection through fossil remains has been long delayed. Even now it rests on a series of fragmentary remains which, when compared with the reptilian, cephalopod, or mammoth record, appears meager. However, taken in connection with the anatomical evidence, there is scarcely room to question the common ancestry of man and the apes.

The oldest remains that indicate an approach toward human characteristics were found on the island of Java in 1894. They consisted of part of the skull, two teeth, and a femur. The femur indicated that its owner walked in an erect posture and was nearly as tall as men of today; but it is the teeth that point most strongly to an advance beyond the simian condition. The name *Pithecanthropus erectus* has been applied to this form. Other remains contemporaneous with it fix the geological time as early Pleistocene, or perhaps half a million years ago.

Homo heidelbergensis, the Heidelberg man, is represented only by a lower jaw with its teeth. This was found near Heidelberg in Germany. Its human character is assigned to it largely from the nature of the teeth, which are certainly not ape-like. The other animals belonging to the same period indicate the time to be the second inter-glacial stage, or perhaps 300,000 years ago. Crude tools appear to have been in use at this time.

The Neanderthal man, *Homo neanderthalensis,* was first found in Prussia in 1856. Several other specimens were subsequently recovered in Belgium, France, Croatia, and at Gibraltar. These relics hail from the third inter-glacial and fourth glacial stage, the former period being probably much more than 100,000 years ago. Large portions of the skeleton have been saved in some of the specimens. The jaws are less massive than the earlier forms, and while the chin still recedes it is more prominent than in the apes. The teeth of the different specimens are variable, but these and the skull characters in general are intermediate between those of the anthropoid apes and modern man. The skeletons were taken from burial places, where ornaments and tools were also found.

Quite recently (1912) fragments of a skull were found at Piltdown, Sussex, England, which seem to antedate the Neanderthal man. But since its status is still much in doubt, it is not placed in this series.

Crô-Magnon men were found first in France and Wales. A number of entire skeletons have been excavated. The skull was narrow, but the face broad, as in the Eskimos of today. The cheekbones were prominent, as was also the chin. The skull was large, and the facial angle indicated high intelligence. Signs of civilization in the form of works of art, methods of burial of the dead, etc., point also to considerable mental development.

The gradual approach toward modern human characteristics which these man-like forms constitute can be better visualized from restorations. Figure 232 represents three members of the series. The restorations of Pithecanthropus and the Heidelberg man are somewhat speculative, since only parts of the skulls are known; the later forms required little conjecture. The expression may not, of course, be correctly estimated but the measurements are reliable. Such features as the prominence of the jaws, the degree of recession of the chin, the height of the cheekbones, and the slope of the forehead are (at least for the forms whose skulls are completely known) correctly portrayed. The figures indicate a

one can only assume that the course of development is brought down from a common forebear. And when the present distribution of animals seems to require that two groups should have sprung from a single antecedent group, it is nevertheless only an assumption that they did thus diverge. The conclusions stated above are plausible, but they are necessarily only inferences. It is otherwise with the facts of paleontology. They leave no doubt that animals were different in different periods; for there are the remains to prove it. There is usually no need to argue which are the earliest forms, for the age of the rocks in which they lie can in general be ascertained in other ways. Often, unless there are long gaps not bridged over, the course of evolution is clearly mapped out; for in successive layers of rock are the remains that show by just what steps a given kind of animal evolved.

Paleontology occupies this favored position as evidence of evolution only so long, however, as it is concerned merely with the fact of evolution and with the course which evolution has taken. As soon as the facts of fossils are used to make incursions into other fields, inference is necessary. From a flat crowned tooth one may infer that the owner was a grazing animal, but that is not proven. Restorations of extinct animals in the flesh are inferences based on a knowledge of modern animals. From a facial angle a certain degree of intelligence may be inferred, but only inferred. The ridges on a bone may indicate heavy muscles, but they lack something of proof. In particular, fossils offer no evidence regarding the cause of evolution. It may be easy to devise plausible explanations for the changes that animals have undergone; but for proof of the correctness or incorrectness of these explanations facts have to be gathered from other sources.

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CHAPTER XVI

EVOLUTION

From specific statements made here and there in the foregoing chapters, and from inferences inevitably drawn from various facts therein related, the student can hardly have escaped drawing the conclusion that the animals of today are not like the animals that once inhabited the earth. Such a conclusion will have been strengthened by much that is discovered at first hand in the laboratory. To explain many of the facts of structure and development in living organisms, the nature of fossils, and the distribution of living animals and plants, it seems necessary to assume that species have undergone gradual changes. This gradual change is called *evolution,* and species are said to have *evolved.* Man has been one of the products of evolution no less than other animals. Not one species of living organism has escaped the modifications that constitute evolution. Though some kinds of organisms have been relatively constant, while others have been altered rapidly and often, there is no species alive now which is not different from its most remote ancestors. Close similarity between modern and ancient life is limited to low forms. Nor has evolution been confined to the past; it is going on today. Not every species is evolving now, so far as can be discovered, but some species are. A few years or a few centuries hence, the species now undergoing modification may have reached a fairly stable condition, and other species, now apparently constant, be in a period of alteration.

Darwin and the Rise of the Evolution Theory.—A brief historical account of ideas of evolution has been given in the first chapter. As was pointed out there crude ideas of evolution were held by individuals even as early as the Greeks. Noteworthy theories were proposed by Lamarck and others at the end of the eighteenth century and in the early nineteenth century. Wide acceptance of the doctrine of evolution, however, dates only from the time of Charles Darwin (Fig. 233) who has the distinction of having brought together so many facts indicating evolution, together with a theory to account for the facts which was so plausible, that thinking people were everywhere driven to adopt his views. The life of Darwin and the history of the evolution idea as developed by him stand, therefore, in much the same relation to the evolutionist as do the great epic poems to the student of literature or the story of the Magna Charta to the historian of constitutional government. A brief account of the origin of modern ideas of evolution may well be added to the general statement made in Chapter I.

Darwin was tremendously influenced by the work of the famous geologist, Sir Charles Lyell (Fig. 234). Lyell attempted to explain past geological changes by processes going on at the present time. If geological changes in the past of which we have present day evidence in the form of rock strata, configuration of land surfaces, continental forms, submerged islands, and the like, could be explained by such processes as erosion, rising or sinking of the land or sea floor, and volcanic action, which are now going on, Lyell insisted that such explanations should be employed. No processes of a different order from those of the present time should be appealed to unless present day occurrences do not explain. This insistence on the application of modern processes to the explanation of past events is known as the doctrine of *uniformitarianism.*

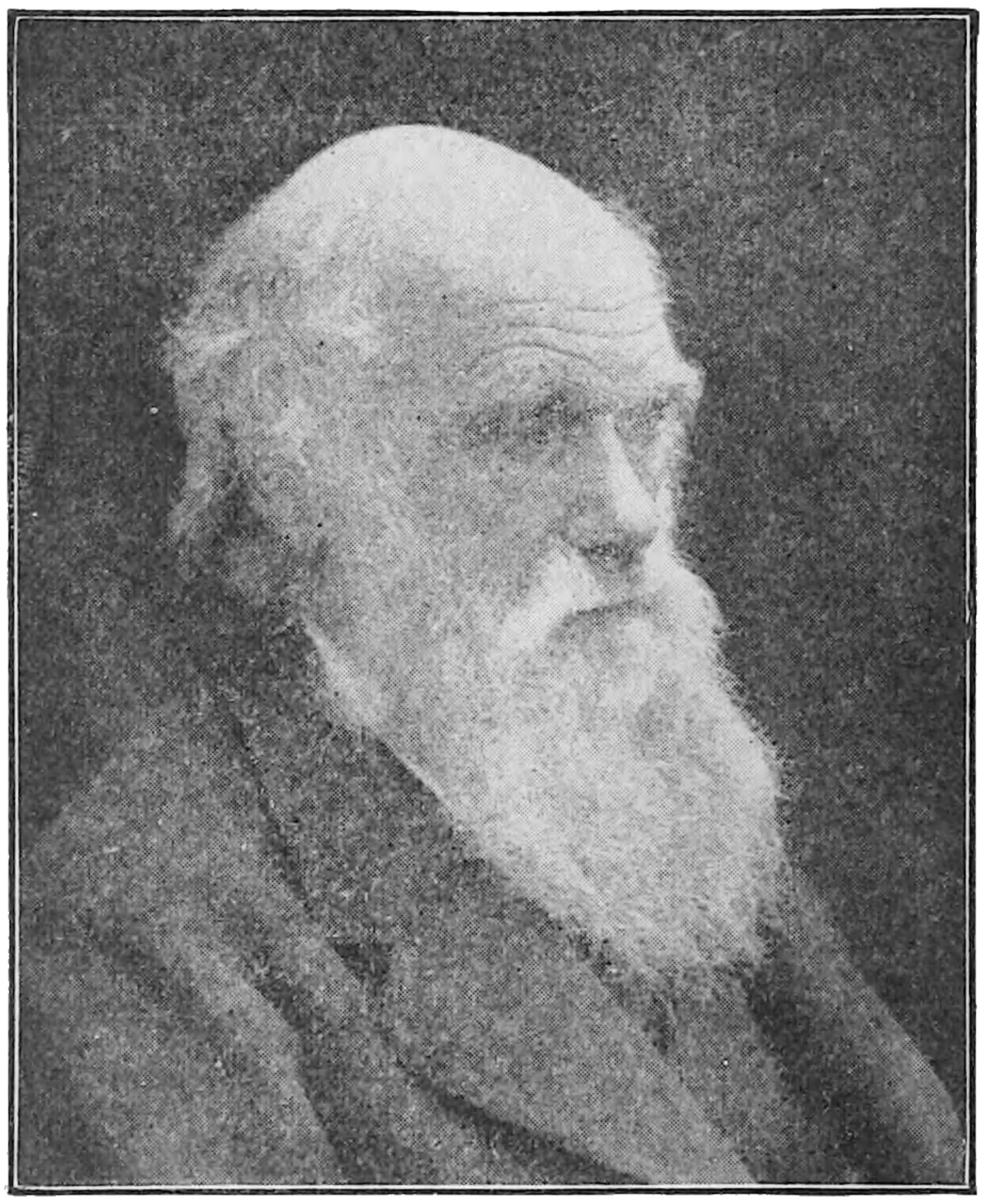

FIG. 233.—Charles Darwin, 1809–1882. *(From University Magazine. Photo by Leonard Darwin.)*

Darwin believed that this doctrine could be applied to living organisms as well as to rocks and hills and shore-lines. He had made a voyage around the world, in 1831 to 1836, as naturalist of a surveying party on the ship *Beagle.* Most of this voyage was devoted to the shores of South America. Darwin had opportunity to make long excursions on land, and observed many remarkable phenomena from which he began to suspect the mutability of species. After he returned from the voyage on the Beagle, he thought it worth while to open a note-book (in 1837) in which he jotted down everything that came to his notice that seemed to bear on the question of the fixity or changeability of species. For twenty years he collected such information as industriously as his health would permit. He had a happy faculty of using others to help him in this

All this time Darwin had published nothing of his discoveries. He wanted to be very sure of his ground. He had confided his ideas to only a few friends, among them the botanist Joseph Hooker and the geologist Sir Charles Lyell. It is doubtful whether he would have published as early as he did but for a curious coincidence. In 1858, Alfred Russel Wallace, an able 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 no other than the theory of natural selection, or survival of the fittest; and as Wallace afterwards related, he 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 Linnæan Society of London, which was done in 1858. History has adjudged practically the entire credit for the theory of natural selection to Darwin; but it is to the immortal honor of both of its authors that neither allowed a dispute regarding priority to mar the launching of their epoch-making hypothesis.

Darwin's theory was developed at length in "The Origin of Species," published in 1859. At intervals after that date he published books on specific phases of the evolution problem. New hypotheses were from time to time advanced, which were intended to supplement the theory of natural selection, such as sexual selection, pangenesis, and others. Of Darwin's writings subsequent to 1859, his "Animals and Plants under Domestication" is at once the most readable and most important. Practically all of these books are so written as to be intelligible to persons without biological training. To this circumstance, more than to any other, perhaps, is due the rapid acceptance of the evolution doctrine. It is true, the time was ripe for such an advance; and then there was Huxley (Fig. 235), who championed Darwin's views in popular lectures. But it is doubtful whether evolution would have occupied the attention of the laity, had it not been for the non-technical presentation of it which Darwin himself gave in his books.

Evolution was not accepted without opposition. The churchmen were reluctant to regard the story of the creation in any other than a strictly literal way. In the main, however, they watched the progress of the new doctrine with good nature, and at present the leading clergy of most churches are as firmly convinced of evolution as are the biologists. Occasionally even now there is a cry that evolution is being abandoned by scientific men, but the arguments in support of such a statement are usually found to confuse the *fact* of evolution with the *cause* or *method* of evolution. When some leading biologist attacks the theory of natural selection, as has been done time and again, some one may proclaim that the doctrine of evolution has been relegated to history. Nothing is farther from the truth. It is only the theories that would account for evolution, or theories that concern the course which evolution has taken, that are still the subject of controversy.

The history of the evolution idea in the last forty or fifty 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. Since a discussion of these later developments often involves the subject matter of the other branches, any further references to the history of the doctrine of evolution that seems desirable will be made in connection with the evidence of evolution and the theories of its causes in the following pages.

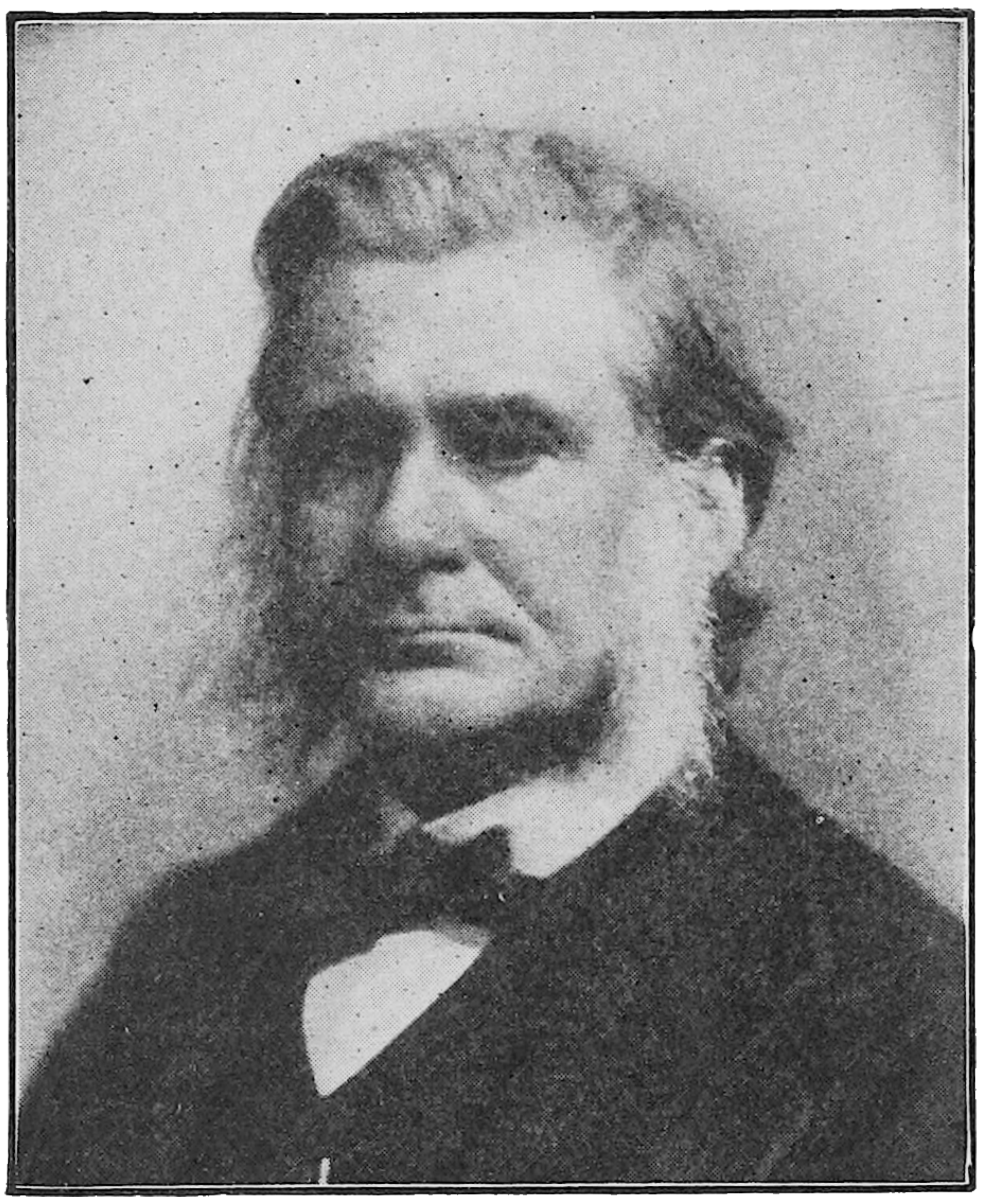

FIG. 235.—Thomas Henry Huxley, 1825–1895.

Evidence of Evolution.—Before proceeding to the implications of evolution, it will be profitable to review the evidence on which belief in the changeability of species is based. The best evidence of any process is to witness it going on. If species can be shown to change while under observation, the best possible evidence of evolution has been obtained. Whenever one or more members of a species possess a characteristic not found in other members of the species in the same generation, or in preceding generations, evolution has occurred, provided the new feature is of such a nature as to be inherited. The heritability of the new feature is insisted upon, as otherwise the change would be temporary. There are numerous differences among organisms belonging to the same line of descent; but in large part these differences are due to the environment and in the main are probably not inherited. Such non-heritable differences are known as *fluctuating variations*, and have no influence upon evolution. Occasionally, however, new characters appear which are inherited. These are called *mutations*, early knowledge of which was largely due to Hugo de Vries, and every mutation is a step in evolution.

Witnessing evolution thus consists in discovering mutations as they occur. This has been done in a considerable number of instances. One of the most fruitful sources of mutations has been the small fruitfly Drosophila extensively studied by T. H. Morgan and others. Owing to the ease with which this fly is reared in confinement, upon fermented bananas, it has been used much for experiments. At first its value as a means of studying evolution was not fully appreciated. It was bred in the laboratories of several universities for the purpose of testing the effectiveness of selection and the influence of the environment, and for experiments upon fertility, length of life, and the like. Then mutations began to appear. It is possible that mutations had been appearing at intervals previously, but if so they did not attract attention. At any rate, mutations so striking that they could not be overlooked occurred. One was a change from the normal red eye of the wild fly to a white eye. Since the flies were examined with a microscope, it is not likely that any such striking alterations escaped observation. The one fly with white eyes was probably the first that had been produced since the stock of flies in which it appeared had been taken into the laboratory. Moreover, when this white-eyed fly was bred with others, the absence of red pigment in the eye was definitely inherited as a recessive trait. Mendelian rules were clearly followed, and the case of white eye in flies might have been used as a simple example of heredity in the chapter on Genetics, instead of albinism in guinea-pigs, were it not for the fact that the possession of white eyes is sex-linked. White eye in Drosophila, then, is a new characteristic which is inherited. It is therefore a mutation and a step in evolution. There are now many white-eyed fruit flies—in captivity. Perhaps, had the first white-eyed fly occurred in nature, it would have perished. Nevertheless, its occurrence would have been a case of evolution. The effect of the death of individuals in which mutations have occurred is discussed later.

Other changes have occurred in the same species of Drosophila (see Fig. 236). Eye colors other than white, to a few of which the names eosin, vermilion, cherry, buff, and tinged have been given, have appeared. New shapes and sizes of wings have occurred. In one the wings were considerably shortened, though they were still functional; in another, the wings were greatly reduced and of abnormal shape, so as to be useless for flight; in still another the wings were inflated like a balloon; in a fourth, wings

features. These alterations affect the size of the flowers; the shape, size and arrangement of the buds; the size and distribution of the seed-capsules (Fig. 237); the size and habit of growth of the whole plant (Fig. 238); the shape of the leaves; the color of the stems; the form of the leaf-rosettes of young plants (Fig. 239); and so on. These new characters have been regarded as mutations for they are inherited. It is true they are not

FIG. 237.—Mutation in Oenothera affecting 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*. (*Photo by Professor H. H. Bartlett.*)

inherited in quite the way that Mendel's law would lead one to expect. Oenothera is a peculiar organism in this regard. Inheritance in the evening primrose is governed by a number of special conditions, which make it an unsatisfactory organism for a first study of heredity; nevertheless the new traits mentioned above are inherited. The new characters are therefore commonly regarded as mutations, although some biologists

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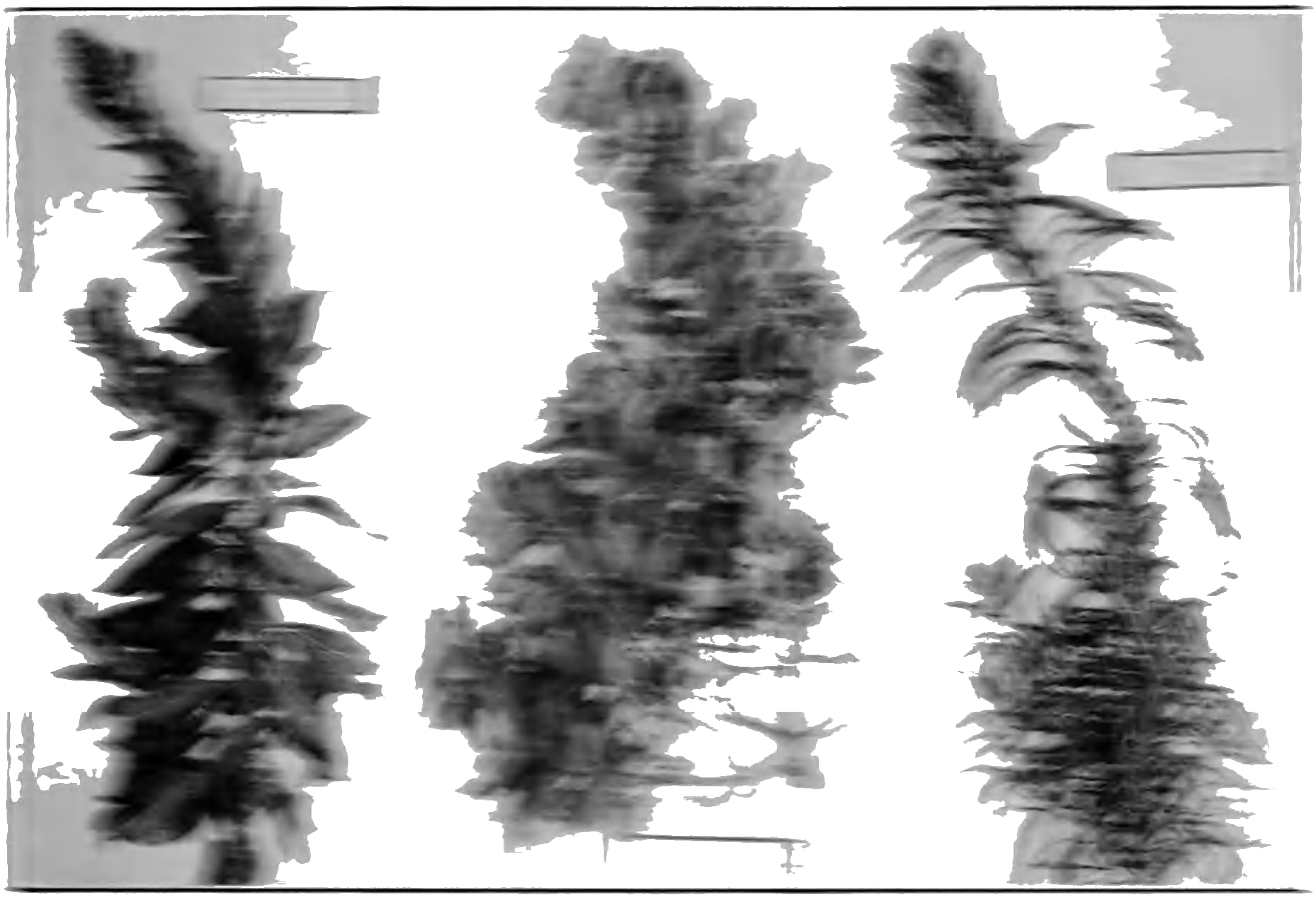

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Many facts of biology are easily explained as due to evolution, but are almost inexplicable on any other assumption. These facts come from various fields of which comparative anatomy is one of the richest.

Comparative Anatomy.—Thus, the similarity of structure in different animals, as revealed by the study of comparative anatomy, is precisely what would be expected if evolution occurred, but would be without meaning in the absence of evolution. The discovery of similar bones in the limbs of practically all vertebrates, though with modifications in each, can hardly mean anything else than that these animals have descended from common ancestors. The similarity of the labyrinth of the inner ear in various vertebrate animals (Fig. 240) is explicable on the same hypothesis. That is why homology is regarded as a certain sign of relationship. The differences found in homologous structures are

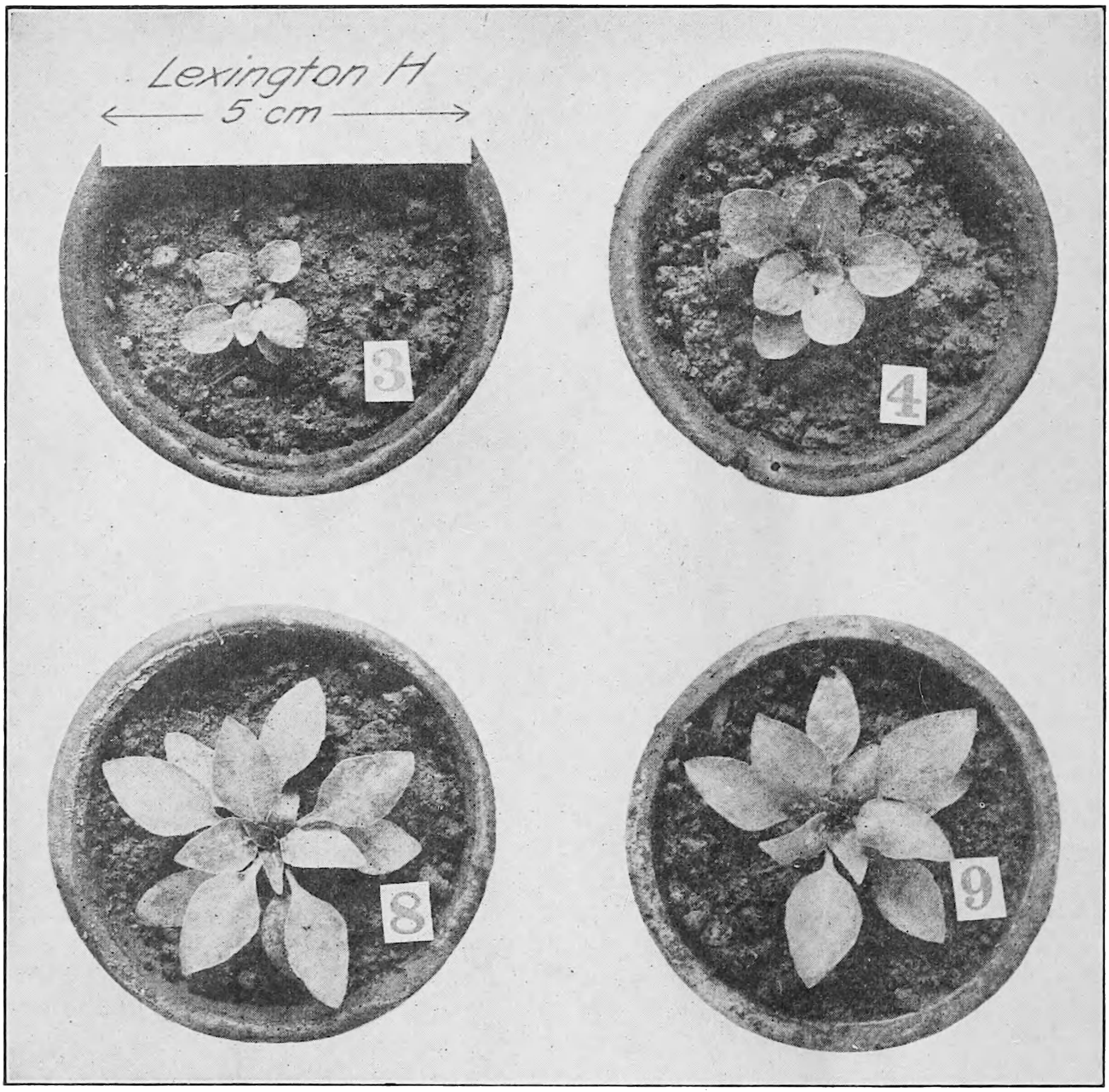

Fig. 239.—Mutation in Œnothera involving the rosettes, or young plants. Below (8 and 9) *Œnothera pratincola;* above (3 and 4) *Œnothera pratincola* mutation *nummularia*, a mutant of the preceding form. (*Photo by Professor H. H. Bartlett.*)

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. 242). Its ancestors, if we may assume evolution to explain this case, were as highly developed as were other barnacles, but by a process of retrograde evolution it has become the degenerate mass of pulp that it is today. Comparative embryology also reveals, not only the fact of evolution, but the course of evolution in some cases. A case in point is the development of gill bars in the embryos of all vertebrate animals, whereas in only a few of the groups do adults have gills. Gill bars in the embryos not only reveal common ancestry, and hence a subsequent evolution, but also indicate that the common ancestors were fish-like animals—fish-like at least to the extent of having gills.

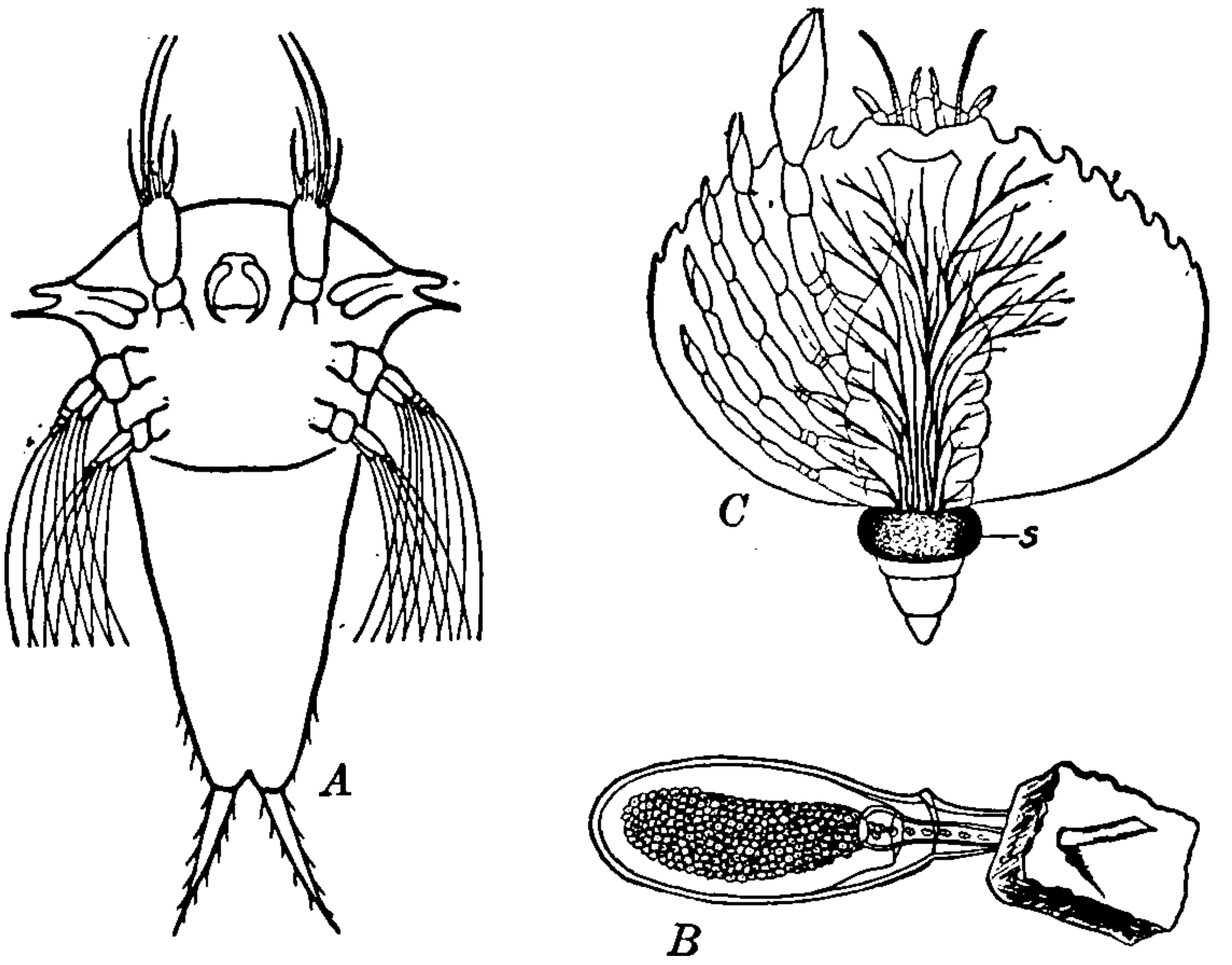

FIG. 241.—Sacculina, parasitic on crabs. *A*, young Sacculina, shortly after hatching, showing that its early development is like that of the Cirripedia (barnacles, etc.). *B*, young animal shown attached to its host, the crab. The projection at the anterior end has penetrated the chitinous ventral wall of the abdomen of the crab, only a small piece of the chitin being shown. Most of the early structure of the parasite is already lost. The mass of cells here shown subsequently passes through the tubular passage in front into the crab's body. *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. These processes absorb nutriment from the body fluids of the host. Practically all of the structure characteristic of the barnacles is lost. Magnification is not the same in the three figures. (*A and B after Delage.*)

COMPARATIVE PHYSIOLOGY.—Similarities in physiological features are to be explained as a result of common descent, but known cases of this kind are less numerous than cases of morphological likeness, probably owing to the difficulty of discovering them. Animals whose blood compositions are very similar, as shown by the results of blood transfusions, are assumed to be closely related. At any rate, similar blood would be a result of common ancestry, and whatever differences now exist are the result of evolution. Fortunately, in general, animals shown by blood tests to be closely related are also known by morphological similarities to have had recent common ancestry.

EXTINCT ANIMALS.—The general relations of fossil animals to each other and to the geological formations are explained by evolution. The fact that, as one passes up through the stratified rocks, the animal remains gradually change, is precisely what evolution would require. The occurrence of fossils similar to living animals, but differing from them in some features, is no longer puzzling if evolution be assumed. Thus, as was pointed out in the preceding chapter, the early mastodons had long protruding faces, while the modern animals most resembling them, the elephants, have the front of the skull much flattened. Fortunately for the explanation of this difference, the later fossil mastodons had much shorter skulls than did the earlier ones. If the later forms evolved from the earlier ones, and if the shortening were continued down to the present time, there is no difficulty in accounting for the evident similarity of the mastodons and elephants in most respects. The differences in the teeth and lower jaw and proboscis and height of skull are explained in the same way. The mastodons and elephants are so much alike in general, that one is practically forced to regard them as members of the same line of descent. But if they are thus related, the form of the skull and the shape and number of the teeth and other features have been altered. The occurrence of horse-like animals in successive geological periods presents precisely the same problem. If the fossils of these animals be arranged in chronological order, there is so little difference between any one animal and those which immediately precede and follow it, that it is difficult to avoid the assumption that they were related to one another as ancestor and descendant. But if this be done, we must assume evolution.

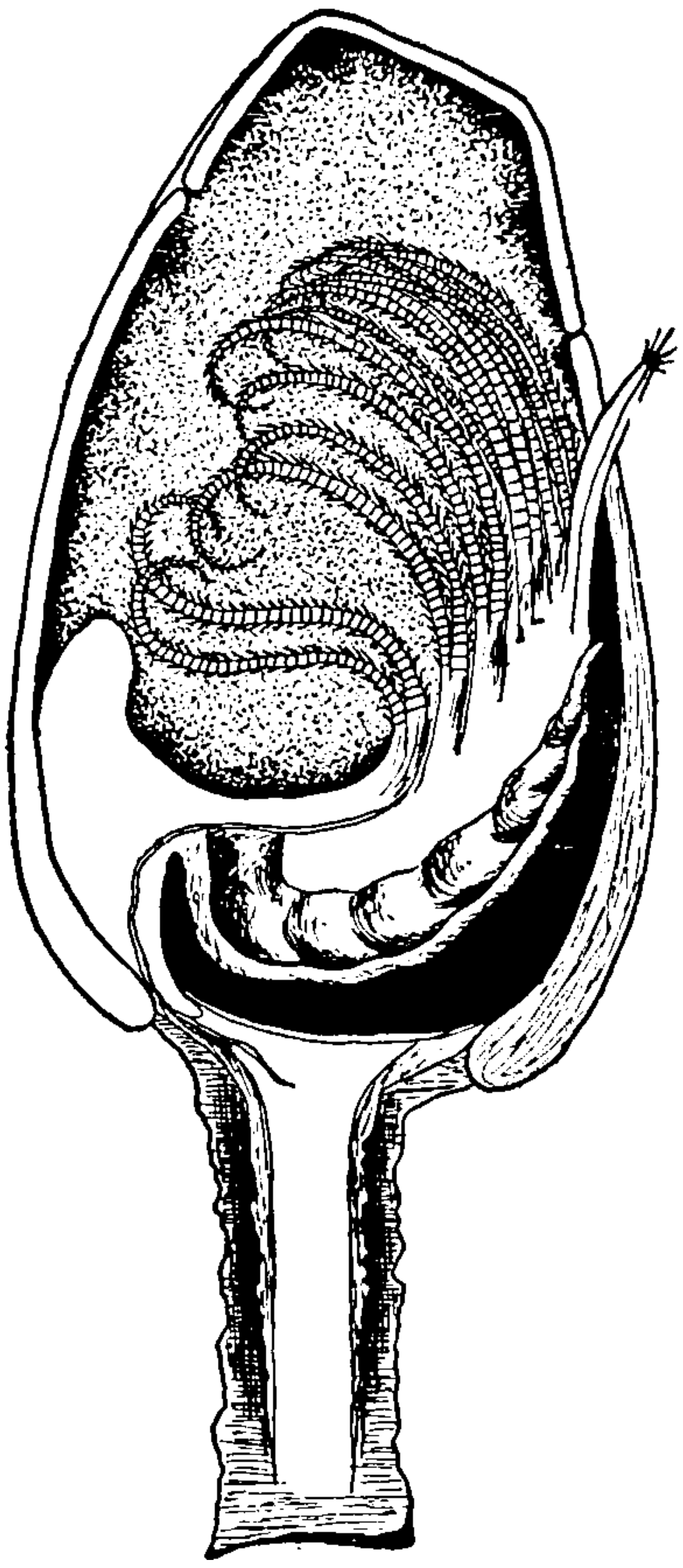

FIG. 242.—Adult free-living barnacle of the genus Lepas, with half of its shell removed. The jointed appendages and some other features make it an arthropod. Its larva resembles that of Sacculina, Fig. 241, *A*. Compare the complex adult of Lepas with the degenerate adult of the parasitic Sacculina, Fig. 241, *C*.

GEOGRAPHICAL DISTRIBUTION.—Many phenomena of distribution which would be meaningless without the doctrine of evolution are entirely natural if modification occurred during descent. Along with the evolution of animals, it is often necessary to assume an evolution of the earth's surface, if the facts of animal distribution are to be made intelligible. Thus, the marsupials (pouched animals, including the opossum and kangaroo) are known to have existed since Mesozoic time. There are reasons for supposing that, at that time, Australia was connected with the American continent by a land bridge across the antarctic region, or indirectly through the other continents (Fig. 243), or by both of these means. As a result, marsupials are found in both Australia and the Americas. But

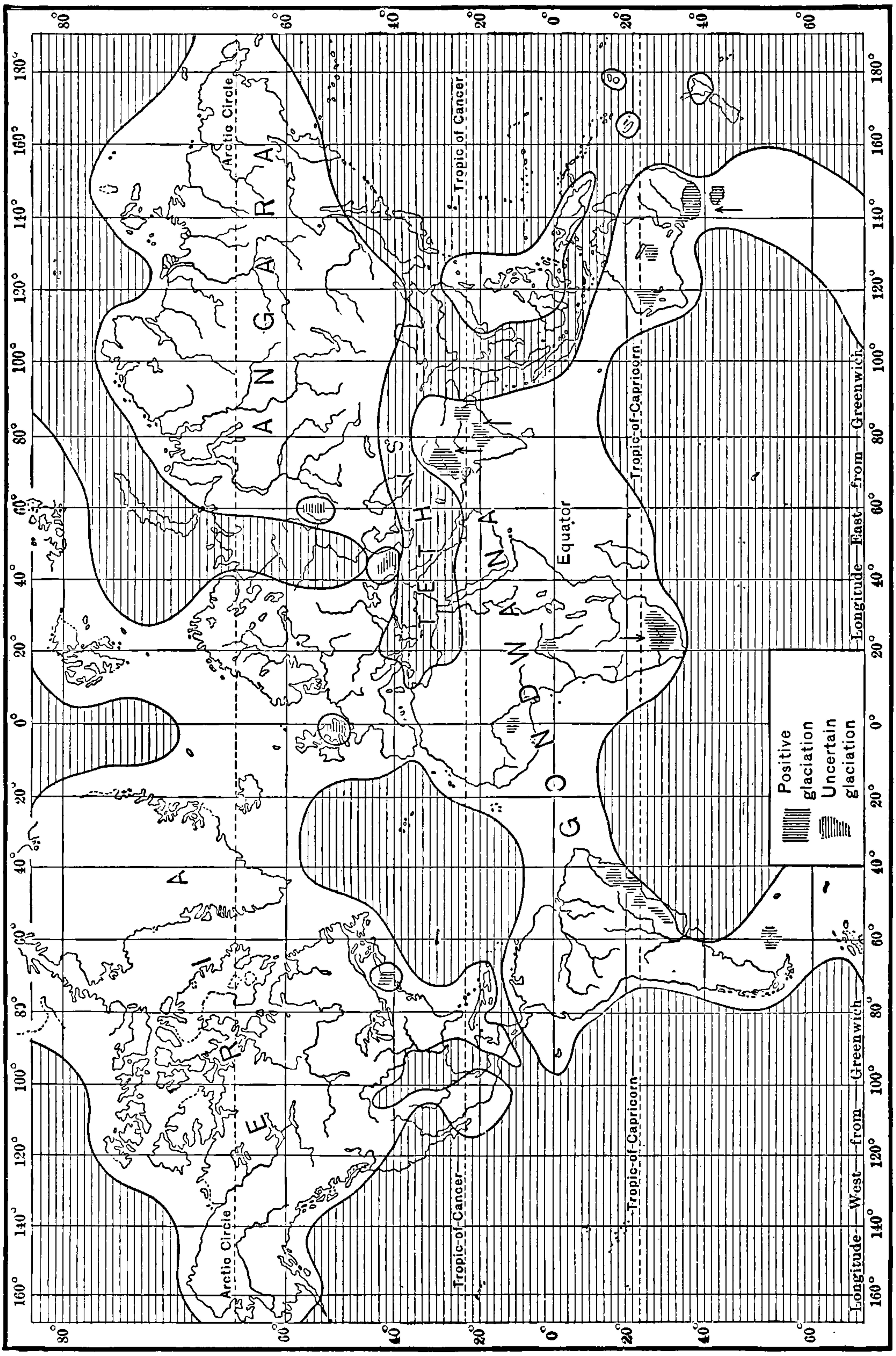

FIG. 243.—The geography of the world in early Permian time. Note the general connection of the continents, especially the union of Australia with the main continental mass. (*From Carnegie Institution of Washington and Schuchert's Historical Geology.*)

separated from the other continents (Fig. 244). No ungulates are native to Australia. If ungulates came into existence in any other way than by evolution from a common stock, there is no apparent reason why they should not have arisen in Australia. But if evolution be assumed as the only method of originating new forms, it is not difficult to understand why Australia never received representatives of this particular group. The ancestors lived elsewhere, and the migration of the descendants to Australia was barred by the sinking of the land.

The facts stated in the foregoing paragraphs, gathered from the provinces of comparative anatomy, embryology and physiology, from paleontology and distribution, receive a very simple and plausible explanation if evolution is assumed. These facts are only a few among a host that would have served equally well. Although these facts have not been specifically designated as evidence of evolution, they constitute such evidence. Facts which may be satisfactorily explained by a theory, and are not readily explained in any other way, are evidence in favor of that theory. To distinguish such evidence from that which comes from direct observation, it may be termed evidence by inference. The time was when inferential evidence was the chief, if not the only, kind advanced to support evolution. The doctrine of evolution was firmly established by evidence from paleontology, comparative anatomy, comparative embryology, and so on; for, at the time of the rise of the evolution theory, new characters had seldom been observed to arise among carefully pedigreed animals. Pedigrees were not common in the experiments of scientific men, and those kept by practical breeders were not always accurate in detail. Very few new characteristics had ever been observed at the time of their origin under circumstances which forbade their being attributed to hybridization or to the environment, until after the evolution theory had been generally accepted by biologists. The evidence which, as stated above, seems to us the best evidence, namely, the observation of mutations at the time of their origin, was not discovered in quantity until near the end of the last century, and since that time.

CAUSES OF EVOLUTION

While no thinking person now denies the fact of evolution, there is still much disagreement regarding the causes or method of the process. There are not wanting facts which bear on the question, but it is probable that a good many more facts are undiscovered or even undiscoverable. The question as to the causes of evolution must therefore be answered, if answered at all, in a rather speculative fashion. Before entering upon such speculation, it is essential to be perfectly clear as to what the problem is. As was pointed out early in the chapter, evolution occurs whenever a new character arises which is capable of being inherited, If it is clearly realized that, in discovering the causes of evolution, it is only the origin of mutations that is being considered, the discussion will be simplified. It matters not, in this connection, what kind of mutation arises, nor whether the one or several animals which possess the new character survive or perish. These are questions which are discussed below under the caption "Course of Evolution." Just now the thing requiring explanation is the origin of heritable changes.

Internal Factors: Mutations.—It has been indicated elsewhere that the characters of an animal are determined by something in the chromosomes of the germ cells from which the animal develops. Although individual characters may be impressed upon an organism by the environment, such features are rarely if ever, in the higher animals, handed on to the offspring. An evolutionary change must therefore presumably begin with a change in the chromosomes of the germ cells. What kind of change this must be is uncertain, for it is not clear what kinds of substances in the chromosomes are responsible for the development of hereditary traits. If the proteins determine development and heredity, a mutation may well result from a rearrangement of the atoms in the molecules. Proteins are very complex substances, their molecules being composed of hundreds or even thousands of atoms. No doubt, as in simpler organic compounds, these molecules have a definite configuration; that is, the proteins possess structure even when the chemist cannot discover it. In such complex bodies, by slight modifications, new molecules could be produced in which exactly the same atoms were present, but in different arrangement. Two or more substances whose molecules have the same number of atoms of each of the same elements, but differently arranged, are known as *isomers*. Isomers are known in many organic compounds, and they invariably differ from one another in some physical or chemical property. A substance may often be easily converted into one of its isomers, as for example, by the application of heat. If the proteins of the chromosomes should suffer any rearrangement of their parts, and their chemical properties be thereby altered, any hereditary traits determined by the modified proteins could hardly escape being different. Moreover, if the rearranged molecules were fairly stable, they would remain in the changed condition in succeeding generations, and the trait which they produced would be inherited. The altered condition would therefore be a mutation, a step in evolution. What sort of change in the adult would follow a given change in the proteins in the chromosomes could not be predicted. A shift of a few atoms to a new position, in the germ cells, might change the color of the eye or the shape of a bone. It is extremely unlikely that a molecular change of the kind hypothecated would not produce any alteration whatever in the adult. In view of the uncertainty regarding the nature of the material basis of heredity, further speculation of this kind would be unprofitable. If these paragraphs have shown what the problem of the cause of evolution is, and what sort of solution of it is to be expected, they have served their purpose.

Changes in the Environment.—Although environment is not generally accepted without reservations by leading biologists as an important cause of evolution, yet from its historical interest and from the belief still held by many biologists, it should be mentioned. Animals are often so obviously fitted for the environment in which they live, that observers are apt to conclude that in some way the environment worked them over until they were fit. Though it is not improbable that adaptation to environment is due to the migration of animals to that environment to which they are best fitted, provided they have had time to reach it and there is nothing in the way, environment as a cause of evolution cannot thus be swept aside without consideration. There are, as stated above, many biologists who firmly believe in the environment as an agent in bringing about evolution. That was Lamarck's view a century ago, and the same view is widely held today. As pointed out in the first chapter, some paleontologists, many medical men, and most of the laity are adherents, even now, of the Lamarckian theory. In support of their position may be cited the work of a few biologists who believe they have been able, in experiments, to produce by artificial means, such as changes of the medium, temperature, nutrition, or moisture, modifications which were subsequently inherited. In so far as these experiments have dealt with bacteria and other simple organisms, or the germ cells have been *directly* affected by the environment, the conclusions are in part apparently justified; but when they involved higher animals, and when the germ cells were not directly influenced, the experiments have never satisfied the majority of experimental biologists. Nevertheless it would be unfair to disregard these experiments. There is no *a priori* ground for supposing that environment could not effect evolution, and it may be that some day evidence so conclusive will be brought forth that everyone will admit its validity. However, that evidence, if it is ever secured, may easily prove unsatisfactory to those persons who most diligently seek it. For the strong appeal to the imagination made by the theory of environmental agency in evolution lies in the possibility that adaptation to environment may thereby be explained. It is well known that changes in the environment cause alterations in the bodies of animals and plants, and that some of these modifications are advantageous to the organisms. But in no case has it been established that one of these adaptive alterations has been transmitted to the descendants. Indeed, it is doubtful whether there exists in organisms any mechanism by which a purely somatic change could produce an effect on the germ-plasm such that the *same* somatic character would appear in the next generation. However, the question whether the environment can produce permanent *adaptive*

Paleontology furnishes perhaps the best evidence of the course of evolution when the series of discovered fossils is fairly complete. But evidence as good as that concerning the horses and elephants is not common. To trace the lines of descent of animals whose ancestors are not abundantly represented among known fossils, reliance is placed on comparative anatomy, comparative embryology, and geographical distribution. In erecting a family tree upon the basis of facts furnished by these sciences there is, however, much uncertainty. It is not difficult, in most cases, to decide what animals have descended from a common ancestor. When two species of garter snake differ only or principally in the number of rows of scales, they may safely be regarded as having been produced from the same stock. But was the ancestral species like the one modern species, or like the other? Or was it different from both? In answering such questions the zoölogist applies certain rules which seem to him to express probabilities. These rules may depend upon the amount of variability in the character which distinguishes the present species, or the present distribution of these and other similar species. But any conclusion based on such rules is subject to risk, and the merits of each case have to be decided separately. In tracing the descent of the larger groups, still greater uncertainty exists. As pointed out above, the vertebrates have plainly come from a gill-bearing animal. But what are the steps by which the present condition, especially in those classes in which gills no longer occur (reptiles, birds, mammals), has been attained? Here opinion differs, and there has been much controversy over questions concerning the mutual relationships and intermediate stages of descent of these groups. When the biologist grows still bolder, and attempts to go back of the ancestors of the phylum, tracing the course of evolution is practically without foundation. It has been held probable, for example, that the annelids and arthropods have descended from common ancestors, partly because the members of both these phyla are segmented. But of the steps in the divergence of the two groups, if they really are related, there is almost no evidence whatever. Tracing such supposed pedigrees was fashionable among zoölogists during the latter third of the nineteenth century, until it was realized how speculative is the process.

Factors Directing the Course of Evolution.—Ideas regarding the agencies that guide evolution are as old as ideas of evolution itself. Speculation as to the reasons for the development of lines of descent is really older than the attempt to build family trees. Evolution was early thought of as a process of becoming perfect, whatever that might mean; and before this idea became concrete, and took the form of specific lines of descent, there was conjecture as to what led animals toward the goal of perfection.

Environment: Use and Disuse.—The early views of the guiding factors involved almost exclusively the environment and the effects of use and disuse. Both of these were embodied in Lamarck's theory of evolution. In some manner the environment was believed to be able to direct the changes, from generation to generation, in certain channels. Lamarck speaks of the "needs" of the animal, or even of its "desire," becoming so great that the body responded by modifications in the required direction. Such a conception now seems to us, of course, the lightest of fancies. In similar manner the effects of use and disuse were believed by Lamarck to be inherited, and so to bring about modifications of the species. The stretching of the giraffe's neck after branches of trees, and the excessive use of the kangaroo's legs for jumping, he thought, caused an over-development which was transmitted to their offspring. Although the increase in length of these organs was presumably small in any one individual, the accumulated increments amounted in time, Lamarck believed, to an enormous change. These views have been largely abandoned by the pure biologists, who realize that a blacksmith's children, if they are stronger than other children, are so because their father was inherently strong, and not because his occupation made him stronger. The strength of the blacksmith, which was his by inheritance, not trade, enabled him both to beget strong children and to follow a vocation requiring brawn. However, as stated in the first chapter, there are those, biologists among them, who still adhere to the Lamarckian view of the effects of use.

Natural Selection: Sexual Selection.—Darwin rejected, in the main, the Lamarckian principles, and proposed in their stead several forms of selection. The best known and the most generally applicable of his theories is that of Natural Selection which, indeed, is often called by the name Darwinism. Animals, he said, naturally varied among themselves. If the variation of certain individuals was such as to give them a better chance in the struggle for existence, those individuals would survive in larger numbers than their less fortunate fellows, or would live longer and produce more offspring. Darwin assumed that, on the whole, the variations which helped these individuals would be transmitted to their progeny. In the next generation, he thought, the selection in favor of this variation would be repeated. In time, by this natural selection, a new race would be established. To explain such useless features as the gorgeous plumage of some kinds of male birds, features that could not help in the ordinary struggle for existence, Darwin postulated sexual selection. The more brilliant males, he thought, were more successful in courtship, and so left more progeny. Assuming variations in coloration to be inherited, a race having highly colored males would thus be evolved. In the hands of Darwin's followers and admirers the idea of selection was developed to an extraordinary degree. The most insignificant features were held to be an aid in the struggle for existence. One gained the idea, from following the arguments of these enthusiasts, that animals possessed no traits that were neutral or harmful, but that every structure and every habit was adapted to some use, and that the present existence of these structures and habits was due to their usefulness. It is now known, however, that such useless or detrimental characters are not uncommon. Through no fault of Darwin's then, but because of the zeal of his apostles, the theory of natural selection came into a degree of neglect. Although careful breeding experiments indicate the effectiveness of artificial selection, there is no marked inclination among leading biologists to attribute to selection in nature, through the struggle for existence, anything but a minor and negative rôle in evolution. Any modification that is very harmful would, of course, probably cause the death of its possessor. But characters that are neither useful nor harmful as well as those slightly harmful and those that are beneficial, might well be preserved. If the destruction of individuals in which very harmful new traits have appeared is all that natural selection accomplishes, it plays a much less important part in directing the course of evolution than Darwin (to say nothing of his more zealous and less discriminating followers) supposed.

Direction of Mutation.—Such negative action by natural selection could not, however, have been responsible for the course of evolution in the development of modern animals from their early ancestors. The direction of this great positive development, with little help or hindrance from natural selection, must have been due to something else. That other agency is believed to lie in the native internal capacity of protoplasm for undergoing change, or producing mutations, which was discussed among the causes of evolution but which must be alluded to here also as a factor determining the direction of evolution. Since mutations, as pointed out in the previous discussion, are probably the result of chemical changes of the chromatin, it will be seen that although a large number of such changes may be possible, there is a limit both to the number and to the kind of changes that may occur, and that the direction of evolution must be one or more of the directions of these possible changes. The kind of chemical change that occurs in a protein, for example, is strictly limited by the structure of its molecule. The kind of mutation that occurs, and hence the direction of evolution, is in turn dependent upon the kind of chemical change that is possible in the chromatin of the germ cells. The direction of evolution is therefore determined by the nature of the chromatin.

Orthogenesis.—What direction the changes in the chromatin, and hence the changes in the adult, will take cannot be foretold. It is possible that the molecular changes of the chromatin take place in a purely random manner. On the contrary, the shifting of the atoms in a particular manner at one time may make a further change of the same kind at a later time more probable. If the latter supposition is correct,

Orthogenesis, if there is such a phenomenon, must not be regarded as an abstruse perfecting principle of any kind, but as being dependent on the chemical composition of the protoplasm. It is therefore to be expected that orthogenesis may occur in some animals, not in others.

Evolution by Hybridization.—Although new characters probably arise regularly in higher animals only by mutation, it is obvious that a form of evolution may take place by combination, in one organism, of features that have previously existed independently in different organisms. They are brought together in one individual by hybridization, producing combinations that did not exist before; for example, rough coat in guinea-pigs may be combined with any of the coat colors. The combination is not always so simple as this, however, even where only two characters are involved. The bringing together in one animal of genes for two characters not previously combined sometimes produces a new character unlike either of those combined. Fowls with pea combs (small combs with a number of low prominences, Fig. 245), breed true to their form of comb. Rose comb (a low but thick comb with a roughened upper surface and a long tapering projection behind) is another true-breeding character. When a fowl homozygous for pea comb is mated with one homozygous for rose comb, the result is not a fowl having both pea and rose combs, but a new comb called walnut. This is a thick, fleshy, rounded comb overhanging the base of the beak. Other inherited features, requiring for their production the presence of half a dozen or more genes for simple characters, are known. The results

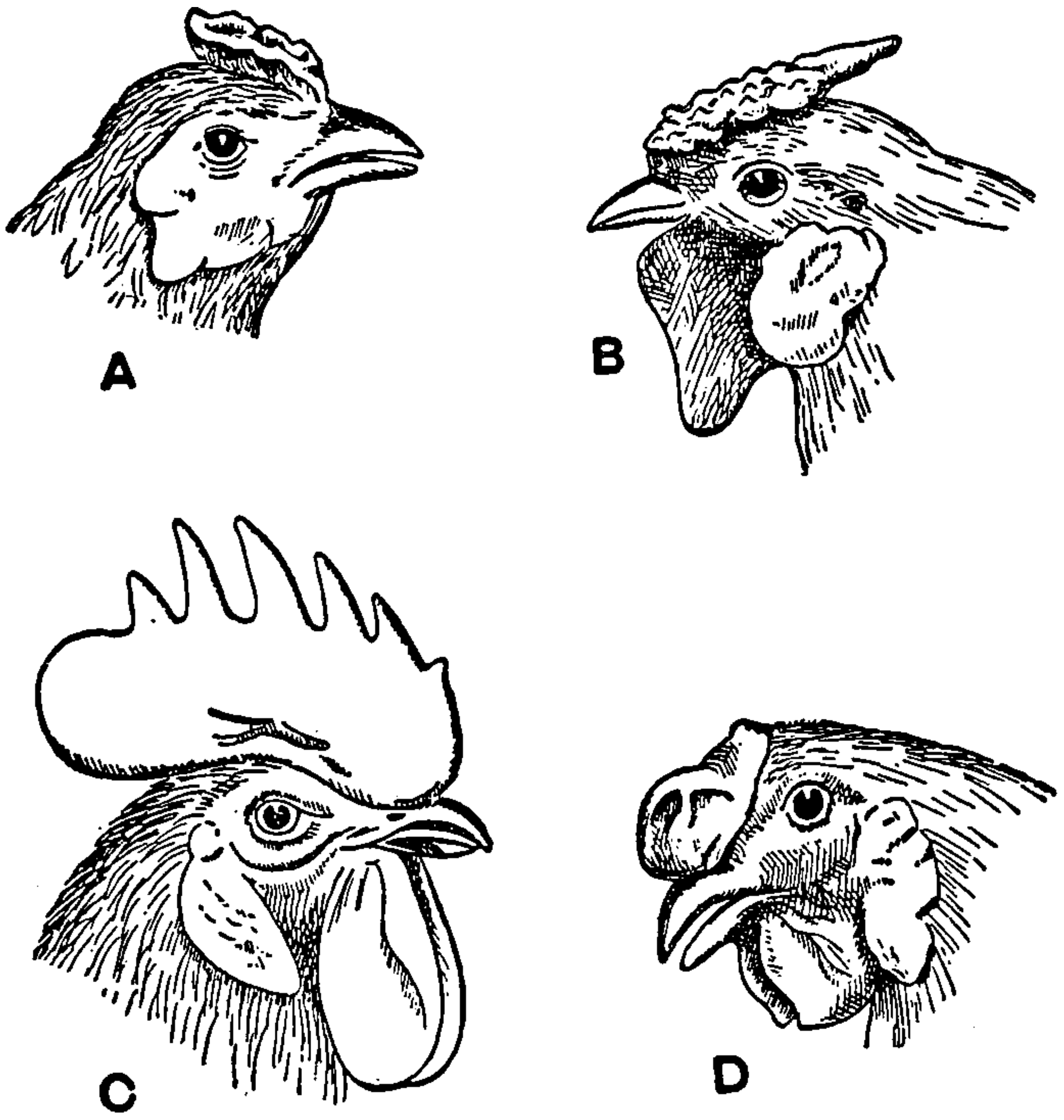

FIG. 245.—Combs in fowls. *A*, pea comb; *B*, rose comb; *C*, single comb; *D*, walnut comb. The walnut comb is a compound character, that is, it is produced by the coöperation of the factors for pea comb and rose comb. (*From Punnett's Mendelism Courtesy of Macmillan Co.*)

of recombination through crossing cannot, therefore, always be foretold. The possibilities of evolution through hybridization are thus greatly increased, and its range enormously widened. In view of these facts, it is not surprising that some biologists have regarded the new characters frequently arising in the fruitfly and the evening primrose as the result of recombinations of genes, and not as mutations at all. But, as pointed out before, even if this view should be correct, it would merely push back to an earlier time the production of the characters whose genes are supposed to be now shifting from one combination to another. For the various factors producing eye color in flies can hardly have existed in their present form from an indefinitely early time, even before flies had come into existence in the evolution of animals. They must have originated sometime in order to be recombined now, if this recombination is all that is happening. Their origin was probably the sort of chemical change which we call mutation.

Artificial Evolution.—The possibility of evolution through hybridization has been seized upon by man for his own advantage. The breeding of animals has occupied his attention in a commercial way for centuries and has resulted in striking improvements. But for a further statement regarding animal breeding the reader is referred to the chapter on Genetics. The attempt to bring about evolution by the artificial production of mutations has been attended with doubtful success. A few biologists, as pointed out above, believe they have altered the hereditary traits of animals by changing such features of the environment as temperature, nutrition and humidity; but their results have seldom been entirely satisfactory. The majority of biologists, on contemplation of their experiments, have usually been impelled to bring in the Scotch verdict of "not proven."

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GLOSSARY

Pronunciations are indicated in this 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 doctrine that living things originate from non-living matter; same as spontaneous generation. In its crude early form the doctrine has been abandoned.

Aboral (*ab o′ ral*). Opposite the mouth.

Absorption (*ab sorp′ shun*). The imbibing of a liquid by osmotic or capillary action.

Acanthocephala (*a kan′ tho sef′ a la*). A group of parasitic worm-like animals usually included with the Nemathelminthes. For definition see Chapter XII.

Acetabulum (*as′ e tab′ u lum*). The socket on either side of the pelvic girdle for the head of the femur.

Achromatic figure (*ak′ ro mat′ ik*). That part of the division figure in mitosis which does not stain deeply, namely, the spindle including centrospheres and asters, but excluding the chromosomes.

Acris (*ak′ ris*). A genus of frogs.

Actinian (*ak tin′ i an*). A sea anemone.

Actinomorphes (*ak′ tin o mor′ feez*). A group of animals in Blainville's early classification; animals with radiating parts, such as the starfish.

Actinophrys (*ak′ ti nof′ ris*). A genus of rhizopod Protozoa, of the order Heliozoa.

Actinosphærium (*ak′ ti no sfe′ ri um*). A genus of rhizopod Protozoa, of the order Heliozoa.

Adaptation (*ad′ ap ta′ shun*). Fitness for the environment. In a concrete sense, an adaptive structure, habit, or function.

Adductor (*ad duk′ ter*). 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 (*ad′ i pose*). Pertaining to fat.

Adrenal (*ad re′ nal*). One of two or more ductless glands in close relation with the kidneys in most vertebrates.

Aeolosoma (*e′ o lo so′ ma*). A genus of worms, phylum Annelida, subclass Oligochæta.

Aganides (*ag′ a ni′ deez*). A genus of extinct cephalopods with bent sutures of the goniatite form.

Agar (*ah′ gar*). A nutrient material used in bacterial cultures, etc.

Agassiz, Jean Louis Rodolphe (*ah′ gah see′*, Eng. *ag′ a see*). Swiss-American naturalist, 1807–1873.

Albinism (*al′ bi niz′m*). The absence of the usual pigments in skin, hair, and eyes; said of individuals having white skin and hair and pink iris in species usually colored.

plants. 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.

Anguis (*ang′ gwis*). A genus of legless lizards.

Animal pole (*an′ i mal 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.

Anisogamy (*an′ i sog′ a mi*). Fusion of unlike gametes in reproduction.

Annelida (*an nel′ i da*). The phylum of animals comprising the segmented worms. For definition see Chapter XII.

Anodonta (*an′ o don′ ta*). A genus of freshwater mussels.

Anodontoides (*an′ o don toi′ deez*). A genus of freshwater mussels.

Antenna (*an ten′ na*)(*pl.,* **antennæ**). One of a pair of jointed appendages projecting forward from the head of an insect or crustacean.

Anthocystis (*an′ tho sis′ tis*). A genus of rhizopod Protozoa, of the order Heliozoa.

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 Cœlenterata, comprising the sea anemones and most of the corals. They have no medusoid form in the life cycle.

Anthropoid (*an′ thro poid*). Man-like; said of certain apes.

Antimere (*an′ ti meer*). One of a series of parts, radially arranged like the spokes of a wheel.

Ant-lion (*ant′ li′ on*). An insect whose larva lives in a conical pit dug in the sand, capturing other insects that fall into the pit.

Anus (*a′nus*). The posterior opening of the digestive tract.

Apoda (*ap′ o da*). An order of Amphibia comprising the legless forms called cœcilians.

Appendicular skeleton (*ap′pen dik′ u ler*). 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 Chapter XII.

Archæopteryx (*ar′ ke op′ ter iks*). An extinct animal of Jurassic time resembling both reptiles and birds, having teeth and feathers.

Archæozoic (*ar′ ke o zo′ ik*). Of the earliest geological period; the oldest known system of rocks is of this period.

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 setæ.

Aristotle (*ar′ is tot′l*). The most famous of the Greek naturalist philosophers, wh lived 384–322 B.C.

Armadillo (*ar′ ma dil′ lo*). An armored mammal of the order Edentata, whic includes also the sloths and ant-eaters.

Artery (*ar′ te ri*). 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 Chapter XII.

Articulate (*ar tik′ u late*). To join; said of bones.

Artificial parthenogenesis (*ar′ ti fish′ al par′ the no jen′ e sis*). The artificial stimulation of an egg to develop without fertilization.

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 round-worms (Nemathelminthes) parasitic in various animals. **A. megalocephala** (*meg′ a lo sef′ a la*), parasitic in the intestine of the horse.

Ascidian (*as sid′ i an*). Any one of a number of degenerate Chordata, members of the subphylum Tunicata, order Ascidiacea.

Asexual (*a seks′ u al*). Not involving germ cells nor fusion of nuclei; said of reproduction, or of an individual employing such a mode of reproduction.

Assimilation (*as sim′ i la′ shun*). The conversion of digested foods and other raw materials into protoplasmic substances.

Aster (*as′ ter*). The star-like figure composed of a centrosome and the radiating lines about it; or the centrosome may be lacking.

Asteroidea (*as′ te roi′ de a*). A class of Echinodermata comprising the starfishes. For definition see Chapter XII.

Astral rays (*as′ tral raze′*). The radiating lines surrounding a centrosome in a dividing cell.

Asymmetrical (*a′ sim met′ ri kal*). Not capable of being divided by a line or plane into halves which are mirrored images of each other.

Asymmetry (*a sim′ me tri*). Absence of any kind of symmetry.

Attraction-sphere (*at trak′ shun sfeer*). A differentiated portion of the cytoplasm of a cell, usually lying near the nucleus, and typically containing a central body called the centrosome. The whole structure is associated with the process of cell division.

Auchenia (*aw ke′ ni a*). The genus to which the llama and vicuna belong.

Auditory (*aw′ di to ri*). Pertaining to hearing; applied to the nerve of hearing and the sensory part of the inner ear.

Auricle (*aw′ ri k'l*). The anterior chamber of the heart in fishes, and one of the two anterior chambers in higher vertebrates.

Autonomic nervous system (*aw′ to nom′ ik*). Same as **sympathetic nervous system.**

Aves (*a′ veez*). A class of vertebrate animals comprising the birds.

Avicularia (*a vik′ u la′ ri a*). Individuals of a Bugula colony, each shaped like a bird's head.

Axial skeleton (*aks′ i al*). 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.

Back cross (*bak′ kros′*). A cross between an F_1 individual and one of its parent types.

Bascanion (*bas ka′ ni on*). A genus of snakes, including the black snake or blue racer.

Belon, Pierre (*be lon′*). French naturalist and traveler, 1517–1564.

Berengario (*ber′ en gah′ ri o*). Italian anatomist and surgeon in University of Bologna, in the sixteenth century.

Biconcave (*bi′ kon kave′*). Having the centrum hollow both in front and behind; said of vertebræ.

Bidder's canal (*bid′ derz ka nal′*). A longitudinal tube near the median border of the kidney of certain Amphibia; into it the collecting tubules open.

Bilateral symmetry (*bi lat′ er al sim′ me tri*). An arrangement of the parts of an object or animal body such that the halves on opposite sides of a certain plane are mirrored images of each other.

Bile (*bile*). The fluid secreted by the liver in vertebrates.

Bile duct (*bile′ dukt′*). The tube through which bile is discharged into the intestine.

Binomial (*bi no′ mi al*). 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 (*bi′ o je net′ ik law′*). The doctrine that animals in their embryonic development repeat the evolutionary history of the race.

Biology (*bi ol′ o ji*). The science of life and of living things, whether plants or animals.

Bionomics (*bi′ o nom′ iks*). The study of the relation of organisms to the environment.

Biota (*bi o′ ta*), The animals and plants of a given area or of a given period of time. (See **fauna** and **flora**, both of which are comprised under the term biota.)

Blainville, Henri Marie Ducrotay de (*blaN veel′*). French naturalist, 1777–1850.

Blastocœle (*blas′ to seel*). The hollow interior of a blastula.

Blastophaga (*blas tof′ a ga*). A genus of wasp-like insects of the order Hymenoptera, certain species of which dwell in figs.

Blastopore (*blas′ to pore*). The opening through which the archenteron of an early embryo (gastrula) communicates with the exterior.

Blastostyle (*blas′ to stile*). The central cellular core of a gonangium.

Blastula (*blas′ tu la*). An early developmental stage, consisting of a hollow ball of cells.

Bolina hydatina (*bo li′ na hi dat′ i na*). A species of ctenophore.

Book gill (*book′ gil′*). See **book lung**.

Book lung (*book′ lung′*). A respiratory organ composed of flat sheets joined together like pages of a book, found in spiders.

Botryllus (*bo tril′ lus*). A colonial marine animal belonging to the subphylum Tunicata. It lives attached to leaves or other flat surfaces.

Bougainvillea ramosa (*boo′ gaN vil′ le a ra mo′ sa*). A species of marine hydroid.

Bowman's capsule (*bo′ manz kap′ sule*). 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 (*brakt*). One of the covering (protective?) members of a siphonophore colony.

Branch (*branch*). Any one of four major groups of animals in Cuvier's early classification.

Bronchus (*brong′kus*) (*pl.,* **bronchi**). One of the two main branches of the trachea in many vertebrates.

Browse (*browz*). To eat the twigs of bushes or trees.

Carnivorous (*kar niv′ o rus*). Flesh-eating.

Carotin (*kar′ o tin*). One of two yellow substances associated with chlorophyll.

Carpal (*kar′ pal*). One of a number of bones in the wrist in vertebrates.

Carpo-metacarpus (*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 (*kar′ ti laj*). 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 (*kast*). 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.

Catalysis (*ka tal′ i sis*). A reaction produced by means of a catalyzer.

Catalyst (*kat′ a list*). See **catalyzer.**

Catalytic agent (*kat′ a lit′ ik*). See **catalyzer.**

Catalyzer (*kat′ a li′ zer*). A substance which brings about a reaction but is not consumed in that reaction. It probably participates in the reaction, but is promptly reformed.

Caudal (*kaw′ dal*). Belonging to the tail.

Caudata (*kaw da′ ta*). An order of Amphibia comprising forms with tails (salamanders, newts).

Cecidomyia (*se sid′ o mi′ ya*). A genus of flies.

Cecidomyiidæ (*se sid′ o mi′ yi dee*) A family of flies.

Cell (*sel*). A mass of protoplasm containing a nucleus or nuclear material.

Cell doctrine (*sel′ dok′ trin*). See **cell theory.**

Cell inclusions (*sel′ in klu′ zhunz*). Non-living objects enclosed in cells.

Cell membrane (*sel′ mem′ brane*). A thin sheet either of differentiated protoplasm, or of some substance produced by protoplasm, surrounding a cell.

Cell theory (*sel′ the′ o ri*). 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 (*sel′ wawl′*). A non-living structure secreted by a cell around itself. It is commonly composed of cellulose or chitin.

Cement (*se ment′*). A binding material in the composition of teeth.

Cenozoic (*se′ no zo′ ik*). Pertaining to the most recent geological time prior to the Psychozoic.

Central nervous system (*sen′ tral ner′ vus sis′ tem*). The brain and spinal cord.

Centrolecithal (*sen′ tro les′ i thal*). Having the yolk in the central portion; said of eggs.

Centrosome (*sen′ tro some*). A minute body often present in a cell, usually near the nucleus in an attraction-sphere, related in some way to the process of cell division.

Centrosphere (*sen′ tro sfeer*). Same as **attraction-sphere.**

Centrum (*sen′ trum*). 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 Chapter XII.

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 head-like 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.

Cercaria (*ser ka' ri a*). The tailed larval form of the liver fluke Fasciola (and similar forms) which is produced by a redia and which develops into the adult fluke.

Cerebellum (*ser' e bel' lum*). A division of the brain of vertebrates developed on the dorsal side anterior to the medulla.

Cerebrum (*ser' e brum*). 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 (*ser' vi kal*). Pertaining to the neck.

Cestoda (*ses to' da*). A class of Platyhelminthes, comprising the tapeworms. For definition see Chapter XII.

Chætogaster (*ke' to gas' ter*). A genus of worms, phylum Annelida, subclass Oligochæta.

Chætognatha (*ke tog' na tha*). A group of marine animals of uncertain kinship, represented chiefly by the arrow-worm Sagitta.

Chætopoda (*ke top' o da*). A class of worms (Annelida) provided with setæ, to which the earthworm and sand-worm belong.

Chara (*ka'ra*). A genus of aquatic plants.

Cheloniidæ (*kel' o ni' i dee*). A family of turtles.

Chelydridæ (*ke lid' ri dee*). A family of turtles.

Chemotropism (*kem ot' ro piz'm*). The response of an organism to chemical substances.

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.

Chlamydomonas (*klam' i dom' o nas*). A genus of unicellular flagellate chlorophyll-bearing organisms.

Chloragogen cells (*klo' ra go' jen*). The cells of the outer layer of the intestine of the earthworm.

Chlorophyll (*klo' ro fil*). The green substance in chloroplasts through whose agency photosynthesis occurs.

Chloroplast (*klo' ro plast*). A green plastid.

Cholesterin (*ko les' ter in*). A substance of fat-like texture common in bile, the chief constituent of gall stones, and found also in blood, nerve tissue, egg yolk, etc. It is often classed with the lipoids.

Choline (*ko' lin*). A hydroxide common in plant tissues and in many animal cells, as egg yolk and nerve tissue, in various combinations.

Chordata (*kor da′ ta*). A phylum of animals including the vertebrates and a few others. For definition see Chapter XII.

Chorophilus (*ko rof′ i lus*). A genus of frogs.

Chromatic figure (*kro mat′ ik*). That part of a mitotic figure which stains deeply, namely, the chromosomes, as distinguished from the spindle.

Chromatin (*kro′ ma tin*). The deeply staining substance of the nucleus of a cell, attached to or imbedded in the linin network.

Chromomere (*kro′ mo meer*). One of the small aggregations of chromatin and other substances collectively forming a chromosome.

Chromoplast (*kro′ mo plast*). One of several kinds of colored structures or organs found in many plant and some animal cells.

Chromosome (*kro′ mo some*). One of the rod-like 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.

Chyme (*kime*). The fluid containing partly digested food found in the stomach.

Cicindela (*sis′ in dee′ la*). A genus of tiger-beetles.

Ciliary (*sil′ i a ri*). Pertaining to cilia.

Ciliata (*sil′ i a′ ta*). A subclass of the Infusoria (Protozoa), in which both young and adult stages are provided with cilia.

Ciliate (*sil′ i ate*) or **ciliated.** Provided with cilia.

Cilium (*sil′ i um*). A minute hair-like motile structure occurring on the surface of certain cells.

Circular canal (*ser′ ku ler ka nal′*). A channel passing around a medusa near its margin.

Circulation (*ser′ ku la′ shŭn*). 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.

Cirrus (approximately *seer′ us*) (*pl.*, **cirri**). A soft tentacle-like projection. Also, a copulatory organ in some animals.

Class (*klas*). A subdivision of a phylum; a group of higher rank than the order.

Clavicle (*klav′ i k′l*). The collar bone in man. One of the bones of the ventral part of the pectoral girdle in vertebrates in general.

Cleavage (*kleev′ aj*). The division or segmentation of an egg.

Clitellum (*kli tel′ lum*). A thickened glandular band encircling the body of an earthworm.

Cloaca (*klo a′ ka*). A common passage-way through which the intestine, kidneys, and sexual organs discharge their products in some fishes, in amphibia, reptiles and birds, and in a few mammals.

Coccidæ (*kok′ si dee*). A family of scale insects.

Coccidium schubergi (*kok sid′ i um shu′ berg i*). A species of parasitic protozoön, one of the Sporozoa.

Cocoon (*ko koon′*). A case in which eggs are stored and in which frequently the larvæ 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.

Cornea (*kor′ ne a*). The transparent bulging membrane at the front of the eye.

Corpora adiposa (*kor′ po ra ad′ i po′ sa*). Fat-bodies, storage places for reserve fatty food.

Cortex (*kor′ teks*). The layer of gray matter which covers the cerebrum and dips into its folds. Also, an outer layer on various other organs.

Costiform (*kos′ ti form*). Rib-shaped.

Cranial nerve (*kra′ ni al nerv′*). One of ten or twelve pairs of nerves arising from the central nervous system within the skull.

Cretaceous (*kre ta′ shus*). Pertaining to late Mesozoic time; so named from the chalk deposits characteristic of it.

Crinoidea (*kri noi′ de a*). A class of Echinodermata, including the feather-stars and sea-lilies. For definition see Chapter XII.

Cristatella mucedo (*kris′ ta tel′ la mu se′ do*). A species of freshwater bryozoön.

Crocodilini (*krok′ o di li′ ni*). An order of Reptilia comprising the alligators and crocodiles and their allies.

Crô-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 (*krop*). 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 (*krus ta′ she a*). A class of arthropods including the lobsters, crabs, water fleas, barnacles, etc. For definition see Chapter XII.

Cryptobranchus (*krip′ to brang′ kus*). A genus of salamanders of large size.

Crystalline lens (*kris′ tal lin lenz′*). A rounded, transparent, refractive body situated behind the pupil of the eye.

Ctenophora (*te nof′ o ra*). A phylum of animals including the comb jellies and sea walnuts. For definition see Chapter XII.

Cubical epithelium (*ku′ bi kal*). Epithelium in which the height and width of the cells are about equal.

Cuticle (*ku′ ti k′l*). Same as **pellicle.** Also same as **epidermis.**

Cuvier, Georges (*kü vyay′*). French naturalist, founder of comparative anatomy, 1769–1832.

Cyclosis (*si klo′ sis*). The rotation of protoplasm about the interior of a cell.

Cyclostomata (*si klo sto′ ma ta*). A class of Vertebrata having an eel-like form, a cartilaginous skeleton, no jaws, and no lateral fins; lampreys and hagfishes.

Cynipidæ (*si nip′ i dee*). A family of gall-producing insects of the order Hymenoptera.

Cyst (*sist*). Any enveloping structure, usually a secreted membrane.

Cytoblastema (*si′ to blas′ te ma*). The name given to a supposed formative or nutritive substance in organisms, from which cells were early thought to be formed.

Cytology (*si tol′ o ji*). The science which deals with the structure of cells.

Cytoplasm (*si′ to plaz′m*). The protoplasm of a cell exclusive of the nucleus.

Dace (*dase*). One of several small species of fish.

Darwin, Charles (*dar′ win*). Celebrated English naturalist, founder of the doctrine of natural selection, author of several works on evolution. Lived 1809–1882.

Darwin, Erasmus (*dar′ win*). English naturalist and poet, grandfather of Charles Darwin. Lived 1731–1802.

Darwinism (*dar′ win iz′m*). The theory of natural selection, propounded by Charles Darwin. (By the German biologists the term is often used to mean evolution.)

Deaminize (*de am′ i nize*). To remove the amino radical (NH_2) from (an amino-acid).

Deciduous (*de sid′ u us*). 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.

Delamination (*de lam′ i na′ shun*). Splitting off; said of a layer of cells.

Demospongiæ (*de′ mo spun′ ji ee*). A class of Porifera (sponges). For definition see Chapter XII.

Dendrite (*den′ drite*). A projection from a nerve cell which ordinarily conducts impulses toward the body of the cell.

Dendritic (*den drit′ ik*). Tree-like.

Dentine (*den′ tin*). The dense bony substance composing the bulk of mammalian teeth.

Dermatemydidæ (*der′ ma te mid′ i dee*). A family of turtles.

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 (*de′ro*). A genus of worms, phylum Annelida, subclass Oligochæta.

Desmognathus (*dez mog′ na thus*). A genus of salamanders.

Devonian (*de vo′ ni an*). Of middle Paleozoic age, next following the Silurian.

Dextrin (*deks′ trin*). Any one of several related carbohydrates derived by hydrolysis from starch; among them being erythrodextrin, achroödextrin and maltodextrin.

Dextrose (*deks′ trose*). Glucose or grape sugar.

Diaphragm (*di′ a fram*). A partition; specifically, the partition between the thorax and abdomen of a mammal.

Diastase (*di′ as tase*). An enzyme that decomposes starch.

Dichogamy (*di kog′ a mi*). The maturing of the male and female germ cells of a hermaphrodite at different times, thus preventing self-fertilization.

Dichotomous (*di kot′ o mus*). Regularly dividing into two parts; said of branching in certain plants, also of a system of classification in which each group is divided into two parts.

Diemictylus (*di e mik′ ti lus*). A genus of salamanders.

Differentiation (*dif′ fer en′ shi a′ shun*). The process of becoming structurally unlike, or of becoming heterogeneous. Also the condition of heterogeneity resulting from differentiation.

Diffusion (*dif fu′ zhun*). The spreading of the molecules of one substance among those of another.

Digestion (*di jes′ chun*). The conversion of food into soluble substances which may diffuse through protoplasm.

Dinobryon (*di no′ bri on*). A genus of colonial flagellate Protozoa in which the individual is enclosed in a sheath.

Dinosaur (*di′ no sawr*). One of an order of extinct reptiles of Mesozoic time, mostly of large size.

Diœcious (*di ee′ shus*). Having the male and female organs in separate individuals; said of species.

Diploblastic (*dip′ lo blas′ tik*). 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 maturation, in bisexual animals. *Cf.* haploid.

Diplozoön (*dip′ lo zo′ on*). A trematode worm parasitic on the gills of fishes.

Dipnoi (*dip′ no i*). A subclass of Pisces, fishes with an airbladder functioning as a lung; the lungfishes.

Dissosteira (*dis′ so sti′ ra*). A genus of grasshoppers.

Division of labor (*di vi′ zhun ov la′ ber*). Distribution of functions among cells, or organs, or individuals.

Dominant (*dom′ i nant*). 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.

Donacia (*do na′ shi a*). A genus of aquatic beetles.

Dorsal (*dor′ sal*). Pertaining to the back; hence, usually, upper.

Dorsal aorta (*dor′ sal a or′ ta*). A large artery formed, in fishes, by the union of vessels coming from the gills, and passing backward in the dorsal region.

Dorsal root (*dor′ sal root′*). The dorsal one of two roots by which a spinal nerve is connected with the spinal cord. Its fibers are sensory in function.

Double refraction (*dub′ ′l re frak′ shun*). The separation of a beam of light into two rays as it passes through a refracting medium.

Drosophila (*dro sof′ i la*). A genus of flies, of which the fruitfly (**D. melanogaster,** *mel′ a no gas′ ter*) is a common species.

Dujardin, Felix (*dü zhar daɴ′*). French naturalist, 1801–1860.

Duodenum (*du′ o de′ num*). The first of three divisions of the small intestine.

Dyad (*di′ ad*). A double body formed by the division of a tetrad into two parts. It may consist of two halves of the same chromosome or of two halves of 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 Chapter XII.

Echinoidea (*ek′ i noi′ de a*). A class of Echinodermata, comprising the seaurchins, sand-dollars, and heart-urchins. For definition see Chapter XII.

Ecology (*e kol′ o ji*). The branch of biology dealing with the relation of animals or plants to their environment.

Ectoderm (*ek′ to derm*). The outer layer of cells of a gastrula, or the representative of this layer in later stages.

Ectoparasite (*ek′ to par′ a site*). A parasite that is attached to the outside of the body of its host.

Ectosarc (*ek′ to sark*). The outer layer of protoplasm in cells in which the outer and inner protoplasm differ distinctly in structure, as in Amœba.

Edaphosaurus (*e daf′ o saw′ rus*). An extinct lizard-like reptile bearing a spiny fin on its back, from Permo-Carboniferous rocks of North America.

Elasmobranchii (*e laz′ mo brang′ ki i*). A class of Vertebrata comprising the sharks, skates, rays, torpedoes, and chimæras. For definition see Chapter XII.

Electrolyte (*e lek′ tro lite*). A substance which in solution is capable of conducting an electric current and of being decomposed by the current.

Elephas (*el′ e fas*). A genus of animals including living elephants and their fossil relatives of Pleistocene time.

Erythrodextrin (*er' i thro deks' trin*). A carbohydrate obtained by hydrolysis of starch.

Erythrosin (*e rith' ro sin*). A red substance used as a protoplasmic stain.

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.

Eudorina elegans (*u' do ri' na el' e ganz*). A species of colonial chlorophyll-bearing organism whose cells are imbedded in a spherical jelly-like mass.

Euglena (*u gle' na*). A genus of green flagellate Protozoa.

Euglypha (*u glif' a*). A genus of rhizopod Protozoa, of the order Foraminifera.

Euplectella (*u' plek tel' la*). A genus of siliceous sponges.

Eustachian tube (*u sta' ki an tube'*). 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 (*e vaj' i na' shun*). The folding of a layer of cells outward from an enclosed cavity.

Evolution (*ev' o lu' shun*). The gradual or sudden change of animals or plants through successive generations.

Evolve (*e volv'*). To change; to undergo evolution.

Excretion (*eks kre' shun*). The elimination of waste substances. As a noun, a substance excreted.

Exhalent (*eks ha' lent*). Breathing out; applied to one of the siphons of a clam or mussel.

Exoskeleton (*eks' o skel' e tun*). A skeleton on the outside of the body, as in the arthropods.

External respiration (*eks ter' nal res' pi ra' shun*). The passage of oxygen from the surrounding air or water to the blood.

Ex-umbrella (*eks' um brel' la*). The convex side of a medusa.

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.*

F_3 (*ef' three'*). An individual or generation of individuals whose parents are F_2 individuals from a previous cross.

Factor (*fak'ter*). Something in a germ cell or other cell which is responsible for a hereditary characteristic. Also called gene. In a general sense, factor means any agent or cause of any phenomenon.

Family (*fam' i li*). A taxonomic group of higher rank than the genus but below the order.

Fasciola hepatica (*fas si' o la he pat' i ka*). A species of parasitic flatworm (Trematoda), commonly called the liver fluke.

Fat (*fat*). A compound of glycerol and one or more fatty acids.

Fauna (*faw' na*). Collectively, the animals of a given region or of a given period of time.

Femur (*fe' mur*). The single bone of the thigh in vertebrates above the fishes.

Feral (*fe' ral*). Escaped from domestication. Also, sometimes, wild.

Fertilization (*fer′ ti li za′ shun*). The union of an egg with a spermatozoön, a process requisite, in the higher animals, to the development of the egg.

Fibril (*fi′ bril*). One of the longitudinal contractile threads of a voluntary muscle cell.

Fibula (*fib′ u la*). The outer one of two bones in the lower leg of vertebrates except the fishes.

Filar (*fi′ lar*). Composed of threads; used in describing some forms of protoplasm.

Fission (*fish′ un*). The division of an organism into two approximately equal parts; or, simply, division.

Fix (*fiks*). To convert into compounds; said of the action of certain bacteria on the nitrogen of the air.

Flagellate (*flaj′ el late*). Possessing flagella, or pertaining to or performed by flagella. As a noun, a flagellate protozoön.

Flagellum (*fla jel′ lum*) (*pl.*, **flagella**). A long whip-like motile projection from a cell.

Flame cell (*flame′ sel′*). A cell having a hollow interior in which a bunch of vibratile cilia are located, forming part of a protonephridium.

Flemming, W. (*flem′ ing*). A German biologist.

Flora (*flo′ ra*). The plants of a given area or of a given period of time, taken collectively.

Fluctuating variation (*fluk′ tu a ting va′ ri a′ shun*). A modification of an organism which is not inherited, and which is presumably due to the environment in a broad sense.

Fluke (*fluke*). Any one of several species of trematode worms.

Foot (*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 ap′ er ture*). In a sponge gemmule, the opening in the shell through which the young sponge escapes when it begins to develop.

Formaldehyde (*for mal′ de hide*). A gas whose formula is HCHO.

Fossil (*fos′ sil*). The remains, or other indication, of a prehistoric animal or plant.

Fungia (*fun′ ji a*). A genus of corals, of the phylum Cœlenterata.

Furcula (*fur′ ku la*). The wishbone of a bird, consisting of the fused clavicles of the two sides.

Galen (*ga′ len*). Famous Greek physician and anatomist, born about 130 A.D. His writings were long the highest authority in medical science.

Gall bladder (*gawl′ blad′ der*). A pouch in which the bile secreted by the liver is stored.

Galvanotaxis (*gal′ van o tak′ sis*). An orientation of an organism with reference to the stimulus of an electric current.

Galvanotropism (*gal′ van ot′ ro piz′m*). The response of an organism to an electric current.

Gamboge (*gam′ boje*). A resinous substance.

Gamete (*gam′ eet*). A germ cell, or other cell which fuses with a second cell in reproduction.

Ganglion (*gang′ gli on*) (*pl.*, **ganglia**). A mass of nerve cell bodies, usually forming a thickening in the course of a nerve.

Gasterosteus (*gas′ ter os′ te us*). A genus of fishes, the sticklebacks.

Gastric (*gas′ trik*). 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 the snails and slugs, mollusks whose bilateral symmetry is often obscured by a coiled body and shell.

Gastrovascular (*gas′ tro vas′ ku ler*). Serving the functions of digestion and circulation.

Gastrovascular cavity (*gas′ tro vas′ ku ler kav′ i ti*). See **cœlenteron.**

Gastrula (*gas′ tru la*). An early developmental stage, formed from a blastula 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 (*gas′ tru la′ shun*). The invagination of the vegetative pole of a blastula into the blastocœle.

Gelatin (*jel′ a tin*). A jelly-like substance obtained by boiling from cartilage, bone, tendon, ligament, connective tissue, etc.

Gemmule (*jem′ mule*). A group of cells forming a reproductive body in freshwater sponges.

Gene (*jeen*). Something in a germ cell or other cell which is responsible for a hereditary characteristic. Also called factor.

Generic (*je ner′ ic*). Pertaining to a genus.

Genetics(*je net′ iks*). The science of heredity, variation, sex determination, and related phenomena.

Genital (*jen′ i tal*). 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.

Geotaxis (*je′ o tak′ sis*). An orientation of an organism with reference to the stimulus of gravity.

Geotropism (*je ot′ ro piz′m*). The response of an organism to the stimulus of gravity.

Gephyrea (*je feer′ i a*). A group of worm-like animals of doubtful rank and relationships. They have sometimes been referred to the Annelida.

Germ cell (*jerm′ sel′*). A cell capable of reproduction, or of sharing in reproduction, as contrasted with the somatic or body cells which are sterile.

Germinal (*jer′ mi nal*). Relating to the germ cells; said of epithelium, for example.

Gill (*gil*). A structure having a surface enlarged usually by branching or folding, which serves a respiratory function.

Gill bar (*gil′ bar′*). The tissue between two gill clefts.

Gill cleft (*gil′ kleft′*). 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 pouch (*gil′ 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 (*giz′ zerd*). In the earthworm, a thick-walled portion of the alimentary tract behind the crop. In birds, the posterior muscular division of the stomach.

Glacial (*gla′ shal*). Pertaining to glaciers, or to the period when glaciers were common in regions now temperate, namely, late Cenozoic time.

Grew, Nehemiah (*groo*). English botanist, 1641–1712.

Grouse (*grous*). One of several species of birds of the family Phasianidae, to which the quail, turkeys, ptarmigans, and prairie-chickens also belong.

Guanaco (*gwah nah′ ko*). A llama-like animal of South America.

Gustatory (*gus′ ta to ri*). Pertaining to the sense of taste.

Habitat (*hab′ i tat*). The kind of place in which an organism lives.

Halysites (*hal′ i si′ teez*). A genus of extinct chain-corals.

Haploid (*hap′ loid*). Single; referring to the reduced number of chromosomes in the mature germ cells of bisexual animals. *Cf.* **diploid.**

Haplozoön lineare (*hap′ lo zo′ on lin′ e a′ re*). A species of mesozoön forming a linear aggregation.

Harvey, William (*har′ vi*). An English physician and physiologist who lived 1578–1657.

Head (*hed*). An enlarged anterior portion. In animals, the part usually containing the principal nervous centers and sense organs. In a spermatozoön, the enlarged part consisting mostly of the nucleus.

Heidelberg (*hi′ del berg*). A city in Germany near which the remains of a man-like being (the Heidelberg man) were found.

Heliotaxis (*he′ li o tak′ sis*). An orientation of an organism with reference to the direction of light.

Heliotropism (*he′ li ot′ ro piz′m*). The response of an organism to the direction of light

Heliozoa (*he′ li o zo′ a*). An order of rhizopod Protozoa.

Helix (*he′ liks*). A genus of snails.

Helminthology (*hel′ min thol′ o ji*). The zoölogy of parasitic worms.

Helodrilus fœtidus (*he′ lo dri′ lus fet′ i dus*). A species of annelid worm found in manure heaps.

Hemoglobin (*he′ mo glo′ bin*). A reddish protein contained in the red blood cells; also spelled hæmoglobin.

Herbivorous (*her biv′ o rus*). Plant-eating.

Heredity (*he red′ i ti*). The occurrence, in offspring, of the same kinds of representatives of physical and psychical traits as were in the parents.

Hermaphrodite (*her maf′ ro dite*). An organism possessing both male and female organs. Also (adjective), possessing the organs of both sexes.

Hermaphroditism (*her maf′ ro di tiz′m*). The state of being a hermaphrodite.

Herpetology (*her pe tol′ o ji*). The zoölogy of reptiles and Amphibia.

Heteromita lens (*het′ er o mi′ ta lenz′*). A species of flagellate protozoön.

Hetermorphes (*het′ er o mor′ feez*). A group of animals in Blainville's early classification; animals of irregular form, mainly sponges and Protozoa.

Heterozygote (*het′ er o zi′ gote*). 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 (*het′ er o zi′ gus*). Of the nature of a heterozygote.

Hexactinellida (*heks ak ti nel′ li da*). A class of Porifera (sponges) whose spicules are composed of silica.

Hexagenia (*heks′ a je′ ni a*). A genus of may-flies. The immature individuals are burrowing aquatic animals.

Hexiology (*heks' i ol' o ji*). The science of the relation of animals and plants to their environment; sometimes erroneously spelled hexicology.

Hipparion (*hip pa' ri on*). An extinct horse-like 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 a horse's head.

Hirudinea (*hi' ru din' e a*). A class of Annelida comprising the leeches. For definition see Chapter XII.

Histology (*his tol' o ji*). The science which deals with the structure of tissues.

Holothurioidea (*ho' lo thu' ri oi' de a*). A class of Echinodermata, comprising the sea cucumbers. For definition see Chapter XII.

Homo (*ho' mo*). The genus of animals comprising man.

Homolecithal (*ho' mo les' i thal*). Having the yolk uniformly distributed throughout; said of eggs.

Homologous (*ho mol' o gus*). Originating in the same way in evolution and hence in the embryo; said of organs or structures.

Homology (*ho mol' o ji*). Similarity of origin in evolution and hence in the embryo; applied to organs that arise in the same way.

Homozygote (*ho' mo zi' gote*). 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 (*hook*). English natural philospher and mathematician, 1635–1703.

Hooker, Sir Joseph Dalton (*hook' er*). English botanist, 1817–1911.

Hormone (*hor' mo ne* or *hor' mone*). A secreted substance which stimulates activity in an organ.

Humerus (*hu' mer us*). The single bone of the upper arm in Amphibia and the higher vertebrates.

Huxley, Thomas (*huks' li*). English biologist and lecturer, 1825–1895.

Hyaliodes (*hi' a li o' deez*). A genus of beetles.

Hybrid (*hi' brid*). The offspring of two parents unlike one another in some heritable character.

Hybridization (*hi' brid i za' shun*). The process of crossing animals having unlike heritable characters, thereby producing animals possessing genes for the traits of both parents.

Hydra (*hi' dra*). A small tubular freshwater animal with tentacles and stinging organs, belonging to the phylum Cœlenterata. Two species are common, **H. oligactis** (*ol' i gak' tis*), and **H. viridissima** (*veer' i dis' si ma*).

Hydractinia (*hi' drak tin' i a*). A genus of marine colonial and polymorphic Hydrozoa, living attached to the snail shells occupied by hermit crabs.

Hydranth (*hi' dranth*). A Hydra-like, tentacle-bearing member of a hydroid colony.

Hydrocorallinæ (*hi' dro kor' al li' nee*). An order of Hydrozoa comprising certain corals.

Hydroid (*hi' droid*). A colonial cœlenterate, the individuals of which resemble Hydra in certain respects.

Hydrolysis (*hi drol' i sis*). A double chemical decomposition in which one of the substances consumed is water.

Hydrolyze (*hi' dro lize*). To undergo, or to subject to, hydrolysis.

Hydropsyche (*hi' dro si' kee*). A genus of insects including certain caddis-flies.

Hydrorhiza (*hi' dro ri' za*). That part of a hydroid colony which is attached to the sub-stratum.

Hydrotaxis (*hi' dro tak' sis*). A response to moisture.

Hydrotheca(*hi' dro the' ka*). The tough transparent sheath surrounding a hydranth of a hydroid; an expansion of the perisarc.

Hydrotropism (*hi drot' ro piz'm*). The response of an organism to water, or moisture.

Hydrozoa (*hi' dro zo' a*). A class of Cœlenterata, including Hydra, the hydroids, jellyfishes, and some corals. For definition see Chapter XII.

Hyla (*hi' la*). A genus of tree frogs.

Hymenoptera (*hi' men op' ter a*). An order of insects, embracing the bees, ants, wasps, ichneumon flies, and others.

Hyoid (*hi' oid*). A bone or group of bones or cartilages located at the base of the tongue or in a corresponding situation.

Hypertonicity (*hi' per to nis' i ti*). The presence of a greater osmotic pressure than normal; for example, in sea water.

Hypodermis (*hi' po der' mis*). An external layer of cells beneath a secreted cuticle, as in the earthworm and in insects and Crustacea.

Hypohippus (*hi' po hip' pus*). An extinct horse-like animal of Miocene time in North America.

Hypostome (*hi' po stome*). A projection from the center of the circle of tentacles in Hydra or one of the hydroids. It is perforated by the mouth.

Hypotonicity (*hi' po to nis' i ti*). The presence of a lower osmotic pressure than normal; for example, in sea water.

Ichneumon fly (*ik nu' mon*). One of a family of parasitic insects of the order Hymenoptera.

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 (*in si' zer*). One of the front cutting teeth of a mammal.

Incubation (*ing' ku ba' shun*). The warming of eggs, resulting in acceleration of their development.

Infusoria (*in' fu zo' ri a*). A class of Protozoa members of which are covered with a pellicle, have a fixed mouth, and are usually covered with cilia; example, Paramecium.

Ingestion (*in jes' chun*). The taking in of food.

Inhalent (*in ha' lent*). Breathing in; applied to one of the siphons of clams and mussels, to certain pores of sponges, and to other passages.

Innominate bone (*in nom' i nate*). 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 (*in sek' ta*). A class of Arthropoda having one pair of antennæ, three pairs of legs, and tracheæ for respiration; the insects.

Insectivore (*in sek' ti vore*). Technically, a mammal of the order Insectivora, including the moles, shrews, and hedgehogs. In a popular sense, any insect-eating animal.

Interalveolar (*in' ter al ve' o ler*). Existing between the alveoli; said of the supporting liquid of an emulsion, in which the alveoli are enclosed.

Lamella (*la mel′ la*). A layer.

Lamprey (*lam′ pri*). An eel-like animal of the class Cyclostomata.

Lampsilis (*lamp′ si lis*). A genus of freshwater mussels.

Large intestine (*larj′ in tes′ tin*). The enlarged portion of the digestive tract following the small intestine.

Larva (*lar′ va*). 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.

Larynx (*lar′ inks*). An enlargement of the anterior end of the trachea, in which the vocal cords are located.

Latreille, Pierre (approximately *lah tray′*). French zoölogist, 1762–1833.

Lecithin (*les′ i thin*). One of a number of lipoid substances common in egg yolk, nerve tissue, and other kinds of cells.

Leeuwenhoek, Antonius von (*la′ wen hook*). Dutch naturalist and microscopist, 1632–1723.

Leiolopisma (*le′ yo lo piz′ ma*). A genus of skinks (lizards).

Lemming (*lem′ ming*). A rodent of the family Muridæ, 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.

Lernæopoda edwardsii (*ler′ ne op′ o da ed wardz′ i i*). A copepod (Crustacea) parasitic on the gills of certain fishes.

Levulose (*lev′ u lose*). Fruit sugar.

Lignin (*lig′ nin*). A substance mixed with the cellulose in the cell walls of woody plants.

Limax (*li′ maks*). A genus of slugs (gastropod mollusks).

Linear (*lin′ e ar*). Arranged in a line or row.

Lingula (*ling′ gu la*). A genus of brachiopods, a group of uncertain relationships.

Linin (*li′ nin*). The substance of the fine network of the nucleus of a cell on which the chromatin is located.

Linkage (*link′ aj*). The occurrence of the genes for two or more hereditary characters in the same germ cell more frequently than the operations of chance would require.

Linnæus, Carolus (*lin ne′ us*). See **Linné.**

Linnê, Carl von (*lin nay′*). Swedish botanist and naturalist, author of the binomial system of nomenclature and an artificial classification of animals and plants, 1707–1778.

Lipase (*li′ pase*). A fat-splitting enzyme.

Lipoid (*lip′ oid*). One of a group of substances whose chemical and physical properties resemble those of fats.

Lipolytic (*lip′ o lit′ ik*). Fat-splitting.

Lister, Joseph (*lis′ ter*). English surgeon, 1827–1912.

Lithobius forficatus (*lith o′ bi us for′ fi ka′ tus*). A species of centipede, phylum Arthropoda, class Myriapoda.

Liver (*liv′ er*). A gland which secretes bile and other substances.

Loligo (*lo li′ go*). A genus of cuttlefishes (mollusks) similar to Sepia; commonly called squids.

Loxoceras (*loks os′ er as*). A genus of extinct cephalopods of the orthocone type.

Lumbar (*lum′ bar*). Pertaining to the loins, the region of the back posterior to the ribs.

Lumbricus terrestris (*lum bri′ kus ter res′ tris*). A species of earthworm.

Lung (*lung*). A respiratory organ in the vertebrates.

Lyell, Sir Charles (*li′ el*). A British geologist, 1797–1875.

Lymnæa (*lim ne′ a*). A genus of snails.

Lymph (*limf*). A clear fluid containing colorless cells found in lymph vessels. It is essentially blood without its red cells and somewhat diluted.

Lymphatic system (*lim fat′ ik sis′ tem*). A system of vessels conveying lymph in vertebrates.

Lymph heart (*limf′ hart′*). One of a number of contractile chambers in the lymphatic system of lower vertebrates which by their pulsation propel the lymph.

Macrogamete (*mak′ ro gam′ eet*). The larger one of two kinds of gametes in species in which these cells differ in size.

Macronucleus (*mak′ ro nu′ kle us*). The large nucleus in a cell or organism having two nuclei of unequal size.

Macrosiphum sanborni (*mak′ ro si′ fum san′ born i*). 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.

Malpighian corpuscle (*mahl pee′ gee an kor′ pus s’l*). 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).

Maltase (*mawl′ tase*). An enzyme splitting maltose into glucose.

Malthus, Thomas Robert (*mal′ thus*). English political economist, author (1803) of “Essay on Population,” who lived 1766–1834.

Maltose (*mawl′ tose*). Malt sugar.

Mammal (*mam′ mal*). One of the Mammalia.

Mammalia (*mam ma′ li a*). 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 (*mam mal′ o ji*). The zoölogy of mammals.

Mammoth (*mam′ muth*). An elephant-like animal of prehistoric times.

Manatee (*man′ a tee′*). An aquatic mammal of the order Sirenia, commonly called sea-cow.

Mantle (*man′ t’l*). A sheet of tissue, typically quite thin, which secretes the shell in mollusks.

Manubrium (*ma nu′ bri um*). A projection from the center of the sub-umbrella of a medusa, corresponding to the hypostome of a hydranth, and bearing the mouth at its end.

Marginal bone (*mar′ jin al*). One of a ring of bones around the margin of the carapace of a turtle.

Marsupial (*mar su′ pi al*). 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 elephant-like animals of Pliocene and Pleistocene time.

Maternal (*ma ter′ nal*). Pertaining to or derived from the mother.

Matrix (*ma′ triks*). The non-cellular material in which the cells of bone and cartilage are imbedded.

Maturation (*mat′ u ra′ shun*). A process which germ cells undergo before they become functional, consisting essentially of (usually) two cell divisions, in at least one of which the behavior of the chromosomes is unlike that in other cell divisions.

Medulla oblongata (*me dul′ la ob′ long ga′ ta*). The enlargement of the anterior end of the spinal cord in vertebrates, commonly regarded as the posterior division of the brain.

Medusa (*me du′ sa*) (*pl.*, **medusæ,** *me du′ see*). A jellyfish; the free-swimming member of many hydroid species.

Megapodes (*meg′ a po′ deez*). Birds of the family Megapodiidæ, the mound-birds and jungle fowls.

Mendel, Gregor (*men′ del*). 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 (*men′ delz 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.

Merozoite (*mer′ o zo′ ite*). One of a number of minute motile cells formed by mutliple division of the nucleus and subsequent fragmentation of the cytoplasm of the cells of Coccidium and similar parasites, while in the intestinal cells of the host.

Merychippus (*mer′ i kip′ pus*). An extinct horse-like animal of Miocene time.

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 (*mes′ o derm*). A layer of cells between the ectoderm and endoderm.

Mesohippus (*mes′ o hip′ pus*). An extinct animal of Oligocene time, ancestral to the horse.

Mesozoa (*mes′ o zo′ a*). A group of degenerate animals of uncertain rank and relationship, once regarded as intermediate between Protozoa and metazoa, hence the name.

Mesozoic (*mes′ o zo′ ik*). 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 (*met′ a kar′ pal*). One of the bones forming the body of the hand or fore foot in vertebrates.

Metagenesis (*met′ a jen′ e sis*). The occurrence of two or more forms of individual in the same species, one or more of which reproduce asexually and one of which reproduces sexually.

Metamere (*met′ a meer*). See **somite.**

Mollusk (*mol′ lusk*). One of the Mollusca.

Monaxon (*mon aks′ on*). Having one axis; rod-like; said of sponge spicules.

Mondino da Luzzi (*mon dee′ no da loot′ see*). Italian anatomist in University of Bologna, in early part of fourteenth century.

Monocystis (*mon′ o sis′ tis*). A genus of gregarines, Protozoa of the class Sporozoa, order Gregarinida. **M. agilis** (*aj′ il is*) is a common species.

Monœcious (*mon ee′ shus*). Having the organs of both sexes in the same individual which is thus a hermaphrodite; said of species.

Monotreme (*mon′ o treem*). One of the Monotremata (Prototheria); an egg-laying mammal having a cloaca.

Morphology (*mor fol′ o ji*). The branch of biology which deals with the structure of living things.

Motor (*mo′ ter*). Pertaining to movement; applied to a neuron which conveys impulses resulting in muscular movement, glandular action, and the like.

Motor root (*mo′ ter 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.

Mucin (*mu′ sin*). A substance from which mucus is derived; it is secreted by certain glands.

Mucosa (*mu ko′ sa*). The layer of cells lining the digestive tract of vertebrate animals.

Muellerian duct (*mül le′ ri an dukt′*). A tube formed in the embryo of most vertebrate animals, becoming the oviduct in the female and degenerating (with few exceptions) in the male.

Müller, Johannes (*mül′ ler*). German physiologist and anatomist, 1801–1858.

Muscle (*mus′ s'l*). An aggregation of contractile cells.

Mutation (*mu ta′ shun*). A heritable modification arising from internal causes in an organism.

Mycelium (*mi se′ li um*) (*pl.*, **mycelia**). The filamentous growths of fungi and related plants.

Myoneme (*mi′ o neem*). One of several contractile filaments in the stalks of Vorticella and its allies.

Myotome (*mi′ o tome*). One of the segments into which certain muscles are divided.

Myriapoda (*meer′ i ap′ o da*). A class of Arthropoda having tracheæ, one pair of antennæ, and many unspecialized legs; centipedes and millipedes.

Myxomycetes (*miks′ o mi see′ teez*). The slime-molds.

Nacre (*na′ ker*). The pearly substance secreted by mollusks upon their shell or other objects.

Nais (*na′ is*). A genus of freshwater worms, phlyum Annelida, subclass Oligochæta.

Nasal pit (*na′ zal pit′*). The ectodermal depression in an embryo which forms much of the nostril.

Natica (*nat′ i ka*). A genus of marine snails.

Natural history (*nat′ u ral his′ to ri*). 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 (*nat′ u ral se lek′ shun*). The doctrine that through natural processes the fittest individuals are enabled to survive.

Nautiloid (*naw′ ti loid*). One of the extinct cephalopods resembling Nautilus.

Nautilus (*naw' ti lus*). An animal belonging to the Cephalopoda, living in a coiled shell divided into chambers.

Neanderthal man (*na ahn' der tahl*). A man-like being whose remains have been found in various places in Europe.

Necator (*ne ka' ter*). 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 (*nek tu' rus*). A genus of salamanders; the mud-puppies.

Nemathelminthes (*nem' a thel min' theez*). The phylum of roundworms and their allies. For definition see Chapter XII.

Nematocyst (*nem' a to sist*). One of the stinging bodies of Hydra and other cœlenterates.

Nematode (*nem' a tode*). Any roundworm of the class Nematoda, phylum Nemathelminthes.

Nematomorpha (*nem' a to mor' fa*). A group of worm-like animals of uncertain affinities. They have usually been doubtfully included in the Nemathelminthes. For definition see Chapter XII.

Nemertean (*ne mer' te an*). Pertaining to the Nemertinea.

Nemertinea (*nem' er tin' e a*). A group of worm-like animals of uncertain relationships. They are regarded by some as a class of Platyhelminthes. For definition see Chapter XII.

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 cœlom with the blood vessels of the kidney in certain Amphibia.

Nereis (*ne' re is*). A genus of marine worms, phylum Annelida.

Neritina (*ner' i ti' na*). A genus of snails.

Nerve (*nerv*). A bundle of axons or dendrites of nerve cells or of both axons and dendrites.

Nervous tissue (*ner' vus tish' u*). Tissue capable of transmitting impulses; as the tissues of the brain, spinal cord and nerves.

Net-knot (*net' not*). A thickened portion of the chromatin of a cell nucleus.

Neural arch (*nu' ral arch'*). That part of a vertebra above the centrum and neural canal.

Neural canal (*nu' ral ka nal'*). The opening in a vertebra through which the spinal cord extends.

Neural crest (*nu' ral krest'*). 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 (*nu' ral fold'*). One of the ridges of ectoderm forming the earliest development of the nervous system.

Neural groove (*nu' ral groov'*). An elongated depression between the neural folds of an embryo.

Neural spine (*nu' ral spine'*). A projection rising from the middle of the neural arch of a vertebra.

Neural tube (*nu' ral tube'*). The tube formed beneath the ectoderm by the union of the neural folds along their crests.

Neuromuscular (*nu′ ro mus′ ku ler*). Combining the functions of contraction and the transmission of impulses.

Neuron (*nu′ rone*). A nerve cell.

Nitella (*ni tel′ la*). A genus of aquatic plants.

Nomenclature (*no′ men kla′ ture*). A system of naming; terminology.

Nostril (*nos′ tril*). 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 fore-runner of the spinal column of the vertebrate animals.

Notophthalmus (*no′ tof thal′ mus*). A genus of salamanders.

Nototrema (*no′ to tre′ ma*). A genus of frogs.

Nuchal plate (*nu′ kal*). In turtles, the median plate of the carapace at the anterior end.

Nuclear membrane (*nu′ kle ar mem′ brane*). A thin film of protoplasm surrounding the nucleus of a cell.

Nuclear sap (*nu′ kle ar sap′*). The liquid forming the bulk of the nucleus of a cell.

Nuclein (*nu′ kle in*). One of a number of protein compounds involving nucleic acid, found in abundance in cell nuclei.

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 (*nu′ kle us*). A highly refractive, deeply staining body of specialized protoplasm found within nearly all cells.

Obelia (*o be′ li a*). A genus of hydroids, or colonial Hydra-like animals of the phylum Cœlenterata.

Octopus (*ok′ to pus*). 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 (*o′ ken*). German naturalist and transcendentalist philospher, 1779–1851.

Oleic (*o le′ ik*). A fatty acid entering into the composition of olive oil.

Olfactory (*ol fak′ to ri*). Pertaining to the sense of smell.

Oligocene (*ol′ i go seen*). Of early Tertiary time, between Eocene and Miocene.

Oligochæta (*ol′ i go ke′ ta*). A subclass of Chætopoda (Annelida), including chiefly terrestrial and freshwater worms with relatively few setæ 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 tracheæ and one pair of antennæ. Peripatus is an example.

Oöcyte (*o′ o site*). A female germ cell subsequent to the initiation of maturation and prior to the second maturation 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 maturation of female germ cells.

Oögonium (*o′ o go′ ni um*). One of the early germ cells of a female animal, prior to the beginning of maturation.

Oösperm (*o′ o sperm*). A fertilized ovum; a term usually applied to plants rather than animals.

Oviparous (*o vip' a rus*). Egg-laying.

Oviposition (*o' vi po zish' un*). The laying of eggs.

Ovisac (*o' vi sak*). 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 (*o' vum*). An egg; a relatively large passive cell which, in preparation for reproduction, has undergone one or two maturation divisions.

Oxidation (*oks' i da' shun*). The chemical process of combining with oxygen.

Oxyhemoglobin (*oks' i he' mo glo' bin*). Hemoglobin in combination with a certain amount of oxygen.

Oxytricha (*oks it' ri ka*). A genus of ciliated Protozoa.

Pædogenesis (*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.

Palæomastodon (*pa' le o mas' to don*). A genus of extinct animals belonging to the elephant ancestry, found in the Oligocene of Egypt and India.

Paleobotany (*pa' le o bot' a ni*). The paleontology of plants.

Paleontology (*pa' le on tol' o ji*). 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 invertebrates were the dominant forms.

Paleozoölogy (*pa' le o zo ol' o ji*). The science which deals with prehistoric animals.

Palinurus (*pal' i nu' rus*). A genus of crayfishes.

Palmitic (*pal mit' ik*). One of the very common fatty acids.

Pancreas (*pan' kre as*). A gland which secretes a fluid containing several digestive enzymes and discharges into the intestine.

Pandorina (*pan' do ri' na*). A genus of colonial flagellate organisms in which the cells are held in a spheroidal jelly-like mass. **P. morum** (*mo' rum*) is one of the species.

Pangenesis (*pan jen' e sis*). The theory that cells of an animal give off minute bodies which collect in the germ cells and later insure inheritance of parental qualities.

Panorpa (*pa nor' pa*). A genus of insects including certain scorpion-flies.

Papilio (*pa pil' i o*). A genus of butterflies; the swallow-tails.

Paramecium (*par' a me' shi um*). A genus of ciliated Protozoa.

Paramylum (*par am' i lum*). A substance related to starch, produced by certain green organisms.

Parapodium (*par' a po' di um*). A fleshy lateral protrusion on the segments of some worms; it bears the setæ.

Parasite (*par' a site*). An animal which lives in or on another species of animal (its host), at the expense of the latter.

Parasitism (*par' a si tiz'm*). The condition of being a parasite.

Parathyroid (*par' a thi' roid*). One of several small glandular bodies associated with the thyroid.

Parenchyma (*pa reng' ki ma*). A loose spongy tissue found in certain low animals.

Parietal bone (*pa ri′ e tal*). One of a pair of bones on the posterior upper part of the skull of vertebrate animals.

Parrakeet (*par′ ra keet*). One of a number of small parrots.

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.

Pasteur, Louis (*pas ter′*). French chemist and bacteriologist, 1822–1895.

Paternal (*pa ter′ nal*). Pertaining to or derived from the father.

Pecten (*pek′ ten*). A genus of bivalve mollusks.

Pectoral girdle (*pek′ to ral ger′ d'l*). A group of connected bones serving to attach the bones of the fore limbs of vertebrate animals to the rest of the skeleton.

Pelagic (*pe laj′ ik*). Pertaining to the open water of a lake or ocean, not near the shore nor far below the surface.

Pelecypoda (*pel′ e sip′ o da*). A class of Mollusca having bivalve shells and a bilobed mantle; the clams and mussels.

Pellicle (*pel′ li k'l*). A thin skin or film on the surface of a cell.

Pelomedusidæ (*pel′ o me du′ si dee*). A family of turtles.

Pelvic girdle (*pel′ vik ger′ d'l*). A group of bones serving to join the bones of the hind limbs of vertebrate animals to the rest of the skeleton.

Penis (*pe′ nis*). The copulatory organ in the male of many animals.

Pentadactyl (*pen′ ta dak′ til*). Having five fingers or toes.

Pentamerous (*pen tam′ er us*). Five-parted, or arranged in groups of five.

Pepsin (*pep′ sin*). An enzyme of the stomach of vertebrate animals, whose function is digestion of many kinds of proteins.

Pepsinogen (*pep sin′ o jen*). An inactive substance from which the enzyme pepsin is derived.

Peptic (*pep′ tik*). Of the nature of pepsin; said of proteolytic enzymes that act in an acid medium.

Peptone (*pep′ tone*). Any of a number of substances, derived by hydrolysis from proteins, which are not precipitated by ammonium sulphate.

Peranema (*per′ a ne′ ma*). A genus of colorless flagellate Protozoa.

Pericardium (*per′ i kar′ di um*). The membranous sac enclosing the heart.

Periodic (*pe′ ri od′ ik*). Occurring at rather regular intervals; said of migration which depends on the seasons or on the age of the migrating animals.

Peripatus (*pe rip′ a tus*). A genus of arthropods with elongated wormlike bodies, belonging to the class Onychophora.

Perisarc (*per′ i sark*). The tough sheath surrounding the stalk and branches of a hydroid.

Peristalsis (*per′ i stal′ sis*). The rhythmical contraction of the walls of the intestine.

Peritoneum (*per′ i to ne′ um*). A sheet of cells covering the viscera and lining the body cavity in many animals.

Perivisceral (*per′ i vis′ ser al*). Around the viscera, or organs contained in various body cavities.

Permeable (*per′ me a b'l*). Permitting the passage of both liquids and dissolved substances.

Permian (*per′ mi an*). Belonging to the close of the Carboniferous age.

Petrifaction (*pet′ ri fak′ shun*). The substitution of mineral matter for organic matter in the remains of 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 (*fo' to sin' the sis*). The construction of carbohydrates from carbon dioxide and water by the energy of sunlight in the presence of chlorophyll.

Phototaxis (*fo' to taks' is*). A response to light.

Phototropism (*fo tot' ro piz' m*). The response of an organism to light.

Phylum (*fi' lum*). 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 (*fi sa' li a*). A very complex colonial cœlenterate, one of the siphonophores.

Physiology (*fiz' i ol' o ji*). The branch of biology which deals with the functions of animals and plants, and the processes going on in them.

Phytogeography (*fi' to je og' ra fi*). The science of the geographical distribution of plants.

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.

Pinna (*pin' na*). A genus of bivalve mollusks.

Pinnule (*pin' ule*). A small feather-like or laterally lobed division or part.

Pinus (*pi' nus*). A genus of coniferous trees including the pines.

Pisces (*pis' seez*). A class of vertebrate animals including the fishes. For definition see Chapter XII.

Piscivore (*pis' si vore*). A fish-eating animal.

Pithecanthropus (*pith' e kan' thro pus*). An extinct ape-like and man-like animal believed to stand in the early ancestry of man.

Pituitary (*pi tu' i ta ri*). A glandular organ beneath the brain composed in part of nervous tissue.

Placenta (*pla sen' ta*). A vascular tissue dove-tailing into the wall of the uterus on one side and connected with the umbilical cord on the other, thus forming an intimate nutritive connection between the embryo and the mother in viviparous animals.

Planaria (*pla na' ri a*). A genus of flatworms, phylum Platyhelminthes.

Planorbis (*pla nor' bis*). A genus of snails.

Planula (*plan' u la*). A ciliated larva consisting of a solid ellipsoidal mass of cells, developed from the fertilized egg of a medusa or similar organism.

Plasmodium (*plaz mo' di um*). The naked mass of protoplasm containing many nuclei, formed by the fusion of many amœboid cells in the Myxomycetes.

Plasmolyze (*plaz' mo lize*). To withdraw water from (a cell) by placing in solutions of higher osmotic pressure.

Porpoise (*por′ pus*). An aquatic mammal closely allied to the whales and dolphins.

Poterioceras (*po te′ ri os′ er as*). A genus of extinct cephalopods of the gomphoceran type.

Precocial (*pre ko′ shal*). Able to run about as soon as hatched; said of certain birds.

Precoracoid (*pre ko′ ra koid*). A ventrally situated bone or cartilage of the pectoral girdle in Amphibia and some reptiles.

Primary (*pri′ ma ri*). For application to spermatocytes, see **spermatocyte.** For application to oöcytes, see **oöcyte.**

Primate (*pri′ mate*). A mammal of the order including man and the ape-like animals.

Priority, Law of (*pri or′ i ti*). 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.

Procœlous (*pro see′ lus*). Having the anterior end of the centrum concave, the posterior end convex; said of vertebræ.

Procyon (*pro′ si on*). The genus of Carnivora to which the raccoon belongs.

Proglottis (*pro glot′ tis*) (*pl.*, **proglottides,** *pro glot′ ti deez*). One of the individuals in a chain of a tapeworm.

Pronuba (*pro nu′ ba*). A genus of moths some members of which feed on Yucca seeds.

Prophase (*pro′ faze*). Any early stage of mitotic cell division, prior to the splitting of the chromosomes.

Prosecretin (*pro′ se kre′ tin*). A substance in the walls of the small intestine from which secretin is produced.

Prostomium (*pro sto′ mi um*). A rounded projection overhanging the mouth of a earthworm.

Protandrous (*pro tan′ drus*). Maturing the male germ cells before the female cells said of an hermaphrodite.

Protein (*pro′ te in*). One of many organic substances, compounds of amino-acids which therefore contain carbon, hydrogen, nitrogen and oxygen and often othe elements. The molecules are large and very complex. Lean meat and eg albumen contain quantities of proteins.

Proteocephalus (*pro′ te o sef′ a lus*). A genus of tapeworms.

Proteolytic (*pro′ te o lit′ ik*). Protein-splitting.

Proteose (*pro′ te ose*). Any one of a number of substances, derived from the hydrolys of proteins, which may be precipitated from solution with ammonium sulphate.

Proterozoic (*pro′ ter o zo′ ik*). Belonging to the era preceding the Paleozoic.

Proteus (*pro′ te us*). A genus of salamanders.

Protogynous (*pro toj′ i nus*). Maturing the female germ cells before the male; said hermaphrodites.

Protonema (*pro′ to ne′ ma*). A thread-like growth originating from a spore of certa plants, as the mosses, and from which arise the leafy sexual shoots.

Protonephridium (*pro′ to ne frid′ i um*). A primitive excretory organ consisting flame cells and connecting tubes.

Protophyta (*pro′ to fi′ ta*). One-celled plants.

Protoplasm (*pro′ to plaz′m*). The living matter of which animals and plants a essentially composed.

Prototheria (*pro' to the' ri a*). A subclass of Mammalia, including the egg-laying mammals such as the duckbill Ornithorhynchus and the spiny ant-eater Echidna.

Protozoa (*pro' to zo' a*). 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.

Protozoölogy (*pro' to zo ol' o ji*). The zoölogy of the Protozoa.

Protylopus (*pro ti' lo pus*). The earliest known ancestor of the camels.

Proventriculus (*pro' ven trik' u lus*). The first division of the stomach of a bird.

Pseudacris (*su dak' ris*). A genus of frogs.

Pseudopodium (*su' do po' di um*) (*pl.*, **pseudopodia**). A blunt finger-like projection thrust out by Amœba and other rhizopods.

Psychozoic (*si' ko zo' ik*). Pertaining to the most recent geological time, that in which man developed as an intelligent being; the time following the Cenozoic era.

Ptyalin (*ti' a lin*). The amylolitic enzyme of the saliva.

Pubis (*pu' bis*) (*pl.*, **pubes**, *pu' beez*) The anterior one of two ventrally placed bones in the pelvic girdle of vertebrate animals above the fishes.

Pulmonary circulation (*pul' mo na ri ser' ku la' shun*). The circulation of the blood through the lungs, as distinguished from that through the body in general (systemic).

Pulmonata (*pul' mo na' ta*). An order of air-breathing snails and slugs.

Pulsating vacuole (*pul' sa ting vak' u ole*). Same as **contractile vacuole.**

Pupa (*pu' pa*). 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.

Pylorus (*pi lo' rus*). The opening from the stomach to the intestine.

Pyrenoid (*pi re' noid*). A small protein body found enclosed in some cells.

Pyrosoma (*pi' ro so' ma*). A colonial tunicate in which the colony is cylindrical in form.

Quadrate (*kwod' rate*). One of the bones of the skull; in birds and reptiles and bony fishes, the bone from which the lower jaw is suspended.

Quaternary (*kwa ter' na ri*). A division of Cenozoic time later than the Tertiary.

Race (*rase*). A group of individuals having certain characteristics in common because of common ancestry.

Radial canal (*ra' di al ka nal'*). One of four tubes extending from the middle to the margin of a medusa.

Radial symmetry (*ra' di al sim' me tri*). 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 longitudinal axis.

Radiating canal (*ra' di at ing ka nal'*) One of a series of collecting channels surrounding the pulsating vacuoles of Paramecium and similar Protozoa.

Radio-ulna (*ra' di o ul' na*). The fused radius and ulna of frogs and toads.

Radius (*ra' di us*). The bone of the lower arm located on the thumb side in Amphibia and the higher vertebrates.

Rana (*ra' na*). A genus of frogs. **R. pipiens** (*pip' i enz*), the common leopard frog.

Range (*rainj*). The area occupied by a species or larger taxonomic group of animals or plants.

Ray, John (*ray*). English naturalist, 1627–1705.

Reaction (*re ak′ shun*). Any response of an animal to a stimulus.

Recapitulation theory (*re′ ka pit′ u la′ shun*). See **biogenetic law.**

Receptacula seminis (*res′ ep tak′ u la sem′ i nis*). Chambers in which one animal stores sperms received from another.

Recessive (*re ses′ siv*). Not being produced when the gene for a contrasted domniant character is also present; said of inherited characters that are concealed in heterozygotes.

Rectum (*rek′ tum*). 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.

Redi, Francesco (*ra′ dee*). An Italian naturalist and poet, 1626–1698.

Redia (*re′ di a*). One of the individuals in the life cycle of the liver fluke Fasciola (and similar forms) which are parthenogenetically produced by the sporocyst.

Reduction (*re duk′ shun*). Cell division in which chromosomes are not split, but merely separated from one another after having previously come together in pairs, as occurs in one of the two maturation divisions in bisexual reproduction.

Reflex (*re′ fleks*). Same as **reflex action.**

Reflex action (*re′ fleks ak′ shun*). An action performed as a result of an impulse which passes over a reflex arc. It is involuntary and is often performed without the consciousness of the organism.

Reflex arc (*re′ fleks ark′*). A group of two or more neurons, one of them sensory, another motor, so connected as to be able to transmit impulses resulting in reflex actions.

Regeneration (*re jen′ er a′ shun*). The production of lost parts by organisms.

Remak, Robert (*re mahk′*). A German neurologist, 1815–1865.

Rennin, (*ren′ nin*). An enzyme produced by the gastric glands and having the property of coagulating milk.

Reproduction (*re′ pro duk′ shun*). The formation of new individuals among organisms.

Reptilia (*rep til′ i a*). A class of vertebrate animals including the snakes, lizards, crocodiles, turtles, and some others. For definition see Chapter XII.

Respiration (*res′ pi ra′ shun*). The absorption of oxygen by protoplasm. The term is sometimes loosely applied also to the forcing of air to and from respiratory organs like the lungs, a process more properly called breathing.

Reticular (*re tik′ u ler*). Of the nature of a network; said of certain forms of protoplasm or cell structure.

Reticulum (*re tik′ u lum*). A network.

Retina (*ret′ i na*). The sensitive inner layer of the eye of vertebrates and some other animals.

Retractile (*re trak′ til*). Capable of being withdrawn.

Rhabdocœle (*rab′ do seel*). A flatworm (Platyhelminthes) of the order Rhabdocœlida.

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, Amœba.

Sciurinæ (*si' u ri' nee*). The subfamily of Sciuridæ comprising the marmots, squirrels, and chipmunks.

Sciuromorpha (*si' u ro mor' fa*). The suborder of rodents comprising the squirrel-like forms.

Sciurus (*si u' rus*). The genus including the arboreal squirrels.

Scolex (*sko' leks*). The "head" or attaching organ from which are budded off the proglottides of a tapeworm chain.

Scolopendra (*sko' lo pen' dra*). A genus of centipedes.

Scyphozoa (*si' fo zo' a*). A class of Cœlenterata, jellyfishes of large size which have no hydroid form in the life cycle.

Secondary (*sek' und a ri*). 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.

Secretion (*se kre' shun*). The act of producing from the blood or other fluids or substances in the protoplasm some new material to be used in metabolism. Also the new substance thus formed.

Sedimentary (*sed' i men' ta ri*). Formed from sediment; said of rocks originally deposited under water, and now found in layers.

Segmentation (*seg' men ta' shun*). Same as **cleavage.**

Segregation (*seg' re ga' shun*). The separation of the genes of a homologous pair at the time of maturation of the germ cells, or at some other time, so that each germ cell receives only one member of the pair. Sometimes applied also to the independent distribution of genes of different pairs to the germ cells.

Self-fertilize (*self' fer' ti lize*). To fertilize the eggs of an individual by sperms of the same individual.

Semi-circular canal (*sem' i ser' ku ler ka nal'*). One of several curved tubes forming part of the inner division of the ear in vertebrates.

Seminal receptacle (*sem' i nal re sep' ta k'l*). An organ in a female animal for the reception and storage of spermatozoa from the male.

Seminal vesicle (*sem' i nal ves' i k'l*). 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 sperms may be stored in various animals.

Semi-permeable (*sem' i per' me a b'l*). Permitting the passage of solvents but preventing the passage of dissolved substances.

Sensory (*sen' so ri*). 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.

Sepia (*se' pi a*). A genus of cuttlefishes (mollusks) from which certain black inks are derived. Also the black substance produced by these cuttlefishes.

Septum (*sep' tum*). A partition.

Sessile (*ses' sil*) Attached directly, as distinguished from stalked. Sometimes, also, attached,as distingushed from free-living.

Seta (*se' ta*) (*pl.*, **setae,** *se' tee*). A spine; specifically, one of the spines projecting from the somites of an earthworm and used for locomotion.

Severino, Marco Aurelio (*sev' er ee' no*). Italian physician, professor in University of Naples, 1580–1656.

Sex-linked (*seks' linkt'*). Associated with sex; said of hereditary characters that are inherited unequally by the two sexes.

Sexual (*seks' u al*). 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.

Sexual selection (*seks' u al se lek' shun*). The supposed preference of animals of one sex for certain qualities in the other sex, leading to the preservation of those qualities in later generations.

Shoal (*shole*). A shallow place in a body of water; also a sandbank or bar which makes the water shallow.

Siagonodon (*si' a gon' o don*). A genus of snakes.

Silica (*sil' i ka*). Silicon dioxide, the material of common quartz.

Silurian (*si lu' ri an*). Of middle Paleozoic time, between Ordovician and Devonian.

Siphon (*si' fon*). 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 (Cœlenterata), the members of which form highly polymorphic colonies (*e.g.*, Physalia, the Portuguese man-of-war).

Siphonops (*si' fo nops*). A genus of cœcilians (Apoda, Amphibia).

Siren (*si' ren*). A genus of salamanders.

Sistrurus (*sis tru' rus*). A genus of snakes; the massasauga.

Slime tube (*slime' tube'*). A sheath of mucous material secreted on the surface of an earthworm at the time of mating.

Small intestine (*smawl' in tes' tin*). That part of the intestine of vertebrates immediately following the stomach, as distinguished from the large intestine.

Smooth muscle (*smooth*). Muscle composed of non-striated, uninucleate, spindle-shaped cells. It is common in the intestine, bladder and glands of vertebrates.

Solanum (*so la' num*). A genus of plants including the common potato, nightshade, and many others.

Solen (*so' len*). A genus of razor-shell clams.

Solute (*so lute'*). A dissolved substance.

Solution (*so lu' shun*). A liquid containing another substance in the form of particles not greater than molecules in size.

Solvent (*sol' vent*). A liquid in which another substance is, or may be, dissolved.

Somatic (*so mat' ik*). Pertaining to the body; when applied to cells, referring to the sterile body cells in contrast to the germ cells which are reproductive.

Somite (*so' mite*). One of the segments into which the body of a worm or arthropod or other segmented animal is divided.

Spallanzani, Lazaro (*spahl' lahn dzah' ne*). Italian naturalist and physiologist, 1729–1799.

Specialization (*spesh' al i za' shun*). Emphasis upon one or a few functions, though not necessarily to the exclusion of others.

Species (*spe' sheez*) (*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 (*spe sif' ik*). Pertaining to a species.

Sperm (*sperm*). One of the male germ cells in an animal or plant.

Spermaducal pore (*sper′ ma du′ kal pore′*). One of the two prominent openings through which spermatozoa issue from the earthworm and similar animals. In the common earthworm they are situated on the fifteenth metamere.

Spermary (*sper′ ma ri*). See **testis.**

Spermatheca (*sper′ ma the′ ka*). See **seminal receptacle.**

Spermatid (*sper′ ma tid*). One of the two cells formed by the second maturation division of the male germ cells. By transformation in shape the spermatids become mature spermatozoa.

Spermatocyte (*sper′ ma to site*). A male germ cell between the beginning of maturation and the second maturation divison. A spermatocyte is called **primary** during the growth period and prior to the first maturation division; **secondary** after the first division but prior to the second.

Spermatogenesis (*sper′ ma to jen′ e sis*). The maturation 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 maturation.

Spermatophore (*sper′ ma to fore*). A mass of spermatozoa, sometimes resting upon a stalk or being otherwise attached, as in some salamanders.

Spermatozoön (*sper′ ma to zo′ on*) (*pl.*, **spermatozoa**). The male germ cell in animals.

Spermophile (*sper′ mo file*). A common term applied to several of the ground-squirrels and gophers.

Sphenodon (*sfen′ o don*). A genus of reptiles of the order Rhynchocephalia. But one living species is known.

Spheroid (*sfe′ roid*). Of nearly spherical shape.

Spicule (*spik′ ule*). A body of various shapes commonly of calcareous or siliceous material, forming part of the skeleton of a sponge.

Spinal cord (*spi′ nal kord′*). That part of the central nervous system of vertebrate animals lying behind the brain and largely enclosed in a channel in the vertebræ.

Spindle (*spin′ d'l*). A group of structures resembling threads, in the form of a spindle, formed in the cytoplasm of a cell during mitosis.

Spiracle (*spi′ ra k'l*). 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 the tracheæ.

Spireme (*spi′ reem*). The coiled or tangled thread formed by the chromatin network of a cell prior to division.

Splanchnic nerves (*splank′ nik*). Three nerves from the thoracic sympathetic ganglion.

Splint (*splint*). A bone at either side of the foot of the horse and some of its relatives, being the remnant of a lost toe.

Spongin (*spun′ jin*). The horny material of the skeleton of the bath sponges.

Spontaneous generation (*spon ta′ ne us jen′ e ra′ shun*). Same as **abiogenesis.**

Sporadic (*spo rad′ ik*). Occurring at irregular intervals, often without apparent reason; said of migration of animals.

Spore (*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.

Sporocyst (*spo′ ro sist*). The bag-like individual into which the miracidium of the liver fluke develops in a snail as host.

Stylonychia (*sti' lo nik' i a*). A genus of ciliated Protozoa.

Sub-epithelial cells (*sub' ep i the' li al*). In Hydra, rounded cells lodged among the epithelial cells, often near the base of the latter.

Sub-umbrella (*sub' um brel' la*). The concave side of a medusa.

Succus entericus (*suk' kus en ter' i kus*). The fluid secreted by the small intestine.

Sucker (*suk' er*). An attaching organ beneath the head of a frog tadpole; a similar organ on the "head" or scolex of a tapeworm colony; also the attaching organ of leeches.

Suctoria (*suk to' ri a*). A subclass of Infusoria which bear no cilia when adult, but have tube-like tentacles.

Sustentative (*sus ten' ta tiv*). Supporting; applied to connective tissue and other supporting tissues.

Suture (*su' ture*). 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.

Swimmeret (*swim' mer et*). One of a number of branched appendages beneath the abdomen of a crayfish.

Syllis ramosa (*sil' lis ra mo' sa*). A species of marine annelid worm which produces colonies by budding.

Symbiosis (*sim' bi o' sis*). The association of two species of animal for their mutual benefit.

Symbiote (*sim' bi ote*). An animal which lives in a symbiotic relationship with another species; called also symbiont.

Symbiotic (*sim' bi ot' ik*). Of the nature of symbiosis.

Symmetrical (*sim met' ri kal*). Of a form that may be divided by a line or plane into two parts which are mirrored images of each other.

Symmetry (*sim' me tri*). The state of being symmetrical.

Sympathetic nervous system (*sim' pa thet' ik*). Two longitudinal nerve cords and associated ganglia in the dorsal region of vertebrates.

Sympheidole (*sim' fi do' le*). A genus of ants.

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.

Syncytium (*sin sish' i um*). An undivided mass of protoplasm containing several or many nuclei.

Synura (*si nu' ra*). A genus of free-swimming colonial flagellate Protozoa, some species of which cause disagreeable odors or tastes in drinking water.

Syrphid (*ser' fid*). A fly of the family Syrphidæ.

System (*sis' tem*). A collection of organs concerned with the same general function, as digestion.

Systematic zoölogy (*sis' tem at' ik*). See **taxonomy.**

Systemic circulation (*sis tem' ik ser' ku la' shun*). 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 (*tad' pole*). The larva of a frog, toad, or certain other animals.

Tail (*tale*). A slender posterior appendage. In a spermatozoön, the whip-like propelling organ behind the head and mid-piece.

Tamarack (*tam' a rak*). The American larch, a bog-inhabiting tree.

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 (*tar' sal*). One of a number of bones in the ankle of most vertebrate animals.

Tarso-metatarsus (*tar' so met' a tar' sus*). A compound bone in the leg of a bird, formed of several of the metatarsals and tarsals.

Taxis (*taks' is*). An orientation of an organism with reference to a stimulus.

Taxonomy (*taks on' o mi*). 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*). Having the yolk massed toward one side; said of eggs in which the yolk is most abundant in the vegetative half.

Telophase (*tel' o faze*). The final phase of mitotic cell division, in which the nuclei are reconstructed.

Tentacle (*ten' ta k'l*). One of a number of arm-like projections from hydroids, Bryozoa, Nautilus, and other animals. Also one of certain elongated individuals of a siphonophore colony.

Tentaculate (*ten tak' u late*). Bearing tentacles.

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 earlier of two divisions of Cenozoic time.

Test (*test*). A hard outer covering, capsule, or shell; as of a sea-urchin.

Testis (*tes' tis*). The organ in which male germ cells are lodged and developed.

Testudinata (*tes tu' di na' ta*). An order of reptiles, comprising the turtles.

Testudinidæ (*tes' tu din' i dee*). A family of turtles.

Tetrabranchiate (*tet' ra brang' ki ate*). Having four gills; applied to a division of the Cephalopoda.

Tetrad (*tet' rad*). A quadruple body formed, during the growth period in the maturation of germ cells, from the union of two chromosomes which at the same time divide in two.

Tetraxon (*tet raks' on*). Having four axes radiating from a common center; said of certain sponge spicules.

Thales (*tha' leez*). A 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*).

Thermotaxis (*ther' mo taks' is*). A response to temperature.

Thermotropism (*ther mot' ro piz'm*). The response of an organism to temperature.

Thigmotaxis (*thig' mo taks' is*). An orientation of an organism with reference to a contact stimulus.

Thigmotropism (*thig mot' ro piz'm*). The response of an organism to the stimulus of contact.

Thoracic (*tho ras' ik*). Pertaining to the thorax or chest.

Thorax (*tho' raks*). 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.

Thymus (*thi' mus*). A ductless gland located near the gill clefts, or in the neck, or in the anterior part of the thorax in various vertebrates.

Thyroid (*thi' roid*). A ductless gland located in the ventral part of the pharynx.

Thysanoptera (*thi' sa nop' ter a*). An order of insects of small size, commonly living in flowers or otherwise concealed on plants.

Tibia (*tib' i a*). The inner one of the two bones in the lower leg of vertebrates except the fishes.

Tibio-fibula (*tib' i o fib' u la*). The fused tibia and fibula of some Amphibia. .

Tibio-tarsus (*tib' i o tar' sus*). A compound bone in the leg of a bird, formed of the tibia and certain of the tarsal bones.

Tissue (*tish' u*). A group of cells of similar structure forming a continuous mass or layer.

Tonsil (*ton' sil*). A glandular organ at the side of the throat.

Tonus (*to' nus*). A state of continuous activity, as in muscle.

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.

Tradescantia (*tra' des kan' shi a*). A genus of plants including the spiderwort and wandering jew.

Transverse process (*trans vers' pros' ess*). 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 (*tri as' sik*). Of the earliest Mesozoic time.

Triaxon (*tri aks' on*). Having three axes diverging from a common point; said of sponge spicules.

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.

Trilophodon (*tri lo' fo don*). An extinct genus of animals from the Miocene of several continents; probably an ancestor of the elephants.

Trimerotropis maritima (*trim' er ot' ro pis ma rit' i ma*). The beach grass-hopper.

Trionychidæ (*tri' o nik' i dee*). A family of turtles.

Tripalmitin (*tri pal' mi tin*). A fat composed of glycerol and three molecules of palmitic acid; the most abundant fat in man.

Triploblastic (*trip' lo blas' tik*). Composed of three fundamental layers of cells.

Triton (*tri' ton*). A genus of salamanders.

Tropism (*tro' piz'm*). A response of an organism to a stimulus.

Trypsin (*trip' sin*). A proteolytic enzyme produced by the pancreas.

Trypsinogen (*trip sin' o jen*). The inactive substance from which the enzyme trypsin is produced.

Tryptic (*trip' tik*). Of the nature of trypsin; said of proteolytic enzymes that act in an alkaline medium.

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 (*vak′ u ole*). A region within a cell occupied by a liquid other than protoplasm, usually water with various substances in solution.

Vagina (*va ji′ na*). The passage leading from the uterus to the exterior in many animals.

Vagus (*va′ gus*). The tenth cranial nerve.

Variation (*va′ ri a′ shun*). In biology, the occurrence of differences among the individuals of the same species; also, sometimes, among the individuals or species of larger groups (genera, families, etc.)

Variety (*va ri′ e ti*). 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.

Vas deferens (*vas′ def′ er enz*) (*pl.*, **vasa deferentia,** *vas′ a def′ er en′ shi a*). A duct conveying sperms 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.

Vegetative (*vej′ e ta tiv*). Concerned with nutrition. When applied to an egg, meaning that side near which the yolk is accumulated (vegetative pole).

Vein (*vane*). A vessel conveying toward the heart blood which has already traversed capillaries since leaving the heart.

Velum (*ve′ lum*). A horizontal circular shelf within the margin of a medusa.

Ventrad (*ven′ trad*). In a ventral direction.

Ventral (*ven′ tral*) Literally, pertaining to the belly; hence, usually, lower.

Ventricle (*ven′ tri k′l*). 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.

Vertebrata (*ver′ te bra′ ta*). A subphylum of the phylum Chordata, comprising the backboned animals. For definition see Chapter XII.

Vertebrate (*ver′ te brate*). *adj.* Possessing a backbone. *n.* An animal having a backbone.

Vesalius (*ve sa′ li us*). A Belgian anatomist and court physician who lived 1514–1564.

Vibracularia (*vi brak′ u la′ ri a*). Individuals of a Bryozoan colony, in the form of a thread.

Vicq d'Azyr, Felix (*veek′ da zeer′*). French comparative anatomist and physiologist, 1748–1794.

Vicuna (*ve koon′ ya*). A llama-like animal of South America.

Virchow, Rudolf (*veer′ ho*). A German physiologist and pathologist, 1821–1902.

Visceral (*vis′ ser al*). 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.

Visual (*viz′ u al*). Pertaining to the sense of sight.

Vitamine (*vi′ ta min*). One of several substances common in leafy vegetables, animal fats, and elsewhere, which are necessary for proper metabolism in animals. Their chemical nature is unknown.

Vitelline duct (*vi tel' lin* or *vit' el lin dukt'*). The duct through which the nutritive material produced in a vitelline gland is discharged.

Vitelline gland (*vi tel' lin* or *vit' el lin gland'*). An organ producing yolk to be supplied to eggs.

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.

Vocal cords (*vo' kal kordz'*). Membranous folds stretched across the larynx, which by their vibrations in forced currents of air cause the voice.

Volvocales (*vol' vo ka' leez*). An order of plants including Volvox, Pandorina, Eudorina, etc.

Volvox (*vol' voks*). 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. **V. aureus** (*aw' re us*) of small size; **V. rousseletii** (*roo' se let' i i*) very large; **V. perglobator** (*per' glo ba' ter*).

Vorticella (*vor' ti sel' la*). A ciliated protozoön attached to a contractile stalk.

Vorticellidæ (*vor' ti sel' li dee*). A family of ciliated Protozoa to which Vorticella, Epistylis, Carchesium and Zoöthamnium belong.

Wallace, Alfred Russel (*wol' las*). English naturalist, 1823–1913.

Xanthophyll (*zan' tho fil*). One of two yellow substances associated with chlorophyll.

Xenophanes (*ze nof' a neez*). A Greek philosopher who lived about 570–480 B.C.

Yucca (*yuk' ka*). A genus of liliaceous plants having long pointed stiff leaves and a panicle of white flowers.

Zoögeography (*zo' o je og' ra fi*). The branch of zoölogy treating of the geographical distribution of animals.

Zooid (*zo' oid*). One of the members of a hydroid or siphonophore colony. Often, in a restricted sense, a particular kind of individual, as a hydranth.

Zoölogy (*zo ol' o ji*). The science of animals.

Zoöthamnium (*zo' o tham' ni um*). A genus of colonial ciliated Protozoa, resembling Vorticella.

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. The posterior pair articulate with the anterior pair of the vertebra next behind.

Zygote (*zi' gote*). A cell or individual produced by the fusion of two cells or their nuclei in the process of sexual reproduction.