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COMPARATIVE ANATOMY

Neal and Rand
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WITH 540 ILLUSTRATIONS

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To

James F. Porter

in admiration and affection
PREFACE

In one of the frescoes of the Sistine Chapel, Michelangelo portrays Adam after his creation by Jahveh. The frontispiece of this book shows only enough of this painting to suggest that Jahveh had a hand in the event; but how Jahveh accomplished his creative work is left to biologists who have tried to solve by scientific methods the problem of the genesis of the human body. Such scientific investigation is not concerned with the question of the ultimate origin of the universe nor of the presence or absence of God in the cosmos, but with the secondary factors which determine physical events in the physical world.

The scientific evidence which bears upon the problem of the genesis of the human body is derived chiefly from the sciences of paleontology, comparative anatomy, and embryology. These sciences provide the factual support of the evolution theory, which in turn furnishes the clue to the origin of species, including the human species. The remarkable development of these sciences since Darwin's day may be attributed to the conviction of biologists that by means of them light may be thrown on the history of organisms in general and of the human body in particular. Today such courses form standard constituents of the biological curricula of universities and colleges.

American undergraduates study comparative anatomy not so much from interest in lower animals as to gain the best approach to an understanding of human structure and function. The details of comparative anatomy in themselves interest the average undergraduate slightly if at all. To elicit the attention of the student the facts must be interpreted for him and given meaning in terms of function or of genetic relations. The earlier books in comparative anatomy served better as works of reference than as college texts. The multiplicity of facts presented in them tended to confuse the student, who consequently was unable to see the woods for the trees.

The facts presented in this book have been selected chiefly because they throw light upon the important problem of man's place in nature and because they help the student to understand the major functions of his body. If greater stress is laid upon morphological than upon physiological matters, this is done, not because students are more interested in morphological problems, but because the authors are convinced that the central problem of life is that of form. The best approach to this problem is through the study of the changes which the body undergoes in ontogenesis and phylogenesis. College and medical courses in physiology usually assume that the student has a basis for them in a knowledge of the facts of anatomy.
Among the difficulties which confront the teacher of comparative anatomy is the reluctance of students to acquire a vocabulary of technical terms. As far as possible in this text familiar, non-technical language is used. Unfortunately, it is impossible to eliminate technical terms wholly from an anatomical text. In defense of their use it should be emphasized that they avoid much circumlocution and thus make for brevity.

This book is not intended to be used as a laboratory manual but as a text to supplement, interpret, and integrate the facts acquired in the laboratory. The foundations of a course in comparative anatomy should be laid in the laboratory so that the student may have first-hand acquaintance with at least a fish and a mammal—and if possible a tailed amphibian also. For such laboratory work a suitable laboratory manual should be used. Since this text deals comparatively with each of the various organ systems in turn, a laboratory manual which follows this plan is desirable.

For some years this text in mimeographed form has had the benefit of student criticism, with the consequent elimination of many obscurities and inconsistencies. The typescript copy has been read by Mr. Edwin Tenney Brewster of Andover, Massachusetts, and by Professors A. Brazier Howell and W. L. Straus, Jr. of the Johns Hopkins University. For what these have done to improve the book the authors are deeply grateful. The authors consider themselves most fortunate to have had the efficient services of John Howell Neal who has drawn or redrawn most of the text figures. All new drawings required for the chapters on reproduction and histology (chapters 2 and 3) were made by Mary B. Marks. Of the text-books in comparative anatomy which have been consulted those of Goodrich, Ihle, Kingsley, Plate, Stempell and Wilder have been especially valuable. For embryological facts and figures, the authors have leaned heavily upon Arey, Corning, Kellicott, MacBride, and Patten. In human anatomy, the text-books of Braus and of Morris have been much used. In histology, Bremer's text, and in neurology, the text-books of Herrick and of Ranson have been most helpful.

In this text-book the discussion of each organ or organ-system is divided into three parts—phylogenesis, ontogenesis, and anatomy. Since it may be assumed that the student has first-hand acquaintance with the anatomy of such a mammal as the cat, and since he presumably is more interested in the human species than in any other mammal, anatomical description in this text emphasizes human anatomy. The descriptions of ontogenesis are also mostly based upon the human embryo. If, as the authors believe, the main purpose of a course in comparative anatomy is to throw light upon the structure of the human body, to ignore it as some text-books do seems like a performance of Hamlet with the Prince left out.

BOSTON, MASSACHUSETTS
INTRODUCTION

"Grant a simple archetypal creature like the mudfish or Lepidosiren, with the five senses and some vestiges of mind, and I believe natural selection will account for the production of every vertebrate animal."  Darwin to Lyell in 1859.

One of Gauguin's best-known paintings portrays a group of human figures, some standing, some reclining, all in an attitude of melancholy thoughtfulness. The picture might well serve as an illustration of Tennyson's "Lotus Eaters." The painter, however, has entitled it "Where do we come from? Where are we now? Where are we going?" These persistent problems interest the biologist also as well as the poet and artist. "The question of questions," says the elder Huxley, "the problem which underlies all others and is more deeply interesting than any other, is the ascertainment of the place which man occupies in nature and of his relations to the universe of things."

The answer is to be found, if it is to be found at all, through scientific methods of investigation and these seem to point inevitably to some form of evolution. Evolution is the scientific theory that organisms have arisen in nature by "continuous progressive change according to certain laws and by means of resident forces." The theory assumes the mutability of species, their blood relationship to one another, and their origin in accordance with natural law by means of resident factors. For its factual support evolutionists appeal to circumstantial evidence. Geological evidence provides the strongest argument for evolution. For the evidence from the rocks demonstrates that the earth has existed for many millions of years, and that during this time the bodies of organisms have progressively changed, so as to resemble, more and more, the forms now living.

Many objections have been raised against the evolution theory, most of them based upon misunderstanding. A few of these may be mentioned. First, it is asserted that the foundations of the theory are weak, since it depends upon circumstantial evidence. In reply to this objection it may be pointed out that there is no more trustworthy evidence than circumstantial. Courts have found that eye witnesses are notoriously unreliable.

It is sometimes asked how it happens, if there has been evolution, that there are any lower animals left. "Why haven't all monkeys turned into men?" This supposed difficulty is evidently based upon the assump-
tion that evolutionary change is bound to occur, under whatsoever circumstances. Evolution, however, is not the notion that organisms are bound to change regardless of conditions. If an animal is adapted to a particular environment, as the monkey is to the forest, and the forest persists, we should not expect the monkey to change. It may be said in this connexion, however, that evolution is not the theory that man came from a monkey, but that the bodies of the two have had a common animal origin.

Evolution is sometimes said to be "only a theory," as if it were no more than an unfounded guess or pure assumption. On the contrary it is doubtful if any other scientific theory has greater factual support.

A frequent objection raised against evolution is that "it cannot explain the origin of life." It may candidly be admitted that we know nothing about the origin of life. But the primary question of evolution is not how life began but how organisms have changed since their origin. The geological record leaves us in no doubt as to the fact of change. As to the origin of life, L. J. Henderson is probably justified in saying that "any theory about the origin of life is nothing but an unfounded guess."

Again, it is charged that the evolution theory "degrades" man by making a monkey of him. In reply to this supposed objection it may be said that the differences between man and monkeys obtain whatever may have been their origin. "A man's a man for a' that." Values are not determined by origins. The value of the Venus of Melos is not affected by the fact that the block of marble from which the statue was carved came from a quarry.

Our ignorance of the causes of evolution has been considered an objection to the theory. It must be admitted that it has been found easier to prove that evolution has taken place than to explain how it has been brought about. Undoubtedly the nineteenth century belief that Darwin's hypothesis of natural selection explained organic evolution led men to accept this theory more readily than they otherwise would have done. Nevertheless, the case for evolution does not depend upon the ability to state its cause any more than the existence of light depends upon our ability to explain how it reaches the earth.

Of the hypotheses advanced to explain evolution, three have best survived criticism. Briefly stated they are:

1. The Lamarckian hypothesis assumes that organic evolution is due to four factors:

   1. The will to live
   2. The use or disuse of organs
   3. The influence of environment
   4. The inheritance of the bodily modifications due to use or disuse or to the influence of environment.
INTRODUCTION

The theory leaves unexplained how bodily modifications effect corresponding changes in the germ cells which transmit inherited traits. On the whole, experimental evidence does not support the assumption of the inheritance of bodily modifications.

2. According the Darwin's hypothesis of natural selection, four factors effect organic evolution:

1. Variation
2. Multiplication
3. Competition
4. The inheritance of useful variations

The theory asserts that no two individuals are precisely alike, and that many more are born than can possibly live. The result is a struggle for existence so severe that only those types survive whose variations favor them in the struggle. These transmit their favorable traits through heredity to their offspring. Carried on through many thousands of generations, such changes would, it is assumed, eventually produce new species.

3. During the twentieth century, Hugo De Vries has advanced a third view, which he calls the Mutation Theory. According to the Mutation Theory, new species arise suddenly, discontinuously, not, as Darwin thought, by slow accumulation of slight differences. De Vries conceives of an organism as a mosaic of traits. A new combination of characteristics constitutes a new species. Breeding evening primroses in his Amsterdam garden, De Vries discovered that mutations are inherited. In other words, mutants breed true. After it arises, a mutant species is subject to natural selection or elimination, but its origin, like that of the fluctuating variations of Darwin, is not dependent upon this struggle for existence. The factors in evolution, therefore, according to De Vries are:

1. Mutation
2. Heredity

The laws of heredity are found to be in accord with the mutation theory. The theory has, however, been criticised as failing to explain the origin of adaptive mutations. Since the cause of adaptive change must affect the germ-cell in order to be inherited, and since biologists are still searching for the factors which determine adaptive mutation, it must be admitted that the cause or causes of evolution are unknown. Of the three hypotheses mentioned, the Lamarckian is least acceptable to biologists.

At the present time two divergent conceptions of evolution are held by biologists—mechanical and emergent.

According to the mechanical conception of evolution, the universe is a machine operating in accordance with "immutable" laws. The entire universe or any part of it consists of particles in motion grouped into
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various systems. Changes in these groupings constitute what we call evolution. Random samplings of all parts of the universe—possible through the spectroscope—prove that all consist of the same kinds of particles moving in accordance with the same laws of motion. Hence from a knowledge of any part of the universe it follows logically that we can know about all the rest. Reduced to its lowest terms, the universe consists simply of matter and energy. Since the total amount of matter and energy is constant and evolution consists of changes in the distribution of matter, it would be theoretically possible, if we knew enough, to calculate the future changes in arrangement, and predict the course of evolution. Since living organisms consist of the same kinds of particles as are found in the lifeless world and no form of energy peculiar to the living has been discovered, prediction of what will happen in the living world involves no new factors.

Against such a mechanical conception of evolution and of the universe most minds revolt. To accept such a conception would mean the rejection of the most cherished beliefs of mankind. If the universe be a great machine, and nothing more, there is obviously no place for freedom, moral responsibility, or for values of any sort. Might and might alone prevails. In a mechanical world, ideas, ideals, and aspirations, if they existed, could have no more influence in the course of events than do shadows cast on a summer day. But, it may be asked, if the universe is in reality a giant machine in which all changes are only alterations of systems of moving particles, how could there be any evolution at all? Mechanical changes undoubtedly do occur in the universe as, for example, in the revolutions of the planets around the sun. But changes like these are not truly evolutionary at all. A mechanical universe which started with matter and energy could consistently have only matter and energy in the end. From such a point of view, the universe could contain only "eternally old things." But evolution is above all else a process of novelty production. Life and consciousness are such novelties. By no hocus pocus could a magician with matter and energy in his hat conjure such entities as mind or ethics. The mechanists, says Carrel, referring to living organisms, have "built a machine, and like the vitalists, they were the engineers of the machine. Then as Woodger pointed out, they forgot the existence of that engineer." Mechanical evolutionists have made the same mistake.

While the mechanical conception of evolution may appear simple, clear, and logical, it ignores too many facts to be true. The facts accord better with the opposing emergent conception of evolution. According to the doctrine of emergent evolution, evolution is above all else a process of novelty-production. The differences which distinguish higher from lower organisms are not simply quantitative but qualitative. The differences are such that it is impossible to reduce the higher to terms of the
lower. Biology is found to be not simply biochemistry and biophysics, but a science in its own right. Mechanism is inadequate to life. The notion that, from a knowledge of masses and motions, the future course of organic evolution might be predicted is ridiculous.

The basis of the emergent conception of evolution is found in the empirical fact that an organized whole—such as a living creature—has characteristics which are qualitatively different from those of the elements which enter into it. The properties of electrons give no clue to the properties of the atoms which they form. The properties of atoms are not found in the chemical compounds which they form. Add ten carbon atoms together and they have the same properties which one atom has. Add hydrogen atoms together and their properties remain the same. But when carbon atoms are combined chemically with hydrogen atoms, the hydrocarbons formed have entirely new properties. It seems increasingly clear that “an organized whole is more and other than the additive sum of its parts.” For the appearance of such new properties science has today no explanation to offer. Indeed, the concept of causation does not seem to apply to such phenomena since cause and effect in the mechanical sense involves a transfer of energy from the cause to the effect. Spaulding has well called this process of formation of new characteristics through the organization of parts into wholes “creative synthesis,” since the properties of the whole, or at least some of them, are new.

“From separate organic compounds to organized living protoplasm,” says G. H. Parker, “we pass from one plane of organization to another and consequently from one set of properties to another. The essential properties of living protoplasm are at present no more to be understood from its constituent compounds than are the properties of water from those of hydrogen and oxygen. The properties of living protoplasm are too manifold for description. They are those properties whereby living protoplasm acts otherwise than its chemical constituents do.”

Nineteenth century mechanism failed because it failed to consider the factor of organization. But, as L. J. Henderson says, “there is that which organizes matter in time and space.” Consequently, if we are to understand how new properties and capacities arise in nature, we must add to the categories of matter and energy (which were considered sufficient in the nineteenth century) a third category of organization. In a strict sense this organizing factor is not “mechanistic.” Certainly, organization has up to the present not been recognized as a mechanistic factor by physicists or chemists. But the evidence of such a factor in life is indisputable. Without it, the evolutionary process is incomprehensible.

As mechanical evolution is a contradiction in terms, so emergent evolution is a redundant expression. If there is no emergence there is no evolution. The facts speak loudly in favor of emergent evolution.
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"Things living," says Jennings, "behave themselves as if emergent evolution were a true doctrine."

The acceptance of the doctrine of emergent evolution has greatly relieved the minds of many who were depressed by "mechanical mythology" as applied to man. According to emergent evolution, man, like all other creatures, is a unique product. Consequently, man's capacities and powers are what we find them to be in experience, and are not to be logically deduced from the properties of lower animals. The doctrine of emergent evolution also relieves the evolution theory of the charge of materialism. If evolution be an emergent process, as it evidently is, we can understand how the "strata" of reality assumed by pluralist philosophers have arisen. Out of the lifeless has emerged the living, out of the living the conscious, out of the conscious the ethical.

This text-book undertakes to answer the questions "Where do we come from?" and "Where are we now?" on the assumption that the human body has evolved. It seems unnecessary and undesirable to present here the mass of evidence gathered by Darwin and his successors in support of this opinion. Most of the facts stated in this book have a bearing, either direct or indirect, upon it. If this book proves anything, it is that the body of man is best understood in the light of its animal origin.

No attempt is made, however, to convey the impression that evolutionary change can be adequately explained at the present time. The hypotheses of Lamarck, Darwin, and De Vries appear today less satisfactory than they did a generation ago, and biologists are still searching for the causes of adaptive evolution. To give students the impression that we know the factors of evolution is to mislead them. A recent text-book states that "it would seem that the immediate cause for the development of dermal bones from tooth-bases . . . was the early need for teeth and tooth supports in the young carnivorous larvae." Such an assertion evidently raises more problems than it attempts to answer. As a causal factor in morphology, need is probably about as effective as it is in economic life in raising our balance at the bank. A future advantage or possibility may influence human behavior, but teleology is ruled out of scientific explanations.

To determine man's ancestry, three kinds of evidence are used—paleontological, anatomical, and embryological. Except for skeletal structures, paleontological evidence is generally incomplete. Consequently, for the history of other organs morphologists have to depend upon anatomical and embryological evidence. Unfortunately, evidence from these two sources is sometimes equivocal or conflicting. Ontogenesis does not always repeat the history of the race. There are too many exceptions to the fundamental law of biogenesis. When embryological
and comparative anatomical evidence conflict with one another, the difficulties of interpretation are enhanced and morphological opinion is likely to be divided. Where evidence conflicts, there is no criterion by which the more reliable clues may be recognized. Anatomists tend to value anatomical evidence more highly; embryologists favor ontogenetic evidence. In such matters, personal opinion looms large. Frequent differences of opinion among morphologists have given the impression that phylogenetic conclusions are exceptionally speculative and uncertain. Much of this divergence, however, is due to lack of sufficient evidence. The history of morphology shows that with increasing knowledge there has been an increase of agreement on controverted issues. As the recent upheaval in theoretical physics has shown, speculation is not peculiar to morphology. Even if it be admitted that the methods of the morphologist resemble those of Sherlock Holmes, this similarity does not invalidate his conclusions.
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Since some of the so-called lower animals, living or extinct, more or less resemble hypothetical ancestors of man, some knowledge of them is necessary for a proper understanding of the history of the human body. Moreover, certain highly complex and obscure organs of man are most easily understood in the light of the simpler conditions of lower forms. Even the plants, so unlike us in outward appearance, contribute something to our knowledge of ourselves.

But the organic world is so enormously complex that no human mind can carry its detail adequately without some system by which facts are classified and summarized. Most useful of such systems are those based on natural relations, which, therefore, exhibit the course of evolution of each species, and place it correctly in an evolutionary scheme. For evolution, nowadays, is the key to all genetic animal relationships.

Such an evolutionary scheme begins by dividing all living things into plants and animals. Plants are creatures which contain chlorophyl, and therefore, can, produce or make their food directly out of inorganic materials, or else they are, obviously, such creatures as have lost their chlorophyl and adopted the feeding habits of the simpler animals. Animals may or may not have descended from plants; only rarely do they contain chlorophyl, hence all their structure and habits rest on other means of obtaining food. There are, however, many simple organisms; for example, the slime molds, which are as much one as the other, plants or animals indifferently. Even some of the higher plants, like the venus fly-trap, catch and devour insects; and some of the unicellular algae also feed like animals.

The animal kingdom as a whole is commonly divided into about a dozen phyla, the precise number and the precise definitions of which have not yet been agreed upon by taxonomists. These phyla, in turn, are split into classes, the classes into orders, the orders into genera, and the genera into species. It is sometimes convenient, also to recognize sub-orders and sub-classes, and to combine similar genera into families.

Scientific naming is by genera and species, a scheme devised by the great naturalist Linnaeus, or Linné, about the middle of the eighteenth
century, and called the Linnaean, or binomial, system. Thus all birches are called by their Latin name Betula, and that is their genus. White, yellow, and black birches are therefore respectively, as species, Betula alba, Betula lutea, and Betula nigra; but the American white birch is Betula papyrifera, that is, the paper birch; and the common gray birch
is *populifolia*, because it has leaves that twinkle in the wind like those of a poplar tree.

The common cat is *Felis domestica*; the lion, *Felis leo*; the tiger, *Felis tigris*; and there are, in all, some forty species more in the genus *Felis*. Linné called us *Homo sapiens*. We belong to the family Hominidae (of which we are the only living species) to the order Primates, the class Mammalia, the phylum Chordata, and the animal kingdom. In a general way, for the larger and more familiar animals and plants, the vernacular name, such as pine or elephant, refers to the genus.

**Phylum I. PROTOZOA**

The protozoa are the simplest of animals, their bodies usually consisting of only a single cell. Since they reproduce by simple fission of the parent body there is no natural death in the group and no protozoon has ever lost an ancestor.

There are, at least, ten thousand species. Most protozoa are microscopic; some are just visible to the unaided eye; a few colonies are millimeters in diameter; the slime molds, which are giant reticulated amoebas and neither quite individuals nor quite colonies, are thin sheets some centimeters in extent.

Among the simplest are the amoebas, which to the superficial observer look like blobs of jelly with no particular shape. They are without skeletons. But some protozoa, such as the not uncommon fresh water *diffugia*, though otherwise like amoebas, have single-chambered shells of chitin or silica. The foraminifera have more elaborate shells, calcareous in most forms, which have accumulated through geologic ages into beds of present-day limestone. The White Chalk Cliffs of Dover, which are composed mostly of protozoan skeletons, are four or five hundred feet thick, and extend nearly to Paris.

More familiar are the forms with cilia or flagella—the slipper animalcule, *Paramecium*, the trumpet animalcule, *Stentor*, and the host of
infusoria that swarm in water containing organic matter. Some are parasitic, and produce sleeping sickness, syphilis, and other diseases. Some contain chlorophyll and might about as reasonably be counted as plants. A few colonial forms, for example, the common green volvox, have their individuals differentiated into vegetative and reproductive cells, and thus take the first step toward the evolution of multicellular organisms.

The protozoa, which are single-celled and, apparently, simple, make a logical starting point for animal evolution. The amoeba, which is among the simplest of the protozoa, is popularly assumed to be "the mother of all living." This assumption is in no wise unreasonable as there is no direct evidence to the contrary.

![Diagrams of embryonic stages illustrating the contrast in the fate of the blastopore in different groups of animals. The forms in which the embryonic blastopore becomes the mouth were grouped together by Grobben as PROTEROSTOMIA. The DEUTEROSTOMIA include those animals in which the blastopore becomes the anus or lies near the anus. The coelenterates, flatworms, annelids, and molluscs are Proterostomians, while echinoderms and chordates are Deuterostomians.]

Multicellular animals or Metazoa have bodies which consist of many cells. Grobben, 1908, divides the metazoa into two main subdivisions:

I. **Proterostomia**, in which the embryonic mouth or blastopore persists as the adult mouth. Proterostomians include the Platyhelminthes, Nemathelminthes, Rotifera, Molluscoida, Annelida, Mollusca, and Arthropoda.

II. **Deuterostomia**, in which the blastopore forms the anus or lies near the anus. The deuterostomians include the remaining groups of animals, —Echinodermata, Hemichordata, Urochordata, Cephalochordata and Vertebrata.

**Phylum 2. Porifera**

The differentiation among individual cells, which began faintly in certain colonizing protozoa, is carried somewhat further in the sponges, which, though rated as multicellular animals, are hardly more than slightly
organized colonies of cells. They are so far independent of one another that a sponge, even after being squeezed through cheese cloth, will reorganize itself and go on living.

Sponges vary from the common Grantia, five to ten millimeters in height and simple in outline, to complex structures larger than a man's head. Nearly all have skeletons, usually calcareous or horný, but siliceous in the glass sponges. The familiar bath sponge is only a skeleton, from which the flesh has been macerated away. Some dozen species of various sizes and textures furnish the commercial product.

Most sponges are marine, but there are some fresh water species, which develop in the form of thin sheets up to the size of one's hand. There are branched forms, and also colonial.

Whatever their size or complexity, most sponges consist essentially of a body-wall that surrounds a central cavity, or cloaca, which communicates with the exterior by, at least, one wide opening, the osculum. The body-wall consists of an external covering (ectoderm); an inner covering (endoderm); and between the two, a thicker covering, or skin (the mesoderm or mesogloea), which secretes the skeleton. There is no nervous system.

In the body-wall are two sets of radial canals. Those of one set open into the cloaca and are lined with endodermal cells. The others open to the exterior, are lined with ectoderm, and have muscle fibers at their mouths. The two alternate, and are interconnected by smaller passages. The endodermal cells bear flagella, which by their motion set up currents of water inward through the canals to the cloaca, and outward through the osculum.

Sexes are separate. The eggs are fertilized in the body of the female, and there develop until they become free-swimming larvae, which finally settle down on the bottom and assume the sessile existence of the adult sponge.

Since the sponges are a side branch of the phylogenetic tree of the animal kingdom and seem not to have been the ancestors of any higher group, they interest the student of the human body chiefly as an example of multicellular organization in very simple terms, intermediate between colonial protozoa and organized multicellular individuals.

Some 2500 living species are recognized, and fossils are somewhat common.

**Phylum 3. COELENTERATA**

The coelenterates include the familiar fresh water hydra and various other polyps, solitary and colonial; corals; jellyfishes; and sea-anemones. The Portuguese man-of-war is a colony in which there are several different sorts of individuals, of which some are specialized for swimming and some
for digestion; some become protective scales, some are reproductive, some become thirty-foot tentacles armed with powerful nettle cells for defense. Such a colony may contain a thousand individuals, whose different kinds simulate the differentiated organs of higher forms and help to explain how such organs arose.

Each polyp, jellyfish, sea-anemone, or coral, like one of the sponges, possesses a central cavity, the enteron. The body wall is at least two-layered, with an ectoderm on the outside and an endoderm lining the enteron. In all except such simple forms as hydra, there is a thick mesogloea which makes up the greater part of the body mass.

Like the sponges, the coelenterates have an enteron, no longer a mere passage for water, from which individual cells pick up food, each for itself, but a digestive organ—hence the name coelenterate. The single opening into the enteron is both mouth and anus. Muscles, also, are more differentiated; so that the polyp waves its tentacles vigorously about, seizes food and conveys it to the mouth, or withdraws suddenly into its capsule. The jellyfishes swim slowly by opening and closing the umbrella. There is also a simple nervous system; and in the jellyfishes, sense organs, both eyes and organs of equilibrium, are arranged along the edge of the umbrella.

The symmetry of the body is generally radial, usually on four or six axes, not on five as in the echinoderms. This radial symmetry may
disguise a possibly primitive bilateral symmetry. But in some of the ctenophores, which are the small jellyfishes whose enormous numbers make the ocean phosphorescent at night, there are beginnings of bilateral symmetry, especially in the tentacles.

The importance of the group for the student of animal evolution lies in the fact that the two-layered gastrula stage of the embryo, of all higher forms, duplicates in all essentials the two-layered adult body of the simpler coelenterates. Coelenterates, therefore, are taken to lie on or close to the main trunk of the ancestral tree of higher animals.

Taxonomists recognize some seven thousand species.

**Phylum 4. Platyhelminthes**

The platyhelminths or flatworms are well described by their name. Included in the group are such diverse forms as liver flukes, planarians, tapeworms, and the nemerteans, which are nearly all marine. The flattened bodies are bilaterally symmetrical, with a well-marked dorso-ventral and antero-posterior differentiation. Nervous centers tend to concentrate as a brain at the anterior end. There is no body-cavity, and usually no anus except in nemerteans. The alimentary canal shows a tendency to form a series of lateral diverticula, thus suggesting the beginnings of the coelomic pouches and gill-pouches of higher animals.

Muscle bundles extend in various directions within the thickened mesogloea. Although most flatworms have neither true circulation nor blood vessels with walls, lacunar spaces filled with liquid occur, and are
thought by some morphologists to represent the beginnings of a circulation. The nemertean, however, have a true blood system in the form of dorsal and lateral vessels with transverse connections.

The parasitic mode of life which has been adopted by many flatworms has led to more or less degeneration and to a great complication of life histories.

Four thousand five hundred species are known.

Phylum 5. Nematelminthes

The nemathelminths or thread-worms are also well characterized by their name. They differ from flatworms, not only in the shape of their

![Diagram of Nematode Cross Section]

Fig. 6.—Monhystera, a type of the Phylum Nematelminths seen in lateral aspect. (Redrawn from Ward and Whipple after Cobb.) Like Monhystera most nemathelminths have an anal opening. As seen in the cross section the alimentary canal is separated from the body-wall by a false body-cavity (pseudocoelom). (Redrawn after Stempell.)

bodies, but also in having a body cavity which, however, instead of lying between two layers of mesoderm, separates the body wall from the endodermal lining of the alimentary canal, and is therefore a pseudocoelom. Most of them have an anus.

Threadworms are much like annelids, but have not their metamerism. Muscles are limited to the body-wall, and consist exclusively of longitudinal fibers, grouped in four bundles. The nervous system is a circumesophageal ring and a dorsal, a ventral, and two lateral longitudinal nerves. Most
have no true circulatory system, but the pseudocoelom distributes digested food and collects wastes. A few possess a closed vascular system. Excretion is effected by protonephridia devoid of flame-cells. The sexes are usually separate.

Nemathelminths are subdivided into three classes, a. Nematodes or round worms; b. Acanthocephala or hook-headed worms; c. Chaetognatha or arrow-worms.

Sixteen hundred species are recognized, mostly parasitic. The thickened cuticula on the outside of the body is probably an adaptation to their parasitic mode of life.

**Phylum 6. MOLLUSCIDA**

Molluscs are animals of ancient ancestry, and the bivalve “lamp-shells” or brachiopods are abundant in the older sedimentary rocks. Living forms are mostly sessile and marine. The valves of the shell, instead of being lateral and paired, as in the clam, are dorso-ventral. The ventral valve is the more curved of the two, and encloses posteriorly an opening for the stalk by which the animal is attached.

Molluscs are coelomate, and the body cavities are bilaterally paired. In them are enclosed the alimentary canal, the liver, and the gonads. Transverse septa divide the coelom into three portions, as in Hemi-chordates and in Sagitta. While some species lack an anus, most have a U-shaped alimentary canal with the anus near the mouth. Paired nephridia function both as excretory and as reproductive outlets. The nervous system consists of a circumesophageal ring with dorsal and ventral nerve chains. The heart is dorsal to the stomach. Some forms, such as the bryozoa, are colonial.

The phylum is subdivided into three classes: Polyzoa, Brachiopoda, and Phoronida.

The origin of molluscs from free-swimming trochophore ancestors is generally assumed. 1700 species have been identified.

**Phylum 7. ROTIFERA**

The rotifers are so named because the cilia that surround or encircle the mouth appear under the microscope to rotate like a wheel. They are little known, partly because of their small size, and partly because they are often confused with ciliated protozoa which they superficially resemble. They are, however, multicellular unsegmented worms with a pseudocoelom. The alimentary canal has both mouth and anus. Usually, the protonephridia and gonadic ducts open into the posterior portion of the intestine. The sexes are separate. Rotifers are frequently com-
pared with the trochophore larva of annelids, but their ontogenetic development does not support this assumption.

Eight hundred and fifty species are recognized.

**Phylum 8. ECHINODERMATA**

The echinoderms include the star-fishes, sea-urchins, sea-cucumbers, and sea-lilies. They are marine coelomate invertebrates with spiny skins and a water-vascular system which they fill with sea-water. Superficially radial in symmetry, the echinoderms are actually bilaterally symmetrical animals which undergo metamorphosis from a bilaterally symmetrical larva. Since the blastopore becomes the anal opening and the mouth is formed secondarily, they are placed among the deuterostomia, the group to which the chordates belong. The coelom is a true enterocoel, that is, develops as an outpocketing of the enteron.

The nervous system consists of a circumesophageal nerve ring from which five nerves radiate. In addition, there is an aboral nervous system. While most echinoderms possess a lacunar blood system, some have radial blood-vessels. Specialized excretory organs seem to be wanting. The sexes are separate and the gonads are interradial in position, with external apertures on the aboral side of the animal. Respiratory organs are varied, among them being dermal papillae which contain outpocketings of the coelom.

Some taxonomists recognize 10,000 species.

**Phylum 9. ANNELIDA**

The annelids include earthworms, leeches, clam worms, and many marine forms. All are metameric, coelomate, and without jointed legs. True nephridia, segmental and ectodermal, are present. In many, the body-wall is beset with bristles or setae. The nervous system is metameric and consists of suprasophageal and subesophageal ganglia, with circumesophageal connectives and a ventral series of ganglia.

Circulation is through a closed system of blood vessels. Blood is pumped forward through a contractile dorsal aorta, and thence around
the pharynx to a ventral subintestinal blood vessel. Smaller branches distribute blood to the body-wall and intestine. External respiration takes place through the skin. External filamentous gills sometimes occur in forms with parapodia. The muscles, both of the body-wall and of the alimentary canal, are divided into circular and longitudinal sets.

The sexes, usually, are separate, and the gonads are limited to a few segments of the body. Germ cells find their way to the exterior either through pores in the body wall, or by way of ciliated tubules, the coelomoducts. Many annelids undergo metamorphosis from a "trochophore" larva.

Four thousand species are known.

**Phylum 10. MOLLUSCA**

Molluscs are coelomate and non-metameric. The body consists of mantle, mantle-cavity, and foot without paired appendages. The mantle cavity receives digestive wastes and the products of the excretory
and reproductive organs, and in most forms contains gills. The foot is muscular and usually is the chief organ of locomotion. The circulation is not closed, but the blood passes through a system of lacunar spaces. The dorsal heart is enclosed in a pericardium which is a part of the coelom. Arteries and veins afford connexions with the gills. The excretory organs bear a fundamental resemblance to the nephridia of annelids. Respiration is by means of gills, which in air-breathing snails are enclosed in a chamber with a narrow opening to form a sort of lung.

The alimentary canal has a muscular pharynx and a stomach enlargement. The anus is posterior or is displaced forward in the mantle cavity.

**Fig. 9.—Diagrams of a Mollusc.** Figure A shows a longitudinal section, while B is a cross section. (Redrawn from Stempell, after Kuhn and Sedgwick.)

The nervous system has a circumesophageal ring and a series of cerebral, pedal and visceral ganglia with their commissures and connectives. Sense organs are varied. Many molluscs are hermaphroditic, the gonads opening into coelomic sacs. Development involves metamorphosis, and the veliger larva resembles the trochophore larva of annelids.

Sixty-one thousand species are recognized.

The phylum contains a number of primitive or aberrant forms, among which are the chitons with eight calcareous plates on the back instead of a single shell, dentalium with a nearly straight tapering shell open at both ends, and certain marine forms that are worm-like and without shells.

Though the molluscs as a group are highly successful in the struggle for existence, as witness the multitude of their species, and the enormous
numbers of individuals of several, they do not lie near the main line of
animal evolution and have contributed nothing to the forms above them.

Three main classes are separated by differences in the structure and
functions of the foot.

Class Gastropoda

The gastropods are the snails. In them, the foot is the familiar
ventral surface on which the animal crawls. Most have a single shell
from which comes their other name, univalves. Commonly, the shell
is coiled; but the Chinaman's cap, patella, has an oval dome. Some are
ear-shaped, suggesting one shell of a bivalve. Some of the land snails,
which are air-breathing, like the common garden slug, have no shells
or only a minute rudiment. In many, the opening of the spiral shell
is closed by an operculum when the animal withdraws itself.

The enormous number of gastropod species, nearly 50,000, the variety
and beauty of the shells, and the ease with which they may be pre-
served and displayed, have long made conchology a favorite branch of
natural history.

Class Pelecypoda

The pelecypods or lamellibranchs are the common bivalves, such as
oysters and clams. They have no heads, and the foot, as their name
indicates, is hatchet-shaped. It functions as a burrowing tool. The
mantle, in addition to secreting the two shells, is often prolonged into a
siphon which, in the common clam, may be elongated to nearly a foot,
and reach the surface of the sand while the rest of the animal remains
safely buried. Commonly, the siphon has two tubes, through one of
which water is drawn into the mantle cavity for respiration and food,
while through the other are ejected the body wastes.

The pelecypods are, in general, less active than the gastropods; but the
fresh-water clams crawl about freely on the muscular foot, and the
scallops, or pectens, swim by flapping their shells together.

This group, also, with some ten thousand species, is sought after by
collectors. Pearls, and mother of pearl for buttons, are obtained from
both marine and fresh-water forms. The ship worm, teredo, which often
does great damage to ships and docks, is a pelecypod.

Class Cephalopoda

The cephalopods are the cuttlefishes, squids, and devilfish. In them,
the mantle is wrapped about the body to form a sac, which is nearly closed
except near the head, where openings admit water to the gills in the
mantle cavity. The foot is divided into long tentacles which surround
the powerful beak. The paired eyes are much like those of vertebrates,
but the retina unlike that of vertebrates is not inverted. Altogether, the cephalopods are much the most highly organized and active of the molluscs.

The class divides into two orders.

The tetramerous or four-gilled forms, have an external shell, coiled in modern species like a snail's, but, unlike a snail's, divided into compartments, only the last and largest of which is occupied by the animal. The chambered or pearly nautilus, of which there are only four species, is the only survivor of a vast assemblage which flourished in the Paleozoic and Mesozoic. Many of the earlier forms had straight shells. Altogether, including the ammonites of the Mesozoic, some two thousand fossil species are known.

The dibranchiates have an internal shell or none. The group includes the squids and cuttlefishes, octopus, and devil-fish.

**Phylum II. ARTHROPODA**

The similar metamerism of their bodies prompted Cuvier to group annelids and arthropods together as articulata.

Arthropods are metameric invertebrates with jointed legs, and covered with a jointed chitinous exoskeleton usually beset with hairs. The general organization of the body resembles, closely, that of annelids, from which, it is believed, that arthropods have descended; but the coelom is secondarily replaced by a pseudocoelom. The eyes are simple and compound, both types often being present in the same individual. The circulatory system is open, that is, the blood vessels open into the lacunar spaces of the pseudocoelom. Comparative anatomy and embryology suggest that, originally, each metamere possessed a pair of appendages, which, however, in the course of phylogensis have become greatly modified by specialization or by reduction.

Species number 400,000 or four-fifths of all known animals.

Owing to the differences in the method of respiration, arthropods are divided into (1) Branchiata, which, having adapted themselves to aquatic life, breathe by means of gills; these gills, usually, being attached to their appendages; and (2) into air breathing Tracheata, which use ectodermal air-tubes that ramify throughout the tissues.

**Class Crustacea**

The crustaceans include all the water-breathing arthropods. Besides the crabs, lobsters, crayfish, shrimps, and prawns, together with several thousand species of smaller creatures allied to them, the group contains the familiar sowbugs of damp woods, five hundred species of barnacles, and some five thousand species of minute creatures, water fleas and the like, in size from 1 cm. down to the limit of comfortable visibility, about half of which are parasitic.
Class Arachnoidea

This division of the arthropods, most of them air-breathing, but without tracheae, in addition to a vast number of minute creatures, contains the harvest men, the scorpions, and over ten thousand species of spiders all with four pairs of walking legs.

The familiar horseshoe or king crab, Limulus, among the largest of arthropods, in length up to 50 cm. is the only surviving relative of the Paleozoic trilobites, which, in their day, dominated the sea. The newly-hatched limulus is strikingly like a trilobite; and yet, the limulus is clearly a much modified spider.

The Limulus has, moreover, a further interest, in that it also resembles, superficially, certain of the Paleozoic ostracoderms, a group which, it is maintained by Patten and Gaskell, contains the long-sought ancestor of all the vertebrates. Limulus belongs to the order Xiphosura (Merosomata). The Eurypterids are a closely related group of extinct paleozoic arachnids of large size.

Class Tracheata

In addition to the insects, all of which as adults have three pairs of walking legs, the group contains many different primitive forms which link the arthropods to the annelids. Of these forms, the most primitive is the genus Peripatus, with fourteen to forty-three pairs of legs, and so strange a body that it has been taken both for a mollusc and for a worm. The familiar centipedes and myriapods have from a dozen to nearly two
hundred body segments, most of them nearly alike, and most bearing
one or two pairs of legs. The common myriapods, an inch or so in length,
are popularly supposed to be worms.

The insects fairly rival the vertebrates as the dominant group in the
modern world. No vertebrate except man has carried social organization
nearly so far. No vertebrate groups and few invertebrates at all approach
the insects in the number of individuals in a single species. In addition,
the number of species is enormous. In North America alone, there are
seven thousand named species of butterflies and moths, ten thousand
beetles, and nearly as many flies. Possibly, in the entire world, known
and unknown species together may number as many as a million.

Fortunately, the individual insect is small. The largest known are a
beetle six inches long, and a grasshopper with a wing spread of ten inches.
But there are fossil dragonflies with a wing spread of two feet. From
these sizes, the insects run down to tiny parasitic creatures that live out
their life-cycle inside the speck-like egg of the coddling moth.

We shall examine later the assumption that the two dominant groups,
the insects and the vertebrates, one of which contains the smallest of
highly organized metazoa and the other the largest, are genetically
related to one another.

Phylum 12. CHORDATA

The chordates are animals which, at least early in life, have a sup-
porting rod, the notochord or chorda dorsalis, between the alimentary
canal and the central nervous system. In higher chordates the notochord
is replaced during ontogenesis by a cartilaginous or bony vertebral
column. All have a dorsal tubular nervous system. The heart is ventral,
and the pharynx has functional or embryonic gill slits. Most chordates
are metameric in structure, although the metamerism may become greatly
obscured in the adult. Segmental excretory organs are generally present.

Nearly 50,000 species are known.
Four sub-phyla are included in the phylum.

Sub-Phylum Hemichorda (Enteropneusta)

The hemichordates or enteropneusta hold a somewhat uncertain
position in the animal kingdom. Morphologists are by no means agreed
that their closest affinities are with the chordates. Some associate them
with the annelids, while the resemblance of their larval stage to that of
echinoderms leads others to place them near that group. Their inclusion
among the chordates rests on their possession of pharyngeal gill-slits,
eteric coelomic pouches, a notochord-like diverticulum of the fore-gut in
the pre-oral lobe, and upon the relations of the blood vessels and nerves. Segmental excretory organs are, however, absent.

There are possibly 50 species.

**Balanoglossus**, the best-known genus, may be taken as representative. The body of balanoglossus is worm-like, and is divided into five regions, proboscis, collar, gill region, “liver” region, and intestinal region. The proboscis is a hollow muscular organ with an opening, a pore, on the left dorsal side of the neck. The mouth lies on the ventral side between the proboscis and the collar. The collar, like the proboscis, contains a division of the coelom, which opens to the exterior by a pair of pores near the mid-dorsal line. Like the proboscis, the collar also is muscular, and used by the organism as a means of burrowing in the sand where it lives.

The pharynx is divided into a dorsal portion that contains the numerous gill-apertures and a ventral portion which functions as the digestive passage of the pharynx. Posterior to the pharynx, the body contains a series of gonadic sacs, each of which has a pore-like opening to the exterior. The sexes are separate.

In the so-called liver region, the intestine shows a series of paired diverticula, each of which produces a corresponding bulging of the relatively thin body-wall. These diverticula are glandular and supposed to have a digestive function, hence their name. Behind the liver-region, the intestine passes without convolution directly to the posteriorly situated anus. The circulatory system resembles that of annelids, but is supplemented by a lacunar system of lymph spaces. (Fig. 532)

The nervous system consists of dorsal and ventral nerve strands containing occasional giant nerve cells. There are no special sense organs. The so-called notochord is a diverticulum of the intestine which extends with a narrow lumen into the proboscis from a point just behind the mouth.

The larva of Balanoglossus, known as Tornaria, shows rather striking resemblances to the larva of echinoderms. As in echinoderms, the blastopore becomes the anus. The sub-phylum, therefore, is included in the group of Deuterostomia.

Cephalodiscus and Rhabdopleura are genera which show resemblances to Balanoglossus but which have a U-shaped alimentary canal. Rhabdopleura is without gill apertures. (Fig. 536)
Sub-Phylum Urochorda (Tunicata)

The urochordates, the tunicates or sea-squirts, are so named because the notochord, absent in the sessile adult, is always limited to the tail region. Another character common to the group is the presence of a tunicin mantle which is secreted by the skin. Tunicin is a chemical substance that resembles cellulose. A coelom is sometimes present, but is limited to the region of the ventral heart. Nephridia or coelomoducts are wanting. The body is unsegmented, and the alimentary canal is bent on itself so that the anus lies near the mouth. The pharynx is perforated by gill-slits, the number of which varies greatly in the different species. The nervous system consists of a nerve ganglion dorsal to the pharynx, from which nerves extend to the various organs. In some forms both sexual and asexual methods of reproduction occur. Individuals however, are usually hermaphroditic. Development generally involves metamorphosis. The sexually-produced tailed larva bears certain striking resemblances to the larva of amphioxus.

Some systematists recognize 1400 species.

Ciona is a sessile tunicate, three or four inches in length, which is attached by tunicin stolons to its substratum. A tunicin test or tunic, which is secreted by the skin, encloses the entire animal as a sac. Beneath the test and loosely connected with it, except in the region of the two apertures of the body, lies the body-wall or mantle. This consists of an
external simple epithelial ectoderm, and beneath this, connective tissue containing a network of muscle fibers which are more abundant in the region of the two apertures of the body, which they serve to close and open.

Of the two external apertures, the more ventral is the inhalent or oral siphon and the other the exhalent or atrial siphon. The former leads directly to the mouth, which is surrounded by a circle of tentacles. The mouth leads into a greatly enlarged pharynx, which is perforated by numerous gill-slits or stigmata. The action of the cilia on the bars of these slits serves to maintain a current of water from the pharynx into the surrounding peribranchial or atrial cavity. Such relations resemble those of similar organs in amphioxus. In the floor of the pharynx extends a longitudinal groove, the endostyle, which morphologists generally homologize with the thyroid gland of vertebrates. A somewhat similar groove extends also along the dorsal side of the pharynx. The alimentary canal consists of a short esophagus, a spherical stomach, and an intestine which leads to an anus situated well forward in the atrial chamber.

The heart lies ventral to the esophagus in the pericardial chamber. There are no closed blood vessels, but the blood is pumped from the heart forward to the pharynx in lacunar spaces the relations of which resemble those of the afferent branchial vessels of vertebrates. The reproductive organs lie in the loop of the intestine, posterior to the stomach. Their ducts extend forward and open into the atrial cavity near the anus. The gonads are hermaphroditic.

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Fig. 13.—Diagrams of stages in the metamorphosis of a urochordate larva. When the larva settles down and becomes fixed by its adhesive papillae, the tail is lost and the notochord disappears. Thus the chordate characters which are so evident in the larva are partly lost in the mature organism. (Redrawn from Korschelt and Heider, after Seeliger.)
The nervous system consists of a ganglion or brain, which lies in the body-wall between the two apertures of the body. Ventral to the brain, is a neural gland which has been compared with the neural part of the hypophysis of vertebrates. The unpaired eye and static organ contained in the brain vesicle of the larva degenerate in the metamorphosis.

Ciona during its ontogenesis, undergoes a striking metamorphosis, which indicates that the animal is a degenerate descendant of a primitive branch of the chordate tree.

Of the four orders of Urochordates the **Larvacea** are of special interest since they develop without metamorphosis, and hence, show no sign of degeneration. Their caudal appendage contains a notochord and spinal cord. That they lie close to the main line of vertebrate ancestry seems not unlikely.

**Sub-Phylum Cephalochorda (Acrania)**

The cephalochordates are those chordates in which the notochord occurs not only in the head, as in hemichorda, or in the tail, as in the urochorda, but throughout the entire length of the body. The group is sometimes called the acrania because, as the name suggests, a brain case is lacking. Metamerism is strikingly manifested in the muscles and nerves, which form an unbroken series from the tip of the snout to the tip of the tail. Segmental protonephridia are metamerically arranged, but are limited to the gill region. As in urochordates, the gills open into a peribranchial cavity. Development involves metamorphosis. (Fig. 539)

There are possibly 25 species.

**AMPHIOXUS.** The lancelet, amphioxus, the characteristic genus of the group and the so-called connecting link between vertebrates and invertebrates, interests morphologists because of its resemblance to the hypothetical ancestor of vertebrates. If the amphioxus had not been discovered, it must have been invented for theoretical reasons. Its resemblance to the larva of cyclostomes is impressive.

The Amphioxus is a lance-shaped animal, not more than two inches long, with a laterally compressed body and a median caudal fin. Its external orifices are an anterior ventrally placed mouth, an anus to the left of the caudal fin, and an **atriopore** somewhat behind the middle of the body. The atrial chamber which surrounds the elongated pharynx is formed by the union of paired lateral folds which meet in the mid-ventral line of the body. Such a structure seems to be an adaptation to the sand-burrowing habit of the adult animal. The atrial cavity ends blindly in front, and opens externally by the atriope just behind the pharynx. In the region of the pharynx, a pair of ventro-lateral **metapleural folds** extend as far back as the atriope.
The body is covered by a thin external cuticula secreted by the simple epithelial epidermis. Beneath the skin and visible through it, are sixty pairs of myotomes which alternate with one another along the two sides of the body. As in the vertebrates generally, these myotomes are greatly thickened along the dorsal side of the body. Each myotome is V-shaped with the apex of the V pointed forward.

The mouth, surrounded by a circle of tentacles, leads directly into the elongated pharynx, the walls of which are perforated by numerous gill-slits. A ciliated groove, which is similar in function and in relations with the endostyle of urochords, extends the entire length of the pharynx. Opposite it, in the roof of the pharynx, is a somewhat similar epipharyngeal groove. The liver is a hollow tubular sac, which opens into the floor of the intestine just behind the pharynx and extends forward to the left below the pharynx. The intestine is straight.

The coelom, considerably reduced in size in the region of the pharynx, extends posteriorly to the region of the anus. Ninety pairs of nephridia, limited to the gill-region, open into the atrial cavity. The solenocytes attached to the nephridia are specialized excretory cells which strikingly resemble those of annelids. Nephrostomes are absent. (Fig. 331)

Sexes are separate. Two dozen or more gonadic sacs surrounded by the peritoneum project into the atrial cavity. Except for the absence of a heart, the circulatory system resembles that of fishes. The blood contains few blood corpuscles.

The nervous system, as in vertebrates, is tubular and dorsal. The brain is a simple vesicle, which may possibly be compared with the forebrain vesicle of vertebrates. The nerves are of two kinds, dorsal (sensory and motor) and ventral (motor). The former pass directly to
the skin and to visceral muscles by way of the myocommata. Dorsal and ventral nerves do not unite. Sympathetic cells and fibers are not segregated to form a sympathetic system.

Sense organs comparable with those of vertebrates are wanting. A median dorsal pit at the anterior end of the brain is mistakenly spoken of as the olfactory pit. A pigment spot on the brain is likewise somewhat uncritically called the cerebral eye. Amphioxus is, however, very sensitive to light. There is no ear.

Sub-Phylum Vertebrata (Craniota)

The vertebrates or craniotes are chordates with a vertebral column and a brain-case. The evolution and perfection of a light and strong endoskeleton has been an important factor in making the vertebrates masters of the world. Exoskeletal structures also appear, as among the invertebrates, but only exceptionally are heavy enough to interfere with the activity of the animal. A many-layered epidermis with various appendages enables the vertebrates to withstand successfully the vicissitudes of weather met by land animals. In correlation with their activity, senses multiply and become acute and the brain is much enlarged. The original metamerism characteristic of lower vertebrates becomes much
obscured in the higher. The heart is ventral and may be either two, three, or four-chambered.

Some 25,000 species are known.

Vertebrates are divided into seven classes.

Class Cyclostomata

Cyclostomes are the round-mouthed lamprey eels and hag-fishes. They have a persistent notochord, lack a biting jaw, and the beginnings of vertebrae appear in the form of cartilaginous neural arches. In the genus Bdellostoma there are often as many as fifteen pairs of gill-slits.

Fig. 16.—Three characteristic genera of Cyclostomes—Bdellostoma, Myxine, and Petromyzon. That they are the most primitive vertebrates is shown in many traits, such as a permanent notochord, absence of paired appendages and jaws, etc. (Redrawn after Dean.)

There are no scales in the skin, and the teeth are horny. Some species are hermaphroditic. Paired appendages are absent.

The lamprey, Petromyzon, is a familiar genus which undergoes metamorphosis during its development. Its larval stage is known as ammocoetes. Other genera are Myxine and Bdellostoma.

Class Ostracodermi

The ostracoderms are fossil forms which, as Stensiö and others have shown, resemble cyclostomes in some striking respects. Unlike the latter, however, their heads were covered by heavy bony armor. Like the lampreys they lacked jaws and paired appendages. As in cyclostomes the nasal aperture was median and dorsal in position. It has been asserted but not demonstrated that the ostracoderms are the ancestors of cartilaginous fishes, which are consequently assumed to have lost their heavy body exoskeletons. Most morphologists, however, consider ostracoderms
rather highly specialized types and not primitive ancestral forms. Cephalaspis and Pterichthys are characteristic genera.

Fig. 17.—Cephalaspis, an Ostracoderm, appears to have affinities with cyclostomes and has been thought by W. Patten to connect vertebrates with arachnids.

Fig. 18.—Types of three sub-classes of fishes—Heptanchus, an Elasmobranch; Polypterus, a Crossopterygian Ganoid; and Scomberomorus, a Teleost. (Redrawn after Dean.)

Class Pisces

Fishes are vertebrates with usually scaly skins, permanent gills, and paired fins. The heart is two- or three-chambered. The skeletons may be cartilaginous or bony. Gill-apertures number four to seven pairs.
Dorsal and ventral spinal nerves join to form mixed trunks. Sympathetic ganglia are differentiated. The liver has at least two lobes.

Of special interest are the orders of fishes which are believed to be in the line of ancestry of land animals. Cartilaginous forms like the Elasmobranchs (sharks and skates) were the common stock from which the remaining orders of fishes were probably evolved.

The extinct Crossopterygians or lobe-finned fishes, which make their first appearance in the Devonian, were air-breathers and possibly the direct ancestors of land animals. Arthrodires are fossil forms possibly related to the modern lung-fishes or Dipnoi. The Dipnoi have either one or two lungs and are in many ways transitional between fishes and amphibia. Ganoids and Teleosts are "ray-finned" forms which include the greater number of living species of fish.

Class Amphibia

Amphibians bridge the gap between land and water vertebrates, since some, like fishes, are lungless, and when lungs are present, either permanent or temporary gills occur. Except in some fossil forms, scales are lacking in the skin. The olfactory pits communicate with the mouth cavity by means of narial passages. The paired appendages are toed. The heart is three-chambered. A postcaval vein is present. The embryo develops without an amnion.

Amphibia are subdivided into urodeles or tailed forms, the newts and salamanders, anura or tailless forms, the frogs and toads, and the gymnophiona or limbless types. Besides these living orders of amphibia, the fossor order stegocephala is important, since they appear to be the direct ancestors of reptiles.

Fishes and Amphibia have been grouped together as Ichthyopsida in contrast with Sauropsida which includes reptiles and birds. The embryos of the latter are protected by fetal membranes, while those of the former are without them.

Class Reptilia

Reptiles are horny-scaled vertebrates which breathe by lungs, the embryos of which develop in a liquid-filled sac, the amnion. The skull
articulates with the atlas vertebra by means of a single occipital condyle. Arterial and venous blood are mixed in the dorsal aorta.

Living reptiles are divided into Rhynchocephalia, Lacertilia, Ophidia, Chelonia, and Crocodilia. Among fossil orders, the Theromorpha are important, since, especially in their dentition, they resemble mammals, and the Dinosaurs because they are the ancestors of the Birds.

Class Aves

Birds differ from reptiles in having both feathers and scales, and in having the anterior appendages modified as wings. The heart is four-chambered, and the single aortic arch on the right. Teeth are wanting in modern forms. The body temperature is higher than in other animals.

Two large divisions are recognized, the flying birds or Carinatae with a keeled sternum, and the running birds or Ratitae which have no keel on the sternum.

Class Mammalia

Mammals are vertebrates with hairs and mammary glands. A few, the monotremes, lay eggs, but all the rest bring forth their young well developed. Mammals have a pair of occipital condyles, a muscular diaphragm, and a chain of three ear bones. The heart is four-chambered, and the aortic arch is on the left. The jaw articulates between the dentary and squamosal bones.

Two major divisions are recognized, placentals, the embryos of which are attached to the mother by a vascular placenta; and the non-placentals, the monotremes and marsupials, most of which lack a placenta.

Sub-Class Monotremes (Prototheria)

The monotremes or ornithodelphia are egg-laying mammals with a cloaca. Teats are lacking.
Ornithorhynchus, the duck-bill of Australia, is the best-known genus; and there are two species of the spiny anteater, echidna. There seem to be no more than a half-dozen species surviving for the entire sub-class.

**Sub-Class Marsupials**

The marsupials or didelphia give birth to their young in a most immature state and nourish them for some time in an external marsupial pouch situated on the ventral side of the body of the female. The brain has no corpus callosum. A loose allantoic placenta occurs in some. Dasyurus has a yolk-sac placenta.

Opossum and kangaroo are well-known examples. All the indigenous mammals of Australia are non-placental.

**Sub-Class Placentalia**

The placentals or monodelphia have a placenta, a corpus callosum in the brain, and no marsupial bones. Urogenital and digestive outlets are separated.

Placentals are subdivided into at least ten living orders.

**Order 1. Insectivora.** The insectivores include shrews, moles, and hedgehogs. They are flat-footed and five-toed, and their dentition is also unspecialized, so that they are apparently nearest of surviving forms to the original placental.

**Order 2. Xenarthra.** The xenartha include part of the group formerly included in the edentates such as the armadillos, sloths and
anteaters. The teeth of adults are either absent or lack enamel and roots. Dentition is limited to a single set.

ORDER 3. RODENTIA. The rodents are gnawing animals, such as rats, rabbits, squirrels, guinea pigs, beavers, porcupines, gophers. Canine teeth are absent, and the incisor teeth in both jaws grow continuously throughout life. The cecum is very large.

ORDER 4. CARNIVORA. The carnivora include the fossil creodonts, the cats, dogs, weasels, bears, raccoons, and seals. Each foot has four or five toes. The canine teeth are sharp and elongated. The clavicle is reduced or absent.

![Lemur Catta](lemur-catta.png)

**Fig. 24.—Lemur, a primitive Primate.** (Redrawn after Shipley and McBride.)

ORDER 5. ARTIODACTYLA. Artiodactyls are such hoofed forms as cattle, deer, swine, sheep, goats, and camels, llamas, hippopotamuses, and giraffes which have an even number of toes on each foot. The third and fourth toes are larger, and the second and fifth reduced or absent. The stomach is complex and the cecum reduced.

ORDER 6. PERISSODACTYLA. The perissodactyls are hoofed forms usually with an uneven number of hoofs, such as horse, ass, zebra, tapir, and the rhinoceros. The third toe is the largest and the only one functional in the horse. The enamel of the back-teeth is complexly folded.

ORDER 7. SUBUNGULATA. Hoofed forms usually with plantigrade feet. Subungulates are the elephants and mastodons, and the hyrax or cony. The proboscidians such as the elephants have five toes on which they walk. Their testes do not descend into a scrotum. Sirenians (Manatee and Dugong) are a suborder of this group.

ORDER 8. CETACEA. The cetaceans include whales, porpoises and dolphins. They are aquatic mammals with fish-like bodies. Hairs and
pelvic extremities are absent in the adult. There are two abdominal teats. Teeth may be replaced by whalebone.

**Order 9. Chiroptera.** Chiroptera are the bats and flying foxes. Their anterior limbs are modified as wings, the fingers are joined by a web, and the sternum has a keel.

**Order 10. Primates.** The primates include lemurs, marmosets, monkeys, baboons, apes, and men. They are mostly arboreal in habit.

![Young Chimpanzee](Image)

**Fig. 25.**—Young Chimpanzee, a type of Anthropoid. (From photograph by Fred Johnson.)

Nearly all have five digits with flattened nails, and in all except the lowest forms the thumb is freely opposable to the fingers. Mammary glands are usually a single pair and thoracic.

Primates are divided into two sub-orders.

**Sub-order Lemuroidea.** The lemuroids include the lemurs and tarsiers. They are arboreal and nocturnal, small and not especially monkey-like. Typical lemurs have a claw on the second digit of the hind-foot. Thumb and great toe are not completely opposable to the other digits. The uterus is two-horned.
Sub-order **Anthropoidea.** Anthropoids include the remainder of the primates. Hands and feet are differentiated, and either the thumb or the great toe is opposable. Finger and toe-nails are flat, except in the marmosets which have claws.

Three chief sections of anthropoids are recognized:

**Platyrrhina.** The South American monkeys, with broad nasal septum, three premolar teeth in each half-jaw (except the marmosets which, like the Old World monkeys, have two), and a climbing foot.

**Catarrhina.** The Old World monkeys and the great apes, with a narrow nasal septum, two premolar teeth, and a climbing foot.

**Bimana.** Also with narrow nasal septum and two premolars, but with the great toe non-opposable and a walking foot.

### CLASSIFICATION OF ANIMALS—SUMMARY

#### ANIMAL PHYLA

1. **Protozoa.** Unicellular. Reproduce by fission.

**Metazoa,** multicellular.


Classes; Crustacea, Arachnida, Onychophora, Myriapoda, Insecta.

12. **Chordata.** Notochord. Dorsal tubular nervous system.

#### SUB-PHYLA OF CHORDATES

**Hemichorda.** Notochord limited to oral and pre-oral region. Worm-like. Body in three primary divisions. **Balanoglossus.**
UROCHORDA. Notochord limited to tail-region. Body-wall covered with cellulose sac. Hemichorda and urochorda together are often called protochordates. Appendicularia. Ascidia.


VERTEBRATA. Chordates with brain case and vertebrae. Squalus.

CLASSES OF VERTEBRATES (Craniota)


2. Ostracodermi, fossil monorhine fishes related to the cyclostomes.

3. Pisces. With paired appendages and movable lower jaw. Skin scaly. Permanent gills. Fishes are subdivided into five sub-classes:
   Elasmobranchii, with naked gills. Skeleton cartilaginous. Sharks, skates, and rays.
   Crossopterygii, fossil forms related to the ganoids.
   Ganoidei, with operculum. Cartilage skeleton largely replaced by bone. Garpike, sturgeon.
   Teleostei, with operculum and bony skeleton. Common bony fishes.
   Dipnoi, with gills and one or two lungs.
   All following are Tetrapods.

4. Amphibia. Living forms are without scales and usually have lungs. Toed appendages instead of fins.
   The Stegocephala are a group of fossil amphibia.
   Fishes and Amphibia grouped together as Ichthyopsida.
   All to this point are Anamnia. All that follow are Amniota, having the embryo protected by an amnion.

5. Reptilia. Adults scaly. Lungs only. Aortic arch on both sides. The Theromorpha are fossil reptiles.

   Reptiles and birds grouped together as Sauropsida.

7. Mammalia. With mammary glands and hair.

   Sub-Classes of Mammals


   Orders of Placentalia

1. Insectivora. Insect eaters.
2. Xenarthra. Toothless or teeth without enamel.
5. Artiodactyla. Generally even number of hoofs.
7. Subungulata. Proboscideans, hyrax, and sirenians.
    Anthropoidea. Thumb or great toe, except in New World monkeys, opposable.

Sub-Orders of Anthropoidea


Bimana. Great toe not opposable.

Species and Genera of Bimana

Pithecanthropus erectus, the Java man.
Eoanthropus Dawsoni, the Sussex man.
Sinanthropus Pekinensis, Pekin man.
Homo Neanderthalensis, Neanderthal man.
Homo Heidelbergensis, the Heidelberg man.
Homo Rhodesiensis, the Rhodesian man.
Homo sapiens, Cro-Magnon and modern man. (Negro, Mongolian, etc.)
<table>
<thead>
<tr>
<th>Eras</th>
<th>Periods</th>
<th>Years (Barrell)</th>
<th>Characteristic Organisms</th>
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</thead>
<tbody>
<tr>
<td>Cenozoic</td>
<td>Recent</td>
<td>1,000,000 to 1,500,000</td>
<td>Modern races of men. Recent plants and animals.</td>
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<td></td>
<td>Tertiary</td>
<td>95,000,000 to 115,000,000</td>
<td>“Age of mammals.” Lemuroids and insectivores appear. First placentals.</td>
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<td></td>
<td>Cretaceous</td>
<td>116,000,000 to 136,000,000</td>
<td>Mammals mostly marsupials. Reptiles highly specialized.</td>
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<tr>
<td></td>
<td>C o m a n -</td>
<td></td>
<td>Bony fishes abundant. Flowering plants appear.</td>
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<td>n c h e a n</td>
<td>120,000,000 to 150,000,000</td>
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<td>Jurassic</td>
<td>155,000,000 to 195,000,000</td>
<td>Diverse reptiles. Ganoid fishes. First birds.</td>
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<td></td>
<td>Triassic</td>
<td>100,000,000 to 240,000,000</td>
<td>Crocodiles and Dinosaurs. Reptiles dominant. First mammals.</td>
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<td>Permian</td>
<td>215,000,000 to 280,000,000</td>
<td>Mammal-like reptiles. Trilobites disappear.</td>
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<td>Pennsylvanian</td>
<td>250,000,000 to 330,000,000</td>
<td>Primitive amphibia and reptiles. Coniferous plants.</td>
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<td>Mississippian</td>
<td>300,000,000 to 370,000,000</td>
<td>Earliest amphibian fossils. Horse-tails and club-mosses.</td>
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<td>Paleozoic</td>
<td>Devonian</td>
<td>360,000,000 to 420,000,000</td>
<td>Amphibian foot-prints. Lungfishes. Earliest land plants.</td>
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<td>Silurian</td>
<td>390,000,000 to 460,000,000</td>
<td>Ostracoderm (armored) fishes. Elasmo-branchs. Land plants begin.</td>
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<tr>
<td></td>
<td>Ordovician</td>
<td>480,000,000 to 590,000,000</td>
<td>Vertebrates appear. First fishes. First insects.</td>
</tr>
<tr>
<td></td>
<td>Cambrian</td>
<td>550,000,000 to 700,000,000</td>
<td>Invertebrate phyla abundant. First trilobites.</td>
</tr>
</tbody>
</table>
Anatomy deals with the structure of the organs of an animal. Structure is described primarily in terms of form. Form is extension in space. The animal, however, exists not only in space but in time. The animal's anatomy is more than the form which it possesses at a particular instant. It is form which passes through a series of definite and characteristic changes beginning with the development of an egg and ending at death. Therefore a description of the anatomy of an adult animal is to be regarded as merely a cross section of its whole anatomy. Embryology deals with the life history during that early period in which the form of the organism is changing rapidly, progressing from the comparative simplicity of the egg to the structural complexity of the adult.

In the anatomy of an adult vertebrate are found many things which remain unintelligible so long as attention is confined to the adult stage of the animal. Why does the chief artery emerging from the heart turn to the right in a bird, but to the left in a mammal? Why are the major blood vessels in the body of mammals, even among individuals of the same species, highly variable in their arrangement? Why does the human diaphragm receive its nerve supply from the neck region of the spinal cord rather than from the neighboring trunk region of the cord? Why does a male dogfish have an apparently useless structure which looks like the anterior portion of the oviduct of the female? These questions and many more of the same sort are answered by embryology. Therefore it is essential that the study of the anatomy of any organ should include the embryonic history of the organ.

**DIFFERENTIATION OF SEXES**

Reproduction in the vertebrates is always sexual. That is, it always involves the differentiation of gonads of two types; the ovary which produces eggs or ova, and the testis which produces sperm or spermatozoa. However, in some members of the Urochorda (tunicates), which are presumably remote chordate allies of the vertebrates, occurs an alternation of sexually produced and asexually produced generations. The sexual individual is hermaphrodite, that is, it possesses both ovary and testis, but the eggs are usually, if not always, fertilized by sperm from another individual. The fertilized egg develops into an adult which, however, is devoid of gonads. Then this asexual individual produces
external bud-like outgrowths each of which develops into a sexual and hermaphrodite adult.

In the very great majority of vertebrates the individual animal is differentiated as either a male or a female—the dioecious condition. Among the lower vertebrates, however, there are a few animals which are normally monoecious or hermaphrodite. The eel-like hag, Myxine, of the class Cyclostomata, has a much elongated median gonad whose anterior region may become a functional ovary while the posterior region remains sexually inactive, or the anterior part may be inactive while the posterior region differentiates as a testis. Self-fertilization is thus impossible. That both regions become functional, but at different times, in the life of the individual hag is not certainly known. It has been claimed that the young hag is functionally male, but later in life becomes female. Among the bony fishes (Teleostei) various hermaphrodite conditions have been described. Serranus, a genus of perch, includes fishes which are normally monoecious and self-fertilizing. Chrysoophrys aurata exhibits "successive hermaphroditism," producing eggs and sperm alternately.

Among fishes which are normally dioecious, the hermaphrodite condition may sometimes occur as an individual variation or abnormality. Such cases have been reported for several fishes, including such common ones as the cod, herring and mackerel. So far as known, no vertebrate above the fishes is regularly and normally hermaphrodite, but many abnormal cases have been reported, especially in amphibians, in which germ cells of both sexes have been found in one individual.

**THE GERMINAL BODIES**

The production of a new individual vertebrate animal is the outcome of the joint activity of a male reproductive body, the spermatozoon, and a female reproductive body, the egg or ovum.

The spermatozoa are derived from cells in the walls of the delicate tubules which are the essential part of the testis (Fig. 27). The ova come from primordial germ cells contained within the tissues of the usually solid ovary (Fig. 28).

The spermatozoön and the ovum each results from the differentiation of a single cell of the gonad. In many respects their differentiation proceeds in quite opposite directions. Nevertheless each retains the essential features of organization of a single cell.

In the course of the differentiation of the spermatozoön (Fig. 29) the cytoplasm (extra-nuclear protoplasm) becomes greatly reduced in volume, very little remaining beyond what is required for the formation of a locomotor apparatus which consists usually of a long filamentous "tail." The "head" of the sperm cell consists of the compacted chromatin
material of the nucleus. The "ripe" sperm cell is essentially a motile nucleus.

**Fig. 27.**—Cross sections of testis tubules of a mouse. *BV*, blood vessel; *F*, fat granules; *IC*, interstitial cells; *S^1*, spermatogonia; *S^2*, spermatocytes; *S^3*, spermatids; *SP*, spermatozoa; *ST*, sustentacular cells. ×360. (Redrawn from Bremer, Text-book of Histology.)

**Fig. 28.**—Section through cortical region of the ovary of a mouse showing young (primary) ovarian follicles and older (vesicular) follicles. ×76.

The egg, in contrast to the spermatozoon, not only retains its original cytoplasmic volume but, while still in the ovary, passes through a long
growth period, the result of which may be a very greatly increased body of cytoplasm (Fig. 38). The volume of the extra-nuclear part of the egg is further more or less increased by the acquisition of special food materials, derived from ovarian sources, which are deposited in the cytoplasm in the form of characteristic coarse granules or globules known collectively as the deutoplasm or yolk of the egg.

Another point of contrast between the ovum and spermatozoon lies in the fact that the latter, consistently with its motile nature, remains a naked cell while the ovum may become invested by membranes or envelopes of various sorts, either protective or nutritive. An egg that possesses a bulky yolk-laden cytoplasm is covered by a delicate but tough vitelline membrane (Fig. 38). The bird’s egg (Fig. 32) is protected by a hard calcareous shell underlaid by a tough fibrous shell-membrane. Nutritive substance also, such as the albumen or “white” of the egg of the common fowl, may be deposited about the egg.

The spermatozoa of the various vertebrates are uniformly minute motile bodies whose differences in size and structure are insignificant when contrasted with the differences exhibited by various ova. Eggs differ most remarkably as to the amount of yolk carried by the cytoplasm and as to their outer investments. The microscopic egg of a mammal and the gigantic ostrich egg encased in its hard shell would hardly be suspected of being essentially similar objects.

**Eggs of Fishes**

Even within the group of fishes the eggs differ widely. In the great majority of fishes the eggs are relatively small (less than 5 mm. in diameter), contain a correspondingly small amount of yolk, and are invested...
by only thin and soft protective membranes. The eggs of sharks and skates, which contain enormous yolk masses, rival in size the eggs of birds, and are enclosed in cases or shells which are secreted by the wall of the anterior portion of the oviduct. These shells consist of a substance resembling chitin or horn. In viviparous sharks and skates the shell is very thin and soft. In those which are oviparous the case (Fig. 30) becomes thick and stiff and usually acquires a curious flattened elongated quadrangular form, often with long curling tendrils extending from each corner. These tendrils serve to anchor the egg by becoming entangled with seaweed or other objects. In some sharks the egg-cases are of even more complicated form.

**Eggs of Amphibians**

The eggs of amphibians, which always contain a considerable amount of yolk, are larger than the eggs of many fishes, but smaller than the average for reptiles and birds. Eggs of various species of frog range in diameter from 1.5 to 3 mm. Eggs of the large salamanders, *Necturus* and *Cryptobranchus* (the hellbender), range between five and six millimeters in diameter. The amphibian oviduct deposits upon the egg a layer of gelatinous substance (Fig. 31) which, after the egg has been extruded into the water, swells to form a thick jelly-like envelope. In some amphibians (e.g., *Cryptobranchus*, most toads) toughened strands of the jelly pass from egg to egg, thus tying many eggs together to form a long string (Fig. 31C).

**Eggs of Reptiles and Birds**

In accord with other evidences of the close relationship of reptiles and birds, the eggs, as well as the methods of development, of the animals of these two groups are closely similar. The eggs are large both absolutely and in proportion to the size of the animal. There is
some correlation between the size of the egg and the size of the animal. Thus, among birds, the humming-bird's egg is smallest, and the largest were produced by certain extinct relatives of the ostriches, the moas of New Zealand and Æpyornis of Madagascar.

The great size of the eggs of reptiles and birds (Fig. 32) is due mainly to the enormous amount of yolk present. In the comparatively small eggs of amphibians (Fig. 31) and most fishes, the yolk substance is dis-

persed throughout the cytoplasm, but there is a tendency—the more marked the greater the quantity of yolk—for the yolk granules to become aggregated at one side of the egg. Thus, a more or less definite polarity of the egg results. The proportion of yolk to cytoplasm is least at the
animal pole and increases to a maximum at the opposite vegetal pole (Fig. 38). The nucleus lies in the animal hemisphere.

In the eggs of reptiles and birds the quantity of yolk is so enormously greater than that of the protoplasm that the dispersion of the yolk granules throughout the protoplasm would be comparable to dispersing a quart of sand grains in a single drop of water. Accordingly the polarizing of these eggs reaches its maximum in that the protoplasm is all aggregated at one spot on the surface of the egg, thus marking the animal pole, while the remainder of the egg is yolk devoid of protoplasm. The localized protoplasm constitutes the so-called germ disc (Fig. 40) which usually appears as a small white fleck on the surface of the large yellow yolk mass. Before the egg is fertilized the germ disc contains a single nucleus, the original egg nucleus.

Such a large ovum, consisting, for the most part, of loosely coherent yolk particles, is necessarily invested by a tough vitelline membrane. External to the vitelline membrane are various additional envelopes. Birds and most reptiles, the lizards and snakes being the exceptions, have a thick layer of albumen (the “white” of a hen’s egg) which doubtless affords the egg some mechanical protection and, in the later stages of development, may be utilized for the nutrition of the young animal. The outermost shell consists of an organic matrix more or less impregnated with salts of calcium. In most reptiles the shell is of a somewhat flexible or leathery texture. In crocodiles and alligators and in birds the shell is highly calcified and consequently hard and brittle. Against the inner surface of the shell lies a thin fibrous shell-membrane.

It should be appreciated that the object referred to in kitchen and market as an “egg” consists of the actual (in strict sense) egg or ovum, plus various extraneous substances and structures. The hen’s ovum, comparable to some small fish egg, is merely the yellow sphere commonly called the “yolk” of the “egg,” enclosed in its vitelline membrane.

**Eggs of Mammals**

In point of size and quantity of yolk, the eggs of birds lie at one extreme. The eggs of mammals, with two exceptions, lie at the other. The exceptions are the duck-bill (Ornithorhynchus) and the spiny anteater (Echidna) of the Australian region. These mammals, presumably of primitive type, exhibit many reptilian features, conspicuous among which is the method of reproduction. Their large eggs contain much yolk, are encased in a tough shell, and are very similar to the eggs of reptiles. With these exceptions, the eggs of mammals contain a minimum of yolk and are of practically microscopic dimensions (0.06 to 0.3 mm. in diameter). The egg (Fig. 33) is covered by a transparent membrane (zona pellucida)
external to which may be a cellular membrane (corona radiata), both contributed by the ovary.

**RELATIVE SIZE**

Comparison of sizes of eggs with little yolk and eggs with much yolk becomes more impressive if stated in terms of volume rather than diameter. The following data illustrate this:

<table>
<thead>
<tr>
<th>Egg of</th>
<th>Approximate diameter, mm</th>
<th>Relative volumes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphioxus</td>
<td>0.1</td>
<td>1</td>
</tr>
<tr>
<td>Some frogs</td>
<td>2.0</td>
<td>8,000</td>
</tr>
<tr>
<td>Domestic fowl (&quot;yolk&quot;)</td>
<td>30.0</td>
<td>27,000,000</td>
</tr>
</tbody>
</table>

The volume of an ostrich ovum would be hundreds of millions of times greater than that of a mouse egg whose diameter is about 0.06 mm.

The comparisons become more significant if every ovum, big or little, is to be regarded as structurally a single cell. There is, perhaps, a little room for question as to whether one of these immense yolk-laden ova, in its entirety, can be properly regarded as a cell. Such an ovum exhibits the extreme limit of that process of polarization (already well advanced in amphibians) which results from increase in the amount of egg yolk. Therefore, viewed with reference to its supposed evolutionary history, it is equivalent to an amphibian ovum which is unquestionably a cell. But, thinking of a cell as a dynamic protoplasmic unit, it is only the germ disc which is organized "living" protoplasm. In a physiological sense, it is only the germ disc which is a cell. The whole ovum, however, can be regarded as structurally analogous to a fat cell, a cell distended by a relatively enormous globule of fatty material.

But the spermatozoon is also essentially a cell. A rabbit spermatozoon, for example, with a "head" about 0.005 mm. long, possesses only an exceedingly small fraction of the volume of a mammal ovum. Therefore, to approach more closely the full range of cell size in the vertebrates, the
volume of the smallest spermatozoon should be compared to that of the ovum of a moa or Æpyornis.

It has been stated above that among birds there is some correlation between the size of the egg and the size of the bird. This is a necessary consequence of the fact that in all birds the yolk must provide the material needed to carry development up to the point of hatching, at which time the young birds have attained roughly corresponding stages in development and growth. When, however, animals of different classes and eggs of different types are brought into comparison, there appears a striking lack of any correlation between size of animal and size of egg. The eggs of some small salamanders are vastly larger than the eggs of some large fishes. From the reasonable assumption that the eggs of elephants and whales are of the typical mammalian sort, it follows that the egg of a humming-bird is tremendously larger than that of one of these gigantic mammals. Egg size is correlated primarily with the method of development. Correlation with body size appears only when the developmental history of the animals is similar.

**Fertilization**

The event which immediately initiates the development of a new individual is the "fertilization" of the egg by the spermatozoon. The motile sperm cell penetrates the egg and the sperm "head," a compact mass of nuclear substance (chromatin), becomes joined with the chromatin of the egg nucleus. In consequence of the so-called "maturation" process through which all germ cells pass, each mature ovum and spermatozoon contains only the "haploid" complex of chromosomes. Therefore the junction of the sperm chromatin and the egg chromatin provides the fertilized egg with a nucleus possessing the "diploid" complex of chromatin—that is, the full complement characteristic of the nuclei of all the body cells of the animal.

So far as known, the cytoplasmic part of the spermatozoon contributes to the functional ovum nothing except, possibly, a single centrosome. However that may be, it is certainly true that the fertilized egg, although it is the product of two cells, possesses the complete mechanism characteristic of a single cell, and it does not visibly possess anything more than that. Its yolk is something characteristic of eggs, but yolk is an inert food substance, not a mechanism. The fertilized egg contains no visible structures which would adequately account for its development into a large complex animal possessing the specific form and characteristics of the parent animals. In fact, as compared with such specialized cells as those of muscle and nervous tissue, the egg cell is strikingly devoid of visible special mechanism.
Developmental Potentialities

The description of the germinal bodies up to the completion of the fertilization process may very well give the impression that the motile spermatozoon is the active and essentially "animal" body while the relatively enormous egg with its burden of inert yolk is a passive and vegetative thing. It is true that, at first, the spermatozoon is the active and aggressive body, but its activity as an independent reproductive agent is very transitory, while the egg, as later events prove, is capable of becoming highly dynamic and continuing so during a long period of constructive development. In fact, the egg possesses this capacity quite independently of any specific action of the spermatozoon. It has been proved that the development of an unfertilized egg may be brought about by any one of a large number of physical and chemical means, such as mere pricking with a needle, or changing the osmotic pressure of the fluid external to the egg, or changing the chemical constitution of the external medium. This "artificial parthenogenesis" may result in the development of a perfectly characteristic adult animal. Its individual peculiarities, however, are only such as may have been derived from the female parent, since its male "parent" may have been a mere needle prick. In normal development the spermatozoon imparts the stimulus which initiates development and provides for inheritance from a male parent, but the egg is fully capable of producing a characteristic adult without the assistance of a spermatozoon.

Means of Exit

The sperm is usually conveyed by way of ducts which lead from the testis to the exterior, but in the cyclostome eels the sperm is discharged from the testis into the body cavity and finds exit by way of abdominal pores which pierce the body wall in the cloacal region. Also in some Teleostei the sperm passes from the testes into the body cavity whence it is discharged through genital pores. The sperm ducts are usually closely associated in one way or another with the duct system of the kidneys. (See Chapter xi.)

The ova are usually liberated from the surface of the solid ovary (Fig. 28) into the body cavity whence they pass into oviducts which lead to the exterior. In the cyclostome eels, however, there are no oviducts, and the ova, like the sperm, find exit by abdominal pores. In some bony fishes (Teleostei) the ovary is hollow, the eggs are liberated into its lumen and pass to the exterior by way of a duct which is an extension of the wall of the ovary. In other bony fishes (the salmon and others) there are no oviducts and the eggs are discharged from the body cavity through abdominal pores. In viviparous vertebrates the eggs develop usually
in an enlarged and more or less specialized region (uterus) of the oviduct, but in a few of the viviparous members of the Teleostei the young develop within an ovarian cavity.

OVIPARITY, VIVIPARITY, IMPREGNATION

The means whereby ovum and spermatozoon are brought together necessarily depends on whether the animal is oviparous or viviparous; also on whether or not the outer investments of the egg can be penetrated by the spermatozoon.

The great majority of fishes are oviparous and produce eggs whose investing membranes can be penetrated by spermatozoa. In such cases there is no copulation. The male discharges the sperm upon, or in the vicinity of, the eggs after they are extruded into the water—"external fertilization." Some oviparous fishes, however, produce eggs whose outer covering can not be penetrated by a spermatozoon. This is true of many skates and sharks. The tough thick egg-case is deposited on the ovum, after it leaves the ovary, by the shell gland or oviducal gland. This gland is a specialized anterior region of the oviduct. In these fishes "internal fertilization" is necessary. There is copulation and the spermatozoa must pass forward and effect fertilization before the egg has arrived in the shell gland, or at least before the deposition of the shell has proceeded to any great extent. After such internal fertilization, the egg may begin to develop and pass through the early stages before it is "laid." Therefore the thing which is "laid" is not, in strict sense, an egg but an early embryo.

Some sharks and skates and a few bony fishes (the guppy, Lebistes, for example) are viviparous and therefore effect internal fertilization.

Among Amphibia there is much diversity. In the great majority of the Anura (frogs and toads) fertilization is external. At present only a very few cases (certain African frogs) are known in which it is internal. In the tailed amphibians (Urodela) fertilization is internal but in most cases it is effected more or less indirectly by means of a spermatophore, a mass of sperm agglutinated together by a secretion from the cloacal glands of the male. The spermatophore may be inserted directly into the female cloaca but more often is attached externally near the cloaca or merely discharged and picked up later by activity of the female. In caecilians (Gymnophiona) fertilization is internal.

In all reptiles and birds the nature of the egg-shell is such as to necessitate copulation and internal fertilization. The substance of the shell is deposited upon the egg in the posterior uterine part of the oviduct. Such eggs as possess a layer of albumen acquire it from a more anterior glandular region of the oviduct. Therefore fertilization must take place before the egg arrives in the uterine part of the oviduct and presumably
before any albumen is deposited around the ovum. If fertilization has occurred, the “eggs” which are “laid” contain not ova but embryos at early stages of development.

Modern mammals, with two exceptions, are viviparous. The exceptions are Ornithorhynchus and Echidna, mammals of obviously primitive type and reptilian in many features. The large egg covered by a thick tough shell makes necessary internal fertilization, as in reptiles. All other mammals, by reason of their viviparity, require internal fertilization. The copulatory apparatus becomes most highly specialized in mammals.

**PROTECTION, NUTRITION, AND RESPIRATION, DURING DEVELOPMENT**

From the beginning of the development of the animal the building up of new protoplasm and the elaboration of it into the organized parts of the animal calls for food to serve as building material. The energy expended in the constructive processes of development is derived from the chemical breaking down and oxidation of organic materials. Therefore food and oxygen are requisite throughout development. The chance that the young animal will attain adulthood depends on the degree of immunity from unfavorable conditions and inimical agencies in the environment. A survey of the whole group of vertebrates reveals the most extraordinary diversity as regards provision for protection, nutrition and respiration during development. Comparing various vertebrate embryos at corresponding stages, the most striking differences are those which relate to protection, food and oxygen. The visible differences which identify one embryo as potentially a fish and another a mammal are insignificant in contrast to the spectacular difference occasioned by the elaborate but merely temporary placental structures of the mammal embryo.

**In Fishes.** In the majority of fishes the eggs, fertilized after they are discharged into the water, are exposed to the hazards of the environment. Mortality is high. The eggs of some fishes (cod, mackerel, haddock, flat-fishes and others) are of such low specific gravity that they float at or near the top of the water (“pelagic” eggs). Others (herring, salmon, trout, most fresh-water fishes, some shallow-water marine fishes) lie on the bottom (“demersal” eggs) until the young hatch. Pelagic eggs do not receive parental protection. Demersal eggs commonly have an investing membrane which is adhesive so that the eggs stick together in masses or may become attached to stones, shells, aquatic plants or other submerged objects.

Many fishes, especially those of fresh water, arrange nests of a simple sort. The eggs may be deposited in a hollow scooped out in gravel, sand or mud. The female salmon covers her eggs with gravel. An Australian cat-fish places the eggs in a hole dug out in the sand and then covers them with
REPRODUCTION

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stones. In many nest-building fishes the nest, after deposit of the eggs, is guarded for a time by one of the parents, usually the male. The eggs of the stickleback are placed in a rude nest which the male builds of weeds glued together by a substance secreted by the kidneys. After the eggs are laid the male stands guard over the nest. In the sea-horse (Hippocampus, Fig. 34) and the pipe-fish (Syngnathus) the male acts as nurse by carrying the developing eggs in a "brood pouch" situated on the ventral surface of the body or tail, an arrangement suggestive of the marsupial pouch of the female kangaroo. In some of the cat-fishes the eggs, during development, are carried in the mouth of one of the parents, usually the male.

Thick tough shells such as enclose the large eggs of oviparous sharks and skates must be highly protective. The curling tendrils (Fig. 30), which such egg-cases commonly possess doubtless serve to attach the egg in a favorable locality. In the somewhat shark-like marine fish, Callo-rhynchus (one of the Holoccephali), the egg-case may attain a length of 25 cm. Its external appearance is suggestive of a strip of kelp.

Most efficient of all is the protection afforded by viviparity, exceptional among fishes, but occurring in many sharks and skates and in a few Teleostei.

The eggs of most oviparous fishes are so scantily endowed with yolk as to be capable of only a small amount of growth until additional food can in some way be obtained from the environment. Such eggs develop rapidly and soon attain functional differentiation of the organs of all systems except the reproductive, but with relatively little growth because of the lack of building material. The resulting miniature fish at once becomes actively free-living and self-supporting. It then enters upon a long period of life concerned mainly with feeding and growth. The bulk of the prospective adult may be hundreds of thousands or millions of times that of the newly hatched young. During the brief developmental period the embryo is directly exposed to the external water so that, until specialized respiratory organs (gills) are developed, the necessary oxygen must be obtained by absorption through such surfaces of the embryo as are in contact with the water.

In many fishes the young differs from the adult in such respects as possession of adhesive discs or long spines or other organs of merely temporary significance, or in form of body or fins, or in gill structure and various other features. These differences may be so marked as to compel
recognition of a definite larval period which is followed by a period of metamorphosis in course of which the adult characteristics are acquired. A famous instance is that of the "glass-fish," a small transparent somewhat eel-like marine animal which was assigned to a genus, Leptocephalus, and for many years failed of recognition as being the larva of common eels of the teleost family, Anguillidae.

The young fish produced by an egg endowed with a large yolk mass attains a relatively large size before it is compelled to obtain food from an external source. Differentiation tends to take place more slowly. Prolongation of this period of functional immaturity and dependence increases the need of protection. In oviparous sharks and skates this need is met by the shell within which the developmental period is passed and from which the well-grown young fish emerges when ready to begin active and independent life. These shells must be sufficiently permeable to allow oxygen to pass from the water through to the enclosed embryo or young fish.

The embryo and young of the viviparous fish not only receives maximum protection but may obtain from the mother some nutriment in addition to the initial supply of yolk, and must somehow obtain necessary oxygen from the maternal blood. In most viviparous sharks and skates the developing young fish lies free in the posterior enlarged uterine region of the oviduct. The walls of this part of the oviduct are highly vascular. Even in the absence of any specialized mechanism for the purpose, it is possible that nutritive materials may diffuse from the maternal blood and pass to the embryo or young fish within, and there appears to be no other way in which the developing fish can obtain its oxygen. In some sharks, however, there is definite provision for transfer of material from mother to young. From the inner surface of the wall of the oviduct develop folds or processes (villi) which are richly vascular. Similar folds may arise in the region of the abdominal wall of the embryo (in relation to the yolk-sac: see page 53) and these two sets of projecting vascular structures, maternal and embryonic, become closely approximated or interlocked in such a way as to facilitate diffusion of materials from the blood of one to that of the other. Respiration, a certain amount of nutrition, and possibly to some extent the removal of excretion products from the embryo are thus provided for. These sharks are sometimes referred to as "placental" sharks because of the striking similarity of this arrangement and the mammalian placenta.

Viviparity in fishes is certainly, in an evolutionary sense, a secondary rather than a primitive condition. This is attested by the fact, among others, that in some viviparous Elasmobranchii the large egg is encased within a shell whose vestigial character is indicated not so much by the extreme thinness and delicacy of the shell as by the fact that it possesses
filamentous extensions which obviously correspond to the "curling tendrils" (Fig. 30) which serve to anchor the deposited eggs of some other elasmobranchs. It is quite certain, too, that there can be no direct genetic relation between the placenta of the mammal and the placenta-like arrangements in some sharks.

In Amphibians. The circumstances attending reproduction and development are, if possible, even more diverse among amphibians than among fishes. In point of initial yolk content, however, amphibian eggs are less variable than fish eggs. The smallest amphibian eggs are much larger than the smallest fish eggs and the largest amphibian eggs are small compared to the eggs of sharks.

Viewing the Class Amphibia as a whole and remembering that it is a very small group compared to fishes, it is probably fair to say that amphibians show much more concern—in a figurative sense—for the survival of their eggs than do fishes. The great majority of them lay their eggs in water, and it is invariably fresh water except in the case of the large toad (Bufo marinus) of the American tropics. The eggs are commonly deposited in a locality which seems to be instinctively chosen as favorable. They may be attached to the under surface of rocks or other submerged inanimate objects or to the leaves of aquatic plants. Some tree frogs (Hylidae) build a low wall of mud to form a rude hollow nest either at the bottom of shallow water or on shore very near the edge of the water. Jamaican tree frogs place their eggs in the small natural aquaria caused by retention of rain water caught by the leaves of certain large-leaved plants. Some frogs of the eastern hemisphere depart from water so far as to deposit the eggs on leaves or stones or in mud but always near water and the newly hatched young go immediately into the water.

Many salamanders deposit the eggs on land. They may be placed in small hollows in soft moist earth under stones or logs, but usually very near some body of water. Some salamanders are wholly terrestrial, depositing the eggs in crevices in logs deep in the woods, or on moss and remote from water. The females of some salamanders and of some caecilians (Gymnophiona) protect their eggs by coiling the body around the mass of eggs, the caecilian eggs being deposited in a burrow.

Certain frogs and toads have various specialized and peculiar ways of caring for the eggs and young. The male of the European "obstetric toad" (Alytes obstetricians) picks up the long strings of eggs extruded by the female and winds them about his body and hind legs. They are carried thus until the tadpoles emerge. The male of the South American frog, Rhinoderma, carries the eggs in his vocal pouch, a capacious recess which communicates with the mouth cavity.

In several instances the back of the female serves in one way or another as a temporary "nest" for the young. The tadpoles of some anurans are
for a time carried by the female parent to whose back they become attached. The male of the toad, Pipa americana, places the eggs on the back of the female where they sink into the soft skin and become completely enclosed, each egg in an individual pouch. Thus protected they pass through the whole developmental period, omitting the development of the gills which are characteristic of the very great majority of amphibian larvae, and finally rupturing the skin pouches to hop forth as fully formed miniature toads. The female of the South American "marsupial" tree-frog, Gastrotheca (Nototrema), likewise temporarily houses the young on her back, but en masse instead of in individual compartments. A fold of skin opening posteriorly forms a capacious chamber into which the eggs are put. In some species the young emerge from the "marsupial pouch" as tadpoles and in others as fully formed frogs.

Fig. 35.—Necturus larva of about 25 mm. length. (After Eycleshymer.)

In a small minority of amphibians, including representatives of each of the three orders, Urodela, Anura and Gymnophiona, the eggs are retained in the oviduct where they are fertilized and pass through the developmental period. This viviparity affords the maximum of protection during development. However, the enclosing of eggs and young in a vocal pouch, in individual dermal sacs, or in a dorsal "marsupium" must be regarded, so far as protection is concerned, as more or less efficient substitutes for true viviparity.

The amphibian egg with its moderate endowment of yolk, whether laid in the open or enclosed in some protective way, develops rapidly into a highly characteristic larva, the tadpole or "polliwog" (Figs. 31B and 35) which, with its functional gills and well developed locomotor tail as well as in many features of internal anatomy, is a distinctly fish-like animal and, if its environment is external water, it lives essentially the life of a fish. During the larval or tadpole period, the chief activities are feeding and growth. The end of the larval period is marked by a metamorphosis during which, and in relatively short time, various more or less profound changes occur, thus transforming the animal to the adult type. The transformation is most radical in frogs and toads, involving the development of legs and lungs, complete absorption of tail and gills, closure of gill clefts, and other changes. Certain frogs, however, produce especially large eggs which are deposited on land and develop directly into the adult form without passing through a tadpole stage. In the Urodela the changes
are less marked, the tail and sometimes also the gills being retained. In some urodeles the changes are comparatively insignificant and such salamanders as adult Necturus are often referred to as "permanent larvae."

The duration of the larval period ranges from a few weeks in some salamanders to a year and more in some frogs. The amount of growth attained during the period varies accordingly. Sexual maturity is ordinarily not attained during the larval period although exceptionally it may be. The Mexican axolotyl, the larva of the salamander, Ambystoma tigrinum, regularly breeds in the larval state.

It is evident, then, that in the development of most amphibians the all-important source of food is the yolk deposited in the egg. This carries development on to the beginning of the larval period or, in fact, the animal may enter the larval period with an important remnant of the yolk still available for further growth. If the larval stage is passed in the open water, the tadpole proceeds to feed, thus augmenting the original food supply. Given a prolonged larval period, a relatively great size may be attained before metamorphosis. When the larval period is spent within the oviduct, or within a dermal sac or a vocal pouch, there is obviously no chance of feeding and less growth is possible before metamorphosis. It should be noted, however, that the extraordinary development of the gills in some of these confined tadpoles opens the possibility that some nutrient as well as oxygen may be absorbed from the surrounding maternal, or sometimes paternal, tissues or fluids. For example, the tadpoles of the "marsupial" frog have enormously expanded bell-shaped gills which expose a large and highly vascular larval surface to the interior of the marsupial pouch. Such a surface might easily serve for absorption of nutrient material as well as oxygen.

Prior to the development of the larval gills the respiration of the embryo must be carried on by diffusion through the general outer surfaces whether the environment be water or some contiguous parental tissues and fluids.

In Reptiles and Birds. In striking contrast to the reproductive arrangements in fishes and amphibians, where the utmost diversity prevails, the corresponding arrangements in reptiles and birds are marked by a high degree of uniformity. The egg, always very large in proportion to the size of the animal, contains a quantity of yolk sufficient to provide for the whole developmental period, thus enabling the young animal to attain a relatively large size (in contrast to the corresponding conditions exhibited by most fishes and amphibians) before being cast upon its own resources for obtaining food. A newly-hatched alligator is gigantic compared to a newly-hatched salmon.

All birds and most reptiles are oviparous. Immediate protection for the egg is provided by the strongly developed shell. Reptiles deposit the
eggs on land, usually in some natural hollow or crevice which will afford protection. Crocodiles and alligators build rude nests of sticks or any available loose materials and the female may guard the eggs. Most reptiles leave the eggs to be incubated by the warmth of the sun.

Many lizards and snakes are viviparous. The utmost protection being afforded by viviparity, the importance of the protective shell is reduced.

A prolonged developmental period in course of which the young animal attains large bulk—all internal organs, except the reproductive, fully formed and highly differentiated before the animal hatches—the heart beating vigorously and the blood circulating rapidly—all of this going on within a thick shell—here is a set of circumstances which make respiration a problem. In warm-blooded birds the maintenance of high temperature during development accentuates the need of suitable provision for supplying abundant oxygen. The outstanding feature of the development of the reptile or bird appears when the embryo itself goes about the business of constructing a complex system of membranes so disposed and so equipped with blood-vessels as to serve very efficiently not only for respiration but for some other and secondary functions.

Early in development, at a time when the main organs are in process of formation (Fig. 84), the outer layer of the embryo, representing the prospective body-wall of the animal, throws up a system of folds which arch over and ultimately enclose the whole of the definitive embryo—much as if an animal should enwrap itself in a highly exaggerated fold of its own skin. Thus are formed the investing membranes known as the amnion and the chorion. The amnion is derived from the inner layer of the fold, the chorion from the outer. The amnion does not fit the embryo snugly. The intervening space is occupied by a watery solution whose chemical constitution resembles that of blood—and also resembles that of sea water. Thus the embryo during its further development is bathed by a fluid whose chemical nature is compatible with that of the embryonic tissues. Further, immersion of the embryo in watery fluid affords the best possible protection from externally caused mechanical pressures and impacts.

Meanwhile the enormous yolk mass has been enclosed (Figs. 84 and 87) by cellular layers which are prospectively the wall of the digestive tube. Then from the hinder region of the embryonic digestive tube a sac bulges out ventrally and, like a great and growing hernia, pushes beyond the ventral body wall. Having thus attained the exterior of the embryo proper, it becomes vastly expanded (by growth) and eventually becomes spread out so that the greater part of its outer surface is, in conjunction with the chorion, in close relation to the inner surface of the egg-shell. This sac is the allantois. It becomes highly vascular, its arteries and
veins communicating with the main vessels of the embryo. A considerable part of the blood of the embryo is diverted into the allantoic arteries and circulates vigorously through a rich system of small vessels lying close to the inner surface of the shell. The shell is porous. Thus ready interchange of respiratory gases between the blood and the external air is provided for. The allantoic sac serves also as a receptacle for embryonic waste. The ducts from the kidneys open into the extreme hind end of the digestive tube whence the fluid excreted by the kidneys readily passes into the cavity of the allantois.

The inner cellular layer (yolk-sac) immediately enclosing the yolk mass is highly vascular and its vessels, like those of the allantois, communicate with the main arteries and veins of the embryo. The blood circulating through these vitelline vessels picks up dissolved yolk materials which are conveyed to all parts of the embryo, thus making the yolk available everywhere for metabolism and growth.

In viviparous reptiles the amnion, the allantois with its vascular system, and the yolk-sac circulation are developed as in the embryos of oviparous reptiles. The oxygen obtained by the allantoic vessels, however, must be derived from the maternal blood in the wall of the oviduct.

In Mammals. Primitive mammals, as indicated by such surviving examples as Ornithorhynchus and Echidna, must have retained reptilian methods of reproduction. However that may be, the two animals just mentioned are oviparous. In size and possession of a protective shell, the eggs resemble those of reptiles. The duck-bill, a burrowing animal, deposits the eggs (usually two) in the burrow. Echidna, producing usually only one egg in a season, places the egg in a fold of abdominal skin, a temporary marsupium, where it is carried and incubated by the warmth of the body until the young hatches. The embryos of these two mammals develop amnion, chorion, allantois, and allantoic and yolk-sac circulations essentially as do reptiles. The material providing for development and growth up to the time of hatching is all derived from the initial yolk content of the egg. The one new thing which these animals do is to provide the young with a convenient source of food to serve for a time immediately after hatching. Milk produced by mammary glands (see page 181) developed in and by the abdominal skin serves to prolong the period of dependence on the maternal food. The additional growth thus made possible renders the young animal the more fit to succeed when it finally starts out for itself.

All known existing mammals except the duck-bill and spiny ant-eater are viviparous. The minute eggs contain so little yolk that they could never pass beyond the very early stages of development unless additional food material were somehow provided. In the great majority of mammals this is done by means of an organ which is one of the most characteristic
features of a mammal. The egg, liberated from the ovary and fertilized, becomes caught and lodged in the superficial tissue of the uterine wall. Here it passes into the early phases of development and very shortly gives rise to an amnion, a chorion and an allantois essentially similar to those structures as developed in reptiles and birds. Curiously, in spite of the absence of any considerable yolk mass, a yolk-sac also, although devoid of yolk, is formed. This is usually interpreted as a relic of reptilian ancestors. The allantoic sac becomes greatly expanded, more or less enwrapping itself around the embryo, and certain regions of it fuse with the adjacent chorion and enter into a very peculiar relation to the uterine wall (Fig. 89). From the conjoined allantoic and chorionic membranes grow out slender extensions (villi) which penetrate more or less deeply into the adjacent uterine wall. They may become more or less branched. These villi are highly vascular, fetal blood circulating in them under the drive of the fetal heart. The surrounding uterine tissue is likewise highly vascular. There is, however, no open communication between the blood vessels of the villi and those of the uterine wall. But the fetal and the maternal blood vessels are so close together that materials readily diffuse from one blood to the other. Dissolved food substances and oxygen pass from the maternal to the fetal blood; waste materials and certain special fetal substances of hormone nature pass from the fetal to the maternal blood. By this placental relation between mother and young the nutrition and respiration of the young animal are provided for through the usually long period of intra-uterine development.

Mammals show many variations in the mode of origin and details of structure of the placenta. The marsupial mammals (Metatheria; the kangaroo and its allies) produce only a weakly developed and briefly temporary placenta or none at all. Accordingly the development of the young cannot proceed beyond what is made possible by the initial small yolk supply plus what nutritive material may be absorbed by the embryo and its investing membranes directly from the neighboring uterine tissues and fluids. The young marsupial is therefore necessarily born at an early fetal stage and while very small. The deficiency of the intra-uterine arrangements is compensated for by the marsupium, a pouch formed by a fold of abdominal skin. The mammary glands are within this pouch. The very immature and quite helpless new-born young (in the great kangaroo, Macropus major, being only about one inch long) is transferred to the marsupium by the mother. The young becomes attached to one of the mammary nipples and feeds passively, the milk being pumped in by contraction of muscle about the mammary gland. This "mammary fetus" inhabits the marsupium for a time which is usually much longer than its period of intra-uterine development. For example, in the great kangaroo the period of intra-uterine gestation is between five and six
weeks, but the young kangaroo is carried in the pouch and nourished by mammary glands for about eight months.

In placental mammals, as compared to marsupials, the young are born at a relatively advanced stage of development and growth. The mammary organs, however, are in all cases an important post-natal provision for bringing the young animal along to a degree of size and strength favorable to ultimate success. They afford the great advantage, too, that the young animal is not thrown upon the world abruptly but may acquire independence gradually.

**EVOLUTIONARY SIGNIFICANCE**

Surveying the whole group of vertebrates, the great diversity in the conditions and arrangements attending reproduction is most impressive. It would be difficult to imagine any practicable reproductive expedient or condition which is not exhibited by some animal. There are microscopic eggs and there are ostrich eggs. The quantity of egg yolk may be vast or it may be next to nothing. The primary food supply, yolk, may in various ways be supplemented by secondary sources of nutriment—egg albumen, maternal blood, mammary milk, pigeon "milk." One egg or millions of them may be produced at a time. They may or may not have shells. Parental care of eggs or young ranges from nothing to the human maximum. Vertebrates may be oviparous or viviparous. A primary oviparity may be succeeded by a secondary substitute for viviparity, as when eggs develop within a fish’s mouth, an amphibian vocal sac, or integumentary pouches of various sorts. Differentiation of organs may precede growth or it may be delayed until the embryo is relatively large. The newly hatched larva of so large a fish as the Atlantic salmon is about 0.65 inch long; a new-born whalebone whale is about twenty feet long. The embryo may develop directly to the adult form or there may be a larval period terminated by a metamorphosis. The embryo may or may not produce a complex set of temporarily functional membranes—amnion, chorion, allantois.

The important point to be appreciated is that the association together of any two or more of these various alternatives in a single animal is not haphazard. If one circumstance is, in itself, inadequate for the success of reproduction, it is supplemented by something else. If a large fish were to produce one single microscopic egg annually and deposit it anywhere in the Pacific Ocean, the species would soon become extinct. On the other hand, there is no unnecessary duplication of highly specialized arrangements. A placental mammal does not produce a large yolky egg. The entire complex of reproductive conditions occurring in any one animal comprises a consistent grouping of alternatives which, as a whole, is adequate. Despite the great differences in methods of reproduction,
the net results are equally good, or nearly so, and generation after generation the life of the world goes on with, at most, only very slow change in the general biological balance and scheme of things.

Among vertebrates may be recognized four fairly sharply defined complexes of reproductive conditions. They may be briefly summarized as follows:

I. Eggs small; very little yolk  
1. As in many Teleostei  
   Oviparity  
   Very many eggs produced—thousands or millions  
   No parental care  
   Rapid development  
   Early differentiation  
   Early self-supporting  
   Long growth period after hatching  
   High mortality  
2. As in higher mammals: minimum yolk  
   Viviparity  
   Few eggs produced  
   Placental development  
   Differentiation mainly pre-natal  
   Growth largely pre-natal  
   Post-natal supplementary nutrition  
   Parental care  
   Self-support deferred  
   Maximum survival

II. Eggs of medium size (1.5–6 mm.): moderate amount of yolk  
3. As in many amphibians, especially Anura  
   Oviparity usual  
   Moderate number of eggs—usually scores or hundreds  
   Parental protection in many cases  
   Free-living self-supporting larva  
   Much growth during larval stage  
   Metamorphosis  
   Considerable mortality

III. Eggs very large: much yolk  
4. As in reptiles and birds  
   Oviparity usual  
   Eggs few—necessarily so because of size  
   Protective shell  
   Amnion and allantois  
   More or less parental care  
   Differentiation mainly before hatching  
   Growth largely before hatching  
   Self-support immediately or soon after hatching  
   Low mortality

There are, as already set forth, a great many modifications of these four types of reproduction.
Highly significant is the fact that so great a degree of diversity can exist within a single class of vertebrates. The fishes and amphibians show this diversity most markedly. Assuming a genetic series from fish to bird and mammal, the evolution of reproduction has not been a direct progress along one straight and narrow path. Instead, the animals within each class, especially the lower, tried (so to speak) a variety of methods. After the many reproductive "experiments" of the lower vertebrates finally emerged two distinct types to which the higher vertebrates fairly closely adhere. Reptiles and birds exhibit one of these types, mammals the other. Yet certain distinctive features of these finally emergent types of reproduction are anticipated by some lower vertebrates. The enormous eggs of oviparous sharks and skates, encased in thick shells, resemble eggs of reptiles. Some viviparous sharks produce vascular uterine structures (see page 48) suggestive of the mammal placenta. Certain viviparous lizards (genus Seps) develop what is practically a placenta. But there can hardly be any direct genetic connection between these structures in sharks and the somewhat similar structures in reptiles or mammals, nor between the "placenta" of a lizard and that of a higher mammal. The exaggerated filamentous gills of the intra-uterine larvae of some viviparous salamanders and the much expanded bell-shaped gills of the larvae of the marsupial frog, Gastrotheca, suggest that the larva may obtain nutriment as well as oxygen from neighboring maternal sources—potentially a "branchial placenta."

The marsupial structures of vertebrates afford another example of convergence in evolution—that is, the independent origin of functionally similar but genetically unrelated things. Defining a marsupium as a brood-pouch developed on the external surface of the body-wall, there are marsupial fishes (sea-horse; pipe-fish), marsupial frogs and marsupial mammals.

Viviparity is commonly thought of as something peculiarly mammalian. Yet there are viviparous fishes, amphibians and reptiles. The only vertebrate class which contains no viviparous members is Aves. In view of the fact that all birds and the most primitive mammals that we know are oviparous and the further fact that oviparity predominates among the lower classes of vertebrates, it is highly probable that the earliest vertebrates were oviparous and that the animals which constituted the main trunk of the vertebrate genealogical tree were oviparous. But viviparity has appeared on twigs of various lower branches of the tree as well as at its mammalian top.

The chordate ancestors of vertebrates must have been small animals and presumably produced small eggs with little yolk. It is likely that primitive vertebrates had small eggs and that large yolk masses have been secondarily acquired. But even within a small group of vertebrates
the yolk content of eggs may be highly variable, being apparently easily susceptible to evolutionary change. In point of size and yolk content, the vertebrate egg has evidently had many ups and downs.

In spite of the diversity of vertebrate methods of reproduction, an evolutionary trend is clearly to be seen. There is a certain extravagance about the primitive method—millions of eggs, perhaps, in a season, but only a small percentage of survival. The evolutionary tendency has been, by introduction of efficient protective, nutritive and respiratory arrangements, together with parental care, to assure the survival of every potential adult. This tendency bifurcates and culminates in two very differently specialized methods, one in birds, the other in mammals. With increase in chance of survival there is reduction in number of eggs produced. This result has the appearance of achieving economy but there is perhaps room for question as to just how and where the economy comes in. Does it cost a cod any more to produce seven million eggs than it costs a viviparous dogfish to bear four or five large "pups"? By either method of reproduction the numerical status of the species may be maintained and so, as remarked above, the net results of the two methods are equally good.

Unquestionably the high degree of efficiency which has been attained by the sauropsidan method of reproduction and also by placental reproduction in mammals is somehow correlated with the necessity of adaptation to the circumstances of living on land and in air. The primitive fish methods would obviously be impracticable. An aquatic larval stage in the development of a horse or an elephant can hardly be imagined—although, developing as it does in the fluid-filled amnion, the terrestrial descendant of ancient aquatic ancestors does spend its early life in a fluid medium. But it is beyond question also that the specialized reproduction of the bird and the mammal emphasizes the importance of the individual animal. The evolution of these highly specialized reproductive methods may very reasonably be regarded as somehow correlated with the fact that the individual bird or mammal is more important.

DEVELOPMENT
CLEAVAGE AND BLASTULA

Development involves great protoplasmic activity. There must be a building up of new protoplasm, rapid dividing of cells, movement and change of form. All of this calls for rapid metabolism. Metabolism requires inter-action of nuclear material and cytoplasm and exchange of materials between the protoplasm and the external medium. The area of the nuclear membrane and area of the external surface of the cell therefore impose a limit on metabolic rate. Two cells are capable of more rapid metabolism than one cell whose nuclear and cytoplasmic volumes
are respectively equal to the combined volumes of the corresponding parts of the two cells because the limiting membranes of the two cells have greater total area than those of the single cell.

The smallest egg-cells are large compared to most tissue-cells of the animal to which the egg belongs. The metabolic rate in an egg before fertilization is relatively low. After fertilization the rate increases. Before entering upon a prolonged period of activity at high metabolic rate the bulky egg-cell increases its surfaces by dividing into small cells. The successive divisions of the original egg-nucleus are, in fact, accompanied by absolute increase in the quantity of nuclear chromatin, a substance which undoubtedly plays an important part in determining the course of development.

In Amphioxus. From the foregoing it follows that the first necessary process in development is the cleavage of the fertilized egg (Fig. 36) into many small cells. Figure 37 illustrates the course of cleavage in Amphioxus. Although sometimes classified as such, Amphioxus is not literally a vertebrate. But it is a chordate and in many respects obviously primitive. The adult is a slender fish-like animal about 5 cm. long (see Fig. 14). The egg is correspondingly small, about 0.1 mm. in diameter, and contains very little yolk.

The plane of the first cleavage of the egg corresponds to the definitive median (sagittal) plane of the future adult. The two cells resulting from the first cleavage therefore represent the right and left halves of the body. The plane of the second cleavage is perpendicular to that of the first, and the third cleavage plane is perpendicular to both the first and second. The second and third cleavages each divide the egg slightly unequally. Further cleavages follow one another in rapid succession, their planes adhering to a fairly rigidly determined order. Meanwhile the cells gradually shift their relative positions and surfaces of contact in such a way that a space opens out at the center of the whole mass. At the thirty-two cell stage the cells are disposed to form a hollow sphere whose wall is everywhere one cell in thickness. Thus every cell of the thirty-two is in direct relation to the exterior, a most favorable position for
respiration and excretion. This hollow spherical shape is retained as cleavage continues (Fig. 37, G–I) until between two hundred and three hundred cells have been formed. This stage of the embryo is called the blastula. The name, blastocoel, is applied to the cavity.

The second and third cleavages introduce inequality of size among the resulting cells. This inequality persists as cleavage goes on. It is correlated with the distribution of yolk in the protoplasm, the larger cells containing the more yolk. The cells of the blastula grade from minimum size at one pole (animal) of the sphere to maximum size at the opposite pole (vegetal). This polarity is established in the egg before cleavage begins.

In Amphibians. Some amphibian eggs (not including the gelatinous envelope) are about 2 mm. in diameter. Such an egg would possess a volume about eight thousand
times that of an egg of Amphioxus. The greater part of the increased bulk is yolk. The egg (Fig. 38) is strongly polarized with reference to the distribution of the yolk in the protoplasm. From the animal pole where yolk is at a minimum the quantity increases toward the opposite vegetal pole where the maximum occurs.

Yolk is a non-living, quite inert substance. The active material in development is protoplasm. The developmental behavior of eggs containing much yolk shows quite clearly that the yolk is an impediment to the free carrying out of developmental operations—just as the necessity of carrying a heavy burden of food supplies may impede the progress of a company of explorers. Figure 39 represents the cleavage stages of a frog's egg. The successive divisions follow the same general order as in Amphioxus. Cleavages succeed one another at intervals of about an hour, but the period varies with temperature. The yolk, however, evidently hinders cleavage, especially in the vegetal hemisphere. The second cleavage begins at the animal pole before the first is completed at the vegetal pole. In fact, the third cleavage may begin while both first and second are still incomplete in the region of the vegetal pole. Further,
the inequality in size of cells at animal and vegetal poles is much greater than in Amphioxus, another consequence of the greater yolk mass.

After the third cleavage a cavity appears in the midst of the group of eight cells. As cleavages proceed this cavity enlarges and the embryo, as in Amphioxus, becomes a hollow sphere or blastula (Fig. 39E). The frog blastula differs from that of Amphioxus. Its cavity (blastocoele) is excentric, occupying approximately the animal hemisphere only. Its wall is more than one cell thick. The great thickness of the wall of the vegetal hemisphere and the consequent excentricity of the blastocoele are obviously due to the yolk.

**In Reptiles and Birds.** In eggs, such as those of reptiles and birds, where the yolk mass greatly exceeds that of the amphibian egg, the polarization with respect to the distribution of yolk reaches its limit in that all the protoplasm is segregated into a thin plate, the germ disc, lying on the surface of the relatively enormous sphere of yolk (Fig. 40). In such an egg, obviously, there is no mechanism for dividing the yolk. Cleavage is confined to the protoplasm of the germ disc which, following fertilization of its nucleus, splits up rapidly and soon consists of hundreds of small cells forming what is then called the blastoderm lying as a thin plate of cells on the surface of the yolk (Figs. 40 and 41). But there is continuity of blastoderm with yolk only around the periphery of the blastoderm. Elsewhere a thin space, the subgerminal cavity, intervenes between blastoderm and yolk (Fig. 41). Comparing this embryo with the blastula stages of Amphioxus and frog, it seems reasonable to interpret it as a
blastula whose blastocele is the subgerminal cavity, while its blastoderm is the animal much-less-than-"hemi"-sphere and the yolk mass is the vegetal much-more-than-"hemi"-sphere. This recognition of a blastula stage, comparable to that of Amphioxus, in the development of a reptile or bird would hardly have been possible but for the intermediate condition exhibited by the amphibian with its moderate yolk mass and total cleavage.

The blastula is to be conceived as an essentially one-layered stage of the embryo, the "layer" being the wall of the blastula, whether one cell thick or more than one cell thick. This stage has two-fold significance. Its immediate importance is in the fact that it gives the embryonic material increased superficial contact with the environment, thus favoring metabolism. Its prospective significance lies in the fact that further development is to consist, to a large extent, in the manipulation of layers of embryonic material. The adult is hollow. It has a body cavity and other cavities. Most of its organs are hollow. The walls of the hollow structures are constituted of layers—skin, epithelium, endothelium, peritoneum, muscle layers, connective tissue layers. For the construction of such a many-layered thing, the embryo naturally proceeds as early as possible to dispose its building material in the form of layers.

Gastrula

In Amphioxus. The blastula stage is briefly transitory. At once changes set in which transform it to a two-layered embryo. In Amphioxus the two-layered gastrula form is attained in a very simple way (Fig. 42). The vegetal hemisphere first flattens, then becomes curved inwards. The infolding (invagination) continues until the material of the original vegetal hemisphere comes into close relation with the inner surface of the wall of the animal hemisphere. The spherical blastula thus becomes an approximately hemispherical embryo whose wall is two layers thick (Fig. 42C). As the process goes on the blastocele is reduced and finally obliterated. The gastrula is hollow. Its cavity, resulting from the invagination process, at first opens widely to the exterior but the width of the opening is rapidly diminished by inbending of the wall about it and it is soon reduced to a narrow blastopore. In consequence of this contraction of the wall around the blastopore, the form of the entire gastrula tends at first to become spherical, but before the contraction is completed the gastrula begins to elongate in the direction of the axis which passes through the blastopore.

An important accessory activity attends this process of narrowing the blastopore. The blastoporal rim is a region of transition from the outer to the inner layer (Fig. 42D). This region is marked by very rapid proliferation of cells, especially at the dorsal edge of the blastopore. Cells
produced within this growth zone or "germ ring" are added, some to the outer layer and some to the inner layer. This growth process, then, is concerned both in the narrowing of the blastopore and the elongating of the embryo. A direct consequence of it is that the material of a certain region of the inner layer immediately adjoining the blastopore attained its internal position not as a result of the primary invagination but by the secondary growth process.

Fig. 42.—Gastrulation in AMPHIOXUS. The figures represent sections through the polar axis of the embryo. A, blastula with vegetal region flattened; B and C, earlier and later stages of invagination of vegetal hemisphere; D, gastrulation completed; with elongation of the gastrula, its long axis becomes the horizontal antero-posterior axis of the embryo. A, archenteron; B, blastocoele; BP, blastopore; EC, ectoderm; EN, endoderm; P, polar body. (After Cerfontaine.)

At the close of the gastrula period (Fig. 42D) the embryo is an elongated ovoid, the slightly larger end being anterior while the now very narrow blastopore marks the posterior end of the long axis. So rapid is development that this stage is attained about seven hours after fertilization.

Significance of the Gastrula. This gastrula form is of utmost significance, certainly prospectively, and perhaps also retrospectively. Reduced to lowest terms, what, essentially, is an organism? It is something which carries on perpetual interchange of material, nutritive and respiratory, with the environment, and it is capable of making such adjustments with
the environment as favor its continuance. Having in mind the necessities of some relatively large animal, nutrition—the digestion and absorption of food—is best effected at an internal surface. The structures and mechanisms immediately necessary for maintaining favorable relations to the exterior—passively protective structures and motor-reaction mechanisms—must lie at the external surface or in relation to it. Respiration can be provided for at either an external or an internal surface. The essential and minimum animal, then, is a two-layered thing. The outer layer is protective, sensory, and may (as it actually does in coelenterates) give rise directly to motor mechanisms. The inner layer is primarily nutritive. It may (as in some coelenterates) share in producing motor structures. Conceivably, and in view of the fact that all the functions of a living thing are carried on by an organism so minute that it is organized as a single cell, one layer might suffice. Given a small hollow animal, its cavity opening to the outside and its single wall being one cell thick throughout, nutrition might be attended to at the inner surface of the layer while the externally superficial protoplasm might provide the necessary contacts and adjustments with the exterior. But the principle of specialization, "division of labor," early became manifest in the evolution of animals. Two layers of cells, each layer specialized for a particular kind of function, work better than one.

The gastrula is the animal in its bare essentials. The outer layer, ectoderm, is potentially protective and nervous. It gives rise to the essential part of the adult skin which produces so many important protective structures and to the whole nervous system, both peripheral and central. The inner layer, endoderm, is nutritive. The cavity within it is the primary digestive cavity or archenteron. It is significant that the wall of the archenteron is derived from the vegetal hemisphere of the blastula. Thus, appropriately, the greater quantity of yolk comes to lie in the lining of the embryonic digestive cavity. In the vertebrates the external aperture of the archenteron, the blastopore, never becomes mouth and rarely becomes anus. The future motor mechanism, muscle, is derived indirectly from the gastrula layers.

The gastrula is strongly suggestive of the two-layer body plan of a coelenterate. A simple coelenterate such as Hydra, two-layered throughout, including even the tentacles, can be regarded as a somewhat elaborated gastrula, the Hydra "mouth" corresponding to the blastopore (Fig. 43). This resemblance, together with the fact that a gastrula stage, modified in one way or another, occurs nearly universally in the development of metazoan animals, gave rise to Ernst Haeckel's "gastraea" theory which proposed that gastrula-like animals (essentially coelenterates) must have been the ancestors of all Metazoa. According to this theory, the occurrence of the gastrula form in the ontogeny of a
vertebrate is a "repetition" of the coelenterate stage in phylogeny. This may very well be true but it is not necessary to hold this view in order to account for the gastrula stage in ontogeny for some such form as the gastrula is the almost inevitable precursor of any adult metazoan which has a skin (ectoderm) and a digestive tube (endoderm).

In Amphibians. Compared to gastrulation in Amphioxus, the corresponding process in the amphibian is very complex. In Amphioxus the entire wall of the blastula is thin. The wall of the vegetal half is only slightly thicker than that of the animal half. The blastocele is very nearly spherical. In the frog the vegetal wall of the blastula (Fig. 39, E–G) is so thick that the vegetal hemisphere is, in effect, solid. It consists of large cells heavily laden with inert yolk. It is not to be expected that such a wall could readily bend inward as does the corresponding thin and labile layer of the Amphioxus blastula.

In the amphibian three processes going on simultaneously effect gastrulation. The beginning of gastrulation is seen when a crescent-shaped groove (Fig. 44.1; I) forms at a certain place on the surface of the blastula. It lies just on the vegetal side of the equator determined by the animal and vegetal poles and extends transversely to the median plane determined by the first cleavage. The equator and a zone extending superficially somewhat into the vegetal hemisphere are marked by especially rapid cell-proliferation. It is in this particularly active region, the "germ ring," that the groove appears. Figure 44.1' represents a section in the median plane of an embryo at this stage. The groove (I) is the result of an invagination which occurs near where the upper thin wall and lower thick wall of the blastula join. The outer layer bounding the invagination consists of smaller cells which have moved inward from

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**Fig. 43.**—Diagrams showing structural similarity of a coelenterate and a gastrula. A, Hydra, longitudinal section; B, gastrula, axial section. A, archenteron, prospective digestive cavity; BP, blastopore; E, enteric (digestive) cavity; EC, ectoderm; EN, endoderm; M, mouth; T, tentacle.
the superficial germ-ring region; the deeper wall of the invagination consists of yolk cells. The groove, initiated as a slight invagination,

Fig. 44.—Gastrulation in the Frog. A, B, C, the whole embryo at successively later stages; viewed toward the vegetal pole. A', B' and C' represent, in somewhat diagrammatic way, sections of corresponding stages cut in the plane including the polar axis and bisecting the gastrular invagination, I; this plane corresponds to the median plane of the adult. During the latter part of the period of gastrulation, as result of shifting of the heavy yolk (compare B' and C'), the embryo rotates so that the axis passing through the blastopore (BP) becomes horizontal (see Fig. 48A). A, archenteron; AN, animal pole; B, blastocoele; BP, blastopore; EC, ectoderm, EN, endoderm; I, invagination; NP, neural plate; VEG, vegetal pole; Y, yolk; YP, yolk plug.

now rapidly deepens (Fig. 44B, B'), not by continued invagination, but by active growth of that upper (for later events prove it to be dorsal) lip
of the groove—that is, the lip resulting from the infolding of germ-ring material. This growth process serves to build out the dorsal lip of the original invagination so that the fold is caused to extend farther and farther downward over the yolk cells. Meanwhile the groove, originally a short crescent as seen on the surface of the blastula, lengthens laterally or in the direction of the curve of the crescent (Fig. 44B) until it describes a semicircle and, continuing, finally completes a circle. As the groove progressively lengthens, the newly arisen region of its outer fold, continuous with the "dorsal lip" of the initial region of the groove, at once begins to grow centripetally over the surface of the yolk cells. Therefore the radius of the curve described by the groove is ever decreasing. The groove is obviously deepest at the region where it began to form and shallower in the successively newer parts of it. Having completed the circle, the centripetal growth of the outer fold of the groove continues until the original vegetal hemisphere is completely covered except for a small aperture through which bulges a mass of yolk cells, the so-called "yolk plug" (Fig. 44C, C').

If the processes just described can be visualized, it will be seen that their result must be the formation of a new cavity in the embryo. This cavity is bounded externally by the two layers of the overgrowing fold, internally by the yolk cells. It potentially opens to the exterior but its actual opening is blocked by the yolk plug. If no process other than those already mentioned were involved the cavity would be exceedingly thin. It is, in fact, greatly enlarged by another process. During the progress of the overgrowth of the vegetal hemisphere, the large yolk cells become extensively rearranged. They move into the blastocoele, finally practically obliterating it. They carry out this movement in such a way that the space left vacant by them is added to the cavity formed by invagination and overgrowth.

Figure 44C' represents a median section of a frog embryo at the close of gastrulation. The embryo is two-layered throughout. The outer layer, ectoderm, is uniformly thin. The inner layer, endoderm, is very thin over approximately the dorsal half of the embryo but thick in the ventral region where the greater part of the original mass of yolk cells persists. The endoderm surrounds a capacious cavity, the archenteron whose external opening, the blastopore, is occupied by the yolk plug. The blastopore marks the posterior end of the embryo. The greater part of the original yolk is now in the endoderm.

This gastrula is essentially like that of Amphioxus. It is formed by the coöperation of several processes of which the more important are (1) invagination, which plays a minor part in the formation of the definitive archenteron; (2) epiboly—that is, overgrowth of the yolk mass by the fold resulting from invagination; (3) rearrangement of the yolk cells
to extend and complete the endodermal sheet produced by the overgrowing fold and, at the expense of the blastocoele, to increase the archenteric space. The difference between gastrulation in Amphioxus and that in the amphibian is essentially this: in Amphioxus the vegetal hemisphere (prospective endoderm) of the blastula actively moves into the interior of the embryo; in the amphibian the eventual interior position of the endoderm material is effected largely by the overgrowing activity of the prospective ectoderm. In Amphioxus the endoderm goes inside; in the amphibian it is put inside by being covered over. Quite clearly, the difference is the necessary consequence of the presence of the great mass of inert yolk in the amphibian blastula.

**In Reptiles and Birds.** A reptilian or avian embryo whose yolk mass may be millions of times that of Amphioxus could hardly be expected to carry out a process of gastrulation similar to that of Amphioxus—if, indeed, anything comparable to gastrulation were to be recognized at all. Yet the original single layer of the blastoderm, formed by cleavage (Figs. 40, 41), must somehow give rise to additional layers. The fact is that the blastoderm does at an early period become two-layered. The details of the mode of origin of the second layer differ considerably in various members of the Sauropsida. In the present connexion the significant fact is that, in all cases so far as known, the deeper layer (endoderm) results, in part if not entirely, from an inward movement of blastoderm cells at the median region of what proves to be the posterior edge of the blastoderm (Fig. 45). This inward movement may consist in the formation of a small pit, an actual invagination, from whose bottom cells move forward and laterally underneath the original blastodermic layer to become the endoderm. In other cases there is merely an in-turning of the mid-posterior edge of the blastoderm without formation of a complete pocket or invagination. In either case the process is confined to the mid-posterior region of the edge of the blastoderm. The endoderm, thus initiated, rapidly spreads over the yolk mass and under the original layer which is now identified as the ectoderm. The growth of the endoderm may be augmented by cells which become detached from the under surface of the outer layer.
It is noteworthy that the place of origin of the endoderm in the sauropsidan embryo is always at the edge of the blastoderm and it is always the posterior edge. If the primary blastoderm is to be regarded as corresponding to the animal hemisphere and the yolk mass to the vegetal hemisphere of the amphibian embryo, then the formation of endoderm in the sauropsidan embryo begins at a point which corresponds very closely to the position of the primary gastrular invagination in the amphibian (Fig. 44A', I). This fact, together with later events in the sauropsidan embryo, justifies the application of the term, blastopore, to the aperture of the little invagination or the slit formed by infolding of the hind edge of the blastoderm.

In the development of the reptile and bird, therefore, there is a gastrula stage which, in spite of the enormous mass of yolk, is essentially similar to the gastrula of an amphibian. It seems fair to say that the process of sauropsidan gastrulation is as nearly as possible—that is, as nearly as the yolk will permit—like that of an embryo in which there is comparatively little yolk (see Fig. 81).

**Comparisons.** Comparison of the early development of Amphioxus, amphibian and reptile or bird compels the conclusion that, were it not for difference in volume of yolk, the several embryos would be practically alike in form, at least through the gastrula stage. It is as if the embryo with the larger yolk mass "tried" to behave like the embryo of Amphioxus but is compelled by the yolk to modify its behavior. Amphioxus with total and nearly equal cleavage; the amphibian with total but very unequal cleavage; the reptile or bird with partial cleavage; the several embryos at corresponding stages exhibiting radical differences in the configuration of their materials—yet analysis of the processes concerned in the development of all these animals reveals a basic similarity.

The actual animal is the protoplasm. Developmental processes are its dynamic expression. Yolk, although necessary, is mere inert luggage. In all these animals its composition is essentially the same. The similarities which exist in spite of variation in yolk volume are certainly much more significant than the differences which exist because of variation in yolk volume. The method whereby the sauropsidan embryo achieves a two-layered condition is not the simplest imaginable. The easy and direct way would consist in the splitting of the original blastoderm to form two layers, an inner and an outer. Such splitting or "delamination" of layers commonly occurs at other stages in development. The fact that the sauropsidan embryo initiates endoderm formation by invagination or infolding at the posterior edge of the blastoderm is open to no better explanation than that there is some necessity of adhering as closely as possible to the developmental methods employed by amphibians and Amphioxus. Such necessity can come only through inheritance. The
embryos thus far—that is, through the gastrula stage—are essentially alike. They are all chordates. They merely carry different quantities of food. Herein lies the reason why so much emphasis is laid on the study of the development of Amphioxus. There is reason to believe that the Amphioxus embryo with its nearly minimum encumbrance of yolk reveals, at least in the early stages of development, the primitive and basic processes which in other chordates become more or less obscured by yolk.

THE THIRD LAYER, MESODERM

The greater extent of the ectoderm of the embryo persists as the essential layer, epidermis, of the adult skin. The endoderm gives rise directly to the lining epithelium of the adult digestive tube. But in the adult animal a great complex of structures—muscle, skeleton, central nervous organs, lungs, liver, and the reproductive, excretory and circulatory organs, making up the greater part of the bulk and weight of the animal—intervenes between the epidermis and the endodermal digestive epithelium. Some of these intermediate organs take origin directly and independently from the primary ectoderm or endoderm. For example, before the close of the gastrula stage the central nervous organs begin to differentiate from the dorsal ectoderm. Later, lungs, liver and pancreas arise as separate localized outgrowths from the endoderm of the early digestive tube. Others of the intermediate organs have an indirect relation to the primary layers of the gastrula. The close of the gastrula stage is marked by the formation of a layer, or system of layers, of embryonic material which comes to be interpolated between the outer and inner layers of the gastrula. This middle and third layer, the mesoderm, spreads extensively between the primary layers and at first appears to be quite undifferentiated throughout. Later it undergoes local differentiation to form muscle, skeleton, kidneys, circulatory organs and various other structures.

Following cleavage the embryo became a one-layered blastula. This form was succeeded by the two-layered gastrula. The next important event is the development of a mesoderm whereby the embryo attains a three-layered stage. The earlier period of development is concerned with laying out the building materials, the embryonic or “germ” layers. In the later and longer period these layers are shaped into organs. The formation of the central nervous organs and the notochord may begin, however, before the mesoderm is fully established.

In Amphioxus. At the close of the gastrula stage the Amphioxus embryo is approximately ovoidal, the long axis antero-posterior with the blastopore at its posterior end. The dorsal surface of the embryo is somewhat flattened. Figure 42D shows a sagittal section of the embryo at this stage. Figure 46A shows a section cutting the embryo transversely and
Fig. 46.—AMPHIOXUS. Transverse sections of embryos at successively later stages, showing origin of notochord, neural tube and mesoderm. A, section somewhat anterior to the middle of the length of an embryo slightly older than that represented in Fig. 42, D, E, from embryo having two pairs of mesodermal pouches, G, section near the middle of the length of an embryo having nine pairs of mesodermal pouches. A, archenteron; EC, ectoderm; EN, endoderm; MES, mesoderm; NC, notochord; NP, neural plate; NT, neural tube. (After Cerfontaine.)
within the anterior third of its length. Except for the dorsal flattening, the configuration of layers is as simple as possible. Figures 46B–G show transverse sections at stages successively later than that of Fig. 46A. Several things are happening simultaneously. A broad band of dorsal ectoderm (NP), slightly thicker than the adjacent regions of the layer, becomes separated, along its right and left edges, from the neighboring ectoderm. This process involves the mid-dorsal ectoderm continuously from the blastopore almost to the anterior end of the embryo. The median ectoderm thus delimited from the lateral ectoderm is the material of the prospective central nervous organ, the neural tube. In this initial stage it is called the neural (or medullary) plate.

The dorsal endoderm is at first flattened in conformity with the neural ectoderm but later (Fig. 46, D–F) it becomes convoluted along three lines extending lengthwise of the embryo. Its median slightly thicker region becomes sharply folded upward. Either side of this median fold a longitudinal groove appears on the inner surface of the endoderm. Then the endoderm in the region of each of these grooves assumes the form of a fold extending outward dorso-laterally. Thus arise three folds, one median and a lateral pair, all convex outward, and extending nearly the whole length of the embryo. As time goes on these folds become more emphasized, but soon a difference arises between the median fold and the lateral folds. The median fold remains continuous throughout its entire length. The lateral folds, however, become interrupted by the formation of sharp deep transverse folds which cut from above downward through each lateral fold. This process of subdivision or segmentation begins near the anterior ends of the lateral folds. Its immediate result is a pair of approximately globular pouches lying symmetrically either side of the median fold, each pouch having a small central cavity opening by a narrow passage into the archenteron. Later this passage is closed and then the pouch becomes detached (Fig. 46F) from the archenteric wall which, at the place where the pouch had formed, closes so that nothing is left to mark the spot (Fig. 46G).

Immediately behind each pouch of the first pair another similar pouch forms exactly as the first did. At this stage of development, marked by the presence of two pairs of these pouches, the embryo escapes from the egg membrane ("hatches"). The period between fertilization and hatching varies considerably, its average being probably not far from twelve hours.

These two pairs of pouches derived from the dorso-lateral endodermal wall of the archenteron constitute the first definitely delimited mesodermal material. The remainder of the dorso-lateral folds, extending back to the blastoporal region, is destined to give rise, after hatching, to additional mesodermal pouches. The median endodermal fold, which has remained
intact during this process of segmentation of the lateral folds, is the material of the future notochord (Fig. 46, NC).

At the time of hatching, then, the embryo has made important progress beyond the gastrula stage. Not only has the segregation of mesoderm begun but two important organs, the central nerve tube and the notochord, are indicated.

After hatching, additional pairs of mesodermal segments are cut off from the lateral mesodermal folds, the addition taking place progressively from anterior to posterior, until a total of ordinarily fourteen pairs have been produced. In several of the more posterior segments cavities do not occur, the mesodermal folds merely breaking up into a succession of solid blocks of cells.

In the formation of these fourteen pairs of mesodermal pouches the material of the original mesodermal folds is completely utilized. These folds, however, terminated posteriorly in the close vicinity of the blastopore (Fig. 47) a region where, since an early gastrula stage, very rapid cell proliferation has been going on. Following, then, the formation of the fourteen pairs of mesodermal segments from the lateral folds, the series of segments is extended backward by addition of successive solid blocks of cells which become detached from the growth zone encircling the blastopore. By this means the number of pairs of mesodermal units, the earlier and more anterior developing as hollow endodermal outgrowths, the later and more posterior as solid blocks derived by ingrowth from the blastoporal rim, is increased to the adult total, usually sixty-one.

In Amphibians. About certain details of mesoderm formation in amphibians there is more or less obscurity. In some respects the process differs conspicuously from that in Amphioxus. On the whole, however,
the similarities seem more significant than the differences. The point of unmistakable correspondence is to be seen in the important part played by the proliferation zone of the blastoporal rim or "germ ring." The amphibian gives little evidence of anything comparable to the paired mesodermal pouches which push out from the dorso-lateral endoderm of Amphioxus. However, about three quarters of the ultimate number of mesodermal segments in Amphioxus have origin in the blastoporal ring. In amphibians the germ ring is the all-important source of mesoderm.

During the process of gastrulation in the amphibian the material destined to become mesoderm lies within the advancing edge of the overgrowing fold (Fig. 44) which is the chief agency in the enclosing of the yolk. As the edge of this fold, the narrowing blastoporal rim, advances, it (in effect) leaves behind it—"behind" being anterior because the fold advances posteriorly—a trail of potential mesoderm which, however, is at first in no way distinguishable from other material destined to be permanently endoderm (Fig. 44C', EN). That is, the two materials together and in no way delimited from one another constitute the deeper layer of the overgrowing fold. Later this layer virtually splits (the process called delamination) to form two layers, an inner one abutting on the archenteric cavity and an outer one which is then recognizable as a definite mesoderm (Fig. 48B). This layer, although now distinct from the endoderm which parallels it, for a time retains continuity with its source, the proliferation zone about the blastopore (Fig. 48A). Initiated in this way, the mesoderm extends into the lateral and anterior regions of the embryo partly by growth within itself, partly by continued contributions from the blastoporal growth zone and possibly augmented by the detachment of cells from neighboring surfaces of the endoderm.
The mesoderm of Amphioxus is segmented at the time of its detachment from the primary gastrular layers and some of the more anterior segments are hollow. The amphibian mesoderm is primarily unsegmented and solid. In view of the fact that it later acquires segmentation and hollowness, these initial differences are outweighed by the essential similarity in the relations to the blastoporal region.

**In Reptiles and Birds.** In reptiles and birds the formation of an endoderm is initiated by a small invagination or infolding at the posterior edge of the early blastoderm (see page 69). The abortive blastopore thus produced exhibits the usual feature of a blastopore in that, in terms of germ layers, it is an indifferent region where ectoderm and endoderm merge together without sharp demarcation (Fig. 45). Following gastrulation the blastodermal layers continue to spread rapidly over the surface of the yolk. In so doing, the growth posteriorly causes the somewhat thickened region of the blastoporal rim to become drawn out into a long streak, the "primitive streak," lying in the median line of the blastoderm (Fig. 49). Along the whole extent of this modified blastoporal region the ectoderm and endoderm merge without sharp demarcation just as they did in the earlier blastoporal wall (Fig. 50).

This primitive streak is the primary seat of mesoderm formation. Rapid cell proliferation within the substance of the thickened "streak" gives rise to masses of cells which move out into the space between ectoderm and endoderm (Fig. 50, MES). These masses of cells increase by continued contribution from the "streak" and by growth within themselves and soon become arranged in a layer which rapidly grows laterally.

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**Fig. 49.**—Surface view of blastoderm of Chick after 15 hours incubation. C, "anterior crescent." occasioned by an irregular fold of underlying endoderm; M, region occupied by mesoderm; O, area opaca whose opacity is caused by adherence of yolk to the blastoderm; P, area pellucida—transparent in absence of adhering yolk (see Fig. 45); PS, primitive streak. X14. (After Duval, Atlas d'Embryologie.)

**Fig. 50.**—Section transverse to the primitive streak of a chick embryo of about 15 hours incubation. The section is taken near the middle of the length of the streak. EC, ectoderm; EN, endoderm; MES, mesoderm; PG, primitive groove of primitive streak; Y, yolk at inner margin of area opaca. X100. (After Duval, Atlas d'Embryologie.)
and forward from the primitive streak and always in the space between ectoderm and endoderm. This layer, like the early mesoderm of amphibians, is unsegmented and devoid of cavity.

In the sauropsidan embryo, then, as in the amphibian, rapid growth and cell proliferation within the blastoporal rim is the primary source of mesoderm.

**Early Development in Placental Mammals**

The early development of placental mammals exhibits features peculiar to the group and more or less difficult of comparison with anything in the development of lower vertebrates. The minute egg (Figs. 28 and 33) contains a bare minimum of yolk. Cleavage is total, more or less unequal and often very irregular in respect of planes and sizes of cells (Fig. 51.4).

The cells resulting from cleavage remain in a solid cluster, the “morula,” until as many as sixty or seventy cells are present. Then, as the number increases further, a cavity appears within the morula (Fig. 51B, C). Most of the cells remain in a solid group at one side of the cavity whose wall elsewhere is only one cell thick. At this stage the embryo looks like a blastula, but further development proves that the stage is not the equivalent of a blastula of a lower vertebrate. The term, blastodermic vesicle, is applied to this stage of the mammalian embryo. The definitive embryo is developed entirely from the thick cell-mass of the vesicle. The thin region (trophoblast, Fig. 51, T) of the wall of the vesicle becomes concerned with the early attachment of the embryo to the wall of the uterus.

The fluid-filled cavity of the blastodermic vesicle rapidly enlarges and meanwhile the thick cell-mass splits off a thin layer adjoining the cavity (Fig. 52). This inner sheet of the thick mass then extends over the inner surface of the thin wall of the vesicle and ordinarily completely lines it. The vesicle as a whole thereby becomes two-layered throughout, a condition which characterizes a gastrula stage. The further history of the two layers identifies them as embryonic ectoderm and endoderm.
However, both in mode of origin and in further history the mammalian embryo at this stage shows perplexing discrepancies as compared to the gastrula of a lower vertebrate.

As stated above, the material which constitutes the definitive embryo is within the thick and solid cell-mass (Fig. 51, 1) of the early blastodermic vesicle. As development proceeds, the behavior of this cell-mass is very much like that of the blastoderm of the embryo of a reptile or bird. If the cavity of the vesicle were occupied by yolk instead of by a watery fluid the whole embryonic complex would resemble closely an early reptilian embryo. The thick cell-mass, lying in relation to the vesicular cavity much as the reptilian blastoderm lies upon the surface of the yolk, flattens and thins out to form the "embryonic shield" (Fig. 53) in the axis of which appears an elongated thickening similar to the primitive streak of a sauropsidan embryo. At the anterior end of this mammalian streak is usually found a small pit or even a perforation extending through the "shield" into the cavity of the blastodermic vesicle—very suggestive of an abortive blastopore. It is along this mammalian primitive streak, as in the similar sauropsidan structure, that rapid cell-proliferation produces a mesoderm (Fig. 54) which progressively interpolates itself between the already separated ectoderm and endoderm and spreads eventually into all regions of the embryo. The mesoderm is at first a continuous layer—unsegmented—and devoid of cavity.

In a rabbit embryo the embryonic shield is established ordinarily by the fifth day of development, the entire blastodermic vesicle then having a diameter of about 1.5 mm.
The early development of the placental mammal presents many perplexing features. It could be expected that the minute egg, unembarrassed by yolk, would revert to the relatively simple and direct methods of early development which, for the most part, characterize Amphioxus. But it does not. Mammalian stages precisely comparable to the blastula and gastrula of Amphioxus or amphibians cannot be recognized. When it comes to the formation of mesoderm, the laying out of the germ layers, and the early shaping up of the embryo, the behavior of the mammal is closely similar to that of a reptile or bird. This similarity exists in spite of the absence of a large yolk mass in the mammal. These facts, taken together with the fact that certain mammals which are in most respects

![Fig. 54.—Transverse section of the embryonic shield of a Rabbit at the stage represented in Fig. 53. The section is taken at the position indicated by the line S-S in Fig. 53. EC, ectoderm; EN, endoderm; MES, mesoderm; PG, primitive groove of primitive streak. ×175. (After Assheton.)](image)

obviously of primitive type produce large yolk-laden eggs whose mode of development is essentially reptilian, point to what may be regarded as a fairly safe interpretation of the conditions in placental mammals.

In connection with the attainment of viviparity the yolk content of the mammalian egg became reduced to almost nothing. Apparently, however, the developmental behavior of the reptilian embryo had become so strongly established in the protoplasm of ancestral reptiles and primitive mammals that it persisted even though the reduction of yolk had removed the immediate necessity for many of its peculiarities. The many millions of years of primitive mammalian and of reptilian lineage constituted a barrier quite impassable by any tendency for reversion to the indefinitely more remote developmental methods of primitive Amphioxus-like chordates. Yet something from these primitive chordates came on down to mammals. If, as seems fairly certain, the reptilian primitive streak is a modified amphibian blastopore and, further, if the axial thickening in the early embryonic shield of a mammal is, as seems likely, a modified reptilian primitive streak—even to the inclusion of a blastopore so belated and so atrophied as to have completely lost its original significance as the aperture of a gastrular invagination—then a heritage from primitive chordates is to be recognized in the embryo of a modern mammal.

Unquestionably the yolk content of the chordate egg is much more readily subject to evolutionary change than is the developmental mecha-
nism of the germinal protoplasm. That mechanism can be changed, but there is a high degree of inertia about it. As the vertebrate egg acquired a bulky yolk mass certain adaptive changes in developmental methods were inevitable. But the primitive methods were so far as possible retained even at the expense of compelling the embryo to adhere to some processes which, under the new circumstances, are indirect and unnecessarily complicated—as when the sauropsidan endoderm arises by infolding at the edge of the blastoderm rather than by some simple and direct process such as delamination from the entire blastoderm. Again, in connexion with the reduction of yolk volume in eggs of recent mammals the developmental mechanism inherited from reptiles has undergone relatively little change beyond what has been immediately forced upon it by absence of the yolk mass and, secondly, by early attachment to the uterine wall in connection with the establishing of the placenta.

The initiation of evolutionary change is evidently not within the embryo itself. The embryo—that is, the living protoplasmic thing, exclusive of inert yolk—is highly conservative. Its inertia is such that it tends always to follow the old methods and it changes only as it must.

In striking contrast to this evolutionary conservatism of the embryo is its capacity for prompt adjustment to immediate emergencies. If one cell of the two-cell cleavage stage of Amphioxus or an amphibian is removed or so damaged as to prevent its development, the remaining cell may produce a complete embryo nearly or quite normal in every particular except size. A large portion of the early blastoderm of a fish egg may be destroyed and yet the remaining fraction of it will develop into a normal young fish.

Organogenesis

Appreciation of the processes whereby a relatively small spherical body of not visibly differentiated protoplasm becomes a large animal having the complex body-plan of a vertebrate requires a knowledge of the early embryonic stages, and especially the origin of germ layers and their characteristic configuration at the time when the shaping up of special organs is about to set in. Given the embryos of vertebrates of the several classes, the three germ layers having been fully established, the development of any major organ proceeds with a high degree of uniformity in all the classes. In view of these facts, the foregoing account of early development has been somewhat detailed while the following description of the embryonic origin of the more important organs can be relatively brief and general. These descriptions will be supplemented, too, in the later chapters dealing with the comparative anatomy of the several systems of organs.
As an introduction to the account of the development of organs in vertebrates reference to Amphioxus will be helpful. Amphioxus, partly because it is so small and partly because it is in so many respects primitive, affords what may be regarded as a simplified and diagrammatic view of the early relations of organs.

Organogenesis in Amphioxus

In the preceding account of the early development of Amphioxus the embryo has been followed to a stage where the mid-dorsal ectoderm has become delimited from the lateral ectoderm to form the neural plate, the mid-dorsal endoderm has given rise to a sharp thick upward fold which is the prospective notochord, and paired mesodermal pouches are in process of formation from the dorsal endoderm either side of the notochordal fold, the pouches increasing in number by addition of new pouches successively from before backward (Figs. 46 and 47).

In the course of further development the thickened ectodermal neural plate becomes depressed slightly below the level of the neighboring lateral ectoderm (Fig. 46, B–D). Along the line of demarcation between neural plate and lateral ectoderm separation occurs following which the lateral ectoderm extends progressively over toward the median plane and external to the neural plate. Eventually the edges of the right and left sheets of ectoderm meet in the median plane and coalesce to form a continuous layer above the neural plate (Fig. 46E). Meanwhile the neural plate transforms itself into a tube by bending its lateral regions upward and inward until the edges meet in the median plane where they become joined (Fig. 46F, G). The neural plate originally extends back to the blastopore. The overarching process whereby the neural plate is covered proceeds

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Fig. 55.—AMPHIOXUS. Median longitudinal section of an embryo having two mesodermal pouches, a stage approximately like that of the transverse section in Fig. 46 E. The blastopore, roofed over by ectoderm, has become the neurenteric canal. A, archenteron; EC, ectoderm; EN, endoderm; NC, endoderm destined to become notochord; NE, neurenteric canal; NP, neural plate; P, neuropore. ×350. (Based on a figure by Hatschek.)
backward and around the posterior margin of the blastopore. Thus neural plate and blastopore come to lie under a common roof of ectoderm and the blastopore, no longer opening directly to the exterior, opens into the small space between the neural plate and its newly acquired ectodermal roof. The resulting relations of layers and cavities are shown in Fig. 55, a sagittal section of an embryo at this stage. Upon conversion of the plate into a tube, the blastopore is left in communication with the lumen of the tube. At its anterior end the closure of the neural tube is delayed so that for a time its lumen is open to the exterior by a small aperture, the neuropore. The extraordinary result of these changes is an embryo whose prospective digestive cavity, still devoid of definitive mouth and anus, communicates via the neurenteric canal (the former blastopore) with the hind end of the cavity of the prospective spinal cord and brain and thence to the outside by the anterior neuropore (Fig. 55, $P$). These relations, however, are merely temporary. Eventually neuropore and neurenteric canal close. The definitive enteric apertures, mouth, gill clefts and anus arise by very similar processes. At the appropriate locality enteric endoderm and superficial ectoderm approach one another and coalesce. The resulting double layer then thins out until perforation occurs.

The notochord, whose development is initiated by an upward folding of mid-dorsal endoderm (Fig. 46$D-F$), early becomes detached from the enteric endoderm and acquires its characteristic cylindrical form. The enteric endoderm meanwhile closes in beneath the notochord and restores the integrity of the dorsal wall of the enteron (Fig. 46$G$). As the embryo increases in length the notochord grows within itself and receives accessions from the active blastoporal region with which its posterior end remains for some time connected (see Fig. 47).

The more anterior mesodermal pouches (or somites), soon after their formation and long before the more posterior somites have been developed, begin to acquire their characteristic differentiation. The pouch expands, especially ventralwards, and its cavity is correspondingly enlarged. That part of its wall lying against the notochord becomes much thickened (Fig. 56) while elsewhere the wall remains relatively thin. The expansion of the pouches continues until the walls of right and left pouches meet in the median plane beneath the enteric endoderm. At this stage three regions of the mesoderm may be distinguished: the thickened part lying alongside the notochord; an outer thin layer contiguous with the ectoderm; and an inner thin layer similarly contiguous with the endoderm. The thick part is destined to form a segment of body muscle and is therefore called the myotome (Fig. 56, $M$). The outer layer—being, in conjunction with the ectoderm, the body-wall of the embryo—is called the somatic or parietal layer. The inner layer, associated with the wall of the
enteron, is called visceral or splanchnic. The now capacious cavity resulting from expansion of the pouch is a segment of the embryonic body-cavity or coelom.

The myotome rapidly thickens and also increases its dorso-ventral extent. As it thickens, the adjacent upper portion of the coelomic space is correspondingly reduced. Eventually the somatic and visceral layers become joined by a horizontal septum formed just below the myotome (Fig. 56). Consequently a lower major part of the original coelomic space is separated from an upper remnant of it, the myocoele (MC), which, with continued expansion of the myotome, is finally obliterated, while only the lower cavity participates in forming the definitive coelom (C). The thin portion of the wall of the myocoele later gives rise to connective tissue including the myocommas which intervene between and tie together successive muscle segments.

As a result of the general expansion of the mesodermal layers, not only, as stated above, are the walls of right and left pouches brought together in the mid-ventral region, but the adjacent walls of successive pouches on the same side of the embryo become closely pressed together. At this stage, then, the paired coelomic spaces of the several pouches are separated from one another by thin partitions, some transverse and others median, each consisting of two layers of cells. These partitions become progressively thinner until they perforate and finally completely disappear except that remnants of the median ventral wall may persist in connection with the development of blood vessels. With the obliteration of these partitions, the several segmentally developed coelomic cavities are all thrown into free communication to form one large space, the definitive coelom, which finally shows no trace of its segmental origin.

Consistently with the fact that the mesodermal pouches arise not simultaneously but in sequence from anterior to posterior, differentiation begins in the most anterior or oldest pouches and proceeds backward at a rate depending on the age of the successively formed pouches. Thus, the myotomes of the first pair of pouches may have differentiated so far as to show the beginning of the development of muscle tissue while as yet not more than ten of the eventual sixty-one pairs of somites have been definitely formed.
An embryo of Amphioxus, at a stage when fourteen or fifteen pairs of mesodermal pouches are present, is a delicate colorless transparent animal having a length of about one millimeter and a diameter of one-eighth that except at the somewhat enlarged head end (Fig. 57). It has a straight digestive tube (enteron) \( I \), extending from an anterior mouth to a posterior anus. There is a single gill cleft, opening from the right side of the anterior region of the digestive tube. The mouth also is unsymmetrical at this stage, opening on the left side. Later, as numerous additional gill clefts are formed, they shift their positions so as to become ultimately a series of symmetrically placed paired apertures. Meanwhile the mouth shifts from its original left to a median position. Just above the digestive tube lies the median rod-like notochord (\( NC \)) extending the entire length of the animal. Immediately above the notochord is the neural tube (\( NT \)), its somewhat enlarged anterior region suggesting a brain. At the anterior end of the neural tube the dorsal neuropore (\( NP \)) is still open. The neuromeric canal (\( NE \)), at this stage, has ordinarily become closed.

![Diagram](image)

In its anterior region, where the differentiation of the mesoderm is most advanced, a coelom intervenes between the enteric tube and the outer body-wall (Fig. 56, \( C \)). The body wall (somatopleure) consists of the ectoderm and the somatic layer of mesoderm. The enteric endoderm together with the contiguous visceral or splanchnic layer of mesoderm constitute the wall (splanchnopleure) of the digestive tube. The somatic and visceral sheets of mesoderm provide the coelom with a continuous and complete lining, the peritoneum. The superficial ectoderm is a skin. The more anterior myotomes contain partially differentiated muscle tissue capable of feeble contraction. The animal is free-swimming but the locomotor mechanism consists merely of long cilia produced by the ectodermal layer.

In its main features this young Amphioxus is like a vertebrate. If its true origin and nature were not known, it might reasonably be expected to proceed to develop directly into a typical vertebrate. But it does not. It acquires no vertebral column; the notochord serves as definitive axial...
skeleton. It develops no structures morphologically similar to the heart, kidneys, specialized sense organs, or paired appendages of a vertebrate. Further, in later development it acquires, especially in the head region, a variety of unique structures which adapt the adult to its peculiar mode of living but make it conspicuously unlike any adult vertebrate. Nevertheless Amphioxus is "vertebrate" in too many features to make it credible that they could have arisen otherwise than in genetic relationship with those of the vertebrates. Herein, then, lies in part the justification for describing the early development of Amphioxus to illustrate the main features of the corresponding stages of vertebrates. Further justification is derived, as already stated, from the fact that the paucity of yolk in the egg of Amphioxus relieves the embryo of the factor which introduces varying degrees of complication into the development of vertebrates and occasions much difficulty and obscurity in the study and interpretation of the processes.

Organogenesis in the Vertebrates

In the late embryo of Amphioxus the main lines of the body-plan of a vertebrate are drawn. There are, however, some noteworthy differences in the mode of origin of corresponding organs of Amphioxus and vertebrates.

Neural Tube. In Amphioxus the neural plate becomes detached from the adjacent lateral ectoderm (Fig. 46) and transforms itself into a tube not until after it has been covered by the lateral ectoderm. In vertebrates a longitudinal folding of the neural plate and adjoining ectoderm occurs in such a way that the movement of the neural material into a deep position, its conversion into a tube, and the covering of it by lateral ectoderm take place simultaneously (Fig. 58). Not until the tubular form is attained does the neural ectoderm of vertebrates become detached from the overlying superficial ectoderm. Figure 59 shows, in diagrammatic way, the characteristic appearance of a recently formed neural tube with its neural crests, dorsolateral extensions of ectodermal material on each side of the tube. Later the neural crest becomes detached from the tube, undergoes segmentation corresponding to that of the myotomes, and gives rise to spinal ganglia. Cells of the crest become ganglion cells whence grow out nerve fibers which constitute the dorsal sensory root of a spinal nerve. The fibers of the other constituent root of a spinal nerve, the ventral motor root, grow out from cells within the neural tube. Some cells of the neural crests migrate into various visceral localities and give rise to ganglia and nerves of the autonomic system.

The anterior region of the tube expands to form the brain. Three enlargements, one behind another, the primary brain vesicles—fore-brain, mid-brain and hind brain (Figs. 61, 63, 85)—characterize the cephalic
part of the tube in all vertebrate embryos. Later subdivision of the first and third vesicles results in the five brain regions universally characteristic of adult vertebrates. The nervous structures (retina and optic nerve) of the paired eye grow out from the second (numbered from in front) region but the lens of the eye is derived from neighboring superficial ectoderm (Fig. 60). The receptor (that is, stimulus-receiving) nervous structures of the ear and olfactory organ originate not from the neural tube but from superficial ectoderm.

**Notochord.** In contrast to the quite definite manner of origin of the notochord in Amphioxus, there is considerable obscurity as to the precise nature of the process in many vertebrates and it must be admitted that the process differs markedly in the several classes. In amphibians the notochord is in part and to greater or less extent folded off or split off from the mid-dorsal endoderm and in part built forward from the actively growing blastoporal region. In amniotes the origin of the notochord is closely related to that of the mesoderm—so much so that the notochord has sometimes been described as of mesodermal nature. Its material, like that of the mesoderm, usually seems to be derived from the primitive streak (see pages 76, 78), a region where ectoderm and endoderm merge indistinguishably. As cells proliferated from the streak laterally give rise to mesoderm, so proliferation forward from the anterior end of the streak produces a median cord of cells which form the notochord. It may, however, receive accessions from the endoderm with which it is usually in close relation.

If it be granted that Amphioxus is a near relative of immediate ancestors of vertebrates, the mode of origin of its notochord does much to
relieve the perplexity occasioned by the variability in the development of the organ in vertebrates. In Amphioxus the anterior part of the notochord is folded up from the endoderm but a considerable posterior extent of it is built on by proliferation at the blastoporal region. The primitive streak of the amniote embryo is open to interpretation as being a modified blastoporal region. The streak is then the equivalent of the blastoporal rim, both actively growing regions. If all this be granted, then the lower vertebrate (amphibian) retains more of the Amphioxus method of forming notochord while in higher vertebrates there is less of direct and obvious origin from endoderm, and proliferation from the blastoporal streak plays the main role—all of which seems quite reasonable.

The Enteron. Gastrulation produces a two-layered embryo whose endoderm surrounds a cavity opening to the exterior by the blastopore. This archenteric cavity is the prospective digestive cavity. As the embryo elongates, the cavity is correspondingly elongated and in later development the enteric tube increases in length faster than the embryo with result that the tube becomes bent or even coiled to adapt itself to the coelomic space.

In the early embryo the ectoderm at a median antero-ventral position gives rise to a shallow depression or pit, the stomodeum, whose deeper wall meets the forward-growing endoderm to form temporarily a two-layered oral membrane separating the external stomodeal cavity from the enteric cavity. Soon a perforation appears at the center of the membrane (Fig. 61, O) and its peripheral remnant is rapidly obliterated. The perforation and obliteration of the membrane apparently result from progressive centrifugal flow or movement of its cellular substance. Thus is formed the mouth. The posterior enteric aperture or embryonic

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**Fig. 59.—Stereogram of embryonic neural tube showing the segmenting neural crest.** e, superficial ectoderm; nc, neural crest; s, central canal. (From Kingsley, *Comparative Anatomy of Vertebrates.*)

**Fig. 60.—Stereogram of the developing eye.** The head of the embryo is cut transversely in the region of the fore-brain. cf, choroid fissure; fb, wall of fore-brain; l, ectodermal thickening which invaginates to form lens; oc, optic cup; os, optic stalk; p, outer thin wall of optic cup, becoming the pigmented epithelium which lies behind the definitive retina; r, inner thick wall of optic cup, becoming the sensory retina of the eye. (From Kingsley, *Comparative Anatomy of Vertebrates.*)
"anus" develops usually by a similar process. The blastopore rarely persists as a definitive posterior aperture although it does so in cyclostomes and possibly in some urodele amphibians. Otherwise, exactly as in Amphioxus, it becomes roofed over by the neural folds and thus converted temporarily into a neurenteric canal (Fig. 61) connecting the hind ends of neural tube and enteric cavity. In reptiles and birds the formation of an actual neurenteric passage is more or less obscured by the presence of the massive yolk but definite traces of the canal may be recognized. An ectodermal pit, the proctodeum, situated just below the neurenteric canal, perforates into the hind end of the enteric cavity to form the definitive hind aperture, either anal or cloacal (Fig. 61). As result of the mode of development of the enteric apertures, the lining of more or less of the mouth cavity is derived from stomodeal ectoderm and that of the posterior region from proctodeal ectoderm. The remaining and by far greater part of the adult enteric tube is lined by endoderm which

![Diagram of Frog Embryos](image_url)
constitutes the essential secreting and absorbing layer of the tube, the digestive epithelium.

It is a noteworthy fact that various organs which have nothing directly to do with digestion have their origin in the enteric endoderm. The anterior region of the embryonic enteron—the part becoming the pharynx of the adult—is concerned particularly with the organs of respiration. Gills of fishes and amphibians develop in relation to paired apertures, the pharyngeal or visceral clefts, which pierce the lateral walls of the enteron and the ectoderm and open to the exterior. A pharyngeal cleft is developed as follows. A deep lateral pouch or furrow of the endoderm bulges outward and meets a similar but shallower pouch or furrow which the ectoderm pushes inward. The resulting two-layered membrane is then obliterated by the same process which removes the oral membrane, leaving a free passage between the pharynx cavity and the exterior. Vascular complications of the endodermal lining of these clefts produce internal gills—although it is possible that some so-called internal gills are derived from ingrowing ectoderm. External gills are ectodermal structures developed in close relation to the external apertures of pharyngeal clefts.

The number of pairs of pharyngeal pouches varies from a maximum of fourteen in some cyclostomes to, in birds and mammals, four or five which are rudimentary in the sense that they exist only temporarily in the embryo and even then may not perforate to the exterior. The clefts of the first pair do not ordinarily produce functional gills in fishes but become the spiracles of sharks and some ganoids. In all amniotes the pharyngeal pouches are merely temporary embryonic features except as those of the first pair are, in a modified way, represented in the auditory passages.

Lungs develop by formation of a mid-ventral pouch in the floor of the pharynx. As the pouch enlarges, it bifurcates forming right and left lungs. The entire epithelial lining, being the essential respiratory membrane, of the adult lung is endodermal and continuous, by way of the lining of bronchi and trachea, with the lining of the digestive tube. In birds the respiratory cavities are continued beyond the lungs into a system of air sacs, branches of which extend into various parts of the body including even the cavities of some of the bones. It seems an extraordinary fact that a bird’s humerus—less often the femur—may contain an air tube whose wall is derived from and is still continuous with the enteric endoderm.

The air-bladders (swim-bladders) of fishes are endodermal sacs which grow out from an anterior region of the embryonic enteron. They are usually dorsal, rarely lateral, or ventral as in the ganoid Polypterus.
The important endocrine glands, thyroid, parathyroid and thymus, and various gland-like bodies mostly of dubious nature and function, arise as outgrowths of the endoderm of the pharyngeal pouches or the wall of the pharynx.

More posterior regions of the enteric endoderm give rise to various accessory digestive organs, most important of which are the liver and pancreas. The liver, uniformly in all vertebrates, develops as a mid-ventral outgrowth, or sometimes more than one, from the anterior region of the prospective intestinal portion of the enteron. Vascular and connective tissues make up a large part of the bulk of the adult liver but the essential liver substance—the hepatic cells which carry on the specific functions of the liver—are endodermal. The position of the opening of the bile duct into the intestine marks the point of origin of the embryonic liver.

The pancreas and liver arise in close relation to one another, but the pancreas commonly has more than one point of outgrowth from the enteron. The secretory tissue of the pancreas is endodermal.

The cloaca of the adult vertebrate is a superficial chamber situated at the hind end of the body cavity and opening ventrally to the exterior. Into it open the intestine and the ducts of the kidneys and genital organs. It is commonly present in vertebrates below mammals except in Teleostei. Mammalian embryos develop a cloaca but only those primitive mammals, Ornithorhynchus and Echidna, retain it in the adult. In other mammals the embryonic cloaca becomes subdivided into a dorsal part connected with the intestine and a ventral part which receives the urinogenital ducts. In course of further development these two divisions of the cloaca are separated and carried apart and acquire independent openings to the exterior so that eventually the anus and urinogenital aperture are far removed from one another, the latter being the more ventral in position. Therefore the more distal portion of the urinogenital passage of the adult, both male and female, is a remnant of the cloaca while another remnant of it persists in the posterior region of the rectum.

In the great majority of vertebrates the cloaca is derived from the extreme hind end of the embryonic enteron. As the kidneys and gonads develop, their ducts acquire connexion into this part of the enteron. It becomes more or less enlarged in diameter as compared to the intestinal region of the enteric tube. The proctodeal perforation provides it with an exit to the exterior and it becomes the definitive cloacal chamber. It has no digestive function other than serving as an avenue for passage of digestive waste as well as the renal and genital products. This cloaca is lined with endoderm. But the cloaca of the frog has been described as developing from the proctodeum, an ectodermal invagination. Such a cloaca would be lined by ectoderm. It is therefore possible that cloacal chambers are not all precisely homologous.
If "anus" is to be defined as the posterior aperture of the digestive tube—digestive in strict sense—then the term should not be applied to the external opening of the cloaca but rather to the internal aperture between rectum and cloaca. By this definition the proctodeal aperture would ordinarily become the external cloacal opening but in some cases would become an external anus (Teleostei) or an internal anus (frog). If the posterior extremity of the adult mammalian digestive tube includes a remnant of the embryonic cloaca, then the mammalian "anus" is in reality a remnant of an external cloacal aperture. There is much confusion and doubt about homologies in this region of the vertebrate and, among authors, there is corresponding confusion of terms.

The Mesoderm. In contrast to the early condition of the mesoderm in Amphioxus, the vertebrate mesoderm is at first devoid of segmentation and ordinarily contains no definite cavity. At an early stage it appears as a somewhat compactly arranged but indefinitely delimited sheet of cells rapidly spreading from its region of origin into the space between ectoderm and endoderm. The layer becomes thickest dorsally alongside the neural tube and notochord (Fig. 62). At an early embryonic stage the mesoderm upon either side splits into two layers; an outer, lying against the ectoderm, and an inner lying against the endoderm. The two layers remain connected, however, at the upper edge of the original sheet (Figs. 63, 64.1). At about the same time the dorsal and thicker part of the mesoderm develops transverse fissures which divide it into a series of paired blocks (somites) lying symmetrically either side of the neural tube (Fig. 63). This segmentation begins in the anterior part of the embryo and progresses backwards just as, in Amphioxus, the mesodermal pouches are formed successively from anterior to posterior. Figure 64B shows a diagrammatic section of an amphibian embryo at this stage. Figure 65

![Image](image-url)
represents a chick embryo after about 33 hours incubation. The mesodermal somites, easily seen through the very thin ectoderm, appear as pairs of denser or darker squarish blocks.

Fig. 63.—Stereogram of the anterior region of a vertebrate embryo showing the segmentation of the mesoderm. The ectoderm has been removed from the left side of the embryo. al, endoderm of alimentary tube; c, coelom; em, epimere; fb, fore-brain; hb, hind-brain; hm, hypomere; m, myotome; mb, mid-brain; mm, mesomere; n, neural tube; nc, notochord; s, stomodeal region; sk, sclerotome; so, sp, somatic and splanchnic walls of coelom. (From Kingsley.)

The process of segmentation involves only the upper part of the mesoderm. As segmentation goes on, the space between the two thin and unsegmented layers becomes wider—a space already recognizable as the coelom bounded externally by a somatopleure consisting of ectoderm and the outer sheet of mesoderm, and internally by a splanchnopleure consisting of endoderm and the adjacent layer of mesoderm. The mesodermal layers upon either side grow down to the mid-ventral
region, carrying with them the coelom, and meet mid-ventrally to form a double vertical layer, a ventral mesentery, extending from the enteron to the outer body wall and separating right and left coelomic cavities (Fig. 63).

The splitting of the original sheet of mesoderm extends so far dorsally as to involve the somite which accordingly contains a more or less definite cavity, the myocele—"myo" because the somite is mainly muscle-
forming. Shortly the somites become detached from the lower somatic and visceral sheets of mesoderm and the myocoeles lose continuity with the permanent coelom (Fig. 64B). Eventually, as the somite differentiates, the myocoele is obliterated.

The differentiation of the mesoderm at the stage just described—dorsally the pairs of quite detached hollow somites; ventrally the unsegmented somatic and visceral layers enclosing between them the coelom—has its exact counterpart in Amphioxus. But in Amphioxus segmentation and hollowness of the mesoderm are primary and continuity of the coelomic space is secondarily acquired. In vertebrates segmentation is secondary and so also is hollowness except that in cyclostomes and some urodele amphibians the early mesoderm appears to have folded outward from the dorsal wall of the enteron and exhibits a thin cavity which may be continuous with the enteric cavity (Fig. 66). This exceptional condition, although it involves no primary segmentation, suggests the mode of origin of the mesoderm in Amphioxus.

In its further history, however, the differentiation of the vertebrate mesoderm is more elaborate than that of Amphioxus, especially in the prospective trunk region. Here a region of mesoderm intermediate between the upper somite or muscle-forming part and the lower peritoneum-forming layers becomes early designated to play a very important role, the formation of the essential structures of the kidneys. In the trunk mesoderm, then, there are upon each side three zones of differentiation: the epimere, a dorsal muscle-forming part; the mesomere, a kidney-forming zone situated just below the epimere; and the hypomere, the most ventral zone, constituting the somatic and visceral layers of peritoneum (Figs. 63 and 64A).

The epimere undergoes three kinds of differentiation. Its heavier inner wall is mainly converted into striated body-muscle. The embryonic myotome gives rise not only to the dorsal but to the ventral body-muscle. The myotome material grows ventral-wards, pushing its way between the ectoderm and the somatic mesoderm, until it reaches the mid-ventral plane (compare Figs. 67 and 68). From the medial surface of the inner or myotomic wall of the epimere numerous cells become detached and give rise to loosely aggregated cellular masses surrounding the notochord and neural tube (Fig. 69). Most of this material enters into the forma-
tion of the supporting structures—connective tissue, cartilage and bone—

Fig. 67.—Diagrammatic transverse section of the body of a vertebrate embryo at an advanced stage. The muscle-forming myotome is beginning to extend into the ventral body-wall of the embryo. c, coelom; g, genital ridge; m, muscle derived from myotome; mc, myocoele; p, peritoneum; pd, pronephric duct; so, somatic layer of somite; v, advancing ventral border of myotome; the finely dotted areas are occupied by mesenchyme. (From Kingsley.)

which are eventually developed around these two axial organs. The outer or somatic wall of the somite breaks up to form loose cellular masses which spread out underneath the ectoderm. As the ectoderm differentiates into the definitive epidermis of the skin, the underlying mesodermal material forms the dermis (or corium), the deeper fibrous and vascular layer of the skin. As the muscle-forming material of the somite is called the myotome, so the medial skeleton-forming region, or the cell-mass derived from it, is conveniently called the sclerotome, and the somatic dermis-forming layer is called the dermatome (Figs. 63 and 67).

The mesomere in lower vertebrates undergoes a segmentation corresponding to that of the epimeres (Fig. 63), but in amniotes segmentation of the mesomereres is obscured or lacking. In anamnia the

Fig. 68.—Diagrammatic transverse section of the body of a vertebrate. av, aorta; c, coelom; e, ectoderm; ep, epaxial (dorsal) muscle; g, gonad; ha, hemal rib; hp, hypaxial (ventral) muscle; i, intestine; mes, mesentery; n, nephridium; o, omentum; r, rib; p, somatopleure; sp, splanchnopleure; s, centrum of vertebra and, above it, neural arch containing spinal cord. (From Kingsley.)
mesomeres become transformed into kidney tubules. The process begins in the more anterior mesomeres and progresses posteriorly. Certain differences in mode of development and in eventual structure compel the distinction between an earlier and more anterior system of tubules, the pronephros, and a later and more posterior system, the mesonephros. In Anamnia the mesonephros becomes the adult kidney and the pronephros disappears except that in a few fishes it is the definitive and only kidney. In amniotes, following development of a pronephros and a mesonephros, the tubule-forming process continues backward, but with some modifications and complications, to form a third kidney, the metanephros, which becomes the adult kidney. The tubular epididymis, associated with the testis of the adult amniote, is a part of the embryonic mesonephros which otherwise disappears except for certain vestiges which are apparently of little functional importance.

In Anamnia each mesomere at first forms a single renal tubule. In what is conceived to be the more primitive method of development of the tubules, the cavity is the original cavity of the mesomere and is therefore a part of the embryonic coelom and continuous with the coelomic space of the hypomere. In amniotes, may be not only unsegmented but devoid of any original cavity. In such case the tubule shapes up as a solid cord, later hollowing out.

Meanwhile, as the pronephric tubules form, the mesomere material on each side of the embryo gives rise to a longitudinal tube (Fig. 64) which extends backward from the pronephric region to the wall of the cloaca into which the cavity of the duct finally opens. The pronephric tubules of each side are joined to the corresponding pronephric duct (Fig. 70) thus putting the coelom into communication with the exterior by way of the cloaca. The coelomic openings or nephrostomes (Figs. 64B, n, and 70, ns) of the pronephros are ciliated. The arrangement apparently serves for drainage from the coelom to the exterior.

The mesonephric tubules develop in many more segments than do the pronephric (Figs. 70 and 71). They acquire connexion with the already-

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**Fig. 60.—Transverse section of the embryo of a lizard (Lacerta muralis) having twenty-eight pairs of mesodermal somites; cut through the tenth pair; much enlarged.**

*Diagram depicting the transverse section of an embryo showing various structures.*

*a*, dorsal aorta; *m*, myotome—muscle-forming part of mesodermal somite; *n*, notochord; *o*, omphalomesenteric vein; *sc*, neural tube (spinal cord); *sk*, mesenchyme derived from sclerotomic part of somite. (From Kingsley.)
REPRODUCTION

Fig. 70.—Stereogram of the developing pronephros and mesonephros. (After Kingsley modified.)

Fig. 71.—Stereogram of the developing mesonephros at a stage later than that of Fig. 70. (After Kingsley modified.)
formed longitudinal duct which, as the pronephros degenerates, then serves at least in part as the *mesonephric* or *Wolffian duct*. In Anamnia each mesonephric tubule has a ciliated nephrostome opening into the coelom (Fig. 72). Near the nephrostome the tubule gives rise to a cup-shaped expansion (Bowman's capsule). The hollow of the cup is occasioned by ingrowth of a dense network of fine blood vessels, the glomerulus. The capsule and glomerulus together constitute a *renal* (or *Malpighian*) **body** or **corpuscle**. The part of the tubule between the renal body and the mesonephric duct eventually becomes much elongated, coiled and locally differentiated. At first there is but one pair of tubules per segment. Later additional tubules are ordinarily formed in each segment by a process of branching from the primary tubules.

![Diagram of renal (Malpighian) corpuscle](image)

In amniote vertebrates, in which the mesomere material ("intermediate mesoderm") is not segmented and not hollow, the pronephric and mesonephric tubules ordinarily do not possess nephrostomes or, at most, exhibit merely vestiges of them.

The amniote metanephros has outlet by way of a duct, the *ureter*, which develops as a forward-growing branch from the cloacal end of the mesonephric duct of the same side of the embryo. The tubular structures of the metanephros are formed partly from mesomere material lying posterior to the mesonephros and largely by outgrowth from the anterior end of the ureter. These tubules produce renal corpuscles similar to those of the mesonephros but do not possess nephrostomes. In the absence of nephrostomes drainage of waste from the coelom does not occur and the function of excretion must be confined to the renal corpuscle, where the glomerulus brings blood vessels into close relation to the lumen of a kidney tubule, and to other vascular regions of the tubule.

The adult kidney consists of the entire system of tubules—mesonephric or metanephric—of one side of the embryo, increased to great number by the branching process, each tubule tremendously elongated and much coiled, the tubules bound together by connective tissue with
blood vessels richly interspersed, and the whole complex ensheathed by connective tissue and thereby delimited from adjacent tissues of the body-wall.

The hypomere mesoderm, later backed up by a layer of connective tissue, becomes the definitive peritoneum. Its somatic layer completely lines the body-wall. Its visceral layer covers the coelomic surfaces of the digestive tube, of such derivatives of the tube as the liver and pancreas, and of all other organs which occupy the coelom. As the originally bilateral coelomic spaces expand to accommodate the developing viscera, the right and left visceral (splanchnic) layers of the hypomere meet one another in the median plane at all regions not occupied by median organs (Fig. 63). Here the two layers coalesce and, later reinforced by formation of connective tissue between them, become the system of membranes or mesenteries which connect and support the viscera. These median mesenteries are usually much more extensive in the embryo than in the adult. In later stages of development they undergo considerable reduction, especially those between the digestive tube and the ventral body wall (Fig. 67).

The mesenteries not only support the major visceral organs but they are important as bridges across which nerves and blood vessels pass from the body wall to organs which are suspended within the coelom, or they may support ducts which traverse coelomic space in passing from one organ to another—the bile duct, for example. In the earlier embryo the establishing of necessary relations of nerves, blood vessels and ducts to their appropriate organs is facilitated by the extensive system of mesenteric bridges. After proper connexions have been made, considerable regions of the mesenteries may be obliterated. A blood vessel which may appear to extend across coelomic space freely and without support is always encased in peritoneum which was left surrounding the vessel after the original supporting mesentery degenerated. The mesenteries of the early embryo to some extent serve as scaffolding, necessary during the period of construction, but removed after the work is finished.

Many complications arise in consequence of the secondary elongation, bending and twisting of the digestive tube. For example, at a given transverse section of the animal, the digestive tube may be cut two or more times (Figs. 67 and 68), one section of it lying above or alongside another and mesentery extending between adjacent regions. Lateral branches of the median mesentery may be developed in relation to lateral organs such as gonads.

Consideration of the relations of the peritoneum to the viscera makes it clear (Fig. 73) that no organ can be said to lie in the coelom except as the peritoneum investing that organ is regarded as a part of the organ. In strict morphological sense, no organ lies in the coelom. The essential organ—that is, the structure constituted of tissues specialized for a
particular function such as digestion or secretion—lies between the peritoneal sheets of the right and left halves of the body. The peritoneum is not so much the property of the organ which it invests as it is specifically the immediate wall or lining of the coelom.

The peritoneum plays a part in the development of the gonads although it is not necessarily the source of the germ cells. At the earliest stage when they are easily recognizable, the prospective gonads appear as longitudinal thickenings or genital ridges in the dorsal peritoneum, one on each side and between the dorsal mesentery and the mesonephros (Figs. 67, 68 and 74). The earlier belief that the germ cells are derived from the peritoneal layer has been shaken by evidence that they are of endodermal origin. The deeper substance of the definitive gonad is derived either from the thickened peritoneum of the genital ridge or, especially in the male, from the mesoderm of the closely adjacent mesonephros (Fig. 75). It has been claimed, however, that the earliest recognizable primordial germ cells, in embryos of various vertebrates, lie in the mid-dorsal enteric endoderm. From this location they are said to migrate.

![Diagram](https://example.com/diagram.png)
then laterally outward to enter the genital ridge. As development progresses, the genital ridges bulge more and more into the coelom and eventually the substance of the gonad becomes entirely detached from the body-wall except as the peritoneal investment of the gonad remains in continuity with the parietal peritoneum forming a two-layered supporting membrane, the mesovarium for the ovary and the mesorchium for the testis.

The gonads find outlet by way of ducts which arise in relation to the kidneys. The seminiferous tubules of the testis acquire connexion with the neighboring mesonephric tubules and thereby gain exit by way of the Wolffian duct which therefore, in adult vertebrates which retain the mesonephros, serves as a urinogenital duct. In amniotes the adult male retains, in the epididymis, that part of the embryonic mesonephros which provided connexion between the testis and the Wolffian duct. With metanephros and ureter serving the urinary function, the Wolffian duct is left as a vas deferens or sperm duct only.

The oviducts of Anamnia and Amniota are perhaps not exactly homologous. In elasmobranchs and probably some amphibians the pronephric
duct splits longitudinally, one portion of it serving thereafter as the Wolffian duct in connexion with the mesonephros while the other portion acquires, by fusion of several pronephric nephrostomes, a wide anterior opening into the coelom in the vicinity of the ovary. The oviduct (Müllerian duct) thus formed has no connection with the kidney in the adult. In other vertebrates, however, the oviduct develops as a fold of peritoneum (Fig. 75, m) closely parallel to the Wolffian duct but independent of it. The Müllerian duct, functional only in the female, develops alike for a time in both male and female embryos but only vestiges of it persist in the adult male.

The Mesenchyme. Reference has been made (pages 94, 95) to the fact that certain regions of the mesodermal somite, the sclerotome and the dermatome, are the source of cellular material which becomes detached from the somite and, becoming eventually more or less densely aggregated in the spaces between the somite and neighboring organs or layers, plays an important part in producing skeletal, connective and integumentary tissues. This secondary mesoderm ("derm" implying a sheet or layer), being usually not disposed in definite layers, is called mesenchyme. But the somite is not the only source of mesenchyme. Quantities of it are produced in all regions of the embryo and from various layers other than the somites.

Beyond question, most of the mesenchyme comes from the mesoderm. The parietal and visceral layers of the hypomere are a prolific source of it, numerous cells becoming detached from the outer (next the ectoderm) surface of the parietal layer and from the inner (next the endoderm) surface of the visceral layer. Also the endoderm contributes to the mass of mesenchyme which accumulates between the enteric wall and the adjacent layers of mesoderm. In fact, any mesodermal surface which faces toward endoderm or ectoderm and any endodermal surface which faces toward mesoderm is potentially a seat of mesenchyme formation. The ectoderm plays a minor part but, especially in the anterior region of the embryo, cells may be detached from the inner surface of the ectoderm. Evidence has been found indicating that mesenchyme of ectodermal origin participates in the development of the skeleton of the pharyngeal region.

But no mesenchyme is produced at the coelomic surface of the mesoderm or at the inner surface of the enteric endoderm. Mesenchyme in the coelom or in the enteric cavity could have no constructive significance.

Mesenchyme spreads from its place of origin and eventually is found in all parts of the embryo. Although late in origin, the importance of the part which it plays is by no means secondary. Chief among its derivatives are the following materials and structures.

Connective Tissue. Fibrous connective tissue is omnipresent in the adult vertebrate. It invests, supports, connects, separates or cushions
parts of the body. Its microscopically delicate ramifications penetrate throughout such massive structures as a liver or kidney, binding together the exceedingly tenuous tubules of those organs and serving as a basis for entrance and distribution of blood vessels. In a modified form it becomes bulky masses of subcutaneous fat. Whale blubber is presumably a derivative of mesenchyme.

**Skeleton.** Every location where cartilage or bone is destined to develop is occupied by mesenchyme. The deeper parts of the skull, the vertebral column, ribs, sternum and the skeleton of the paired appendages are first constructed of cartilage. The entire endoskeleton is permanently cartilaginous in elasmobranchs. Cartilage is a direct product of mesenchyme. Cells of the mesenchyme become cartilage cells (Fig. 76) and deposit the ground substance or matrix of the cartilage. In the great majority of vertebrates the primary cartilaginous skeletal structures are, in later development, more or less completely replaced by bone. The process of replacement involves the destruction of the greater part of the cartilage. The remnants of the cartilage are in form of a spongy meshwork whose strands become calcified and serve as a framework upon which bone is deposited (Fig. 77). The bone-producing cells, osteoblasts, seem to be derived mainly, if not entirely, from the perichondrium, the membrane which invests the surface of any cartilage. In the development of one of the long bones of an appendage, the perichondrium produces a shell of bone upon the external surface of the cartilage (perichondral bone) while extensions of the perichondrium burrow into the degenerating cartilage and provide the osteoblasts which build up endochondral bone on the calcified remnants of the cartilage. The process of ossification involves at first only the middle region or shaft of the developing long bone. The terminal regions (epiphyses) remain for some time cartilaginous and do not become wholly ossified until growth is completed.
Osteogenic tissue.

Hyaline cartilage (cells in groups).

Hyaline cartilage (cells enlarged)

Calcified matrix of hyaline cartilage.

Periosteum.

Perichondral bone.

Osteoblasts.

Osteoblasts.

Blood vessels.

Osteoclasts.

Endochondral bone.

Marrow cells.

Fig. 77.—Development of cartilage bone (primary bone). Part of a longitudinal section of a phalanx of the first finger of a human embryo of the fourth month. Ossification within the cartilage produces endochondral bone; the perichondrium deposits bone superficially to the cartilage, perichondral bone, and thereby becomes the periosteum. X220. (From Bremer, Text-book of Histology.)
Since the perichondrium is produced by mesenchyme, the bone is indirectly a derivative of mesenchyme.

In the development of certain of the more superficial bones of the cranium, the outer bones of the jaw skeleton and some parts of the shoulder girdle, no cartilage is formed. At the site of the prospective bone, mesenchyme produces a fibrous tissue whose fibers become calcified (Fig. 78). Mesenchyme cells, becoming osteoblasts, congregate on the surfaces of the strands or spicules of this calcified spongy matrix and, using it as a foundation, build up successive delicate lamellae of the calcareous material which constitutes bone. Occasionally an osteoblast will become enclosed in a minute space or lacuna between bone lamellae and persists there as a bone cell.

Most of the bones which develop in the manner last described are derived from the embryonic mesenchyme of that same general superficial layer which otherwise gives rise to the dermis (or corium) of the skin. They are accordingly called dermal bones. In course of evolution they apparently originate by expansion and fusion of the basal plates of calcareous placoid scales of elasmobranchs. Certain bones—for example, the clavicle of the shoulder skeleton—which develop without intervention of cartilage occur in positions so deep that the bones are not obviously and literally "dermal." They are called membrane bones, a term which is, however, often expanded to include all bones which arise directly from mesenchyme. Presumably deep "membrane" bones had their phylogenetic origin in dermal bones. Assuming this, all bones developed directly from mesenchymatous fibrous tissue may be called dermal, as is commonly done. It follows from all of this that no distinction can be maintained.
between "dermal" and "membrane" bone. "Dermal" seems the more significant descriptive term.

Bone resulting from replacement of cartilage is called cartilage bone. It is sometimes called primary bone because its cartilage precedes dermal ossification whose product, therefore, may be called secondary bone.

**Muscle.** Mesenchyme is the source of nearly all unstriated or "smooth" muscle whether in the walls of viscera or in the body wall. Most visceral organs are hollow. In their early embryonic stages their primary and essential walls are either endoderm as in the case of the digestive tube, lung or urinary bladder; or mesoderm as in the urinogenital ducts. The outer surfaces of these primary walls are always adjacent to regions occupied by mesenchyme. The unstriated muscle fibers which constitute the muscle layers of the walls of these hollow organs are differentiated from cells of the adjacent mesenchyme. In such organs as the stomach and uterus the muscle layers become thick and strong. They are relatively thin in a lung, air bladder or urinary bladder. The walls of the larger blood vessels in all parts of the body contain unstriated muscle whose fibers lie in planes transverse to the axis of the vessel so that their contraction decreases the diameter of the vessel. Unstriated muscle occurs in the walls of some integumentary glands, serving to expel the contents of the gland. Hairs and feathers are erected by contraction of delicate muscles attached to the follicles in which the organs are inserted. These muscles are unstriated or possibly sometimes striated in case of feathers. Most unstriated muscle of integumentary organs is derived from mesenchyme. The changes in diameter of the pupil of the eye are effected by unstriated muscle in the iris. The dilator fibers in the human iris, however, are apparently of ectodermal origin. Mesenchymatous unstriated muscle, wherever situated, is innervated by fibers from the autonomic system.

**Circulatory Organs.** The general statement that the circulatory vessels are derived from mesenchyme is probably admissible although some vessels seem to arise fairly directly from the mesoderm. There is apparently much diversity in the manner of origin of the vessels. They may arise as solid cords of cells, later becoming hollow, or they may be hollow from the beginning. The essential wall or endothelium having been established, the outer layers of connective tissue and unstriated muscle are provided by adjacent mesenchyme. The heart develops as a large blood vessel. In the region just behind that where the pharyngeal clefts are forming, the right and left hypomeres of the mesoderm push ventralwards and toward one another just as they do in a more posterior region of the body. But instead of meeting to form a median ventral mesentery, they bulge away from one another (Fig. 79) so as to give rise to a median ventral space between them. In this space accumulate
cells derived from the adjacent mesodermal layers, therefore essentially mesenchymatous in nature. These cells arrange themselves to form the very thin wall of a relatively large vessel. The wall is the endothelial lining or endocardium of the prospective heart. In some cases, at first two endothelial tubes are formed, lying side by side, later coalescing into one. The thick muscular layer (myocardium) of the wall of the heart is derived from the adjacent hypomeric mesoderm, but this muscle, unlike that of blood vessels, is striated. In details of structure it differs from the striated muscle of the body walls. The coelomic space on either side of the developing heart remains as the pericardial cavity. The visceral layer of the hypomere, not wholly consumed in giving rise to the myocardium, forms an outer layer on the wall of the heart, the epicardium, which remains in continuity with the somatic layer of the hypomere. The latter constitutes the lining or pericardium of the pericardial cavity. The pericardium and epicardium evidently correspond to the peritoneum of the more posterior region of the coelom. The right and left hypomeric layers, meeting above and below the heart, produce mesentery-like connexions (dorsal and ventral mesocardium) between the heart and pericardial walls. Later these mesocardia are largely, or usually entirely, obliterated leaving the heart in an undivided pericardial cavity. Later a transverse septum (Fig. 80) arises to wall off the pericardial cavity from the more posterior coelomic cavity.

Concerning the origin of the earliest blood cells or corpuscles in the embryo, there is some uncertainty but it seems probable that they have common origin with the walls of the vessels.

Head, Neck, Diaphragm, Tail. The development of the head region presents many problems of which the most perplexing is that of the segmentation of the head. This problem is discussed in other chapters of this book. The mesoderm of the head is less definitely organized than that of the trunk. It presents some obscure evidences of segmentation, but it is difficult to ascertain how many segments are present and their

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**Fig. 79.**—Diagrammatic transverse sections of developing heart. In A the descending right and left mesodermal hypomeres have nearly met; mesenchyme cells appear between them. In B the layers have met ventrally forming the ventral mesocardium; the enclosed mesenchyme has formed the endocardium. In C the layers have met dorsally to form a dorsal mesocardium; meanwhile the ventral mesocardium has disappeared and the right and left coelomic spaces have become the pericardial cavity. c, coelom; ec, ectoderm; en, endoderm; end, endocardium; m, ventral wall of hypomere; p, pericardial cavity; v, mesenchyme cells. (From Kingsley, Comparative Anatomy of Vertebrates.)
fate. The six muscles, consisting of striated fibers, which effect the movements of the eyeball in its orbit are developed from head mesoderm which is probably the equivalent of three somites or epimeres of the trunk. But there is nothing corresponding to the mesomere of trunk mesoderm.

The neck region, whether or not differentiated externally, corresponds approximately to that of the embryonic pharyngeal pouches. In this region there is, on each side, a lateral sheet of mesoderm corresponding, except as to its derivatives, to the hypomere of the trunk. Whereas the trunk hypomere forms no muscle other than (indirectly by way of mesenchyme) the unstriated muscle of the digestive tube and other visceral parts, the pharyngeal hypomeric mesoderm produces striated muscle

![Fig. 80. — Diagrams showing the relations of the coelomic cavities (black) in fishes (A), amphibians and sauropsida (B), and mammals (C). L, liver; P, lungs; S, septum transversum; D, diaphragm. In B the lungs lie in the peritoneal (or pleuroperitoneal) cavity; in C they occupy special pleural subdivisions of the coelom. (From Kingsley.)](image)

which constitutes an elaborate system of muscles related to the skeleton of the jaws and to the visceral skeleton which supports the gill region of the enteron. These muscles effect the movements of the jaws and of the branchial apparatus. They are commonly referred to as "visceral muscles," a designation which is, however, unfortunately misleading, for "visceral" implies a position much deeper than that occupied by certain of these muscles which lie quite superficially and just under the skin of a fish. In amniotes various muscles of the neck and facial region, including in man the very delicate superficial muscles which control facial "expression," can be recognized as derivatives of certain of the "visceral" muscles of a fish—which makes the term the more inappropriate. To call the muscles of this system "branchiomeric," as urged by H. H. Wilder, would obviate confusion.

The diaphragm of the mammal is not the exact equivalent of the septum transversum of other vertebrates. The latter arises as merely a fold of peritoneum. The diaphragm is muscular. The muscles are striated. The muscular part of the diaphragm is formed by ingrowth
from the body wall so that it is derived actually from epimere mesoderm. The somatic folds which are involved in forming the diaphragm arise far forward and shift back to the definitive position of the organ. This fact accounts for the innervation of the diaphragm by cervical spinal nerves.

In vertebrates other than mammals there are two divisions of the coelom, the pericardial and the peritoneal (abdominal or pleuroperitoneal), and the lungs lie in the posterior division (Fig. 8o). In mammals that part of the coelomic space lying on the cephalic side of the diaphragm is subdivided into three cavities, the pericardial and the right and left pleural cavity containing the corresponding lobes of the lungs.

The tail is produced by growth of ectodermal and mesodermal parts backward from the region of the blastopore or neurenteric canal. Growth of the mesoderm keeps pace with that of the neural tube and notochord. The mesoderm forms somites, more or less numerous depending on the length of the tail, but these produce only the segmental striated caudal muscle and the mesenchyme which goes into the formation of skeletal, vascular and connective tissue structures of the tail.

**Effect of Massive Yolk on Organogenesis**

In the description of the earlier embryonic stages of reptiles and birds attention has been given to the peculiarities which are imposed upon the earlier developmental processes by the massive yolk of the egg. Elasmobranchs, with their large yolk-laden eggs, exhibit similar peculiarities. Cleavage, gastrulation and the mode of origin of the mesoderm and the notochord are necessarily much affected by the presence of the bulky and inert yolk (Fig. 81). Once the germ layers have been established, however, the development of organs proceeds in vertebrates of all classes with only minor differences in details of the processes. Apparently each germ layer is capable of producing certain structures and no others, and those particular structures arise from that layer in all vertebrates, whether fish or man. Indeed, there is so much evidence of rigid necessity in the germ-layer origin of organs that, in cases where homology of adult organs is in question, the germ-layer relations of those organs are generally regarded as the safest criterion for homology. Yet at early stages of development the embryonic material may not be so rigidly determined. By appropriate operations at sufficiently early stages of embryos, both vertebrate and invertebrate, it has been proved that a certain region of germ material may be caused to produce structures other than those which it would have produced normally.

While a particular organ develops in essentially the same way in vertebrates of all classes, regardless of the quantity of yolk, yet the presence of a large yolk mass does profoundly affect the general configuration and topography of the layers of the embryo. Sections of embryos of
amphibian and bird at similar stages and at corresponding planes may appear to be so unlike as to be hardly comparable. Yet careful study of them reveals that the differences are mainly quantitative. They are

**GASTRULATION IN FORM WITH ISOLECITHAL EGG HAVING ALMOST NO YOLK—AMPHIOXUS.**

**GASTRULATION IN FORM WITH TELolecITHAL EGG CONTAINING MODERATE AMOUNT OF YOLK—AMPHibia.**

**GASTRULATION IN FORM WITH TELolecITHAL EGG CONTAINING LARGE AMOUNT OF YOLK—BIRDS.**

Fig. 81.—Diagrams illustrating the differences in gastrulation depending on whether the egg is isolecithal (having little yolk uniformly distributed) or telolecithal (having much yolk more or less concentrated toward one pole of the egg). bld., blastoderm; bld., blastocoele; bld., blastopore; ect., ectoderm; ent., entoderm; mit., cell undergoing mitosis; yk., yolk; yk.g., cells containing yolk granules; yk.p., yolk plug. (From Patten, Embryology of the Chick.)

differences in proportions and extent of layers. The essential relations of layers and developing organs are the same. View a mid-trunk transverse section of an early frog embryo and imagine that the mass of yolk
cells in the wall of the enteron is increased in diameter thirty or more times, meanwhile the layers of the splanchnopleure and somatopleure

stretching to accommodate themselves to the swollen enteron. The result would be a section essentially like the corresponding section of some bird.

Yolk is food. In an animal having an enteron, the appropriate place for food is in the enteron. In an amphibian embryo the relatively small

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**Fig. 82.**—Diagrams representing median longitudinal sections of chick embryos after incubation for approximately one day, A; two days, B; three days, C; four days, D. The four stages show progressive differentiation of the regions of the enteron and progressive constriction between the yolk-sac and the shaping body of the embryo. (From Patten, Embryology of the Chick.)
amount of yolk is contained within cells which, although more or less encumbered by the yolk, are yet capable of developmental activity. Gastrulation having established the enteron, the greater part of the embryonic food is then present, not in the enteric cavity but, even better than that, within the cells which constitute the wall of the enteron where it may be directly acted upon by the endodermal protoplasm and made available, as the blood system develops, for transportation to all parts of the growing embryo.

The enormous yolk of the egg of a reptile or bird is morphologically a part of the original ovum. But by the time cleavage of the germ disc has progressed so far as to produce a many-celled blastoderm spreading out thin and flat on the surface of the yolk, the cells of the blastoderm can be regarded as, at most, merely joint proprietors of the food supply and the yolk is essentially extra-cellular. As development proceeds, the blastoderm differentiates into the typical germ layers, the mesoderm splits to form somatic and visceral sheets with coelomic space between them, and all of these layers progressively spread over and around the non-living yolk (Figs. 86 and 87) until eventually it is entirely enclosed by splanchnopleure and somatopleure with coelom between them.

In the amphibian the food supply is, from the beginning, not only inside the embryo but, for the most part, inside the prospective wall of the enteron. In reptile and bird the food is external to the early embryo. Therefore the embryo is put to the necessity of building not only its enteron but its body wall around its prospective food.

As development proceeds the yolk is assimilated and utilized in the building of new protoplasm. It therefore steadily decreases in bulk both relatively and absolutely. As the body of the embryo begins to take form, a constriction, involving both somatopleure and splanchnopleure, appears between the yolk-sac and the remainder of the embryo (Fig. 82). The constriction deepens until the embryo presents the appearance of a
small animal having a narrow-necked globular sac suspended from the under side of the body (Fig. 83). In amniotes the amnion is concerned in this constriction (Fig. 84). As the embryo increases in size the shrinking yolk-sac is drawn up into the body. The inner wall (splanchnopleure) of the sac finally constitutes a small region of the wall of the intestine. In elasmobranchs the somatopleure of the yolk-sac finally flattens out and persists as a part of the abdominal wall. In reptiles and birds the corresponding region of the somatopleure is concerned in the formation of the amnion and chorion. At the time of hatching the somatopleure is ruptured at the constriction between the definitive body and the extra-embryonic structures and everything external to the rupture is abandoned.

Embryonic and Fetal Membranes

In the general account (pages 51–55) of the reproductive arrangements in vertebrates mention was made of the embryonic membranes, amnion, chorion and allantois, which occur in reptiles, birds and mammals. The foregoing account of the origin of the germ layers and the shaping up of the embryonic body now makes possible more explicit statements concerning the manner of formation of the embryonic membranes.

All eggs are invested by protective membranes or coverings which are either produced by the egg-cell itself or are deposited about the egg by secretory activity of the walls of the oviduct. Such membranes consist of material which is not cellular and not in any sense living. They have merely passive functions. The unique thing about these other membranes, the amnion, chorion and allantois, is that they are produced by the germ layers at a relatively advanced stage of the embryo, they are therefore constituted of living cellular material and they are actively concerned with such important functions as nutrition, respiration, excretion and circulation.

The amnion and chorion of reptiles and birds are simultaneously produced by an up-rising fold of the embryonic body wall or somatopleure (Fig. 84). A chick embryo in the second day of incubation shows a crescentic transverse fold of somatopleure just beyond the head (Fig. 85). As development goes on, the head grows forward into the fold and at the same time the fold grows backward over the head. Meanwhile the fold extends backward along either side of the embryo. On the third day a similar fold arises just beyond the tail and begins to grow forward over the caudal part of the embryo. Head-fold and tail-fold having become joined by lateral folds, the embryo is then surrounded by one continuous fold which grows in centripetally from all directions and finally completely encloses the embryo. Where opposite edges of the fold meet above the embryo they become coalesced. Reference to
Fig. 84.—Diagrams illustrating the development of the amnion and allantois. The upper Figure (A), a cross section of an earlier stage, shows the amniotic folds rising above the embryo. The lower Figure (B), a longitudinal section of a later stage, shows the allantois as well as the completely closed amnion. In most mammals the fused allantois and serosa (chorion) form the foetal placenta. Ectoderm in diagram is striped, mesoderm stippled in black, endoderm stippled in white.
Figs. 86 and 87 will serve better than description to make clear the relations of layers and spaces resulting from the development of these folds.

The somatopleural folds which give rise to the amnion and chorion are, at the time of their formation, a living part of the embryo. The statement that the folds eventually enclose the embryo anticipates the fact that the amnion and chorion do not become any part of the adult. Therefore "the embryo" which the folds enclose is the definitive body region of the embryo. Everything else is conveniently referred to as extra-embryonic.

Since it is a fold of somatopleure which covers the embryo, there are necessarily, at the completion of the process, two layers of somatopleure external to the embryo. The inner one, the amnion, has its ectodermal surface toward the embryo. The outer one, the chorion or serosa, has its mesodermal surface toward the embryo. Between outer and inner layers of the fold the mesoderm-lined space is obviously a part of the coelomic cavity but, because it becomes no part of the adult coelom, it is described as "extra-embryonic."

The allantois is a sac formed as a mid-ventral outgrowth from the hind or cloacal region of the embryonic enteron (Figs. 84, 86–88). It is
therefore a product of the splanchnopleure and is lined by endoderm. It grows rapidly, swelling out into the space between the yolk-sac and the chorion and eventually acquires more or less extensive and intimate fusion with the chorion. In the apposed mesodermal layers of the allantois and chorion is developed a rich network of fine blood vessels which are connected by the allantoic arteries and veins to the main blood vessels of the definitive body of the embryo. In this way an extensive circulation is

![Diagram of extra-embryonic membranes of the chick](image_url)
established in close relation to the inner surface of the shell of the egg of a reptile or bird, providing for exchange of respiratory gases between the blood and the external medium. As development proceeds the albumen

becomes much reduced in bulk. The expanding allantois apparently pushes the remainder of it out of most of the peripheral territory within the egg shell and causes it to become concentrated at one spot (Figs. 86
and 87) thus leaving the greater part of the inner surface of the shell membrane free to make close contact with the vascular and respiratory chorio-allantoic membrane. The now localized remnant of albumen is gradually absorbed by the embryonic layers adjacent to it.

Before the time of hatching the shrinking yolk-sac is drawn up into the growing body. The umbilical stalk—that is, the whole complex of connections between the definitive body of the embryo and the extra-embryonic membranes—becomes narrowly constricted. At time of
hatching the amnion and the slender neck of the allantois are ruptured at the umbilicus. As the young animal emerges into free life the amnion and chorion and the extra-embryonic part of the allantois are abandoned. The proximal portion of the allantois, remaining within the body, becomes enlarged and serves as the urinary bladder of such adult reptiles as possess that organ. In birds, the adult having no urinary bladder, the proximal remnant of the allantois degenerates.

Among mammals there is considerable diversity as to the manner of origin of the amnion and chorion. Once established, however, these membranes possess the same relations to the germ layers and to the definitive body of the embryo as in reptiles. The allantois develops, as in reptiles, from the cloacal region of the enteron. An abortive yolk-sac is present but devoid of yolk except in those presumably primitive mammals, Ornithorhynchus and Echidna, whose manner of development is essentially reptilian.

In most eutherian mammals the allantois expands until it becomes apposed to the inner surface of the chorion and the two membranes undergo more or less extensive fusion of their contiguous mesodermal layers.
The main facts concerning the development of a placenta by the chorio-allantoic membrane have already been stated (see page 54). The essential structures of the placenta are the highly vascular villi produced by the chorio-allantoic membrane (Fig. 89). These villi may be merely lodged in depressions in the uterine wall or they may pierce more or less deeply into its tissues. Their terminal regions may lie within a vascular connective-tissue layer of the uterus and the surface of a villus may be in close contact with the very thin wall of a blood vessel. These deeper penetrations of the villi are attained at the expense of actual eroding or destruction of uterine tissue. In extreme cases there is destruction of walls of uterine blood vessels and the extravasated blood fills large spaces or sinuses in the uterine wall. The branched ends of villi project into these sinuses so that the villous surfaces are directly bathed by maternal blood, an arrangement providing maximum efficiency in the exchange of materials between fetal and maternal blood. In general the extent of penetration of the villi and the degree of intimacy of their relation to the maternal blood is an index of the degree of specialization of the placenta. In the human placenta the villi are long, much branched, and exposed directly to maternal blood which fills capacious sinuses in the uterine wall.

Mammals exhibit various types of placenta, depending on the distribution of villi in the chorionic surface. When the villi are uniformly distributed over the chorion, as in the horse, pig and many other ungulates, the placenta is called diffuse. In many ruminant ungulates, such as cattle, the villi are localized in numerous patches or clusters of varying sizes—the cotyledonary placenta. In carnivores the placenta usually takes the form of a broad band or zone encircling the chorion at a position about midway between head and tail of fetus—the zonary placenta (Fig. 90). A discoidal placenta, in which villi are restricted to a single relatively large area of the chorion, occurs in insectivores, bats, rodents and higher primates including man.
The terms deciduate and non-deciduate, as applied to the placenta, refer to conditions which obtain at time of birth. A fetal placenta whose villi do not penetrate deeply into the uterine wall separates from it readily and without loss or destruction of uterine material. Such a placenta, called non-deciduate, occurs in most ungulates, in the whale and dugong, and in lemurs. When, however, the fetal villi are deeply imbedded in the uterine wall, at time of birth the involved layer of the uterus is split off and discharged with the fetal placenta. This deciduate condition of the placenta occurs in the carnivores, in the elephant, and commonly in animals having a placenta of the discoidal form.

In marsupial mammals few or no villi are produced on the chorion and there is merely contact of chorion and uterine wall without actual connection. Usually, too, the chorion does not become vascular. It is a noteworthy fact, however, that in some marsupials (Perameles) the allantois, in conjunction with the chorion, forms a limited vascular area which becomes closely related to the uterine wall, while in others (Dasyurus) it is the splanchnopleure of the yolk-sac which joins the chorion and forms a placenta-like vascular area which is apposed against the uterine wall. These facts suggest that in early mammals both the yolk-sac and the allantois were potentially placenta-forming. In higher Primates, however, the allantoic sac is rudimentary and the fetal portion of the placenta is of chorionic origin only; yet the allantois develops far enough to bring its blood vessels into connection with the chorionic vessels of the placenta.

At time of birth the amnion and chorion are ruptured and the young mammal is expelled, along with the amnionic fluid, by muscular contraction of the uterine walls. The amnion, chorion, allantois, fetal placenta, and more or less uterine tissue in a placenta of the deciduous type are discharged later as the "after-birth." The umbilical cord is the much elongated and attenuated connexion between the body of the fetus and the extra-fetal membranes. It includes somatopleure, extending from the fetal body wall to the amnion, and the stalks of the yolk-sac and allantois with their vitelline and allantoic blood vessels. During later fetal life the yolk-sac degenerates. Its cavity is obliterated, its blood vessels close and it becomes reduced to a slender solid cord contained within the umbilical cord. After birth the umbilical cord is, in one way or another, severed and such remnant of it as remains attached to the body shrivels up and is sloughed off at the navel. That portion of the allantois remaining within the body becomes the urinary bladder.

Functions of the Embryonic and Fetal Membranes. The amnion is protective in mechanical ways. It provides a fluid medium in which the embryo is suspended and so protected from deforming pressures and impacts. The amnionic mesoderm produces unstriated muscle fibers
which impart contractility to the amnion. Its gentle undulations keep the amnionic fluid moving, thus preventing local stagnation in the fluid and possible adhesions of embryonic parts.

The main importance of the chorion is in its serving, in conjunction with the allantois (rarely the yolk-sac), to form respiratory, excretory and nutritive membranes.

The allantois in reptiles and birds is the embryonic respiratory organ. In viviparous reptiles its circulation may pick up some nutrient material from the uterine wall or fluids. The cavity of the allantois serves as receptacle for waste from the embryonic kidneys. Consistently with this function its proximal portion may persist, after hatching, as the urinary bladder.

In mammals, although primitively the yolk-sac may have had placental possibilities, the allantois came to be the all-important agency in establishing the placenta. The placental villi are primarily chorionic but their vascular structures are usually derived from the allantoic circulatory system. In the placenta, then, are concentrated the vital functions, nutrition, respiration and, at least in part, excretion.

The vascular splanchnopleural wall of the yolk-sac is the essential nutritive membrane in reptiles, birds and primitive mammals, but becomes rudimentary in later mammals.

**SUMMARY AND INTERPRETATION**

A backward glance over the foregoing account of vertebrate development suggests emphasis on the following points.

Cleavage may be described as a process of mobilizing the agencies within the fertilized egg. The smallest egg is a large cell. Nutrition, respiration and excretion involve the limiting surfaces of cells. Metabolic rate is high during development. Cleavage increases cell surface. Nuclear material is certainly somehow important. Cleavage increases the quantity of nuclear material both absolutely and relatively to the amount of cytoplasm.

In the blastula stage the embryonic material becomes arranged in form of a layer. The increased exposure of surface to the external medium favors metabolism. The disposition of cells in a layer is especially significant in view of the fact that the adult animal is constituted essentially of layers of cells.

Gastrulation transforms the one layer of the blastula into two, an outer and an inner. The cavity of the blastula has no permanent significance. The new cavity produced by gastrulation is the definitive enteron. The ectoderm, potentially protective and nervous, provides for necessary relations of an animal to its environment; the endoderm is nutritive. At the gastrula stage, therefore, a minimum metazoan animal is established.
Respiration and excretion may be carried on at all surfaces, without specialized organs, as in Coelenterates.

Ectoderm and endoderm provide for the bare necessities of animal life. The addition of a mesoderm provides for some of the luxuries, especially that of being large and powerful. Swift movement of massive bodies demands powerful motors. Muscles are necessarily bulky. To meet the metabolic requirements of cells which are deep within some bulky mass of tissue such as a muscle, a circulatory system is necessary. Blood carries to deep-seated tissues the food and oxygen which are otherwise not directly accessible to them, and removes wastes from them. In order that the blood stream of a large animal may be properly supplied with oxygen and freed of waste materials, it must be related to efficiently specialized respiratory organs—gills or lungs, and excretory organs, kidneys. With increase in bulk and in structural complexity provision for mechanical support becomes necessary. There must be tensile connective tissues and rigid supporting structures—skeleton.

Mesoderm is the main source, directly or indirectly, of these organs which are of accessory nature. There are, admittedly, small animals which possess a mesoderm, but there are no very large animals which do not have mesodermal structures.

Mesoderm produces directly the striated musculature of the body wall and the essential tubules of the kidney. Indirectly, by way of the mesenchyme (receiving some very minor contributions from endoderm and ectoderm), arise circulatory organs, connective tissues, and skeleton. Respiratory organs are essentially vascular and insofar derived from mesenchyme, but aeration of the respiratory blood demands the intermedation of a layer which is directly or indirectly in relation to the external medium. The endoderm plays this role for internal gills and lungs, the ectoderm for external gills. It is particularly the pharyngeal endoderm which is the seat of development of specialized respiratory organs, gills and lungs, in vertebrates. In general, therefore, the vertebrate endoderm is concerned with the business of dealing with those materials, food and oxygen, which the animal must receive from the environment.

There may seem to be some inconsistency between the fact that the notochord, that most fundamental structure of the vertebrate skeleton, is derived wholly or in part from endoderm and the fact that cartilage and bone, the definitive skeletal materials of vertebrates, are derived from mesenchyme. But the notochord is very ancient. Its presence and condition in such animals as Amphioxus and the urochordates makes that certain. While the notochord is not derived from already-formed mesoderm, it develops, not only in Amphioxus but in all vertebrates, simultaneously with the mesoderm and the two are very closely similar in their
manner of origin in the embryo. But Amphioxus has very little that can be regarded as corresponding to the mesenchyme of vertebrates. Unquestionably cartilage and bone are phylogenetically new skeletal materials as compared to the notochord. Consistently with this assumed fact, the mesenchyme, which is the embryonic source of cartilage and bone, is the last of the germinal building materials to be differentiated in the embryo.

The principle of "recapitulation" was formulated by Ernst Haeckel (1874) in the phrase "Ontogeny is a brief repetition of Phylogeny." Nineteenth century biology was perhaps inclined to over-work the idea. Nevertheless many facts of vertebrate development justify, or even compel, the inference that there is some direct relation between the phylogenetic and the ontogenetic order.

Early embryos of reptiles, birds and mammals develop briefly transitory pharyngeal clefts (or pouches). These clefts are not accompanied by the formation of functional gill structures such as occur in connexion with the pharyngeal clefts of adult fishes. But they are closely similar to those embryonic pharyngeal clefts which in fishes come to be associated with vascular filaments and the other structures which, altogether, constitute functional gills.

The notochord is developed in the early embryo of all vertebrates. In shark-like fishes (Elasmobranchii) wholly cartilaginous vertebrae are developed around the notochord of which traces persist in the adult. In reptiles, birds and mammals the embryonic notochord becomes surrounded by cartilaginous vertebral structures. In later development the cartilage is replaced by bone. The adult vertebrae consist of solid bone. Ordinarily no traces of notochord remain. Nowhere else in the body is bone preceded by any such structure or tissue as notochord. Many bones other than vertebrae are produced directly from mesenchyme without the intervention of cartilage. It seems clear, then, that in general the formation of bone is not inherently dependent on preëxisting cartilage or notochord.

Elasmobranch fishes have an all-cartilaginous skull. The skull of adult amniotes is nearly all bone. But the amniote embryo develops first a cartilaginous skull whose general plan resembles that of an elasmobranch. In later development the cartilage is almost wholly replaced by bone and numerous dermal bones are developed superficially to the cartilage. The geologic record shows that elasmobranchs existed long before any vertebrates with bony skeletons came upon the scene.

In the phylogenetic history of the axial skeleton of vertebrates, notochord is the oldest structure and bone is most recent. In the development of the bony vertebral column of a modern animal, notochord, cartilage and bone succeed one another in phylogenetic order. In all
vertebrate embryos the notochord is one of the first three organs to be established, the two others being the enteron and neural tube. It appears simultaneously with the mesoderm. But it is not until long afterward that mesenchyme, the source of cartilage and bone is produced. The early formation of the notochord in the vertebrate embryo and the relatively late appearance of mesenchyme, followed by cartilage and bone, is in accord with the phylogenetic order.

It is, however, not safe to assume that the embryo always adheres to the phylogenetic order. Cartilage is a very ancient skeletal material. The amnion is phylogenetically recent. Yet in an amniote embryo the amnion develops long before any cartilage is formed. Some of the departures from phylogenetic order are so glaring as to shake faith in the principle of recapitulation. Yet, on the whole, it would seem that the instances of adherence to the phylogenetic order are more striking and more significant than the departures from it.

It cannot be too much emphasized that the embryo of a later vertebrate resembles or "recapitulates" not the adult stage of an ancestor but the embryo of that ancestor. The mammal embryo does not have gill pouches; it has pharyngeal pouches similar to those which, in a fish embryo, develop into gill clefts. Karl Ernst von Baer in the first quarter of the nineteenth century recognized the fact that the early embryos of vertebrates of all classes are fundamentally similar and that the special features which identify the animal as a member of a particular class appear relatively late in ontogeny.

The embryo whose development may be observed in the laboratory today has had unbroken protoplasmic continuity with ancestors hundreds of millions of years remote. Herein is the physical basis for recapitulation. Nevertheless protoplasm seems such a fragile and labile thing that it is almost incredible that it should be able to retain the impress of structures which, long ages ago, lost all functional significance for the adult animal.
CHAPTER 3

HISTOLOGY

The material, source and basis of everything that an animal is or does is the chemically specific and complex "living substance," protoplasm. In such very small animals as Protozoa the protoplasm of the minute body exhibits an organization similar to that of a single one of the structural subdivisions or "cells" of the body of a large animal. Within the body of one of these so-called "unicellular" animals there is more or less localizing of functions and a corresponding structural differentiation of regions. There may be contractile fibrils, digestive vacuoles, excretory vacuoles and other localized intracellular organs. Similarly, the body of a large animal is locally differentiated for the carrying on of various functions. The specialized regions, more or less definitely delimited from one another and each characterized by a configuration which is consistent with its special function, we call organs. But these organs, in contrast to the intracellular organs of a protozoan, comprise many cells, and the cells of any one organ, so far as they are concerned in carrying on one common function, all exhibit intracellular differentiation of the same kind. Such a group or system of cells, coordinated in one common function and alike in their internal differentiation, constitutes a tissue.

An ideally simple organ would consist of only one tissue. As a matter of fact, nearly all organs are concerned with more than one function. An organ's primary function usually demands certain accessory functions and a corresponding diversity of tissues enters into the constitution of the organ. The primary function of a liver is secretion of bile. But secretion calls for blood supply, and a complex of hepatic tubules and blood vessels requires mechanical support. Therefore vascular tissue and connective tissue make up a large part of the substance of the liver. In a stomach, the primary tissue is the digestive epithelium. Muscular, nervous, vascular and connective tissues play accessory but nevertheless necessary roles. Vascular and connective tissues enter into the constitution of all major organs. A certain tissue may be the primary and essential tissue in one organ and occur as an accessory tissue in another organ. Nervous tissue is the essential tissue in a brain or spinal cord but it appears as an accessory tissue in nearly all other organs.

Anatomy deals with organs as such. It considers their form, relations and all those grosser features of structure which are external to tissue structure or cell structure.
**Histology** concerns itself with the internal and specific structure and organization of tissues. Since the tissue is constituted of cells, histology is necessarily concerned with those specific intracellular differentiations which collectively create a tissue.

**Cytology,** narrowly defined, deals with cells as such—that is, with that fundamental cell mechanism which is common to all cells and independent of tissue specialization. In practice, however, it is impossible to maintain a sharp distinction between cytology and histology. The anatomist, too, never hesitates to become, upon occasion and temporarily, a histologist or a cytologist.

Most vital functions involve **the surface between protoplasm and the medium external to it.** Food enters from without. Respiratory gases pass in and out. Waste is expelled from the surface. Special secretions are produced at the surface. External forces impinge upon the surface and give rise to internal progressive changes (nerve conduction) which may result in a reaction directed toward the exterior. Consistently with these facts, as the size of animals increases above that of the unicellular protozoans the substance of these larger animals is so disposed as to present, directly or indirectly, an adequate amount of surface to the exterior. **Indefinite increase in size of cells and nuclei is rendered impossible by the necessity of maintaining appropriate relations of cell surface to cell volume as well as of nuclear surface to nuclear volume,** for the necessary interaction of nucleus and cytoplasm must take place through the nuclear membrane. Therefore the protoplasm of the larger animal must be subdivided into many cells.

In the preceding chapter on embryology it was pointed out (page 123) that a large and powerful animal necessarily possesses various specialized organs. To say that an animal is large because it has many organs and is complex is the reverse of the truth. Attainment of relatively large size together with capacity for powerful movement and diversified activities compels the differentiation of various organs and results in a high degree of anatomical and histological complexity. Protoplasm being what it is and under necessity of maintaining certain surface relations with the exterior, larger animals **must be** multicellular and **must be** complex.

Among the coelenterates are found the simplest of multicellular animals, consisting of two layers of cells, an outer which is essentially protective and an inner which is nutritive. The double wall encloses a cavity which has a single external opening for admission of food and expulsion of waste.

The gastrula is a form attained by the early embryo of nearly all metazoan animals, both invertebrate and vertebrate. At the gastrula stage all of the embryonic material is arranged in two layers, an ectoderm, prospectively protective and nervous, and an endoderm, nutritive. The
double wall encloses a cavity which is the primitive enteron. Very soon the gastrula adds a mesoderm, a third layer, and for some time thereafter all of the embryonic material continues to be disposed in layers of cells more or less widely separated by spaces. There is no important departure from this arrangement until the myotomes begin to thicken, preparatory to forming muscle, and mesenchyme cells begin to aggregate around the notochord and neural tube preparatory to forming skeleton—and by this time the circulatory system is beginning to develop.

Most of the organs of the adult animal are hollow. They contain something or they convey something—food, air, blood. Even such organs as the liver and pancreas, upon casual inspection apparently quite solid, are minutely hollow. The essential liver tissue consists of tubules whose bore is, however, exceedingly small. Upon the other hand, muscles are solid. Connective and skeletal tissues may form bulky solid masses—solid, that is, except insofar as they are penetrated by blood vessels. Bone may, indeed, contain cavities, but these cavities have not the same significance as those of such organs as, for example, blood vessels whose cavities are essential to the functioning of an organ whose tissues are actively alive. Fully developed bone consists mainly of non-living material and the cavities within it have a merely passive mechanical significance. The occupation of bone cavities by a blood-forming marrow makes advantageous use of what might otherwise be mere waste space in the animal, but this marrow tissue has no direct relation to the skeletal function of the bone.

Such nervous organs as brains, ganglia, central nerve cords, and nerves need not be hollow and ordinarily are not. The hollowness of the brain and spinal cord of the adult vertebrate is an incident of the development of those organs from an embryonic neural tube. The cavities of the brain and cord serve as a channel for a cerebro-spinal fluid which has some metabolic significance, but in the absence of such cavities the metabolic needs of the nervous tissue could doubtless be provided for, as in other massive tissues, by the usual blood and lymph channels.

Every surface of the animal, whether apposed directly to the external medium or to some internal cavity, is a critical region of the organism. It is a surface on the one side of which is living substance while on the other side of it may be food, water, air, blood or something else between which and the protoplasm is being carried on some vitally necessary activity—digestion, respiration, absorption, secretion, excretion, diffusion. Or it may be a surface at which the underlying protoplasm deposits a non-living substance which serves as a passive mechanically protective barrier between the living substance and the adjacent space, as when skin produces an external cuticula or a horny layer for protection against external agencies, or as when the lining of a bird’s gizzard deposits a tough
horn-like layer which prevents abrasion of the walls of the organ when its powerful muscles grind up hard seeds with the aid of ingested pebbles.

Provision for the adequate carrying on of these diverse and important surface activities can be afforded only by the presence of a superficial membrane constituted of living material and specialized appropriately for the functional requirements of the particular surface. Tissue highly specialized for motor, skeletal or nervous functions could not at the same time meet the requirements of a surface layer. Consequently, with very rare exceptions, every free surface of an animal, external or internal, is the surface of a more or less specialized cellular layer, an **Epithelium**.

**EPITHELIAL TISSUES**

In view of the foregoing considerations, it is clear that epithelia are tissues of primary importance. They are the immediate agencies concerned in the necessary interactions between protoplasm and the materials and agencies external to it. They provide a barrier against invasion by disease-producing organisms. They are important also in serving to seal the surfaces of the animal against leakage of the omnipresent intercellular lymph of deeper tissues. If human skin is abraded so slightly as not to cause bleeding, nevertheless a clear watery fluid, lymph, exudes. The outer portion of an intact epidermis prevents such leakage.

Epithelia are, in double sense, the most primitive of tissues. The smaller simpler coelenterates consist merely of an outer and an inner epithelium. There is much reason for believing that all other metazoans are descended from some ancient and primitive coelenterate. The gastrula of animal embryos consists of two epithelia. All tissues of the adult are derived from the primary ectoderm and endoderm. Hence, presumably in phylogeny and certainly in ontogeny, all tissues are derived from epithelia.

It is evident, therefore, that epithelium provides for all animal needs, and therefore all-epithelial animals may and do exist. But there are no non-epithelial animals—unless protozoans be considered as such, but even a unicellular protozan may be regarded as a minimum epithelium, being one cell thick and one cell in extent!

The outer layer of the gastrula, while it is the source of various glandular and other structures which attain a deeper position, otherwise persists as the **epidermis** which is the external epithelium of the adult body. The inner layer of the gastrula, which gives rise to various organs such as the liver, pancreas and lungs which grow outward from the enteron, otherwise persists as the lining of the digestive tube, the **digestive epithelium**, which is the innermost epithelium of the adult body. These two layers, then, the very thin epidermis and the even thinner digestive epithelium, which together constitute only an extremely small fraction of the bulk of the
animal are the gastrular layers persisting in their original relations to space. By far the greater part of the massive adult has been inserted between the two primary layers.

In view of the foregoing facts, the significance of the outer and innermost epithelia of the body and their immediate derivatives is such that attempts have been made to recognize it in terminology. The embryologist, Wilhelm His, in 1865, proposed to apply the term *endothelium* to all mesodermal limiting layers, thus restricting "epithelium" to the ectodermal and endodermal epithelia and their immediate derivatives. At present, however, the term endothelium is rarely used except to designate the lining layer of blood vessels and lymphatic vessels. To designate the mesodermal layer lining the coelom, that is, the peritoneal epithelium, the term *mesothelium* has been proposed.

In present usage, the term endothelium may be correctly applied to the lining layer of blood vessels and lymphatics. "Mesothelium" may be used for the peritoneal epithelium.

In certain localities are found tissues whose cells, in their appearance and arrangement, resemble epithelial cells, but they do not abut upon a cavity. The insulin-producing "islands" or "islets" in the pancreas, the deeper tissue or medulla of the suprarenal gland, and the tissues of some other endocrine glands are of this nature. These are glands whose secretion is not collected in a cavity but transmitted directly to the blood in closely adjacent vessels. To such tissues, which are not typically epithelial, is applied the adjective *epithelioid*.

The most notable exception to the rule that all free surfaces of the animal are epithelial is found in lymph glands whose irregular internal spaces do not have a continuous endothelial covering. Its absence is intelligible. Cells proliferated from the spongy deep tissue of these glands float away in the lymph stream to become new white blood cells. An
endothelium would interfere with easy release of these cells. Also in the spleen and smaller blood glands—that is, glands whose spaces are occupied by blood instead of lymph—there is more or less interruption of the endothelial lining.

Epithelia carry on functions of most diverse kinds. The diversity is reflected in the structure of epithelia. Only a few of the more general features of structure can be mentioned here.

**Simple Epithelium.** Most epithelia are only one cell in thickness. Such layers are termed **simple**. There is, however, great variation in the thickness of simple epithelia. The cells may be of such form that, seen in sections perpendicular to the surface, their outline is approximately square. Such an epithelium is commonly called cuboidal (Fig. 92), but unfortunately so, for the cells are not cubes. They are prisms of usually hexagonal form and with bases at opposite surfaces of the layer. Or a simple epithelium may consist of greatly elongated cells with long axes extending from base to free surface of the layer (Fig. 91C). Such a layer is called **columnar**—but incorrectly called cylindrical for the cells are elongated prisms, approximately hexagonal. At the extreme of thinness are epithelia each of whose cells is a broad flat plate, hexagonal in outline (Figs. 91B and 92), but so thin that, as seen in section perpendicular to the surface, even under high power of a microscope it has scarcely perceptible thickness except where the nucleus, itself much flattened, occasions a bulge in the outline. Such a layer is called **flat** or **squamous**.

Many columnar epithelia depart from being strictly "simple" in having relatively small or short **basal cells** interposed among the basal ends of the taller columnar cells (Fig. 93).

Most of the ectodermal and endodermal epithelia are relatively thick, ranging from tall to low columnar. The squamous form occurs commonly...
among the mesodermal epithelia. The endothelium of blood vessels is one of the thinnest of layers. In studying sections of a tissue it is often difficult to ascertain whether or not a certain space in the tissue is lined by endothelium. The peritoneal epithelium of a frog tadpole is of utmost thinness.

In such organs as the digestive tube and urinary bladder the lining epithelium is stretched as the wall of the organ becomes distended and the form of the individual epithelial cell varies accordingly. A cell which is tall-columnar when the organ is contracted may be cuboidal or even flat when the wall is stretched.

![Image](image_url)

**Fig. 93.—Columnar ciliated epithelium from human trachea.** Most of the cells are slender, with axes more or less curved, and extend from the basement membrane to the free surface of the epithelium. Occasional short cells, basal cells, lie at or near the basement membrane and do not extend to the free surface. Several swollen mucous cells ("goblet" cells) are shown. (From Bremer, Text-book of Histology.)

**Stratified Epithelium.** On Amphioxus, a slender marine animal only four or five centimeters long, an epidermis one cell thick affords adequate protection. On an elephant it would not. In such large arthropods as crabs and lobsters the epidermal epithelium is simple but it attains considerable thickness by virtue of the fact that its columnar cells are exceedingly tall. These cells secrete the characteristic "shell" consisting of organic chitinous material hardened by deposit of calcium salts. As the animal grows, the shell is periodically cast and, until the new shell becomes hardened, the animal is in a somewhat precarious "soft-shelled" state. While this arrangement serves the crab passably well, it would have obvious disadvantages for, again, the elephant. Certain surfaces of large heavy animals are exposed to excessive mechanical friction and impact. The inevitable loss of material at the surface is best compensated for by a
stratified epithelium whose lower layers persistently grow to replace the loss.

A stratified epithelium may be two or several or many cells in thickness (Fig. 91, D–F). In all vertebrates the epidermis is stratified (Fig. 94). Its thickness varies with the size and habits of the animal, and in a particular animal it varies locally depending upon the degree of exposure to mechanical wear. The epithelial lining of the vertebrate mouth, pharynx and esophagus is stratified. Sebaceous glands, associated with the roots of hairs, have walls several cells in thickness. The deeper cells, becoming quite filled with the oily secretion, break down and pass out with the discharged product of the gland. The outer cells replace those lost. In general, an epithelium which, for any cause, is subject to loss of cells at the surface, is likely to be stratified. The fact remains, however, that in fishes there is no constant or periodic shedding of epidermal material and yet the epidermis is stratified.

The cells of the bottom tier in a stratified epithelium are usually columnar (Fig. 95), their deeper ends resting on a non-protoplasmic basement membrane which gives the layer a flat and smooth surface. At the free surface of the epithelium the cells are more likely to be flat or squamous. In a thick stratified epithelium the cells of several or many of the outer layers may be more or less flattened (Fig. 95). The form of cells in the intermediate level of the epithelium is usually such as would result from crowding tightly together a mass of compressible spheres, that is, polyhedral. And yet the cells are not actually packed tightly together. They are separated by excessively thin intercellular lymph spaces through which seeps lymph derived from underlying blood vessels and serving to provide for the metabolic needs of the individual cells. Cells on opposite sides of the intercellular space are connected by most delicate strands of solid, or at least dense, substance. Presumably protoplasmic, the strands are called protoplasmic bridges or plasmodesms.

Epithelium, even when stratified, is very rarely vascular. Nutrition, respiration and excretion of its individual cells depend on movement of intercellular lymph derived from blood vessels of some adjacent vascular connective tissue. In amphibians, however, the skin is more or less important as a breathing surface. In the lung-less salamanders, also gill-less
in the adult stage, the integument and the pharyngeal lining carry on all of the respiratory interchange. Accordingly capillaries penetrate to some extent into the epidermis and pharyngeal epithelium, thereby bringing blood into closer relation to the external medium.

Many epithelia, although "simple" in the sense of being only one cell thick, are not the ideally simple tissues of the definition (page 126), constituted of cells all "alike in their internal differentiation." Among the

![Fig. 95.—Epidermis from the sole of the foot of an adult man. Section perpendicular to surface of skin. External to the stratum germinativum, the strata show successive stages in the production of the stratum corneum. X360. (From Bremer, Text-book of Histology.)](image)

special functions of an epithelium are the following: (1) production of a superficial covering of protective, non-living, mechanically resistant substance; (2) production of special secretions such as mucus; (3) reception of external stimuli; (4) provision for motile activity. Two or more of these functions may be carried on by one "simple" epithelium or by a stratified epithelium. Within the epithelium, then, cells will exhibit differentiation of as many types as there are functions.

(1) Most epithelia produce at the free surface a protective covering which ranges from a very thin and delicate cuticula, such as occurs on the epidermis of a small fish, to the massive horny layer on a large reptile or the hoof of a horse.
A cuticula is a dense, tough or hard material formed at the exposed surface of an epithelial cell. The cuticular products of adjacent cells are perfectly continuous thus giving rise to an uninterrupted layer over the epithelium. Such a layer occurs, as stated above, on the stratified epidermis of fishes (Fig. 94), and is found also, in varying degrees of development, on many internal epithelia.

Keratin is a nitrogenous organic substance which may be formed by epithelial cells. It is the basis of horny structures. Its most characteristic development is seen in the epidermis of vertebrates. Produced within the cell, the keratin is deposited in the peripheral region of the cell and at the expense of the cytoplasm. As the process reaches its limit, the nucleus and remnant of cytoplasm die and dry up. What was a living cell is then merely a minute horny scale—in contrast to the fact that cells which produce a cuticula remain alive. As the keratin is deposited, adjacent cells somehow become strongly adherent so that the entire keratinized or “horny” layer (stratum corneum) acquires a high degree of mechanical resistance. The process may involve only the outermost tier of cells of the epidermis, as in some amphibians, or, as in reptiles, several or many of the upper layers of cells become horny. On the human body the stratum corneum varies from a thin and flexible layer, as on the back of the hand, to a thick hard and tough layer, as in the callosities of the palm and sole (Fig. 95).

The stratum corneum is one of the most important epithelial products of a vertebrate. Fishes have merely a cuticular outer layer on the epidermis. Apparently amphibians introduced the stratum corneum. The characteristic superficial scales of reptiles, and feathers, hair, claws, hoofs, nails and the hollow horns of ruminant ungulates are all differentiations of the stratum corneum—they are epithelial products.

In amphibians and reptiles the horny layer is shed periodically and either entire or in large fragments. In birds and mammals minute particles of the layer are constantly sloughing off. The material thus lost is replaced by growth in the deeper part of the epidermis. In animals which shed periodically, a new horny layer is well established beneath the old before the old is shed. The animal therefore passes through no such critical period as the “soft-shelled” stage of a crab. It is this ease of repair and replacement of the outermost layer of the body which makes the stratum corneum incomparably superior to a cuticular layer for the uses of large heavy land animals.

Calcified structures may be formed by an epithelium. The shells of mollusks are epidermal products. In vertebrates the enamel which caps the spine of a placoid scale of a shark and covers the crown of a tooth is an epithelial product. But, in contrast to cuticular and horny layers which are produced at the free surface of an epithelium, enamel is deposited at
the basal surface and in coordination with the building of the dentine of the scale or tooth by the adjacent dermal or mesenchymal layer (Fig. 96).

(2) A glandular epithelium is one in which certain of the cells are specialized for secretion. Single glandular cells may be scattered more or less abundantly throughout an epithelium, either simple or stratified. In stratified epithelium such cells are at or near the surface (Fig. 94, u) and open upon it, usually a prolonged and narrow extension of the cell serving as a ductule. The mucus which coats the surface of an earthworm or fish is produced by such unicellular epidermal glands. Many internal epithelia are mucous.

(3) A sensory (or neuro-) epithelium is one in which certain cells are specialized for reception of stimulation by some agency in the cell's environment. Such a cell is usually elongated and slender and characterized by one or more exceedingly delicate "hairs" or "bristles" at its distal end (Fig. 97). The hair, which is evidently an important part of the receptor mechanism, extends through the cuticula (if present) or is otherwise disposed so as to be readily accessible to the appropriate stimulating agency.

Sensory cells may occur in either simple or stratified epithelia. They may be scattered singly throughout an epithelium as in the epidermis of various invertebrates. In the olfactory epithelium of the nasal cavity of mammals the non-nervous cells are of very elongated form and interspersed among them are the even more attenuated olfactory sensory cells (Fig. 97).
Epithelial sensory cells may be grouped in small clusters forming specialized sense organs. Such are the sense organs of the lateral-line system of fishes and amphibians (Fig. 98) and the "taste buds" in the mouth of higher vertebrates (Fig. 99).

The essential layer of the internal ear is derived from embryonic ectoderm. This auditory epithelium produces sensory cells in localized groups which become the special sensory organs of the ear, the maculae and cristae acusticae (Fig. 97A). The organ of Corti in the spiral cochlea of the mammalian ear is a highly specialized sensory epithelium.

The retina of the vertebrate eye is produced by outgrowth from the wall of the embryonic forebrain and consists of two ectodermal epithelia (Fig. 60). The outer is a simple pigmented and non-nervous epithelium. The inner is the most complex of all sensory epithelia, all the cells at its outer surface becoming the sensory rods and cones, while the deeper cells become specialized as nerve cells arranged in two layers intervening between the rod and cone layer and the optic nerve (Fig. 100). The epithelial nature of the adult retina is obscured by the fact that the original open space between the outer pigmented epithelium and inner sensory epithelium is obliterated, thus bringing the two epithelial surfaces into close contact.
contact. In the adult state, then, they are epithelioid, but in origin and essential nature they are truly epithelial.

Most receptors of external stimuli—that is, the exteroceptors of the body—are more or less specialized sensory epithelia.

(4) Cilia are extremely delicate motile filaments borne by the free end of an epithelial cell (Fig. 93). A single cell may carry from one (called flagellum if especially long) to over a hundred cilia.

The vibratile beating of a cillum is caused by a motor mechanism which may be either at the base of the cillum or within the filament itself. As in rowing a boat, the stroke of a cillum is effective in one direction only. The beat of all cilia in a region is not simultaneous, but progressive waves of ciliary motion pass along the epithelial surface.

Beating of cilia may cause motion of the body on which the cilia are carried, or of an external fluid medium within which the cilia beat, or it may transport small solid bodies along the ciliated surface. The gastrula of Amphioxus is propelled through the sea water by beating of ectodermal cilia. The ciliated nephrostomes of the mesonephros (page 98) cause a flow of coelomic fluid toward the mesonephric duct. Certain regions of kidney tubules are ciliated. The cilia on the lining of the trachea and bronchi propel inhaled foreign particles upward and outward. Oviducts, efferent sperm ducts and many other hollow organs are lined by ciliated epithelium.

Fig. 100.—Retina of a mammal. The upper part of the figure is a simplified representation of a section through the retina; much enlarged. Below are shown the relations of individual elements of the several layers. The cavity of the eye-ball is toward the left. c, cone; cc, cone cell; g, nerve cells; ig, inner “granular” layer, the granular appearance being due to numerous small nerve cells; in, inner “molecular” layer consisting of the processes of the nerve cells of adjoining layers; m, basal membrane; nf, nerve fibers of optic nerve; og, outer “granular” layer, the “granules” being the deeper nucleated portions of the rod cells and cone cells; om, outer “molecular” layer; r, rod; rc, rod cell. (From Kingsley.)
The simple external epithelium of the earthworm and the stratified epidermis of a fish combine cuticular, glandular and sensory specializations. Cilia and mucous glands commonly occur together in the same epithelium. An epithelium, either simple or stratified, may be rendered sensory by the presence of free nerve terminations, that is, the terminal twigs of a nerve fiber ramifying amongst the epithelial cells (Fig. 101). These nervous structures, however, are not produced by the epithelium itself but invade it from adjacent tissue. The term "sensory epithelium" should be restricted to those whose specialized sensory structures are certain of the cells of the epithelium.

**Glands**

The name "gland" is applied to various organs which have little in common beyond a superficial similarity which may cause a lymph gland to be mistaken for a salivary gland. In general, glands produce or discharge something. But organs whose products are as different in nature and significance as are sweat, eggs and blood cells hardly merit the same name. Accepting the name, it is at once necessary to distinguish the following fundamentally different types of glands: (1) **secretory glands** whose products are retained, at least temporarily, and serve the animal in some useful way—e.g., mucous, salivary and thyroid glands; (2) **excretory glands** which eliminate waste from the body—the kidneys; (3) **cytogenic glands** whose products are living cells—the reproductive glands which produce sperm cells and egg cells, and the various lymph and hemal glands, including the spleen, which produce white blood cells. The products of these cell-producing glands may either be retained to serve useful purposes as are secretions, or discharged as are excretions. Blood cells are retained, but reproductive cells are discharged by means of ducts which are identical with or closely related to those which discharge waste from the kidneys.

**Secretory glands** are of most diverse sorts. The simplest and presumably primitive type of gland is the **unicellular gland** of a glandular epithelium. The association of numerous secreting cells together to form a glandular organ provides for a more efficient carrying on of the secreting process. Such an organ is called a **multicellular gland** (Fig. 94, g).

Nearly all multicellular secretory glands arise directly from epithelia and retain their epithelial character. Certain of the endocrine glands, whether arising directly from epithelium or not, are epithelioid.
The great majority of secretory glands arise directly from the ectodermal and endodermal epithelia and discharge at the surface of their native epithelium. Such are the many kinds of integumentary glands and the digestive glands. The mesoderm gives rise to some secretory glands, especially in connection with the reproductive system—e.g., the albumen glands and shell glands of oviducts and the mucous glands of the mammalian uterus.

A multicellular secretory gland, other than endocrine, is an invagination of an epithelium into adjacent tissue (Fig. 102). The secretory activity is usually limited to cells of the deeper part of the gland, the more superficial part of it serving merely as duct.

Fig. 102.—Types of multicellular glands. A–D, tubular; E, F, alveolar or acinous. A, simple; B, coiled; C–F, branched. The duct pierces the epithelium from which the gland has been produced. (From Kingsley.)

Varying in the form which the invagination assumes, two main types of gland are recognized. A tubular gland (Fig. 102, A–D) is one in which the secretory portion and the duct are of approximately the same diameter. An alveolar or acinous gland (Fig. 102E, F) has an enlarged and more or less nearly globular secretory region. Glands of either type, complicated by branching, are called compound.

The larger multicellular glands, and especially those which are compound, require certain accessory structures. A good blood supply must be provided. Therefore the gland may have an outer investment of connective tissue containing blood vessels and lymphatics. A thin layer of unstriated muscle fibers may be present on the wall of a gland which discharges its contents abruptly. The muscle would be accompanied by nerve fibers and in some glands nerves may be traced to the secretory cells.

Secretory glands in vertebrates range from unicellular mucous glands in the skin of fishes and amphibians and in the digestive epithelium of all vertebrates to such massive compound multicellular glands as the mammary glands and the liver.

**NON-EPITHELIAL TISSUES**

The primarily essential parts of a metazoan animal are the epidermal epithelium and the enteric epithelium. Certain of the organs which, in
the adult, lie between these two layers consist of tissues which do not retain the epithelial character of the embryonic tissues from which they are derived, but give rise to more or less bulky and solid masses of material. Non-epithelial tissues also play an important part in providing structures accessory to the primary epithelia, as when connective tissue forms a dermal layer of the skin, or muscular and connective tissues become associated with the enteric epithelium to form the wall of the digestive tube.

The important types of adult non-epithelial tissues are the following: (1) muscular; (2) nervous, exclusive of neuro-epithelial structures; (3) tissues serving for mechanical support—the connective and skeletal tissues; (4) adipose tissue or fat; (5) blood.

Muscular Tissue

Locomotion in some protozoans is effected by beating of cilia. The movements of large animals depend on contractile mechanisms. Contractility is inherent in protoplasm. The least specialized protoplasm is apparently able to contract in the direction of any of its axes. When protoplasmic mechanism for effecting vigorous, quick or long continued contracting is established, the ability to contract becomes restricted to one axis. The protoplasmic structures which seem to be somehow immediately concerned with contraction are exceedingly fine fibrils, the myofibrils, which extend through the cell parallel to the axis of contraction. Some unicellular animals exhibit fibrils which are apparently of the nature of myofibrils and serve as intracellular motor elements. In metazoa certain cells become more or less elongated and differentiate myofibrils extending lengthwise of the cell—a muscle cell (Fig. 103). In the simple small coelenterate Hydra, however, the contractile fibers which effect the movements of the animal are not independent muscle cells but are merely long processes from the basal ends of the epithelial cells. It is significant that, in the absence of a mesoderm, the primary epithelia are able to provide a motor mechanism. Such epithelial motor processes may have been the forerunners of muscle cells.

Among invertebrates the usual type of muscle element is a much elongated cell having a single nucleus, more or less numerous myofibrils
extending through the protoplasm lengthwise of the cell, and having the usual cell wall devoid of any special membranous covering. Such cells, associated together to form layers, bundles or masses, constitute the muscles of the body wall and the viscera. Certain invertebrates, however, whose muscles are, in one way or another, especially efficient have muscle cells of much more complex sort. The myofibrils become strongly developed and each fibril exhibits an alternation of darker and lighter zones. The zones of either type lie exactly alongside one another on adjacent fibrils so that they give the impression of transverse bands or striations extending continuously across the cell. Muscle cells of this sort are called **striated**. Uninucleate striated fibers occur in the heart of some mollusks. In arthropods, especially insects, striated fibers attain great length, are multinucleate, and exhibit a most complex system of transverse striations.

Vertebrates possess both striated and unstriated (or "smooth") muscle (Fig. 103). In general the muscle of the body wall is striated and visceral muscle is unstriated. But unstriated muscle occurs in the walls of blood vessels which lie in the body wall, in connection with some skin structures such as hair and certain glands, and also in the iris of the eye. The muscles in the walls of the mouth, pharynx and at least the upper part of the esophagus are striated, and it is said that striated muscle occurs in the wall of the stomach of some fishes. Also the external anal muscle is striated. The muscular part of the diaphragm is derived from the embryonic body wall (see page 108) and its muscle is accordingly striated. And in all vertebrates all of the muscle of the wall of the heart is striated.

In general, striated muscle is innervated by nerves of the cerebro-spinal system and unstriated muscle, even in the body wall and skin, is innervated by autonomic nerves. The old distinction to the effect that striated muscle is "voluntary" and unstriated "involuntary" is inaccurate. The striated muscles of the heart, diaphragm and esophagus are involuntary. The striated muscles of the vertebrate body wall and appendages are capable of quick and powerful contraction. Heart muscle is notable for its capacity for long-sustained rhythmic action.

Unstriated muscle fibers in vertebrates are much like those of invertebrates. They are ordinarily not over a fraction of a millimeter in length and, in man, much less than a hundredth of a millimeter in diameter. They are usually spindle-shaped (Fig. 103A), lying in the tissue with their tapering ends overlapping.

The somatic striated fibers of vertebrates are enormously larger than unstriated fibers. Their diameter may approach a millimeter and their length, not accurately known, doubtless reaches several or many millimeters. But these great fibers are not, in strict sense, single cells. They contain scores or hundreds of nuclei. In lower vertebrates the nuclei are
ordinarily scattered throughout the interior of the fiber, but in higher vertebrates the nuclei are at the surface of the fiber as if crowded out of the deeper regions by the closely packed myofibrils (Fig. 104). Probably, however, the fiber is the product of a single mesoderm cell of the embryo and many nuclei are derived, by repeated divisions, from the original mesoderm nucleus. The fiber, therefore, is a syncytium rather than a cell.

The myofibrils of striated fibers are much coarser than those of unstriated fibers. They are imbedded in a peculiar fluid sarcoplasm.
which is probably a nutrient medium rather than ordinary cytoplasm. The wall of the fiber, much more prominent than an ordinary cell-wall, is called the sarcolemma. Some investigators maintain that extraneous connective-tissue cells may give rise to a second investing membrane reinforcing the inner sarcolemma which is a product of the fiber itself.

The alternate dark and light bands on the individual fibril are due to physical differences such that, in polarized light, the dark bands are doubly refractive (anisotropic) while the lighter bands are singly refractive (isotropic). Both the dark and the light bands are traversed by finer markings, as seen under high magnification, so that altogether a very complex structure in the fibril is indicated.

In the act of contracting, profound changes occur in the appearance and relations of the striations. Undoubtedly the contraction of a fibril is due to specific chemical and physical differentiation within the fibril; the contraction of a fiber is the collective contraction of its fibrils; and the contraction of a muscle is the resultant of the action of its numerous fibers.

The relation of an unstriated fiber to its nerve is apparently of the simplest sort. A terminal twig of nerve merely attaches to the surface of the fiber, the end of the nerve often showing a knob-like enlargement. Presumably every striated fiber has a nerve connected to it. The nerve, however, enters a small flat plate of nucleated protoplasm lying superficially on the muscle fiber. Within this motor plate (Fig. 105) the nerve ramifies into fine twigs which seem to terminate in the substance of the plate.
Striated fibers are bound together in bundles enwrapped by a connective-tissue perimysium. Thick muscles consist of several or many such bundles wrapped together.

Cardiac muscle has striations which resemble those of somatic muscle but the fibers are relatively short and they are branched. The sarcolemma is less strongly developed than in somatic fibers. A peculiar feature of the cardiac fiber is the presence of conspicuous transverse bands, the intercalated discs (Figs. 106 and 107), which are quite distinct from the ordinary striations. Their significance is not known. A cardiac fiber develops from a syncytium of mesenchyme cells so that the adult fiber is the product of several mesenchyme cells.

Nervous Tissue

The proper relating of an animal to its environment depends upon a nervous system whose outposts must be at the surface of the animal, therefore in, or at least very near, the external epithelium. Central nervous organs, presumably in evolution and certainly in ontogeny derived from ectoderm, retreat to a protected deep position. Stimuli set up by impact of external agencies must be carried to deep central organs which must, in turn, cause appropriate muscular or other reaction. For complete coordination of all parts of a large complex animal it is necessary that deep-seated visceral activities be controlled in accord with the external situation, and equally necessary that external actions fit the internal state. Therefore the animal must have a system consisting of receptors connected by conductors (nerves) to a coordinating central nervous organ whence other conductors extend outward to the effectors which are such organs as muscles, glands and the electric organs of fishes. Receptors are distinguished as exteroceptors which are stimulated by external agencies, interoceptors which pick up visceral stimuli, and proprioceptors which lie within the motor mechanism of the body-wall—the muscles, tendons and joints. The central nervous organ of an automobile is the driver. His own eyes and ears serve as exteroceptors for the moving car. Certain interoceptors register on the instrument board the condition of the gasoline and water which are concerned with the metabolism of the car. Then there are proprioceptors which, registering in the speedometer and oil gauge, give information concerning the performance and intrinsic condition of the motor mechanism.
Fig. 108.—Types of nerve cells. A, multipolar cell; B, portion of nerve fiber with sheaths; C, unipolar cell (such a cell may arise by modification of a bipolar cell as shown in Fig. 110); D, pyramidal cell (from cerebral cortex); a, axon; c, collateral; d, dendrites; cb, cell body; m, medullary sheath; n, nucleus of cell of Schwann’s sheath; r, node of Ranvier; s, sheath of Schwann; t, telodendron. (From Kingsley.)

Fig. 109.—Cell-bodies of neurons showing arrangement of neurofibrils. A, from human spinal ganglion; two cut fragments of the neuraxon lie near the cell-body. B, “giant pyramidal cell” from human cerebral cortex. Highly magnified. a, neuraxon. (From Morris, Human Anatomy.)
Nerves which conduct impulses from receptors toward the central nervous organ are called sensory or afferent. Those which conduct from a central organ to some effector are called motor or efferent.

Nerves conducting impulses from exteroceptors or proprioceptors to the central organ are somatic sensory (afferent); those conducting from the central organ to the striated muscle of the body wall are somatic motor (efferent). Similarly visceral sensory and visceral motor nerves are distinguished.

All nervous functions are carried on by protoplasm organized, as always, in cells. To say, as is often done, that nervous tissues consist of nerve cells and nerve fibers is inaccurate. So far as known, every fiber which conducts nervous impulses is developed as an outgrowth from a cell and can function and survive only so long as it remains in physical and physiological continuity with the nucleated region of the cell of which it is an integral part. Any cell engaged in nervous operations, together with all conducting fibers which have grown out from it, is called a neuron.

A central nervous organ is a more or less complex system of physiologically related neurons serving for the proper association, coordination and integration of nervous impulses. A ganglion is a minor localized nerve center consisting of the cell-bodies of neurons together with the adjacent regions of their nerve processes. The neurons of such ganglia as the dorsal or spinal ganglia of vertebrates apparently serve only for conduction—that is they do not initiate nerve impulses.

Neurons are of various types depending on the form of the cell-body and the number of nerve processes (Figs. 108 and 109). Unipolar cells, of comparatively rare occurrence, have a single process; bipolar neurons are usually spindle-shaped and have a process at each end; multipolar cells have several processes of which one, the neuraxon (axon or neurite), is relatively long, while the short dendrites branch out into fine twigs which end within a short distance of the cell-body. The dendrites seem to be protoplasmic but the neuraxon is devoid of the granules which characterize the protoplasm of the cell-body. The neuraxon may give off lateral branches (collaterals) and its distal extremity breaks up into fine branches forming the terminal arborization.

The unipolar cell characteristic of the dorsal ganglia of adult vertebrates is apparently a "disguised bipolar" cell. At least in some animals it develops from an embryonic bipolar cell which, in effect, becomes bent.
upon itself so that the two processes are joined into one which divides into two near the cell-body (Fig. 110).

Most types of receptor neurons are epithelial. In some of these the receptor cell itself produces a nerve fiber which conducts to the central organ (e.g., an olfactory cell and its fiber). In such case, one neuron serves as both receptor and conductor. In other cases, as in the auditory organ, the epithelial receptors do not produce nerve fibers but are intimately related to the terminal twigs of afferent nerve fibers whose cell-bodies lie in some deep ganglion such as the acoustic ganglion or a spinal ganglion.

Between the receptor neuron and an ultimate motor neuron may intervene a chain of several neurons, the nerve impulse being relayed from one member of the chain to another.

Nerve cells vary greatly in size, but in general are relatively large. They are often the largest cells in the body exclusive of eggs. When the possible length of a neuraxon is considered, the dimensions of some neurons become impressive as contrasted with the usual microscopic size of cells. A neuron whose body lies in a spinal ganglion of the giraffe presumably has a nerve process extending to the extremity of a front leg.

Some of these very large nerve cells have two or more nuclei. Their cytoplasm sometimes exhibits a system of very narrow branching canals apparently serving for circulation of lymph which enters from the adjacent intercellular lymph space. The cell may be supported by a delicate close-fitting membrane of connective tissue, strands of which may enter the cytoplasm.

The most striking characteristic of the body of a neuron is the presence of large masses of a granular substance which has a strong affinity for the anilin dye, methylen blue. These Nissl's bodies (Fig. 111) have been shown to become reduced in neurons which have been excessively active, indicating that the bodies contain something which is a source of energy for nervous activity. Less conspicuous are the neurofibrils (Fig. 109), extremely fine fibrils which are ordinarily seen only after use of special staining methods. Such neurofibrils may form an elaborate system within the body of the neuron and may be traced into the neuraxon and larger dendrites. The appearance and arrangement of these neurofibrils strongly suggest that they are specialized avenues for conduction of impulses. The objection has been made, however, that they are artificial products of the special preserving and staining technique which is employed.
The neuraxon is a delicate thread consisting of a probably modified protoplasm in which, as just mentioned, neurofibrils may be demonstrated. It may be surrounded by one or even two special ensheathing layers. The medullary or myelin sheath is a relatively thick layer of fat-like substance, myelin, fitting the neuraxon closely. The neurolemma or sheath of Schwann is a cellular layer wrapped around the neuraxon. Its cells are so exceedingly thin that the layer could hardly be detected were it not for the nuclei which at intervals occasion roundish bulges in the contour of the nerve fiber.

A neuraxon may possess either, both, or neither of these two sheaths. When both are present the myelin sheath is always next the nerve fiber and, at fairly regular intervals (in man averaging about 0.5 mm.) along the fiber, it seems to be nearly or quite interrupted so that the neurolemma there comes into close relation with the nerve fiber (Fig. ro8B). The neuraxon therefore presents a segmented appearance due to these nodes of Ranvier. Usually only one neurolemma nucleus can be found between successive nodes. A single internodal segment therefore probably represents the territory covered by one sheath cell.

Nerves whose individual fibers possess the myelin sheath appear more nearly white than do non-medullated nerves. The so-called "white" parts of the brain and spinal cord consist mainly of medullated nerves. Non-medullated fibers and the cell-bodies of neurons are the chief constituents of "gray matter."

On medullated nerves within the brain and spinal cord no neurolemma can ordinarily be found, but medullated fibers in nerves external to the brain and cord commonly have both sheaths except in the vicinity of the terminal arborization of a neuraxon. The myelin sheath stops short of the arborization. The neurolemma may continue alone somewhat further, but the terminal twigs of the neuraxon are always bare.

Most autonomic fibers and the fibers of the olfactory nerve are non-medullated. A cellular neurolemma may occur on a non-medullated fiber.

The sheaths doubtless serve for the protection, insulation and nutrition of the nerve fiber. The source of the myelin is not definitely known.

A nervous organ is constituted of neurons supported by connective tissues accompanied by vascular tissues. In the brain and spinal cord of vertebrates occurs not only the usual mesenchymal connective tissue but another which is unique in that its cells have ectodermal origin in common with the nerve cells. Some of the cells of this neuroglia possess branched processes which make them confusingly similar in appearance to nerve cells. The neuroglia cells form, by means of their processes, a supporting network for the nerve cells.

A nerve is a bundle of neuraxons, each of which may be ensheathed as described above, and all wrapped together within a sheet of connective
tissue, the perineurium (Fig. 112), extensions of which (endoneurium) may penetrate into the bundle. Larger nerves consist of several or many bundles all tied together by connective tissue and enwrapped by a relatively thick epineurium. Small blood vessels traverse the connective-tissue layers of the nerve.

The component neuraxons of a nerve may include one or more of the four types of conductor, somatic afferent and efferent and visceral afferent and efferent. All four kinds of "nerve components" occur in a spinal nerve. In cranial nerves fibers which are connected with the special sensory mechanisms of the head are designated as "special" components.

![Diagram of a nerve](image)

**Fig. 112.—Structure of a nerve.** The figure represents a small part of a transverse section of a large nerve constituted of many bundles of medullated fibers. X20. (From Bremer, Text-book of Histology.)

### Tissues Serving for Mechanical Support

Protoplasm is a substance of semi-fluid or gelatinous consistency. An elephant constituted of protoplasm only would be a mechanical impossibility. Large animals, especially if they are land animals, require mechanical support. That essentially protoplasmic and socially organized being which is mankind provides for certain of its physical needs, both individual and collective, by use of various mechanical, architectural and engineering contrivances which are external to the human body and constructed of non-living materials derived from the environment. Similarly the organized cellular protoplasm which is an animal appropriates various materials from the environment and builds them into non-living structures which are external to the cells and physically adapted to the mechanical needs of the animal as a whole and of its parts. Just as man uses steel wires, various cements and masonries, so the animal has its connective-tissue fibers, intercellular cements and that most delicate masonry, bone.
The basis of the material of these supporting structures consists of various nitrogenous or protein substances. By impregnation of the material with inorganic salts, chiefly those of calcium, hard or rigid supporting structures are produced. The protoplasmic or cellular agencies concerned in building the supporting tissues are mesenchyme cells, except in the cases of the notochord and the peculiar connective tissue of nervous organs, the neuroglia (page 149) which is ectodermal.

The embryonic precursor of supporting tissues other than the exceptions mentioned is a more or less spongy mesenchyme (Figs. 69 and 113A) whose individual cells have branching processes by means of which the cells are joined together. The spaces within the meshwork of cells is filled by a homogeneous fluid substance, the matrix. Presumably the cells are the source of the matrix.

Connective Tissue

Connective tissue consists essentially of fibers. The source of the fibers has long been a matter of controversy. The earlier belief that they are formed in the protoplasm of cells has largely given way in view of much evidence that they arise in the intercellular matrix by some process resembling precipitation, the cells probably serving merely to bring about the reaction in the matrix.

The ordinary connective tissue which is present throughout the body of a vertebrate serves to bind structures together or to ensheath them, provides internal support for massive soft structures or, in general, affords
resistance to tensile strain. The essential mechanical structures in such tissue are relatively coarse white fibers (Fig. 114) consisting of an albuminoid substance, collagen, the source of gelatin and glue. These collagenous fibers are only slightly elastic. They may be branched. Each fiber is a bundle of very delicate fibrils. Exceedingly flattened cells with flat nuclei appear as if clinging closely to the surface of a fiber. These connective-tissue cells or fibrocytes are presumably the agencies which have brought about the production of the fiber.

Elastic fibers (Fig. 114, e) are much finer than collagenous fibers and differ from them chemically in being composed of elastin which is not a source of gelatin. An occasional elongated fibrocyte may be seen stretching along the surface of a fiber (Fig. 115). Elastic fibers commonly occur intermingled with collagenous fibers. The elasticity of a connective tissue as a whole depends upon the relative abundance of elastic fibers in it.

Connective tissue forming a loose open mesh-work, as does the subcutaneous tissue lying between the skin and the muscle of the body, is called areolar tissue.

Reticular tissue is composed of cells whose branched processes join to form a network. Associated with the processes are comparatively short fibers which seem to be similar to collagenous fibers.
This tissue forms the supporting framework of such organs as lymph glands and the spleen. In form and arrangement its cells resemble embryonic mesenchyme cells. The spaces within the network are occupied by a fluid substance in which are numerous lymphocytes and other cells.

**Tendons** and **ligaments** are connective-tissue structures highly adapted to resisting tensile strain. Tendons (Fig. 113C) consist of coarse collagenous fibers lying parallel to one another in compact bundles. Tendons are inelastic. The elasticity necessary to a ligament is due partly to a certain degree of elasticity in the individual fiber and partly to the fact that the fibers are wavy in contour when not under strain and are more or less interwoven.

**Chromatophores**, pigment cells (Fig. 113B), may occur in connective tissue, especially in the dermal layer of the skin. The specific pigment appears as granules lying in the cytoplasm. Black pigment (melanin) is most common and cells containing it are called **melanophores**. Chromatophores are usually richly branched. The pigment may at one time be distributed throughout the processes (“expanded” phase), at another time densely massed in the central part of the cell (“contracted” phase). Some pigment cells are migratory.

**Skeletal Tissues**

**Notochord.** Among skeletal structures the notochord is histologically unique in that its tissue is for the most part neither hard nor even solid; it is fluid. It is exceptional also in its embryonic origin. It is not a product of mesenchyme but arises simultaneously with the mesoderm and in much the same way although independently of it (see page 86).

The essential notochord material consists of cells each of which contains a relatively enormous vacuole occupied by a substance of fluid or possibly gelatinous consistency. The cytoplasm of the distended cell is so stretched that it appears as the thinnest possible layer surrounding the vacuole. The very flat nucleus occasions a bulge in the contour of one side of the cell (Fig. 116). The outer cell-membrane, while very thin, is probably of semi-rigid consistency. Seen under the microscope, this tissue looks like a mass of soap bubbles crowded closely together, the cytoplasm and cell-membrane of each cell being the wall of a bubble.

The vacuolated notochord tissue is enclosed by sheaths which differ in number and nature in various animals. There is commonly an inner elastic sheath (Fig. 116, ei) composed of material secreted by an outer epithelioid layer of the notochord tissue, and a thick outer sheath of dense fibrous connective tissue.

The capacity of the notochord as a whole to resist deforming strains is doubtless due in part to the cell walls of the vacuolated tissue, these walls
collectively forming an alveolar framework for the inner tissue. It must, however, be due largely to the enclosing sheaths which, taken all together,

**Fig. 116.—**Developing vertebrae of the amphibian, Ambystoma; I, earlier; II, later. Longitudinal sections. Cartilage and bone are forming around the notochord. *cc.* cartilage in center of vertebra; *ei,* epithelioid internal elastic sheath of notochord; *i,* incisure cutting through *ic,* intercentral (intervertebral) cartilage; *n,* notochord; *ns,* outer notochordal sheath; *v,* developing bone (black) of centrum of a vertebra. (From Kingsley.)

are tough and not highly elastic. Mechanically, the notochord resembles a length of rubber tubing, closed at the ends, and filled with liquid under some degree of pressure.

**Cartilage.** In development of cartilage, mesenchyme cells become densely massed and then produce an abundant intercellular substance whose accumulation causes the cells to become more or less widely separated from one another (Figs. 76, 117, 118). The intercellular substance, the matrix, becomes solid and acquires a firm or even hard consistency. Chemically it is a complex of collagenous, albuminoid and other protein substances. The cartilage cells remain imbedded in the matrix, each occupying a close-fitting space, a *lacuna.* In some cartilages have been described

**Fig. 117.—**Hyaline cartilage with cartilage cells lying in lacunae enclosed by the matrix. Thin section highly magnified. (From Kingsley.)
exceedingly fine canals penetrating the matrix and putting any one lacuna into communication with neighboring lacunae.

The external surface of cartilage is invested by a membrane, the perichondrium, consisting of collagenous connective-tissue fibers, densely arranged and for the most part parallel to the surface of the cartilage.

The perichondrium contains blood vessels but they do not penetrate into the cartilage. Hence cartilage cannot occur in thick masses.

In growing cartilage, cells from the adjacent surface of the perichondrium become cartilage cells and add cartilage to the exterior of the mass already formed. At the same time growth may take place within the mass. A deep cartilage cell divides. The resulting two cells secrete matrix substance whereby they become separated, each to lie in a lacuna of its own. In growing cartilage, therefore, the matrix substance is not so firmly "set" that it may not expand as a result of such internal or interstitial growth.
Several types of cartilage are distinguished. **Hyaline cartilage** (Fig. 118), appearing bluish and clear or translucent, has a matrix which is quite or nearly devoid of fibrous material. **Fibro-cartilage** is, so to speak, a hybrid of cartilage and connective tissue. Its matrix consists partly of hyaline material but largely of fibers similar to those of ordinary connective tissue. **Elastic cartilage** contains numerous elastic fibers which impart to it a yellowish color and a more or less elastic texture. **Calcified cartilage** is rendered white and relatively hard by deposit of calcium salts in the matrix.

**Bone.** Cartilage and bone are similar in that their essential skeletal material is an intercellular matrix within which are imbedded the cells which produced it. Bone differs from cartilage in that the matrix is highly calcified and correspondingly hard and also in that it never exhibits the apparent homogeneity of the matrix of hyaline cartilage but is disposed in very thin parallel layers. Usually the deeper substance of a bone is of a porous or spongy texture (**cancellous bone**) while the outer region is dense or solid (**compact bone**).

A section of fully developed compact bone, seen under high magnification, shows the matrix layers or **lamellae** arranged in parallel or concentric order (Figs. 119B and 120). Between adjacent lamellae are minute cavities, the **lacunae**. A lacuna is broad in any direction parallel to the surface of a lamella but very thin in the direction perpendicular to that surface. Exceedingly fine canals, the **canaliculi**, extend between each lacuna and neighboring lacunae, piercing the intervening lamellae. In bone of a living animal each lacuna is occupied by a living bone cell (**osteoblast**) from which processes extend into the adjoining canaliculi and may even unite with similar processes from the occupants of neighboring lacunae. It follows, therefore, that the bone is penetrated by a system of continuous spaces and it is probable that in young bone the bone cells, joined by their processes, constitute a continuous network of protoplasm throughout the bone.

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**Fig. 119.—**A, stereogram representing a sector of the shaft of a long bone. B, transverse section, much more enlarged, showing part of one Haversian system. bl, bone lamellae; c, canaliculi; h, Haversian canal; l, lacuna. (From Kingsley.)
All external surfaces of bone are covered by a membrane, the periosteum (Fig. 77), of dense fibrous connective tissue well supplied with blood vessels. Most bones, notably the long bones of the appendages, have internal cavities (Fig. 208) occupied by a more or less vascular soft tissue, the marrow. The "yellow marrow" of long bones contains much fat. "Red marrow" is very highly vascular and contains little fat. Marrow has a framework of reticular tissue in whose spaces occur marrow cells (myelocytes) and various types of blood cells.

Blood vessels from both the periosteum and the marrow enter and branch throughout the bone. From these vessels substances necessary for the metabolism of the bone cells diffuse through the system of connected lacunar spaces.

In long bones the larger blood vessels lie approximately parallel to the long axis of the bone. Around such a vessel the bone lamellae are arranged in concentric order (Figs. 119 and 120) forming a so-called Haversian system. The central space, occupied by the blood vessel, is called a Haversian canal. These concentric systems are much less prominently developed in flat bones.

The matrix of bone consists of commingled organic and inorganic materials. Collagenous and other protein substances constitute the
organic part while various salts of calcium, mostly the phosphate and carbonate, are the most important inorganic ingredients. The stratified structure of the matrix is primarily due to the arrangement of collagenous fibers in the organic basis of the matrix. The subsequent depositing of calcareous substance in relation to the stratified fibrous material produces the laminated structure of the finished bone.

The development of bone has been briefly described (pages 103-106) and the distinction between cartilage bone and dermal or membrane bone has been made. Differing in mode of development, bones of the two kinds, when fully developed, are histologically alike. Just as the perichondrium adds cartilage at the surface of an already-formed mass, so the periosteum builds lamellae at the surface of a bone. But bone, because of the rigidity of its calcified matrix, is incapable of such interstitial growth as occurs in cartilage, unless it be at stages of bone formation so early that the matrix is not yet fully calcified. A further difference between cartilage and bone lies in the fact that the cartilage cell produces matrix in all directions and thus surrounds itself by its own product, whereas the osteoblast produces matrix only at such part of its surface as is adjacent to the already-formed bone. A layer of bone cells building up lamella upon lamella of bone may be likened to a group of masons laying course upon course of stone at the unfinished top of a wall. But, in the case of the bone, every now and then one of the masons, an osteoblast, is left behind and buried between successive courses of the wall, remaining there in his little lacuna as a permanent bone cell.

Bone once formed may be broken down or "resorbed." By this means the marrow cavity of a long bone is enlarged as the bone grows. The nature of the resorption process is not definitely known, although it has been attributed to action of cells called osteoclasts (Fig. 77).

Adipose Tissue

Adipose tissue or "fat" consists of cells each of which contains a globule or vacuole of oil so large that the cytoplasm appears as merely an exceedingly thin layer surrounding the vacuole (Fig. 121). The flat nucleus lies in the peripheral layer of cytoplasm. The irregular polyhedral form of the cells is doubtless the result of their mutual pressures. As seen in sections, fat looks very much like notochord tissue, the individual cell of each being greatly distended by its fluid vacuole.

Fat develops in richly vascular regions, as along the course of large blood vessels and in the subcutaneous connective tissue.

Blood

Blood is the circulating medium which provides for the metabolic needs of tissue cells which are remote from the source of food and oxygen
and must be relieved of their waste products. Its circulatory function requires that it be fluid but various special services are rendered by cells suspended in the fluid, some of them passively carried by it, others capable of independent motion somewhat like that exhibited by an ameba.

The fluid part of blood, the **plasma**, is water containing all the other substances which enter into the constitution of protoplasm. In its inorganic chemical constitution, the plasma resembles sea water. Derived from the food are various proteins and carbohydrate substance (sugar),

![Diagram](image.png)

**Fig. 121.**—Fat cells in subcutaneous tissue of a human embryo of four months. *bl.v.*, blood vessel; *c.t.*, white connective-tissue fibers; *fib.*, young fibrocyte; *mes.*, mesenchymal cell; *x*, young fat cell, nucleus not in section; 1, 2, 3, developing fat cells. (From Bremer, Text-book of Histology.)

while fat may be carried as minute droplets suspended in the plasma. Other important constituents of the plasma are hormones produced by such endocrine glands as the pituitary, thyroid and suprarenal, and the various wastes of metabolism.

In the coagulation of blood, on exposure to air or under some other circumstances, a nitrogenous substance, **fibrinogen**, carried by the plasma in solution, becomes transformed into fine solid filaments of **fibrin** (Fig. 122). The uncoagulated portion of the plasma is called **serum**. The “clot” is a mass of fibrin with blood cells caught in its meshes.

Blood cells are of two main kinds, **red corpuscles** or **erythrocytes** and **white corpuscles** or **leucocytes**. The red cells are much more numerous.
In human blood the red cells outnumber the white in the ratio of five or six hundred to one.

Erythrocytes (Figs. 122 and 123) are relatively small and usually have the form of flat discs with elliptical outlines. These blood cells are heavily loaded with hemoglobin, a very complex protein substance containing iron and having a strong affinity for oxygen which the cells pick up at the respiratory surfaces of the animal. The red cells are therefore the oxygen-carriers. Their color is due to the hemoglobin. The mature erythrocytes of all vertebrates except mammals are nucleated, although the nucleus

![Coagulated blood. Biconcave red corpuscles arranged in "rouleaux"; filaments of fibrin radiating from minute blood plates. (From Bremer, Text-book of Histology; after Da Costa.)](image)

seems to be in a more or less degenerate condition. But in adult mammals the red cells in course of their differentiation lose their nuclei, thereby acquiring the form of concavo-convex discs (Fig. 122).

Erythrocytes are produced in mesenchymal tissue in the liver and in the spleen of embryos, but in the adult their chief source is probably the red bone-marrow. They serve as oxygen-carriers for a limited time and

![Cells from smear preparation of normal human blood, Wright's stain. In the center: adult red blood corpuscles, blood platelets and a polymorphonuclear neutrophile. At left above: two polymorphonuclear basophiles and two polymorphonuclear eosinophiles. At right above: three large and four small lymphocytes. At left below: polymorphonuclear neutrophiles; two of these cells, the uppermost and lowermost of the group, are young, with merely crooked nuclei; the mature cells have multilobed nuclei. At right below: six monocytes; in the younger cells the nuclei tend to be rounded, in the adult cells they are horseshoe-shaped, indented or lobed. (From Bremer, Text-book of Histology.)](image)
Fig. 123.—(See page 160 for description).
then break down and are removed from the blood by action of phagocytic cells in the hemal glands and spleen.

**Leucocytes** are permanently nucleated and do not carry hemoglobin. Several types of leucocyte are recognized (Fig. 123):

- **Lymphocyte**; usually small (occasional larger ones), cytoplasm scanty and usually non-granular, nucleus spherical and relatively large.
- **Large mononuclear leucocyte** (monocyte); larger than lymphocyte, non-granular cytoplasm, nucleus excentrically placed in the cytoplasm and spherical, or indented on the side adjacent to the larger cytoplasmic mass.
- **Polymorphonuclear leucocyte**; large, with conspicuous granules in cytoplasm, nucleus indented, lobulated, irregular or separated into two or more parts. Several kinds of polymorphonuclear leucocytes are distinguished on the basis of the reaction of their granules to anilin dyes. **Basophiles** have granules which take basic stains; **eosinophiles** have an affinity for eosin, an acid dye; the granules of **neutrophiles** take both basic and acid dyes.

Most leucocytes are capable of active ameboid motion and many are phagocytic. Some of them are apparently capable of penetrating the wall of a blood vessel and emerging into intercellular spaces in neighboring tissue. They are produced in the lymph glands, in bone marrow, and in lymphoid tissue variously situated throughout the body.

**Blood Plates.** In addition to the red and white blood cells, blood contains minute bodies which seem to be protoplasmic and yet are not nucleated. These **blood plates**, much smaller than the smallest blood cells, probably result from fragmentation of cells in bone marrow or elsewhere. Their function is not certainly known but they seem to have some relation to the clotting of blood as indicated by the fact that the filaments of fibrin tend to radiate from blood plates.

**Lymph**, as found in the lymphatic vessels, resembles blood but differs from it chiefly in lacking erythrocytes and therefore being colorless. The fluids occupying the several coelomic spaces and the cavities of brain and spinal cord, the aqueous humor of the eye and the amnionic fluid are all of the general nature of lymph but contain relatively few cells and differ from one another in details of chemical constitution.

**HISTOLOGICAL SPECIFICITY**

In general, histological differences are less conspicuous than the corresponding anatomical differences—that is, tissue of a particular sort may enter into the constitution of most unlike organs. Bricks from the same kiln may be used in the construction of either a church or a brewery.
Unstriated muscle fibers appear much the same whether they are in the wall of a stomach or of a lung.

Nevertheless tissues and cells may exhibit characteristics which mark them as belonging to a particular organ or animal. The nerve cells of a spinal ganglion differ from the motor nerve cells in the spinal cord of the same animal. The striated muscle of the vertebrate heart differs from that of the body wall. Further, vertebrate cardiac muscle differs from cardiac muscle of a lobster. Epidermal tissue of a fish differs from that of a reptile. Anyone familiar with the nervous tissues of annelids could easily distinguish ganglionic tissue of an earthworm from that of a leech.

It follows, therefore, that the individual tissue cell may, in its visible structure, exhibit characteristics reflecting as many as four grades of organization. First there are those cell organs, such as nucleus and chromatin bodies, which are common to all cells and which represent the fundamental organization of protoplasm as cells. Then there are those intracellular structures such as myofibrils or neurofibrils which mark the cell as belonging to a particular tissue—muscular or nervous. Thirdly, there may be features which identify the tissue as that of a certain organ; for example, the intercalated discs in the heart muscle of vertebrates. Finally, the individual tissue element may have peculiarities which are specific for animals of a certain group; for example, the striated muscle fiber of an insect differs in details of structure from that of a vertebrate.

Beneath all of this structural differentiation there is chemical specificity. Although it does not necessarily always manifest itself in visible structural differentiation, there must exist from top to bottom of this series of levels of protoplasmic organization a chemical specificity corresponding to a specific genetic group of animals—or, indeed, corresponding even to the individual animal.
CHAPTER 4

THE INTEGUMENTARY SYSTEM

EVOLUTION OF THE INTEGUMENT

Since all life involves continual adjustment of processes within the organism to conditions outside, the skin and its appendages which mediate this relation are highly important organs.

Even among the protozoa, an external semipermeable membrane separates the living protoplasm from the surrounding medium. Most protozoa have in addition an outer differentiated layer of clearer cytoplasm, the ectosarc, analogous in function to the skin of the higher animals though without genetic relation.

A true multicellular skin appears first in sponges and coelenterates, the ectodermal layer of hydra being a familiar example. Even in so simple a skin as this, there is some differentiation among cells. Most are epithelial covering cells, each commonly prolonged at its base into a contractile thread. But among these are gland cells, which by their different secretions in different coelenterates indicate a wide difference in metabolic processes. The secretion of lime salts by the skin of coelenterates may be regarded as the beginnings of the exoskeleton of many higher invertebrates.

Most invertebrates retain essentially unaltered the simple epithelial ectoderm of coelenterates. Some have a ciliated epidermis which aids locomotion. Many secrete an external cuticula, in which lime may or may not be present.

The evolution of a simple epithelium into a stratified epidermis, such as occurs in vertebrates, results, presumably, from a change in the direction of cleavage planes during cell multiplication. So long as cell walls form perpendicular to the surface, a simple epithelium results. When, however, cleavage planes form parallel to the surface, the membrane becomes stratified. The outer layers of cells serve to protect the lower layer where growth and cell multiplication take place. In animals exposed to dry air, an outer layer of dead cells is obviously adaptive. Yet the beginnings of a protective outer layer appear in the exoskeletons of water-dwelling invertebrates. Among invertebrates appears also, though exceptionally, a connective tissue layer or corium beneath the epidermis.

The lowest chordates (balanoglossus, ciona, amphioxus), have both an outer epidermis and an inner corium; but the epidermis is only a single
layer of cells. Gland cells are numerous in the epidermis of amphioxus, and they secrete a thin cuticle like that of annelids. The corium in amphioxus is gelatinous.

Although the epidermis is stratified in all vertebrates, such low forms as cyclostomes do not have the outer dead horny layer, and they do have the thin cuticular layer of the invertebrates and amphioxus. The skin of fishes is like that of cyclostomes, except for differences in gland secretions. See Fig. 124.

The outer dead horny layer of the epidermis, the corneum, appears first in amphibia, correlated apparently with the land habit, since most

land animals have it. As the amphibian skin is fundamentally like that of higher vertebrates, the evolution of the skin beyond the amphibia presents no serious difficulties. The striking differences are in the secretions of the glands. It is indeed difficult to imagine how the skin mucus of amphibians could have evolved into the milk of mammals. It should, however, be remembered that slight chemical differences often result in striking differences in properties; so that we should not be surprised to find chemical differences in the skin secretions of vertebrates that are far greater than any morphological differences in the glands themselves.

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Fig. 124.—Cross sections of the skin of four chordates, amphioxus, petromyzon, squalus, and rana, showing the fundamental differentiation of the skin into corium and epidermis. The differentiation of the epidermis into a dead outer layer and an inner living layer began in aquatic animals. (Redrawn mainly after Plate and Schimkewitsch.)
The skin of man, together with its appendages, hair, nails, teeth, membrane bones, and glands, is only about four per cent of the body weight. Like that of other mammals, it consists of two tissues, an outer epidermis and an inner connective tissue corium.

A cross section of the epidermis shows under the microscope a many-layered epithelium, which varies greatly in thickness in different parts of the body. Even where it is thinnest, as for example on the back, at least two layers of cells are distinguishable, an inner, growing stratum germinativum and an outer, horny stratum corneum. The cells of the stratum germinativum are columnar in shape; those of the stratum corneum are flattened and scale-like. The former are alive, and by their constant proliferation on division planes parallel to the surface of the skin, they make continual additions to the stratum corneum. The living cells in
their turn, as by the wearing off of the outer layers they come nearer and nearer the surface, alter their living protoplasm into keratin, and become the horny scales of the outer epidermis. In man as in most mammals, the stratum corneum wears away as rapidly as it is formed and never becomes greatly thickened on most parts of the body. Amphibia, however, shed the stratum corneum in sheets, sometimes sloughing off the entire covering of the body at once. Serpents do the same thing, scales and all.

Sections of the thick epidermis of the palms and soles show between the stratum germinativum and the stratum corneum, two intermediate layers, a stratum granulosum and a stratum lucidum. These, however, are merely transitions between the inner growing layer and the outer lifeless horn. See Fig. 125.

Corium. The deeper layer of the skin, the corium, cutis, or dermis, is connective tissue, with a much greater variety of cell elements than the epidermis, and, unlike the epidermis, richly supplied with blood vessels. Where it touches the epidermis, especially on the palms and soles, the corium is thrown up into many fine papillae, the capillaries of which feed the cells of the stratum germinativum. In some of these papillae, are tactile corpuscles and other nerve terminations. Cutaneous glands and the roots of hairs, both derived from the epidermis, become embedded in the corium, and from it they are fed. Fat cells are numerous especially in the lower layers.

The greater portion of the corium is made up of connective tissue fibers, both elastic and non-elastic. Most of these lie parallel to the surface, interwoven like the fibers of felt; but some bundles are perpendicular to the surface. The fibers are more compactly set in the outer parts of the corium than in the inner. The deepest layer is the loose or areolar connective tissue by which the entire skin is attached to the underlying muscle or bone. Skin muscles are few, and are mostly connected with the bases of the hairs. The elasticity of the skin decreases with age.

Leather is made from the outer, compact layer of the corium of animals. The epidermis is removed by maceration, and the connective tissue fibers are toughened by tanning.

DEVELOPMENT OF THE SKIN

Notwithstanding the close connexion between the two main layers of the skin, their origin in the embryo is diverse, the epidermis developing from the ectoderm, the corium from mesenchyma. Since the mesenchyma is derived chiefly from the mesoderm, this contrast in origin is fundamental.

Epidermis. The embryonic epidermis arises directly from the ectoderm, and is at first a simple cuboidal epithelium. By the end of the first month, as the result of cell divisions in a plane parallel to the surface,
this epithelium becomes two-layered, the outer and thinner layer being the periderm.

By the continued multiplication of the basal cells, the number of layers gradually increases, until by the fourth month, all four layers of the thicker parts of the adult skin have appeared. The cells of the stratum corneum contain a fatty or waxy substance, which helps to form the pasty vernix caseosa which covers the body of the new-born infant. Developing hairs, instead of penetrating this layer, lift it as a continuous sheet, the epitrichial layer.

Corium. In most parts of the body, the mesenchyma which produces the corium is derived from cells which have migrated from the parietal layer of the mesoderm. For this reason, that part of the epimere which forms the corium is called the dermatome. Some observers, however, assert that in mammals the entire epimere forms muscle and there is no dermatome in embryos of the group. Moreover, in some vertebrate embryos, if not in all, the ectoderm also contributes to the mesenchyma of the head and possibly, therefore, to the corium.

Embryonic mesenchyma consists of scattered, stellate cells, separated by wide spaces. It becomes the connective tissue of the corium by secreting intercellular fibers, both elastic and non-elastic. By the fourth month, the compact fibrous layer of the corium is distinguishable from the loose areolar tissue under it. Blood vessels and nerves invade the corium from below, hairs and glands grow into it from the epidermis. Abnormalities in the distribution of blood vessels cause birthmarks.

FINGER-PRINTS

In all primates, the entire surface of the palms and soles, but no other portion of the body, is marked with fine parallel ridges separated by equally fine grooves.

At definite places on hands and feet, these ridges form concentric lines or loops. Eleven distinct "friction-ridge patterns" have been distinguished, five on the finger tips, four at the base of the fingers, two near the wrist or ankle. Those of the finger tips are most familiar, since they are used for identification. Since no function has ever been proved for these designs, their presence and their constant position has stimulated much interest and discussion. To useless organs, the hypothesis of special creation gives no clue. Are they, then, rudiments of structures functional in the lower animals? See Fig. 126.

The significant fact about these patterns is that they match precisely, both in number and position, the concentric rows of horny scales on the foot-pads of insectivores, a group which, for various reasons, is thought to be near the direct line of man's ancestry. In the insectivores, the position and arrangement of the scaly ridges is clearly adaptive and
the best possible one to prevent slipping in any direction. These fingerprint patterns, therefore, serve to convict men of animal ancestry, as they have on occasion served to convict them of crime.

On the sides of the fingers, the friction ridges merge into rows of wart-like elevations. This has been interpreted as confirming the opinion that the ridges are remnants of rows of horny scales. That the ancestors of the mammals were scaly is, however, supported by more convincing evidence than this.

Throughout almost the entire animal kingdom the skin tissues form various calcareous, chitinous, or horny structures—shells, spines, teeth, bones, scales, hair, feathers, horns—which serve for defence, support of tissues, or attachment of muscles. The limy shells of molluscs and the chitinous exoskeletons of arthropods serve all three purposes.
Among vertebrates, the placoid scales, which first appear in certain sharks of the Upper Devonian, are especially important because of their further evolution. Each of these scales has a flat basal plate of dentine embedded in the skin, and each has commonly also a projecting spine coated with hard enamel like a tooth. From these minute placoid scales of ancient sharks have evolved all the multiform teeth of all the higher vertebrates.

From these and other types of scale have evolved also, by simple enlargement, the heavy continuous dermal armor of ganoids and other fishes. These same bony plates survive also in man and the higher vertebrates as "membrane bones" which, unlike most parts of the skeleton are not pre-formed in cartilage but develop directly in connective tissue.

HORNY SCALES

Vertebrates, besides bony scales, have also horny; but these have played a much less important part in evolution, and are confined to amniotes, more especially, reptiles.

In reptiles, the stratum corneum forms a continuous scaly layer over the entire body, the separate scales being local thickenings which continue to grow by the addition of new keratin from underneath. Serpents commonly shed this scaly coat twice a year. But the rattlesnake retains
bits of the old skin at the tip of the tail. These become the rattle, which therefore grows two rings a year.

Most reptiles have substituted horny scales for the bony scales characteristic of fishes. But crocodiles have both sorts on the same individual. On the ventral side of some snakes, large scales are attached to muscles and become organs of locomotion.

The largest reptilian scales are those of chelonia, in which horny scales fuse with the bony carapace and plastron. In birds horny scales cover the feet.

Among mammals, the East Indian manis, and the tails of rats and mice are scaled.

![Diagram](image)

**Fig. 129.**—Section of developing scales of lizard, *Sceloporus.* e, papilla of corium; e, outer layer of epidermis which later becomes cornified; f, fibrous layer of skin; m, Malpighian (stratum germinativum) layer; p, periderm; ts, tela subjunctiva. (From Kingsley’s “Comparative Anatomy of Vertebrates.”)

It is a curious fact that while horny scales are purely epidermal structures, their development is initiated, like that of bony scales, by the corium.

**Horns**

To produce such diverse structures as hairs, feathers, scales, nails, and hoofs, demands most exceptional evolutionary potentialities on the part of the horny layer of the skin. Among the surprising developments of keratin-forming tissues are the horns of ruminants and rhinoceroses. Those of rhinoceroses are formed wholly of keratin produced by the stratum corneum on the snout. The hollow horns of cattle have, in addition to external keratin, a bony base and core, which grows from the frontal bone into the cavity of the horn. The antlers of the deer tribe are bony outgrowths with no covering of horn, but only the skin or “velvet” which is soon lost.

Horns are best interpreted as weapons of defense and offense.

**Nails, Claws, and Hoofs**

Nails are scale-like thickenings of the stratum lucidum at the ends of the fingers and toes, formed of homogeneous keratin identical with that of the stratum lucidum from which they develop.

Nails and claws are strikingly alike except in form. Both develop from a matrix at the base, which in man appears as the whitish “lunula.”
Both have their bases surrounded by a fold of skin, the "nail wall." In both, a convex outer plate on the upper side of the digit may be distinguished from a concave "ventral plate" on the under side, each being morphologically a reptilian scale. The ventral plate in man is reduced to a narrow fold of skin between the nail and the finger pad.

Claws appear first in urodele amphibia. In some Anura, they are limited to certain hind toes. But certain male frogs, at mating time, develop horny papillae on their thumbs, which serve to hold a slippery female. Reptiles have claws on all toes. Those of mammals are like those of reptiles, except where the mammalian claw has altered into a hoof, or become retractile, as in cats, which walk on foot-pads and keep their claws sharp by raising them off the ground. Claws of mammals intergrade with nails, so that it is difficult to draw a line between the two.

Some primates have both claws and nails on the same foot. Nails are then rudimentary claws, modified to correlate with the increased sensibility of the ends of the digits and their use as organs of touch.

Some mammals, such as the horse and deer, which run on their toes, have hoofs instead of claws. The structure, development, and relations of hoofs, however, prove that they are nothing more than enlarged and modified claws. Both have dorsal and ventral plates. The attempt to divide mammals into hoofed and clawed types encounters the difficulty that at least one animal, Hyrax, has both claws and hoofs.

FEATHERS

Feathers, which are characteristic of birds, are modified scales, and their early development is the same. A corium papilla initiates both; but the feather anlage, instead of flattening to a scale, becomes an elongated cylinder, which splits into the plumes, barbs, and barbules of the developed feather. A down feather, in fact, suggests an elongated and frayed out scale.
Birds, which have descended from reptilian ancestors, still have scales on their feet, and even their bills and claws are presumably enlarged and modified scales.

HAIRS

Hairs, which are characteristic of mammals, are not comparable morphologically with either feathers or scales, since their development is initiated by the epidermis and not by the corium. When, as in Manis, hairs and scales occur together, the hairs are at the apices of the scales. That scales are older phylogenetically than hairs, is indicated by the fact that scales develop earlier in the embryo; and fossil evidence demonstrates that mammals have evolved from some scaly Stegocephalan-like Cotylosaurian. But since neither the skin nor its non-bony appendages are commonly fossilized, their history has to be made out chiefly from embryology and comparative anatomy.

All mammals have hair; and man's relative hairlessness is by no means a distinctive human trait, since some mammals, for example the whales, have less hair than man. It is well known that changes in the secretion of the endocrine glands affect profoundly the growth of hair, and man's loss of hair may have been thus brought about.
Hair Structure. The hair of all mammals is essentially similar. There are, however, such differences of detail as enable an expert to identify different species.

Each hair consists of a "root" buried in the skin, and an external shaft. Microscopic examination shows a multicellular structure, with the cells in three layers, an outer cuticle, a cortex, and a central medulla. The cells of the cuticle are scale-like, overlapping one another like shingles on a roof. Cortex cells, greatly elongated, make up the greater portion of each hair. The medulla occurs only in the "contour hairs" and is wanting in the finer. It is made up of cuboidal cells usually in a double row.

The root is surrounded by epithelial and connective tissue sheaths. It ends in a swollen "bulb," from which it grows and which contains a connective tissue papilla, with capillaries which feed the hair.

Hairs of different human races differ in cross section. In general, the rounder the hair, the straighter it is; the more compressed, the curlier. It has not been shown that these differences have been developed either by natural or by sexual selection.

Hair Direction. Hairs, instead of projecting vertically from the skin, emerge at an acute angle, have a slant in some special direction, and thus form streams in various parts of the body. Where such currents meet, either "rhomboids" or "vortices" may form, the latter being commonly called "cowlicks." The fact that such rhomboids and vortices appear on the human body in regions where the hair is short, has been interpreted to mean that man's hairy covering was once longer than at present.
Although in general the direction of hair growth is such as to make gravity the determining influence, it is a curious fact that the hair on the human forearm suggests his animal ancestry. The hair of the forearm slants from the wrist toward the elbow, in the reverse direction to the slant on the upper arm. Man shares this peculiarity with the apes alone. All other mammals have the same hair direction on both parts of the limb. Why this resemblance of man to the apes unless they share a common ancestry? The peculiarity is not adaptive, and it is not easy to see why, if man and apes were independently created, they should resemble one another in this detail.

**Hair Arrangement.** That the arrangement of hairs on the human body has any evolutionary meaning is, to say the least, surprising. Indeed, since such patterns can have no use, we should hardly expect to find them at all. No less surprising is an arrangement of hair in mammals that indicates descent from scaly ancestors.

In most mammals, the hairs occur in groups of three or more. These groups are arranged in parallel rows in such wise that each cluster lies opposite an interval in the rows in front and behind. In short, the arrangement is imbricated, like the universal arrangement of scales. This arrangement, though quite useless, is precisely what we should expect if mammals have descended from scaly ancestors.

**Histogenesis of Hairs.** Hairs are, in origin, epidermal, and therefore ectodermal. Each begins as a minute epidermal papilla, which has arisen by local cell proliferation in the *stratum germinativum*. Continued proliferation gradually converts this papilla into a cellular column, which extends obliquely downward into the underlying mesenchyma which is to become the corium. The growing end swells into a bulb, in which later develops the corium papilla from which the hair is to grow. Cellular differentiation of the hair column results in an inner sheath and the hair-shaft, all surrounded by an outer sheath. From the bulb to the point in the hair column where the sebaceous gland develops, the cells of the hair-shaft become cornified. Above this point the central cells degenerate to form a canal in which the hairshaft grows towards the surface. Continued cell multiplication of the *stratum germinativum* of the papilla elongates the central hair shaft to extend beyond the skin.
Each hair thus formed continues to elongate throughout its life of some months or years, the rate of growth varying greatly in different parts of the body. But finally, growth ceases, the hair dies, and is shed. If the hair papilla retains its stratum germinativum, a new hair grows.

Each hair column, in addition to producing a hair, may form as lateral outgrowths one or more sweat or sebaceous glands. Muscle cells developed from the mesenchyma of the corium attach themselves to the hair-roots and become arrectores pilorum.

![Diagram of skin structure](image_url)

**Fig. 134.**—A vertical section of skin of a five month human embryo, showing four early stages in the development of a hair. The growth of a hair is initiated by the formation of an epidermal papilla projecting (down) into the underlying corium. (Redrawn from Bremer after Stöhr.)

The human foetus has before birth a hairy covering, the "lanugo," which is shed shortly before or soon after birth. The coat persists, however, in certain types of "hairy men." The evolution theory affords the only rational explanation of the lanugo.

**PIGMENT**

Skin color in man is due in part to the blood in the capillaries of the corium. In addition, there are two pigments in the skin and hair, a brown, sometimes darkened to a black, both in granules, and a yellow, that may strengthen to a red, both diffused in the tissues. All are products of cell metabolism.

The pigments of the hair are confined to the cortex. The epidermis and the outer parts of the corium are both pigmented. Not until shortly after birth do pigment granules appear in the stratum germinativum, so that even negroes are born white.

Moles and freckles involve excessive local pigmentation. Freckles are small local patches of excess pigmentation, which are more likely to occur in light-skinned individuals who have been exposed to strong sun-
light. A mole or nevus is an elevation of the skin due to local proliferation of epidermis and corium, and is usually excessively pigmented. When a mole is congenital and involves blood capillaries, it forms a "birthmark."

Since pigments like those of vertebrates are found also in invertebrates, there is no reason to question their common origin. Many animals below the mammals have their pigments in special cells, the chromatophores, which expand or contract under the influence of hormones and thus alter the color of the skin. The colors of lizards, which are often brilliant, are not in their scales, but in chromatophores of the underlying corium.

Widely among vertebrates, pigments of scales, skin, hair, or feathers often show striking and elaborate patterns that serve for protection, warning, recognition, or sexual allure; but in man chiefly the region of the nipples and the external genitals are slightly darker than the rest of the body. In man and some other hairless mammals, such as the elephant, the function of the skin pigment is to check ultraviolet light before it penetrates to living cells. Everyone has observed the effect of the sun's rays upon unwonted skin, and the promptness with which the skin responds by tanning. Lacking skin pigment, men could not live in some parts of the earth.

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**Fig. 135.**—A series of hypothetical stages in the phylogensis of cutaneous appendages of vertebrates. A common origin of placoid scale, horny scale, feather, and hair from a corium papilla is assumed. (Redrawn after Matvieveff.)
**Color in Races and Individuals.** The blue of the iris of human children and new-born kittens is an interference color, like the blue of the sky or the eyes of a peacock’s tail. Later, as the iris fibers thicken, the interference is less perfect, and the eye is gray. Brown pigment in some fibers only, gives hazel. Brown eyes are evenly pigmented. Dark brown eyes are called black.

There is also the yellow pigment, which, nearly free from brown, gives the amber eyes of some blondes. The same color intensified, makes the red iris that sometimes accompanies red hair. The interference blue slightly masked by yellow, gives that rarest of all eye colors, green.

In general, among Europeans, the eyes are less pigmented than the hair, so that dark hair with gray-blue eyes is common. But some blondes have a striking color scheme, eyes darker than the hair.

Hair is colored by the same two pigments, both usually present, with the brown-black, masking the red-yellow, except in strong light. But some dark hair lacks the red and is blue-black.

Some blondes have no brown pigment, and little yellow. Most have brown also, along with varying amounts of yellow. The tow head with a touch of dark, is the ash blond. Yellow with some red is golden; and starting from this, the red may strengthen to a rather unadored carrot or orange. More brown carries the red over into auburn; still more gives bronze.

Hair that has lost its color is white, for the same reason that snow is, the crystal faces of the one and the cell walls of the other scatter the light.

Skin color is like hair color except that the blood color below the pigment may show through, and that sunlight, which fades the lifeless hair, stimulates the living skin to turn dark.

Primitive man was dark as the ape ancestor was, and as most races are still. Reducing the black pigment with the yellow retained, gives the Mongolian skin color. The stronger yellow, together with a good deal of brown, is the traditional hue of the Red Man, though as a matter of fact, most Indians are brown, like most White Men.

The blond White Man is a local race that originated in some region near the Baltic, apparently since the last Ice Age. Being highly energetic and uncommonly well endowed, the descendents of these blond giants have made their way all over the world, and, much diluted with darker blood, still appear in most civilized countries of the world.

Why their blondness, nobody knows. It cannot be due to climate, for the Eskimos, Samoyads of Siberia, the Patagonians, and the people of northern China are all dark. Naturally, a blond race could hardly survive in the tropics; but a white skin is no obvious advantage anywhere. Yet certain studies of Chicago children show that the highly pigmented
Italians are more liable than lighter stocks to rickets, which is a sunlight deficiency disease. So it may be that in high latitudes, in a wooded country or one that has much cloud and fog, a fair skin that is still able to tan may have a selective value and be accounted for on Darwinian principles.

Skin color plays queer tricks. Any two parents, even two Negroes, may have an albino child; two dark-haired parents may somehow miss with the brown pigment and have red-haired offspring. The most that anyone can say is that "Nordic" man probably began as a mutant from a dark stock. Possibly, after the mutation appeared, it was admired and selective mating kept it to the fore.

**Fig. 136.**—A diagram illustrating the nervous mechanism of temperature regulation in man. The quantity of secretion of tubular glands (and consequently the amount of sweat which may evaporate to cool the body) depends upon the quantity of blood in the capillaries associated with the glands and dermal papillae. Through a reflex arc the circulation is regulated by the temperature of the skin. (Redrawn after Hough and Sedgwick.)

**CUTANEOUS GLANDS**

Since among invertebrates most glands are unicellular, it has generally been assumed that the multicellular glands of vertebrates have evolved from such beginnings, an increase in the size of the secreting cells tending to carry them into the underlying corium, where together with other epidermal cells, they become multicellular organs.

Be this as it may, cutaneous glands develop, much as hairs do, from solid cords, which are proliferated from the *stratum germinativum* and grow downward into the underlying corium. The lumen of the gland forms later, to connect with the exterior, and the gland anlage differen-
iates into a secretory portion and a lining for the duct. The secretory cells become intimately associated with blood vessels and nerves.

**Sweat Glands.** In man sweat glands occur in most regions of the body, and are especially abundant on the palms and soles. They are, for the most part, of the simple tubular type, much coiled to increase the secreting area; but those of the axillae are branched and greatly enlarged. They are of the “vitally secretory” type, that is, the cell protoplasm merely produces the secretion, but is not converted into it, and the cell continues alive indefinitely. The sweat is usually oily, but becomes watery under the influence of the nerves. See Fig. 136.

![Diagram of different kinds of nipples](image)

**Fig. 137.**—Scheme of different kinds of nipples. Single line, ordinary integument, double line, that of primary mammary pocket. A, primitive condition, found in *Echidna*; B, human nipple; D, *Didelphys* before lactation; C, same at lactation E, embryonic, F, adult conditions in cow. B and C are true nipples, F a pseudo-nipple (teat). (Based on figures by Weber from Kingsley.)

**Sebaceous Glands.** Sebaceous glands in man also occur on most parts of the body, but are wanting on the palms and soles. Most hairs have sebaceous glands connected with their follicles.

They are of the acinous type, and necrobiotic, that is, their protoplasm forms the fatty secretion, which the cell extrudes, and then dies.

**Other Glands.** Besides the sebaceous and sweat glands, there are other highly specialized cutaneous glands, the lacrimal glands of the eye and the Meibomian of the eyelids, the wax glands of the auditory meatus, besides preputial, vaginal, anal, and mammary glands, which occur in most mammals.

Of the organs which have evolved from glands, none are more surprising than the luminous organs or photophores of deep sea fishes. These are true dark lanterns since they have a condensing lens and a reflecting
membrane. The light is produced by the oxidation of luciferin secreted by the gland. No carbonic acid and little heat are evolved in the process.

![Diagram of the integumentary system](image)

Fig. 138.—The presence of supernumerary teats (polymastism) in man supports the theory of the animal origin of the human body. Their repeated occurrence has received no other rational explanation. They are reversions or atavisms. (Redrawn after Wiedersheim.)

![Diagram of mammary gland development](image)

Fig. 139.—A figure illustrating the development of the mammary gland in man. A 13.5 mm. embryo shows the "milk line", a ridge which extends from the axillary region to the groin. The definitive gland develops only from the anterior portion of this line. Taken with the evidence of supernumerary teats in man, the line is interpreted as proof that the ancestors of man had more than a single pair of mammary glands. (Redrawn from Arey, after Kollmann.)

A, B, and C are sections of the definitive mammary gland in successive stages of ontogenesis. A is from a two-months embryo, B from a four-months embryo, and C from a seven-months embryo. From its development the mammary gland is seen to be a compound tubular gland. (Redrawn from Arey, after Tourneux.)

**Mammary Glands.** Mammary glands first appear in monotremes, as a pair of milk-secreting organs on the ventral side of the body. They are without nipples, and in Echidna they pour their secretion into a
depression, the "mammary pocket," surrounded by a fold of skin. From this condition in monotremes, the teats of the higher mammals have evolved, either by elevating the milk-field at the bottom of the pocket into a "true teat," as in man, or else by elevating the surrounding ridge to form the "false teat" of ruminants. The number of teats corresponds roughly to the number of young in a litter.

Functional differences among the glands of vertebrates are much greater than morphological, and their physiological evolution is a difficult problem in biochemistry.

Certain abnormalities in the milk glands of man, however, confirm strongly the theory of the animal origin of the human body. Supernumerary nipples appear in man with a certain statistical frequency. But these extra teats, instead of being placed at random, are usually set in two ventral rows, precisely like two rows of nipples which form the milk lines of lower animals. They are, then, best interpreted as reversions to an animal ancestor. The theory of special creation gives no clue whatever to their occurrence in human beings. See Fig. 138.
CHAPTER 5

TEETH

No invertebrate has teeth at all comparable, save in function, position, and material, with the teeth of vertebrates. Some annelids, like Nereis, have horny pharyngeal teeth that act like pincers. A circle of calcareous teeth surrounds the mouth of the vegetarian sea-urchin to form the lantern of Aristotle, but each tooth has its own muscles and there is no jaw. Some snails have a radula with which they rasp their food. Many arthropods, notably the biting insects, have their appendages modified into hard mouth-parts that are both jaws and teeth. But a series of independent teeth operated by a movable jaw is peculiar to chordates.

Nor do all chordates possess such teeth. The protochordates have no teeth of any sort. Cyclostomes have within the oral hood horny ectodermal teeth, with which they cling to their prey or bore their way into its flesh. In this absence of calcareous teeth attached to jaws, as in so many other characteristics, the cyclostomes exhibit their primitive nature.

The larvae of some amphibia have upon their jaws horny teeth in the form of papillae. Most reptiles have true teeth; but the chelonia have replaced those of their ancestors with horny beaks. So, too, have all modern birds, although their ancestors of the Jurassic and Cretaceous had typical reptilian teeth. The embryo of the duck-billed platypus has rudimentary teeth which it does not use. Even among the placental mammals, the edentates either have no teeth or have them without enamel. In the toothless whales, teeth are present in the embryo, but the adult has only whalebone strainers.

EVOLUTION OF TEETH

Since the protochordates are without teeth, the cyclostomes have horny ones, and all attempts to discover any sort of rudimentary calcareous teeth in cyclostomes have proved unsuccessful, it seems clear that teeth of the vertebrate type are a new acquisition with no homologs anywhere among invertebrates.

Typical or "true" vertebrate teeth have their beginning in the innumerable, minute placoid scales, which so roughen the skin of sharks that in former time shark skin, under the name shagreen, was widely used as an abrasive.
In elasmobranchs, on the edges of the jaws, these minute scales become enlarged into formidable biting teeth or sometimes inside the mouth into bony pavements that are used for grinding the food.

That the biting tooth of elasmobranchs is a modified placoid scale is obvious from inspection, since the two look alike, and there is a transition in size and form between them. This identity is further borne out by other evidence. Like true teeth, placoid scales have a base of dentine, which contains a pulp-cavity filled with connective tissue. Both scales and teeth have a spinous process, covered with enamel, which protrudes through the skin. Moreover, their development is similar, in that, in both, the enamel is secreted by the ectoderm and the dentine by mesenchyme, and both arise in that portion of the mouth where the ectoderm has invaginated to line the digestive tube. See Fig. 141.
This evidence for the identity of teeth and placoid scales is not invalidated by the fact that the endodermal lining of the pharynx of some elasmobranchs is also beset with placoid scales like those of the external skin. This simply shows that the potentialities of the germ-layers are greater than was formerly supposed. The lining of the pharynx has also taste-buds, although sense organs usually develop from the ectoderm. The presence of scales and of taste-buds in the pharynx has led some morphologists on a priori grounds to assume that ectoderm has invaded mouth, pharynx, and even the esophagus. There is no question that the lining of the pharynx is primarily endodermal, and no one has ever been able to discover evidence that this primary lining degenerates and

![Fig. 141.—Comparison in development and structure between a placoid scale and a tooth. a, b, and c represent the scale; d, e, and f the tooth. In all the figures the stratum corneum is dotted, the stratum germinativum is represented by a layer of large cells with nuclei; and the cutis is presented as composed of fibers with scattered cells. x, enamel membrane; y, cutis papilla; e, enamel; d, dentine; p, pulp cavity. (From Wilder's "History of the Human Body," Henry Holt & Co.)](image)

is secondarily replaced by ectoderm. Until such evidence is presented, we have no alternative to the conclusion that the endodermal lining persists and produces both taste-buds and enamel. Whatever the origin of the enamel of these pharyngeal scales, there is no doubt that the enamel of the teeth, like that of dermal scales, is of ectodermal origin.

Originally, in vertebrates, the teeth were for seizing and holding prey. Grinding and cutting teeth, tusks, and fangs, are all modifications of the primitive mouth trap.

The number of these holding teeth is indefinite in elasmobranchs, which may have as many as one hundred. They are not attached to the jaws, but merely imbedded in the skin of the mouth. They are all about alike; and when one is lost, another moves forward into its place.
In teleosts, the number of teeth is somewhat reduced, although all parts of the mouth and even the pharynx may carry them. The special advance made by the teleosts is to set the teeth more firmly by fusing their bases with the membrane bones of the mouth.

Amphibia still farther reduce the number of teeth; but retain them on premaxilla, maxilla, mandible, vomer, and palatine bones, and more rarely on the paraphenoid. But toads have no teeth whatever. A striking feature of certain ancient and long extinct amphibians, the labyrinthodonts, which arose in the Coal Period and survived into the Triassic, was the enormously complicated folding of the tooth enamel and dentine, which anticipated, yet went far beyond the similar arrangement in some mammals.

Reptiles make two important advances toward the condition in mammals. Some of them, like some of the amphibia, have their teeth set on a ledge on the inner side of the jaw—pleurodont dentition. Or they may have the tooth set directly on the bone, acrodont dentition. But the crocodiles and some fossil reptiles attain to a thecodont dentition, in which each tooth is fixed in a separate socket, as in mammals. In addition, some lizards and numerous fossil reptiles abandon the original homodont dentition, with all teeth about alike, and have their teeth more or less differentiated into incisors, canines, and molars, as in mammals, a heterodont dentition. The differentiation of teeth is obviously an adaptive division of labor, the incisors acting as cutters or chisels, the canines as daggers, and the molars as grinders. The reptiles, moreover, limit their teeth to the two jaws.

An especially elongated tooth occurs in the lower jaw of lizard and snake embryos, which is used to break through the tough membranous shell. A hardened tip of the horny beak of birds is used for the same purpose. The two structures are, however, morphologically quite different.

Especially remarkable in reptiles are the highly specialized poison fangs of certain snakes. These are modified from the ordinary conical tooth, first by a folding of the tooth to form a groove along which the venom from a modified salivary gland flows into the wound. In other snakes, by a still further folding the edges of the groove unite, and the tooth becomes a hollow needle. One pair only is functional at any one time, others up to nearly a dozen pair being held in reserve to take the place of the large fangs when these are lost. All the vipers including the rattlesnakes fold back the functional pair of fangs when the mouth is closed, and only in the act of striking pull them erect by special muscles.

Mammals, besides having nearly always a heterodont dentition, with incisors, canines, and molars well differentiated, have adopted also a distinction between a milk and a permanent set, as a means of adjusting to an enlarging mouth solid teeth of limited size.
The elasmobranchs, indeed, do have a certain succession of teeth, but only one at a time as single teeth are lost. Lower vertebrates, reptiles conspicuously, have a somewhat indefinite number of sets, and are said therefore to be polyphyodont. Only the mammals have two definite sets, and are therefore diphyodont. But monotremes, sirenians, and toothed whales retain their milk teeth throughout life, have no second set, and are said to be monophyodont.

In general, then, the course of evolution has been from a large and indefinite number of simple teeth all alike, not fixed firmly in place, and borne by any part of the mouth, to a reduced and definite number, set firmly in alveoli, confined to the jaws only, and differentiated into three sorts. Along with this, has gone a shortening of the jaws and a change of food habits. But whether the change in diet caused the change in teeth, or the change in teeth made possible the change in foods, is still an unsolved problem.

**EVOLUTION OF COMPOUND TEETH**

Compound teeth resembling the molars of mammals first appear in certain late Permian and early Triassic reptiles, the theromorphs. Since amphibia and the earlier reptiles had simple conical teeth, the conclusion has been drawn that compound teeth are derived from conical teeth, and morphologists have advanced two theories as to how this evolution came about.

The **Differentiation Theory** of Cope and Osborn assumes that the teeth of vertebrates were originally of the simple conical type found in most Reptiles. Such were the teeth of the premammalian Stegocephala and of primitive Theromorph reptiles.

The first multitubercular type of molars of modern mammals appears in such a Triassic mammal as Dromatherium, the teeth of which had a large median cone or **protocone** in line with two smaller cones, a **paracone** in front and a **metacone** behind. Corresponding parts in the teeth of
the lower jaw are called **protoconid, paraconid** and **metaconid**. Teeth of this sort are known as **triconodont**. Besides the three cones, triconodont teeth have a basal rim, the **cingulum**, which forms part of the crown. Marsupial-like mammals of the Tertiary had teeth of this triconodont sort. See Fig. 143.

The secondary tubercles of such teeth show a tendency to enlarge to the size of the protocon. A further advance occurs when the three cones assume a triangular relation to one another, the secondary cones of the upper jaw migrating inwards, those of the lower jaw outwards. Teeth of this **tritubercular** sort occur in Amphitherium of the Jurassic period.

Later, in mammals, appeared a posterior projection or talon, and a fourth tubercle, the **hypocone** and **hypoconid**. With these additions, the molar teeth assumed more and more the modern form with six cusps.

![Fig. 143](image)

**Fig. 143.** — A, triconodont tooth of *Dromatherium*; B, tritubercular tooth of *Spalacotherium*; C, interlocking of upper (dark) and lower (light) tritubercular molar teeth (after Osborn); D, molar of *Erinaceus*; E, of horse (selenodont type); c, cingulum; m, metacone (metaconid); pa, paracone (paraconid); pr, protocone (protoconid); t, talon. (From Kingsley's "Comparative Anatomy of Vertebrates."")

It took many million years to accomplish these changes, which were naturally based upon change in the form of the tooth-germ and involved budding of that organ.

The **concrescence theory** accounts for the multitubercular molar teeth of mammals by supposing a fusion of the anlagen of conical teeth, the number of cusps corresponding with the number of conical teeth involved. Some observers claim to have found evidence of fusion of tooth-germs in vertebrate embryos, but most investigators are sceptical. It must be said, however, that tooth fusion is known to occur in the case of the massive pavement teeth of dipnoi. At the present time the concrescence theory seems to have less factual support than does the differentiation theory.

According to Bolk, in a modified form of the concrescence theory, compound teeth are formed by the fusion of the germs of successive sets. His theory assumes that the ancestors of mammals had more than two generations of teeth like the milk and permanent sets, that is, their dentition was **polyphyodont**. Under these conditions, the germs of
successive sets might fuse with one another. The factual foundations of the theory, however, are weak.

**TEETH OF MAMMALS**

Teeth of mammals are especially important for the paleontologist, partly because they are hard and therefore likely to be preserved, but more because mammalian teeth are closely correlated with feeding habits. But feeding habits, in their turn, are correlated with the entire bodily structure, so that teeth are a key to the whole organism. Moreover, mammalian teeth are so highly specialized and so diverse in size and structure, that a single one is often sufficient to identify a species.

In general, the tendency has been to reduce the number and to do away with the division into two sets, and at the same time to specialize and elaborate individual teeth. An ideally complete set for a placental mammal would consist of three incisors, one canine, four premolars, and four molars in each half-jaw. The distinction between premolars and molars is that the premolars replace milk teeth, and are therefore of the second set, like the teeth in front of them; but the molars have no predecessors, and are therefore really of the first set. Functionally, however, and often in size and shape, there is little difference, and the two groups are conveniently lumped together as cheek teeth.

But while 3-1-4-4, 48 teeth in all, is ideal, no placental mammal conforms to it, 44 being the usual limit in any actual animal and 3-1-4-3 a common formula. Nevertheless, it is convenient to think of each actual tooth as one particular member of the ideal set. Thus can the history of each tooth be followed throughout all the placental mammals, and each be identified wherever it occurs. But the marsupials are aberrant, opossums, for example, having four and five incisors, so that their teeth cannot always be homologized with those of placentals.

Starting, then, with the ideal dental formula: $i_3$, $c_1$, $p_4$, $m_4$, the little hyrax or cony allied to the elephants is one of the few mammals to retain the full eight cheek teeth. But its incisors are reduced to one in each half-jaw and it has no canines. On the other hand, the ungulates tend to have the typical four front teeth, but to lack one molar and sometimes a premolar also. They usually, have the canine like the incisors, and so have practically, though not morphologically, four incisors. But all hollow-horned ungulates lack upper canines, and many, like domesticated sheep, have lost all four incisorform teeth from the upper jaw. Their dental formula is, therefore, in brief form: $2-0-3-3$.

The pigs, with forty-four teeth in all, are peculiar in having the canines in both jaws grow throughout life as fast as they wear away, and are kept sharp by whetting against one another. The walrus makes
tusks of the upper pair only, which also are unrooted. The narwhal, for a like purpose, uses one incisor, its mate growing indefinitely in size, and has no other teeth.

The carnivora make the canines, especially the upper pair, into long curved daggers, which reach their extreme development in the extinct saber-toothed tiger of the Pliocene but are noteworthy even in the domestic cat. With each canine, in the flesh eaters, goes a "carnassial" tooth, especially developed in the cats, a premolar above and a molar below. Other cheek teeth, especially in the cats, tend to be reduced almost to rudiments.

Moreover, the carnivora, though uniform as to incisors and canines, differ somewhat widely in the cheek teeth. Thus, while the dog is $\frac{3}{1}-\frac{4}{2}$ the cat is reduced to $\frac{3}{1}-\frac{3}{1}$. The lynx is made a separate genus from the cats because it has lost the minute first premolar of the upper jaw and brought its dentition down to $\frac{3}{1}-\frac{2}{1}$. On the other hand, some of the whales have gone back to primitive conical teeth used only for holding, are virtually or quite homodont, and have fifty or more pegs in each jaw.

Characteristic of rodents is the complete absence of canines, and the reduction of the incisors to one functional pair in each jaw. The single pair, however, is a remarkable tool. Each tooth grows from a permanent germ, that is set far back in the jaw, so that each passes under all the cheek teeth, before it emerges at the front of the mouth. Enamel coats the front surface only, so that as the tooth wears, the dentine wears most, and the thin plate of enamel remains always sharp. Since these teeth grow throughout life, if they are not worn away by gnawing, they become too long and the animal cannot feed.

No rodent has more than six cheek teeth, many have only four, and an Australian mouse so far depends on its incisors, that it has brought its dentition down to $\frac{1}{0}-\frac{0}{0}$. But the hares and rabbits, and some other rodents, as if to exhibit their affinities with other mammals, have two more incisors, very minute, behind the large pair in the upper jaw.

Probosidians. The most specialized of all teeth are those of elephants. Incisors and canines are completely lacking in the lower jaw. In the upper jaw, one pair only of incisors become the tusks, but the other two pairs have so completely vanished that it is not known certainly which pair remains. The tusks are rootless, and grow from far up in the skull. They elongate throughout life, growing faster than they wear away, until in some instances, they have reached a length of eight feet and a weight of more than 150 pounds each. Certain extinct elephants had tusks even larger, up to twelve feet and two hundred pounds. In the Indian elephant, only the males have tusks. But the larger African species, which
uses the tusks for digging roots, has them in both sexes. The famous African elephant Jumbo, in a fit of rage, broke off both tusks inside his cheeks. When they grew out again, they made new holes through the flesh, but the original holes remained for the rest of the animal’s life.

Two extinct proboscidians, tetrabelodon and dinotherium, had tusks on the lower jaw also, those of tetrabelodon nearly parallel with the upper pair, those of the dinotherium turned downward like those of a walrus.

Curiously, the small milk tusks of the young elephants, which are shed early, are rooted like ordinary teeth—another illustration of Von Baer’s law that the young in a specialized group tend to resemble generalized ancestors. The cheek teeth of proboscidians, less conspicuous than the tusks, are even more remarkable. There are six in each half jaw, i.e., twenty-eight teeth in all including the tusks and four evanescent incisors. But of the six grinders not all are in use at one time. As the foremost wears down and is shed, a second and larger moves into its place, only to be followed by the remaining teeth in succession. Thus an old animal, since there are no canines, may have only the two tusks and four grinders.

The grinders themselves are remarkable for their enormous size, the largest being more than a foot from front to rear and four inches wide. Each tooth is highly complex, with intricate folding of enamel and dentine, so that as the softer dentine wears away faster, the tooth keeps always its sharp grinding ridges. The same arrangement on a smaller scale appears in various other vegetarian mammals, notably in the horse. The huge single teeth coming successively into use are a device for prolonging the life of the animal long after any set of teeth all functional at once would wear away. Apparently as a result, the elephants are among the longest lived of mammals.

**Primates.** The primates, except for their hands, feet, and brains, are a somewhat unspecialized group, and their teeth, though reduced in number to conform to the shortened jaws, are little differentiated and the enamel is not folded. The dental formula for the Old World monkeys is 2-1-2-3 in both jaws. But the New World monkeys have another premolar, and sometimes lack one of the three molars. It is a curious fact, which no special creationist has attempted to explain, that man, also an Old World primate, has exactly the dental formula of the others.

The canines in monkeys are somewhat longer than the other teeth, and in the male gorilla are much like those of the less specialized carnivores. Significantly, in man, although even the upper canines are hardly larger than incisors, they have nevertheless the long roots of the animal tusk.

That general tendency to shorten the mammalian face which has brought down the cats to three and four cheek teeth and the higher
primates to five, continues in man by a general reduction in size of all the teeth and by closing the diastema, the open space next the canines.

Fig. 144.—Dental arcades of ape, Negro and Caucasian. The form of the Negro arcade is transitional between that of the ape and white man. With the shortening of the human jaw the diastema between incisor and canine teeth seen in the ape jaw is lacking. The refinement of the face is one of the most striking results of primate evolution. (Redrawn after Wiedersheim.)

Fig. 145.—Human teeth viewed from the left side. The human dental formula is: \( i\frac{2}{3}, c\frac{1}{3}, pm\frac{3}{3}, m\frac{3}{3} \). As a result of the shortening of the human jaws the third molars frequently do not erupt. The elongated root of the canine tooth suggests that as in lower primates the ancestors of man may have had fangs. (Redrawn after Braus.)

Consequently, human teeth are a continuous series and no tooth is very much larger than another, for the canines ceased to be tusks at the begin-
ning of human evolution. Along with these, has gone a change in the
direction of the incisors, correlated with the appearance of a chin. In
the apes, the incisors protrude, in man, they stand upright. Incidentally,
the human bite becomes horseshoe-shaped, with the rows of cheek teeth
no longer parallel, as in all lower forms, even the apes. In addition, the
triangular upper molars of the apes, with three cusps, become in man
quadrangular with four, and, correlated with the reduced size of the single
teeth, their pulp cavities become relatively still farther reduced, not to
sacrifice unduly the thickness of the tooth wall. Ape teeth are, then,
taurodont, so that the X-ray sometimes identifies a fossil human tooth
when other tests fail.

All these differences between apes and men are, however, bridged by
various fossil creatures, on the whole human, some of the genus Homo
but not our species, others quite outside the genus, but still within the
family.

TEETH OF MAN

Human teeth are in structure substantially like those of most other
mammals, and very like indeed to those of other primates.

In each tooth three parts are distinguishable, an external enamel-
capped crown,—a root buried in a bony socket or alveolus,—and a neck
or constricted region between root and crown. The number of cusps or
tubercles on the crown varies in the different teeth. The incisor and
canine teeth have a single cusp, the premolars have two, and hence are
known as bicuspids, and the molar teeth may have as many as five. The
number of roots also varies in the different teeth. Incisors, canines, and
premolars have but one, although the roots of the premolars are some-
times divided into two. The lower molars have two roots, and the upper
molars three.

The finer structure of a tooth may be best seen in a thin longitudinal
section (See Fig. 146). The central portion, the pulp-cavity, is filled
with connective-tissue containing blood capillaries and nerve-fibers, which
enter the tooth through a minute foramen at the end of the root. The
larger mass of the tooth is formed by a bone-like substance, the dentine
or ivory. Unlike bone, however, dentine is devoid of cells. In section,
the dentine takes on a somewhat prismatic appearance from the presence
of parallel tubes, the dental canaliculi, which radiate from the pulp-
cavity through the dentine. At their peripheral terminations in the
dentine, the canaliculi branch profusely. The sensitivity of the dentine
to the dentist's drill is probably due to the living protoplasm in these
canaliculi, which acts in the manner of nerve fibers. The larger part
of the dentine, approximately 75%, consists of inorganic mineral salts
such as calcium phosphate and calcium carbonate. The remaining 25%
is organic material. At no place on the tooth does the dentine reach the surface, since the crown and neck are covered with enamel, while the root is surrounded by a heavy cement.

Enamel is the hardest substance in the human body, since it contains only three and a half per cent of organic substance. It is thickest at the apex of the crown, and thins out towards the neck and root. High magnification shows that the enamel consists of minute parallel hexagonal prisms which rest on the dentine and extend to the outer surface of the crown. Increase in the amount of enamel toward the outside of the crown is effected by means of increase in the number of enamel prisms and not by their enlargement or branching. In this way the solidity
of the enamel is maintained throughout the crown of the tooth. The mineral constituents of enamel are identical with those of dentine.

**Cement** is a bone-like substance covering the root of the tooth as a thin layer which becomes thickest at the apex. Like other bone, the cement contains lacunae connected with one another by canaliculi. The mineral constituents are identical with those of bone. Surrounding the cement, is a connective tissue **dental sac** or membrane continuous with the periosteum of the alveolus and at the neck connected with the covering of the gum, gingiva.

**Development of Teeth**

When the human embryo has attained a length of about 11 mm., that is, by the end of the sixth week, the ectodermal epithelium covering the upper and lower jaws grows rapidly down into the underlying connective tissue to form a horseshoe-shaped ridge or lamina extending along the edge of the jaw. As growth continues, the lamina divides into an outer **labial lamina** and an inner **lingual lamina**. The two ingrowths,
however, soon separate, one growing in labially, the other lingually.

The latter forms the **dental ridge** or **lamina**. As in development of a hair, the dental ridge is formed by cell multiplication in the stratum germinativum of the epidermis.

Early in the development of the dental lamina, a series of bell-shaped enlargements, ten in each jaw, appear along its labial border (Fig. 148). These are known as **enamel organs** since they secrete the enamel covering of the crowns of the teeth. Each of the twenty milk teeth has a separate enamel organ, and all of them are present in a $2^{1/2}$ months embryo. Each enamel organ contains a mesenchymatous **dental papilla**, the outer cells of which, the odontoblasts, secrete the dentine of the tooth. The remaining cells of the papilla become the **pulp** of the tooth. As development proceeds, each enamel organ recedes from the dental lamina with which it retains a transient connexion by means of a "neck" or cord of cells.

The free edge of the dental lamina, losing connexion with the anlagen of the milk teeth, forms a second set of enamel organs lying on the lingual side of the primary set. In this way, the anlagen of the thirty-two permanent teeth come to lie embedded in the connective tissue of the jaws on the lingual side of the primary set. The permanent teeth are, however, relatively slow in development, the third molar usually not forming in the jaw before the fifth year.

Soon after the enamel organs emerge from the dental lamina, they become differentiated into three layers, an inner **ameloblast** layer which secretes the enamel, a mesenchymatous enamel pulp, and a layer of outer enamel cells. The ameloblast cells which line the enamel organ are columnar epithelial cells derived directly from the stratum germinativum of the epidermis. Viewed from the inner surface, each ameloblast cell is hexagonal and each secretes a simple hexagonal prism of enamel. As the enamel increases in thickness, the multiplication of ameloblast cells
results in an increase in the number of enamel prisms. The twisting and curvature of the prisms in the developed tooth is a consequence of the torsion of the ameloblast layer during active secretion. While the enamel grows by addition from the outside, the dentine increases in thickness from within. Consequently as the tooth is formed the ameloblast and odontoblast layers are pushed farther and farther apart. During the secretion of the dentine, protoplasmic strands from the odontoblasts are retained within the dentine to form the dental canaliculi. The odontoblast cells persist throughout life, and by their continued secretion may in old age entirely obliterate the pulp cavity of the tooth.

The crown of the tooth is the first to develop, and for a while the tooth resembles a silver-plated thimble, the thin enamel coating corresponding to the silver plate covering, the dentine to the bare metal. As the tooth grows, it increases in length as well as in thickness, adding first a neck and later a root. The opening into the inner pulp cavity becomes more and more restricted as the root elongates until finally only a minute foramen remains to admit blood-vessels and nerves. The nerves grow into the pulp and acquire free terminations among the odontoblast cells. The cement layer is the last to be added. Cement is secreted by bone-cells which penetrate the connective tissue sac enclosing the tooth. Membrane bone is formed around the root of the teeth to form the alveoli of the jaw-bone and to hold the teeth firmly in place.

The mechanics of the eruption of teeth is a problem which needs further elucidation. Among the factors which operate is the elongation
of the root, although teeth erupt before the root has completed its growth. The eruption of the deciduous teeth begins during the seventh month after birth, and is usually completed by the end of the second year. Of

the permanent set, the first to erupt are the first molars which appear during the sixth year. The last to erupt are the third molars, which frequently become impacted in the jaw-bone so that eruption is impossible.
Fig. 152.—A section of the jaw of a nine-months human embryo, showing the anlage of a canine tooth. The enamel organ of the permanent incisor is seen on the lingual side of the milk-tooth. (Redrawn after Corning.)

Fig. 153.—The teeth of a five-year-old child. Portions of the jaws have been removed so as to expose the roots of the milk teeth and the anlagen of the permanent teeth. The latter are stippled in the figure. (Redrawn after Sobotta.)
The shape of a tooth is determined by that of the tooth-germ. If the layer of ameloblasts is folded, the enamel is correspondingly modified, and teeth such as those of ruminants and elephants, which become ridged by wear as the result of the difference in hardness of enamel and dentine, owe this adaptive characteristic to the folding of the ameloblast and odontoblast layers. The multiplication of roots as in molar teeth is produced by the budding of the odontoblast layer of the dental papilla.
CHAPTER 6

THE SKELETAL SYSTEM

Some creatures, jelly fish for example, have no skeleton. In some, as in many molluscs and more conspicuously the corals, the skeleton is heavier than all the soft parts combined. In man, the bones make up about a fifth of the entire weight of the body, and this is not far from the average for active air-breathing vertebrates that do not have dermal armor.

All skeletons support or protect the softer parts. Supporting skeletons occur even in such lowly creatures as protozoa and sponges. Protective skeletons are conspicuous in echinoderms and molluscs, are universal among the arthropods, and are found among vertebrates in such diverse groups as the Paleozoic ostracoderms, ancient and modern ganoids, dinosaurs, turtles, and armadillos.

Skeletal parts, which are also jointed levers used in locomotion, occur in arthropods and vertebrates alone.

Arthropods solve the problem of locomotion by means of a chitinous exoskeleton with the muscles inside it. Such a skeleton is highly efficient as attachments for muscles, and it has the further advantage of providing armor at the same time. Its disadvantage is that it cannot grow, so that all the arthropods, by one device or another, shed their exoskeletons as their bodies enlarge. This leaves them for a time helpless. Furthermore, since the tissues of the molting arthropod are unsupported, no arthropod can attain any considerable size. Among arthropods the largest air-dwellers are foot-long centipedes; and although among water-dwellers the eurypterids of the lower Paleozoic and earlier were more than a yard long, a twenty-pound lobster is about the limit for a modern form. The typical arthropod is a tiny insect.

The endoskeleton of vertebrates, light and strong, and capable of indefinite growth, has the single disadvantage that skeletal armor must be developed independently. But vertebrates have for the most part abandoned armor. Their success as a group has depended not a little on their admirable endoskeleton. To its usual functions, the vertebrates add the production of blood cells by the marrow, especially of the long bones.

The Two Parts of the Skeleton. Historically, the vertebrate skeleton consists of two parts, which begin independently, have evolved separately,
and not even in the higher forms have become completely integrated. These are the appendicular skeleton of the four limbs with their girdles; and the axial skeleton, which includes the skull with the jaws, and the vertebral column, the sternum, and the ribs. The individual bones number in man, sixty-four for the shoulder girdle and the arms, sixty-two

![Diagram of Comparative Anatomy](image-url)

**Fig. 154.**—Diagrams illustrating two theories of the origin of chondrin in the formation of cartilage. According to one opinion (A) chondrin is of intracellular origin. According to the other view (B) chondrin is of intercellular origin. (Redrawn after Bremer.)

in the pelvic girdle and the legs, twenty-three in the skull, twenty-six in the backbone, and twenty-five for ribs and sternum, with six ear bones besides, over two hundred in all.

![Diagram of Vertebrate Skeleton](image-url)

**Fig. 155.**—A diagram of the vertebrate skeleton, showing the division of the skeleton into axial, visceral, and appendicular. Membrane bones are shown in black, cartilage bones stippled.
THE AXIAL SKELETON

Evolution of the Vertebral Column. Nothing like a vertebral column appears in any invertebrate, so that the earlier portions of its history are unknown; though, if amphioxus gives the clue, it was once no more than a medial dorsal fold of the alimentary canal. Its first certain beginnings are

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Fig. 156.—Diagram of the skeletogenous tissue in the caudal region of a vertebrate. *bv*, blood-vessels; *d*, corium; *epmu*, epaxial muscles; *hs*, horizontal septum; *hymy*, hypaxial muscles; *msd*, *msv*, dorsal and ventral median septa; *mys*, myosepta; *n*, spinal cord; *nc*, notochord. (From Kingsley's "Comparative Anatomy of Vertebrates.")

Fig. 157.—A, The skeleton of a cyclostome, Petromyzon; B, The skeleton of an elasmobranch, Cestracion. Elasmobranchs were the first animals to invent paired appendages and the skeletal elements to support them. Marked differences in the axial and branchial skeletons of cyclostomes and elasmobranchs also appear. (Redrawn after Dean.)
the notochord of the lower chordates, the hemichorda, urochorda, and cephalochorda. In the cyclostomes, the notochord is still the main part of the axial skeleton. Since the cyclostomes have cartilaginous neural arches, it is probable that neural arches are the earliest vertebral elements.

Elasmobranchs, both fossil and modern, show a considerable advance over the cyclostomes. Cartilaginous haemal arches and centra appear, with both neural and haemal spinous processes. The anterior trunk vertebrae of elasmobranchs have short lateral or “costal” processes which extend between the myotomes and which suggest the future ribs of mammals. Since in fossil and living forms two centra may occur in each body segment, and since each centrum usually develops in ontogenesis by the fusion of antero-posterior anlagen, it is possible that two centra in each segment (diplopondyly) may have been the original arrangement in vertebrates. Elasmobranchs, moreover, begin the long process of vertebral differentiation, the vertebrae of the tail being unlike those of the trunk, the difference correlated with a difference in the relation of the coelom to the vertebrae. In the trunk region, where the body cavity lies, the haemal arch of each vertebra is incomplete, while in the caudal region each arch is complete with a median spinous process. The notochord persists intervertebrally and the centra are biconcave. The skeleton is still cartilaginous, but the cartilage is often hardened with lime.

Bony vertebrae make their appearance in Ganoid fishes, some of which however retain a cartilaginous vertebral column. Ball and socket joints between the centra are developed in Lepidosteus (Gar-pike) as in some Amphibia. Amphicoelous or biconcave vertebrae, however, predominate in all groups of fishes. Centra are wanting in the Dipnoi.

With the amphibia, bone succeeds cartilage; and the vertebrae are differentiated into cervical, trunk, sacral, and caudal. The single sacral vertebra is but slightly modified for attachment to the pelvic girdle. A single atlas represents the cervical series of higher forms. Zygapophyses, for articulating each vertebra with its two neighbors, first appear in this group. Articulation with the ribs is effected by two sorts of processes,—diapophyses from the neural arches and parapophyses from the centra.

Lumbar vertebrae are first differentiated in reptiles, which also have two sacral vertebrae. Here also appear vertebrae with centra flattened...
on both anterior and posterior sides and with the centrum of the atlas fused with the axis, as in mammals.

The vertebral column of mammals shows little advance beyond that of reptiles. A few Insectivora have intercentra in the lumbar region,—

![Diagram of endochondral bone formation]

*Fig. 159.*—Endochondral bone formation at the end of a long bone. Destruction of cartilage is followed by the secretion of lime in the form of thin lamellae. Osteoblasts then lay down bone upon these lamellae. In this way cancellous bone replaces cartilage. (Redrawn after Dahlgren and Kepner.)

a diplopondyloous condition reminiscent of elasmobranchs. Parapophyses are reduced to shallow pits for articulating the heads of the ribs.

The human spine differs little from that of other mammals, except that the tail is reduced to a coccyx with a few variable muscles attached. Man’s only distinctive feature is the sigmoidal curve, which bends his spine in two directions, instead of one only as in other creatures. In
addition to the two main spinal curvatures, thoracic and lumbar, man also has two lesser curvatures, cervical and sacral, in the region of the neck and sacrum respectively.

Fig. 160.—Diagrams of (A and B) fish vertebrae and (C) vertebra from higher groups. b, basal stumps; c, centrum; ch, capitular head of rib; d, diapophysis; ha, hemal arch; hr, hemal rib; n, notochord; na, neural arch; p, parapophysis; r, rib; t, tubercular head. (From Kingsley's "Comparative Anatomy of Vertebrates.")

Fig. 161.—Two caudal vertebrae of alligator. c, centrum; ha, hemapophysis; hs, hemal spine; na, neurapophysis; ns, neural spine; poz, prz, post- and prezygapophyses; t, transverse process. The arrow passes through the neural arch. (From Kingsley's "Comparative Anatomy of Vertebrates.")

The Vertebral Column in Man. In the backbone of a child there are thirty-three vertebral elements. During growth the last nine fuse to form two adult bones, the sacrum and the coccyx. The other twenty-four vertebrae remain separate throughout life and become differentiated into seven cervical vertebrae, twelve dorsal or thoracic, and five lumbar. These are sometimes called "true" vertebrae in contra-distinction from those of the sacrum and coccyx which are called "false" vertebrae. Although the vertebrae are separate bones, they are nevertheless so firmly fastened together by ligaments and fibrous cartilages as to make the
backbone a fairly rigid column. Four curvatures appear in the adult—cervical, thoracic, lumbar, and sacral.

The Structure of a Vertebra. A typical vertebra consists of a cylindrical body, the centrum, which is flattened on its superior (cranial) and inferior (caudal) surfaces. A neural arch arises from the dorsal side of the centrum and surrounds a vertebral canal. That part of the neural arch which connects with the centrum is the pedicle. A spinous process extends backwards and downwards from the mid-dorsal side of the neural arch. That part of the neural arch between the spinous process and the pedicle is the lamina. Anterior and posterior notches or incisures constrict the pedicles so that the incisures of two successive vertebrae form the foramina for the spinal nerves which pass out between the vertebrae. Articular processes or zygapophyses project forwards and backwards from the neural arches. A postzygapophysis of one vertebra overlaps a prezygapophysis of the next vertebra and the two are bound together by ligaments: thus the backbone is strengthened, but at the same time made less flexible. On each side a transverse process projects from the neural arch laterally into the muscles of the body wall. See Fig. 164.

The Kinds of Vertebra. There are five kinds of vertebrae, cervical, thoracic, lumbar, sacral, and caudal or coccygeal. A distinguishing feature of cervical vertebrae is a transverse foramen which in the upper six vertebrae transmits the vertebral artery. The lateral border of this foramen is formed by the fusion of a rudimentary rib with the vertebra. The first two cervical vertebrae are the atlas and the axis or epistropheus. A peculiarity of the two is that the centrum of the atlas fuses with that of the axis to form the odontoid process upon which the atlas rotates. The
forms and arrangement of the cervical vertebrae permit greater freedom of movement than is possible in other parts of the column. The spinous process of each cervical vertebra except the last is forked or bifid.

Only the twelve thoracic vertebrae carry ribs. A pit in the centrum articulates with the head of the rib and a similar pit at the extremity of the transverse process articulates with the tubercle of the rib. The head of most ribs articulates with two adjacent centra.

The five lumbar vertebrae are the largest. Short ribs fuse with them to form conspicuous transverse processes. The neural arches of these vertebrae have mammillary and accessory processes in addition to articular.
The **sacrum** is a spade-shaped bone formed by the fusion of five vertebrae. Its lateral wings are modified ribs fused together and also articulated with the hip bones. Spinous processes are much reduced. Between the costal processes four pairs of sacral **foramina** provide exit for nerves and blood vessels. The **sacral canal** is the continuation of the vertebral canal.

The coccyx consists of four fused centra which lack neural arches and processes. Frequently the first of these vertebrae fuses with the sacrum, and only the last three form the coccyx.

Successive vertebrae are connected to form a continuous column by intervertebral discs of fibrous cartilage. Interconnexions are further strengthened by numerous vertebral ligaments.

**Development of the Vertebral Column.** In man as in other vertebrates the primary axial skeleton is the notochord. Around this the definitive axial skeleton is built; and the notochord disappears, slight traces only being left as **nuclei pulposi** of the intervertebral cartilages. The processes involved in this replacement are complicated, beginning with the appearance of mesenchyma cells around the notochord and the neural tube. In this mesenchymal matrix, cartilage develops only to be destroyed in its turn and replaced by bony vertebrae.

The mesenchyma from which the vertebrae arise is produced by proliferation of the sclerotome, the cells of which migrate into the space...
between the mesoderm and the notochord. Later, by a continuation of the same migration, the neural tube becomes completely surrounded by mesenchyma.

Before cartilage is secreted in the mesenchyma, the sclerotome median to each myotome becomes differentiated into a denser posterior portion and a less dense anterior half. As the definitive vertebrae are formed, the posterior half of each vertebral anlage fuses with the anterior half of the following one. By this process the definitive vertebrae come to lie intersegmentally, alternating with the myotomes. The result is obviously adaptive, since only by this arrangement could each myotome become connected with two vertebrae and with two successive ribs.

![Diagram](image)

**Fig. 167.**—A diagram showing the relations of myotome and sclerotome as seen in a horizontal section of a vertebrate embryo. The upper half of the figure shows the relations in an earlier stage of development, while the lower half represents a later stage. The posterior half of each sclerotome unites with the anterior half of the following sclerotome to form a centrum which thus alternates in position with the adjacent myotome. Thus each myotome becomes attached to two vertebrae.

The chondrification of each vertebra starts in six centres, two in each centrum, two in each neural arch, and two in the costal processes. During the third month ossification of the vertebrae begins; but it is not completed until several years after birth. At about the seventeenth year, bony epiphyses arise as separate ossifications of the anterior and posterior surfaces of the centra. In the twenty-first year, these fuse with the centra and elongation of the vertebral column ceases. Of the original cartilaginous matrix only the intervertebral regions persist. The fusion of the sacral vertebrae is deferred until the twenty-fifth year.

**The Ribs.** Man has twelve pairs of ribs, which form a basket surrounding the thoracic cavity. Each rib is a curved flat bone ending ventrally in a costal cartilage. By means of these **costal cartilages** the
first seven pairs connect directly with the sternum and are therefore called sternal or true ribs while the five remaining pairs are distinguished as false ribs. The last two pairs, the eleventh and twelfth, do not connect with others, and are known as floating ribs. Each rib has a head or capitulum, which articulates with the vertebral centrum, and a tuber-
culum, which articulates with the transverse process. As the rib basket rises and falls in breathing, each rib rotates on an axis running through the tuberculum and the capitulum.

Each rib has a **costal groove** extending along its lower or posterior border. To the ridges which border this groove are attached the external and internal intercostal muscles.

**The Development of Ribs.** Ribs develop in the embryo as **costal processes** of the vertebrae in the intermuscular septa or myocommata. Primarily, the cartilaginous anlagen of the ribs are continuous with the cartilaginous vertebrae. The short costal processes in the cervical, lumbar, and sacral regions unite with the transverse processes and are indistinguishable from them in the adult. In the thoracic region, separate centers of ossification in the ribs are formed and articulations with the vertebrae develop. Epi-

![Diagram](image-url)  
**Fig. 169.—Diagrammatic section of a vertebrate to show the relation of ribs to the muscles of the body wall. av, aorta; c, coelom; e, ectoderm; ep, epaxial muscles; g, gonads; ha, hemal rib; hp, hypaxial muscles; i, intestine; mes, mesentery; n, nephridium; o, omentum; r, true rib; p, somatopleure; sp, splanchnopleure; v, vertebra. (From Kingsley's "Comparative Anatomy of Vertebrates,")**

The Evolution of Ribs. Ribs are wanting in chordates below the elasmobranchs, and even in elasmobranchs they occur only in the anterior trunk region as short cartilaginous processes lying in the horizontal septum separating epaxial and hypaxial muscles. Such true ribs should not be confused with the hemal arches of fishes which are median to the lateral trunk muscles and adjacent to the peritoneal lining of the body cavity. See Fig. 169.

The ribs of modern amphibia show little advance above those of the elasmobranchs, and in many Anura continue as short cartilaginous processes of the vertebrae. But bony ribs are present in urodeles such as Necturus and the attachment to the vertebrae is, as in the higher vertebrates, by means of tubercular and capitular processes. In some fossil amphibia the ribs were elongated and extended around the body to the ventral side. Abdominal ribs were also present, as in some modern reptiles.
In reptiles, ribs increase in number, and in some forms encircle the abdominal cavity. Abdominal ribs are common. The ribs of snakes are especially numerous. In mammals and man, ribs which articulate with the vertebrae and extend around the body cavity are limited to the thoracic region.
The Sternum. The sternum is a flat, dagger-shaped bone lying mid-ventrally of the chest.

Three parts are distinguished. 1. The manubrium or presternum, triangular, the widest portion and the most anterior. It articulates with the clavicle. 2. The gladiolus or mesosternum, the longest portion, formed by the fusion of four sternal elements or sternebrae. 3. The posterior metasternum, xiphoid or ensiform process. The xiphoid process is sometimes perforated by a foramen and is sometimes forked posteriorly.

Development of the Sternum. The sternum arises from connective tissue which is afterwards chondrified to become a pair of cartilaginous bars, which secondarily unite in the mid-ventral line and only later connect with the costal cartilages. Ossification begins in a series of paired centers, but the manubrium usually has one center only. Ossification of the metasternum or xiphoid process remains incomplete until very late in life.

Evolution of the Sternum. Opinion is divided as to the beginnings of the sternum. Some morphologists take the median portion of the elasmobranch pectoral girdle to be the homologue of the mammalian presternum, notwithstanding the fact that in some urodeles the sternum is a midventral plate of cartilage quite unconnected with the pectoral girdle. Since, however, the median ventral portion of the elasmobranch pectoral girdle is limited to a single intersegment, while the sternum of higher vertebrates extends through several segments and in mammals is clearly metameric, this hypothesis leaves the metamерism of the sternum unexplained. To meet this difficulty, it would be necessary to assume an
antero-posterior extension of the sternum along the mid-ventral line, and a secondary segmentation. But the fact that in urodeles, where the sternum makes its first appearance in the vertebrate series, the sternum is independent of the pectoral girdle, and the additional fact that the sternum develops in ontogenesis independently of the pectoral girdle, makes it difficult to accept this hypothesis. See Fig. 172.

A second more plausible hypothesis assumes that the sternum arose by the fusion of the ventral ends of a series of ribs. In favor of this opinion it is pointed out that in such a primitive amphibian as *Necturus* the sternum is represented by a series of four or five pairs of cartilages near the mid-ventral line. Like ribs these cartilages are intermyotomic. While in *Necturus* ribs do not extend from the vertebrae to the ventral side of the body, it is believed that there were primitive fossil amphibia in which the ribs were so extensive. The hypothesis that the sternum is a rib-sternum has at least this much foundation.

The facts of mammalian ontogenesis, however, do not appear to support this view. As stated above, the mammalian sternum arises independently of the ribs by the union of a pair of longitudinal cartilages which arise near the mid-ventral line. The connexion of these cartilages with the ribs is secondary.
If an opinion were to be based upon the relation of the sternum in Necturus and of the ontogenesis of the mammalian sternum alone, we should have to conclude that the sternum arose from paired segmented cartilages formed near the mid-ventral line independently both of the girdle and of the ribs. Under the circumstances, and until more decisive evidence is discovered, suspension of judgment is necessary.

In the reptiles the sternum is converted into a metameric structure composed of a series of sternebrae and connected with the ribs as in mammals.

Fig. 173.—Diagrams showing the development of the primordial skull. Since this organ develops primarily beneath the brain as a support the figures represent the ventral aspect. (A) Early stage, before the appearance of cartilage. The notochord is seen lying along the nerve cord as far forward as the hypophysis. The three sense-organs, nose, eye, and ear, have already appeared. (B) This stage shows the trabeculae (t), the parachordals (p), and the capsules around the sense-organs. (C) In this the trabeculae, the parachordals, and the nasal and otic capsules have fused into a single mass, the primordial skull, or chondrocranium. The anterior end of the notochord is imbedded in this. The cartilaginous capsule of the eye remains free to allow the necessary movements of the eyeball. (From Wilder's "History of the Human Body," Courtesy of Henry Holt and Co.)

The mammalian sternum differs little from that of reptiles. It is divided into the same three elements as those of reptiles and man, pro-meso-, and meta-sternum.

The Skull. There are two chief parts to the skull, which have different origins and a different history. One of these is the cranium or brain-case, together with the bones of the face except the two jaws. The other is the visceral skeleton, that is to say, the two jaws, the hyoid bone, the ear bones, and the cartilages of the larynx.

The Evolution of the Cranium. In the early part of the nineteenth century it was generally assumed by morphologists that the skull consists of four or five enlarged vertebrae. Originally suggested by the poet
Goethe, this “vertebral theory” of the skull was developed by Oken in Germany and by Owen in England. The basis of this theory may be seen in any mammalian skull, which consists of four bony rings beginning with the nasal region and ending with the occipital. Owen pictured an archetypal vertebrate, the axial skeleton of which consisted of a series of typical vertebrae, the anterior four being enlarged to form the skull. The vertebral theory received its death blow, however, when Huxley called attention to the fact that in the skull of such lower fishes as the elasmobranchs there is nothing remotely resembling a vertebra. The absence of vertebrae where they should be most evident, together with the lack of cranial vertebrae in vertebrate embryos except in the occipital region, led morphologists to abandon the theory. Failure to demonstrate vertebrae in the skull has not, however, altered the opinion that head and trunk had at one time a similar metameric structure. See Fig. 174.

The notochord forms in chordates the primary skeleton of the head as well as of the trunk. Evidence from comparative anatomy and embryology also indicates that the next step in evolution was the appearance of the parachordal and trabecular cartilages. The former as their name suggests parallel the anterior end of the notochord while trabecular cartilages lie anterior to the notochord beneath the forebrain vesicle. Enlarging these cartilages and fusing them with the cartilaginous nasal and otic capsules formed the primordial chondrocranium. The loosely constructed cartilaginous skull of cyclostomes represents roughly this stage of evolutionary development. In the cranium of cyclostomes, however, in addition to the parachordal and trabecular cartilages there is an ethmoid plate anterior to the trabeculae, and the beginnings of a tectum covering the brain in the region between the otic capsules. (Fig. 173)
A further advance towards the skull of higher vertebrates is presented in elasmobranchs, where the fusion and extension of cranial cartilages has produced a brain case which covers the brain except for an anterior and a posterior fontanelle. Among novelties in the skull of elasmobranchs are cartilages homologous with those which give rise to the alisphenoid bones of higher vertebrates. The beginnings of a dermal skeleton appear in this group in the form of placoid scales. The bone-like basal plates of these scales are considered as the beginnings of the dermal skeleton and of the membrane bones of the higher vertebrates.

In ganoid fishes the dermal scales of the head fuse into bony scutes, a number of which (nasal, frontal, parietal, squamosal, etc.) may be traced directly into the membrane bones of man and mammal. The cartilaginous brain case within these dermal plates differs in no essentials from that of elasmobranchs; but a progressive integration and fusion of cartilaginous and dermal constituents explains the two modes of development of bones in the mammalian skull. Intermediate stages in this evolution appear in living and fossil vertebrates. (Fig. 175)
Among the noteworthy changes in the skull during its evolution from fishes to man is the considerable reduction in the number of bony elements. Professor W. K. Gregory points out that the primitive fishes have as many as 180 skull bones while higher fishes have only about 100. In amphibians they number from 95 to 50. The skulls of earlier fossil reptiles had 80 bones while those of the highly specialized modern snakes have only 50. There were 70 bones in the skulls of (tertiary) reptiles from which mammals evolved; but mammals in general have half that number and the skulls of primates do not have more than thirty bones. Pre- and postfrontals are present in the reptilian skull but are wanting in mammals. Curiously the peccaries, like the birds, have the entire skull fused to a continuum and only the lower jaw a separate bone.

This reduction is especially striking in the evolution of the dermal skeleton. As the dermal scales sink into the deeper layers of the skin, they unite with the bony elements which are preformed in cartilage so that there frequently results a complex bone that has both cartilaginous and membranous elements.

The tendency of the primitive cartilaginous brain case to become bony begins in the ganoids, advances in amphibia and reptiles and is nearly completed in birds and mammals. Although the advantages of a bony skeleton for land animals is obvious, it is difficult to explain by any hypothesis of Lamarck, Darwin or De Vries the substitution of bone for cartilage in aquatic animals. Elasmobranchs such as the dogfishes seem as successful in the struggle for existence as are the teleosts. The former have a cartilaginous and the latter a bony skeleton. Cartilage is not a prerequisite condition for the appearance of bone since membrane bones develop directly from mesenchyma without an intermediate cartilaginous stage. The difficulty of explanation of the emergence of bony skeletons from cartilaginous beginnings is greatly increased by the complexity of the processes by which in ontogenesis, and therefore presumably in
Fig. 177.—Membrane bones of typical tetrapod; chondrocranium in dotted outline. *interp*, interparietal; *premx*, premaxilla; *postf*, postfrontal; *postorb*, postorbital; *pref*, prefrontal; *qj*, quadratojugal; *zyg*, zygomatic. (From Kingsley’s “Comparative Anatomy of Vertebrates.”)

Fig. 178.—The diagrams A–D illustrate the growth and enlargement of the membrane bones of the skull and their encroachment upon the chondrocranium. Cartilage and pro-cartilage bones are stippled, membrane bones black. Membrane bone is represented in the basal plates of the placoid scales of elasmobranchs (A). In the ganoid (B) the scales have fused and enlarged to form bony skutes, but the chondrocranium remains cartilaginous. In amphibia (C) the cartilage is largely changed to bone and the two kinds of bone become fused together. In mammals (D) very little cartilage is left and the two kinds of bone unite to form bone complexes. Most of the covering bones of the mammalian cranium are membrane bones.
**Fig. 179.**—Dorsal and ventral views of the skull of turtle, *Trionyx*. bo, basioccipital; bs, basisphenoid; eo, es, exoccipital; f, frontal; j, zygomatic (jugal); m, mx, maxilla; n, prefrontal; opis, opisthotic; p, (behind orbit) postfrontal, (others) parietal; pal, palatine; pmx, premaxilla; pno, prootic; pt, pterygoid; q, quadrate; s, supraoccipital; v, vomer. (From Kingsley’s “Comparative Anatomy of Vertebrates.”)

**Fig. 180.**—Skull of hake in left lateral aspect. Membrane bones are cross-hatched, pro-cartilage bones stippled. Compared with the skull of ganoids, that of teleosts shows an increasing dominance of membrane bones over those preformed in cartilage.
Fig. 181.—Diagram of the bones of the mammalian skull. Cartilage bones dotted, membrane bones lined; 2–12, nerve exits. (Altered from Flower, from Kingsley’s “Comparative Anatomy of Vertebrates.”)

Fig. 182.—A series of fossil skulls (A–G) which are believed to represent fairly well the phylogenetic changes of the human skull. (Redrawn after Romer’s “Man and the Vertebrates,” University of Chicago Press.)
phylogenesis, cartilage is gradually destroyed and later replaced by bone.

Since reptiles have only a single occipital condyle to articulate the skull with the atlas vertebra, while mammals have two, the descent of mammals from reptiles has on this account been questioned. Also for this reason, the attempt has been made to prove that mammals have evolved directly from amphibia, which also have two occipital condyles. But some reptiles have a tripartite condyle, and mammals may have derived their two condyles from this tripartite reptilian condyle by the disappearance of its median basioccipital element.

One of the most conspicuous evolutionary developments of the skull has been the relative enlargement of the membrane bones and the reduction of the cartilage elements. The only cartilage bones which persist are those which support the brain, those which cover the brain being exclusively dermal. This change is correlated with the increased size of the brain. See Fig. 178.

Except in proportion, there is little difference between the skull of man and that of other mammals. The enlargement of the brain and the correlated enlargement of the roofing bones of the skull carries the olfactory lobes, the foramen magnum and the otic capsules to the floor of the

Fig. 183.—Stages in the recession of the internal nares (choanae) are represented in the Tertiary reptiles, Dimetrodon and Cynognathus. By the growth of a horizontal septum from the maxillary and palatine bones the narial passages become separated from the mouth cavity in higher reptiles and mammals. Thus the internal nares or choanae finally open, not into the mouth cavity directly as in amphibia, but into the pharynx. (Redrawn from Romer's "Man and the Vertebrates," University of Chicago Press.)
Fig. 184.—Skulls of fossil men restored, left lateral aspect. Australopithecus, however, as its name implies, is an ape rather than a man. Opinions differ as to whether pithecanthropus is man or ape. Sinanthropus is indisputably human. While none of these fossil types is believed to be in the direct line of ancestry of modern man (Homo Sapiens), their discovery proves that more than one species of man has inhabited the earth. It is also significant that, with the exception of Cro-Magnon man, the earlier species of men were more ape-like than is modern man, as would be expected if apes and men have had a common ancestry. (Redrawn after Romer's "Man and the Vertebrates," University of Chicago Press.)
cranium. Among other changes is an increase in the facial angle from an acute to a right angle. The facial angle is the angle between a line from the frontal bone to the maxilla and one from the basioccipital to the base of the nasal septum. Apes and fossil species of men, however, help to bridge this contrast. See Fig. 184.

The heavy superciliary crests characteristic of the chimpanzee and gorilla, but lacking in modern species of men, are present in fossil Neanderthal and Rhodesian man. Furthermore, the usual contrast between apes and man disappears in the orang-utan which, like modern man, has rudimentary superciliary ridges. Furthermore, the contrast between the skulls of apes and man holds for the adult only, not for the young, the differences increasing with age.

Against the evolution theory as applied to the human species it used to be urged that there are no connecting links between man and apes, contrary to expectation if man and apes have evolved from a common ancestry. The contrast in brain size between man and apes is especially striking. The brain of the gorilla is never larger than 600 cc., while the smallest human brain is not less than 1000 cc. and the normal male brain is 1400. The discovery of the cranium of the Java man with a brain capacity of between 800 and 900 cc. helps to reduce this contrast. The striking fact revealed by fossil human skulls is that the characteristics which distinguish them from the skulls of modern man tend to bridge over the gap between man and apes. In other words, all fossil skulls, except that of the Cro-Magnons which is like that of modern man, are more ape-like than those of modern races. The dental arch of Negroid races is intermediate between that of apes and Europeans. The chin which is such a striking feature of the modern human jaw is lacking in some fossil men as in the great apes.

Another contrast between the skull of man and apes is in the relation of the skull to the backbone. The skull of modern man is poised on the occipital condyles at about its center of gravity, but the condyles of apes lies far behind the center of gravity of the head. Therefore are the neck muscles of modern man relatively weak, those of the ape massive. It is an interesting fact from the evolutionary point of view that the skull of Neanderthal man shows an intermediate condition.

**Bones of the Cranium.** Eight bones in man enclose the brain, frontal, occipital, ethmoid, and sphenoid and the paired parietals and temporalis. The facial skeleton includes twelve bones, the lower jaw or mandible, the vomer, and the paired maxillaries, zygomatics, nasals, lacrimals, and palatines. Since the turbinal bones of the nose are extensions of the ethmoid they are not counted as separate bones.

The frontal bone forms the front of the cranium. Ridges of this bone above the orbits of the eyes are the superciliary crests. Within the
frontal bone are the large frontal sinuses. Articulating with the frontals and forming the greater part of the roof and sides of the cranium are the paired **parietals**. Curved ridges on the sides of the parietals mark the origin of the temporalis muscle. See Fig. 185.

The **occipital** bone articulates with the parietals and forms the most posterior of the roofing bones of the skull. Through a large median aperture, the **foramen magnum**, the spinal cord passes from the vertebral canal into the cranium to connect with the brain. Many of the neck muscles are inserted on the basal portion of the occipital. On each side of the foramen magnum the occipital condyles form the articulation of the cranium with the atlas vertebra.

The **sphenoid** bone, at the base and sides of the cranium in front of the occipital, is in form the most complex of the cranial bones. It has a median body and two pairs of wings, the lesser and the greater. Paired **pterygoid** processes project downward and backward toward the pharynx.
The pituitary gland or hypophysis occupies a median depression of the sphenoid, the **sella turcica**. A number of nerves and blood vessels have their foramina of exit through the sphenoid, and a large foramen, the **foramen lacerum**, marks its posterior boundary.

The **temporal** bone is conspicuous on the sides of the skull, articulating with the sphenoid in front, the parietal above, and the occipital behind. Among its varied functions, it provides an articulation for the mandible and a protection for the sensory ear. Its three divisions are the **squamous**, **mastoid**, and **petrosal**. The squamous element covers the temporal lobe of the brain and contains a fossa for the articulation of the mandible. Several neck muscles, including the sterno-cleido-mastoid, are inserted on the mastoid process of the temporal. The inner cavity or **antrum** of the mastoid connects with the Eustachian tube and is consequently liable to infection from the throat. Within the petrous portion of the temporal are contained both the sensory and the bony portions of the inner ear. The middle ear, lying between petrous and squamosal elements contain the three ear bones, **malleus**, **incus**, and **stapes**, which belong to the visceral skeleton.

The **ethmoid** is a bone of delicate texture lying at the anterior end of the brain case and articulating with the frontal, sphenoid, and other bones. It consists of a dorsal, horizontal perforated plate, the **cribriform plate**, a vertical **mesethmoid** plate which divides the nasal passages, and paired lateral plates from which are derived the turbinal bones or conchae of the nose. The inferior conchae, although fused with the maxilla in the adult, are believed to be derived from the ethmoid.

The vomer or "ploughshare" bone derives its name from its resemblance to a plough. It articulates with the mesethmoid and forms the lower portion of the nasal septum. The lacrimal bones lie on the medial surface of the orbit and are so named because the naso-lacrimal ducts pierce them. They are the smallest bones of the cranium. The two **nasal** bones form the bridge of the nose. They articulate with the frontal above and the maxilla on the sides.

The **maxilla**, in addition to its function as the upper jaw, helps also to form the orbits, the palate, and the narial passage. As a part of the visceral skeleton (splanchnocranium) its description will be taken up later.

The posterior part of the hard palate is formed by the **palatine**, an L-shaped bone, consisting of a vertical and a horizontal member, the **sphenopalatine** notch dividing it into dorsal and ventral portions. It articulates with sphenoid, maxilla, vomer, and ethmoid.

The **zygomatic** or malar bones are quadrangular, with processes articulating with the frontal, maxillary, and temporal bones.

**Development of the Cranium.** The history of the vertebrate skull revealed by the study of its comparative anatomy is amply supported
by its embryology. Both prove it to be a complex formed by the union of diverse elements, capsules that contain the sense organs, and supports for the gills, underpinning and protective covering for the brain, while in the occipital region vertebrae appear to have fused with the brain case. The primordial cartilaginous cranium of the human embryo arises as a pair of parachordal cartilages and a pair of prechordal cartilages or trabeculae. These fuse together; later they combine with two pairs of sensory capsules, the olfactory and the auditory. This formation of the cartilaginous basis of the cranium, the chondrocranium, takes place during the second month of intra-uterine life. Ossification from separate centers begins with the third. See Fig. 173.

Evidence from comparative anatomy proves that the bones of the human skull correspond to a much larger number of separate bones which appear in the fishes and have been progressively reduced by fusion with one another during the course of evolution. This also is borne out by the development of the human cranium.

Ossification of the occipital bone, for example, begins in four centers corresponding with the basioccipital, the paired exoccipitals with their condyles, and a supraoccipital of lower vertebrates. To these are later added a membranous interparietal. Ossification of the occipital begins in the third month but is not completed until the seventh year.

The development of the sphenoid bone is even more complex, no fewer than ten centers of ossification are recognized. Six of these arise in the body of the bone and four more in the two paired wings. Membrane bone is added both to the pterygoid processes and to the great wings. Fusion of the separate elements is completed before the second year.

Ossification of the ethmoids remains throughout life incomplete. Three centers of ossification corresponding to the pro-, epi-, and opisthotic bones of lower vertebrates develop in the otic capsule and help to form the petrosal and mastoid portions of the temporal bone. The styloid process of the temporal is an ossified portion of the hyoid cartilage which fuses with the temporal. The squamous portion of the temporal is membranous in origin. An outgrowth of the epithelium of the middle ear penetrates the mastoid process to form a cavity or antrum.

The rest of the cranium is membrane bone. Because the roofing bones of the brain case ossify slowly and expand from centers, uncovered regions or fontanelles persist for some months after birth as "soft spots" between the frontal, parietal, and occipital bones.

**Evolution of the Visceral Skeleton.** Evidence from both comparative anatomy and embryology indicates that the upper and lower jaws, the hyoid bone, the ear bones, and the laryngeal cartilages of man have evolved from the skeletal gill supports of primitive fishes.
Cartilaginous supports for the respiratory system are lacking in the lowest chordates. In amphioxus, the velum in which the mouth lies, and the gill arches are supported by slender rods of a material which from its resemblance to cartilage is called pro-cartilage. A truly cartilaginous visceral skeleton first appears in cyclostomes in the form of a gill-basket in which the number of cartilage rods corresponds with the number of gill-arches. Bdellostoma may have as many as fifteen of these, other cyclostomes eight or nine.

In elasmobranchs the number of visceral cartilages is reduced to correspond with the reduced number of gill apertures. The maximum number is nine, in heptanchus, of which the first, the mandibular, is modified to become the cartilages of the upper and lower jaws, while the second arch, the hyoid, functions slightly as a gill arch, and its dorsal division, the hyomandibula cartilage, acts as a suspensory apparatus for the lower jaw.

The dorsal division of the first visceral arch, which forms the cartilage of the upper jaw, is called the palato-pterigo-quadrato cartilage, since palatal, pterygoid, and quadrate bones develop from it in amphibia and reptiles. The lower half of the first visceral arch forms cartilage of the lower jaw, Meckel’s cartilage. An articulation is formed between the two, so that in elasmobranchs a biting mouth replaces the sucking mouth of cyclostomes. Nevertheless, the upper jaw does not fuse with the cranium.
in elasmobranchs but remains independent. The suggestion that the labial cartilages of elasmobranchs are rudiments of cartilages which supported pre-oral gill arches in the ancestors of elasmobranchs has too slender a foundation to be taken seriously. This, however, is not to deny the possibility that there were preoral segments in such ancestors.

Posterior to the hyoid arch, the visceral cartilages persist in elasmobranchs as supports of the branchial or gill arches. The number is commonly reduced to five, but whether the loss takes place at the end or in the middle of the series is a disputed point. Most teleosts have only four functional branchial arches, and in some the number is reduced to two. Perennibranch amphibia have either two or three. Land animals have lost their gills entirely, but cartilaginous and bony skeletal supports persist and are turned to new and diverse uses.

In amphibia, both upper and lower jaw cartilages are at least in part converted into bone, and the upper jaw becomes firmly fastened to the cranium. The hyomandibular in this group ceasing to function as a suspensory apparatus of the jaw, slips into the tympanic cavity to form a connexion between the ear-drum and the inner sensory ear, the columnella or stapes. The hyoid cartilage forms the basis of attachment of the tongue muscles. With the disappearance of the gills as functional organs in land amphibia, the remaining visceral cartilages become further reduced and associated with the larynx.

Some advance towards the mammalian visceral skeleton appears in living reptiles. The teeth both in upper and lower jaws become lodged in alveolar sockets in two membrane bones, the premaxillary and maxillary

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Fig. 187.—Branchial arches of (A) Heptanchus; (B), Chlamydoselachus; and (C) Cestracion. c, ceratobranchial; e, epibranchial; h, hyoid; hb, hyobranchial; hc, hyoid copula; chbr, cardiobranchial (posterior copula); p, pharyngobranchial; 1–7, branchial arches; m, Meckel’s cartilage. (A and C after Gegenbaur, B after Garman from Kingsley’s “Comparative Anatomy of Vertebrates.”)
of the upper jaw and the dentary or mandibula of the lower. These membrane bones, however, do not extend as far as the articulation of the jaw which, as in amphibia, is between the quadrate of the upper jaw and the articulare of the lower.

In mammals a new articulation of the jaw is formed between two dermal bones, the dentary of the lower jaw and the squamosal of the brain-case. The evidence for this change in the articulation of the jaw is too strong to permit of any reasonable doubt. How such a change could occur while the jaw was still functioning has been one of the vexed questions in vertebrate morphology. Thanks, however, to recent discoveries of fossil reptiles which bridge the gulf between reptiles and mammals, the way in which the shift was effected is now fairly clear. (Fig. 188)

D. M. S. Watson and others have found that in Tertiary reptiles changes in the articulation of the jaw occurred which involved reduction of the articulare element and a corresponding enlargement of the dentary. The relation of the two bones is such that the lower jaw at one time was probably hinged by both. The enlargement of the dentary and the diminution of the articulare set free the latter to pass into the tympanic

Fig. 188.—Jaws of Tertiary reptiles viewed from their inner and outer aspects. Dimetrodon belongs to the lower Tertiary, while Scymnosuchus and Cynognathus belong respectively to the middle and upper Tertiary. A notable increase in the size of the dentary and relative diminution in the size of the articular element is seen. Such changes suggest how in the ancestors of mammals the articulation of the lower jaw shifted from the articulare to the dentary. Thus the articular was set free to become the malleus of the ear. By similar changes in the upper jaw the squamosal bone replaced the quadrate, which then became the incus. The teeth of the three jaws also show a change in the dentition in the direction of that of mammals. (Redrawn after D. M. S. Watson.)
cavity and join the chain of earbones as the malleus. By a similar piracy in the upper jaw, the squamosal replaced the quadrate which also was freed to pass into the tympanic cavity and become the incus. (Fig. 190)

The evidence, therefore, compels us to believe that the skeletal elements which primarily functioned as supports of the visceral arches in connexion with respiration have been converted through evolutionary change into organs of mastication, sound-conduction, speech, and support of tongue muscles. That the cartilage of the external pinna of the ear is a derivative of the hyoid arch has been asserted on the basis of doubtful evidence.

The Visceral Skeleton in Man. The visceral skeleton is that part of the axial skeleton which is related to the mouth and pharynx. In man it includes upper and lower jaws, the hyoid bone, the cartilages of the voice box, and the ear bones, malleus, incus, and stapes. The maxilla or upper jaw is really a pair of bones fused together along the middle line. It is nearly cubical in shape, has a body and four processes and encloses the maxillary sinus. The upper surface of the maxilla forms the lower surface of the orbit of the eye. From its inner surface the inferior concha projects into the nasal passage.

Of its four processes, the frontal articulates with the frontal bone, the zygomatic with the zygomatic bone, the palatine with the palatine bone, while the alveolar process bears the sockets for the teeth of the upper jaw. Near the incisor teeth each half of the maxilla is perforated by an incisive canal through which the nose communicates with the mouth. The maxilla also contains a large sinus, the antrum of Highmore, which opens into the narial passage.

The mandible or lower jaw consists of a body and two rami, which extend upwards nearly at right angles with the body. That portion of the jaw in which the teeth are set is the alveolar limbus. One of the distinguishing characteristics of the mandible of modern man, Homo sapiens, is the presence of a chin or mentum, which is lacking in most fossil types. Near the chin on the side of the jaw is a mental foramen through which nerves and blood vessels penetrate the jaw. See Fig. 189.

Each flattened ramus of the mandible has two prominent processes, the condyloid and coronoid. The head, capitulum, of the condyloid fits into the mandibular fossa of the temporal bone to form the articulation of the jaw.

The hyoid is a small, flattened, U-shaped bone located in the throat between the larynx and the base of the tongue. Like the mandible, the hyoid consists of a body, corpus, and two paired "horns." The anterior horns are much smaller than the posterior and frequently remain cartilaginous. Each lesser horn is connected by a stylohyoid ligament with the styloid process of the temporal bone.
Included in the visceral skeleton of man are the cartilages of the larynx or "voice-box." The largest and most prominent of the laryngeal cartilages is the thyroid or shield-shaped cartilage. The right and left halves of this cartilage stand at approximately right angles to one another. From its dorsal borders extend paired superior and inferior horns.

The cartilage immediately below the thyroid has the shape of a sealing-ring and consequently is called the cricoid cartilage. The cricoid expands into a broad lamina on its dorsal or posterior surface. Articulating with the cricoid on its anterior surface is a pair of pyramid-shaped arytenoid cartilages, so-called because of their resemblance in section to a funnel. A fifth cartilage supports the epiglottis.

In addition to these, two small paired cartilages usually occur in the larynx, the corniculate and cuneiform cartilages. The corniculate cartilages lie at the apices of the arytenoids. The cuneiform cartilages are of variable occurrence. The cartilages which support the trachea may also doubtfully belong to the visceral skeleton. They form a series of incomplete rings extending along the trachea.

The three ear bones are named malleus, incus, and stapes from their fancied resemblance to hammer, anvil, and stirrup. Within the cavity
of the middle ear they extend in the order given from the ear drum or tympanum to the oval window or fenestra vestibuli of the internal ear. Thus they serve to carry vibrations from the ear drum to the liquids of the internal ear. Their arrangement is such as to reduce the amplitude of vibrations and to increase their intensity. See Fig. 496.

**Development of the Visceral Skeleton.** In the human embryo a series of visceral arches separated by pharyngeal pouches appear in relations corresponding to those of aquatic vertebrates. In the first of those arches the maxilla of the upper jaw and the mandible of the lower jaw develop as membrane bones. The mandible, however, surrounds a cartilage, Meckel's cartilage, which corresponds to the mandibula or cartilage of the lower jaw of elasmobranchs. While most of Meckel's cartilage disappears during ontogenesis, that portion which extends into the cavity of the
ear ossifies in two centers one of which forms the malleus and the other the incus.

The so-called Meckel's cartilage of the mammalian embryo appears therefore to correspond not only to the mandibular or Meckel's cartilage of lower vertebrates, but with their quadrate element also. The quadrate element develops into the incus while the articular portion or articular element of the mandibula ossifies as the malleus. All this agrees completely with the evidence from comparative anatomy, which makes the malleus homologous with the articulare bone of the lower jaw, and the incus the modified quadrate of the upper jaw of reptiles, so that the articulations of the reptilian jaw become in man and mammals a part of a sound-conducting apparatus. See Fig. 190.

The cartilages of the remaining visceral arches in the human embryo have a diversified fate. The dorsal part of the second, the hyoid, ossifies...
to form the stapes of the middle ear, while the ventral portion forms the lesser horn and a part of the body of the hyoid bone. The intermediate portion of the hyoid cartilage forms the stylohyoid ligament by which the hyoid bone is suspended from the petrosal bone of the cranium. The cartilage of the third visceral arch fuses with that of the second, and later ossifies to form the greater horn and part of the body of the hyoid bone. The cartilages of the fourth and fifth arch persist as the thyroid and arytenoid cartilages of the larynx, and also form the cuneiform and corniculate cartilages. The cartilage of the fifth arch is said to form the cricoid cartilage also. Other observers claim that the cartilage of the sixth arch also contributes to the formation of the cricoid. That cartilages of posterior visceral arches form the ring cartilages of the trachea has been asserted on insufficient evidence.

Just as no theory of special creation can explain why there should be both cartilage and dermal bones in the same human skull, so no theory except evolution can explain why a bone in man should ossify from several centers, each of which corresponds to a separate bone in a lower form.

II. THE APPENDICULAR SKELETON

Evolution of Paired Appendages. The cyclostomes have no paired appendages and, so far as the evidence goes, never have had them. We are, consequently, forced to conclude that the paired appendages of vertebrates have no genetic connexion with those of invertebrates, but have arisen independently as vertebrate novelties. Unfortunately for the speculative morphologist, the beginnings of these appendages are obscure. Those of elasmobranchs are the simplest in living vertebrates, but even these are highly differentiated.

The most promising attempt to solve the problem of the origin of paired fins is the so-called fin-fold theory. According to this, paired fins began as paired folds of skin extending from the region posterior to the gills back to the anus. The paired metapleural folds of amphioxus are often mentioned, with dubious justification, as structures which suggest how the fin-folds may have had their origin. Pectoral and pelvic fins are supposed to be formed by enlarging the end portions of these folds and suppressing the intermediate region. In favor of this hypothesis is the presence of longitudinal paired "Wolffian" folds in vertebrate embryos, and the fact that the anlagen of the appendages extend through more segments of the embryonic body than do the appendages of the adult, the base of the appendages becoming constricted during ontogenesis. Some morphologists have used the continuous fin-folds of skates as evidence supporting the fin-fold theory, while others doubt their significance. The continuity of the folds, as Goodrich has suggested, is probably not an essential element in the theory. See Fig. 193.
The alternative theory of Gegenbaur that the paired fins of fishes arose from modified gill arches and their associated rays has too little evidence in its support to make it worthy of serious consideration.

The second step in this evolution was the invasion of connective tissue and muscle into the fin-folds. A similar migration actually occurs

ontogenesis. In elasmobranchs the muscle buds which invade the fin-folds are metamerically arranged.

The third step in this evolution was the appearance of a series of inter-myotomic cartilage rays like those which support both median and paired fins of elasmobranchs. The universal occurrence of skeletal material in connexion with muscle, and indeed wherever in an organism stresses occur, may possibly be taken as explaining these radial cartilages. The position between the myotomes is obviously adaptive, as is also their position
between the dorsal extensor muscles of the appendage and the ventral flexor muscles.

Further steps in the evolution of the appendicular skeleton involve the thickening and fusion of the basal or proximal portions of the radial cartilages and the extension of the basal cartilages thus formed into the body wall and towards the mid-ventral line. The result of this appears today in the pelvic fin of elasmosbrachys. The beginnings of a girdle are seen in a ventral cartilaginous plate, the ischio-pubis. A doubtful beginning of the ilium may be seen in the so-called iliac process. The

**Fig. 194.—Diagrams illustrating the hypothetical evolution of the extremities of Dipnoan (I), Ganoid (H), and Elasmobranch (G) from a fin-fold supported by a series of similar radial cartilages. By fusion basal elements are differentiated. The skeletal supports of fins eventually differ in the relations of the basal elements to the radialis. (Redrawn after A. Brazier Howell.)**

evolution in the pectoral girdle seems to have been more rapid than in the pelvic girdle, if we may base our conclusion on the fact that in elasmosbranchs the scapula or dorsal arm of the pectoral girdle is already well developed when there is little, if any, indication of a dorsal arm, the ilium, of the pelvic girdle. In both girdles in the elasmobranch, however, a ball-and-socket articulation between girdle and free extremity has already made its appearance.

An advance towards the pectoral girdle of higher vertebrates appears in living and fossil gnoids in which a membrane bone, the *clavicle*, is added to the pectoral girdle. There is no structure in the pelvic girdle homologous with the clavicle.

A tripartite pectoral girdle makes its first appearance in amphibia. The ventral arm, which in fishes was single and undivided, becomes in
amphibia differentiated into posterior and anterior moieties, the coracoid and precoracoid. The dermal clavicle becomes closely apposed to the precoracoid. The dorsal scapula and suprascapula remain undivided as in fishes.

The dorsal arm of the pelvic girdle, the ilium, articulates with the transverse process of a single sacral vertebra. In its most primitive form in amphibia, the ventral portion of the pelvic girdle resembles that of ganoid fishes, and consists of a broad cartilaginous plate with which the femur articulates. Centers of ossification corresponding with ischium and pubis arise successively in this plate. The attempt of morphologists to discover in ganoid and dipnoan fishes transitional stages leading from the pelvic girdle of elasmobranchs to that of amphibia has had little success. Fossil remains also throw little light on the problem. See Fig. 197.

The girdles of reptiles are essentially like those of amphibia. In the turtle they become definitely Y-shaped. The clavicle fuses with the precoracoid and becomes indistinguishable from it. The ilium connects with two sacral vertebrae. In pythons, a rudimentary hip girdle connects with a pair of rudimentary claws in the anal region. Both are useless; both go to prove descent of serpents from tetrapod ancestors.

In mammals, the coracoid is reduced to a process of the scapula. In man in addition to the coracoid process a remnant of the coracoid bone survives in the coracoid ligament which extends from the coracoid process to the sternum, and in which occasional pieces of cartilage are found as rudiments of the coracoid. The clavicle has supplanted

![Fig. 195.—Ventral surface of Cladoselache. In this fish the skeletons of both pectoral and pelvic fins are extremely primitive. (After Jaeckel from Kingsley's "Comparative Anatomy of Vertebrates.")](image-url)
the precoracoid, remnants of which, however, usually occur within the clavicle. See Fig. 196.

Fig. 196.—Diagrams illustrating the fundamental similarity of the human (B) and amphibian (A) pectoral girdle. In man the coracoid element has degenerated into a process (coracoid) and a connective tissue ligament containing occasional cartilage nodules. (Redrawn after Huntington.)

The mammalian hip bone differs little from that of reptiles. The number of sacral vertebrae to which the coxal bone is attached increases in

Fig. 197.—A series of six appendicular skeletons illustrating the gradual emergence of the elements of the pelvic girdle found in reptiles and mammals. They probably represent fairly well stages in the evolution of the human pelvis. First came the separation of girdle and extremity (A and B); then the fusion of the paired elements of the girdle into a median ventral cartilaginous plate (C and D); the differentiation of bony ischium, pubis, and ilium (D and E); and finally the appearance of the obturator foramen (F). There is no essential difference between the reptile and mammal girdle. (Redrawn after Wilder, "History of the Human Body"; Henry Holt & Co.)

mammals. In man there are five sacral vertebrae, to three of which the hip bone is attached.
Evolution of the Free Extremities. Two contrasting types of free extremity appear in vertebrates, the fins characteristic of fishes and the toed appendages such as are found in the remaining classes from amphibia to man. The conversion of the one into the other continues to be a vexed question of vertebrate morphology. Technically stated, the problem has been to determine how the evolution of the *ichthyo*pterygium into the *cheiro*pterygium has occurred. Interest has centered especially in the transformation of the skeleton.

Primarily the fish fin like that of the fossil shark Cladoselache was supported by radial cartilages which articulated with basalia, of which one or more articulated with the girdle. In the pectoral fin of modern elasmobranchs three basalia, propterygium, mesopterygium, and meta-ptygium, connect the fin with the girdle. Morphologists, however,
Fig. 200.—Diagrams illustrating theories of origin of appendages. A, B, C, origin of biserial appendage (C) from gill arch (A); D, biserial appendage (archipterygium); E, F, evolution of elasmobranch fin; G, dotted lines indicate parts involved in origin of leg from fin; H, dotted parts show another view of origin of elements of leg. (From Kingsley's "Comparative Anatomy of Vertebrates.")

Fig. 201.—Diagrams of the pectoral appendages of lower and higher vertebrates. A persistent problem of morphology is how the fish extremity or ichthyopterygium was transformed into the fingered extremity (cheiropterygium) of land vertebrates.
disagree as to the skeleton of the primitive extremity, the archipterygium. While some suppose it to have been uniserial, i.e., the radial cartilages were limited to one side of the basal cartilages or axis as in elasmobranchs, other morphologists regard the biserial fin skeleton of dipnoi as the more primitive. Conclusions in regard to the evolution of the skeleton of the extremity differ, therefore, as one or other of these two types of fish-fin skeleton is assumed as more primitive.

Fig. 202.—Goodrich's solution of the problem of the transformation of the ichthyopterygium into the Cheiropterygium. The diagram (B) of the ichthyopterygium is based upon the fossil fish Sauripterus. The main axis of the appendages is indicated by a dotted line. A and C are diagrams of cross sections showing the relations of girdle and extremity. D represents the appendicular skeleton of Tetrapods. (Redrawn after Goodrich.)

There is also extreme divergence of opinion as to the exact homologies between the elements of the ichthyopterygium and of the cheiropterygium. The skeleton of the latter invariably articulates in a socket of the girdle by a single skeletal element, the humerus or the femur. The fish extremity, on the contrary; usually articulates by more than a single skeletal element. While the forearm and shank of tetrapods have respectively two elements, radius and ulna and tibia and fibula, the number in the ichthyopterygium is usually considerably greater than this. Obviously, in the evolution of the skeleton of the fish extremity into that of land animals there has been a loss of skeletal elements as well as a great elongation of the appendage. It is difficult to determine which elements have persisted and which have disappeared. See Fig. 200.
Summary of Skeletal Evolution. Most animal phyla, even the protozoa, have some sort of skeletal structures. But there seems to be no genetic connexion between the skeletons of invertebrates and those of vertebrates. In the evolution of a skeleton, vertebrates have been given carte blanche. In the process of acquiring a skeleton, chordates first converted the roof of their alimentary canal into a supporting rod, and later used this as a foundation upon which to build a vertebral column of cartilage. The replacement of cartilage by bone in higher vertebrates is an astonishing engineering feat for which our current theories of adaptation seem quite inadequate.

To the notochord, cyclostomes added neural arches and the rough beginnings of brain case and visceral skeleton. Elasmobranchs show a marked advance towards a more elaborate skeleton. To the vertebrae they added hemal arches, centra and spinous processes. They converted a gill arch into a biting jaw, and invented paired fins and a scaly dermal skeleton. Ganoids went to extremes in dermal armor, but made a permanent contribution to our skulls. In this group, bone began to replace cartilage.

Crossopterygian ganoids of the Devonian suggest the beginnings of the tetrapod extremity. The extremities of two of these, Sauripterus and Eusthenopteron, are especially significant. The skeletal elements of the pectoral extremity of these forms consisted of a single proximal element, and articulating with this two distal elements. Furthermore, the proximal element, interpreted as a humerus, articulates in a socket of the pectoral girdle. From the evolutionary standpoint this evidence is most important since it shows that in fishes even before locomotion on land was adopted the arrangement of the proximal bony elements in the extremity had already come to resemble that of land animals. Thus Sauripterus and

![Fig. 203.—The pectoral girdle and fin of Sauripterus, an upper Devonian Crossopterygian fish. Interest in this type of fish fin lies in the similarity of relations of the proximal elements of the extremity to those found in the pectoral extremity of tetrapods. (Redrawn after Broom.)](image-url)
Fig. 204.—Skeleton of gorilla viewed from in front. The bones of the gorilla are identical with those of man. Differences of proportion, however, are seen. Among these differences, that of the relative length of arm and leg bones is most striking. The limb proportions of the human infant, however, tend to resemble those of the ape. (Redrawn after Brehm.)
Eusthenopteron help to bridge over the structural gulf separating the ichthyopterygium and the cheiropterygium.

The emergence of animals from the water to the land was accompanied by momentous changes in their skeletons. Somehow or other fins were changed into fingered appendages capable of supporting the weight of the body. This transition was probably accomplished by amphibians, which because they had lungs and could breathe air, were able to meet this crisis in animal life. Legs and not tails became the locomotor organs. Even the vertebral column was affected by these developments. The pelvic girdle became attached to the vertebral column and sacral vertebrae were differentiated. Speed was of life-saving value and legs elongated. All organs,—heart, kidneys, brains, and all the others—were improved.

Profound changes in the visceral skeleton also occurred. With the replacement of gills by lungs as organs of respiration, the skeletal supports of the gills were set free for other uses. Fishes had already demonstrated that a cartilaginous gill arch could be used for seizing food. Land animals turned the remaining arches to other divergent uses. The tongue became attached to the hyoid arch. The hyomandibular element in amphibia became a sound-conducting apparatus. Some of the arches were used to support the vocal cords and the voice box.

Amidst all the many adaptive changes which affect the skeleton of the appendages in land animals, both pectoral and pelvic extremities retain their fundamental similarity to one another. Even the differentiation of hand and foot does not obscure this fact. The diversities of form and function of the tetrapod appendage do not concern us in this discussion. It is, however, interesting to note that notwithstanding the high degree of specialization of the extremities of man they differ little in fundamental structure from those of amphibia.

To assist their hind legs, amphibia connected the pelvic girdle with the sacrum; to assist their hearing, they converted the suspensorium of the jaw into an earbone, the columella. Tripartite girdles made their appearance in amphibia. The sternum also is a novelty in this group. In the thermomorph reptiles, changes in the articulation of the jaw began to take place, so that when mammals appeared, the old hinge between articular and quadrate had been lost, and a new hinge between dentary and squamosal had taken its place. Thus were articular and quadrate set free to become malleus and incus of the ear. The beginnings of hands and feet appear in arboreal mammals in adaptation to life in the trees. In man, the backbone becomes vertical and the skull is balanced on the occipital condyles. The facial angle, in correlation with the great enlargement of the brain, increases to a right angle; and a sigmoid flexure makes its appearance in man’s spine.
The Appendicular Skeleton in Man

1. Upper Limb. The upper limb is divided into four regions, pectoral girdle, upper arm, forearm, and hand. The pectoral girdle consists of two bones, the scapula and clavicle or collar bone.

The Scapula. The scapula or shoulder blade is a triangular bone embedded in the muscles of the back and forming the chief skeletal support of the shoulder. It consists of a flattened body with two processes, the coracoid and the acromion. The dorsal surface of the scapula is divided unequally by the spine into a smaller upper supraspinous fossa containing the supraspinatus muscle, and a larger lower infraspinous fossa in which is the infraspinatus muscle. The concave inner or costal surface of the scapula lodges the subscapularis muscle. The three borders of the scapula are the superior, vertebral, and axillary.

At the outer or lateral angle of the scapula is a shallow depression, the glenoid fossa, which provides the articulating surface for the "bend" of the humerus. The spine of the scapula terminates laterally in the acromion process, where it forms the summit of the shoulder and serves as the origin of parts of the deltoid and trapezius muscles. The clavicle articulates in a concavity in the acromion process. The coracoid process, shaped like a bent finger, projects laterally and forward from the "neck" of the scapula.
The Clavicle. The ventral element of the pectoral girdle is the clavicle or collar bone. Laterally, the clavicle articulates with the acromion process of the scapula; medially, with the manubrium just above the first costal cartilage. The clavicle, with its two curvatures, roughly resembles the italic letter $f$. Several muscles have their origin at least in part on the clavicle, among them the trapezius, deltoid, pectoralis, sterno-mastoid, and sterno-hyoid.
The Humerus. The humerus, which forms the single skeletal element of the upper arm, is the longest and largest of the bones of the upper extremity. It articulates in a ball-and-socket joint with the scapula and in a hinge joint with the radius and the ulna of the forearm. Like other long bones, the humerus consists of a shaft and two extremities. The upper or proximal extremity has a hemispherical head and two tuberosities, greater and lesser, of which the lesser, although smaller, is the more prominent. Shoulder muscles are inserted on these tuberosities.

The distal end of the humerus is somewhat flattened and divided by a ridge into a trochlea and a capitulum. The trochlea provides the articulating surface for the ulna while the capitulum articulates with the radius. On the dorsal surface just above the trochlea is a deep pit, the olecranon fossa, which receives the olecranon process of the ulna when the arm is extended. Similar depressions on the ventral surface receive the coronoid process of the ulna and the head of the radius when the forearm is completely flexed.

Radius and Ulna. The skeletal elements of the forearm are the radius and the ulna. The radius is lateral in position and smaller, the ulna median and larger. The radius is smaller at the elbow and larger at the wrist, the ulna is larger at the elbow and smaller at the wrist.

The proximal end of the radius is the head. It articulates both with the capitulum of the humerus and with the radial notch of the ulna. The head of the radius is connected with the shaft by the “neck.” Between the two, projects the tuberosity for the insertion of the biceps muscle. Distally the radius articulates with the navicular and lunate wrist bones and with the extremity of the ulna. From the extremities of both the radius and ulna project styloid processes which afford attachment for wrist ligaments.

The proximal end of the ulna is distinguished by the olecranon process to which the tendon of the triceps muscle is attached. By means of a concave semilunar notch the ulna articulates with the trochlea of the humerus. The lower border of this notch is formed by the coronoid process. An adjacent fossa, the radial notch, serves for articulation with the radius. Radius and ulna are so related that the palm may be turned either up or down. In supination of the hand, the palm is up, and the two bones are parallel. In pronation of the hand, the palm is down, the radius crosses the ulna, and the position of their distal ends is reversed.

The Carpus. The wrist has eight bones arranged in two rows, a proximal and a distal. Beginning on the radial side of the wrist, the four proximal carpals are the navicular, lunate, triquetrum, and pisiform. The four distal carpals are the greater multangular, lesser multangular, capitate, and hamate. Except the pisiform, which is inside a tendon, each of the carpals has six surfaces. Articulating surfaces with the bones
of the forearm are provided by the navicular and lunate. The triquetrum is separated from the head of the ulna by an interarticular cartilage.

**Metacarpus and Phalanges.** The metacarpus consists of five cylindrical bones which articulate with the distal carpals on one side and with the proximal phalanges on the other. In form the metacarpals are miniature long bones.

All the digits except the thumb have three phalanges each.

2. The Lower Limb. The bones of the lower extremity are also divided into four groups, hip, thigh, leg or shank and foot. The skeletal elements corresponding are the coxal or hip bone, femur, tibia and fibula, tarsus, metatarsus, and phalanges.

**The Coxal Bone.** The hip or coxal bone consists of three parts, a dorsal ilium, and two ventral elements, **pubis** and **ischium.** The ilium articulates dorsally with the sacrum, the two pubic bones meet in the mid-ventral line in the **pubic symphysis.** The pubis and ischium articulate with one another above and below the large **obturator foramen.** Laterally, in the region where the three elements of the coxal bone meet, is a cup-like depression, the acetabulum, with which the head of the femur articulates. The concavity of the acetabulum is divided into a smooth articular portion and an **acetabular notch** to which the head of the femur is attached by the
teres ligament. Many muscles of the thigh and body wall are attached to the coxal bone, which also serves to support the abdominal viscera. The two coxal bones together with the sacrum and coccyx form the pelvis, the shape of which differs somewhat in the two sexes.

**Femur.** The *femur* or thighbone, which is the largest bone of the body, has a shaft and two extremities. The upper extremity includes a hemispherical head, a neck, and two trochanters, the greater and lesser. The large *gluteus* muscle of the buttocks is inserted on the greater trochanter while the psoas muscle is connected with the lesser trochanter. Between the two extends the ridge of the *intertrochanteric crest*. On the anterior side of the femur, the tendonous capsule of the hipjoint is attached to the *intertrochanteric line* which separates neck and shaft.

![Diagram of the structure of a long bone](https://example.com/diagram.png)

Among the remarkable adaptations manifested in the femur none is more amazing than the arrangement of bony lamellae within the calcaceous bone of the upper extremity in such wise as to withstand the stresses and strains of supporting the weight of the body with a maximum of strength and minimum weight of material. The relations of the parts resemble those of a Fairbairn’s crane. In addition, the femurs together with the coxal bone and sacrum form a natural arch of which the sacrum is the keystone.

The shaft of the femur is nearly cylindrical but on its dorsal side the *linea aspera* extends as a ridge throughout its entire length. Several muscles have their insertion along this line. The lower extremity of the femur is distinguished by two articulating condyles, the *median* and the *lateral*, separated by an *intercondylar fossa*.

**Patella.** The knee-pan is a flattened bone which develops in the tendon of the quadriceps femoris muscle at the lower extremity of the femur. It has median and lateral facets, which articulate with corresponding facets in the lower end of the femur.

**The Tibia.** The *tibia* is considerably the larger of the two bones of the shank. Its function is to transfer the weight of the body from the
femur to the foot. Two flattened condyles articulate with the femur. The ligament of the patella is attached to the ventral surface of the upper extremity of the tibia. The shaft of the tibia is triangular having an anterior sharp crest from which the tibialis anterior muscle has its origin. The lower extremity of the tibia is smaller than the upper. Articulation

is with the talus bone of the ankle. The large process of the medial malleolus extends from its lower outer border. (Fig. 206)

The Fibula. The fibula is the slenderest of the long bones. It functions chiefly as a basis of attachment of leg muscles which serve as extensors and flexors of the toes. Its upper extremity articulates with the tibia, its lower is prolonged into a conspicuous lateral malleolus.

The Tarsus. The tarsal or ankle bones number seven. The proximal tarsals are the talus and calcaneus. Three cuneiform bones and a cuboid form the distal tarsals. Between the two on the inner side of the instep
is the navicular. Each of the seven tarsals has six surfaces. The tibia rests upon and articulates with the talus. The largest bone of the foot is the calcaneus, which articulates with the talus and cuboid. To the posterior tuberosity of the calcaneus is attached the tendon of Achilles. Since the calcaneus acts as a lever with the talus as a fulcrum, it is not surprising that the size of the calf muscle which provides the power varies inversely with the length of the heel bone.

**Metatarsus and Phalanges.** The metatarsal and phalanx bones differ little from the corresponding bones of the hand, except that the phalanges are considerably shorter in the foot and the great toe has much less freedom of movement than the thumb.

**Homologies of the Limb Bones.** The striking similarity of the bones of the upper and lower limbs, notwithstanding their great diversity of function, is interpreted by morphologists as indicating a primary similarity in use. Their present differences in form, size, and function have arisen secondarily and adaptively.

**Development of the Appendicular Skeleton.** The paired appendages of vertebrates arise from two Wolffian folds, which extend along the sides of the embryo at approximately the level where the hypomere connects with the mesomere. Only the end portions of these folds,
however, go to form the limbs; the intermediate region atrophies and disappears.

The Wolfian folds consist of an external covering of ectoderm and a core of mesenchyme, which in man is of uncertain origin. Although in elasmobranchs myotomic buds grow into the fin-folds, no such buds occur in mammalian embryos. So far as can be seen, the mesoderm of the paired appendages in man and mammals is proliferated as loose mesenchyma from the hypomere and not from the epimere as in the lower vertebrates. However the somatic motor innervation of appendicular muscles throughout the vertebrate series suggests that they are homologous. (See p. 289.)

In their early development, arms and legs take the form of shovel-shaped outgrowths. At this stage two surfaces may be distinguished, of which the dorsal forms the extensor surface of the appendage while the ventral side becomes the flexor surface. During development, however, each appendage is rotated on its long axis. The rotation of the arm is, however, the reverse of that of the leg, with the result that the flexor muscles of the arm are in front and the elbow bends back, but the extensor side of the thigh is in front and the knee bends forward. In the meanwhile, the elongation of the appendages is correlated with division into proximal and distal portions. Fingers and toes appear as early as the second month. Up to this point there has been little difference in the skeletons of the two appendages. (Fig. 210)
Development of the Upper Limb. The anlagen of the arms extend through five myotomes of the cervical region. During the second month indications of an appendicular skeleton appear as axial thickenings of the mesenchyme. In this compact mesenchyme, as early as the sixth week cartilage forms between the cell masses which are to become the muscles on the upper and lower sides of the limb. By the end of the seventh week the entire cartilaginous matrix of the skeleton of the arm is formed except the third phalanx of the fingers. At this stage, however, it is impossible to distinguish sharply individual elements, and the cartilage of the entire appendicular skeleton is virtually continuous.

Ossification begins in the seventh week but is not completed in all bones of the body until the twenty-fifth year. Ossification of the clavicle begins before the third month, but in the coracoid process not before the end of the first year, and of the acromion process only at puberty. The shaft or diaphysis of the humerus is usually the only portion ossified at birth. The distal epiphysis fuses with the diaphysis during the sixteenth year and the proximal epiphysis during the twenty-fifth.
The shafts of the radius and ulna begin to ossify about the middle of the second month. The bony epiphysis of the olecranon process appears at ten years and unites with the shaft at sixteen years. The epiphyses of the radius appear earlier and fuse with the diaphysis later. (Fig. 211)

The wrist bones are cartilaginous at birth but begin to ossify during the first year, the pisiform last of all during the tenth to twelfth years. Metacarpals and phalanges ossify relatively early, beginning with the third month. Diaphysis and epiphyses are formed as in all long bones.

![Diagram of bone development](image_url)

**Fig. 213.**—Diagrams illustrating the development of the thigh-bone from birth to the twenty-fifth year. Since the marrow cavity of the adult bone is large enough to contain the entire bone of the new-born infant, it is obvious that the growth of the bone involves continuous destruction of the bone from within as well as additions to the outside. (Redrawn after Keith.)

**Development of the Lower Limb.** The concentration of connective tissue to form the anlage of the pubis and femur begins in the fifth week of fetal life. At the time when cartilage first appears, the axis of the coxal bone, which primarily stood at right angles to the vertebral column, shifts backward and comes to lie parallel with the backbone. Connexion with the sacrum begins with the sixth week. By the end of the second month, all of the elements of the pelvic appendage including the coxal are performed in cartilage. Ossification of the shaft of the femur usually occurs by the end of the second month.
Beginning with the ninth week, the coxal bone ossifies from three centers corresponding with ilium, pubis, and ischium. In the region of the acetabulum, ossification is not completed before the tenth year, and ossification of the coxal bone continues until the twenty-fifth year. The bones of the leg and foot develop in a manner resembling the manner of growth of bones of the arm and hand. The bones are mostly long bones and develop from the usual three centers, a diaphysis and two epiphyses. Separate epiphyses are formed for the head of the femur and the greater and lesser trochanters. Ossification of the patella begins in the third year.

The tarsal bones begin to ossify before birth, but the epiphysis of the calcaneus not until the ninth year. Metatarsals and phalanges begin to ossify in the third month.

Malformations of the hand and foot are not uncommon. Most of them result from a duplication or a fusion of parts. They include fusion of digits, extra digits, and even duplication of entire hands or feet.

The Development of Joints. While the precartilaginous anlage of the skeleton is usually described as a histological continuum, the statement needs qualification. For in the regions where joints appear, the connective tissue does not assume the characteristics of cartilage. Such undifferentiated tissue resembles histologically, and is continuous with, the perichondral sheath which surrounds each embryonic cartilage. When such a joint persists throughout life without motion, the condition is known as synarthrosis, and the connective tissue of the joint may change little throughout life. With increasing age, however, such immovable joints tend, as in the case of the sutures of the cranium, to close up or ankylose, so that the bone becomes a continuum.

When, however, a movable joint is formed between cartilages such as those which form the phalanges, the connective tissue of the joint first becomes gelatinous and then disappears leaving a liquid-filled cavity or cleft between the phalanges. The connective tissue which surrounds the joint, and which is continuous with the perichondrium of the phalanges, persists and becomes differentiated as the ligamentous capsule of the joint. Most of each phalanx is eventually converted into bone, but the articulating surface of the joint remains cartilaginous throughout life.
This not only insures some degree of elasticity at the joint but also provides a means of lubrication. As the cartilage wears down through use, the cartilage cells are converted into one of the best lubricants known to man.

In the development of some joints, a cartilaginous disc primarily divides the liquid-filled cavity in two. Later this disc disappears and a single cavity is formed.
CHAPTER 7

THE MUSCULAR SYSTEM

The muscular system of an active vertebrate makes up nearly half the entire body-weight, in man slightly more than forty per cent.

A muscle can do only one thing—contract. It cannot expand; and having once contracted, must be pulled out to its resting length by one or more antagonistic muscles. Each skeletal muscle consists of a fleshy part or belly, each end of which if attached to a bone or cartilage, either directly to the periosteum or indirectly by means of a tendon. The attachment which moves most when the muscle contracts is its insertion; the other is its origin. Each muscle is surrounded by a connective tissue membrane or perimysium, from which septa may grow into the muscle and divide it into several muscle slips, each of which has a separate function.

Muscles vary greatly in shape according to the arrangement of their fibers and the way these are attached. Muscles may be segmented into a series of similar units such as appear in the body muscles of fishes.

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Fig. 215.—A diagram of the biceps muscle taken as a typical muscle, showing its nervous and vascular relations. Each skeletal muscle is attached to a bone either directly to the periosteum or indirectly—as in the case of the biceps—by means of tendons. (Redrawn after Keith.)
Fig. 216.—Diagrammatic outlines to illustrate various types of muscle architecture and the relations of the main nerve branches to the fiber-bundles of the muscle.  
a. Two segments of the rectus abdominis muscle of a small mammal.  
b. Portion of sheet-like muscle with two nerve-branches and intramuscular nerve plexus.  
c. Typical quadrilateral muscle with nerve passing across the muscle about midway between the tendons.  
d and e. Two triangular muscles with different types of innervation.  
f. Long ribbon-like muscle with interdigitating fiber-bundles.  
g. Unipenniform muscle.  
h. Bipenniform muscle.  
i. Typical fusiform muscle.  
The main intramuscular nerve-branches are distributed to the fiber-bundles about midway between their origins and insertions.  
(From Morris' "Human Anatomy.")
They may spread out in thin sheets that are ribbon-like, triangular, pinnate, or fan-like. Appendicular muscles are more frequently spindle-shaped and massive.

Each muscle is well supplied with capillaries and with both motor and sensory nerves.

As to origin, muscles are sharply divided into two kinds; 1. Skeletal (epimeric or myotomic), derived from the dorsal or epimeric portion of the mesoderm; and 2. Visceral (hypomeric) derived from the hypomere. In the trunk region in contrast with the head visceral muscles arise from the splanchnic layer of mesoderm only.

Skeletal muscles are composed of striped fibers which respond to stimulation by rapid contraction. Most visceral muscles, on the other hand, consist of slow-acting smooth or non-striped fibers. The former are voluntary and under control of the will, the latter are usually involuntary. Exceptions are found in the heart muscle which is visceral and involuntary, but formed of striped fibers, and in the chewing and facial muscles which are visceral and at the same time striped and voluntary.

**EVOLUTION OF THE MUSCULAR SYSTEM**

The muscles of man and mammals are the last term in the series of transformations of the mechanism of contraction, the evolution of which it is now possible to sketch in fairly firm outlines.

Contractility appears to be one of the original properties of living cells. Touch an amoeba, and it responds by drawing together into a sphere. There is no single axis, but contraction takes place from all directions towards a center. In some protozoa, however, progressive advance in the function appears in the differentiation of contractile fibrils. A cluster of such fibrils in the stalk of vorticella is so arranged as to contract in one direction only, like a muscle fiber.

True muscle cells first appear in the animal series in the sponges. The primary independence of muscle and nerve is indicated by the presence of muscle cells in this group which lacks nerves altogether. The epithelio-muscular cells of coelenterates are essentially similar to those of sponges.

The next step in the evolution of muscles appears in the flatworms, in which muscle cells are aggregated into clusters. The bilateral symmetry characteristic of the muscles of higher animals also appears in this group.

Transitional evolutionary stages between flatworms and chordates are, it must be admitted, highly speculative. Even if we accept the assumption that annelids resemble the ancestors of vertebrates, there still remains a wide gulf to be filled between flatworms and annelids. In certain characteristics, the muscles of annelids, it is true, strikingly resemble those
of vertebrates. Among these are the segmentation of the muscles, and their separation by a body cavity into somatic and visceral divisions. It is impossible, however, to be sure that these similarities are not cases of convergence. The eyes of cuttle fish and of man are similar in many respects, but this does not prove a genetic connexion. Moreover, there are striking dissimilarities between annelids and vertebrates, such as the circular trunk muscles of annelids which have no homologues in vertebrates, and which consequently make it difficult to accept the hypothesis of the annelid ancestry of vertebrates.

While the pre-chordate history of muscles is obscure, the evolutionary changes of muscles in chordates are fairly clear. Since the lower chordates, the hemichorda and urochorda, are non-metameric, we must assume that the metamerism of amphioxus and vertebrates is a new acquisition in the group. The trunk muscles of Amphioxus form an unbroken series of segments extending throughout the entire length of the animal. Each muscle segment or myotome is a mass of muscle fibers which extends around the sides of the body nearly to the mid-dorsal and mid-ventral line. Each myotome terminates anteriorly and posteriorly in connective tissue septa, the myocommata, which separate successive myotomes. A sharp bend near the middle of each myotome
gives it in side view the shape of a letter V. All alike are innervated by somatic motor nerves.

The visceral muscles connected with the intestine are non-metameric, and are differentiated into an inner circular and an outer longitudinal group. In the region of the gills, the visceral muscles are connected with
the gill cartilages, and are differentiated into levators, depressors, and constrictors of the gills.

The lateral trunk muscles of cyclostomes strikingly resemble those of amphioxus. In the region of the body cavity, on the ventral side, an external layer of oblique muscles is differentiated. The most important evolutionary advance, however, appears in the differentiation of six eye muscles. Paired eyes first appear in this group, and with them the same six eye muscles as in all vertebrates up to man. All six are formed from the first three embryonic myotomes. It is generally assumed that, like the eye muscles of higher vertebrates, they are innervated by the 3rd, 4th, and 6th cranial nerves. Since in cyclostomes the fourth myotome of the embryo forms the first permanent trunk myotome, all the myotomes of the embryo persist in the adult. Of none of the higher vertebrates is this true. (Figs. 218, 219, 220.)

Hypobranchial muscles, lacking in amphioxus, first appear in cyclostomes. They arise from postbranchial myotomes which send myotomic buds ventrally and anteriorly below the gills as far forward as the mouth. The development and nerve relations of this hypobranchial musculature prove that it is the homologue of the tongue and throat muscles, which in higher vertebrates, are innervated by the twelfth nerve, the hypoglossal. Cyclostomes, however, have no true tongue. The hypobranchial muscles function as a part of the lateral trunk muscles. (Fig. 218.)

A further evolution of muscles also appears in elasmobranchs. The embryos of this group provide a clue to the history of the eye muscles, by demonstrating that the differentiation of the three anterior myotomes into the six eye muscles involves primarily a longitudinal splitting of the myotomes into dorsal and ventral moieties such as happens also in the first and second post-otic myotomes of cyclostomes. The facts suggest that the splitting occurred along the series of lateral line sense organs, which at one time may have included the lens of the eye and the ear capsule. Each of the two divisions of the first myotome splits again lengthwise, thus making the four eye muscles innervated by the oculo-
motor nerve. The dorsal of the two moieties of the second myotome forms the superior oblique muscle innervated by the trochlearis nerve, while the ventral portion unites with the third myotome to form the external rectus muscle innervated by the abducens nerve. The myotomes of the fourth, fifth, and sixth somites break up into connective tissue, so that the first persistent trunk myotome is the seventh. In this way, a hiatus is left in the series of myotomes, and the eye muscles are left as an isolated group which owe their persistence to the fact that they become functionally connected with the eyeball. (Fig. 220.)

If we may draw phylogenetic conclusions from these facts of ontogenesis, we must consider the eye muscles not as relatively young muscles or as post-otic muscles which have migrated into the pre-otic region, but as the first three myotomes of the vertebrate body. Their present isolation may be interpreted as a consequence of the enlargement of the otic capsules. The ontogenesis of cyclostomes and elasmobranchs supports the assumption that in the ancestors of vertebrates, as in amphioxus today, the myotomes formed an unbroken series extending throughout the entire length of the body.

Are the three myotomes which form the eye muscles exactly homologous with the first three myotomes of amphioxus? On account of the absence of eyes, ears, and brain vesicles in amphioxus, it is difficult to answer this question categorically. It is not even agreed that the mouth of amphioxus is the homologue of the vertebrate mouth.

That the first myotome of amphioxus may be compared with the first myotome of elasmobranchs is supported by the evidence that these myotomes have the same relation to the anterior endodermic diverticula of amphioxus that they have to the anterior head cavities of ganoids and elasmobranchs. In ganoids the anterior head cavities, like the anterior endodermic diverticula of amphioxus, are paired outpocketings of the anterior blind end of the enteric cavity and only secondarily acquire openings to the exterior, as also do the proboscis cavities of the hemichorda and the left cavity of amphioxus. Since, therefore, these cavities are the most anterior in the chordate body and share the peculiarity of opening by pores to the exterior, and since they have similar topographic relations to the first permanent myotomes and to the mouth, the assumption of their exact homology seems justified.

If, then, we make this assumption, the history of the eye muscles sums up as the transformation of the first three myotomes of an amphioxus-like ancestor into the six eye-muscles of the vertebrates. Primarily, as in amphioxus, the three anterior myotomes were members of an unbroken series of segmented muscles extending throughout the entire length of the body. When lateral line organs and enlarged cranial ganglia associated with them evolved, the anterior myotomes became split lengthwise
Fig. 220.—Diagrams based upon cyclostome and elasmobranch embryos illustrating the phylogenesis of the six eye muscles. Myotomes are cross-hatched. Those which degenerate in ontogenesis are cross-hatched with broken lines. In C the eye muscles are shown as if viewed from the median side of the eye.
into dorsal and ventral moieties. Further separation and displacement followed the enlargement of the optic and otic vesicles. In this way, eventually, two sets of muscles, one dorsal and one ventral, were brought into close proximity to the enlarging optic vesicles with which they finally became functionally associated.

During the phylogenetic transformation of myotomes into eye muscles noteworthy changes come about in their nerve relations. While the first myotome retains throughout phylogenesis its primary connexion with the oculomotor nerve, the nerve of the second myotome, the trochlearis, acquires a dorsal chiasma and retains connexion only with the dorsal moiety of the myotome which becomes the superior oblique muscle. There is no satisfactory explanation of the appearance of this chiasma. The cells which by their outgrowth produce the fibers of the trochlear

nerve are located in the base of the brain posterior to those which form the oculomotor nerve. But the fibers of the trochlear nerve instead of growing directly to the muscle of the same side, as do those of the oculomotor nerve, grow around the wall of the brain and cross above the brain to connect with the superior oblique muscle of the opposite side. In the days when it was assumed that there is a primary connexion between nerve and muscle, some morphologists thought it necessary to assume that not only the nerves but the muscles had interchanged sides—a sort of internal leap-frog for which there is not a particle of evidence. But even our present knowledge that muscle and nerve become connected with one another secondarily gives us no clue as to how the chiasma was formed during phylogenesis.

Another difficult problem is presented in the nerve relations of the external rectus muscle, which is formed from the ventral moieties of the second and third myotomes. The nerve of the external rectus muscle is

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**FIG. 221.**—The mesodermal somites 1–3 from which the eye muscles develop, as seen in a wax reconstruction of a 5–6 mm. Squalus (elasmobranch) embryo made by Alton F. Chase. The somites are viewed from the left side. The anterior somite of Miss Platt later breaks up into mesenchyme.
not the trochlear, which is the nerve of the second myotome, but the abducens, the sixth nerve. We appear to have here to do with a case of nerve piracy, in which a nerve of one myotome has invaded the territory and usurped the place of another nerve. Similar cases of nerve substitution are not unknown, and the innervation of a myotome by nerves of more than one segment is the rule rather than the exception. A difficulty which is perhaps more serious is that the abducens nerve appears not to be the original nerve of the third myotome, but to be a post-otic nerve which has invaded pre-otic territory. The causes of such a nerve substitution are as obscure as those of the trochlearis chiasma (Fig. 505).

**Muscles in Elasmobranchs.** The metamerism which is such a characteristic feature of the musculature of cyclostomes is retained with slight

![Diagram of superficial muscles in the shoulder region of Squalus.](image)

Fig. 222.—The superficial muscles in the shoulder region of Squalus. From such relatively simple beginnings have evolved the complex muscles of the arm and shoulder of man. The flexor protractor muscle which corresponds to the deltoid muscle in mammals is covered in the figure by the posterior gill constrictor. (Redrawn after A. Brazier Howell.)

modification in elasmobranchs. A more elaborate folding of the myotomes of elasmobranchs, however, greatly complicates their form. The cause of this folding is unknown. The total amount of muscle remains the same; and although the myocommata are folded along with the myotomes, so that the surface of attachment of the muscles is increased, it has not been proved that this increase is adaptive.

A novelty first appearing in this group, is the division of the lateral trunk myotomes by a horizontal connective tissue septum into epaxial and hypaxial groups of muscles. Five post-branchial myotomes send buds anteriorly into the floor of the pharynx to form the hypobranchial musculature innervated by the hypoglossal nerve.

The most important advance, however, made by the elasmobranchs is the first appearance in vertebrates of the muscles of pectoral and pelvic fins. As the myotomes extend ventrally in the body-wall, hollow epithelial buds branch off laterally into the fin anlagen. The appendicular
muscles are thus seen to be derivatives of lateral trunk muscles. Differentiation of the muscles thus formed takes place in two directions in elasmobranchs and higher animals. First, the appendicular muscles are subdivided into intrinsic muscles which lie within the fin and extrinsic muscles which are connected with the fin but lie within the body-wall.

Both groups are subdivided into levators and depressors. On the anterior side of the fin, a muscle is formed which pulls the fin forward towards the head. No special antagonistic muscle is differentiated in elasmobranchs, the adduction of the fin being effected by the combined action of the posterior part of the levator and depressor groups acting together. The extension of the extrinsic muscles of the fins in fan-like form over the lateral trunk muscles tends to obscure the metamerism of these in the region of the appendages. The trapezius muscle which extends from

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Fig. 223.—Diagrams illustrating the hypothetical evolution of the branchiomeric muscles. A. Hypothetical ancestral form. B. Branchiomeric muscles in urodele amphibian. (Redrawn after Wilder’s "History of the Human Body," Henry Holt & Co.)
the scapula anteriorly above the gills makes its first appearance in this group.

In the head region, the visceral muscles become specialized in relation to the jaws. The levators of the first two visceral arches form the jaw muscles, including the masseter, temporalis, pterygoids, while the depressors of these arches become the intermandibularis muscles. The muscles of the remaining visceral arches remain relatively unmodified. (Fig. 223.)
In the urodeles, the metamerism of the lateral trunk musculature persists as a striking characteristic. The extrinsic muscles of the appendages, however, become widely extended anterior and posterior to the legs. Such definitive muscles as the pectoralis and the latissimus dorsi now appear, and the intrinsic muscles subdivide into those of the arm and thigh, the forearm and shank, and the feet. By further splitting of the original muscle mass within the limb, many new muscles arise, some of which may be homologized with those of man. On the sides of the body, the lateral trunk muscles become delaminated into layers, some amphibia having as many as four. The 'epaxial muscles of the trunk divide into longitudinal bundles connected with the head.

Fig. 225.—Superficial muscles of dog. b, brachialis; bc, brachiocephalic; bf, biceps femoris; cc, cleidocervical; d, digastric; dt, deltoid; g, gluteus; i, intercostals; ld, latissimus dorsi; m, masseter; mk, mylohyoid; oc, external oblique abdominal; ot, omotransversarius; p, pectoralis; pg, parotid gland; ra, rectus abdominis; s, sartorius; sc, sternocleidomastoideus; sg, submaxillary gland; sh, sternohyoideus; sm, semimembranosus; sl, semitendinosus; t, trapezius; tb, triceps brachialis. (From Kingsley's "Comparative Anatomy of Vertebrates," after Ellenberger and Baum.)

A further novelty in amphibia is a movable tongue. Its intrinsic muscles are those which, as we have seen, grow from occipital myotomes into the floor of the throat and are innervated by the hypoglossal nerve. In this group also we find sternohyoid and geniohyoid muscles, which connect sternum and lower jaw respectively with the hyoid, differentiated.

No very striking developments affect the muscles of reptiles. The three sets of epaxial muscles of the trunk,—transverso-spinalis, lumbo-costalis, and ilio-costalis, appear. The fusion of the lateral trunk myotomes and the consequent loss of metamerism leads towards the conditions in mammals. An extreme degree of delamination affects the lateral trunk muscles, some reptiles having as many as eight layers in the body-wall.

With the great enlargement of the appendages of mammals, there appears a corresponding increase in the appendicular musculature and
trunk muscles become relatively reduced. Subdivision and migration of muscles increases. Caudal muscles dwindle with the reduction of the tail. In the trunk region, metamerism is preserved only in the intercostals, the rectus abdominis, and the intervertebral muscles.

Integumental (Dermal or Cutaneous) muscles in the form of a panniculus carnosus group appear suddenly in monotremes and marsupials only to disappear in the higher primates except as rudiments. In the head and neck region, however, the platysma and facial muscles persist in man and apes. In the trunk region, these integumental muscles are outgrowths of the pectoralis minor complex. In the head region, however, they are visceral in origin.

The most important muscular novelty contributed by mammals is the diaphragm. Its innervation by branches of cervical spinal nerves proves that it is a derivative of cervical myotomes.

There is no essential difference between the muscles of man and those of other mammals. The presence in man of such useless muscle rudiments as the sacro-coccygeal and ear muscles suggest a mammalian
derivation. The evolutionary process of subdivision, fusion, migration, and splitting of muscles reaches its climax in primates, forearm and hand being especially noteworthy.

Figure 227.—Mimetic muscles in monkey (ateles) and man. A. Ateles (redrawn from Wilder after Ruge) and B. Homo. The similarity of these muscles both in function and relations attests their similar genetic derivation.

**Muscles in Man**

In the human body are nearly four hundred paired or bilaterally symmetrical muscles, of which forty-seven pairs are visceral and the rest skeletal. In addition to these, four unpaired muscles are recognized.

**Muscles of the Head.** One of the most distinctive features of the head is the presence of numerous integumentary muscles, visceral in origin, inserted in the skin of the head and neck, innervated by the facial
nerve, and used chiefly for the expression of the emotions. The facial muscles arise chiefly, if not exclusively, from the mesoderm of the hyoid arch, from which they spread to the face and scalp. Although most visceral muscles are involuntary, those of the face are under the control of the will.

Among the best developed of the facial muscles are those connected with the lips. The **platysma** is a broad sheet extending from the corners of the mouth along the sides of the neck. When it contracts it depresses the corners of the mouth as in grief. The **orbicularis oris** encircles and closes the mouth. The **risorius**, connected with the corners of the mouth, is not a laughing muscle as its name suggests, but is used in drawing back the corners as in pain or grief. The **buccinator**, which also radiates from the corners of the mouth, is used in compressing the cheeks to keep food between the teeth. The **caninus** raises the corners of the mouth as in sneering. The **zygomaticus** runs from the corners of the mouth to the zygomatic bone and is the true smiling muscle. The **triangularis** depresses the corners of the mouth as in grief.

A few weak slips of muscle surround the nasal orifices, among which the **nasalis** functions both as constrictor and dilator of the nares.

One of the facial muscles, the **orbicularis oculi**, closes the eyelids. But the muscle which raises the upper lid, the **levator palpebrae superioris**, is innervated by the oculomotor nerve and is therefore not regarded as one of the facial muscles. The **corrugator** muscle, however, which serves to wrinkle the forehead in frowning, is a facial muscle.

Of the muscles of the scalp, the **frontalis** draws the scalp forward and wrinkles the forehead, the **occipitalis** draws the scalp back. A number of **auricularis** muscles retract or raise the ears. The six eye muscles,— the superior, inferior, internal, and external rectus, and the superior and inferior oblique, do not belong to the integumentary group. The function of the oblique muscles is thought to be to prevent rotation of the eyeball when the rectus muscles contract.

A number of visceral muscles associated with the jaw and innervated by the trigeminal nerve are used in mastication. These include the
masseter, which raises the mandible; the temporalis, which raises the mandible and draws it back. The chief function of the pterygoids, internal and external, is in moving the jaw from side to side, as in chewing. The digastric lowers the jaw.

Some of the tongue muscles are intrinsic but most are extrinsic. The intrinsic lingualis forms an interwoven complex extending longitudinally, vertically, and transversely. Of the extrinsic group, the hyoglossus and styloglossus retract the tongue, while the genioglossus, which forms most of the body of the tongue, both extends and retracts it, depending upon which part of the muscle contracts.

Another group of muscles lies in the floor of the throat between the mandibles and the hyoid bone, among them the anterior belly of the digastric, the geniohyoid, and the mylohyoid. The stylohyoid and the posterior belly of the digastric extend from the hyoid to the styloid process. Food is forced into the esophagus by a group of constrictor muscles of the pharynx.

Muscles of the Neck. In addition to the cutaneous platysma, the neck contains sixteen paired muscles. Underneath the platysma on the side of the neck, the conspicuous sternocleido-mastoid bends and rotates the head. The trapezius, strictly a muscle of the shoulder, extends well up on the back of the neck. Another shoulder muscle, the levator scapulae, draws the shoulder blade towards the head. (Fig. 229.)
The **dorsal muscles** of the neck extend the head and bend the neck. Included in this group are the **spleenius, longissimus, semispinalis, multifidus**, and the long and short **rotators**, the most powerful being the **semi-spinalis**. Also on the back of the neck, connecting the occipital bone with the first two cervical vertebrae, are the **rectus and obliquus**.
muscles of the head. Between the spinous and the transverse processes of the neck vertebrae, are inter-spinales and intertransversarii muscles.

On the ventral side of the throat, between the sternum and hyoid bones, are the sternohyoid, sterno-thyroid, thyrohyoid, and omohyoid muscles, which pull the hyoid toward the sternum. The longus capitis, longus cervicis, and the scaleni, anterior, middle, and posterior, are a deeper group, ventral to the vertebrae, which bend the neck.

Muscles of the Back. The dorsal muscles of the back extend from the sacrum to the neck. Starting posteriorly as the sacrospinalis muscle, the mass divides into a medial longissimus and a lateral iliocostalis, both of which as they extend into the neck region give off slips to all the ribs. Closely connected with the iliocostalis, is a more medial muscle, the spinalis, which also extends along the backbone. In the groove between the spinous processes of the vertebrae and the transverse processes, is a group of muscles which have already been mentioned as the semi-spinalis group in the neck. In the lumbar region this group is known as the transversospinalis muscle. A deep subdivision of this group is the multifidus. Between the vertebrae, connecting spinous and transverse processes, are the interspinales and intertransversarii muscles which stiffen the spine.

The prevertebral group of muscles of the trunk, immediately ventral to the vertebral column, are less developed than those just mentioned, so that the backbone is bent chiefly by other muscles not closely related to the vertebrae. Prevertebral muscles are wanting in the thoracic region. In the lumbar region, this group is represented by the major and minor psoas. The psoas major is, however, more concerned with bending the thigh than with flexing the back. The quadratus lumborum bends the back sidewise.

In the coccygeal region, the rudimentary and variable sacrococcygeus muscles appear to be functionless but interest the morphologist as remnants of the powerful caudal muscles of man's ancestors.

Abdominal Muscles. The muscles of the lateral abdominal wall are split into three layers, the external and internal obliqui, and the transversus. The contraction of these muscles lowers the ribs, compresses the abdomen, and by pushing the viscera against the diaphragm, expels air from the lungs. Extending from the ribs to the pubic bone along the ventral wall of the abdomen, is the segmented rectus abdominis, the function of which is to lower the thorax and to flex the backbone. Although this muscle is innervated by six or seven spinal nerves, it is divided by inscriptions tendineae into only four or five segments, which are interpreted as remnants of the primitive metamerism of the trunk musculature. The lateral halves of the rectus abdominis are separated in the medial line by a connective tissue linea alba. In the region where
the linea alba is attached to the pubis, a small muscle, the *pyramidalis*, is usually present. When well-developed its length is 7 to 8 cm., but rarely it may extend craniad to the sternum. Its relations and variable size suggest that the pyramidalis is a remnant of the muscle attached
to the marsupial pouch of didelphians. On the sides of the abdomen, the **quadratus lumborum** muscle extends from the last rib to the

![Diagram of the muscular system](image)

**Fig. 232.**—Deeper trunk and neck muscles of man, viewed from the left side. (Redrawn after Sobotta.)

ilium. Its function is to depress the thorax and bend the backbone backwards.
Thoracic Muscles. The intrinsic muscles of the thorax are covered by the extensive muscles of the shoulder and chest. When these are removed, the same three muscles found in the abdomen are exposed. The outer of these, corresponding with the external oblique of the abdomen, is the external intercostal; the internal intercostal is the homologue of the internal oblique of the abdomen; the m. transversus thoracis corresponds to the transversus abdominis. In addition to these, an external sheet of muscle which is continuous in many marsupials is represented in

![Diagram of the human diaphragm viewed from above. Only the peripheral region of the diaphragm is muscular. The central portion is tendinous. The diaphragm is dome-shaped with the convex side uppermost. (Redrawn from Braus.)](image)

man by the serratus posterior, which is divided into superior and inferior moieties. When certain parts of the intercostal muscles contract, the rib-basket is raised, the thoracic cavity enlarged, and air is inspired to fill the space thus created. The levators of the ribs are twelve pairs of triangular muscles which connect the ribs with the transverse processes of the vertebrae and are used to raise the ribs. (Fig. 232)

Diaphragm. The diaphragm is a dome-shaped muscle separating thoracic and abdominal cavities. The central portion is tendinous and only the outer portion which is attached to the ribs is muscular. When the muscles of the diaphragm contract, the dome is flattened and the
the thoracic cavity is enlarged. The curvature of the diaphragm is restored when the intercostal muscles relax and the abdominal muscles push the viscera against the diaphragm.

**Shoulder and Chest Muscles.** The muscles of the shoulder and chest function chiefly in relation to the arms. The most superficial of these on the back is the trapezius which elevates the shoulder and in conjunction with the rhomboideus draws the shoulder blade towards the backbone. Underneath the trapezius, the rhomboideus major and minor also draw the shoulder blade towards the backbone. The deltoideus is the shield-shaped muscle which covers the shoulder and extends from the scapula to

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![Diagram of the Muscular System](image_url)

**Fig. 234.**—Thoracic and lumbar muscles of man as seen in cross section. Thoracic muscles on the right, lumbar on the left. (Redrawn after Braus.)
brachialis bend the elbow. The biceps brachii is also the most powerful supinator of the forearm.

**Muscles of the Forearm and Hand.** There are many more muscles in the forearm than in the upper arm, and the diversity of function is also much greater. Two groups are distinguished, a radio-dorsal which straightens the wrist and supinates the forearm, and an ulno-volar group which flexes the wrist and pronates the forearm. On the medial side of the arm, the two groups are separated by the ulna bone.

Among the extensor muscles of the forearm are the **extensor carpi radialis longus**, and the **extensor carpi radialis brevis**, which lie on the radial side, the **extensor carpi ulnaris** of the ulnar side, and intermediate between these, the **extensor digitorum communis** and **extensor digitii quinti proprius**. Deeper muscles beneath these include the **supinator**, **abductor pollicis longus**, **extensor pollicis longus**, **extensor pollicis brevis**, and **extensor indicis proprius**.

Included in the flexor-pronator group of muscles are the **pronator teres**, **flexor carpi radialis**, **palmaris longus**, **flexor carpi ulnaris**, **flexor digitorum sublimis**, **flexor digitorum profundus**, **flexor pollicis longus**, and
the **pronator quadratus**. An additional muscle is the **brachioradialis**, which, although belonging with the extensor group, has come to have flexor action. Altogether there are nineteen muscles in the forearm.

Besides these muscles of the forearm most of which act upon the hand, there are nineteen intrinsic to the hand. Four of these are inserted on the thumb, the **abductor pollicis brevis**, **opponens pollicis**, **flexor pollicis brevis**, and **adductor pollicis**. Three muscles are inserted on the little finger, **abductor**, **flexor brevis**, and **opponens digiti minimi**. In the palm of the hand are four **lumbrical** and seven **interosseus** muscles. The **palmaris brevis** is usually considered an integumentary muscle like those of the face.

**Hip Muscles.** The muscles of the hip, like those of the shoulder, may be divided into dorsal and ventral sets. The dorsal muscles have their origin on the vertebral column and the ilium. Of these, the **iliopsoas** protracts the thigh, and the **gluteus maximus** extends it. Other dorsal muscles, are the **gluteus medius**, **gluteus minimus**, **piriformis**, and **tensor fasciae latae**, all of which are inserted on the femur.

The ventral muscles of the hip have their origin on the pubis and the ischium, and their insertion on the femur. Among them are the **obturator externus**, **obturator internus**, **quadratus femoris**, and the **gemelli**, all of which both adduct and rotate the thigh. The obturator externus, here included in the hip muscles is sometimes regarded as a thigh muscle.

**Muscles of the Thigh.** There are three groups of thigh muscles, anterior—extensor, medial—adductor, and posterior—flexor muscles. Their relations are such that they act upon both the thigh and the lower leg.

The anterior extensor group includes five muscles, the **sartorius** or “tailor muscle,” and the four divisions of the **quadriceps femoris**, the **rectus femoris**, **vastus lateralis**, **vastus medialis**, and **vastus intermedius**. In the medial adductor group are five muscles, **gracilis**, **pectineus**, **adductor brevis**, **adductor longus**, and **adductor magnus**. The posterior or “ham-string” muscles which bend the leg and extend the thigh, are the **semi-tendinosus**, **semimembranosus**, and **biceps femoris**.

**Muscles of the Lower Leg and Foot.** There are thirteen muscles in the lower leg, four of which form an anterior group which bends the ankle and lifts the toes, the **tibialis anterior**, **extensor digitorum longus**, **peroneus tertius**, and **extensor hallucis longus**. Two lateral muscles, the **peroneus longus** and **brevis**, extend the foot. Three superficial calf muscles, the **gastrocnemius**, **soleus**, and **plantaris**, connect with the calcaneus by the tendon of Achilles, and extend the foot. Beneath them are four deeper muscles, the **popliteus**, which rotates the leg medially, and the **flexor digitorum longus**, **flexor hallucis longus**, which bend the toes, and **tibialis posterior**, which extends the foot.
The muscles of the foot strongly resemble those of the hand. The extensor digitorum brevis, which extends across the top of the foot from the heelbone to the four lateral toes, has, however, no homologue in the hand. On the top of the foot also are four dorsal interosseus muscles.

The most superficial muscle of the sole is the flexor digitorum brevis connected with the four lateral toes. The quadratus plantae is inserted upon the tendons of the flexor digitorum longus. The four lumbricales are flexors of the four lateral toes. Three muscles, abductor, flexor, and adductor, connect with the great toe. The little toe also has three special muscles, abductor, flexor, and opponens. The three ventral interossei lie between the metatarsals.

Pelvic Muscles. Muscles of the pelvic diaphragm, of the urogenital diaphragm, and of the external genitals are, from their position, regarded as pelvic.

Those of the pelvic diaphragm are the coccygeus, which connects the coccyx with the ischium, the levator ani, a muscle with three divisions which lifts the anus, and the sphincter ani externus, consisting of three muscular rings surrounding the anus. All are supplied with branches of sacral nerves. The levator ani complex represents the caudal flexor-abductor musculature of tailed mammals, which in man, as in the anthropoid apes, with the reduction of the tail, has gained new relationships with the pelvic viscera. The coccygeus represents the proximal ventral caudal abductor of tailed mammals.

The urogenital diaphragm has two muscles, a transversus perinei and a sphincter urethrae. The latter closes the urethra and is under voluntary control. In the male, the sphincter also compresses the prostate and bulbo-urethral glands. In the female, it compresses the vagina and the glands of Bartholin.

The external genital muscles include the bulbo-cavernosus, which in the female compresses the vagina and in the male increases the turgescence of the penis, and the ischio-cavernosus, which serves to maintain the turgescence of the penis or clitoris.

Development of the Muscles

The classification of muscles into striped and smooth upon the basis of their finer structure, like that into voluntary and involuntary, does not correspond with a classification into skeletal and visceral based upon their embryonic development.

Somatic Muscles, Derived from the Epimere. The Eye Muscles. The details of the development of the six eye muscles in man are not fully known. The fact, however, that they are innervated by the same somatic motor nerves, III, IV, and VI, as in the lower vertebrates has led morphol-
ogists to assume that their development corresponds in essentials throughout the vertebrate series.

![Diagrams A-F illustrating the ontogenesis of muscles in vertebrates.](Based upon figures by Hatschek and Kingsley modified.)

Their development has been most thoroughly investigated in elasmobranchs. In embryos of this group, as well as in higher vertebrates to

![Diagram of muscle segments in head of embryo vertebrate, based upon a shark.](The anterior myotomes tend to divide into dorsal and ventral moieties; persistent myotomes lined, transient with broken lines; central nervous system dotted, nerves black. a, premandibular somite; abd, abducent nerve, hyp, hypoglossal musculature; hypn, hypoglossal nerves; om, oculomotor nerve; sp, spiracle; 1-6, first six somites (4, 5, 6, functional in Petromyzon); I-VIII neuromeres. (From Kingsley's "Comparative Anatomy of Vertebrates," after Neal.)

mammals, the eye muscles develop from somites or "head cavities." The first head cavity (somite 1) gives rise to the four muscles innervated by the oculomotor nerve, the superior oblique muscle comes from the
second head cavity, while the third head cavity combining with the
second forms the external rectus muscles. (Figs. 237, 238.)

The serial homology of the head cavities or somites with trunk somites,
which for many years was a controverted problem, has now been demon-
strated by the fact that in the embryos of lower vertebrates the head
somites form a series of mesodermal segments continuous with the trunk
somites. Like the latter, they become differentiated into myotome and
and sclerotome, are innervated by somatic motor nerves, and are dorsal
to notochord and dorsal aorta. Furthermore, their segmentation is
independent of that of the visceral arches. Another point of resemblance
is that the first and second head cavities divide during ontogenesis into
dorsal and ventral moieties precisely as do the first and second post-otic
myotomes in petromyzon. The fusion of portions of two myotomes, the
second and the third, to form the external rectus muscle of the eye resem-
bles the fusion of trunk myotomes such as occurs in the formation of the
tongue muscles. (Fig. 238)

Lateral Trunk Muscles. The lateral trunk muscles of man develop
from myotomic segments which first appear in the fourth week of onto-
genesis, and by the end of the second month, have increased to nearly
forty pairs. The original metamerism of the myotomes, which persists
even in the adults of the lower vertebrates, becomes largely lost in adult man and mammals as the result of a number of processes among which fusion is the most important. As the myotomes grow in size and thickness through cell multiplication, the connective tissue septa between them disappear. In this way are formed such elongated muscles as the spinals and iliocostalis. Among the processes tending to obscure the original metamericism is the degeneration of myotomes into connective tissue fasciae and aponeuroses which may be very extensive. Migration of muscles may accompany their fusion, as in the case of the tongue and throat muscles which develop from four or five occipital myotomes. In man,
group including obliquus and transversus sets. The muscles of the diaphragm, which are peculiar to man and mammals, migrate into the chest from the neck, as is evidenced by the fact that they are innervated by branches of the third, fourth, and fifth cervical nerves.

**Tongue Muscles.** The origin of the hypoglossal muscles in the human embryo is somewhat uncertain. Since, however, they have the same innervation as in lower vertebrates, it is generally assumed that their development is essentially similar. In all vertebrates below mammals, muscle buds grow from four to five occipital myotomes ventrally into the floor of the throat. From the mass of cells thus formed, arise the intrinsic muscles of the tongue, innervated by the twelfth nerve, the hypoglossus. In man and mammals evidence is lacking of muscle buds in the formation of the hypoglossus muscles. It may be assumed that cell migration takes the place of bud formation and extension.

**Appendicular Muscles.** In the embryos of lower vertebrates, elasmobranchs to reptiles, as the myotomes grow ventrally in the body-wall and reach the level of the lateral folds from which the appendages develop, they give off lateral buds into the appendicular folds. After they have entered the folds, these buds lose their connexion with the trunk muscles, although they still retain their epithelial character. Within the anlage of the appendage, the appendicular muscle buds subdivide into dorsal and
ventral moieties, from which develop respectively the levator and depressor muscles of the appendage. (Figs. 241, 242)

The appendicular muscles of man and mammals, on the contrary, do not develop from myotomic buds, but arise by cell migration. The two methods are after all not radically different. In fishes, for example, where most of the appendicular muscles arise from myotomic buds, some muscles which develop later than the others come from migrant mesenchymatous cells as they do in mammals. Similarity of innervation, however, attests the homology of the appendicular muscles throughout the vertebrate series.

The fact that the arm muscles of man are innervated by the last four cervical and the first thoracic nerves further justifies the assumption that
they are derived from the myotomes of these segments. To the group of muscles derived from this source, are added other, such as the trapezius, sternocleidomastoid, and levator scapulae. The pectoralis and latissimus dorsi muscles spread out from the arm. Most of the muscles of the shoulder, chest, and arm appear early in the second month, and are differentiated by the beginning of the third.

From the connexion of the muscles of the lower leg with spinal nerves, including the last four lumbar and first three sacral, it may be assumed that their cellular anlagen are derived from the corresponding myotomes. In all essentials their development resembles that of the muscles of the arm. A common mass of cells within the limb-bud differentiates into dorsal and ventral muscle anlagen. The muscles from the ventral group become innervated by the femoral nerve while the dorsal group are connected with the obturator. The subdivision of the primary muscle mass into the separate muscles of the adult limb is mostly completed by the end of the second month.

**Visceral Muscles, Derived from the Hypomere.** The visceral or hypomeric include those of the heart and main blood vessels as well as those associated with the alimentary canal. While most of them consist of smooth muscle fibers, the visceral muscles of the head and heart are striped.

The muscles of the wall of the alimentary canal are formed from mesenchymatous cells proliferated from the visceral layer of the hypomere. Such cells fill the space between the mucous epithelium lining of the alimentary canal and the adjacent hypomere. They also differentiate into both the connective tissues and the blood vessels of the wall of the alimentary canal and into its circular and longitudinal muscles. The circular layer of muscles is formed before the longitudinal layer. The histogenesis of smooth muscle in some respects resembles that of striped muscle. The mesenchyma cells elongate and within them rows of cytoplastic granules are converted into myofibrils. Unlike the fibrils of striped muscle, however, light and dark bands are not formed. As the fibers elongate into spindle-shaped cells there is no nuclear division and the fibers remain mono-nucleate. The protoplasmic bridges (plasmodesms) by which the mesenchymatous cells were connected with one another persist and bind the muscle fibers together.

The fate of the hypomere in the head is much more complex than in the trunk. Besides forming the heart and pericardium, the head hypomere gives rise to the chewing muscles, the muscles of expression, and the pharyngeal and laryngeal muscles. In general, the processes involved are similar in lower and higher vertebrates.

In embryos of lower vertebrates, e.g., elasmobranchs, the coelom extends throughout head and trunk. In the head region, as a result of the outpouching of pharyngeal pouches, the hypomere becomes divided...
into a series of cavities each of which lies in a visceral arch. This hypo-
meric segmentation (branchiomerism) is independent of the segmentation
of the epimere (mesomerism), and should not be confused with this,
although it is possible that the two types of segmentation may originally
have coincided. From the mesoderm of the visceral arches arise the
muscles, connective tissues, and blood vessels of the arches. In the
fishes, these muscles are differentiated into levators, depressors, and
constrictors of the gills. In the process of conversion the epithelium of
the hypomere breaks up into mesenchyme and the coelomic cavity
disappears.

In mammals and man, the coelom is absent in the visceral arches and
the muscles are formed from masses of mesenchymatous cells. From
the first visceral arch arise the muscles innervated by the mandibular
branch of the fifth nerve, the masseter, temporalis, pterygoid, mylohyoid,
and tensor veli palatini. From the same source come the tensor tympani
of the ear and the anterior belly of the digastricus. The muscles innerv-
ated by the facial nerve are derived from the second visceral arch, the
hyoid. They include the muscles of expression, the stylo-hyoid, stapedius,
and the posterior belly of the digastricus. From the third visceral arch
arise the stylopharyngeus muscle innervated by the glossopharyngeus
nerve, and the constrictors of the pharynx innervated by the vagus nerve.
The laryngeal muscles innervated by the vago-accessory nerve originate
from the fourth and fifth visceral arches. As already explained the
muscles of the tongue and throat innervated by the hypoglossal nerve
are myotomic, not visceral, in origin.
CHAPTER 8

THE DIGESTIVE SYSTEM

Life depends upon an unceasing intake and outgo of matter. Each living thing takes in food or the raw materials for food, assimilates this into its own peculiar sorts of protoplasm, and after forming these chemical substances, promptly burns them up into simpler chemical substances, which finally leave the body as the wastes and ashes of life. Upon this fundamental chemical process of metabolism, all other vital functions depend. The foundations of life are chemical.

The products of plant metabolism, on their way back to the inorganic world, become, directly or indirectly, the food of animals. Thus all animals are parasites on the green plants. But their feeding habits are varied. Some marine organisms live on the mud as well as in it; earthworms pass through their digestive tract enormous quantities of soil for the sake of the organic matter which they extract from it. But leeches live chiefly on blood. Oysters sweep bacteria into their mouths by ciliary action. Barnacles kick food into their mouths by means of their six pairs of legs. Some insect larvae feed on cellulose, some on fur and wool. Some whales eat minute swimming crustacea, which they strain out by means of the whalebone. Others live chiefly on gigantic cuttle-fish. Some mammals are herbivorous; some are carnivorous; others, like man, are omnivorous. Man alone cooks his food.

Digestion. The first chemical change which ingested foods undergo is a process by which insoluble substances are made soluble, so that they may be absorbed through the lining membranes of the small intestine. The agents in this chemical process are certain remarkable enzymes which, like other and inorganic catalysts, are able to bring about chemical changes without appreciable effect on themselves. During digestion, these enzymes split up the huge molecules of colloids into simpler molecules, small enough to pass through animal membranes. Their composition is unknown; but they are thought to be rather simple colloids derived from proteins. The specificity of their action is remarkable, each enzyme affecting only one food substance. All are secreted by glands connected with the alimentary canal.

EVOLUTION OF THE DIGESTIVE SYSTEM

The protozoa have no digestive system. The single cell merely engulfs the food particle, surrounds it with protoplasm, digests and assim-
ilates it, and extrudes what remains. The porifera, though they have a cloacal cavity, do their feeding essentially like protozoa, each cell for itself.

The first real step in evolving a proper digestive system is taken by the coelenterates. These, as their name affirms, have a cavity or enteron which is also the digestive tract. This has but one opening to the exterior, which serves both as mouth and anus.

Most flatworms, like coelenterates, have a single opening to the digestive cavity (enteron), and this opening serves as both mouth and anus. A few species of flatworms, however, possess an anus—some indeed have two ani—the invention of which therefore should be credited to flatworms. Threadworms, with few exceptions, have both mouth and anus, and their alimentary canal is separated from the muscular body wall by a space, a false body-cavity or pseudocoelom. The digestive tube in threadworms is purely epithelial and non-muscular.

A muscular digestive tube, one of the important steps in animal evolution, is contributed by the annelids. In these for the first time in the phylogensis of animals an epithelium-lined coelom or "body cavity"
proper separates the alimentary canal from the body wall. In annelids as in all the higher animals there is no connexion between the two cavities, enteron and coelom. The single tube that forms the body of lower forms has become double, and the muscular activities of the alimentary canal are carried on independently of those of the body wall.

Among the forms which lie near the main line of human ancestry, pharynx, esophagus, and stomach are first differentiated in urochordates. A liver arises in the cephalo-chordates. What is possibly a new mouth, not homologous with the mouth of amphioxus, appears in cyclostomes. But this mouth is still a sucking one, without jaws. The cyclostomes contribute also a pancreas and a bilobed liver.

Elasmobranchs, utilizing dermal scales as teeth and transforming a visceral arch into a jaw, convert the sucking mouth into a biting one. They develop also a new cavity, the cloaca, to receive the wastes and secretions of the urogenital and digestive systems.

The amphibia fasten their teeth in a groove in the jaw bone, invent salivary glands, utilize hypobranchial muscles to make a mobile tongue, and differentiate small from large intestine.

Mammals greatly elongate the intestine, and by suppressing the cloaca separate the rectum from the urogenital sinus. The result is a muscular, epithelium-lined alimentary canal, differentiated into nearly a dozen different organs, and having about the same number of different glands associated with it.

THE HUMAN DIGESTIVE SYSTEM

MOUTH

The mouth cavity is divided into an anterior vestibule or labial cavity lying between the lips and the teeth, and a posterior mouth cavity proper or buccal cavity underlaid by the tongue and extending to the posterior margin of the soft palate. The roof of the mouth cavity proper is formed
by the hard and soft palates, which separate the mouth cavity from the narial passage above.

Development of the Mouth

At a relatively late stage of ontogenesis, at the anterior end of the fore-gut where the mouth is to break through, the ectoderm invaginates to form the stomodeum, the depth of which, in amniotes, is considerably increased by the expansion of the fore-brain in front and the heart behind. At the bottom of the stomodeum, ectoderm and endoderm are in contact as a two-layered membrane, which ruptures and disappears leaving no trace in the adult. Thus, in forming the mouth, the ectoderm takes the initiative, whereas the gill-slits are primarily outpocketings of the endoderm.

The covering of the lips and gums is derived from the ectodermal stomodeum, while that of the rest of the mouth is endodermal. The salivary glands arise from the epithelial lining of the mouth and are generally supposed to be ectodermal in origin. The enamel of the teeth is a product of the stomodeal wall, and therefore, although within the digestive cavity, ectodermal.

Evolution of the Mouth

There is no doubt that the mouths of all vertebrates are homologous, the sucking mouth of cyclostomes being no exception. Cyclostome and gnathostome mouths have the same fundamental structure, development, and relations to other parts, and must therefore be considered homologous.
The ectodermal horny teeth of cyclostomes like the movable lips and cheeks in mammals, are merely details which do not affect the general issue.

But concerning the question of the homology of the mouth of vertebrates with that of the lower chordates, opinion is divided. Van Wijhe (1914) suggested that the mouth of Amphioxus is not homologous with that of vertebrates, but is comparable with the left spiracle of elasmobranchs.

The foundations of this assumption, however, are weak. The enormous enlargement of the larval mouth of amphioxus, as well as its asymmetry are best interpreted as larval adaptations.
Beard and Von Kupffer are persuaded that vertebrates have had two mouths—an old paleostoma, and new neostoma. The paleostoma, in their opinion, may be represented by the hypophysis, which in some Cyclostomes, e.g. Bdellostoma, opens directly into the pharynx. Furthermore, the presence of a pre-oral gut in vertebrate embryos is interpreted as a support of this hypothesis. Von Kupffer thinks that the hypophysial mouth may be homologous with the mouth of Urochords, while Dohrn assumes that it is comparable with the mouth of annelids. Such views have seemed to morphologists to have a rather insecure support, and have therefore been regarded as speculations. (Figs. 248, 250)

That the chordate mouth is not homologous with the mouth of invertebrates has generally been assumed, especially by those who have upheld either the annelid or the arachnid hypothesis of vertebrate ancestry. Each of these theories seems to need to assume a reversal of dorsal and ventral surfaces. But were such a reversal to occur, the ventrally situated mouth of the invertebrate would take a dorsal position, and would consequently lie dorsal to the central nerve cord, whereas in all chordates the mouth is ventral to the central nerve cord. Hence the assumption is made that a new ventral mouth must have arisen when the worm turned over and became a chordate. Minot has sought to avoid this theoretical necessity by assuming that the lateral halves of the supra-esophageal ganglion of the annelid became separated and converted into the eyes of vertebrates, while the old mouth migrated to its present position on the ventral side of the vertebrate, which is the former dorsal side of the invertebrate.

Whether we accept or reject either the annelid or the arachnid theory of the origin of vertebrates, we must believe that there have been at least two mouths in the course of vertebrate phylogensis. The reason for this conclusion is that the original coelenterate mouth becomes the mouth in no vertebrate, while only in Cyclostomes, dipnoi, and possibly some amphibia does it become the anus. But the coelenterate mouth becomes the blastopore of chordate embryos. And the blastopore of chordates lies at the posterior end of the body and forms the neurenteric canal, which connects the neural tube with the enteron, while the chordate mouth develops at the anterior end of the enteron. Consequently, it seems indisputable that there have been at least two mouths in the history of vertebrates.

While, however, all agree that the vertebrate mouth is not the primary animal mouth, and that at least two mouths have successively appeared, some morphologists believe that there have been at least three mouths. Delsman (1922) reviving an earlier suggestion of Kowalevsky (1877) claims that “in the ontogeny of vertebrates we see three successive mouths appear in the same succession as they appeared in phylogeny,
viz., the blastopore (Urmund), the neuropore (the annelidian mouth), and finally the definitive mouth.” According to this view, the neural tube was formerly a part of the digestive system, and its anterior embryonic external opening, the neuropore, once functioned as a mouth. For a part of the digestive system to become nervous in function is indeed a surprising assumption, yet scarcely more so than many other transformations assumed by evolutionists. The digestive apparatus postulated by Delsman on the basis of the relations presented in the Amphioxus embryo has seemed to zoologists too impractical for daily use by any adult animal. The notion that the neuropore of chordate embryos represents a former
mouth or that it is homologous with the annelid mouth lacks sufficient evidence to convince most zoologists that it is more than an interesting speculation.

According to Von Kupffer, the hypophysis of vertebrates represents a paleostoma which functioned as a mouth in prechordates, following their abandonment of the blastoporic mouth. In support of this assumption, he points out that the definitive mouth of vertebrates arises late in ontogenesis in such relation to the series of gill-slits that it might have been formed from a pair of coalesced gill-slits; that the presence of a pre-oral gut in vertebrate embryos suggests that the alimentary canal formerly extended anterior to the present mouth; and, finally, that in the Myxinoids and the embryonic sturgeon the hypophysis actually opens into the pharynx, and like the mouth of urochordate larvae, has a dorsal external opening. Kupffer, however, does not waste time guessing as to the cause of this substitution of a new mouth for an old one. It is possible that the development and enlargement of the pre-oral lobe was a factor in effecting the displacement of the mouth from a dorsal to a ventral position. Diagrams showing the position of the four mouths mentioned in this discussion are shown in Fig. 249. The objection to the idea that there have been a series of mouths in the course of animal phylogensis, on the ground that the chances are against the appearance of more than one ingestive opening into the enteron, loses much of its weight in view...
of the fact that many openings such as the gill-slits have made their appearance in the course of phylogenesis.

The fate of the original blastoporic mouth of Coelenterates, has been mentioned in connection with the classification of animals. In most invertebrates, the blastopore becomes the mouth, while in echinoderms and chordates it either becomes the anus or lies in the anal region. Animals in which the coelenterate mouth persists as the definitive mouth are known as Protostomians, while those in which a new mouth is formed are called Deuterostomians. The two main branches of the animal kingdom shown in Fig. 1 are separated on the basis of this distinction.

According to the protostoma theory of Adam Sedgwick (1884) the oral surface of coelenterates with its encircling nerve ring becomes the ventral, and neural, surface of non-chordates, while in chordates it forms the dorsal, and neural surface. Thus the theory assumes that the non-chordates are the descendents of coelenterates which moved with the oral side down, while the chordates have come from coelenterates which moved around with the oral side up. Sedgwick holds that the two sides of the elongated slit-like mouth of the coelenterate (such as an actinian) have become the right and left sides of the bilaterally-symmetrical bodies of higher animals. He finds that in the primitive worm-like arthropod Peripatus the elongated gastrula mouth closes along the median line of the embryo, but anterior and posterior dilatations persist as the definitive mouth and anus. In this way the alimentary canal is formed with two external openings. The concrescence of the right and left halves of the vertebrate embryo is taken as a confirmation of the theory. It seems
impossible, however, to compare the definitive mouth and anus of vertebrates with the mouth and anus of Peripatus, since the former lie outside of and ventral to the ring of nervous tissue which forms the central nervous system, while the latter lie within the nerve-ring. Only the neuropore and neurenteric canal of vertebrates could be compared with the mouth and anus of Peripatus.

The phylogeny of the vertebrate mouth remains, therefore, an unsolved problem. That there have been at least two mouths in the course of animal evolution, all morphologists agree. These are the coelenterate mouth, which is the blastopore, and the definitive vertebrate mouth. Evidence is however not wanting that the embryonic neuropore and the hypophysis may have served as mouths. Such assumptions are considered to have a relatively insecure foundation.

The Lips. The lips are fleshy folds of skin surrounding the mouth of tetrapods. They are immovable in amphibia and reptiles. In mammals, however, slips of muscle derived from the sphincter coli migrate into the lips, which as a result become movable, and useful in sucking and in the prehension of food. Their increased size in mammals is correlated with the habit of mastication; and they, together with the cheeks, restrict the opening of the mouth. In man, the lips become an important aid to articulate speech.

The Salivary Glands in Man

As food enters the mouth, it is moistened by the secretion of a number of salivary glands, in addition to which are lingual, labial, buccal, palatine and molar mucus-secreting glands. Besides moistening the food, the chief salivary glands contain serous cells which secrete the starch-splitting enzyme ptyalin and the sugar-splitting enzyme maltase. The sublingual and submaxillary glands secrete mucus also.

The largest of the salivary glands is the parotid, which lies below the ear. It is a serous tubulo-acinuous gland, and empties by Stenon's duct into the vestibule of the mouth opposite the second upper molar tooth. It is innervated by fibers from the otic ganglion and has nervous connexion both with the fifth and ninth cranial nerves. Inflammation of the parotid is the cause of mumps.

The submaxillary is a mixed (mucous and serous) tubuloacinous gland located in the floor of the mouth near the angle of the lower jaw. Its secretions are carried by Wharton's duct to the frenulum at the front margin of the tongue near its median line. The cells of the gland are mostly serous, mucus-secreting cells occurring irregularly and constituting only a minor portion. The slender intercalated ducts present in the parotid are absent in the submaxillary.
The **sublingual** is also a mixed tubulo-acinous gland lying below the tongue in the front of the mouth near the median line. Mucus and serous cells are about evenly distributed. In each acinus, the mucus cells are central and the serous peripheral so that the serous tend to form demilunes. The openings of the sublingual ducts lie in front of the tongue near those of Wharton’s ducts.

**Development.** From their position and the relations of their ducts, it is generally assumed that the chief salivary glands are of ectodermal origin. This is probably not true, however, of the numerous glands of the tongue, all of which are formed by the local proliferation of the stratum germinativum of the mucous lining of the mouth.

**History of Salivary Glands.** Salivary glands are not unknown among the invertebrates. Multicellular mucus glands connected with the mouth are present in molluscs. Malaria is transmitted by the saliva of mosquitoes. It is doubtful, however, if the salivary glands of invertebrates have any genetic relation with those of vertebrates.

Lower chordates have no salivary glands, and fishes only unicellular mucus glands. It has generally been assumed that the multicellular glands of the higher vertebrates have their beginnings in such unicellular glands.

Multicellular oral glands appear in amphibia. Besides the mucus-secreting cells of the tongue, most amphibia have an intermaxillary gland,
the duct of which opens between the intermaxillary bones. In some amphibia, e.g., Rana, mucus glands are also located in the posterior narial passages. That enzymes are secreted by the mucus cells of fishes and amphibia has, however, not been demonstrated.

In the reptiles, there are serous cells in the oral glands, and lingual, sublingual, and palatine glands occur. Glands connected with the teeth are differentiated as the poison glands of some snakes.

True salivary glands secreting enzymes are limited to mammals. There seems no good reason to doubt, however, that the salivary glands of mammals are derived from the oral glands of reptiles. Labial and buccal glands become abundant, and possibly the parotid is an enlarged buccal gland. In addition to the lingual and palatine glands, the sublingual and submaxillary glands are present; and in general, the glands of man resemble those of other primates.

The Tongue

The tongue is a muscular organ of miscellaneous functions—digestive, sensory, conversational—lying in the floor of the mouth cavity and attached to the hyoid bone. It consists of an apex or body directed towards the teeth of the lower jaw, a root of muscular attachment, a dorsum divided by the sulcus terminalis into an anterior papillated portion and a posterior tonsillar and glandular portion, and an inferior surface below the apex. The sulcus terminalis is a V-shaped groove with the apex of the V pointing backwards and marking the position of the foramen coecum. Fig. 255.

The dorsum of the tongue anterior to the sulcus is covered with numerous papillae which give the tongue its characteristic rough appearance. Four kinds of papillae are distinguished, vallate, filiform, foliate, and fungiform. The vallate papillae are the largest, and are distinguished also by the deep depression or fossa which surrounds each of them. On
their sides they bear numerous taste-buds. Their number varies from six to twelve, and they occur in a V-shaped row just in front of the sulcus terminalis. Of the various forms of papillae on the tongue the **filiform papillae** are the most numerous. Each filiform papilla is covered with filamentous processes. **Foliate papillae** are three to eight parallel folds on each side of the tongue. Like the vallate papillae, the foliate papillae have taste-buds. The **fungiform papillae** are scattered over the entire dorsum of the tongue, and are distinguished by their reddish color and their globular mushroom shape. They also bear taste-buds. No papillae occur on the posterior and inferior surfaces of the tongue. (Fig. 255)

Most of the mass of the tongue consists of striated muscle. In the connective tissue corium of the tongue, both mucus and serous glands are abundant. The lingual tonsils lie on the posterior dorsum.

**Development of the Tongue.** The apex and root of the tongue, which develop from separate anlagen, remain throughout life divided by the sulcus terminalis. The apex of the tongue is formed by the union of a median **tuberculum impar** with the basal portions of the two halves of the

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**Fig. 255.**—The dorsal surface of the tongue. The sulcus terminalis divides the body or apex of the tongue from the root. The two regions have a different embryonic origin. (Redrawn after Sobotta.)
mandibular arch. The root of the tongue arises from portions of the second, third and fourth visceral arches. The tongue muscles, however, are not formed from those of the visceral arches, but from post-occipital myotomes which send buds downward and forwards into the tongue.

**History of the Tongue.** None of the lower chordates has a tongue, so that the vertebrate tongue seems to be an emergent organ like the notochord. The so-called tongue of cyclostomes is a muscular piston associated with the sucking mouth and cannot be compared with the tongue of higher vertebrates since the hypobranchial muscles which form the mass of tongue muscles in higher vertebrates, though present in cyclostomes, have no connection with the so-called tongue.

**Fig. 256.**—Two stages in the development of tongue and pharyngeal floor of man. The body of the tongue comes from paired and unpaired anlagen of the mandibular arch; the root from second and third visceral arches. That the fourth arch is involved is doubtful. (After Kallius.)

Gnathostome fishes have an immovable tongue, which forms a swelling in the floor of the mouth and is supported by the basihyal, or os entoglossum. Although it lacks muscles, this fish tongue is generally regarded as homologous with the root of the tongue of tetrapods.

The tongue of tetrapods beginning with amphibia consists of an apex and root as in man. While the root is derived from the tongue of fishes, the body is a new formation derived from the mandibular arch united with a median outgrowth from the floor of the mouth.

The tetrapod tongue is further modified by the ingrowth of hypobranchial muscles by which it attains a high degree of mobility. Consequently, in addition to its other functions of moving food in mouth and swallowing, it serves as a means of capturing food. Its gustatory function continues throughout the entire vertebrate series. Some have assumed that the primary function of the tongue muscles was that of squeezing secretions out of the lingual glands. Papillae appear first in amphibia, but become more highly differentiated in mammals.
The Pharynx

The pharynx is that part of the alimentary canal where the respiratory and digestive passages cross one another. The constricted opening through which the mouth cavity communicates with the pharynx is the **isthmus faucium**. It is bordered by the soft palate above, the tongue below, and the **glossopalatine arch** on each side. The glossopalatine arch partially covers the **palatine tonsil**, a mass of adenoid tissue pitted with numerous crypts which tend to be a source of infection. The isthmus is surrounded on all sides by adenoid tissue, the lingual tonsil being included in the ring. The hypertrophy of adenoid tissue, especially that of the soft palate in childhood, interferes with breathing and often requires surgical treatment. (Fig. 257)

The **soft palate** is a muscular partition separating digestive and respiratory portions of the pharynx. From its posterior border hangs the **uvula**. By the action of the palatine muscles, the food pushed by the tongue into the pharynx is forced backwards towards the esophagus and prevented from entering the nasal portion of the pharynx.
Seven cavities open into the pharynx, the mouth, the two nasal passages, the two Eustachian tubes, the larynx, and the esophagus. Three divisions may be distinguished, oral, nasal, and laryngeal. The palatine tonsils lie in the oral portion, the nasal passages and Eustachian tubes open into the nasal portion, while the larynx opens into the laryngeal portion. When food enters the pharynx the entire pharynx is raised by the contraction of the stylo-pharyngeal muscles while the constrictor muscles of the pharynx squeeze the bolus towards the esophagus. The nerve supply of the pharynx comes chiefly from the glossopharyngeal. Like the mouth cavity, most of the pharynx is lined by stratified squamous epithelium. The nasal portion, however, is lined with ciliated columnar epithelium.

Since the pharyngeal region is closely associated with the respiratory organs of vertebrates, the description of the evolution and development of the pharynx is omitted here and will be found in the following chapter.

The Esophagus

The esophagus is that portion of the alimentary canal which extends from the pharynx to the stomach. It is nearly ten inches in length and is the narrowest part of the digestive tract. From the pharynx it passes just beneath the back bone through the mediastinum and diaphragm to the cardiac region of the stomach.

The wall of the esophagus consists of the four layers characteristic of the digestive tract, tunica mucosa, tunica submucosa, tunica muscularis, and tunica adventitia; but the serous layer which covers the stomach and intestine is wanting in the esophagus, since the body cavity lined by the serosa does not extend into the neck. The tunica mucosa includes not only the stratified squamous epithelium which lines the esophagus, but also a connective tissue tunica propria and a muscularis mucosae, a thin layer of longitudinal muscle fibers. The muscular coat of the esophagus consists of striped fibers in the upper third, while those of the lower two-thirds are smooth. In the contracted state of the esophagus, the mucosa is thrown into longitudinal folds like those of the stomach. (Fig. 258)

The submucosa is a layer of loose connective tissue containing glands and many blood and lymph vessels. The tunica muscularis consists of an inner layer of circular muscles and an outer longitudinal layer. The connective tissue between them contains a plexus of sympathetic nerve fibers. By the wave-like peristalsis of the circular muscles food is conveyed from the pharynx to the stomach.

Development of the Esophagus. Beginning with the fourth week, the esophagus develops as an elongation of the fore-gut between pharynx and stomach. Its single-layered columnar epithelium becomes gradually converted into a stratified squamous epithelium like that which lines
the pharynx. During this change, its lumen becomes occluded temporarily, a new lumen arising secondarily through the union of a number of vacuolar spaces. Ciliated epithelial cells occur in the esophagus until relatively late (10th week) stages of development.

**History of the Esophagus.** There is little to distinguish the esophagus of a fish from its stomach, except the relative scarcity of glands, and the fact that its muscle fibers, like those of the pharynx, are striated, while those of the stomach are smooth. In amphibia, the esophagus becomes slightly elongated. Its considerable elongation in reptiles and mammals is correlated with the elongation of the neck. In these groups, it becomes constricted in diameter and most of its muscle fibers become smooth.

**The Stomach**

The stomach, lying between the esophagus and small intestine, is the most expanded part of the alimentary canal. Its shape in man varies greatly, depending upon the quantity of food contained. The human stomach lies almost transversely across the abdominal cavity with a
greater curvature on the left side of the body and a lesser curvature to the right. The opening of the esophagus into the stomach is the cardiac orifice, that into the small intestine is the pylorus.

The anterior more enlarged portion of the stomach is the cardiac portion, the posterior more constricted portion is the pyloric portion. In the cardiac division, may be distinguished a main body and a blind pouch, the fundus. The pyloric portion of the stomach diminishes in size towards the pylorus, which is reduced to a small aperture by a local ring-like thickening of the mucous lining and of the layer of circular muscle. By this mechanism, only finely divided material is allowed to pass in jets into the duodenum, forced by the peristalsis of the stomach.

The wall of the stomach contains the same four layers of tissue as are seen in the esophagus, plus an external serous layer. These beginning with the outermost are the serosa, including the adventitia, the tunica muscularis, tunica submucosa, and the tunica mucosa. The tunica serosa is a connective tissue layer covered with the peritoneal epithelium. In it are many blood vessels, with branches of the vagus nerve and the celiac plexus of sympathetic nerve fibers.

The tunica muscularis contains three layers of muscle, longitudinal, circular, and oblique. By their combined action under the stimulus of the sympathetic nerves, the stomach maintains a peristaltic churning action as long as food is present. The tunica submucosa consists of loose areolar connective tissue richly supplied with blood vessels and with a

![Diagram of the stomach](image)

Fig. 250.—The right half of the human stomach, viewed from within. (Redrawn from Braus, after Elze.)
plexus of sympathetic nerve fibers. The mucosa is divided into a mucous columnar epithelium, a tunica propria, and a muscularis mucosae containing circular and longitudinal muscle fibers. The tunica propria includes considerable adenoid tissue.

The simple mucous epithelium which lines the stomach joins abruptly the stratified epithelium of the esophagus. Viewed with a hand-lens, the inner surface of the stomach appears to be filled with minute pores, which are the apertures of the ducts of the gastric glands. Three kinds of stomach glands are distinguished, cardiac, gastric, and pyloric. The

![Diagram of stomach glands](image)

*Fig. 260.—Cross sections of the wall of the human stomach, showing A, the structure of the gastric (fundus) glands, and B, that of the pyloric glands. While the secretions of gastric glands are chiefly digestive (gastric juice), the pyloric glands secrete mucus chiefly. (Redrawn after Braus.)*

cardiac glands occupy a relatively small area near the cardiac orifice and resemble closely the glands of the esophagus. Each cardiac gland consists of a group of parallel tubules opening into a single duct or pit. The walls of the tubules are formed of cells which secrete zymogen or pepsinogen granules, of parietal cells which secrete the chemical precursor of hydrochloric acid, and of mucus-secreting cells.

Most of the glands of the stomach are gastric each of which, like the cardiac glands, consists of a duct or pit connected with a group of straight or slightly curved tubules. During life, the number of pits is multiplied, while the number of tubules connected with each crypt is correspondingly reduced. The pits are relatively short and are lined with mucous gland cells like those which cover the inner surface of the stomach, while the
tubular glands are relatively elongated and their walls are formed of granular chief cells and of peripheral parietal cells. The chief cells secrete two kinds of zymogen granules—pepsinogen and prochymosin. When mixed with hydrochloric acid secreted by the parietal cells, pepsinogen becomes pepsin, which splits the molecules of albumen into peptones, and the prochymosin becomes chymosin or rennin, which changes casein into paracasein. It is also asserted that the gastric glands secrete lipase, a fat-splitting enzyme.

The pyloric glands are limited to the pyloric portion of the stomach. Their chief secretion is mucus, but the presence of some chief and parietal cells suggests that they may also secrete some gastric juice. They differ from gastric glands also in having relatively long pits and short, branched and twisted tubules. Thus they resemble duodenal glands.

**Development of the Stomach.** During ontogenesis, beginning with the fifth week, the stomach arises as a local enlargement of the fore-gut. Its lining, therefore, together with the glands derived from it, is endodermal. The external peritoneal membrane is mesodermal; the remainder
of the stomach wall, including the submucous and muscularis layers, is mesenchymatous. The mesentery which attaches the stomach to the dorsal body wall becomes the greater omentum of the adult, while the ventral mesentery between the stomach and liver becomes the lesser omentum. The more rapid growth of the dorsal wall produces the greater curvature of the stomach and results in its left-sided displacement. The lesser curvature develops from the ventral side. In this way the original dorsal side shifts to the left side of the body, while the primitive ventral side comes to lie towards the right. Gastric glands begin to appear as local proliferations of the lining epithelium during the seventh week.

**History of the Stomach.** Since stomachs are not unknown among invertebrates, it might be assumed that the stomach of vertebrates is derived directly from that of invertebrates. However, among the protochordates, the hemichordates and some urochordates possess a stomach, while the cephalochordates do not, the pharynx passing immediately into the intestine. The liver of amphioxus develops as a ventral outgrowth a short distance behind the pharynx. Consequently, if we consider amphioxus as an ancestral type, the stomach of vertebrates must have arisen from the short portion of the alimentary canal which in cephalochordates lies between pharynx and liver. The esophagus must likewise have developed from this region. Furthermore, the innervation of the stomach by a cranial nerve, the vagus, is regarded by some as a proof of the derivation of the stomach from the anterior portion of the alimentary canal.

In the cyclostomes, the stomach is a slight enlargement of the alimentary canal. As in the dipnoi, there is no flexure. In most fishes, however, the stomach becomes J-shaped by the bending of the pyloric region, and this curvature persists throughout the vertebrate series. The complications of stomachs such as are found in ruminants are of considerable importance and interest. The stomach of the cow, for example, is divided into four functional divisions, rumen, reticulum, omasum (psalterium), and abomasum. Since, however, such adaptations to a special diet throw no light on the problem of human phylogensis, detailed description is omitted.

**The Intestine in Man**

The intestine is the portion of the alimentary canal from the pylorus to the anus. Its length averages about thirty feet, of which five feet are included in the large intestine and the remainder in the small intestine.

**Small Intestine.** The small intestine extends, gradually diminishing in diameter, from the pylorus to the ileocolic valve of the colon. The small intestine is distinguished not only by its smaller diameter but also
by the presence of numerous villi which cover its inner surface and give it a velvety appearance. Somewhat arbitrarily three regions are distinguished, duodenum, jejunum, and ileum. The duodenum, the anterior portion of the small intestine, averages about nine inches in length, and is characterized by the presence of tubulo-acinous glands located in the submucosa and known as duodenal or Brunner's glands. The duodenal glands secrete an alkaline mucus which neutralizes the acidity of the food which enters the duodenum from the stomach. Zymogenic cells are also found in the duodenal mucosa.

The jejunum, which forms two-fifths of the remainder of the small intestine, contains numerous transverse crescentic folds, the valvulae conniventes, covered with large villi. These serve to retard the passage of food and also to increase the absorptive surface. In the ileum, the crescentic folds disappear, and villi become smaller and more scattered. Lymph nodules are abundant in the tunica propria.

The four layers of tissue characteristic of the alimentary canal are present in the small intestine. The mucous epithelium is of the simple columnar sort, and each cell has a striated border on its inner free surface. Throughout the entire length of the intestine are numerous tubular mucus-secreting glands, perpendicular to the surface of the intestine, the intestinal glands or crypts of Lieberkuehn. Goblet-shaped cells distended with mucus are abundant in the walls of these glands. The secretions of these glands are said to stimulate peristalsis of the intestine as well as lubricate its surface.
Each villus is covered with a mucus epithelium containing numerous goblet-cells, and each villus has a core of connective tissue filled with capillaries and lymph vessels. A single lymphatic or lacteal occupies the center of each villus, and a network of capillaries lies just below the basement membrane of the mucous epithelium. Each villus is therefore a mechanism admirably adapted for absorbing the digested food which bathes it. Besides the peristaltic waves which pass along the intestine squeezing the food backwards towards the large intestine, divisive or churning movements are also carried on, bringing the digested food into contact with the villi.

Absorption takes place in the small intestine, in accordance with the law of osmosis. The dissolved foods pass through the lining membranes, are taken up by the blood capillaries and the lymphatics, enter the general circulation, and are absorbed into the cells of the various tissues.

The Large Intestine. The large intestine or colon differs from the small not only in its great diameter but also in the absence of villi in the
adult. The walls of the large intestine are sacculated, and they bear externally numerous fatty appendages, the *appendices epiploicae*. The longitudinal muscles do not form a continuous layer as in the small intestine, but are arranged in three longitudinal bands, the *teniae*. Transverse crescentic folds, the *plicae semilunares*, are abundant. Between these the wall of the colon bulges out to form *haustra*.

The large intestine is divided into cecum, vermiform appendix, colon, rectum, and anus. The cecum is a blind sac, about two and a half inches in length, lying near the ileocolic valve in the right iliac fossa. The *vermiform appendix* of the cecum is an elongated worm-shaped tube between three and four inches in length, attached to the apex of the cecum. The structure of the appendix is similar to that of the large intestine in having numerous Lieberkuehn's glands and lymph nodules. In the majority of persons, the lumen becomes occluded in later life. The appendix appears to be a rudiment of a more extended cecum functional in the ancestors of man.

The *colon* is divided into four regions, *ascending, transverse, descending* and *sigmoid colon*. The ascending colon passes up the right side of the abdominal cavity as far as the liver, where it bends to the left

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**Fig. 264.**—Vertical section of the mucous membrane of the descending colon of an adult man. The fat has been blackened with osmic acid. (From Bremer's "Text Book of Histology.")
to form the transverse colon. Reaching the lower end of the spleen on the left side, it curves sharply downwards, to become the descending colon. Passing down the left side to a point below the kidney, the descending colon bends towards the median plane of the body and enters the pelvic cavity, where it forms the sigmoid flexure. The rectum is continuous with the sigmoid colon and extends to the anus. In the rectum, a number of transverse folds of the wall tend to prevent fecal

matter from pressing into the anal canal. In the anal region, the layer of circular muscles is thickened to form the sphincter ani, which, unlike that of the lower rectum, is non-striated and not under control of the will. The external sphincter of the anus, however, is striated and voluntary.

Development of the Intestine. Except in the mouth and anal regions, the mucous lining of the alimentary canal and the secretory epithelium of the glands connected with it develop from the endoderm. Primarily, the endoderm of the embryonic area is continuous with that which lines the yolk-sac. In correlation with the development of head fold and tail fold, a fore-gut and hind-gut are formed in connexion with the yolk-sac by
means of anterior and posterior intestinal portals. From the fore-gut develop pharynx, esophagus, stomach, and the anterior part of the small intestine; from the hind-gut the remainder of the intestine. Early in development, an allantois arises as a ventral outpocketing of the hind-

gut, with which it retains connexion by an allantoic stalk. The cloaca is the posterior portion of the hind-gut into which allantois and intestine open, and which is closed to the exterior by the cloacal membrane.

The later development of the intestine involves its elongation and twisting. The opening into the yolk-sac becomes reduced to a slender
vitelline duct, which disappears during the second month. Becoming at first too long for the body cavity, a loop of the intestine pushes down into the umbilical cord. In a six weeks' embryo, the beginning of a cecum is indicated by a swelling posterior to the vitelline duct. Later a horizontal septum grows backward to divide the cloaca into a dorsal rectum and a ventral urogenital sinus. Thus an important evolutionary change is briefly repeated in ontogenesis. The septum forms the perineum of the adult. During the second month, an anal canal is formed by the invagination of an ectodermal proctodeum and the rupture of the cloacal membrane. The elongation and torsion of the intestine continue, and result in the many convolutions of the small intestine and the ascending, transverse, and descending portions of the colon. (Figs. 261, 266)

The four layers of the intestinal wall develop as has been described for the stomach. During the second month, the lumen of the small intestine becomes temporarily occluded. Muscle fibers first appear in the second month, and intestinal glands during the third month.

**History of the Intestine.** The intestine as a region for the digestion and absorption of food is present in the great majority of animals from flatworms to man. An anal aperture makes its first appearance in flatworms, some of which, indeed, have two ani. Can the intestines and anal apertures of invertebrates be homologized with structures having the same name in vertebrates? Is an anus which lies near the mouth, as in cephalodiscus, rhabdopleura, and in molluscoïds, homologous with that which, as in vertebrates, lies near the posterior end of the body? In view of the present uncertainty in regard to the ancestry of vertebrates, it is obviously hazardous to-day to attempt to homologize any vertebrate structure with any organ of invertebrates.

We may take as a test case the question of the origin of the vertebrate anus. Is the vertebrate anus derived directly from that of any invertebrate type? Can we homologize the anus of cyclostomes and some urodeles, which develops directly from the embryonic blastopore, with that of an elasmobranch the anus of which does not develop from the blastopore? Ignoring this difference in origin, Dohrn suggested that the vertebrate anus, like the vertebrate mouth, may have been a new structure formed by the coalescence of a pair of gill slits. The suggestion was made notwithstanding the fact that in no chordate do gill slits extend as far back as the anus. The fact that, assuming amphioxus as a primitive form, the lower the chordate, the larger the number of gill slits, seemed to Dohrn a sufficient foundation for the hypothesis. That the vertebrate anus is secondary has seemed further attested by the fact that there is a postanal gut in vertebrate embryos and that the definitive anus arises relatively late in ontogenesis. Vertebrate morphologists generally regard the anus of vertebrates as homologous throughout the group not-
withstanding differences in ontogenetic development in different groups. The post-anal gut may be interpreted as a special modification correlated with the elongation of the tail, and not as a primitive trait. The assumption of a partial homology of the vertebrate anus with the blastoporic mouth of invertebrates seems to be in harmony with all known facts.

The uncertainty of pre-chordate homologies will explain why most vertebrate morphologists take the intestine of amphioxus as the starting point for intestinal evolution. Yet it is obvious that the intestine of amphioxus is an inheritance from some prechordate ancestor of whatsoever sort. The intestine of amphioxus extends as a straight tube from the region of the liver directly to the left-sided anus. The intestine of cyclostomes is almost as simple. A spiral fold projecting into the cyclostome intestine, however, suggests the beginning of a small intestine, since the small intestine of elasmobranchs contains a spiral valve. Intestinal elongation has its inception in the sigmoid flexure of elasmobranchs. A similar functional result is effected in elasmobranchs and ganoids through the development of a spiral valve in their small intestine. A finger-like rectal gland makes its appearance in elasmobranchs near the anus. The rectal gland is sometimes homologized with the cecum of higher vertebrates, and its position consequently is held to mark the boundary between large and small intestines. A cloaca also makes its first appearance in this group. A further step in advance is seen in the teleosts, which have a convoluted small intestine, intestinal ceca, and a somewhat enlarged colon. Most amphibia except gymnophiona have small and large intestines. All have a cloaca. Some have in their small intestine intestinal glands, valvulae conniventes, and villi.

The intestine of reptiles is relatively short. Their large intestine is short, and they retain a cloaca.

In mammals, the small intestine becomes greatly elongated and differentiated into duodenum, jejunum, and ileum. Valvulae conniventes, villi, and intestinal glands become very numerous. Duodenal glands make their appearance. Colon and rectum are differentiated. In many mammals, especially herbivorous forms, the cecum becomes much elongated and forms an important organ of absorption. In others, as in man, it degenerates in size and serves as an adenoid organ.

**Mesenteries and Omenta**

The peritoneum lining the abdominal cavity is a serous membrane formed from the embryonic hypomere. It not only lines the body wall, but is reflected over the viscera, so that parietal and visceral portions are distinguishable. The complex relations of the peritoneum are due chiefly to the complications of the alimentary canal with which it is connected. These are best understood by tracing their development in
the embryo. In the region of the pharynx the splanchnic layers of mesoderm unite in the median plane to form the tubular heart and the mesocardial membranes in which the embryonic heart is suspended. In the abdominal part of the coelom the splanchnic layers of mesoderm unite above and below the alimentary canal to form dorsal and ventral mesenteries. The dorsal mesentery persists throughout life, but the greater
part of the ventral mesentery disappears in ontogenesis. The anterior portion which connects stomach, liver and ventral body wall only is retained. With the differentiation of the successive regions of the alimentary canal corresponding portions of the dorsal mesentery are recognized as mesogaster, mesentery, mesocolon, and mesorectum. The mesenteries serve not only as means of attachment of the intestine to the body wall, but also as a passage for the blood vessels of the alimentary canal. In the adult the mesenteries become very complex in relations as the result of the elongation of the intestine, formation of omenta, and local adhesions.

As the stomach develops its greater curvature it rotates on its long axis so that its left side becomes ventral and the right side dorsal. As a result the dorsal mesogaster is stretched to the left and a pouch or bursa between the mesogaster and the right side of the stomach is formed. The pancreas and spleen which lie in the dorsal mesogaster are also carried over to the left side of the body where they form adhesions with the dorsal body wall. As the sacculcation of the mesogaster progresses, dorsal and ventral layers become distinguishable. The two-layered sac thus formed grows ventrally and posteriorly between the viscera and the ventral wall of the abdomen as an apron-like membrane, the greater omentum. Much of the original cavity of the omentum is lost through the fusion of dorsal and ventral layers. In the region of the stomach, however, the cavity persists as the bursa omentalis, which opens by the foramen epiploicum into the coelom of the right side. The omentum becomes the seat of deposit of considerable fat and serves as a blanket to keep the viscera warm.
As the intestine elongates the mesentery becomes pleated and several adhesions are formed. With the growth of the colon the mesocolon twists around the superior mesenteric artery as an axis of rotation.

**The Liver**

The functions of the liver are diverse. During early ontogenesis, it forms red blood corpuscles. Later in life, it becomes an agent in the elimination of blood-cells. It transforms both sugar and protein into a polysaccharid, glycogen, which it stores in its cells for later use. It also secretes bile, which aids in the emulsification of fats, in the activation of lipase secreted by the pancreas, and in the stimulation of peristalsis of the intestine.
The liver is a reddish brown organ lying between the stomach and the diaphragm and is the largest gland in the body, weighing between two and three pounds. It is wedge-shaped, and divided into a smaller left lobe and a larger right lobe. The two lobes are separated by the falciform ligament, which is developed from the ventral mesentery and attaches the liver to the diaphragm and the ventral body-wall. Two smaller lobes, the caudate and quadrate, lie between the right and left lobes on their inferior surface. Impressions are made on the inferior surface of the liver by the pressure of the stomach, colon, kidney, suprarenal, and duodenum. The gall bladder lies below the right lobe near the duodenum. The postcaval vein passes through the right lobe.

Secretions pass from each lateral lobe by a single duct, the two uniting to form the hepatic duct. Nearer the intestine, the hepatic duct joins the cystic duct from the gall bladder to form the common bile duct or ductus choledochus, which opens into the duodenum at a point about three or four inches from the pylorus.

The liver is a compound tubular gland, the tubules of which are arranged radially around branches of the hepatic vein. Each cluster of tubules around a central intralobular vein forms a lobule. The numerous lobules of the liver are bound together by interlobular connective tissue containing interlobular veins, which are branches of the portal vein, interlobular ducts carrying bile, and branches of the hepatic artery. Connexions between intralobular and interlobular veins are effected by means of intralobular capillaries or sinusoids, which bathe the liver tubules and supply them with the materials for secreting the bile. The relations may best be understood by the examination of the diagram.
(Fig. 272). While branches of the vagus nerve reach the liver, most of its nerves belong to the sympathetic system.

In most microscopic preparations of the liver the branching tubules appear as solid cords of epithelial cells. In microscopic preparations made by the Golgi method, however, the bile capillaries which carry the secretions of the liver cells are stained black and contrast strongly with the lightly colored cells. In such preparations, the bile capillaries are seen to be minute passages between the gland cells leading to the inter-lobular ducts and the hepatic ducts, which carry the secretions to the gall bladder where they are temporarily stored. (Fig. 270)

The gall bladder is a pear-shaped muscular sac between three and four inches in length, holding about 30 cc. Its inner surface is lined by a mucous epithelium which is thrown into folds. Crescentic folds in the neck of the bladder and in the common bile duct form a sort of spiral valve. When food enters the duodenum from the stomach, the muscles of the gall bladder squeeze the bile into the intestine. This action is sometimes impeded by gall stones formed by constituents of the bile such as cholesterol. Pressure from the intestine caused by constipation may have the same effect, and result in "bilious" disorders.
Development of the Liver. The anlage of the liver appears in a 2.5 mm. human embryo as a ventral outpocketing of the foregut near the anterior intestinal portal, between the two vitelline veins. The liver diverticulum projects into the ventral mesentery and the mesoderm of the septum transversum which separates the pericardial cavity from the abdominal cavity. The outgrowth soon becomes differentiated into an anterior mass of branching tubules surrounded by branches of the vitelline veins, and a posterior hollow sac which later becomes the gall bladder. The multiplication of the tubules correlated with that of the blood capillaries associated with them produces the lobules. Mesenchyme cells

form the interlobular connective tissue which binds the lobules together. Bile capillaries appear within the cell cords, and the blood capillaries acquire endothelial walls. As a result of this, the lumen of each bile capillary is separated from that of each blood capillary by a layer of gland cells and a layer of endothelial cells. (Figs. 261, 267, 272)

The multiplication of tubular cords and of blood spaces results in a rapid enlargement of the liver, which begins to bulge out from the septum transversum and the ventral mesentery and to push into the abdominal cavity between the septum and the stomach. In this way, the liver becomes covered by the peritoneum and acquires its two chief lobes. The ventral mesentery into which it originally grew forms the falciform ligament. (Fig. 267)
History of the Liver. The vertebrate liver has no homolog among invertebrates, though many of these have organs which are called livers. That the so-called liver or digestive gland of the urochordates is the homolog of the vertebrate liver has not been demonstrated. The liver of amphioxus is generally regarded as representing the beginning of that of vertebrates. This is a ventral outpocketing of the intestine immediately behind the pharynx, which grows ventrally and forwards beneath the pharynx, and remains a hollow sac throughout life. Its relations to the blood vessels resemble those of the liver of vertebrates.

The liver becomes bilobed in cyclostomes and elasmobranchs, and a gall bladder is differentiated. In the higher vertebrates and man no important morphological changes occur. The form, however, varies with the shape of the abdominal cavity and the pressure of surrounding organs. In snakes, for example, it becomes reduced again to a single lobe.

The Pancreas

The pancreas is a light pinkish organ about five inches in length, extending across the abdominal cavity from a loop of the duodenum on the right side to the left colic flexure. Three regions are distinguished, a head lying in the intestinal loop, a body, and a tail. In man, the pancreas usually has two functional ducts. One of these, the pancreatic or Wirsung’s duct, generally opens into the common bile duct; the other, the accessory or Santorini’s duct, opens into the duodenum about an inch above the opening of the bile duct.

The pancreas secretes trypsinogen, which is converted into trypsin through the action of enterokinase secreted by the intestinal glands. Trypsin splits proteins into amino-acids. The enzyme amylolysin secreted by the pancreas splits starch into monosaccharids. Another enzyme, lipase or steapsin when activated by enterokinase breaks fats into fatty acids and glycerine. Another enzyme, ereptose or erepsin, splits proteoses and peptones. The digestive activity of the pancreas is stimulated through the endocrinal effect of secretions poured into the blood by the intestinal glands when the acid chyme enters the intestine from the stomach.

Besides this digestive function, the pancreas acting as an endocrine gland regulates the sugar metabolism of the body by means of the endocrine insulin.

The histological structure of the pancreas strikingly resembles that of the parotid gland, both being compound acinous glands divided into lobes and lobules by connective tissue septa which contain interlobular ducts, blood vessels, and nerves. The acini of the pancreas, instead of being hollow, contain central cells. The secretory pancreatic cells of the acini are wedge-shaped in section and contain zymogen granules largely con-
centrated near the lumen of the acinus. Secretions pass from the lumina of the glands into fine intercalated ducts, and from these into secretory ducts like those of the parotid.

Scattered irregularly among the acini of the pancreas are clusters of lightly-staining cells. The area of these clusters in section is considerably greater than that of a single acinus. These are the islands of Langerhans, endocrinal organs which secrete insulin.

**Development of the Pancreas.** Like the liver, the pancreas develops from the endoderm. It is formed by the fusion of two separate outgrowths of the intestine, a ventral bilobed outpocketing from the bile-duct, and a dorsal evagination of the intestine slightly anterior to that of the liver. By the proliferation of the cells of these anlagen, two pancreases are formed, which secondarily unite, but retain usually the two primary connexions with the intestine, the ventral becoming Wirsung's duct and the dorsal Santorini's, the two connecting within the body of the gland. The dorsal pancreas grows much faster than the ventral, and forms the body and tail of the gland and part of the head. The connective tissue of the gland comes from mesenchymatous cells which penetrate between the acini and lobules.

**History of the Pancreas.** The pancreas seems to be an emergent trait of vertebrates, since no comparable structure is found in the invertebrates or even in the lower chordates. In cyclostomes, the pancreatic tissue remains buried in the substance of the liver or in the wall of the small intestine. Since no duct appears in these forms, it is assumed that the pancreas was primarily endocrinal and not digestive. Higher vertebrates, beginning with the elasmobranchs, have both dorsal and ventral pancreases.
CHAPTER 9

THE RESPIRATORY SYSTEM

Introduction. Living protoplasm, that is to say a living organism, burns slowly and continually. When oxidation ceases, life ceases also. Galen in the second century saw the similarity between respiration and burning. But it was many centuries before Lavoisier (1771-1780) proved its chemical nature. Breathing is but a subordinate part of respiration. Respiration is the process of gaseous exchange which occurs in a living body through the oxidation of carbon compounds. This exchange involves an intake of oxygen and an outgo of carbon dioxide. This process requires uncombined oxygen, which forms one fifth of the air. Aquatic organisms obtain their oxygen from air dissolved in water.

Two kinds of respiration may be distinguished, external and internal. In external respiration, animals make use either of a moist skin or of specialized respiratory organs such as lungs and gills in which blood capillaries are brought into intimate relation with moist membranes. Under these conditions, respiration goes on in accordance with the law of diffusion of gases separated by semipermeable membranes. In internal respiration, in accordance with the same law, gaseous exchange takes place within all the tissues of the body which are bathed with blood or lymph. Cells draw on the oxygen in these just as a burning match gets its oxygen from the air. The living cell, however, unlike the match, is the master of the oxidative process and not its servant.

The necessity for two kinds of respiratory organs, one adapted to aquatic and the other to land and aerial life has produced in chordates two distinct but possibly not entirely independent respiratory systems to complicate evolutionary history. These are the pharyngeal gills of the lower and the lungs of the higher classes. Chordates have not inherited their respiratory system from their invertebrate forbears, but have invented new ones of their own.

Fortunately for the land vertebrates, their fish ancestors were already prepared for the transition from water to land life before the event occurred. By a change of function and some modifications of structure and relation, the bilobed air bladder of the crossopterygian fishes was made to serve as a lung. Furthermore the advantage of nasal passages in air breathing was probably already anticipated by the fish ancestors of amphibia. This assumption seems justified by the fact that some fishes, such as the
Dipnoi, have narial passages. But it is not generally believed that the Dipnoi are in the direct line of amphibian ancestry.

The story of gills is one of great multiplication in number in forms like the protochordates which use the pharynx both for obtaining food and for gaseous exchange. In the fishes and amphibia, however, the gills are considerably modified, are reduced in number and finally in higher vertebrates disappear. Startling changes of function occur. Supporting skeletal elements are converted into a sound-conducting apparatus. Gill-slits degenerate into blind pharyngeal pouches, which in turn become endocrinal glands.

The transformation of a ventral air bladder into lungs is sufficiently well attested to be plausible. The chief evolutionary change which lungs undergo is an enormous increase of respiratory surface so that, even within the limits of the mammalian chest, they expose many square yards of moist surface for gaseous exchange.

To meet respiratory needs, two sorts of organs have emerged in animals, branchial organs or gills found in aquatic animals and pulmonary organs characteristic of land forms.

A. The Branchial System. The fact that lungs are wanting in all classes of protochordates as well as in the more primitive groups of vertebrates, proves that the primary respiratory system is that series of paired pharyngeal gills which form the branchial system of chordates. Remnants of this system persist in all higher vertebrates. The transition between gilled and lunged forms occurs in the amphibia most of which, at least at some time in their individual development, have both gills and lungs and which thus bridge the gap between aquatic and terrestrial life.

Gills, like lungs, function as respiratory organs by bringing a network of blood capillaries in close contact with moistened membranes through which gaseous exchange takes place. Their efficiency is increased either by the activity of cilia which cover the surface of the gills or by the contraction of muscles which pump a stream of water through the pharynx, or by waving the gills to and fro, as in Necturus.

It may be doubted whether we have any adequate explanation of the substitution of lungs for gills as respiratory organs. The fact that lungs are much better adapted to the needs of land animals than gills which tend to dry in air does not explain their origin. It is to be noted however that in this change of life animals have played safe. Even before they abandoned the water for a land life, they had acquired an organ, the air bladder, which would serve as a substitute for gills.

Gills are not the pharyngeal openings through which water passes in respiration; these are gill slits or gill clefts. Two sorts may be distinguished, internal gills within the body wall and external gills. Those of most animals are internal; a few fishes and amphibians have external.
The gills of elasmobranchs may be taken as typical. They are modifications of the branchial bars or arches which alternate with the gill-slits and serve to keep them open. Each branchial arch consists of an interbranchial septum of connective tissue which is covered on the surface of the body by skin, and which includes near the pharyngeal lining a cartilaginous arch as a support. Within the septum are branches of the dorsal and ventral aortae which supply the gills with blood. The septa are further supported by skeletal gill-rays extending from skeletal branchial arch laterally towards the skin.

Each interbranchial septum bears on each surface a half-gill or hemibranch, which together constitute a holobranch. Each hemibranch is a mucous membrane folded into minute parallel lamellae or branchial filaments, each of which has parallel secondary folds containing a capillary network. Between the capillaries and separating them are pilaster cells peculiar to the gill filaments. In the ganoids and teleosts the interbranchial septum becomes reduced and tends to disappear, leaving only the portion containing the skeletal arch and branchial blood vessels. In these forms, the gill slits do not open separately to the exterior as in elasmobranchs but are covered by an operculum formed by the backward growth of the septum of the hyoid arch. (Fig. 274)
The mechanism of breathing differs considerably in fishes which, like the elasmobranchs, have modified the first gill slits into spiracles, and those which have not. In all fishes, through the action of antagonistic pharyngeal muscles, the cavity of the pharynx is alternately expanded and contracted, so that water is sucked in through the mouth or the spiracles and forced out through the gill slits. In forms with an operculum, this functions as a valve, and prevents the entrance of water through the gill slits. Gaseous exchange takes place through the thin mucous epithelium which covers the gill lamellae. The gills of fishes function also as excretory organs, excreting nitrogenous waste as do the kidneys.

**Fig. 275.**—Diagram of the relations of external and internal gills in the anuran tadpole. ab, eb, afferent and efferent branchial arteries; h, heart; o, ear cavity; ph, pharynx; ra, radix aortae. (From Kingsley's "Comparative Anatomy of Vertebrates," after Maurer.)

**Fig. 276.**—Frontal (horizontal) section of a 16-day petromyzon embryo, showing seven pairs of gill-pouches (1–7) formed as lateral diverticula of the pharynx. Slight invaginations of the ectoderm to meet the gill-pouches are seen. Between the successive gill-pouches the mesoderm is divided into a series of branchiomeric segments, from which the muscles and skeletal arches of the gills develop.

**External Gills.** External gills are of two sorts, external gill filaments such as occur in elasmobranch embryos as prolongations of the posterior gill lamellae, and external gills which characterize some adult urodeles and the larvae of some fishes and amphibians. The evidence on the whole supports the opinion that they are secondary derivatives of the
internal gills developed in adaptation to special conditions. They have no genetic relation to any human structure.

**Development of Gills.** Gill slits develop from a series of paired endodermic diverticula of the pharynx which meet corresponding invaginations of the ectoderm. By the disappearance of the double membrane thus formed the pouches are converted into gill slits. The branchial arches develop from the regions between the gill slits. Each arch has an endodermal pharyngeal lining and an external ectodermal covering. The core of each arch is mesodermal. The difficulty of distinguishing the boundary between ectoderm and endoderm of each branchial arch has resulted in a difference of opinion in regard to the origin of the gill lamellae. Some embryologists assert that these are ectodermal, while others claim that they are endodermal. Sewertzoff (1916) distinguishes "endobranchiate" cyclostomes from "ectobranchiate" gnathostomes. The issue does not appear to be important since Cook (1921) has found that the pharyngeal endoderm of fishes produces such characteristic ectodermal structures as taste-buds and placoid scales. Consequently we are forced to conclude that the contrast in the potencies of the two germ layers is not as great as has sometimes been assumed.

The levator and depressor muscles of the gills are developed from the hypomeric mesoderm enclosed in each branchial arch. The connective tissue, the cartilage or bone, and the blood vessels of each arch are derived from the mesenchyma. The origin of this mesenchyma has been a subject of controversy, but the evidence favors the opinion that the mesenchyma of the branchial arches is proliferated from both mesoderm and ectoderm, not exclusively from the mesoderm as was once supposed.
History of the Gills. Pharyngeal gills are peculiar to chordates and are one of the most constant characteristics of the group. This should not be understood to imply that invertebrates are without structures from which gills might have evolved. The origin of gills from endodermic diverticula suggests the possibility that their beginnings may be seen in the intestinal diverticula of flatworms. Were these diverticula to meet the skin and become perforate, apertures similar to gill slits would be formed.

Gill slits first appear in the hemichordates. Rhabdopleura has none, but cephalodiscus has a single pair. In most hemichordates the number is considerable and increases throughout life. Early in their development, their number is doubled by the growth of "tongue-bars" which extend from the dorsal side of the gill aperture to the ventral side. Later the
gill bars thus formed become interconnected by cross rods or synapticulae such as occur also in urochordates and cephalochordates.

In urochordates, the number of gill slits varies from a single pair in Appendicularia to the many characteristic of most genera. The gill slits of this group open into an atrial cavity developed by an ectodermal ingrowth along the dorsal side of the body.

Amphioxus, the typical genus of cephalochordates, has as many as one hundred and eighty paired openings or stigmata. As in hemichordates, the number is doubled by the growth of secondary gill slits. Before metamorphosis the number of primary gill slits in the larva of amphioxus is nineteen pairs. The large number of gill slits in the protochordates is apparently an adaptation, since these organisms use their gills not only for respiration but also as a mechanism for obtaining food by ciliary action. The multiplication of branchial bars means a corresponding increase in the number and efficiency of the cilia which cover
their surface. The fact that the peribranchial cavity of amphioxus develops from the ventral side of the body, makes it seem impossible to compare this with the atrium of the urochordates which arises on the dorsal side. See p. 661, Fig. 535.

The history of gills in vertebrates is one of continuous reduction in number and modification in function. The transformation of their skeletal supports has been described in the history of the skeletal system. Even in amphioxus, some of the gill pouches of the embryo are modified or lost. The first pair become the endostyle while the second pair form the larval club-shaped gland. The third left slit never has a corresponding right slit and disappears early in ontogenesis. The first permanent gill slit of amphioxus is therefore the fourth of the ontogenetic series.

Fig. 280.—Four stages in the development of the endostyle of amphioxus. The evidence indicates that the endostyle is developed from a pair of modified gill-pouches. The evidence is equally strong that the endostyle is the homolog of the thyroid gland of vertebrates. The conclusion is drawn that the thyroid has evolved from a pair of gill-pouches. There is no evidence, however, that endostyle and thyroid are functionally similar. (Redrawn after van Wijhe.)

There are cogent reasons for homologizing this slit with the spiracle of elasmobranchs, but there is little agreement among morphologists in regard to the exact homology of serial organs in chordates.

The popular belief among morphologists that the vertebrate mouth has been formed by the coalescence of a pair of gill slits is supported by the mode of development of the mouth in amphioxus. The endoderm takes the initiative in the development of the mouth of amphioxus, as would be the case if it were a gill slit. In this respect, the mouth of amphioxus differs from that of vertebrates, in which the ectoderm initiates development. Later the mouth of amphioxus assumes a left-sided position and becomes enormously enlarged. Partly from the fact of its left-sided position, van Wijhe (1893) homologized the mouth of amphioxus not with that of vertebrates, but with the left spiracle of elasmobranchs. Other morphologists have not accepted this homology, but are not wholly agreed that the mouth of amphioxus is homologous with that of vertebrates. At metamorphosis, the mouth of amphioxus assumes a position
in the center of the velum and becomes greatly reduced in size. The asymmetrical position and the hypertrophy appear to be larval adaptations.

The question whether or not gills are metameric structures has been an open one. The metamerism of chordates is manifested primarily in the mesodermal somites. Since there are none of these in hemichordates and urochordates, it is impossible to demonstrate in these forms a correspondence between mesomerism and branchiomerism, and thus to establish the metamerism of the latter. The case is different, however, in amphioxus, where the mesodermal segmentation is one of the most striking features. In the adult animal, there is no correspondence between gills and myotomes. But in the larva, the gill slits not only take an intermetameric position in relation to the myotomes, but also are innervated by metameric nerves. A similar metameric correspondence is strikingly shown in the embryos of cyclostomes. The conclusion drawn is that mesomerism and branchiomerism correspond.

The number of gills varies greatly in different cyclostomes. In the genus Bdellostoma, the number ranges from fourteen to six pairs. The number in myxine and petromyzon is respectively six and seven, or one more counting the spiracular pouch which does not become perforate. By the backward growth of the hyoid septum, the external apertures in myxine becomes reduced to a single pair, a condition not unlike that in bony fishes. The posterior displacement of the gills in bdellostoma is an adaptation to the parasitic habit of this animal, which burrows with its head into the flesh of its host.

Among elasmobranchs, Heptanchus has seven pairs of gill slits in addition to the spiracles, which are evidently modified gill slits since they bear rudimentary hemibranches. Hexanchus and Photorema have six pairs of gill slits. Most elasmobranchs have five pairs of gill slits plus spiracles. In bony fishes the number is reduced to four pairs and the spiracle is absent.

Gill slits disappear in adult tailless amphibia, but are present in some aquatic urodèles. The number however is reduced. Some adult urodèles have three pairs of gill slits, some two, and some only one. In the newts they disappear entirely. Cutaneous respiration is common.

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**Fig. 281.** Diagram of relations of esophagus and respiratory tracts in (A) Myxine and *Amphioxus*, and (B) *Petromyzon*. 1, branchial duct ("bronchus"); 2, esophagus; 3, thyroid gland. (From Kingdon's "Comparative Anatomy of Vertebrates,")

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in the group, and some respire by means of a highly vascular pharynx. Nevertheless, even in those adult forms which are devoid of functional gills, gill pouches occur in the embryo, and the embryos of gymnophiona may have as many as six such pouches, suggesting a corresponding number of functional gills in their ancestors. Most amphibian larvae have functional gills.

Functional gills are lacking in amniotes, but rudiments of gills are represented by transient embryonic gill pouches and their intermediate visceral arches. In the embryos of reptiles, some of the gill slits usually become perforate and later close. The perforation of gill slits in mammals is abnormal. Pharyngeal pouches are, however, always formed in the human embryo, and when these become perforate fistulae in the throat, they may persist and require surgical treatment. The presence of five pharyngeal pouches and six visceral arches alternating with them receives its only reasonable interpretation in the evolution theory.

As has already been explained, the disappearance of the visceral arches in man and mammals is incomplete. The skeletal elements are converted into ear bones, attachment for the tongue, and support of the larynx. Three of the aortic arches also persist, as will be shown in the next chapter. Moreover, in addition to these rudiments there are certain derivatives of the gill pouches which require special discussion.

Pharyngeal Derivatives. From the epithelial lining of the embryonic pharyngeal pouches arise some of the important endocrinial glands, thyroid, parathyroid, thymus, and the ultimobranchial bodies. In addition to these which occur in man, some vertebrates have also epithelial bodies and suprapерicardial bodies. From the second pair of pharyngeal pouches come the palatine tonsils. The history and development of these pharyngeal derivatives will be taken up in the chapter on endocrinial organs.

B. The Pulmonary System. The respiratory system of man and mammals includes lungs, larynx, trachea, bronchial tubes, narial passages, and diaphragm.

Lungs. Lungs are the essential respiratory organs of land vertebrates. Man, like virtually all land animals except snakes, has two, the left having two lobes and the right three. The absence of a middle lobe on the left side appears to be an adaptation to the presence of a left-sided aorta. The lungs lie within the rib basket, and when expanded obliterate the potential pleural cavities. They are separated from one another by the mediastinum or interpleural space, which contains the heart, esophagus, and the great blood vessels which leave the heart. In childhood, the color of the lungs is pinkish, but becomes slaty grey in the adult as the result of the accumulation of soot. Each lung is conical with an apex and base. However, two surfaces, costal and mediastinal, and three
borders are distinguished. The heart and pericardial cavity produce a deep concavity on the mediastinal surface of each lung, while the costal surface is convex in conformity with the inner surface of the chest. The base of each lung is concave to correspond with the diaphragm with which it is in contact.

The structure of the lungs is admirably adapted to the need of exposing to the air a large amount of surface, estimated to equal that of a balloon ten feet in diameter, and a section of the lungs shows that the volume of air space greatly exceeds that of solid tissue. The required moisture is supplied by mucous glands.

The trachea or wind-pipe subdivides into bronchi, both structures having cartilaginous supports. The bronchi divide into bronchioli, the bronchioli into alveolar ducts, the alveolar ducts into atria, alveolar sacs, and alveoli, which form the ultimate subdivisions. Exchange of gases occurs chiefly in the alveoli, although the thin respiratory epithelium is found also in the atria and alveolar sacs and may extend even into the
bronchioli, which in general are lined with a simple cuboidal non-respiratory epithelium. There is an elaborate network of capillaries in the walls of the alveoli, so that only two extremely thin membranes separate the blood in the capillaries from the air in the alveoli. J. S. Haldane has shown that during this exchange a constant quantity of carbon dioxide is maintained in the alveoli and that the rhythm of breathing is dependent upon this factor.

Lungs are very elastic, and their elasticity is increased by the smooth muscle fibers which extend into the connective tissue of the lungs as far as the alveolar sacs but not into the walls of the alveoli.
The respiratory blood vessels of the lung are branches of the pulmonary arteries and veins. The bronchial artery and vein supply the connective tissues of the lungs. The innervation of the lung is through branches of the vagus and of the sympathetic.

On the outside of the lung the **pleura**, corresponding to the peritoneal lining of the abdominal cavity, consists of a subserous connective tissue which extends into the lobules of the lung, and of an external epithelial **serosa**. The pulmonary pleura is reflected back on the inside of the chest as the **parietal pleura**.

**Larynx.** The **larynx** or voice-box lies between the root of the tongue and the **trachea**, and opens into the pharynx by the **glottis**. Nine cartilages support it, the unpaired epiglottic, thyroid, and cricoid cartilages, and the paired arytenoids, corniculate, and cuneiform cartilages. Small paired triticeous cartilages also sometimes are found. Numerous muscles are attached, some extrinsic and some intrinsic. The extrinsic muscles are chiefly to lift the larynx in swallowing. Among the intrinsic

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**Fig. 284.**—Cross section of a bronchus 2 mm. in diameter, from a child. (From Bremer's "Text-book of Histology.")
muscles are the thyro-arytenoid or vocalis and the cricothyroid, which affect the pitch of the voice. At puberty in the male, the larynx becomes enlarged and the vocal cords within it elongated so that the voice is deepened. The epiglottis and vocal cords are covered with the same kind of squamous stratified epithelium as that which lines the pharynx, but the rest of the larynx is lined with ciliated columnar epithelium similar to that of the trachea. The action of the cilia is such as to carry the secretions of the mucous glands of the lungs together with particles of dust out into the pharynx. Mucous glands are numerous. The nerve supply is from the vagus and the sympathetic.

**Trachea and Bronchi.** The trachea or windpipe is a membranous tube, four to five inches long, supported by fibrous connective tissue and incomplete U-shaped rings of cartilage. It carries air to and from the lungs. The cartilages vary in number from sixteen to twenty and are incomplete on the side next to the esophagus. The trachea divides to form the right and left bronchi. The lining of the trachea is a mucous ciliated stratified columnar epithelium. Below this is a submucous connective tissue containing many mucous glands derived from the

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**Fig. 285.—**A median longitudinal section of the human head showing the relations between digestive and respiratory passages in the pharyngeal region. (Redrawn after Braus.)
mucous layer. Between the cartilage and the mucosa is a layer of circular muscle fibers.

**Nasal Passages.** Air is taken in and expired through the nasal passages. The external orifices are the external nares and the openings into the pharynx are the choanae. The paired nasal passages are separated from one another by the nasal septum and the median plates of the maxillary and vomer bones, and from the cavity of the mouth by maxillary and palatine bones. They are lined with a ciliated columnar epithelium containing many mucus-secreting goblet cells.

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**Diaphragm.** Air is drawn into the lungs under atmospheric pressure as the result of the contraction of the muscles of the diaphragm and ribs. Their contraction raises the rib-basket and flattens the dome-shaped diaphragm. As a result, the size of the pleuropertoneal cavity is increased. To fill the enlarged space thus formed air enters the lungs and inflates them to the size of the chest cavity. The diaphragm is a muscular partition which divides the cavity of the chest from that of the abdomen and which occurs only in man and other mammals. Lacking a diaphragm the amphibia must swallow their air. The phrenic nerve, a branch of the cervical plexus of nerves, innervates the diaphragm.

**Development of the Lungs.** During the fourth week of development a laryngo-tracheal groove is formed in the floor of the pharynx immediately behind the fourth gill-pouch. Externally this groove appears as a ridge which is bordered on either side by a groove or furrow. By the approximation of these paired lateral grooves and their union in the median plane, the lung anlage is separated from the pharynx, except anteriorly where connexion with the pharynx is retained. The posterior blind end of the

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**Fig. 286.—Stages in the development of the trachea, bronchi and lungs in the pig.** The pulmonary arteries are shown in black; the veins are cross hatched. *E.p.* bud of eparterial bronchus. (From Patten’s “Embryology of the Pig,” after Flint.)
diverticulum swells to form the lung anlage while the less expanded anterior portion becomes the larynx and trachea. The lung anlage later divides into two lateral buds which, by successive subdivision, gradually assume the adult structure. (Fig. 286)

The cartilages which support the larynx correspond exactly with those which in aquatic vertebrates support the fourth and fifth branchial arches. The muscles of these arches form the laryngeal muscles. Vocal cords appear during the eleventh week.

Beginning with the fifth week, the paired lung-buds branch in the manner of a compound tubular gland. In this way, the entire lining of

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**Fig. 287.**—A–D Stages in the development of lungs in vertebrates. A is a horizontal section of a salamander embryo showing the series of paired pouches which form the gill slits after Goette. The last pair of pharyngeal pouches are the anlagen of the lungs. Such evidence suggests that lungs may have arisen in phylogenesis from a pair of gill pouches which failed to reach the surface. B and C are earlier and later stages in the development of the lungs in an amphibian. D is a cross section of the lung anlage in a reptile, after Wiedersheim. (Redrawn from Ihle.)

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the lungs is derived from the pharyngeal endoderm. The connective tissue develops from the surrounding mesenchyma. The splanchnic mesoderm forms the serosa, which covers the lungs and lines the chest cavity. As the two lungs enlarge, they push laterally into the body cavity and by their ventral extension nearly surround the heart, from which they remain separated by the pericardium. With the development of the diaphragm, the pleural cavity containing the lungs becomes separated from the more posterior peritoneal cavity. According to Broman the diaphragm arises from four sources, the septum transversum anterior to the liver, the pleuroperitoneal membranes, the body-wall, and the dorsal mesentery.

The nasal passages of lower vertebrates, such as the dipnoi and amphibia, develop from nasobuccal grooves similar to those seen in some adult elasmobranchs. In the embryo an ectodermal groove extends from
each olfactory pit to the corner of the mouth. Later the groove deepens, its edges meet and fuse together and convert the groove into a tubular passage which connects the pit with the mouth cavity (Fig. 471).

The development of the narial passage in the human embryo is slightly different. In the month-old embryo a similar nasobuccal groove makes its appearance. The narial passage, however, is not formed by the closure of this groove, but by the backward extension of the epithelium of the olfactory pit, which thus acquires a secondary connexion with the mouth (Fig. 473).

That this method of formation of the narial passage is a modification of the method found in lower vertebrates is indicated by the not infrequent occurrence of hare-lip in infants. Hare-lip is best explained as a reversion to the more primitive mode of development of the narial passage from a groove. The hare-lip arises when the groove fails to close over. In some infants the defect in growth is so extensive as to cause a perforate or “cleft” palate and to necessitate surgical operation.

History of the Pulmonary System. Invertebrates have no organs comparable with the human pulmonary system, the so-called lungs of pulmonate molluscs being modifications of the mantle and not outgrowths from the alimentary canal. Opinions are divided as to the origin of the lungs. According to some, a pair of gill pouches which failed to reach the skin have been converted into lungs. Others suppose that lungs have evolved from the air bladder of fishes. Some seek to reconcile these two divergent opinions by asserting that the air bladder is itself derived from a pair of modified gill pouches.

Goette (1875) was the first to suggest that lungs are modified gill pouches, on the ground that in some amphibian embryos the lungs develop from a pair of posterior endodermal pouches in series with the gill pouches. A number of observers have confirmed this observation and reached the same conclusion. In support of Goette’s hypothesis is the fact that the pulmonary arteries develop from the sixth pair of aortic arches. Further-
more, it is obvious that if a gill pouch were to fail to reach the skin and were to grow backwards into the body cavity it would assume the relations of a lung.

On the other hand, supporters of the air bladder hypothesis emphasize the fact that the air bladder of such a fish as the Nile bichir (Polypterus) develops like the lung as a median ventral outgrowth of the pharynx.

Its bilobed adult form is secondary, as is also its vascular connexion with the sixth aortic arch. Basing the homology of air bladder and lung upon their similar development as median ventral outgrowths from the pharynx, the supporters of this view are skeptical of the attempt to compare a median organ with paired structures such as gill pouches.

To meet this difficulty, it may be pointed out that the transformation of a paired organ into a median one is not unknown. For example the thyroid gland in all vertebrates develops as a median ventral outpocketing of the pharynx, yet all morphologists agree in homologizing the thyroid with the endostyle of amphioxus. The endostyle, however, in amphioxus develops from a pair of gill pouches. Likewise it is sometimes assumed that the median and unpaired pineal organ of the brain arose by the union of paired diverticula of the brain.
While some uncertainty remains in regard to the origin of the lungs, the facts on the whole seem to accord with the gill pouch hypothesis. If it is assumed that the crossopterygian air bladder is a pair of modified gill pouches, the rest of the problem of the history of the lungs is easily solved, since there are among living vertebrates all intergradations in complexity between the simple air bladder of polypterus and the mammalian lung. The evolutionary changes which occur involve chiefly a great increase in the lung surface effected through the branching and subdivision of the primary lobes. The facts of embryology and comparative anatomy are in complete agreement. An evolutionary series based upon evidence from comparative anatomy is shown in Fig. 289.
CHAPTER 10

THE VASCULAR SYSTEM

The Vascular System. While the blood of many invertebrates fills intercellular spaces without specialized walls, the circulation in vertebrates is a closed system, the essential components of which are a circulating fluid, a heart with receiving and propulsive chambers and valves so arranged as to permit the blood to flow in one direction only, arteries to carry blood away from the heart, veins to bring blood back again, and microscopic capillaries to connect arteries and veins. The walls of the capillaries are so thin that they permit passage of plasma from the blood into the tissues. This fluid in the form of lymph is restored again to the veins by way of special vessels, the lymphatics, which like veins, permit flow in only one direction.

It was William Harvey (1616) who first demonstrated the circulation of the blood. Before Harvey's day it had been assumed that the blood ebbs and flows in the arteries and veins like water in tidal streams. Harvey was able to demonstrate that the valves in the heart and blood vessels permit a one-way movement only; that a cut artery spurts blood from the cut end nearer the heart, while a cut vein bleeds most from the end farther from the heart; that pressure of a finger on a vein results in distension on the side farther from the heart; and that in a dead body liquid injected into an artery will return to the heart by a vein, while the liquid injected into a vein will not return to the heart by an artery. Later, following the invention of the microscope, Malpighi (1661) discovered the interconnexion of arteries and veins by way of the capillaries.

Blood. The human body contains about one gallon of blood, one twentieth of the weight of the body. Blood has two constituents, a fluid
plasma and blood corpuscles which are cells. Blood is, therefore, regarded as a tissue composed of cells (corpuscles) and of a liquid intercellular material. The plasma consists of a liquid serum and a coagulable material, fibrinogen. By stirring blood it is possible to separate these two elements. Blood corpuscles are of two sorts, red erythrocytes and white leucocytes. To every cubic millimeter of blood there are from four and one-half to five million erythrocytes, and from five to seven thousand white corpuscles. Variations from this proportion are of diagnostic value in disease.

Functions of the Blood. The blood vessels and blood constitute an organic transportation system. Blood is a common carrier of foods and wastes to and from all parts of the body. Among its numerous functions are equalizing the temperature of the body, regulating the water content of the various tissues, distributing endocrines and thus assisting in the integration of the body. The red corpuscles carry oxygen, the white act as scavengers of the blood. The color of red corpuscles is due to hemoglobin, a nitrogenous substance with an affinity for oxygen. Most, if not all, white corpuscles are amoeboid, and like amoebae surround and engulf bacteria. Foods and wastes are carried in the plasma and not by the corpuscles. The plasma also contains mineral salts of the same sorts and in nearly the same proportions as those of somewhat dilute sea water. Among other constituents of the blood are enzymes, antibodies, antitoxins, antithrombin, etc. Antibodies are substances produced in the tissues in response to the poisons caused by bacteria. They are regulatory in their action and help to preserve the normal chemical balance of the blood. Antithrombin is a substance, normally present in blood, which prevents the clotting of the blood by preventing the action of thrombin on fibrinogen.

Evolution of the Blood Vessels. Two types of circulation may be distinguished in animals, intracellular and intercellular. The former occurs in all cells alike as foods enter the cell and are distributed to the various cell-organs and as the cell wastes are excreted. Intracellular circulation is similar in protozoa and metazoa. A true vascular system, however, is multicellular and therefore limited to the metazoa.
The simpler metazoa, such as the sponges and coelenterates, are devoid of a vascular system. In an animal such as hydra in which the body-wall forms the alimentary canal, a vascular system is unnecessary. With only two layers of cells in the body-wall, the diffusion of food stuffs from the digestive cavity into the cells may take place by osmosis. The excretion of wastes is likewise direct and requires no special system of transportation.

A circulatory system is necessary and is present in all animals in which the body-wall is separated from the lining of the alimentary canal either by a mass of mesoglea or by a body-cavity. In other words, the emergence of a circulatory system in animals is conditioned by increase in size of body and of mass of tissue, as well as by the separation of the body-wall from the alimentary canal by a coelom. Stages in the evolution of blood vessels are represented in living invertebrates.

Metazoa have two kinds of vascular systems, an open lacunar system such as occurs in most invertebrates and a closed system like that of vertebrates. The facts support the assumption that the lacunar system is the more primitive. A lacunar system is well represented in flatworms, in which a fluid plasma fills the spaces between loose mesenchymatous cells. No heart is present and no true circulation occurs. The contraction of the muscles of the body wall and the movements of the worm bring about more or less irregular currents in the plasma. In many flatworms, numerous diverticula of the intestine bring digested food near most parts of the body so that a vascular system is unnecessary. The beginnings of blood vessels, however, make their appearance in nemerteans which are sometimes classified with flatworms. Nemertean worms have in addition to lacunar spaces in the mesenchyma three longitudinal blood vessels, two lateral and one dorsal. Interconnexions between these vessels occur at the anterior end of the worm. The fluid contained in these vessels is a
sort of lymph, without blood corpuscles and without hemoglobin. It may be assumed that the walls of these vessels are formed directly from the surrounding mesenchyma and that the vessels therefore are evolved from lacunar spaces. In the nematodes, a pseudocoelem provides an adequate mechanism of circulation in animals which have no thick masses of tissue to nourish.

Most of the invertebrate phyla above the nematodes have composite circulatory systems, partly lacunar and partly closed. Before Malpighi (1661) discovered the capillary circulation in vertebrates and thereby demonstrated in them a closed circulation, it was assumed that the vertebrate circulatory system was likewise partly lacunar and partly closed. That the lacunar system of invertebrates is comparable with the lymphatic system of vertebrates has been more recently suggested. Such a suggestion however is obviously based upon erroneous assumptions. The facts accord better with the assumption that both blood-vascular and lymphatic systems have had a common origin from the primitive lacunar systems of invertebrates. While in the invertebrates the circulatory system has remained partly open, in the vertebrates on the other hand the circulatory system, both blood-vascular and lymphatic, has become wholly closed.

The vascular system of annelids is fundamentally like that of chordates. In both groups occur two main longitudinal vascular trunks, one above and one below the alimentary canal, connected with one another by aortic arches around the pharynx. In the earthworm, there are five pairs of aortic arches. It is true that the direction of flow of blood in annelids is the reverse of that in vertebrates. But this difference in blood flow is nullified if the dorsal and ventral sides of the worm are reversed. Reversal of the annelid is also necessary in order to bring the central nervous systems of annelids and chordates into a similar position, dorsal to the alimentary canal. It is therefore not surprising that proponents of the annelid hypothesis of vertebrate ancestry have stressed the similarity of the vascular systems of the two groups as a strong support of their views. The absence of a heart in annelids and its presence in vertebrates is not a serious objection to this view, since the dorsal blood vessel of annelids is contractile throughout its length and it may be reasonably assumed that this contractile function is concentrated and localized in the vertebrate heart.

Such a diagram of the hypothetical primitive vertebrate blood-vascular system as is shown in Fig. 291 is based, however, not on the assumption of an annelid ancestry of chordates but upon evidence from comparative anatomy and embryology. While the circulation of blood in the ancestral chordate was probably due, as in annelids, to the contractility of the walls of the blood vessels, a contractile heart such as is found in all vertebrates
is added to the diagram. Blood is pumped by the heart towards the head through a median ventral truncus arteriosus from which pass the series of aortic arches, which connect around the pharynx with the median dorsal aorta. In fishes and in amphioxus, the aortic arches are divided by a network of capillaries in the gills into ventral afferent and dorsal efferent arteries. The carotid arteries carry blood forward to the head while the dorsal aorta carries it posteriorly to the trunk and tail, giving off metameric intersegmental arteries to the body-wall and median unpaired splanchnic vessels to the alimentary canal. In the tail, venous blood is carried towards the heart by the caudal vein. In the primitive circulation, the caudal vein is assumed to be connected by intersegmental vessels with the caudal artery. When the caudal vein reaches the region of the anus it encircles the alimentary canal. From this point blood may return to the heart either by a subintestinal vein (which also collects blood from the intestine) or by an abdominal vein which extends along the median ventral body-wall. These two vessels parallel one another and both connect anteriorly with the heart. Venous blood from the body-wall is returned to the heart by the cardinal veins, anterior and posterior.

**Amphioxus.** In most details the vascular system of amphioxus resembles the hypothetical ancestral system just described. But amphioxus is heartless, and the circulation of its blood is dependent upon the contractility of the walls of its main blood trunks. Blood is carried forward beneath the pharynx by a contractile ventral blood vessel, the truncus arteriosus, and distributed to the numerous gills by a series of paired afferent vessels, the aortic arches. Contractile enlargements or bulbils of these vessels aid in the propulsion of blood to the gills. Nephridia similar to those of annelids are associated with the gills and presumably assist in the elimination of nitrogenous wastes. From the efferent vessels the blood passes to the paired dorsal aortae, the anterior extensions of which correspond to the internal carotid arteries of vertebrates. Posterior to the gills the paired aortae unite to form the median dorsal aorta of the trunk region. From the dorsal aorta paired intersegmental vessels are given off to the body-wall and a series of median unpaired vessels to the alimentary canal. In the tail region the caudal artery has intersegmental connexions with the caudal vein. Beginning at the anal region blood from the caudal vein may be returned to the heart either through the right postcardinal vein or by the subintestinal vein. Like the hepatic portal vein of vertebrates, the subintestinal vein of amphioxus breaks up in capillaries within the liver. Anteriorly the hepatic capillaries unite to form the hepatic vein which carries blood to the sinus venosus and the truncus arteriosus. Amphioxus has no renal portal system such as occurs in fishes and amphibians. Venous blood is brought from the anterior part of the body by the precardinal veins and from the
posterior body-wall by the postcardinal veins. The two unite with the sinus venosus by means of paired common cardinal veins or ductus

Cuvieri. The vascular system of amphioxus thus resembles that of cyclostomes and elasmobranchs. The blood however lacks hemoglobin and is colorless. Blood cells are scarce. (Fig. 294, A)
Cyclostomes. The vascular system of cyclostomes shows little advance above that of amphioxus. An S-shaped heart with three chambers, sinus venosus, atrium, and ventricle, is a novelty in this group. A conus with valves makes its appearance at the root of the truncus arteriosus. The common cardinals drain into a thin-walled sinus venosus. In the adult the left common cardinal degenerates and both precardinals connect with the right common cardinal or precava as in some mammals. The two posterior cardinals unite into a common cardinal which passes to the left side of the body and unites with the sinus venosus. In the heart atrio-ventricular valves prevent a reverse flow of blood. With the development of a septum transversum the coelom becomes divided into

![Diagram of the primitive (fish) heart](image)

Fig. 295.—A diagram of the primitive (fish) heart, as seen in a median longitudinal section. Anterior is to the right. The course of blood in the heart—indicated by arrows—takes the form of a letter S. (Redrawn after Keith.)

an anterior pericardial cavity and a posterior abdominal cavity. Red blood corpuscles make their appearance in this phylum and the blood is consequently red. A renal portal system is wanting in cyclostomes, the caudal vein draining directly into the postcardinal veins.

Elasmobranchs. The blood vascular system of elasmobranchs differs little from that of cyclostomes and with slight changes may easily be derived from the latter. Associated with the appearance of paired fins the subclavian and iliac arteries and veins are present. The arteries are connected with the dorsal aorta. The subclavian vein is a branch of the precardinal, while the iliac vein drains into the lateral abdominal vein. The latter is believed to have been developed from the median ventral abdominal vein of the primitive chordates. Internal jugular veins parallel the precardinal veins are a novelty in this group. The caudal
vein of Elasmobranchs divides anteriorly into the paired renal portal veins which break up in capillaries within the mesonephroi. The heart resembles that of cyclostomes. The branches of the dorsal aorta are subclavians, intersegmentals, celiac, anterior and posterior mesenterics, spermatics and ovarians, and renals. (Fig. 294, B)

**Dipnoi.** In the dipnoi with the emergence of lungs some advances towards the mammalian circulation are seen. In the heart of lung fishes both atrium and sinus venosus become partly divided by incomplete longitudinal septa. Impure blood from the veins enters the right atrium while aerated blood from the lungs flows into the left atrium. Atrio-ventricular valves are lacking but the conus contains a series of valves.

![Diagram of vertebrate circulation based on a urodele](image)

**Fig. 296.**—Diagram of vertebrate circulation based on a urodele. Arteries cross-lined; veins black except the pulmonary vein, white. *av*, abdominal vein; *c*, celiac artery; *ca, cv*, caudal artery and vein; *d*, dorsal aorta; *ec*, external carotid; *g*, gonad; *h*, hepatic vein; *ha*, hepatic artery; *hy*, hypogastric artery; *ic*, internal carotid; *il*, iliac artery and vein; *j*, jugular; *lv*, liver; *m, mv*, mesenteric artery and vein; *pa*, pulmonary artery; *pec, postcardinal; pcv, postcava; *pv*, hepatic portal vein; *r*, rectal artery; *ra*, renal advehent (portal) vein; *sc*, subclavian artery and vein. (From Kingsley’s “Comparative Anatomy of Vertebrates.”)

Immediately in front of the conus the truncus divides into four pairs of aortic arches, the third to the sixth of the original series. In the dipnoi pulmonary arteries make their first appearance in the vertebrate series as posterior branches of the last pair of aortic arches. As another novelty in fishes, the right postcardinal vein degenerates and a new vein, the postcava, drains most of the posterior part of the body. The caudal vein in this group bifurcates into the left postcardinal and the postcaval veins. The iliac veins as they leave the pelvic fins divide into pelvic and renal portal veins. The two pelvic veins unite to form a median abdominal vein. Venous blood from the fins may thus reach the heart either by way of a capillary network in the mesonephroi or by the abdominal vein. The efferent renal veins drain into the postcava and into the left postcardinal veins. Thus in the appearance of an atrial septum, of pulmonary arteries and veins, and of a postcaval vein the dipnoi make notable advances towards the circulatory system of the higher vertebrates. The differences between the dipnoan and amphibian circulation are slight.
**Amphibia.** In the amphibians the connexion of the sinus venosus is shifted to the right atrium while the pulmonary veins connect with the left atrium. The two atria are divided by a septum which is usually perforate in urodeles. There is however little mixing of impure and pure blood in the atria. In the undivided ventricle some mixing of the two kinds of blood does occur. A spiral septum in the truncus arteriosus shunts the venous blood from the right side of the ventricle chiefly into the pulmonary arteries while that which passes to the dorsal aorta and systemic arteries is mostly aerated blood. Of the six original aortic arches of the embryo the last four persist in some adult amphibia while in others only the third and fourth arches persist. One of the most important changes in circulation which occurs within the group is the abandonment by the higher amphibia of the capillary branchial network characteristic of fishes. In the perennibranch amphibia most of the blood in the aortic arches short-circuits the gills, and with the loss of gills in the anura the aortic arches form direct connexions between ventral and dorsal aortae. In the anura as in most amniotes that portion of the dorsal aortae between the carotid (third) and systemic (fourth) arches degenerates. In urodeles as in dipnoi the pulmonary arteries form posterior branches of the sixth aortic arch while in the anura the connexion by a ductus arteriosus with the dorsal aorta is lost as in mammals. Several splanchnic arteries convey blood from the dorsal aorta to the intestine. In anura however they are reduced to three, celiac, anterior, and posterior mesenteric arteries. In urodeles three veins drain the mesonephroi, the right and left postcardinal veins and the postcava. The connexion of the iliac veins with the renal portal or advehent veins which made its appearance in dipnoi is also present in amphibia. Impure blood from the hind-legs may thus return to the heart either through the mesonephroi, or by the abdominal vein. The increased flexure of the heart brings the atria anterior as well as dorsal to the ventricle. (Fig. 296)

**Reptiles.** The reptilian vascular system strikingly resembles that of amphibia. The main arteries and veins are homologous in the two groups. The chief differences appear in the heart and truncus arteriosus. The ventricle is partly divided by a septum in lower reptiles and more or less completely divided into the crocodiles and alligators. Consequently pure and impure blood are separated in the two sides of the heart as in mammals. A peculiarity of the reptilian circulation, however, is manifested in the triple splitting of the truncus arteriosus. Three arteries instead of the two characteristic of mammals leave the heart. One of these is the pulmonary artery carrying venous blood from the right ventricle to the lungs. The remaining two vessels are the systemic arteries, one of which comes from the right, and the other from the left, ventricle. Soon after leaving the heart each artery crosses to the opposite
side of the body. Thus the right aortic arch comes from the left ventricle and conveys pure blood to the dorsal aorta and the head. The left aortic arch comes from the right ventricle and carries mixed blood into the dorsal aorta. Consequently, the dorsal aorta of reptiles contains mixed, and not pure, blood. Since both celiac and mesenteric arteries are given off from the left aortic arch which carries mixed blood, they carry mixed blood to the stomach and intestine. In some reptiles a foramen Panissae connects the blood streams in the two ventral aortae so that some mixing of the blood in the two vessels may take place. In the lower reptiles
systemic and carotid arches are connected with one another, as in urodeles, by the dorsal aortae. In the crocodiles this connexion is lost, as in mammals. The connexion between the postcava and the postcardinals is lost in reptiles and the blood from the kidneys returns to the heart by the postcava as in mammals. Both right and left common cardinals (ductus Cuvieri) persist and bring blood from the head and anterior limbs into the sinus venosus. Thence it passes to the right atrium. Blood from the hind legs as in amphibia may return to the heart either by the renal portal veins or by the lateral abdominal veins.

**Mammals.** The complete division of the heart into a right venous half and a left arterial half which was attained by reptiles is retained by mammals. In mammals, however, the sinus venosus merges into the right atrium. In this region is located the *sino-auricular node*, a bundle of muscular and connective tissue richly supplied with nerve fibers, which is said to be the "pace-maker" of the heart-beat. Mammals have a single ventral aorta. Of the paired systemic arches of amphibians and reptiles only the left one persists. The renal portal system has disappeared and with it the abdominal veins. The latter however form the transient umbilical veins of the fetal circulation. The right and left iliac veins establish connexions with the postcava by way of the posterior cardinals and of their transverse anastomosis in the lumbar region.

The postcava of mammals appears to be only in part homologous with that of lower vertebrates. As is shown in Fig. 320, four distinct embryonic vessels unite to form the mammalian postcava. These are the anterior hepatic portion, the subcardinal anastomosis, the supracardinal veins (in part), and the posterior portion of the right postcardinal vein. The supracardinal veins seem to be mammalian novelties, arising in the embryo dorsal to the post- and subcardinal veins. There is difference of opinion in regard to the first appearance of subcardinal veins, whether they are new in mammals or present in vertebrates from amphibia to man. According to McClure subcardinal veins are present in all vertebrates.

The origin of the azygos and hemiazygos veins is also in doubt. Most textbooks regard these vessels as persistent remnants of the postcardinal veins together with their transverse anastomosis. The researches of Huntington and McClure however indicate that the azygos and hemiazygos veins are limited to mammals and that they are in chief part persistent portions of the supracardinal veins which appear to be mammalian novelties. The renal veins of mammals are not the homologs of the renal veins of lower vertebrates but are new vessels formed from the intersubcardinal anastomosis.

In the lower mammals both common cardinals occur as in lower vertebrates. In the higher mammals and man, however, a transverse anastomosis between the precardinals or jugulars is converted into the
left innominate vein which brings venous blood from the left arm and left side of the head across to the right jugular vein. The left common cardinal consequently degenerates but persists in part as the coronary vein.

**Evolution of the Heart.** The chief changes which the heart has undergone in phylogenesis may be briefly summarized as follows: The vertebrate heart is a differentiated portion of a median ventral blood vessel. The contractile function which originally extended throughout the length of this vessel became localized and concentrated in the subpharyngeal region. Primarily the heart had neither valves nor chambers but consisted of a two-layered tube with a muscular wall and an endothelial lining. The first subdivision of the heart was into a receiving chamber or **atrium** and an anterior propulsive division, the **ventricle.** Later were added a posterior **sinus venosus** and an anterior **conus.** Atrioventricular and semilunar valves in turn made their appearance, thus ensuring a one-way flow of blood. With the elongation of the heart in confined space a sigmoid flexure was formed and the atrium consequently came to lie dorsal to the ventricle. Fishes added a muscular bulbus anterior to the conus. In the dipnoi and amphibia the connexion of the sinus venosus was shifted to the right atrium while aerated blood from the lungs entered the left atrium. In the dipnoi and amphibia the atrium became divided by an incomplete septum into right and left atria while the ventricle remained undivided, so that some mixing of aerated and impure blood occurs. The increased flexure of the heart brings the atria in amphibia anterior to the ventricle. In the crocodilian reptiles the complete division of the heart into arterial and venous halves is effected, but the beneficial effects of this separation are partly neutralized by the mixing of the two
kinds of blood in the dorsal aorta. In mammals the sinus venosus becomes merged with the walls of the right auricle.

**Evolution of the Aortic Arches.** The device of oxygenating blood in pharyngeal gills is peculiar to chordates. Nevertheless aortic arches connecting ventral and dorsal aortae in the pharyngeal region occur in annelids. It is a matter of opinion whether this point of resemblance between annelids and chordates has a phylogenetic significance or is simply a case of convergence. In chordates the number of aortic arches is correlated with the number of visceral arches. Amphioxus has the largest number, nineteen pairs, of primary visceral arches among chordates. The aortic arches are correspondingly numerous. The largest number of aortic arches in vertebrates occur in some species of cyclostomes, fifteen pairs in bdellostoma stouti. Although some elasmobranchs have
more, it is customary to assume six pairs as the primitive number of aortic arches in gnathostomes. Of these the first two pairs belonging to the mandibular and hyoid arches partly lose their respiratory function and, consequently, the associated aortic arches. In fishes the persistent aortic arches are broken up into a capillary net-work in the gills. In urodeles the last four pairs of aortic arches persist, the blood from the ventral aorta largely short-circuiting the gills. In anura gills are lost and blood passes directly through the aortic arches to the dorsal aorta. In the anura the fifth pair of aortic arches degenerate. That portion, the ductus arteriosus, which connects the pulmonary branches of the sixth aortic arch with the dorsal aorta also atrophies. The third pair of arches persist as the roots of the carotid arteries. In reptiles as in anura three pairs of aortic arches persist, the 3rd, 4th, and 6th in part as pulmonary. In reptiles the common carotid arteries connect with the right and not with the left systemic or fourth aortic arch. In mammals portions of

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**Fig. 300.—A section through a human ulnar artery and vein, showing the wall of the artery on the left and of the vein on the right. The upper part of the figure (a–d) is from a section of the same vessels stained with resorcin-fuchsin, an elastic tissue stain.**

- a. Circular, and b. radial elastic fibers of the media of the artery; c. external elastic membrane; d. elastic fibers in the media of the vein; e. circular, and g. longitudinal muscle fibers of the media; f. endothelium. X 550. (From Bremer's "Text Book of Histology.")
three aortic arches persist in the adult, 3rd, 4th, and 6th as in reptiles. The systemic arch of the right side, however, forms the right subclavian artery while that of the left side becomes the arch of the aorta. Since this is connected directly with the left ventricle it carries only aerated blood to the dorsal aorta. The aortic arches in man resemble those of other mammals. (Fig. 299)

**The Evolution of Arteries.** Aside from the transformation of the aortic arches the phylogenetic changes in the arterial portion of the vascular system have not been profound. The main trunks persist throughout the series proving that nature holds fast to that which is good. The appearance of the subclavians and iliacs is correlated with that of the paired fins, but once invented these vessels persist in man to nourish the arms and legs. In the dipnoi pulmonary arteries make their debut as branches of the sixth pair of aortic arches when the lungs which they supply emerge from air bladders. The connexion of the pulmonary arteries with lungs persists throughout the vertebrate series. With the substitution of a definitive kidney for the mesonephroi of lower vertebrates new renal arteries are formed. The history of the caudal artery is one of degeneration until in man it becomes the rudimentary median sacral artery. The number of splanchnic arteries supplying the intestine in man remains the same—three—as in elasmobranchs. (Fig. 297)

**The Evolution of Veins.** The phylogenetic alterations of the veins are much more radical than those of the arteries just described. Few veins persist throughout the entire chordate series. Included among such persistent veins are the jugulars, the precava (the right common cardinal or right ductus Cuvieri) and subintestinal, a part of the portal vein. The usual assumption that the postcardinals persist as the azygos and hemiazygos, except in part, is not supported by the evidence from embryology.

The primary veins are paired, e.g., the precardinals, postcardinals, lateral abdominals or umbilicals, vitellines, and even the subintestinal vein which is paired at the time of its first appearance in vertebrates. The portal vein is one of the primitive veins of amphioxus and the modifications of its development in connexion with the right vitelline vein appear to be recent adaptations. The postcava appears as a new vein in dipnoi and undergoes considerable reconstruction in mammals through the addition of parts of the subcardinal anastomosis, right postcardinal, and supracardinal veins. The views of investigators in regard to the origin of the subcardinal veins are divergent. The evidence seems to support the opinion that the subcardinals make their appearance with that of the renal portal veins and that they persist throughout the vertebrate series and in part are incorporated in the postcava of mammals. In man, and to a lesser degree in other mammals, veins become differenti-
ated into a superficial set which drain the skin and outer organs, and a
deep set which carry blood away from the deeper organs of the body.

Evolution of the Lymphatic System: Little is known of the relations
of chordate lymphatics to those of prechordates. The contrast between
lymphatics and blood vessels is less marked in invertebrates than in
vertebrates. It seems not unreasonable to assume that primarily there
was no distinction between blood vessels and lymphatics and that the

![Image](image_url)

**Fig. 301.**—The lymphatics of the scrotum. Showing the transition of the capillaries to
the vessels with valves (a, a, a). (From Morris, after Teichmann.)

two systems have had a common origin. As in the case of most blood
vessels it is impossible at the present time to homologize particular
lymphatic vessels in chordates and pre-chordates.

In amphioxus the lymphatics surround the blood vessels and occur
also in the metapleural folds, dorsal fin, and around the central nervous
system. In vertebrates the distribution of lymphatics corresponds
roughly with that of veins, although lymphatics are far more variable in
position than are veins. Like the veins the lymphatics are divided into
superficial and deep systems. The deep system develops in close relation
to the cardinal veins and acquires connexions with them and with the
superficial system.

Lymphatic vessels occur in cyclostomes and fishes. They surround
the veins in elasmobranchs, while their relations to the veins are less
intimate in other fishes. One or two main trunks may parallel the dorsal
aorta in this group and therefore be compared with the paired thoracic
ducts of mammals. Lymph sinuses surround the heart and nervous system. Some fishes have lymph hearts serving to assist the circulation of the lymph. But fishes do not have lymph glands.

A thoracic duct is present in amphibia. Larger subcutaneous sinuses occur in this group possibly as an adaptive arrangement which prevents dessication. Lymph hearts may occur in various parts of the body. Reptiles have large paired lymphatic trunks. Lymph hearts are also found in this group.

Most mammals have paired thoracic ducts. In man the left duct persists throughout life in connexion with the left subclavian vein, while

![Fig. 302.—Diagrams illustrating the chief lymphatic trunks and their relations to the veins in mammals and man. A, South American monkeys; B, Mammals (Lepus) in which postcaval-renal communications are wanting; C, Mammals in general; D, Man. In all mammals lymph enters the veins at the point of junction between the jugular and the subclavian veins. In most mammals there is also communication between the lymph vessels and the postcaval and renal veins. In man the right thoracic duct degenerates in part and the only communication with veins is at the root of the jugulars.

the right duct is rudimentary having a length of only a few centimeters. One lymphatic sinus, the cisterna chyli, also persists in man. The lymph is returned to the veins at the point of least pressure, where subclavian and jugular veins meet. Lymph glands are numerous in man and mammals and generally occur in clusters in the axillary region and in the groin and neck. Lymph hearts are wanting in mammals and man. Lymphoid or adenoid tissue is found in all vertebrates. Lymph-nodes however make their first appearance in reptiles.

**Evolution of Hemopoietic Tissues.** Hemopoietic or blood-forming tissues are found in several phyla of invertebrates. Blood-cell formation consequently appears not to be a novelty in chordates. Identical highly
Fig. 303.—Human blood corpuscles. Left hand column, as seen after Zenker's fixation and haematoxylin and eosin stain; at the right, as seen in smears stained by Wright's triple stain. 1, neutrophiles; 2, mononuclear leucocytes; 3, lymphocytes; 4, eosinophiles; 5, basophiles. (From Bremer's "Text Book of Histology," after Mallory.)
specialized blood cells occur both in pre-chordates and chordates. The lymphocytes of cyclostomes resemble those of some annelids. The erythrocytes of gephyreans are similar to those of vertebrates and some echiuroids have enucleated red blood corpuscles like those of mammals.

The primordial blood cell of animals appears to have been a lymphocyte from which the various types of blood cells—erythrocytes, granulocytes, monocytes, etc.—are differentiated. The original lymphocytes in vertebrate embryos are derived from the splanchnic mesoderm. All blood cells of vertebrates are therefore believed to be mesodermal. That the first blood cells of vertebrate embryos appear in the wall of the yolk-sac is not surprising since the yolk-sac is a herniated portion of the alimentary canal and its mesodermal wall therefore splanchnic.

The spleen is the fundamental blood-forming organ. In cyclostomes, the splenic tissue lies in the submucosa of the stomach and intestine, in the lamprey within the spiral valve. In the dipnoi, splenic blood-forming tissue is concentrated in the stomach wall. In elasmobranchs and ganoids, the spleen becomes attached to the mesentery and in amphibia remains the chief erythrocytopoietic organ. In some amphibian larvae, however, the mesonephros also functions as a blood-forming organ.

With the appearance of hollow bones in the anura, the spleen begins to lose its importance as an erythrocytopoietic organ. In mammals,
this function is vestigial in the spleen, and bone-marrow has usurped the function. Bone-marrow is well-adapted for erythrocyte formation, since the blood there is relatively static and the carbon dioxide tension is high. Blood-cells, however, whether derived from spleen or bone-marrow, become vascular elements only following migration. Hemoblasts are transformed into erythrocytes in the venous sinuses of the bone marrow.

**Development of the Vascular System.** It is now agreed that the blood and blood vessels are mesenchymatous in origin. The heart, however, with possibly the exception of its endothelial lining, develops from the visceral layer of mesoderm and is therefore of epithelial origin.

**Fig. 305.—Drawings to show the cellular organization of blood islands at three stages in their differentiation.** A, from blastoderm of 18-hour chick; B, from blastoderm of 24-hour chick; C, from blastoderm of 33-hour chick. (From Patten's "Embryology of the Chick.")

**Development of Blood and Endothelium.** Blood makes its first appearance in the form of solid masses of mesenchymatous cells known as blood islands in the visceral layer of the mesoderm adjacent to the endoderm in the extra-embryonic yolk-sac. These blood-islands consist of cell masses which secondarily unite to form a network of solid cords. In this condition, they constitute the angioblast or source of the primary blood cells. The central cells of the cords are transformed into both red and white blood corpuscles, while the peripheral cells become the endothelial lining of the blood-vessels. The first blood vessels are, therefore, extra-embryonic, and those within the embryo are secondary.
The differentiation of blood corpuscles is correlated with the appearance of an intercellular fluid plasma. Thus the blood becomes a liquid tissue. Connexions of the vitelline vessels are soon established with those formed within the embryo and similar vessels extend into the body-stalk and chorion. Blood is already present in a human embryo of three to four weeks. The extension of the angioblast and the formation of blood channels is believed to occur, not by the sprouting and elongation of the primary trunks, but by the confluence of separate cords of cells, as a drain is built of separate tiles placed end to end. Some blood vessels, however, appear to be formed out of capillary networks by the enlargement of a single channel and the disappearance of the others. Primarily, the walls of the blood vessels consist of a single layer of endothelium. The muscular and connective tissue layers are added from the surrounding mesenchyme.

There is a divergence of opinion as to the origin of the various types of blood cells of the adult blood. According to the monophyletic theory, both leucocytes and erythrocytes come from a primitive hemoblastic cell, and thus have a common origin. According to the alternative polyphyletic theory, red and white corpuscles have a diverse origin. Difference of opinion has also arisen as to whether or not the blood corpuscles of the adult are the direct descendants of the primary blood cells of the embryo which have migrated to the various hemopoietic organs and centers of proliferation. The evidence on the whole favors the conclusion that the blood cells of the adult have diverse sources of origin (red marrow, endothelium, lymph nodes, spleen, etc.) and are not the direct descendants of the primitive angioblast cells.

In the embryo, blood cells arise successively from diverse centers, including the blood islands, vitelline blood vessels, the adenoids, liver, spleen, and finally from bone-marrow. Proliferation of blood cells continues throughout life in the bone-marrow, lymph glands and spleen, but ceases early in other organs. It has been calculated that erythrocytes are manufactured in the adult body at the rate of ten to thirty thousand every second.

The primary type of blood cell is the hemoblast cell, which contains a relatively large vesicular nucleus and relatively small surrounding cytoplasm. During its histogenesis, the nucleus of the hemoblast shrinks, while the cytoplasm increases in volume. In this way, the hemoblast is converted into a normoblast, if the cell is to become an erythrocyte. The nucleus of the normoblast, in correlation with the concentration of its chromatin, stains intensely. Eventually, the nucleus of the erythrocyte is extruded bodily, though whether by active migration from the cytoplasm or by being abandoned by the cytoplasm is uncertain. As a consequence of its loss of a nucleus, the life of an erythrocyte is relatively
short—possibly a month. The first enucleated erythrocytes appear during the second month, mostly from the liver. Up until that time all embryonic blood cells are nucleated, as in the adults of lower vertebrates.

White blood corpuscles are of two types, granular and non-granular. Most of the non-granular are lymphocytes which have about the same
diameter as the erythrocytes. Their source is both in the bone-marrow and the lymph glands. The granular leucocytes arise in the bone marrow as myelocytes. They become differentiated mostly into neutrophiles, the nuclei of which have diverse shapes while the cytoplasm is neutral in its staining reactions. A small proportion of the myelocytes become eosinophiles, which have a coarsely granular cytoplasm with a strong affinity for eosin and other acid dyes. The cytoplasm of other leucocytes stains with basic dyes. They are, consequently, known as basophiles.

Fig. 307.—Sections cut transversely through the cardiac region of pig embryos of various ages to show the origin of the heart from paired primordia. A, 5-somite embryo; B, 7-somite embryo; C, 10-somite embryo; D, 13 somite embryo. (Projection diagrams X50, from series in the Carnegie Collection.) (From Patten's "Embryology of the Pig."

**Development of the Heart.** The heart makes its appearance as a two-layered tube ventral to the pharynx, so that the early embryo has its heart in its throat. Of the two layers, the inner becomes the endothelial lining of the heart, while the outer forms the epicardium and the muscular myocardium. The right and left halves of the heart begin as longitudinal folds of the splanchnic mesoderm. Between these mesodermal folds and the adjacent endoderm, scattered mesenchyme cells appear, and soon become arranged as a thin-walled endothelial tube in each of the folds.

The paired mesodermal folds with their enclosed endothelial tubes arise before the ventral wall of the pharynx is formed. The union of the two halves occurs in correlation with the formation of the floor of the
pharynx from the endoderm. Successive stages in the process are shown in Figs. 306 and 307.

Soon after the tubular heart forms below the pharynx, its wall becomes three layered by proliferation of cells from the outer or epimyocardial layer. In this way, a thick muscular layer is formed between the endo-

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Fig. 308.—Ventral views of the heart of chick embryos at successive stages to show its changes of shape and its regional differentiation. Abbreviations: a.v., constriction between atrium and ventricle; i.v., interventricular groove. (From Patten’s “Embryology of the Chick.”)

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thelial lining and the outer serosa. By the union of the visceral layer of mesoderm above and below the heart, dorsal and ventral mesocardia are formed in a manner resembling the formation of mesenteries in relation to the intestine. By the time the embryo is a month old, the ventral mesocardial membrane disappears and the right and left halves of the pericardial cavity are thus brought into direct connexion with one another. By the formation of septum transversum and diaphragm, the pericardial cavity becomes separated from the abdominal cavity. (Fig. 311)
Soon after the two halves of the heart are united in the mid-ventral line, the heart itself becomes S-shaped as a consequence of its elongation in a confined space. The dorsal curve is posterior and connects directly with the paired vitelline (omphalomesenteric) and umbilical veins. The ventral curve is anterior and extends forward beneath the pharynx as the truncus arteriosus. Circulation has already begun when the heart is in this tubular condition. By the time the embryo is two months old, the heart, although its size is minute, has reached its adult form and structure. (Fig. 308)

The processes involved in converting a tubular heart into a four-chambered one include: 1. The increased flexion of the heart so that the posterior atrial portion becomes anterior, while the morphologically anterior ventricular portion lies posteriorly. 2. The formation of a longitudinal septum which divides the heart into right and left chambers. 3. The relative hypertrophy of the two atria, that of the right side enlarging the more rapidly. 4. The separation of atria and ventricles by the growth of the atrio-ventricular valves. 5. The inclusion of the posterior division of the heart, the sinus venosus, within the right atrium. 6. The division of the anterior portion of the heart, the conus, into aorta and pulmonary artery. The changes thus briefly summarized are best understood from diagrams of the successive stages. (Figures 298, 308.)

During intra-uterine life, the septa which divide the heart into right and left halves are perforated to permit blood from the right side to pass through foramina into the left side, and thus to make possible a systemic circulation even when the pulmonary circulation is small. In the atrium, two longitudinal septa arise, the one first formed (Septum I) being on the left. Since relatively little blood comes from the lungs, the blood
pressure in the right atrium is greater than in the left atrium and consequently the septum on the left is pushed back like a swinging door into the left atrium, and blood enters freely from the right atrium through the foramen ovale in Septum II. (Fig. 321)

When, however, the child is born and the pulmonary circulation is augmented, the increase in the amount of blood in the left atrium equalizes the pressure in the two atria, the left septum (Septum I) is forced back against the right (Septum II), and the foramen ovale is closed. The blood in the two atria is therefore no longer mixed. After a few months or years the two septa normally unite to form an imperforate septum.

Development of Valves. The processes involved in the development of the atrio-ventricular valves are complicated. The valves arise from thickened folds of the heart-wall lying in the constricted passage between atrium and ventricle. The folds from which the valves develop are lip-

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**Fig. 310.**—Section through the heart of a 9.4 mm. pig embryo, at the level of the atrio-ventricular canals. ×45. (From Patten's "Embryology of the Pig.")
like, one dorsal to the other. Both are known as endocardial cushions. The extension of the interventricular septum described above results in its fusion with the endocardial cushion and in the division of the single atrio-ventricular foramen into right and left atrio-ventricular foramina. The endocardial cushions guarding the right atrio-ventricular foramen become the tricuspid valve, while those of the left foramen form the mitral valve. The chordae tendineae and the papillary muscles which are con-

![Diagram](image)

**Fig. 311.**—Schematic diagrams showing the manner in which the pleural and pericardial region of the coelom become separated. (From Patten's "Embryology of the Pig.""

connected with the valves are derived from the inner walls of the ventricles, which primarily are spongy masses of muscular trabeculae. As the walls of the ventricles are converted into the compact muscle of the outer heart-wall, the inner trabeculae become papillary muscles and chordae tendineae.

**Descensus Cordis.** When the heart begins its development, it lies well forward beneath the pharynx. As it takes on adult form and structure, it shifts backward into the thorax. During its migration the atria which were primarily posterior to the ventricles come to lie anterior to them.

**Development of Aorta and Pulmonary Artery.** Extending anteriorly from the ventricle, the *bulbus* and *truncus arteriosus* carry blood from
the heart to the aortic arches. The bulbus and truncus are primarily a single vessel. During the second month of foetal life, however, a spiral

Fig. 312.—A–F show successive stages in the development of the aortic arches in human embryos. The arteries are shown in black, the pharynx and lung anlagen are stippled. A is an embryo of four weeks, B of four and a half weeks, C of five weeks, D of six weeks, E of six and a half weeks, and F at birth. (Redrawn from Romer, after Streeter.)

Fig. 313.—A diagram of a 4.2 mm. human embryo showing five aortic arches. (Redrawn after W. His.)

septum is formed, dividing them lengthwise into two trunks, the aorta and the pulmonary artery. At the time when this occurs, four thickenings of the wall of the bulbus are converted into the six semilunar valves, three
in the aorta and three in the pulmonary artery. As a result of the spiral splitting of the bulbus, the pulmonary artery is made to connect with the right ventricle, and the aorta with the left.

**Development of the Aortic Arches.** In very early stages of ontogenesis, in 1.5 mm. to 2.00 mm. embryos, before the two halves of the heart are completely united in the mid-ventral line, connexion between ventral and dorsal aortae is established around the pharynx by means of a single aortic arch, the first. In a 2.6 mm. embryo, a second aortic arch, the hyoid, is added. Others are added in succession until in a 4.2 embryo there are five aortic arches. But the fifth or last of these is really the sixth arch, the true fifth aortic arch being a rudimentary vessel which appears only transiently in the 7.0 mm. embryo. By this stage, however, the first two
aortic arches have degenerated. Consequently, while all six aortic arches arise, they are not present simultaneously in the human embryo.

Only three of the six embryonic aortic arches are represented in the adult, the third, fourth, and in part sixth. The right and left third aortic arches become respectively the root of the right and left internal carotid arteries, the external carotids coming from the ventral aorta. The left fourth aortic arch becomes the arch of the aorta of the adult, while the right forms the right subclavian artery. The dorsal aorta between the third and fourth arches degenerates and disappears. Posterior branches of the sixth pair of aortic arches connect with the lungs and form the pulmonary arteries. Until birth, the remainder of the left sixth aortic arch persists as the ductus arteriosus connecting the pulmonary artery with the dorsal aorta. The vessel which connects the right pulmonary artery with the right dorsal aorta degenerates. The fifth pair of arches degenerate soon after their appearance.

**Changes in the Embryonic Circulation.** The vascular system of a 1.5 mm. to 2.0 mm. embryo includes paired dorsal aortae from which are given off intersegmental vessels to the body-wall, and a series of vitelline arteries to the yolk-sac. Blood is returned to the sinus venosus of the heart through vitelline veins from the yolk-sac and paired umbilical veins from the placenta.

In embryos of 2.0 mm. to 2.5 mm., blood is returned from the head to the heart by the paired precardinal veins. At this stage, six pairs of vitelline arteries carry blood to the yolk-sac. In embryos of 2.6 mm., postcardinal veins join the precardinal veins to form the common cardinal veins, the ductus Cuvieri. These, together with the umbilical and vitelline veins, return blood to the sinus venosus. Also, at this stage, the paired dorsal aortae begin to unite into a median unpaired trunk. In the head region, however, this fusion does not occur, and the paired dorsal aortae persist as the internal carotids of the adult body. The vitelline...
arteries become reduced in number to a single vessel formed by the coalescence of a pair of arteries. This vessel persists as the superior mesenteric artery of the adult. In a 2.6 mm. embryo, there are two pairs of aortic arches, and by the time the embryo is 7 mm. long, five pairs of aortic arches are present. A series of twenty-seven branches of the dorsal aorta form the intersegmental arteries of the body-wall. Celiac, superior mesenteric, and inferior mesenteric arteries develop from the vitelline arteries. Three types of branches develop from the dorsal aorta, somatic or intersegmental, lateral or intermediate, and ventral or visceral branches. Lateral or intermediate branches are limited to the trunk region. From the dorsal branches arise the metameric vertebral, costal, and lumbar arteries. The vertebral arteries below the brain combine as the basilar artery. The subclavian arteries develop from the seventh cervical intersegmental arteries of the embryo.

From the intermediate branches of the dorsal aorta come the renal, adrenal, phrenic, and spermatic or ovarian arteries. The vessels which supply the intestine, the celiac and mesenteric, are derived from the ventral visceral arteries. The aortic arches, limited to the head region, are also visceral. The umbilical arteries during ontogenesis change greatly in their relations. They arise in a 1.5 mm. embryo opposite the fourth cervical myotome. In a 5 mm. embryo, they have been shifted backward to a connexion opposite the fourth lumbar vertebra. In the adult, they persist as the iliac arteries. The median sacral artery is the continuation of the dorsal aorta into the sacrum and coccyx. (Fig. 315)

The arteries of the upper and lower extremities grow into them from the dorsal aorta. The brachial artery of the arm is formed by the union of three segmental vessels, the middle of which belongs to the last cervical segment. Extending into the forearm, this artery becomes the interosseous artery. In the hand region five branches are given off to the five fingers. Through the growth of a median artery paralleling the interosseous artery, the latter loses its connexion with the digital arteries. The ulnar artery is added as a third vessel in the forearm, and in the hand.
becomes connected with the median artery by a volar arch. A fourth vessel, the radialis, grows from the brachial artery into the hand. Diagrams of these stages (Fig. 317) summarize these changes.

Fig. 317.—Diagrams of the development of the arteries in arm and leg. A–E, stages in the development of the arteries in the arm; F–I, stages in the development of the arteries of the leg. Proximal is to the right, distal to the left. (From Corning, after McMurrich in Piersol’s “Anatomy.”)

Fig. 318.—Three stages in the development of the hepatic portal system. A, primitive; B, liver tubules beginning to develop, right omphalomesenteric interrupted; C, definitive condition, liver not indicated. dc, Cuvierian ducts; hp, hepatic portal vein; hv, hepatic vein; l, liver; lo, ro, left and right omphalomesenteric veins; si, sub-intestinal veins; sv, sinus venosus. (From Kingsley’s “Comparative Anatomy of Vertebrates.”)

The arteries of the lower extremity differ somewhat in their development from those of the upper. Two primary arteries make their appearance in the thigh, the femoral and ischiadic arteries. The latter extends
into the foot and ends in the five digital arteries of the toes. From the femoral artery, a saphenous artery grows diagonally across the leg and by making connexion with the digital vessels supplants the ischiadic vessel, which now becomes the peroneal artery of the calf. As a consequence of the union of the saphenous artery with the ischiadic, the latter partly atrophies. In the knee region, the saphenous becomes the popliteal

artery, and in the leg, the tibialis posterior artery. By an outgrowth of the popliteal artery, the tibialis anterior artery is formed.

Development of the Veins. At the time of its first appearance in a 2 mm. embryo, the sinus venosus receives blood from two pairs of veins, the vitelline veins from the yolk-sac and the umbilical veins from the chorionic villi of the placenta. A third pair of veins connected with the sinus appear in a 2.6 mm. embryo. These veins are the common cardinals,
Fig. 320.—Diagrams illustrating stages in the development of the systemic veins of the pig. The cardinal and omphalomesenteric veins are shown in black, the subcardinal system is stippled, the supracardinals are horizontally hatched, and vessels arising independently of these three systems are indicated by small crosses. A, Ground plan of the veins of a young mammalian embryo; B, Cross section (at level of arrow in A) showing dorso-ventral relations of the various veins; C, Diagrammatic plot of veins of
5–6 mm. pig embryos; D, Arrangement of veins in 6–7 mm. pig embryos; E, Cross section (at level of arrow in D) showing dorso-ventral relations of vessels; F, Veins in 12–13 mm. embryos; G, Veins in 16–19 mm. embryos; H, Veins in 22–24 mm. embryos; I, Veins in 30–35 mm. embryos; J, Cross section of 17 mm. embryo at level of arrow in G; K, Plan of veins in adult pig. (From Patten’s “Embryology of the Pig,” after Butler.)
the ductus Cuvieri. The blood from the head is returned by the precardinals or jugulars and that from the trunk by the postcardinals. The subclavian, renal, and external iliac branches of the cardinals soon make their appearance. At a later stage, transverse anastomosing vessels connect right and left pre- and postcardinal veins. Another transverse anastomosis is formed in the region of the iliac veins.

The rapid growth of the liver effects radical changes in the vitelline and umbilical veins which pass through it, both breaking up into capillary networks within the organ. Three transverse connexions between the parallel vitelline veins are formed. Of these the first and last are dorsal to the duodenum while the middle anastomosis is ventral to the intestine. The united veins thus form a figure 8; but the left half of the anterior loop and the right half of the posterior loop atrophy, and the resultant portal vein assumes the shape of a letter S. With the atrophy of the yolk-sac and its associated vitelline veins, and with the appearance of splenic (lienal) and superior mesenteric branches from the intestine, the portal vein attains its adult relations. The right umbilical vein disappears, while the left umbilical acquires direct connexion with the hepatic portal vein. In this way, a ductus venosus is formed carrying blood directly from the intestine and placenta to the postcava and the heart. (Fig. 319)

The precardinal veins, which drain the blood from the head, are primarily paired and symmetrical. In an eight week embryo, a transverse anastomosis is established and later converted into the left innominate vein. Eventually the left common cardinal atrophies, but occasionally persists as the oblique vein of Marshall. The left common cardinal persists also as part of the coronary sinus.

In the older texts it is stated that the posterior cardinals persist as the azygos and hemiazygos veins. The more recent researches of Huntington and McClure, however, indicate that the ontogenesis of the veins below the heart is extremely complicated. The changes may be more clearly expressed in a series of diagrams of successive stages than from a description (see Fig. 320). Postcardinal, subcardinal, and supracardinal veins make their appearances successively in the embryo and acquire complex connexions with one another. The adult postcava is formed by the coalescence and anastomosis of four primarily separate veins, the hepatic, subcardinal, postcardinal, and supracardinal. In addition to these, a sub-supracardinal anastomosis is built into the wall of the postcava. These changes are seen in the stages represented in Fig. 320.

Changes in Circulation at Birth. In the fetus oxygenated blood is returned to the heart by the umbilical vein, ductus venosus and the postcava. In the postcava, venous blood from the lower part of the body mingles with the pure blood from the placenta. Further dilution of the oxygenated blood occurs in the heart by the addition of venous blood from
Fig. 321.—Diagrammatic plan of circulation of mammalian foetus just before birth. (From Patten's "Embryology of the Pig.")
the head. Some of the mixed blood in the right auricle finds its way through the foramen ovale into the left auricle and thence to the left ventricle from which it is pumped to all parts of the body. The blood which is pumped from the right ventricle into the pulmonary artery also finds its way mostly into the dorsal aorta by way of the ductus arteriosus. The pulmonary circulation, it is assumed, is reduced in amount, since the lung sacs are not fully inflated while the embryo is in utero.

At birth, when the child draws its first breath the lungs become filled with air and expanded, with consequent increase in their capillary circulation. As a result, the blood which had been flowing through the ductus arteriosus into the aorta passes to the lungs and returns to the heart by the pulmonary veins. The consequent increase in pressure in the left auricle forces septum I of the auricle against septum II and closes the foramen ovale. (See Fig. 321 and description on page 372.) Thereafter the blood in the left side of the heart is aerated blood, while that of the right side is venous blood. As a result of these changes in circulation the lumen of the ductus arteriosus usually disappears. The walls of the vessel, however, persist as a connective tissue cord, the ligamentum arteriosum of adult anatomy.

Following the birth of the child the placental circulation stops. That portion of the umbilical vein which extends from the navel to the liver loses its lumen and becomes the ligamentum teres of the liver. The two umbilical arteries are reduced to the lateral umbilical ligaments of the adult body. The ductus venosus of the liver becomes the ligamentum venosum. Some of these changes occur slowly so that in most infants the ductus arteriosus becomes imperforate only at three months. The fusion of the interauricular septa occurs still more slowly, and is complete at three months after birth in only one third of all individuals, and even at maturity is incomplete in a quarter of the population. The failure of the septa to close the foramen ovale results in a "blue" baby, for which the chances of life are small.

Development of the Lymphatic System. Lymphatic vessels are thin-walled channels which, like arteries and veins, have an endothelial lining and terminate in fine capillaries. In addition to vessels and capillaries lymphatics have nodular swellings or lymph-nodes which act as "filters of lymph" and centers of lymphocyte formation. Since, however, lymph nodes or glands are supplied with blood capillaries, it cannot be said that they are peculiar to the lymphatic system.

The origin and differentiation of lymphatics have long been matters of dispute, and some of the issues still remain unsettled. Although lymphatics at the time of their first appearance as well as in later life are closely associated with veins, it seems to be increasingly evident that they are not formed as outgrowths of the veins. They arise as independent
spaces in the mesenchyma, and the mesenchymal cells surrounding them are converted into the endothelial lining of the lymphatic vessel. Since connexions with veins appear very early and the number of connexions diminishes in later stages, it was formerly thought that lymphatics are outgrowths of veins. Today, however, this evidence seems less convincing than it did to earlier investigators.
The separate mesenchymal spaces which form the anlagen of lymphatic vessels secondarily unite with one another to form the continuous channels of the adult lymphatics. Later in their development, however, there is good evidence that the extension of the lymphatic system involves branching and sprouting of the primary lymphatic trunks.

In the two-months human embryo paired thoracic ducts already appear near and parallel to the posterior cardinal veins. They arise in connexion with the paired jugular lymph sacs which lie lateral to the internal jugular veins. Later the thoracic ducts become connected with posterior lymph sacs and with the cisterna chyli in the pelvic region. From these main trunks as a basis lymphatic vessels grow into all parts of the body—head, trunk, and appendages. The jugular lymph sacs acquire direct connexion with the jugular veins and retain it throughout life. Although blood cells are abundant in the anlage of the lymphatic vessels these cells largely disappear during ontogenesis. The lymph sacs of the embryo are later replaced by lymph glands or nodes.

During the third month of development paired lymph glands make their appearance in the axillary, iliac and maxillary regions. In their formation the cells of the lymph vessels or sacs do not appear to participate. Adenoid tissue becomes intercalated in the course of the lymphatic vessel and after its envelopment by the lymphatic to form a peripheral sinus, the gland becomes differentiated into an outer nodular cortex and an inner mass of medullary cords. The development involves an ingrowth both of lymphatic capillaries and blood capillaries, which are thus brought into close relation with the adenoid, lymphocyte-forming cells. The ingrowth of capillaries takes place by a process of sprouting.
The Heart in Man. The human heart is a hollow muscular organ about the size of the closed fist, weighing from nine to eleven ounces. It is shaped like a truncated cone with its apex pointing downwards to the left. It is placed asymmetrically behind the sternum, with its apex just above the left fifth rib. A muscular partition extending from apex to base divides it into right and left cavities, each of which is subdivided into an anterior atrium or auricle and a posterior ventricle. Externally the division of the heart into atria and ventricles is indicated by a groove, the sulcus coronarius, and the two are separated internally by atrioventricular valves. Two large veins, the precava and postcava, enter the right atrium, while four pulmonary veins return blood from the lungs to the left atrium. The pulmonary artery connects with the right, the aorta with the left ventricle.

The walls of the ventricles are thicker than those of the atria, and the wall of the left ventricle is thicker than that of the right, for the right ventricle pumps blood only to the lungs, while the left ventricle forces blood to all other parts of the body and is correspondingly more muscular.

The heart-wall has three layers, endocardium, myocardium, and epicardium. The endocardium consists of a thin layer of connective tissue and an endothelial layer continuous with that of the blood vessels. The myocardium is the thick muscular layer. The fibers of cardiac muscle are striped, and are peculiar in having anastomosing connexions with one another. The epicardium is a thin layer of connective tissue covered with the serous membrane which lines the pericardial cavity.
A similar serous epithelium is reflected on the outer side of the pericardial cavity. The cavity between contains a small amount of fluid.

The muscles of the myocardium are wound circularly around the heart and arranged in layers. The fibers of the outer layers run at approximately right angles to those of the inner layers, thus insuring a maximum contraction of the heart cavities during contraction or systole.

The muscle of the atria is mostly independent of that of the ventricles and the two are separated by a connective tissue septum. There is, however, an atrioventricular bundle of specialized muscle fibers which extends from the atrial septum to the ventricular septum and serves to convey to the ventricles the rhythm of contraction of the atria.

The atrio-ventricular valves are attached by chordae tendineae to the walls of the ventricles in such a manner as to open freely into the ventricles but to prevent the return of blood when the ventricles contract. The attachment of the chordae tendineae to the heart-wall is by means of
special papillary muscles, anterior and posterior, in each ventricle. The
right valve is partially divided into three "cusps" and the left into two.
Hence they are known respectively as tricuspid and bicuspid or mitral
valves.

At the opening of the aorta and of the pulmonary artery crescentic
semilunar valves prevent the return of blood into the ventricles. Each
artery contains three of these valves so arranged that under pressure of
the blood they meet together and occlude the lumen completely. Near
the semilunar valves lie the openings of the coronary arteries which
supply blood to the wall of the heart. This blood is returned to the
coronary sinus of the right atrium by coronary veins which parallel the
coronary arteries.

Course of Blood in the Heart. The blood from the systemic veins,
the precava and the postcava, enters the right atrium and by the con-
traction of the atrium is pumped through the tricuspid valve into the
right ventricle. From the right ventricle the blood is carried by the
pulmonary artery to the lungs, returning from the lungs by the four
pulmonary veins to the left atrium. Forced by the contraction of the
atrium through the bicuspid valve into the left ventricle it is pumped into
the aorta and to all parts of the body.

PULMONARY CIRCULATION

The pulmonary artery carries impure or venous blood from the right
ventricle to the lungs. Near the heart it divides into right and left
branches which connect with the corresponding lungs. At the point of
separation of right and left pulmonary arteries the ligamentum arteriosum
connects them with the aorta.

From the lungs, blood is returned to the left atrium by pulmonary
veins which, unlike other veins, convey aerated blood. While there are
usually four pulmonary veins, occasionally there are five and the blood
from the middle right lobe enters the atrium independently. Within
the lung lobes the pulmonary veins parallel the arteries.

Arteries. Arteries convey blood away from the heart, and because
they are subjected to considerable pressure when the heart contracts,
their walls are correspondingly thick and elastic. A cross section shows
three layers, an intima, a relatively thin layer consisting of the lining
endothelium and a connective tissue layer with elastic fibers, a media, a
relatively thick layer of muscle and elastic fibers, and an externa, a
layer of loose connective tissue consisting largely of white inelastic fibers.
Because of the strength and elasticity of their walls, arteries usually do not
collapse after death. (Fig. 300)

Arteries have their own circulatory and nervous supply. The capil-
laries of the walls are the vasa vasorum. The nerves are branches of the
autonomic system, and are of two sorts, vasoconstrictor nerves which stimulate the contraction of the blood vessels and thus check the flow of blood, and vasodilator nerves which act as inhibitors and thus permit the dilation of the blood vessels.

SYSTEMIC CIRCULATION

The Arteries. All of the blood of the head, trunk, and limbs leaves the heart by way of the aorta, the largest artery of the body, with a diameter of over an inch where it leaves the heart. Beginning at the left ventricle, the aorta ascends to the level of the second rib, curves to the left over the bronchial tube, and then descends along the backbone to the fourth lumbar vertebra, where it divides into right and left common iliac arteries. The divisions of the aorta near the heart are known successively as the ascending aorta, aortic arch, and descending or dorsal aorta. From the ascending aorta in the region of the semilunar valves, two small arteries, the right and left coronary arteries, are given off to the walls of the heart. From the upper side of the aortic arch three large arteries arise. The first is the innominate artery, which extends towards the head for a short distance and then divides into right subclavian and right common carotid arteries. Near the origin of the innominate the left common carotid artery leaves the aorta and passes to the head. Immediately to the left of the origin of the left common carotid the left subclavian artery extends from the aorta into the left arm. From the lower side of the aortic arch near the ligamentum arteriosum the upper and lower bronchial arteries pass to the right and left bronchial tubes. (Fig. 326)

The two common carotid arteries extend towards the head to about the level of the larynx and there each divides into internal and external carotids. The internal carotid supplies chiefly the brain, while the external carotid carries blood to the remaining parts of the head and face. Among the many branches of the external carotid artery are superior thyroid, ascending pharyngeal, lingual, external and internal maxillary, sterno-cleido-mastoid, occipital, posterior auricular, and superficial temporal arteries. The names of these vessels suggest their distribution.

The subclavian artery extends beneath the clavicle giving off as branches vertebral, internal mammary, superficial cervical, thyroid axis, and costo-cervical arteries. The vertebral arteries, after passing through the costo-transverse foramina of the cervical vertebrae, unite beneath the brain to form the basilar artery which, with the internal carotids, supplies the brain. The internal mammary artery conveys blood to the sternum, diaphragm, and intercostal muscles. The thyreo-cervical or thyroid axis artery supplies thyroid gland, esophagus, trachea, and muscles of the shoulder blade and neck.
Fig. 326.—The chief arteries of the human body viewed from in front.
As the subclavian artery passes out from under the clavicle towards the arm it becomes the axillary artery. In the five inches of its length the axillary artery gives off the superior thoracic, thoraco-acromial, lateral thoracic, subcapular, anterior circumflex humeral, and posterior circumflex humeral arteries to the muscles of the shoulder and chest. Continuing into the arm the axillary artery becomes the brachial artery which extends to the elbow and there divides into radial and ulnar arteries. Its branches supply the bone muscles and skin of the upper arm. The radial and ulnar arteries are the chief arteries of the forearm; those of the hand are the volar and digital arteries, their branches supplying chiefly muscles and skin. The pulse is usually taken from the radial artery in the wrist.

The thoracic portion of the dorsal aorta extends from the aortic arch at the level of the fourth thoracic vertebra to the level of the twelfth thoracic vertebra, where it passes through the diaphragm and becomes the abdominal aorta. The chief branches of the thoracic aorta are ten pairs of intercostal arteries, which not only supply the intercostal muscles but also the vertebral canal and the skin of the thoracic region. Small arteries are given off to the bronchi, lungs, esophagus, and mediastinum.

The abdominal aorta extends from the diaphragm to the fourth lumbar vertebra. As it passes downwards it gives off in succession right and left inferior phrenics, celiac, right and left middle adrenal, right and left first lumbar, superior mesenteric, right and left renal, right and left internal spermatic, right and left second lumbar, inferior mesenteric, right and left third and fourth lumbar, right and left common iliac, and middle sacral arteries. Of these the phrenics and lumbar are parietal in distribution while the remainder, except the iliac and sacral, are visceral.

The right and left inferior phrenic arteries supply the diaphragm and adrenals. The lumbar arteries supply the lumbar vertebrae and the lumbar muscles. One branch anastomoses with the renal artery. The celiac artery divides into three chief branches, the left gastric, the hepatic, and splenic (lienal) arteries. The left gastric artery supplies the lesser curvature of the stomach and the lower part of the esophagus. The hepatic artery supplies the liver, duodenum, pancreas, and the right half of the greater curvature of the stomach. The third branch of the celiac is the splenic which, as its name implies, supplies the spleen and also the pancreas and the stomach wall.

The superior mesenteric artery extends for most of its course in the mesentery and gives off five chief branches, inferior pancreatice-duodenal, intestinal, ileo-colic, right colic, and middle colic. The inferior pancreatic-duodenal artery anastomoses with the superior pancreatico-duodenal artery, a branch of the hepatic. The intestinal arteries supply
the jejunum and ileum as well as the mesentery. The colic arteries carry blood to the colon.

The renal arteries supply kidneys, adrenals, and the upper portion of the ureters. Thus the adrenals receive blood from three sources, phrenic, renal, and middle adrenal arteries. The internal spermatic arteries are given off just below the renals and pass along the spermatic cord to the testes. From them branches are given off to the ureters, cremaster muscle, and epididymis. The ovarian arteries in the female correspond to the spermatic arteries of the male. Branches from the ovarian arteries pass to the ureters, ovaries, uterine tubes, uterus, and to the round ligaments of the uterus.

The inferior mesenteric artery leaves the abdominal aorta about an inch and a half above its division into the iliacs. It is distributed chiefly to the colon and rectum. Arising just above the bifurcation of the abdominal aorta, a median sacral artery supplies the last lumbar vertebra, sacrum, and coccyx.

The common iliac arteries are formed by the bifurcation of the abdominal aorta when it reaches the level of the fourth lumbar vertebra. At the level of the lumbo-sacral articulation, the right and left common iliacs divide into internal or hypogastric and external iliac arteries. From the internal iliac arteries both visceral and parietal branches are given off. The visceral branches are the umbilical, inferior vesical, middle hemorrhoidal, uterine, and internal pudendal arteries. The parietal branches are the ilio-lumbar, lateral sacral, obturator, and gluteal arteries. The ilio-lumbar arteries are serially homologous with the lumbar arteries and have a similar distribution to the vertebrae and lumbar muscles.

The lateral sacral arteries, as their name suggests, supply chiefly the sacrum. The obturator artery supplies the bladder, iliac and pubic bones, and obturator and adjacent muscles. The gluteal arteries supply gluteal and neighboring muscles.

Of the visceral branches of the hypogastric artery the umbilical artery supplies chiefly the bladder. The inferior vesical artery sends branches to the bladder and prostate gland. The middle hemorrhoidal artery carries blood to the rectum and, in the female, to the vagina. The uterine artery after a tortuous course supplies the uterus and vagina. The internal pudendal artery is distributed to the muscles of the perineum, penis or clitoris, and to the scrotum or labia majora.

The external iliac artery is the larger of the two vessels into which the common iliac artery divides. In its course it gives off inferior epigastric, deep circumflex, iliac, as well as smaller branches to adjacent muscles. As the external iliac passes into the thigh it becomes the femoral artery. Continuing to the knee it becomes the popliteal artery.
Fig. 327.—The chief veins of the human body viewed from in front. Superficial veins are shown on the right side, deeper vessels on the left side of the body.
Below the knee the popliteal artery terminates in the **posterior** and **anterior tibial** arteries which are deeply situated beneath the calf muscles.

The **posterior tibial** artery extends to the foot. In the leg its branches supply the leg muscles and the skin of the lower leg. One of its branches, the peroneal artery, parallels the **posterior tibial** artery as far as the ankle. In the foot the latter terminates as the **lateral** and **medial plantar** arteries. The **anterior tibial** artery extends along the front of the leg to the foot where it terminates as the **dorsalis pedis** artery with its metatarsal and other branches.

**The Systemic Veins.** Blood is returned to the heart from the head, the upper part of the body, and from the arms by the precaval vein or vena cava superior. The **precava** is formed by the union of the right and left innominate veins. From the thorax blood is returned to the precava by the azygos vein. (Fig. 327)

Each of the innominate or brachiocephalic veins is formed by the confluence of the internal jugular and subclavian veins. The left **innominate** crosses the median plane of the body just above the arch of the aorta, and unites with the right innominate vein immediately to the left of the aortic arch.

Blood from the anterior part of the scalp and face is returned to the facial vein, a branch of the internal jugular. Venous blood from the back of the scalp and neck enters the **external jugular** veins, and thus is carried to the subclavian vein. The two chief veins tributary to the **common facial** vein are the **anterior** and **posterior facial** veins.

The **external jugular** vein is formed by the union of the **posterior auricular** vein and the communicating branch of the posterior facial vein. Other tributaries of the external jugular are the occipital, posterior external jugular, transverse scapular, and anterior jugular vein. For purposes of description, it is customary to divide veins into two classes, superficial and deep. Most of those of the head and neck mentioned belong to the group of superficial veins.

The deep veins of the head include the veins of the diploë, which drain the cancellous bones of the skull, the venous sinuses of the brain membranes, and the veins of the brain, nose, eye, ear, pharynx, and larynx. The chief deep veins of the neck are the **internal jugular** veins, which have as tributaries the **lingual** from the tongue and the **superior thyroid** from the thyroid gland. The **vertebral** veins which bring blood from the vertebrae unite with the innominate veins, which also receive blood from the deeper neck muscles through the **deep cervical** veins. From the thyroid gland come the **inferior thyroid** veins and the **thyroidea ima** vein which is usually single and median. Veins from the thymus gland, trachea, and esophagus also open into the left innominate vein.
In the thoracic region are the azygos, hemiazygos, accessory hemiazygos, ascending lumbar, vertebral, and internal mammary veins. The azygos vein extends along the thoracic vertebral column, receiving blood from the right intercostal veins, from the hemiazygos vein and from the accessory hemiazygos vein. It opens anteriorly into the precava. The hemiazygos vein receives blood from the left intercostal veins, and joins the azygos at about the level of the eighth rib. The accessory hemiazygos vein crosses the backbone from left to right just above the hemiazygos vein. In the region below the diaphragm, the azygos and hemiazygos veins continue as right and left ascending lumbar veins. The vertebral column in the thoracic and lumbar regions is drained by the vertebral, intercostal, lumbar, sacral, and intervertebral veins. The internal mammary veins drain the superficial veins of the thorax as well as the anterior intercostal, bronchial, and pericardiac veins and open into the right and left innominate veins.

The chief superficial veins of the upper extremity are the cephalic and basilic veins. The cephalic vein joins the axillary vein below the clavicle. The basilic vein unites with the brachial vein at about the middle of the upper arm. The deeper veins of the arm, forearm, and hand parallel the arteries of these regions. Each artery, however, is accompanied by a pair of veins, venae comitantes. Beginning with the volar veins of the hands, the veins of the upper extremity, in order, are the metacarpal, ulnar and radial, brachial, axillary, and subclavian. The tributaries of these veins correspond closely in number and relations with arteries of the same name.

Most of the blood from the legs, abdomen, and viscera is returned to the right auricle by the postcava. The tributaries of the postcava are the right and left common iliac veins, which return blood from the legs, the lumbar veins from the lumbar body-wall, the right spermatic or ovarian vein from the gonad, the renal veins from the kidneys, the right adrenal vein (the adrenal vein of the left side and the left spermatic or ovarian veins are tributaries of the left renal vein), the inferior phrenic veins, of which the left usually opens into the left renal vein, and the hepatic veins which are largest of all.

The portal vein is unique in having capillaries at both of its ends. The portal collects blood from the intestine, stomach, and spleen and delivers it into the capillaries (sinusoids) of the liver. Its branches parallel those of the mesenteric arteries and some of those of the celiac artery. The chief tributaries of the portal vein are the superior mesenteric vein, the splenic vein which drains the spleen, stomach, and pancreas, the inferior mesenteric vein (the relations of which correspond to those of the artery of the same name), the coronary or gastric vein from the
stomach, the pyloric vein from the pylorus, pancreas, and duodenum, and the cystic vein from the gall-bladder.

The **common iliac** veins parallel the arteries of the same name and are formed by the union of the external and **hypogastric** or internal iliac veins. The **middle sacral** vein, which is thought to be a rudiment of the caudal vein of lower vertebrates, returns blood from the sacrum and lower pelvis into the left common iliac vein. The **hypogastric** vein parallels the artery of the same name. Its tributaries are the hemorrhoidal vein from the rectum, uterovaginal vein, vesical from the bladder, and the pudendal vein from the external genitals. The hypogastric also receives blood from the inferior and superior gluteal, obturator, lateral sacral, and ilio-lumbar veins, the distribution of which is similar to that of the arteries of the same names.

In the leg the chief superficial vein is the **great saphenous** which returns to the femoral vein most of the blood from the surface of the thigh, leg, and foot. The veins of the skin beginning with the digital veins of the foot form plantar and dorsal networks which combine on the inner side of the leg into the **great saphenous** vein. The **small saphenous** vein extends from the foot along the back of the calf to the knee where it combines with the **popliteal** vein.

The deep veins of the leg parallel the arteries and are given corresponding names. In the region of the shank there are two veins to each artery. Beginning with the plantar veins in the foot, the more important of the deep veins of the leg are the **anterior** and **posterior tibial** veins, which unite in the knee region to form the popliteal vein. In the upper part of the thigh, the popliteal vein in turn becomes the **femoral** vein which directly continues as the external iliac.

**The Lymphatic System.** The circulatory system thus far described is closed, in contrast with the open or lacunar systems of invertebrates. That is to say, the blood vessels of vertebrates form a system of tubes the walls of which are continuous and without openings. But to nourish the cells in the tissues the blood vessels must be permeable. Loss of fluid plasma from the blood takes place in the capillaries, which are formed of a single layer of endothelium. It is generally thought to be due to three factors, blood pressure, osmosis, and diffusion; but active secretion by the endothelial cells may also be involved.

The fluid which passes from the capillaries forms lymph. Lymph is essentially blood plasma from which the corpuscles, except a few leucocytes, have been removed. The lymph lost from the blood capillaries is taken up by the lymphatic capillaries which like the blood capillaries are microscopic vessels whose walls consist of a single layer of endothelium. Unlike blood capillaries, however, the lymphatics vary
greatly in size, and in the translucent mesentery are visible to the naked eye when distended with the milky lymph absorbed from the intestine after a meal. (Fig. 301)

The lymphatic system includes capillaries, collecting vessels, and lymph nodes. Like blood capillaries, lymph capillaries exchange dissolved substances with the surrounding tissues. They form complicated plexuses, of which few parts of the body are devoid.

From the lymph capillaries, the lymph passes into lymph vessels or ducts by which it is conveyed to the innominate veins. The largest of the lymph trunks is the thoracic duct, which extends along the backbone and enters the left innominate vein. The wall of a lymph vessel resembles that of a vein, having three coats, intima, media, and adventitia. The lymph vessels, however, have more valves than the veins to insure flow in one direction only.

On its way through the lymph vessels, lymph before it enters the vein passes through one or more lymph nodes consisting chiefly of adenoid tissue. Lymph vessels enter as vasa afferentia into the cortex of a node, where they form lymph sinuses surrounding lymph nodules. Within the lymph node, the lymph vessels pass from the outer cortical sinuses into the medulla of the node, where they again form sinuses surrounding medullary cords of adenoid tissue. The vasa efferentia which convey lymph away from a node are relatively large vessels. Each lymph node has on one side an indentation or hilum where arteries enter and veins and efferent lymphatic vessels emerge. Lymph nodes have a double function. They are centers of proliferation of lymphocytes, and they serve as lymph filters. The gland cells have the capacity, it is believed, to ingest bacteria and to neutralize the action of foreign substances in the lymph. Fig. 324.

The thoracic duct extends from the second lumbar vertebra along the spinal column to the point where the jugular and subclavian veins unite to form the left innominate vein. Here the lymph is restored to the veins in the region of least pressure. Into the thoracic duct flows lymph from the lower part of the body as well as the lymph brought by the left jugular and subclavian lymph vessels. At its lower extremity the thoracic duct expands into a cisterna chyli or receptaculum. (Fig. 302)
CHAPTER II

THE UROGENITAL SYSTEM

EVOLUTION OF THE UROGENITAL SYSTEM

The evolution of urinary and reproductive systems may be conveniently discussed as if the two were independent.

THE URINARY SYSTEM

Metabolism furnishes the necessary chemical foundation of life. But the oxidation of nitrogenous compounds, essential to the process of metabolism, results also in poisonous nitrogenous wastes, which must be removed. It is, therefore, not surprising that all animals have mechanisms for removing the ashes of life, intra-cellular mechanisms in the protozoa, porifera, and coelenterates, multicellular in higher animals.

Protozoa. The characteristic excretory organ of protozoa is the contractile vacuole. Usually each cell contains a single vacuole, but there may be two in protozoa with elongated bodies. The position of the vacuole just beneath the ectosarc is constant and its external orifice permanent. Liquid wastes formed within the cytoplasm stream toward the vacuole from all directions. When the tension of liquid within the vacuole reaches a maximum, the external orifice is forced open and the liquid passes to the outside. The rate of contraction is a function of the temperature, warmth increasing and cold retarding excretion. There is, of course, no genetic connexion between the intracellular organs of protozoa and the multicellular organs of metazoa.
Lower Metazoa. While specialized excretory organs are not present in coelenterates, they do occur in flatworms, where they assume the form of branched tubules which carry liquid wastes to the exterior. In many flatworms, their apertures, usually paired, open on the dorsal side of the body near its anterior end. One peculiarity of the excretory system of flatworms is the flame cells located at the terminations of the branched tubules. These are relatively large hollow cells containing numerous long cilia which extend into the cavity of the cell and which sometimes unite to form a single long flagellum. The function of the cilia appears to be to drive the secretions of the cell towards the excurrent canal and the exterior. Many invertebrates besides flatworms possess flame cells in connexion with their excretory systems. The flame cells of flatworms are probably the prototypes of those of the highly specialized solenocytes of annelids and amphioxus. (Fig. 328)

Annelids. Two sorts of excretory organs occur in annelids, protonephridia and metanephridia, the former, as their name suggests, considered the more primitive. (Fig. 329)

Protonephridia. The protonephridia of annelids and molluscs are branched or unbranched excretory tubules which end blindly within the body cavity or in the connective tissues. In the annelids they are segmentally arranged and are ectodermal in origin. Their inner blind ends are beset with numerous solenocytes. Each solenocyte is prolonged into a tubular capillary containing an elongated flagellum, which extends throughout the length of the capillary into the cavity of the nephridial tubules. The solenocytes gather liquid wastes from the surrounding tissues, and pass them to the nephridium and thus to the outside. Thus
protonephridia resemble the branched tubules of flatworms not only in structure but also in function. (Fig. 331)

**Metanephridia.** Many annelids also have *metanephridia*, which are nephridia devoid of solenocytes and opening not only to the exterior but also into the coelom. The internal aperture is the *nephrostome*. In oligochaetes the metanephridia are much convoluted, and the nephrostome opens into the coelom of the segment anterior to the one which contains the external aperture. The metanephridia are paired and occur in most segments of the body throughout its length. Cilia surrounding the nephrostome sweep wastes from the body cavity into the nephridium and thus to the exterior. Like the protonephridia, the metanephridia are ectodermal in origin. It is assumed that they are genetically related to the protonephridia.

**Coelomducts.** In addition to the two kinds of nephridia just described, many invertebrates have a third type of tubules, *coelomducts*. These in annelids, however, are not excretory in function but serve as reproductive ducts. Like the metanephridia, they have coelomostomes which are ciliated and open into the coelom. Like nephridia, also, they are paired and metameric in arrangement. Their mesodermal origin, however, makes it impossible to compare them with nephridia. Consequently, they must be considered as novelties first appearing in annelids. Their special interest to morphologists lies in the fact that they resemble the kidney tubules of vertebrates and are consequently regarded as prototypes of the latter. If this comparison is valid, we must assume that, in the course of phylogenesis, they have changed from a reproductive to an
excretory function. In this connexion it is interesting to note that the coelomoducts of molluscs are excretory in function, and that in male vertebrates some of the anterior tubules of the mesonephros serve as reproductive outlets.

**Acrania.** Among the protochordates, the urochordates appear to have no organs comparable with either nephridia or coelomoducts. The hemichordates, with the possible exception of rhabdopleura, have no paired excretory organs. The proboscis cavity of rhabdopleura contains a couple of ciliated tubules which are usually denominated nephridia. We find, however, in acrania, protonephridia strikingly similar to those of annelids. Their presence in chordates is frequently interpreted as supporting the assumption that chordates have an annelid ancestry. It seems more likely however that we have here another case of convergence. The nephridia of amphioxus are protonephridia associated with the secondary gill-arches. They are short branched tubules which open into the peribranchial cavity, sometimes as many as ninety pairs. The fact that they are ectodermal in origin and are limited to the gill-region, while the excretory tubules of vertebrates are mesodermal and postbranchial, is sufficient to show that the two are not homologous. That the nephridia of amphioxus are protonephridia comparable with those of annelids is evidenced by the fact that they are ectodermal and metamERICally arranged and have their blind terminations beset with solenocytes almost identical in structure with those of annelids.

**Craniota.** Three successive kidneys make their appearance in vertebrates, pronephroi, mesonephroi, and metanephroi. That the tubules of these three kidneys are comparable with coelomoducts is sufficiently

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**Fig. 331.**—Diagrams of the protonephridia of Amphioxus. *A* is a section in the pharyngeal region—through a gill septum on the left and through a gill slit on the right. *B* is an enlarged section of a protonephridium showing the attached solenocytes. Such a protonephridium is practically identical in structure with a protonephridium of annelids. (Redrawn after Boveri and Goodrich.)
attested by their mesodermal origin and with the exception of the tubules of the metanephros, their metameric arrangement. The pronephros in vertebrates is an embryonic structure which persists only in the adults of some cyclostomes, teleosts, and dipnoi. The mesonephros becomes the functional kidney of adult anamnia, the metanephros of adult amniotes.

Comparative embryology and anatomy suggest therefore, that the function of excretion has phylogenetically migrated from the anterior to the posterior part of the body. The possibility, however, cannot be excluded, that originally every metamere in chordates, as in annelids, contained a pair of excretory organs. But this assumption is weakened by the evidence that the excretory tubules of acraniia are not serially homologous with those of craniotes. The possibility that the gonadic sacs of amphioxus may be homologous with coelomoducts and kidney tubules has, however, been suggested somewhat plausibly.

**Fig. 332.**—A diagram illustrating the four types of kidneys which occur in chordates. The excretory tubules of amphioxus are ectodermal in origin like the protonephridia of annelids, while they are mesodermal in vertebrates. In the course of phylogenesis the excretory organs of chordates have migrated farther and farther back in the body, as is shown in the diagram.

**Pronephros.** The first vertebrate kidney to develop in ontogenesis, and possibly also the oldest in phylogenesis, is the *pronephros* or head kidney. This consists of three to fifteen pairs of segmental tubules, each of which opens by a nephrostome into the body cavity. Each tubule is connected laterally with the primitive pronephric duct which carries excretions posteriorly to the cloaca. It is generally assumed that originally each pronephric tubule, like the coelomoducts of annelids, had its own aperture. The elimination of liquid wastes by a common pronephric duct must be considered as a secondary condition. The factors in this phylogenetic development are obscure. Similar relations, however, are found in some annelids. In some oligochaetes and hirudinea, a longitudinal duct conveys the products of the testes to the outside. In others, the nephridia may join a longitudinal duct which opens into the cloaca. If, as is generally believed, the nephridia are ectodermal in origin, we have here another case of convergence of structures which have a diverse origin—the nephridia from the ectoderm, pronephros and duct from the mesoderm.

The pronephros functions in few adult vertebrates, but it appears to function in the early ontogenesis of those craniotes which have little yolk
Fig. 333.—Diagram of possible connexions of coelom with the exterior. c, coelom; cl, cloaca; g, glomerulus of kidney; i, intestine; n, nephrostome; pa, porus abdominalis. (From Kingsley’s “Comparative Anatomy of Vertebrates,” modified after Bles.)

A. PRONEPHROS

B. MESONEPHROS

C. MESONEPHROS

D. METANEPHROS

Fig. 334.—Diagrams illustrating the relations of A, pro-, B-C meso-, and D, metanephridial tubules. The primary or pronephric tubules remove wastes from the body-cavity, while the mesonephric tubules get their wastes directly from the blood; many of them, however, retain the original connexion with the coelom. The metanephric tubules lose all connexion with the coelom. (Redrawn after Corning)
in their eggs and which consequently have a prolonged larval period. Usually pronephric tubules are not connected with glomeruli. The associated glomeruli, instead of connecting directly with the tubules through a Bowman’s capsule, project into the body cavity in the neighborhood of the nephrostomes. In this way wastes excreted into the body cavity find their way indirectly to the tubules of the pronephros and thus to the cloaca. In some cyclostomes and bony fishes, however, the pronephros includes a segregated portion of the body cavity. This becomes a **pronephric chamber** into which an **inner glomerulus** projects.

It has been suggested that the glomeruli of the pronephros originally belonged to the gills and not to the urinary system, and only with a reduction in the number of gills came to serve the pronephros. Such a suggestion is quite consistent with the fact that the gills of fishes supplement the kidneys as excretory organs.

**Mesonephros.** The fact that the mesonephric tubules arise later than the pronephric tubules during ontogenesis by no means proves that they are phylogenetically younger, since the difference in time of appearance in the embryo may be only an instance of the law of antero-posterior differentiation in accordance with which anterior structures in the embryo develop earlier than posterior ones. The chief reason for thinking that the pronephros is phylogenetically older than the mesonephros is the fact that the pronephros is more conspicuous in cyclostomes than in fishes and amphibia.

The mesonephros is the functional kidney of anamnia. Its tubules, like those of the pronephros, are mesodermal and derived from the intermediate cell mass, the nephrotome. They utilize the primitive (pronephric) duct as an outlet. From their structure, development, and relations, they are seen to be serially homologous with the pronephric tubules. This is one of the facts which has led morphologists to postulate an **archinephros** which consisted of a series of homologous tubules extending throughout the length of the trunk, and possibly, as in annelids, throughout the entire length of the body. If the latter assumption is made, it is also necessary to assume a pair of nephridia and a pair of coelomoducts in each metamere, as in some annelids, and that in acrania coelomoducts have degenerated while in the gill region nephridia have persisted.

It may be reasonably assumed that, like the pronephric tubules, those of the mesonephros were metameric in origin. Indeed, they are metameric in the embryos of elasmobranchs. In amniotes, however, the mesonephric tubules branch repeatedly and lose their primary metamericism. In the posterior portion of the mesonephros, the intermediate cell mass, nephrotome or mesomere, does not divide into segments, but forms its tubules from an unsegmented mass. The mesonephric tubules differ from pro-
nephric tubules also in the fact that they acquire connexions with glomeruli and thus are enabled to eliminate liquid wastes directly from the blood vessels and not indirectly by way of the body cavity.

In the male the anterior portion of the mesonephros changes its function from that of an excretory organ to that of a reproductive organ. In other words, the tubules of the anterior part of the mesonephros return to the original function of the coelomoducts from which, assuming an annelid ancestry, they are derived. (Fig. 335)

Metanephros. The third kidney or metanephros appears not to be an amniote novelty, since transitional conditions between mesonephros and metanephros occur in some amphibia in the form of a combined mesonephros-metanephros, the opisthonephros. In the amniote embryo, the nephrogenic tissue from which the excretory tubules of the metanephric kidney arise resembles that which forms the mesonephros. The tubules of the metanephros, like those of the posterior portion of the mesonephros, arise from the nephrotome and are non-metameric in origin.

Fig. 335.—Diagrams of urogenital structures in (A) indifferent and in female elasmobranchs and amphibians; (B) male elasmobranchs and amphibians; (C) male amniote (mammal); (D) female amniote (mammal). b, urinary bladder; c, cloaca; e, epididymis; f, Fallopian tube; g, gonad; h, "stalked hydatid"; k, kidney (metanephros); l, longitudinal tubule; m, Mullerian duct (oviduct), rudimentary in B and C; mn, mesonephros; o, ovary; ot, ostium tubae abdominale; pd, paradidymis; po, paroophoron; pe, parovarium; r, rectum; ti, testis; u, uterus; ua, urethra; ur, ureter; va, vasa aberrans; vd, vas (ductus) deferens; w, vasa efferentia; w, Wolffian duct, urinary in A, urogenital in B, genital in C and rudimentary in D. (From Kingsley's "Comparative Anatomy of Vertebrates.")
Even the ureter of amniotes seems not to be a novelty in the group. In some elasmodobranchs, a secondary renal duct arises as an outgrowth from the primitive duct in a manner similar to that of the ureter. A urinary duct, which in the embryos of some reptiles drains the posterior portion of the mesonephros, develops like the ureter of amniotes as an outgrowth of the mesonephric duct. The fact that in some mammals and in man a number of ureters may develop, suggests the possibility that ureters were primitively multiple but that they have become reduced in number in mammals. The present ureter has been regarded also as an elongated renal tubule which secondarily acquires functional connexions with the numerous tubules of the metanephros.

In the female amniote, the mesonephros disappears except in the form of functionless rudiments, the epoöphoron, the paroöphoron, and the duct of Gartner. In the male, the primitive mesonephric duct is utilized as a ductus deferens. The anterior part of the mesonephros becomes the epididymis. Such relations are inherited from those of anamnia. Remnants of the posterior portion of the mesonephros may persist in the adult as the rudimentary paradidymis and ductus aberrans.

In vertebrates except most mammals, the excretions are poured into the cloaca. This is also true of monotremes. A bladder comparable to that of mammals makes its first appearance in amphibia as a hollow outgrowth from the floor of the cloaca. In neither the amphibia nor reptiles, however, is the bladder directly connected with the excretory ducts, so that excretions reach it only by way of the cloaca. In those mammals which are without a cloaca, the ureters acquire direct connexions with the bladder and open upon its dorsal surface.

**The Reproductive System**

Cells specialized as reproductive elements make their first appearance in colonial protozoa. Sexual reproduction, however, involving the union of two gametes occurs in all classes of protozoa. Protozoa conjugate periodically. The beginnings of differentiation of gametes appear also in protozoa. In unicellular organisms transitional stages between the union of similar gametes, isogamy, and that of specialized eggs and spermatozoa, heterogamy, may be recognized. Such a differentiation of gametes is generally interpreted as adaptive. The ovum contains the food supply for the developing embryo and consequently loses the motility which is retained by the spermatozoan as a way of insuring union of gametes. Biologists are not agreed in regard to the meaning of sexual reproduction. Some hold that it increases variability, while others assume that it increases stability of species by checking extreme variation.

**Coelenterates.** Among coelenterates the individual may be hermaphroditic as in the case of hydra, or sexually differentiated as in the case of
Fig. 336.—Diagram illustrating the hypothetical evolution of the urogenital system of vertebrates, beginning with the gonadic sacs of flatworms. The diagram assumes that the gonadic sacs of flatworms have become the coelomic pouches of chordate embryos. The latter in turn unite to form the extended coelom of vertebrates. Coelomoducts appear first in annelids and become in vertebrates the renal tubules. Vertebrates "invent" a longitudinal (primitive) excretory duct. During phylogensis the region of proliferation of germ-cells becomes greatly restricted.
most jelly-fishes. Vegetative methods of multiplication are common in the group. Some have a regular alternation of sexual and asexual methods of reproduction. In the jelly-fishes, eggs and spermatozoa arise in the endoderm and are discharged to the outside through the mouth. In vertebrates a similar endodermal origin of primordial germ cells has been asserted.

**Flatworms.** An advance towards the reproductive organs of chordates is made by the flatworms, in which the gonads take the form of a series of paired gonadic sacs. Sexes in the nemerteans are separate and the gonadic sacs contain either ova or spermatozoa. Germ-cells are proliferated from the epithelial lining of the gonadic sacs, and are discharged to the exterior through paired apertures. It is possible that the metameric characteristic of vertebrates had its origin in such a series of paired gonadic sacs. (Fig. 336)

**Annelids.** The number of metameres in which germ-cells develop is much reduced in annelids. The region of proliferation of eggs and spermatozoa is also limited to restricted areas of the peritoneal lining of the coelomic cavities. Paired and metamERICally arranged coelomoducts provided with ciliated internal apertures convey the germ-cells to the exterior. In some species, the nephridia join longitudinal paired ducts which in their development and relations resemble the primitive kidney ducts of vertebrates. Their mesodermal origin, however, seems doubtful. Consequently their presence may not be used as evidence to support the annelid theory of vertebrate ancestry.

**Protochordates.** The gonads of balanoglossus have a striking resemblance to those of flatworms. Like the latter, they form a series of paired sacs each of which opens to the exterior by an external aperture. The gonads of amphioxus also are metamERICally arranged in segments 10 to 35. From them the germ-cells escape to the peribranchial cavity and through the posterior atrio pore to the exterior. It has been suggested that the relations of the gonads of amphioxus resemble those of the coelomoducts of annelids as well as those of the pronephric tubules of vertebrates.

**Cyclostomes.** The gonad of cyclostomes is peculiar in being a median and unpaired organ which extends through nearly the entire length of the body cavity. In myxine the right gonad alone persists in the adult. Metamerism is, however, not evident. That vertebrates have metameric gonotomes as well as myotomes has not been demonstrated. It is, however, possible to believe that the elongated gonads of cyclostomes and of some fishes have been formed by the fusion of primarily separate metameric gonadic sacs of invertebrates. The early gonad of cyclostomes appears to be hermaphroditic, but during ontogenesis changes into either an ovary or a testis. The factors which determine which of the two shall
arise are obscure. Sex in cyclostomes, however, appears not to be as definitely predetermined in the chromatin constitution of the fertilized egg as it is assumed to be in higher vertebrates.

No special reproductive ducts are found in cyclostomes. The eggs collect in the body cavity and pass to the outside by way of paired abdominal pores, which in structure and relations resemble the paired pores of the gonadic sacs of flatworms. The elongated body cavity of vertebrates may be considered as formed by the fusion of the cavities of a similar series of paired coelomic sacs. Indeed, evidence that this assumption is correct is furnished by the ontogenesis of the body cavity in amphioxus. In the embryos of this animal each mesodermal somite contains a separate cavity (coelom). As the somite extends around the side of the body its ventral wall meets that of the somite opposite below the intestine. By the disappearance of the double membrane thus formed the coelomic cavities of the two somites become continuous. Later, on the ventral side of the body in the trunk region, the series of partitions which separate the cavities of successive somites disappear and a continuous body cavity or coelom extending through many metameres is formed. The extended body cavity of vertebrates is believed to have had a similar phylogenetic origin through the fusion of such serial gonadic sacs as occur in flatworms and nemerteans. This assumption is further justified by the fact that the relations of the abdominal pores in vertebrates resemble those of the gonadic pores of flatworms. Moreover, their function is similar. In petromyzon both the primitive pronephric ducts

![Diagram of the urogenital system of a young leopard frog showing a stage in the transformation of the primitive gonad into a testis. In the left gonad the metamorphosis is nearly completed. Only the small posterior lobe contains eggs. In the right gonad, which appears like a young unpigmented ovary, some crypts containing spermatozoa have already made their appearance. Most of the lobules, however, are filled with ova as if the gonad were to become an ovary.](image)
and the abdominal pores open posteriorly into the urogenital sinus and to the outside through a urogenital papilla.

Elasmobranchs. The gonads of elasmobranchs are paired, and in some species greatly elongated, especially in the male. The testes acquire secondary connexions with the anterior part of the mesonephros, and use the mesonephric ducts as an outlet for the sperm. Elasmobranchs retain abdominal pores, but they appear to be functionless. In this group, the primitive pronephric duct splits longitudinally to form Wolfian and Muellerian ducts. In the female the Wolfian ducts are purely excretory, while the Muellerian ducts form the oviducts. In the male, the Wolfian ducts combine both urinary and reproductive functions, while Mueller's ducts atrophy to form the uterus masculinus. Many elasmobranchs are viviparous, and the eggs are retained until hatched within uterus-like enlargements of the oviducts. In some species, the embryonic yolk-sac, which is richly supplied with blood-vessels, unites with the wall of the oviduct to form a yolk-sac placenta.

Amphibia. The gonads of amphibia resemble those of elasmobranchs. As in the latter, the testis becomes connected by means of vasa efferentia with anterior tubules of the mesonephros, and this part of the mesonephros tends to atrophy and lose its excretory function. The Wolfian duct serves as a urogenital outlet in the male. The Muellerian ducts, which persist as rudiments in the male, become the oviducts of the female.
As in elasmobranchs, the oviducts open far forward in the body cavity near the liver. The primary gonads show the hermaphroditic potencies manifest in cyclostomes. Ovaries and testes at first resemble one another and have the appearance of ovaries, but either before or after metamorphosis of the larva, the ovary-like gonad of the male is transformed into a testis. In exceptional instances, this metamorphosis is retarded and may take place in a full-grown individual. Frequently the transformation of an ovary into a testis may occur on one side before it has begun on the other. Such an individual may appear superficially as a unilateral gynandromorph. The so-called fat-bodies of the frog are formed from the anterior portion of the genital ridges and appear to serve as a reserve food-supply for the germ-cells. (Figs. 337, 338)

**Reptiles.** The differences between the reproductive systems of amphibia and reptiles are relatively slight. In the reptiles the gonads of both sexes have shifted posteriorly. Also the beginnings appear of a division of the cloaca into a dorsal rectal, and a ventral urogenital moiety; but these affect only the anterior part of the cloaca, which remains undivided posteriorly. The excretory and reproductive ducts which in amphibians open on the dorsal side of the cloaca, shift their connexions ventrally in reptiles so as to open into the new urogenital passage.

A phallus comparable with that of mammals also appears first in reptiles, notably in chelonia and crocodiles, in the form of a shallow "seminal" groove in the floor of the cloaca. This groove is bordered by paired "seminal" ridges, each of which contains erectile tissue. Posteriorly the groove terminates in a free swelling or **glans** which also contains erectile tissue. When the erectile tissue of the seminal ridges is distended, the groove between them is converted into a tubular passage which serves as an intromittent organ to convey the semen to the cloacal cavity of the female.

**Mammals.** The genital system of monotremes differs little from that of reptiles and is readily derived from it. In the male, the genital portion of the mesonephros is converted into an epididymis, while the mesonephric duct becomes a ductus deferens. The remainder of the mesonephros atrophies, although remnants persist as a paradidymis. In higher mammals, the testes migrate into a scrotal sac.

In the female monotreme, the gonad produces large yolk-laden ova similar to those of reptiles. In the placental mammals, however, the ova are reduced in size, and the embryo depends for its nourishment upon the mother. The proliferation of oocytes ceases early in the life of the mammal, and the number of mature eggs produced by the ovary is greatly reduced as compared with the number in anamnia. Like the testis, the ovary acquires connexions with the mesonephros; but the connexion never becomes functional, and the mesonephros persists only
in the form of a rudimentary *epoöphoron* and *paroöphoron*. The mesonephric duct in the female becomes the functionless Gartner's duct. The descensus of the ovaries is slight compared with that of the testes.

With the development of a horizontal longitudinal septum, the cloaca disappears in placental mammals, and two cavities, the urogenital and rectal, take its place. As this change occurs the ureters shift their connexions from the cloaca to the bladder while the ductus deferentes open into the urogenital cavity or urethra.

![Diagram of uteri](image)

**Fig. 339.—** Four types of uteri occurring in different groups of mammals. *A*, duplex, the type found in rodents; *B*, bipartite, the type found in certain carnivores; *C*, bicornate, the type found in most insectivores and prosimians; *D*, simplex, the type characteristic of the primates. (From Patten’s “Embryology of the Pig,” after Wiedersheim.)

In female mammals a tendency of the Muellerian ducts—which parallel the Wolffian ducts and lie medial to them—to fuse in the median line is evident. Beginning with the monotremes the posterior part of the Muellerian ducts fuse into a single *uterus*, while their anterior portions remain separate as the paired uterine or Fallopian tubes. The monotreme uterus opens into the urogenital sinus. In the higher mammals a vagina for the reception of the penis is differentiated between the uterus and the urogenital sinus. The vagina is therefore seen to be a portion of the united Muellerian ducts. The duplex character of the vagina appears in the marsupials (didelphians) which have two vaginas. In placental mammals, however, the vagina is single. Four stages in the increasing
fusion of the uteri are represented in the placental mammals—uterus duplex, bipartitus, bicornis, and, in primates, uterus simplex. Even in the primates, however, the original duplex character of the Muellerian ducts is retained in the paired uterine tubes. (Fig. 339)

External genital organs also make their appearance in mammals. Copulatory organs are, however, not wholly new in this group. Some of the flatworms have an intromittent organ by which sperm is conveyed to the seminal receptacle of another individual. In elasmobranchs, the pelvic fins of the male are modified as claspers which in copulation are inserted into the cloaca of the female. None of these structures however are morphologically comparable with the phallus of mammals.

The free posterior extremity of the paired erectile folds in the floor of the cloaca of chelonia forms a glans. In monotremes likewise, the phallus points posteriorly and is contained in the floor of the cloaca. In the walls of the monotreme cloaca, the seminal groove of the reptile has become a tubular canal surrounded by erectile tissue, the corpus cavernosum urethrae. This canal is used in

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Fig. 340.—Diagrams of male urogenitalia in I, monotreme; II, marsupials; and III, monodelphs. a, anus; b, bladder; c, cloaca; cu, corpus cavernosum urethrae; cp, corp. cav. penis; cd, Cowper’s gland; p, perineum; pg, prostate gland; r, rectum; s, symphysis pubis; t, testis; u, ureter; v, vas deferens; vg, vesicular gland; wm, ventral muscle. (From Kingsley’s “Comparative Anatomy of Vertebrates,” after Weber.)
monotremes for the passage of sperm only, while urine passes from the bladder to the cloaca by way of a **urinary canal**. In addition to the erectile tissue of the **corpus cavernosum urethrae**, paired masses of erectile tissue, the **corpora cavernosa penis**, make their appearance in the phallus of monotremes. The posterior free portion of the phallus of monotremes becomes more elongated than in reptiles, and is surrounded by an integumentary fold, the **preputial sac**, which disappears during erection. (Fig. 340)

In marsupials and placental mammals, with the disappearance of the cloaca the phallus becomes more independent as an external penis. The urinary canal of monotremes disappears, and the urine is conveyed to the outside through the urogenital canal or **urethra**. The glans penis with an enlarged corpus cavernosum urethrae persists. In the female, it forms the rudimentary **glans clitoridis**. In the marsupials, in correlation with the presence of a double vagina, the penis has a forked termination.

While the preputial sac of the phallus of monotremes, marsupials, and lower placental mammals is directed posteriorly, in most higher mammals, the sac shifts its direction so as to point anteriorly. Finally, in primates the penis is released from the skin of the abdominal wall, the organ becomes pendulous, and the preputial sac opens downwards.

In the female, the external genitals correspond with those of the male but in a rudimentary form. The **clitoris** is the homolog of the glans penis of the male. The remainder of the male phallus is represented in the female by the labia minora. A corpus cavernosum urethrae is lacking in the female. The labia majora correspond to the scrotum of the male.

**THE UROGENITAL SYSTEM OF MAN**

Although the excretory and reproductive systems of mammals are so closely associated that it is difficult to describe them separately, their wide divergence in function makes this desirable.

**Urinary Organs**

The urinary apparatus of man and all placental mammals consists of four parts: excretory glands, the **kidneys**; urinary ducts, the **ureters**; a urinary reservoir, the **bladder**; and the external outlet of the bladder, the **urethra**.

**The Kidneys.** The kidneys in man are bean-shaped organs, lying in the lumbar region, closely pressed against the dorsal body-wall, and on account of the large amount of blood in them, of a deep reddish color. Each is approximately four inches long, two inches wide, and an inch and a half thick. The upper end of each kidney overlaps the twelfth rib, the left kidney being usually somewhat higher than the right. The lateral border of each kidney is convex; the medial border is concave,
with a slit-like aperture, the hilum. The kidneys are held in position both by the peritoneum and by a connective tissue renal fascia. Only upper (anterior) and lower (posterior) surfaces of the kidneys are covered with peritoneum, the middle of the right kidney being crossed by the colon, that of the left by the pancreas. These relations, however, are subject to considerable variation.

**Structure.** A cross section of the human kidney in the region of the hilum shows that under its peritoneal and fatty investments the kidney is covered with a thin but tough fibrous capsule, which in a young kidney may be pulled off like the skin of an orange.

The substance of a kidney consists of an outer cortex and an inner medulla. A variable number, three to twenty, of renal pyramids form the medulla. Straus has shown that among Primates man and the spider monkey are peculiar in having a multipyramidal kidney, while the anthropoid apes have monopyramidal kidneys. Each pyramid has its base upon the cortex, and a cone-shaped apex which projects as a papilla into the renal sinus. The cortex, which is about half an inch thick, appears striated from the presence of cortical rays. Between the renal pyramids, the cortex extends to the renal sinus in the form of renal columns in which blood is conveyed to and from the cortex. The renal sinus is filled by the expanded termination of the ureter, the pelvis.

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**Fig. 341.**—A diagram of the finer structure of a kidney. *A* is a section of the entire kidney showing the contrast between cortical and medullary regions. The relations of the chief arteries and veins are indicated. *B* is a reconstruction of a single tubule, showing its relations to the blood and the pelvis of the kidney. (Reproduced in modified form from "The Human Body" by Dr. Logan Clendening. Copyright 1927, 1930 by Alfred A. Knopf, Inc.) by permission of and special arrangement with Alfred A. Knopf, Inc., authorized publishers.)
Renal Tubules. The structure of the kidney as just described is determined by the arrangement of the kidney tubules, which are the functional units of the kidney. In the cortex, the renal tubules are convoluted and connected with knots of blood capillaries, the glomeruli. The pyramids, on the other hand, consist chiefly of straight collecting tubules, which open into the renal pelvis by numerous apertures lying at the ends of the papillae.

Each renal tubule begins in a spherical capsule surrounding a glomerulus, the combined structure being known as a renal corpuscle. The swollen termination of a tubule is a Bowman’s capsule. The portion of the tubule adjacent to the corpuscle is convoluted and thickened, and is known as the proximal convoluted part of the tubule. Passing into one of the pyramids, the tubule becomes slender and straight, and is
known as the descending limb of Henle's loop. Bending sharply, it forms the ascending limb of Henle's loop, and returns to the cortex, where it becomes convoluted again, the distal convoluted portion, and unites with a **collecting tubule.** As an element in a cortical ray, each collecting tubule passes from the cortex into a pyramid. Usually a group of collecting tubules unite and open by a common aperture into the pelvis of the ureter. There is evidence that the secretion of urine takes place chiefly in the renal corpuscles and in the convoluted portions of the tubules, while the limbs of Henle's loop are chiefly absorptive in function. The high degree of concentration of the constituents of urine leads physiologists to assume that the quantity of water excreted by the renal corpuscles is many times greater than that which finds its way through the collecting tubules into the ureter, and consequently to conclude that most of this water is reabsorbed by the tubules. Their great length is assumed to be an adaptation to this absorptive function. (Fig. 341)

**Blood Supply.** Arteries enter and veins leave the kidney by way of the hilum on the median side of each kidney. Within the renal columns, branches of the renal artery form **interlobar arteries.** Passing between the medulla and cortex, these, in turn, become the **arcuate arteries,** and give off branches both to the medulla and the cortex. In the cortex, they are known as **interlobular arteries,** from which branches supply the glomeruli. The arteriole which carries blood to a glomerulus is larger than that which leaves the glomerulus. By this arrangement, blood pressure in the glomerulus is considerably greater than that in capillaries generally, so that filtration through the glomerular capillaries is increased. The renal veins parallel the arteries and receive the same names. Lymphatics and sympathetic nerves are abundant.
Ureters. The renal ducts or ureters convey the secretions of the kidneys to the bladder. Each ureter is a tube about a quarter of an inch in diameter and about twelve inches long. Within the sinus of the kidney, each ureter enlarges into a renal pelvis, which fills the sinus and branches into the renal calyces. The human kidney has two major calyces, superior and inferior, and each of these subdivides again in three to five minor calyces. Each of the minor calyces is connected with one or more renal papillae and in this way receives the urine from the collecting tubules. The two ureters open into the bladder on its posterior surface, about an inch from the beginning of the urethra. Three layers appear in a cross section of an ureter, an inner mucosa of transitional epithelium, a muscularis coat of longitudinal and circular muscles, and an outer adventitia of loose connective tissue.

The Bladder. The bladder is a muscular sac, the shape and size of which vary greatly since, when distended with urine, it may increase twenty to thirty times its size when empty. A median connective tissue ligament, the urachus, a rudiment of the embryonic allantoic stalk, extends from the bladder to the umbilicus. The hypogastric arteries of the embryo degenerate to form lateral umbilical ligaments connected with the bladder. Other ligaments in addition to these serve to hold the bladder in position. Viewed from within, the dorsal wall of the bladder shows a triradiate figure called the trigone, formed by three ridges extending from the two openings of the ureters and from the urethra.

The lining of the bladder is a layer of transitional epithelium capable of greater distension. Next to this is a layer of loose connective tissue with many elastic fibers. The greater portion of the thickness of the wall of the bladder is, however, a coat of smooth muscle fibers arranged in three layers, to which nerve fibers are distributed from both the spinal cord and the sympathetic system. At the origin of the urethra, a thickened ring of muscle forms a sphincter. In the act of urination, nerves stimulate the muscles of the bladder to contract, and inhibit the contraction of the sphincter muscle of the urethra.

Urethra. The passage from the bladder to the external orifice is the urethra. Its length differs in the two sexes, being about four inches long in the male and an inch to an inch and a half in the female. In the male urethra, three portions are distinguished, a prostatic portion, which is surrounded by the mass of the prostate gland and into which the ejaculatory ductus deferentes open; a membranous portion, which is constricted where the urethra passes through the urogenital trigone or diaphragm; and a cavernous portion surrounded by the corpus cavernosum urethrae. The diameter of the urethra differs considerably among these regions.
Fig. 341.—Schematic diagram of mammalian ovary showing the sequence of events in the origin, growth, and rupture of the ovarian (Graafian) follicle, and the formation and retrogression of the corpus luteum. Follow clockwise around the ovary starting at the arrow. (From Patton's "Embryology of the Pig."

- Primary Follicle
- Secondary Follicle
- Ovum
- Corpus Luteum
- Corpus Alveolare
- Blood Vessels
- Germinal Epithelium
- Ovarian Tissue
- Fallopian Tubes
- Ovary
- Corpora Lutea (in various stages)
Reproductive Organs: Female

Ovaries. The ovaries are paired whitish almond-shaped organs from one to two inches in length lying on the sides of the pelvis, usually with the long axis parallel to that of the body. Each ovary is attached by a thick membranous mesovarium to the broad ligament which supports the uterus. The ovary is also attached to the side of the uterus by an ovarian ligament. Another suspensory ligament carrying blood vessels and nerves extends upwards from the ovary along the wall of the pelvis.

![Diagram of an ovarian (Graafian) follicle approaching maturity, showing details of its structure and relations. (From Patten's "Embryology of the Pig.")](image-url)

The ovary is covered by a layer of columnar epithelium, which is regarded as a special modification of the peritoneum. Most of the substance of the ovary is a connective-tissue stroma containing some smooth muscle fibers. In the cortex are ova in various stages of development, surrounded by follicle cells. As an ovum approaches maturity, the follicular layer of cells which surrounds it increases in thickness. Eventually, a liquid-filled cavity appears in the follicle and the ovum is crowded to one side. As the follicular liquid increases, the follicle migrates toward the surface of the ovary. The pressure is finally sufficient to burst the follicle, and the ovum escapes into the uterine tube, the coelomic opening of which, the ostium tubae, almost completely surrounds the ovary. Sections of mature ovaries show their Graafian follicles in various
stages of growth. That portion of the follicle which remains in the ovary is converted into an endocrinal tissue the corpus luteum. If the ovum is not fertilized and therefore does not become implanted in the uterus, the corpus luteum soon degenerates to form a corpus albicans, which eventually disappears. (Figs. 344, 345)

Remnants of the embryonic mesonephros remain associated with the ovary throughout life, as the epoophoron, paroophoron, and the stalked hydatid of Morgagni. So far as is known, these are functionless rudiments of organs functional in lower vertebrates. Ovarian arteries and veins enter the ovary besides a branch of the uterine artery. The nervous supply is sympathetic. In addition to the reproductive function, it is generally assumed that the ovaries serve as endocrinal organs which in ontogenesis determine the secondary sexual characters of the female.

Uterine Tubes. The uterine tubes, which convey the ova to the uterus, vary in length from three to five inches. Near the uterus each tube is straight, but as it approaches the ovary it becomes sinuous and enlarged in diameter. The termination of each tube is a funnel-shaped structure, the infundibulum, which opens into the body cavity and...
partially surrounds the ovary. The margin of this opening is prolonged into numerous **fimbriae** which surround the ovary and convey the ova into the uterine tube. A ciliated columnar epithelium lines the tubes, the cilia beating towards the uterus and carrying the ova in that direction.

**Fig. 347.**—Diagram illustrating the passage of the fertilized egg from the ovary to the uterus. The ovum is a week in the tube and three days in the uterus before implantation takes place. (Redrawn after Dickinson's "Sex Anatomy," Williams & Wilkins Co.)

The number of cilia is greatly increased by the complex folding of the lining of the tubes. It has long been a question how spermatozoa make
their way up the tubes against the action of these cilia; but the walls of the tubes have strong circular and longitudinal muscular layers, so that it is possible that spermatozoa are carried up the tube by peristaltic waves. The blood supply of the tubes comes from ovarian and uterine vessels. The nerves are sympathetic. (Fig. 347)

The Uterus. The uterus is a median pear-shaped organ suspended in the broad ligament. Round and uterosacral ligaments form additional supports. The body of the uterus is normally bent forward so that it rests upon the bladder. By a constriction, the isthmus, the uterus is divided into an upper body and a lower cervix. Its cavity is connected with that of the vagina below and those of the paired uterine tubes above.

The cavity of the uterus is lined with a simple ciliated columnar epithelium, from which numerous tubular glands of unknown function
grow down into the underlying connective tissue. This mucous lining, the endometrium, is partly lost during menstruation with some extravasation of blood. The thick muscular wall of the uterus consists of interwoven masses of smooth muscle fibers. Uterine and ovarian vessels provide the blood supply. The nerve supply is sympathetic.

The Vagina. The vagina provides the outlet of the reproductive apparatus. It is a highly distensible muscular canal between two and three inches in length, extending from the lower end of the uterus, the os uteri, to the vestibule. Previous to sexual congress its external opening is more or less completely occluded by a membranous hymen. The vagina is lined with squamous stratified epithelium free from glands. Its muscles are divided into circular and longitudinal layers of smooth fibers. Near its orifice the bulbo-cavernosus muscle acts as a sphincter.

External Genitals. The external genital organs in the female form a median longitudinal groove extending from the mons pubis in front nearly to the anus behind. This groove is bordered by two fleshy folds, the labia majora, which contain considerable fatty tissue, and which are somewhat beset with hairs both on their inner and outer surfaces. Usually, the median edges of the labia majora are in contact with one another, thus concealing the remaining parts of the external genitals. Sebaceous and sweat glands are numerous on the median surfaces. (Fig. 350)

Between and more or less concealed by the labia majora is a second pair of integumentary folds, the labia minora, which are devoid of fat
and of hairs. The space between the two labia minora is the vestibule, at the ventral end of which projects an erectile organ, the clitoris. Both urethra and vagina open into the vestibule. On the sides of the vestibule, are the openings of the greater vestibular glands or glands of Bartholin, which correspond with the bulbo-urethral glands of the male.

**Male Reproductive Organs**

**Testes.** The male reproductive glands are lodged in an integumentary pouch, the scrotum, which is divided by a median septum into two compartments. This septum develops through the union of two fleshy folds of skin comparable with the labia majora of the female, the line of fusion being marked externally by a ridge, the raphe. Included in the wall of the scrotum, is a cremaster muscle, the fibers of which are striped, and by contraction lift the scrotum and testes.

The testes are oval glands which have migrated into the scrotum from the body cavity through the paired inguinal canals, and which have both reproductive and endocrinial functions. Attached to the posterior border of each testis is a mass of efferent tubules forming the epididymis. Each testis is enclosed in a tough connective tissue capsule, the tunica albuginea, which penetrates into the substance of the testis as septula and divides the testis into lobules.

The testis is a compound tubular gland composed of convoluted seminiferous tubules which are held together by interstitial connective tissue. In each lobule several of the seminiferous tubules unite into a common efferent tubular outlet. These efferent tubules, the tubuli recti, in turn combine into a network of efferent tubules, the rete testis. From the rete testis pass the efferent ducts which convey the sperm from the testis into the ductus epididymidis. These relations are shown in Fig. 352.

The seminiferous tubules are lined with an irregular many-layered epithelium from which the spermatozoa are proliferated, the multiplica-
tion of cells beginning in the basal layers. During this process a reductional or maturation division takes place previous to the metamorphosis of the cells into mature spermatozoa. All transitional stages in the conversion of epithelial cells into spermatozoa may be seen in a cross section of the seminiferous tubules. The Sertoli cells which occur among the germ-cells are usually assumed to have a nutritive function. As the spermatozoa lose connexion with the epithelium, they pass into the lumen of the tubules, and thus find their way to the epididymis, in which they may be retained for some time. They are contained in a mucous alkaline liquid, also secreted by the epithelium of the seminifer-

![Diagram of the Urogenital System](image)

**Fig. 352.**—The urogenital system—male. The glandular complications of the male urogenital system appear to be in part an adaptation to the double function of the urethra—excretory and reproductive. The alkaline secretions of the glands serve to neutralize the acidity of the urethra caused by the acid urine. (Sobotta.)

uous tubules. Diminution in the activity of the tubules is seen in old age, and may begin as early as thirty-five years.

The interstitial tissue between the seminiferous tubules is believed to have an endocrinal function and to influence the development of secondary sex traits and the vigor of the individual.

Also associated with the testes are certain rudimentary organs, ductuli aberrantes, paradidymis, hydatid of Morgagni, the significance of which will be better understood after the description of their development. Each testis is attached to the scrotum by a connective tissue cord, the gubernaculum.

**Ductus Deferens.** By the efferent ducts of the testis, sperm is carried to the ductus epididymidis, a much convoluted tube twenty or more feet
in length, which together with the efferent ducts forms the **head** of the epididymis. The ductus epididymidis is the beginning of the ductus deferens and, like it, lined with ciliated columnar epithelium. The cilia beat towards the urethra and carry the spermatozoa to the seminal vesicles where they may be temporarily stored. Layers of circular and longitudinal muscles are present in the wall of the duct. At the lower end of the testis the ductus loops back along the tail or cauda of the epididymis, and then leaves the epididymis to join the spermatic cord. As a component of the spermatic cord it passes through the inguinal canal. Entering the body cavity, the ductus leaves the spermatic cord and passes medially to the ureter to enter the prostate gland where it becomes the **ductus ejaculatorius**. As it approaches the prostate, it enlarges into an ampulla and is joined by the duct of the seminal vesicle. Each seminal vesicle is about two inches in length and three quarters of an inch in diameter, formed by an elongated tube four to five inches long coiled within a connective tissue capsule. It secretes continuously an alkaline mucous fluid. (Fig. 352)

**Prostate and Bulbo-urethral Glands.** At the point where the ductus ejaculatorius opens into the urethra, this passage is surrounded by a conical mass of glandular and muscular tissue, the **prostate gland**. The glandular portion of the prostate is formed by fifteen to thirty branched tubular glands. These are embedded in connective tissue containing compact masses of smooth muscle fibers. The development of the prostate shows that it is a modified portion of the wall of the urethra. Its alkaline mucous secretion, produced at times of sexual excitement, has a stimulating effect upon the movement of spermatozoa. Characteristic albuminoid concretions are formed in the alveoli of the gland. In later years of life these concretions increase in size and number and become calcified, so that the lumen of the urethra tends to become occluded by the pressure of the prostate. Embedded in the prostate is a median pouch, the **prostatic utriculus** or **uterus masculinus**, which opens by a median aperture near the openings of the ejaculatory ducts. The utriculus is a rudiment of the embryonic Muellerian ducts which in the female become the uterus.

The **bulbo-urethral** glands or **Cowper's glands** are tubulo-alveolar glands less than half an inch in diameter, embedded in the connective tissue of the urogenital diaphragm near the bulbus urethrae. Their ducts open into the cavernous portion of the urethra. At times of sexual excitement they secrete an alkaline mucous liquid. They appear to be the first portion of the urogenital apparatus which ceases to function in old age.

**The Penis.** The male urethra extends into the intromittent organ, the **penis**. Thus in the male the urethra serves both as an excretory and
as a reproductive outlet. Three portions of the urethra are recognized, prostatic, membranous, and cavernous portions. (Fig. 352)

The body of the penis consists of three masses of erectile tissue, paired corpora cavernosa penis and the unpaired corpus cavernosum urethrae. The latter enlarges at the root of the penis into a bulbus urethrae and terminates at the extremity of the penis as a swollen mass of erectile tissue, the glans penis. In its flaccid condition the glans is covered by the foreskin or prepuce. The paired corpora cavernosa are prolonged into the peritoneal region as far as the tuberosity of the ischium.

![Diagram](image-url)

In this way they form the fixed portion of the penis, the crura penis. To each crus is attached an erector muscle, the ischio-cavernosus.

The nerves of the penis are several. Branches of the second, third and fourth sacral (spinal) nerves are known as erector nerves since their stimulation causes the erection of the penis. Pressure upon the sympathetic centers of the hypogastric plexus also stimulates erection. In a flaccid penis the arterial blood supply is reduced through occlusion of the lumen of the vessels by the contraction of local thickenings of their walls. When, however, the artery is dilated, a free flow of blood into the venous spaces of the corpora cavernosa causes them to become engorged with blood and the penis consequently erected.
DEVELOPMENT OF THE UROGENITAL SYSTEM

The Urinary System

The urinary organs, except the lining of the bladder, are mesodermal in origin, both urinary tubules and ureter being formed from the nephrotome. Strangely enough, three renal organs, pronephros, mesonephros, and metanephros, develop in succession in the human embryo as well as in all amniote embryos. The pronephros in man is a functionless rudiment.

Pronephros. The pronephros or “head kidney” is the anterior-most of the three, and in the human embryo develops from the nephrotomes of segments seven to fourteen. The first of the pronephric tubules makes its appearance in a 1.7 mm. embryo, and all eight tubules are formed by the time the embryo has reached a length of 2.5 mm. Degeneration begins soon and the anterior tubules disappear before the posterior ones are differentiated.

The development of pronephric tubules is initiated by the parietal layer of the nephrotome or intermediate cell mass from which cells are
THE UROGENITAL SYSTEM

Fig. 355.—Stereo,ram of the developing pronephros and mesonephros. (After Kingsley modified.)

Fig. 356.—Drawings to show structure of nephric tubules. A. Pronephric tubule from section through 12th somite of a 16-somite chick embryo. (After Lillie.) B. Diagram of functional pronephric tubule. (After Wiedersheim.) C. Primitive mesonephric tubule with rudimentary nephrostome, from section through 17th somite of 30-somite chick embryo. D. Schematic diagram of functional mesonephric tubule of the primitive type which retains the nephrostome. (After Wiedersheim.) (From Patten's "Embryology of the Chick."
proliferated towards the ectoderm. The nephrotome loses its connexion with the epimere above, and together with the lateral outgrowth just mentioned forms a pronephric tubule. In most vertebrate embryos, pronephric tubules are primarily solid, but become hollow later. As they grow laterally towards the ectoderm, the pronephric tubules also grow posteriorly and unite to form a mass of rapidly dividing cells which continue to extend posteriorly as a cellular rod until they reach the cloaca. Connexion with the cloaca is established and a lumen forms. In this way is produced the **primitive** or **pronephric duct**. Although the pronephric tubules which produced the primitive duct degenerate soon after their appearance, the duct itself persists as the Wolffian or mesonephric duct, so-called because it forms the outlet of the tubules of the mesonephros. In some vertebrates, but apparently not in the human embryo, the pronephric tubules open into the body cavity and persist, at least in part, in the adult as the **ostium tubae** (the anterior opening of the oviduct).

**Mesonephros.** The tubules of the mesonephros are formed from nephrotomes posterior to those which form the pronephros. At its full development in the human embryo, the mesonephros extends from the sixth cervical to the third lumbar segment. Since as many as eighty-
three pairs of mesonephric tubules occur in human embryos, it is obvious that, unlike the pronephros, the mesonephros is not metameric in its origin. While the anterior nephrotomes are segmented, the most posterior mesonephric tubules are derived from a continuous unsegmented nephrogenic cord or intermediate cell mass. At their first appearance, the anlagen of the mesonephric tubules are budded off as solid spherical cell masses, which secondarily attain connexion with the primitive duct, now become the mesonephric duct.

The differentiation of mesonephric tubules takes place thus: The spherical cell-masses elongate towards the mesonephric duct and at the same time acquire a lumen. While the medial portion of the anlage enlarges into a vesicle, the Bowman's capsule, the lateral end unites with the mesonephric duct and finally opens into it. Each vesciculated enlargement is converted into a renal corpuscle by the ingrowth of a knot of capillaries derived from the dorsal aorta. A sharp bend of the mesonephric tubule near the Bowman's capsule divides it into a distal secretory portion and a collecting portion proximal to the duct. These changes, in conjunction with the growth of capillary networks derived from postcardinal and subcardinal veins and the associated enlargement of the genital folds, cause the combined organs to bulge into the body cavity as urogenital folds.

Most of the mesonephric tubules degenerate, only twenty-six pairs remaining in a 20 mm. embryo. In the male, some of these are converted into the efferent ductules of the testes, and in this sex the mesonephric

Fig. 358.—Drawings showing the development of the mesonephric tubules in the pig. d, mesonephric duct; t, mesonephric tubule; cap., glomerular (Bowman's) capsule. (From Patten's "Embryology of the Pig," based upon figures by McCallum and Lewis.)
or Wolffian ducts become the ductus deferentes. It is generally assumed, but not demonstrated, that the mesonephros functions as an excretory organ in the embryo.

**Metanephros.** The definitive kidney of man and other amniotes, the metanephros, is the last to appear in ontogenesis. Like the mesonephros, it has a double origin. The collecting tubules and the ureter are derived from an outgrowth of the mesonephric duct. The cortex of the kidney, on the other hand, arises from the posterior portion of the nephrogenic cord in the lumbar region. In a 6 mm. human embryo, the ureter appears in the form of a hollow outgrowth from the mesonephric duct near its posterior end. At its anterior end, this outgrowth expands into a vesicular enlargement. Growing dorsally, the vesicle comes in contact with the nephrogenic cord which covers it as a cap. As the ureter elongates, the nephrogenic cap is pushed anteriorly, and takes a position dorsal to the posterior portion of the mesonephros. (Fig. 360)

The vesicular enlargement of the ureter becomes the **pelvis.** Two outgrowths from it, one anterior and one posterior, form two **major calyces.** Two more are added later between the first two. Minor calyces arise by the continued subdivision and branching of the major calyces. Further branching to the twelfth generation produces the **collecting tubules** and the medullary portion of the kidney. Those of the fifth generation to the number of twenty to eighty for each renal calyx

![Diagram](image-url)
become the **papillary ducts**, which convey urine from the collecting tubules and which open directly into each of the renal calyces. (Fig. 362)

Each of the collecting tubules terminates in a slight swelling or vesiculated enlargement, upon which a mass of nephrogenic tissue rests as a cap.

From this mass arise excretory tubules, which subsequently acquire connexion with the collecting tubule. Differentiation of the excretory tubules begins with the formation of vesicular cell-clusters which separate from the remaining nephrogenic tissue. These vesicles elongate into excretory tubules; and their ends enlarge to form Bowman’s capsules. Subsequent changes involve the attachment of the tubule to the adjacent collecting tubule, the elongation of the excretory tubule, and the ingrowth
of a glomerulus into the Bowman's capsule. Arterial and venous connexions are subsequently established similar to those of the mesonephros. These changes occur in the later months of intra-uterine life. (Fig. 365)

**Fig. 361.**—Profile reconstructions of lizard (Lacerta agilis) (A) 16 mm. long; (B) 20 mm. long; and (C) human embryo 115 mm. long. a, allantoic stalk; c, cloaca; cc, cranial collecting tubule; cd, caudal collecting tubule; k, permanent kidney (metanephros); mct, median collecting tubule; ms, mesonephros; mt, metanephric (nephronegenic) tissue; mtb, mesonephric tubules; pct, primary collecting tubule; pu, Wolffian duct (primitive ureter); r, rectum; s, secondary collecting tubule; u, ureter; cm, u and pu, common portion of primitive and permanent ureters. (From Kingsley's "Comparative Anatomy of Vertebrates," after Schreiner.)

**Connexions with the Bladder.** During the earlier stages of its development, each ureter shares with a mesonephric duct a common lateral opening into the cloaca. Between 10 mm. and 17 mm. stages, the cloaca becomes divided by a septum into a dorsal rectum and a ventral urogenital
sinus. The septum, which is completed during the seventh week, becomes the perineum of the adult. After the septum is formed the mesonephric ducts and ureters retain their connexion with the urogenital sinus. Even before the development of the septum is completed, in an 11 mm. embryo, the urogenital sinus becomes subdivided into a vesico-urethral portion into which the ureter and mesonephric ducts enter, and a phallic portion which extends into the genital tubercle. By the time the embryo attains a length of 25 mm. (2 months), the ureters and mesonephric ducts are separated, the ureters open into the bladder, and the mesonephric ducts into the urethra. The bladder, therefore, arises not from the allantois
Fig. 365.—Diagrams A–E illustrating the development of collecting and secretory tubules of the kidney. Vesicles derived from nephrogenic tissue become attached to the collecting tubules and thus functionally connected with them. The swollen termination of each secretory tubule encloses a glomerulus and forms a renal corpuscle. E represents an earlier, D a later stage of development. (Redrawn after Corning's "Human Embryology."

Fig. 366.—Diagrams of three stages A–C in the growth and differentiation of a uriniferous tubule. The collecting tubule is shown unshaded. (Redrawn from Arey, after Huber and Stoerck.)
but from the cloaca. The bladder anlage, however, is continued ventrally as the allantoic stalk, which subsequently atrophies to form the middle umbilical ligament.

Fig. 367.—Diagrams illustrating the development of the mesonephros and gonadic ridge. (From Patten's "Embryology of the Pig.")

Reproductive Organs

The human embryo is usually characterized as sexually indifferent. This popular view is based upon the similarity of the anlagen of male and female reproductive glands in the early embryo, and upon the occasional appearance of hermaphroditic adult individuals. According to modern genetical opinion, however, sex is definitely predetermined in the fertilized
egg and is only exceptionally modifiable. Nevertheless, ovaries and testes develop from morphologically similar genital folds, located between the mesonephroi and the mesentery. At their first appearance, the genital folds are elongated masses of epithelial cells, which become differentiated into an external many-layered epithelium and an inner epithelial mass derived from the peritoneum. Together with the mesonephros, the gonad forms a urogenital ridge, the prominence of which is increased by the growth of underlying adrenal tissue. (Fig. 367)

As the genital folds increase in size, longitudinal grooves develop separating them from the lateral mesonephros and the median mesentery. Connexion of the gonad with the mesonephros and with the body-wall is finally reduced to a thin mesentery-like membrane. In the male, this membrane forms the mesorchium and in the female the mesovarium through which blood and nervous connexions are retained. The gonads remain undifferentiated in a ten to twelve millimeter embryo.

**Histogenesis of the Testis.** By the time the male embryo has reached a length of 13 mm., the gonad assumes characteristics which differentiate it as a testis. One of these is the connective tissue tunica albuginea beneath the peritoneal epithelium. Within the medullary region of the gonad, branched and anastomosing testis cords appear, separated by less compact intermediate cords. Two kinds of cells may soon be seen within the testis cords, primordial germ-cells and indifferent cells. Opinion is divided whether the testis cords are formed by ingrowths from the peritoneum or by concentration of epithelial cells within the medulla. Uncertainty also prevails as to the source of the primordial germ-cells. Some assert that they are derived from cells which migrate into the gonad from the intestine. Others claim that they are peritoneal cells which have entered the medulla. The latter opinion seems to have the greater support. The fate of these cells is equally in doubt. Some assume that they are the progenitors of the definitive germ-cells, the spermatogonia, while others believe that they disappear and that the indifferent cells become spermatogonia.

The testis cords converge towards the mesorchium as a center. At the base of the mesorchium, they combine to form the tubules of the rete testis. These in turn unite with tubules of the mesonephros. Finally the testis cords become hollow and differentiated as seminiferous tubules. Epithelial cells within the intermediate cords form interstitial cells which are believed to have an endocrinal function. (Fig. 368)

**Histogenesis of the Ovary.** Differentiation of the ovary is slower than that of the testis. The female embryo is from ten to eleven weeks old (50 mm.) before ovarian characteristics appear. In contrast with the testis, the ovary lacks a tunica albuginea and epithelial cords. At three to five months, the primordial germ-cells in the medullary region
begin to disappear, and a new cortical zone is formed, probably derived from the peritoneum. Rows of primordial ova known as Pflueger's egg tubes extend through the cortex to the medulla. Their arrangement suggests that the egg-tubes are proliferated from the peritoneal epithelium, which therefore is known as germinal epithelium. In late fetal life the primordial ova become surrounded by indifferent follicular cells and differentiated as the definitive ova. The changes in the Graafian follicles have already been described (p. 421). Medullary cords and a rete ovarii comparable with the testis cords and rete testis appear as transient structures in the ovary.

Reproductive Ducts. The mesonephric or Wolffian ducts are utilized by the male as reproductive ducts, the ductus deferentes. Mueller's ducts are also developed in both sexes. Each Mueller's duct arises from a longitudinal groove on the lateral side of the mesonephros. The peritoneal epithelium sinks into the underlying mesenchyma. Except at its anterior end, where it remains open as the ostium tubae, the groove closes over and grows posteriorly as far as the cloaca into which it acquires an opening.

Male Reproductive Ducts. In a three month embryo, the anterior and posterior regions of the mesonephros differ. In the anterior region, which consists of five to twelve renal tubules, the collecting portions of the tubules separate from the excretory portions and acquire connexion with the tubules of the rete testis. In this manner, anterior mesonephric tubules form the ductuli deferentes and serve as outlets for the secretion of the testis. The remaining, posterior, portion of the mesonephros mostly degenerates, remnants persisting as the paradidymis and ductuli aberrantes. The cranial portion of the mesonephric duct increases greatly in length to form the ductus epididymidis. The posterior portion becomes the ductus deferens.

In the male, Mueller's ducts begin to atrophy in the third month. In the adult, remnants of the anterior and posterior extremities may
persist as functionless rudiments. The former is the **appendix testis** and the latter the **uterus masculinus**.

Remnants of the mesonephros also persist in the female. Some anterior mesonephric tubules unite with the rete ovari to form the **epoöphoron**. The posterior part of the mesonephros becomes the rudi-

Fig. 369.—Schematic diagrams to show the relations of pronephros, mesonephros, and metanephros at various stages of development. In the adult male the mesonephric (Wolfian) duct is retained as the ductus deferens. (From Patten's "Embryology of the Chick.")

mentary **paroöphoron**. The functionless remnant of the Wolfian duct in the adult is known as Gartner's duct.

**Female Reproductive Ducts.** Mueller's ducts parallel the mesonephric ducts and open into the urogenital sinus median to them. The position of the primary opening marks the place where later the **hymen** is located. During the fourth month, the posterior portions of the paired Muellerian ducts unite to form **uterus** and **vagina**. The anterior portions form the uterine tubes.
Descensus of Gonads. A comparison of earlier and later stages reveals the fact that the gonads shift their position posteriorly in the body cavity. The prime factor in this backward migration is the continued growth of the posterior portion of the gonads and the associated atrophy of the anterior portion. These processes result in the change of the gonads from an abdominal to a pelvic position. The ovaries retain this position throughout life but the testes migrate into the scrotal sac.

The testis is originally an abdominal organ like the ovary, and its position in the scrotum the result of a migration or descensus in which it drags with it blood vessels, lymphatics, nerves, and the cremaster externus and internus muscles, which, together with the ductus, constitute the spermatic cord.

During the third to the sixth month of development, paired out-pocketings of the body cavity, vaginal sacs, extend ventral to the pubic bones into the scrotal sacs. During the seventh to the ninth month, the testes descend into the scrotal sacs. This "descensus" occurs not into the vaginal sacs but beneath the peritoneum dorsal to the vaginal sacs. Normally, the passage between the body cavity and the vaginal sac is obliterated soon after the migration of the testis (7th to 9th month). Failure to close results in liability to inguinal hernia. The condition of undescended testes is known as cryptorchism and is accompanied by sterility since spermatozoa are unable to survive the normal temperature of the body. The scrotal sac appears to act as a thermoregulator.

The factors involved in the descensus of the testes are complex. Chief among them appears to be the contraction of the connective tissue gubernaculum testis which extends from the testis to the posterior wall of the scrotum. The gubernaculum contracts to one quarter of its original length and after the descensus almost completely atrophies. During the course of its descent, each testis rotates through an arc of 180° so that its anterior and posterior ends are reversed.

Rarely, the ovaries undergo a similar descent into the labia majora. Normally, however, the enlargement and relations of the uterus prevent this migration.
External Genitals. The external genitals of the two sexes, like the gonads, have similar beginnings. Slight differences, however, quickly make their appearance. In an 8 mm. embryo, a rounded eminence, the genital tubercle, develops between the tail and the umbilical cord. Along its caudal surface extends a shallow urethral groove bordered by urethral folds, the inner genital folds. Labial or scrotal swellings, the outer genital folds, border the urethral folds laterally. When the embryo has reached a length of 15 mm., the urethral groove is perceptibly longer in the male. In both sexes the tubercle elongates to form a phallus, the termination of which enlarges as the glans penis or the glans clitoridis.

In the male the urethral folds unite along the median line to form an enclosed tubular urethra, the line of fusion persisting as the raphe of the adult penis. Closure takes place last in the region of the glans and is completed during the fourth month. Some observers state that the scrotal swellings subsequently migrate posteriorly and unite behind the penis, but this is denied by others. An external raphe and an internal septum persist along the line of union of the scrotal swellings. At the end
of the phallus the **prepuce** or foreskin, which encloses the glans, is formed by an ingrowth of epidermis around the glans. By the degeneration of the central cells of this ingrowth the prepuce is separated from the glans except on its anal side, where the glans and the prepuce remain connected by the **frenulum** of the prepuce.

In the female, changes occur more slowly. Instead of closing as in the male, the urethral groove remains permanently open as the **vestibule**, and the urethral folds persist as the **labia minora**. The labial swellings elongate and become in part the labia majora. The elongation of the phallus characteristic of the male does not occur in the female. The glans however persists as the **clitoris**. Consequently, in respect to external genitals, the female is the undeveloped male.

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**External Genitalia**

| | | |
| Genital tubercle | Glans penis | Glans clitoridis |
| Urethral folds | Corpus penis | Corpus clitoridis |
| Labioscrotal swellings | Raphe | Labia minora |
| | Scrotum | Labia majora |
CHAPTER 12

THE ENDOCRINAL ORGANS

One problem of a living organism is to get its organs to work together. In fact, the difference between a living creature and a dead one is that the living organism is integrated and the dead is not. Moreover, the more complex an organism, the more difficult it is to secure functional correlation among its different but interdependent parts, and the more complicated is the mechanism which accomplishes this end.

![Diagram of endocrrinal glands in man.]

This functional integration of the animal body is brought about by two means, one nervous, the other chemical. In general, quick adjustments, muscular activities and correlations, and responses to the outward environment are controlled by the nervous system. But growth, for example, metabolism, and in general the adjustment of the several tissues to one another, is largely taken care of by the ductless or endocrine glands, which secrete into the blood stream minute quantities of so-called hormones that speed up ordinary chemical reactions. With the discovery
that nerves produce neurohumors which act in the manner of hormones, the contrast between nervous and endocrinial action does not appear as great as was formerly thought.

In a sense, every organ acts as an endocrine gland toward every other. All, for example, as a result of their metabolism, form CO₂, which diffuses into the capillaries, and is carried by the blood stream to other parts of the body. But any increase in the CO₂ content of the blood affects the respiratory center in the medulla and increases the activity of the breathing muscles. Strictly, however, the term endocrine organ is restricted to those only which secrete hormones that act somewhat specifically and usually on particular tissues. But there is no hard and fast line to be drawn.

The word "hormone" was first used by Bayliss and Starling in their description of the chemical regulation of the secretion of the pancreatic digestive juices. They discovered that when hydrochloric acid enters the intestine from the stomach, the digestive secretion of the pancreas is poured into the intestine. But the same effect was produced even when all nervous connexions had been previously cut. Therefore, they concluded, the connexion must be chemical, by way of the blood; and they were led to postulate a chemical messenger or hormone produced by the epithelial cells lining the duodenum. They gave to this substance the name secretin. Their results have been repeatedly confirmed, and endocrinologists include the duodenum in the list of endocrine organs.

THE PANCREAS

General interest in endocrine organs was increased by the important discovery that the pancreas has an endocrinial as well as a digestive function. Scattered among lobules of the pancreas, are aggregations of lightly-staining cells, the pancreatic islands or islands of Langerhans. It has been shown that these islands secrete a hormone, named by its discoverers insulin. While its chemical formula remains uncertain, the substance has been extracted from the pancreas of animals, and is used in the treatment of diabetes. Insulin poured into the blood has the function of regulating the oxidation of carbohydrates in the tissues and the storage of glycogen in the liver. How this is done is an unsolved problem.

Both deficiency and excess of secretion of insulin is dangerous, and often fatal. Diabetes results from too little insulin. The liver fails to convert sugar into glycogen, and the excess of sugar in the blood is eliminated by the kidneys, so that sugar in the urine and excessive urination are among the symptoms. As a result of this loss of sugar, the tissues are obliged to burn their reserves of fat and protein, and the patient becomes emaciated. Acidosis and death follow in the absence of
proper medical treatment. Today, however, as a result of the discovery of insulin and the part it plays in life, thousands of people who a generation ago were destined to prolonged suffering and premature death are able to live a fairly normal life.

Pancreatic islands occur in all classes of vertebrates, usually in connexion with the pancreas, though in some bony fishes the two glands are independent. Both arise from the endoderm, but there is no evidence that pancreatic gland cells are ever converted into cells of the blood-islands.

THE GONADS

Male Sex Glands. The structure and development of the male gonads have already been described in detail. We are now concerned with their endocrinal function. It has long been known that removal of the gonads in childhood prevents the appearance of secondary sex characters of the male, such as beard, deeper voice, broadened shoulders, etc., the castrated individual becoming a eunuch and lacking the virile traits of the normal male. Evidently, then, the appearance of those traits which distinguish male from female depends upon some physiological action of the testes. That this is an endocrinal effect of the interstitial Leydig cells of the testes and not of the seminiferous tubules which produce the spermatozoa, may be inferred from the fact that male traits develop in the absence of the seminiferous tubules, provided only that the interstitial tissue is
present. The individual without seminiferous tubules must, indeed, be sterile, but he has the secondary traits of the male. This condition occurs when the testes fail to descend into the scrotal sac.

Although, according to present genetical opinion, primary sex differences are already determined in the fertilized egg by the chromosome complex, there is, nevertheless, plenty of evidence that endocrines influence the secondary sex traits, the first striking evidence appearing at puberty when the boy assumes some of his adult male characteristics. That the chromatin constitution of the body cells has little or no influence on sex is proved by the fact that, if ovaries are grafted in place of testes, the individual takes on female characteristics. Crew cites the case of a fowl which was successively a mother and a father as a result of the destruction of the ovary by disease and subsequent growth of a testis in place of the ovary. Further evidence of the influence of endocrines early in development is afforded by the "freemartin." When a cow gives birth to twin calves, one male and one female, the latter is sterile and shows some male characteristics. In this case, the primary sex is probably determined in the fertilized eggs. But since the twin calves are attached to a single placenta and share a common blood stream, the male endocrine not only sterilizes the female, but also gives her masculine traits from which she never recovers. Precisely how the male endocrine dominates over the female is as yet an unsolved problem.

THE FEMALE SEX GLANDS

In the ovary, as in the testis, interstitial and germ cells may be distinguished. That the interstitial cells have an endocrinal function, is suggested by the fact that they increase during pregnancy. The argument from analogy with the testis has less weight.

There is also the following evidence that the Graafian follicles have an endocrinal as well as a reproductive function. Before puberty, the follicles mature in the ovary, but are not discharged. Instead, they atrophy and the follicular liquid is reabsorbed into the blood, so that any endocrine which the liquid may possibly contain enters the blood stream to influence growth and development.

At puberty, however, when a follicle, instead of degenerating, discharges its egg, the follicular liquid stimulates changes in the uterus, which prepare it for the implantation of the fertilized egg. At the same time, correlated changes take place in the ovary. Of the follicular cells which are left behind in the ovary when the ovum is discharged, some undergo rapid multiplication and become converted into the fatty cells of a corpus luteum. (Fig. 344)

The fate of the corpus luteum depends upon that of the ovum discharged. If the ovum is fertilized and pregnancy occurs, the corpus
luteum persists throughout pregnancy and for some time subsequently. If, on the other hand, the ovum is not fertilized, the corpus luteum degenerates in a few months and forms a transient structure, the **corpus albicans**.

Observed facts convince physiologists that at least two hormones, the follicular and the luteal, are secreted by the ovary. The causal relation between follicular secretion and menstruation is demonstrated by the fact that menstruation follows the discharge of the follicular secretion and ceases when the ovaries are removed. Furthermore, the follicular hormone, theelin, is used in cases of delayed menstruation and puberty. Definite physical changes in a woman follow the menopause when ovulation stops. Facial hairs tend to grow. Fat is deposited on parts of the body. The breasts tend to atrophy. Nervous and mental disturbances are likely to arise.

A mature animal from which the ovaries are removed fails to manifest the normal reproductive instincts, for example, estrus or "heat." An immature animal which is ovariotomized fails to develop secondary sexual traits, and remains throughout life infantile and sexually neutral. Experiments indicate that estrus in animals depends upon the follicular hormone. Follicular liquid injected into young female rats brings them to sexual maturity in a few days. Injected into adult

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**Fig. 375.**—A diagram of the interactions of pituitary, follicular and luteal hormones. (Redrawn after Dickinson’s “Sex Anatomy,” Williams & Wilkins Co.)
females from which the ovaries have been removed, the estrus which had been lost recurs.

The follicular hormone, theelin, has the chemical formula C\(_{18}H_{21}O_3\) and is a fatty substance, soluble in alcohol and other lipoid solvents. It is used hypodermically to induce puberty and menstruation. It is now sold as Theelin, Progynon, and under other names. Its use may cause abortion.

One of the names for the corpus luteum hormone is progestin. Its action is antagonistic in some effects to that of theelin, for, while theelin acts as a sex stimulant, progestin prepares the uterus for the reception of the ovum. In animals, experimental removal of the corpus luteum early in pregnancy causes abortion. Progestin prevents ovulation and menstruation in pregnancy.

Fig. 376.—Shows the suprarenals in relation to the kidneys as seen when the fat which normally encloses them is removed. The relations of the blood vessels which supply them are also shown.

THE SUPRARENAL GLANDS

Anatomy. The suprarenals or adrenals of man are two small glands, each averaging only four to five grams in weight, and each, as the names suggest, lying like a cap upon the upper end of a kidney, embedded usually in the same mass of fat. Accessory adrenals also occur not infrequently near the kidneys or the gonads. From their relation to kidneys, the adrenals were once assumed to be also excretory. Later discovery that their removal or destruction results in death has made them objects of much interest and research.

The adrenal gland has a rich blood supply. Arterial blood comes from three sources, phrenic, aortic, and renal vessels, which give off respectively the superior, middle, and inferior suprarenal arteries. The gland is drained by the right and left suprarenal veins, the former connected with the postcava, the latter with the left renal. Lymphatic vessels are abundant.
**Histology.** An adrenal has two kinds of tissue, an outer yellowish cortex and an inner brownish medulla. The cortex is subdivided into three layers, an outer glomerular layer composed of rounded clusters of epithelial cells, a middle fasciculate layer of rounded cells arranged in cords perpendicular to the surface, and an innermost reticular layer in which the cellular cords unite in a network. The central or medullary portion of the adrenal is characterized by relatively large "chromaffin" cells, so-called because they have a strong affinity for chromic salts, which stain them brown. They are arranged in clusters separated by numerous lacunar blood spaces. A compact connective tissue capsule encloses the glandular tissues. (Figs. 377, 378)

**Physiology.** The adrenals have a double function corresponding with their histological differentiation into two tissues. The cortex secretes an endocrine, cortin, of unknown chemical composition, which is essential to life. Destruction of the cortex by tuberculosis or tumor is followed by Addison's disease, which is characterized by a deep pigmentation of the skin and great weakness. Death comes rapidly unless cortin is administered. The effect of cortin is, however, immediate, and the patient suffering from adrenal failure promptly arises as though from the dead.

The cortex of the adrenal is, relatively to the medulla, largest during foetal life, and there is little doubt that its secretions have a strong influence upon growth. Excessive activity of the gland induces precocious development. The stages of life are so speeded up that a child of four or five may look like an old person. Hyperactivity of the cortex also...
intensifies masculine traits, so that a woman may acquire the beard and deep voice of the male. The "bearded lady" of the side show is a familiar example.

The endocrine secreted by the medullary tissue of the adrenal is epinephrine or adrenin, its empirical chemical formula being \( C_{9}H_{13}O_{3}N \).

**Fig. 378.**—A diagram illustrating the complex interrelations of the endocrine organs. The multiplicity of pituitary influences is only partially indicated. For the sake of clearness the diagram over simplifies the relations. The pancreatropic, ketogenic, and parathyreotropic factors are not thoroughly understood. (Adapted from Therapeutic Notes through courtesy of Parke, Davis & Company.)

Most commercial adrenin is now made synthetically and not derived as an extract from animal tissue. Like the sympathetic nerves, adrenin has a stimulating effect upon smooth muscle. Since sympathetic nerves and the chromaffin cells of the medulla have a common origin in the embryo, this similarity of function might be expected. It is so potent a drug that its physiological effects appear even when it is diluted to one part in 400,000,000 of blood.
Cannon's well-known experiments upon animals led him to his emergency theory of adrenal action. He found that in a quiet undisturbed animal adrenin is absent from the blood. When, however, the animal is excited by pain, fear, or anger, adrenin increases. As a result, the heart beats more strongly, breathing becomes deeper and more rapid, intestinal action ceases, the liver releases sugar more rapidly, the muscles respond more quickly to stimulation, the tonus of the blood vessels is raised, the coagulability of the blood increases, and so the animal is prepared either to run or fight. Thus the medullary secretion reinforces the action of the sympathetic nerves.

Cannon has also shown that a substance which resembles adrenin in its effects is given off by organs stimulated by the sympathetic nervous system. This substance, the chemical nature of which is unknown, has been called sympathin.

Development. Corresponding with its double function and its division into cortex and medulla, each adrenal has a double origin. The cortex develops from mesoderm, while the medulla is derived from sympathetic ganglia and is therefore ectodermal in origin. In the human embryo of 6 mm., the cortical substance makes its first appearance as a proliferation of the coelomic epithelium near the root of the mesentery. The cells of the anlage lose their connexion with the epithelium and take positions at the sides of the abdominal aorta. There is no evidence of a segmental origin.

The cells of the medulla, on the other hand, come from the chain of sympathetic ganglia. In a 6 mm. human embryo, the cells which later form the adrenal medulla may be distinguished in the ganglia by their affinity for chromic acid which stains them brown while other cells of the ganglia remain unstained. The migration of chromaffin cells into the adrenal cortex begins in embryos of seven weeks (17 mm.) and may continue until after birth. In embryos of the third month, the adrenals are more conspicuous organs than the kidneys, but as development proceeds, they fail to keep pace with the enlargement of the body.

Evolution. Adrenal glands are limited to vertebrates. Homologous organs are lacking in invertebrates and protochordates. In Cyclostomes, both the cortical layer and the chromaffin are present, but are spatially separated. The cortical substance is represented by clusters of cells, the interrenal bodies, which lie throughout the length of the body cavity near the post-cardinal veins. The chromaffin cells, on the other hand, are arranged as strands along the dorsal aorta. In the Elasmobranchs, the interrenal bodies tend to aggregate in the posterior part of the body cavity, while the chromaffin cells are arranged in metameric groups near the sympathetic ganglia.
In the amphibia the organization of the adrenals is intermediate between that of elasmobranchs and that of amniotes. Chromaffin and interrenal cells lie in close proximity to one another. The two kinds of tissue are usually interspersed and extend along the surface of the mesonephroi. In some amphibia the chromaffin tissue surrounds the interrenal cells. The relations of the two tissues vary considerably in reptiles. In some, though not in all, the chromaffin cells, as in fishes, are separate from the interrenal bodies. In crocodiles and tortoises, however, the two tissues are mixed as in amphibia. Strands and clusters of chromaffin cells are embedded within the interrenal tissue. In birds also the two kinds of tissue are intermingled. Finally, in mammals, the interrenal tissue forms a cortex which encloses the chromaffin cells as a medulla. The quantity of cortical tissue in mammals greatly exceeds that of medullary (chromaffin) tissue.

THE THYROID GLAND

Anatomy. The thyroid gland of man is a bilobed brownish organ closely apposed to the trachea just below the larynx. The lateral lobes are generally connected by an isthmus across the trachea, so that the shape of the gland varies from a "U" to an "H," depending upon the relative position of the isthmus. Not infrequently, especially in younger persons, there is a median pyramidal lobe. The accessory thyroids which sometimes occur are usually remnants of this pyramidal lobe. There is, also, occasionally another accessory gland beneath the upper end of the sternum.

Although the size of the thyroid varies greatly in different individuals, the average weight is thirty-four grams. The connective tissue capsule surrounding the gland is a double membrane. Suspensory ligaments of connective tissue attach the thyroid to the tracheal and laryngeal cartilages.

The blood supply of the thyroid, like that of the adrenals, is exceptionally abundant. Four, and frequently five, arteries connect with the organ; seven veins drain the blood away. The arteries are the paired superior and inferior thyroid, and the occasional thyroidea ima. On the surface of the gland, a plexus of veins gives rise to paired, middle, and inferior thyroid veins and to the unpaired thyroidea ima. Lymphatics are abundant. The nerve supply is sympathetic.

Histology. The thyroid is formed of numerous spherical masses of glandular tissue, separated from one another by connective tissue partitions. The glandular tissue consists of rounded follicles, each enclosed by a single layer of cuboidal epithelium. Loose connective tissue filled with blood vessels and lymphatics binds the follicles together. Each follicle is filled with jelly-like colloid material which has a strong affinity
for acid dyes such as eosin. The colloid is evidently a secretion of the cuboidal epithelium and is generally assumed to be a store of the hormone.

**Physiology.** The most important, if not the exclusive, endocrinal secretion of the thyroid gland is an iodine compound thyroxine, the empirical chemical formula for which is $\text{C}_{15}\text{H}_{11}\text{O}_4\text{N}_4\text{I}_4$. A substance with identical properties has been made synthetically, and it is generally the synthetic drug which is used in medical practice.

One function of thyroxine is to control metabolism, especially of the carbohydrates, a thirtieth of a grain increasing oxidation by one percent. Many commercial flesh-reducing preparations, therefore, contain thyroxine, often in dangerous quantity. It regulates also growth before birth, through infancy, and at puberty, so that, in no small measure, we are what we are in virtue of our thyroid glands. Tadpoles fed with thyroid may become frogs no larger than flies.

Excessive activity of the gland is a common malady, manifested by extreme nervousness, rapid pulse, insomnia, and basic metabolism above normal, so that the patient loses weight. In man, exophthalmic goitre is one of the common manifestations.

As too much thyroxine speeds up the life processes, too little slows them down. Basal metabolism is low, so that the tendency is to put on fat. In the young, both growth and development are retarded; and if the deficiency is very great, a child, unless given thyroid artificially, may become an idiotic dwarf not unlike a cretin.

Iodine is needed for the production of thyroxine, and in regions where iodine is lacking in the food, as in the central states of America and in the Alps, the glands may attempt to make up the deficiency by enlargement and increased secretion. This results in the more usual form of goiter. The remedy is to add potassium iodide to the diet.

**Development.** In man, as in other Vertebrates, the thyroid gland arises as a median ventral outgrowth from the floor of the pharynx at the

![Fig. 379.—A portion of a section of the thyroid gland enlarged, showing the secretory epithelium and the colloid-filled follicles.](image)
level of the first visceral pouch. For a while the anlage of the thyroid retains connexion with the floor of the pharynx by means of the thyroglossal duct. When, at a considerably later stage of the development, the tongue forms, the point of connexion of the thyroglossal duct is indicated by a pit, the foramen cecum, near its posterior border. The thyroglossal duct persists for some time in the embryo, and becomes gradually elongated as the gland anlage grows backward to take its definitive position on the sides of the trachea. Eventually, however, connexion with the tongue is lost. The median lobe of the gland, if present, develops from the thyroglossal duct, and the accessory thyroids frequently come from the same source. The lateral lobes increase in size more rapidly than the median portion which persists as the isthmus. (Fig. 380)

**Fig. 380.—Longitudinal section of head of 19-day Petromyzon embryo. ch, optic chiasma; ep, epiphysial outgrowth; h, hypophysial ingrowth; mes, mesenteron; n, nasal epithelium; nc, notochord; oc, oral cavity; op, oral plate; sc, canal of spinal cord; th, thyroid. (From Kingsley's "Comparative Anatomy of Vertebrates.")**

**Evolution.** The thyroid gland is a peculiarity of chordates, and is found in all classes of this phylum. Since no homologous structure is known in non-chordates, we must assume that the gland, like the notochord, emerged with the phylum from unknown non-chordate ancestors. In the hemichordates, the only possible homologue of the thyroid is a groove apparently functionless in the floor of the pharynx. The urochordates and cephalochordates have a ciliated groove, the endostyle, in the floor of the pharynx. This groove is morphologically, if not physiologically, comparable with the thyroid.

In Amphioxus, a typical cephalochordate, the endostyle is lined by columnar epithelial cells of two sorts, glandular and ciliated. Four rows of gland cells alternate with rows of ciliated cells which extend the entire length of the pharyngeal floor. Particles of food caught up in the mucus are swept forward towards the mouth, and are carried by a ciliated circumpharyngeal groove to a median epibranchial groove, which carries them posteriorly to the intestine. It has been suggested that the epibranchial groove is represented in vertebrate embryos by the **hypochorda**, a transient embryonic structure below the notochord, which disappears during ontogenesis.
The endostyle of petromyzon larvae, like that of amphioxus, is a mucus-secreting organ with four rows of mucus-secreting cells alternating with rows of ciliated cells. This larval endostyle, however, is a transient structure which develops into the thyroid gland of the adult animal. Connexion of the anlage with the pharynx is eventually lost, and the organ becomes vesiculated like the thyroid of higher vertebrates. The vesicles secrete colloid, and the function is evidently endocrinial. The homology of the thyroid gland and endostyle is further attested by the fact that in the cyclostome Bdellostoma the median groove from which the thyroid gland develops extends the entire length of the floor of the pharynx, precisely as does the endostyle of Amphioxus. In fishes, as in cyclostomes, the thyroid is usually unpaired. A subdivision into two lobes is, however, characteristic of Amphibia.

In reptiles, the gland is again unpaired and remains unpaired in most mammals, with a tendency to form lateral lobes as in man. The position of the gland is fairly constant, ventral to the trachea and just below the larynx.

Evidence has been given (p. 335) that the endostyle is a modified gill pouch. The history of the thyroid therefore reveals a complete change of function such as we have already seen to be a general characteristic of pharyngeal structures.

**THE PARATHYROID GLANDS**

**Anatomy.** The parathyroid glands in appearance resemble lymph nodes, and are usually four in number in man. Their diameter varies from three to thirteen millimeters. Their position is also variable. They generally lie dorsal to the thyroid, but may be occasionally enclosed within its connective tissue capsule. This relation, however, is purely topographical; there is no functional similarity. Their blood supply is from the inferior thyroid arteries.

**Histology.** Unlike the thyroids, the parathyroids are formed of masses and cords of polygonal epithelial cells, among which numerous blood vessels are interspersed. Colloid-filled follicles are rare; but they multiply in number when the thyroid is removed, and may take over the function of the thyroid in an emergency.

**Physiology.** While, therefore, an animal may lose its thyroid glands without necessarily fatal consequences, the removal of the parathyroids is followed by convulsions and death unless parathyroid extract is administered intravenously. The effects of loss of parathyroids resemble those which follow the use of strychnia or the bite of a mad-dog. There is a marked fall in the calcium content of the blood, followed by cramps and muscular tetany. Apparently calcium salts act as a nerve sedative to prevent acute stimulation of muscular contraction, so that hypopara-thyroidism has been thought to be one of the causes of extreme irrita-
bility and "touchiness." The injection of parathyroid extract into the blood is followed by a rapid increase in blood calcium, so rapid that a slight overdose may cause death, for the chemical balance of the blood must be delicately regulated to maintain normal health. The chemical nature of the parathyroid endocrine is not yet known.

On the other hand, even a slight over activity of the parathyroids may have serious consequences. The reserve supply of calcium for bodily use is limited, and excess of parathyroid endocrine in the blood may cause the withdrawal of calcium from the bones and teeth, which lose their hardness and become fibrous.

![Diagram](image_url)

**Fig. 381.**—Diagram to show the derivatives of the branchial pouches. *Ie, Ile, IIIe. IVe, Ve, external branchial grooves; II, IIIi, IIIi, IVi, internal branchial pouches; TA, auditory tube and tympanic cavity; Tons., palatine tonsil; EpIII, EpIV, parathyroid glands; Ub, ultimobranchial body; Th., thyroid gland. D.th.gl., ductus thyroglossus. (From Morris, after Keibel and Mall.)

Since calcium and phosphorus metabolism are also dependent upon the presence of vitamin D in the food, the problem of calcium balance is not simply a problem of endocrinology.

In brief, the action of the parathyroid endocrine resembles that of a catalyst which facilitates the manufacture of calcium salts in the body and thus helps to regulate the irritability of the nerves.

**Development.** In the human embryo, the parathyroid glands are formed from the epithelium of the third and fourth pharyngeal pouches. By proliferation from the dorso-lateral wall of these pouches are formed masses of cells which soon lose connexion with the pouches and migrate caudally. In this migration they become closely associated with the anlagen of the thymus gland. The cells of the third pouch are carried
back as far as the posterior border of the thyroid gland. The migration of the cells of the fourth pouch is less extensive, and they usually come to lie near the anterior border of the thyroid. The epithelial character of the cells of the parathyroid is retained during the histogenesis of the gland. Mesenchyme cells work their way into the anlage, forming blood vessels and breaking up the cellular mass into cords. (Fig. 381)

**Evolution.** Parathyroid glands occur in all vertebrates except fishes, making their first appearance in Amphibia in which the gills have begun to degenerate. The factors involved in the emergence of their endocrinal function are at present speculative, since to say that they owe their origin to gill degeneration means little. Comparison of lower with higher vertebrates reveals a progressive reduction in number but apparent increase in endocrinal importance.

**THE ULTIMOBRANCHIAL BODIES**

Among the pharyngeal derivatives which may have an embryonic endocrinal function are the ultimobranchial bodies, called also postbranchial and suprapostcardial bodies. These are paired glands which arise from or near the fifth pair of gill-pouches. They come to lie near the posterior border of the thyroid and attain a vesicular structure.

**Evolution.** Ultimobranchial bodies occur in all gnathostomes except possibly teleostome fishes. In Amphibia, the gland may be paired or unpaired. It is not unlikely that, as its name suggests, it represents a posteriormost pair of gill-pouches modified as an endocrinal organ. In man it persists only as a transient embryonic structure the function of which has become that of an endocrinal organ. (Fig. 381)

**THE THYMUS GLAND**

**Anatomy.** The thymus glands or throat sweetbreads are paired organs located where the throat joins the chest. They are pinkish in color in childhood, but become yellow in old age from fatty degeneration. They enlarge up to puberty and thereafter gradually shrink. Contrary to earlier opinion, the gland does not completely disappear in the adult, but persists as a shrunken remnant within the mediastinum.

Branches of the subclavian or of the internal mammary artery supply the gland with blood. Its numerous veins drain into the internal mammary or the inferior thyroid. Lymph vessels are abundant. The nerves are sympathetic nerves derived from the vagus.

**Histology.** From the connective tissue capsule of the gland, partitions extend inwards and divide it into lobes and lobules. In each lobule a cortex and medulla are distinguishable as in a lymph node, but the large lymph sinuses in the medulla, and the germinal centers which are present in lymph nodes, are lacking in the thymus. The resemblance of the
thymus tissue to adenoid tissue makes it probable that it is a lymph-forming organ, whatever other functions it may have. The most striking histological characteristic of the thymus is the presence of thymic or Hassall's corpuscles, relatively small clusters of concentrically arranged epithelial cells, usually assumed to be degenerate and non-functional.

**Physiology.** The endocrine function of the thymus is doubtful, since removal of the gland is not followed by disturbances of normal functions. The enlargement of the gland in early life and its later atrophy suggest that its functional activity may be limited to stages of growth and differentiation.

Hypertrophy of the thymus sometimes accompanies that of other lymphatic organs, the condition being known as **status thymicolymphaticus.** It results in serious metabolic disturbances and sometimes even death. Adults in whom the thymus does not atrophy may die suddenly under ether.
**Development.** Thymus glands first appear in a six-weeks embryo as hollow tubular outpocketings of the third pair of pharyngeal pouches, dorsal to those of the parathyroid glands. As they grow caudally, the anlagen become solid and considerably elongated, the anterior part atrophies, and the posterior enlarges. In the tenth week, after the gland attains its definitive position in the mediastinum, thymic corpuscles appear. By the third month, cortex and medulla are differentiated, and the gland assumes the appearance of a lymph gland. Enlargement continues until puberty. (Fig. 382)

**Evolution.** Thymus glands are peculiar to vertebrates but occur in all members of that sub-phylum. In cyclostomes all gill-pouches give rise to thymic tissue and the gland persists dorsal to the gills throughout life. Ventral anlagen have also been described. In fishes there is a reduction in the number of thymus anlagen, since some of the gill-pouches make no contribution to the thymus. In amphibia the thymus is further reduced, and comes to lie at the angle of the jaw. The thymus glands of reptiles are lobular organs located in the sides of the neck. In mammals the third pair of pharyngeal pouches, or sometimes the third and fourth, produce the cells which form the thymus. The gland assumes its definitive position in the mediastinum at the base of the neck. The history of the thymus is thus one of reduction in the number of gill-pouches which contribute to the gland. However, in some orders of mammals, such as marsupials, rodents, ungulates and prosimians, a new type of thymus gland appears, the cervical thymus, which is said to be of ectodermal origin. It is of relatively small size and of unknown function.

**THE PITUITARY GLAND**

**Anatomy.** The pituitary gland is a flattened oval body, its longest diameter averaging 10 to 12 mm., located at the base of the brain near the optic chiasma, where it is attached by a stalk to the lower end of the infundibulum. Lodged in a cavity, the sella turcica, in the sphenoid bone, the pituitary is as safe from injury as possible. (Figs. 285-383)

Like the suprarenals, the pituitary is formed of two elements of diverse origin and function. The chief parts are a larger anterior glandular lobe, which develops from the ectoderm of Rathke's pouch, and a smaller posterior nervous lobe derived from the floor of the brain and partly surrounded by the anterior lobe. Between the two major lobes are two smaller glandular masses, the pars intermedia and the pars tuberalis. Blood is richly supplied from the adjacent arterial circle, while numerous veins drain the blood into the venous circle and the basilar plexus of veins. Nerves are supplied from the carotid plexus and the infundibulum.

**Histology.** The anterior lobe consists of cords of epithelial cells interspersed among numerous blood and lymph spaces. In their staining
properties, these cells vary from cells with strong affinity for dyes to those with weak affinity. Some are acidophilic, some basophilic. The acidophilic cells are conspicuous in cases of gigantism, while sex derangement is associated with changes in the basophilic. In the pars intermedia some colloid-filled follicles resembling those of the thyroid occur among the cell cords. The cells of the posterior lobe are chiefly neuroglia cells with numerous connective tissue fibers. (Fig. 384, F)

**Physiology.** One of the important functions of the anterior lobe is the stimulation of growth. Enlarged pituitary in early life is accompanied by excessive bone growth. Deficient secretion, on the other hand, produces a certain type of dwarf, the ateliotic dwarf or “midget.” Administration of anterior lobe extract has in some instances increased the height of such dwarfs.

After the growth of the long bones has ceased, as in the normal adult, it is of course impossible to stimulate further growth in height. But when, as the result of tumorous enlargement, anterior lobe secretion is increased, a local growth of bone, sometimes asymmetrical, may occur. Such cases of acromegaly are not infrequent. Another effect of excessive pituitary secretion is increased hairiness, like that caused by hypertrophy of the adrenal cortex.

Removal of the anterior lobe in young animals is followed by cessation of growth and by increase in fatty tissue. In this way it is possible to produce ateliotic dwarfs experimentally. Experiments also demonstrate that deficiency of anterior lobe hormone in young animals results

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**Fig. 383.—The human brain in median section and aspect.** The pituitary gland (hypophysis) is attached to the infundibulum of the brain and embedded in the sella turcica of the sphenoid bone. (Redrawn after Sobotta.)
in failure of sexual development and atrophy of the sex glands. Another effect is reduced secretion by the suprarenal and thyroid glands, so that it is quite possible that the effect of the pituitary upon sexual development is indirectly through the effect upon suprarenals and thyroid.

While the histological structure of the posterior lobe does not suggest a glandular function, treatment with extract of the posterior lobe causes a marked rise in blood pressure. Two kinds of substances which act as endocrines have been obtained from the posterior lobe of the pituitary. One of them, vasopressin, increases blood pressure; the other, oxytocin, stimulates the contraction of the muscles of the uterus and is now used following childbirth to bring the uterus back to normal size. Posterior lobe extract is found to reduce obesity and certain types of obesity are now ascribed to deficiency of this hormone. Increase of posterior lobe secretion causes decreased urination, possibly brought about indirectly through the nervous system.

The wide-spread and contrasting effects of the secretion of the pituitary, which may have as many as eight different hormones, taken together with the experimental evidence of the mutual interaction of endocrinial organs, demonstrates the enormous complexity of the problem of the biology of endocrines. Under the circumstances, we may follow Hoskins in suggesting that "To those who, in the present state of our knowledge, would glibly re-write physiology and psychology in terms of pituitary functions the timorousness of the proverbial angel is commended."

**Development.** The pituitary gland has a double origin. The anterior lobe comes from an ectodermal sac, Rathke's pouch, in the roof of the mouth, while the posterior lobe is formed as an outgrowth of the base of the diencephalon. Rathke's pouch makes its appearance in a 3 mm. embryo. The posterior end of this sac comes into contact with the infundibular outgrowth from the base of the brain. As development proceeds, Rathke's pouch loses connexion with the ectoderm and breaks up into vesicles, the cavities of which are remnants of the pouch cavity. In this way, the anlage of the anterior lobe assumes its definitive position anterior to the infundibulum. The ventral end of the infundibulum becomes thickened as the anlage of the posterior lobe. The anterior lobe enlarges and partly surrounds the posterior lobe. The cells which later become differentiated as **pars intermedia** and **pars tuberalis** are derived from the anlage of the anterior lobe. By the end of the fourth month, the gland attains its adult form and appearance. Blood vessels and connective tissue capsule are of mesenchymatous origin.

**Evolution.** The pituitary gland occurs only in vertebrates. No comparable structure has been identified in the protochordates. The elements of the pituitary make their first appearance in cyclostomes. In myxinoids (Myxine, Bdellostoma) the neural (posterior) lobe is repre-
sent by the epithelial ventral termination of the infundibulum. The anterior lobe is represented by the hypophysial duct, an ectoderm-lined tube, which opens in front of the mouth anteriorly and into the pharynx posteriorly. Into this duct the paired olfactory pits open. The only element of the myxinoid pituitary which is glandular is the intermediate lobe, represented by clusters of cells lying between the infundibulum and the hypophysial duct. These cells are proliferated from the ectoderm of the hypophysial duct, just as in embryos of the higher vertebrates the cells of the intermediate lobe are proliferated from the hypophysis (Rathke's pouch). The scarcity of blood-vessels in the region of the intermediate lobe of the pituitary in cyclostomes makes it seem likely that, if it has an endocrinal function in this group, its secretions are poured into the infundibulum. Since the epithelium of the infundibulum and of the hypophysial duct is not thickened but remains single-layered in myxinoids, there is no evidence that these elements in this group have an endocrinal function. Stendell, therefore, seems justified in the conclusion that the intermediate lobe is the first part of the vertebrate pituitary which is differentiated as an endocrinal organ. (Fig. 384)

An advance in the evolution of the pituitary is found in Petromyzon. In this animal, as in all higher vertebrates, connexion of the hypophysial duct with the pharynx is lost and the organ ends blindly at its posterior end. From it, however, are proliferated cells into the region between the duct and the infundibulum. The cells which take a position next
to the infundibulum form the intermediate lobe. Other clusters of
cells nearer the hypophysial duct produce hollow vesicles which are
believed to represent the beginning of a glandular anterior lobe. Since
the remainder of the embryonic hypophysis persists in the adult as a
blind pouch and is not, as in higher vertebrates, converted into anterior
lobe, it is evident that the anterior lobe of the pituitary of Petromyzon
is only partially homologous with that of the higher vertebrates. The
nervous lobe of the pituitary can hardly be said to exist in Petromyzon.
In this animal where the infundibulum is in contact with the cells of the
intermediate lobe, the epithelium is slightly thickened and the infundibu-
num shows a well-marked hypophysial recess.

The evolution of these elements which have their inception in cyclo-
ostomes may be briefly summarized. As one passes through the verte-
brate series from fishes to man, all three elements seen in cyclostomes are
present. The anterior lobe steadily increases in relative size while the
intermediate lobe shrinks. An increase takes place in size and differentia-
tion of the posterior lobe. The presence of colloidal material in the
pituitary in all vertebrate groups justifies the assumption that the gland
has an endocrinal function throughout the series. In elasmobranchs
the nervous portion of the gland is only slightly indicated. The region
of the infundibulum to which the intermediate lobe is attached is thickened
in ganoids. The posterior lobe becomes more conspicuous as we pass
up the vertebrate series to mammals.

According to the view just expressed, the evolution of the hypophysis
involves the metamorphosis of a tubular hypophysial duct into an endo-
crine organ. Another view is that the hypophysis was in the beginning a
gland which opened into the mouth, but for this opinion there seems to be
less evidence.
CHAPTER 13

THE NERVOUS SYSTEM

Of the two agencies which integrate the various functions of the body the nervous system is the more important. In addition, however, to this integrative function the nervous system, with the intermediation of the sense organs, serves to bring the organism into relation with its environment.

The general protoplasmic properties upon which the actions of nerves depend are merely the irritability and conduction which are characteristic of all cells. An amoeba, for example, responds to a stimulus by contracting. If one of its pseudopodia is touched, all pseudopodia withdraw. Obviously, both irritability and conduction are involved in this reaction. All cells of higher animals presumably retain these two powers, but they become the special functions of nerve and sense cells.

ELEMENTS OF THE NERVOUS SYSTEM

In simple colonial animals such as volvox nerves are wanting, and impulses are transmitted from cell to cell by means of intercellular bridges or plasmodesms. Special nervous cells first appear in coelenterates, in the form of neurosensory cells located in the skin. Each neurosensory or receptor cell is connected with deeper tissues, such as muscle fibers, by an elongated process or neurite, which carries nervous impulses to the effector cell. In a characteristic reflex action in worms, a ganglion or transmitter cell, comparable with the motor cell of vertebrates, is interpolated between the receptor and effector cells. A similar reaction in vertebrates usually involves four cells:—1. a receptor cell in the skin or sense organ; 2. an afferent or sensory cell; 3. an efferent or motor nerve cell, which is connected with 4. an effector cell by a neurite. Further complications arise by the chaining together of additional nervous units within a central nervous system, until, in vertebrates, so few cells are devoid of nervous connexions that, if all were destroyed except the nervous tissues, the general form of the body would still be preserved.

The steps in the evolution of a reflex nervous system such as that of worms and vertebrates involve, first, the differentiation of a neurosensory cell in the ectoderm. The body of such a cell remains in the ectoderm, and one or more protoplasmic hairs may extend above the surface. The most characteristic feature of such a cell, however, is the neurite, which
Fig. 385.—A general view of the nervous system of man as seen from behind.
grows away from the surface towards the underlying muscles. By branching into terminal **telodendria**, such a neurite may increase the number of its connexions.

A second evolutionary step is taken when the body of the neurosensory cell sinks below the surface into the underlying connective tissue, but retains connexion with the superficial epithelium by means of a process with branched terminations or **dendrites** attached to the skin.

Further advance appears when the dendrites, instead of ending freely among the epithelial cells, become connected with special receptor or **secondary sense cells** in the skin. The somatic sensory cells of vertebrates are at this evolutionary stage.

The so-called **primitive ganglion cells** of coelenterates exhibit another line of differentiation. That these cells derive from neurosensory cells is a conclusion supported by considerable evidence. That they are more differentiated than neurosensory cells is indicated by the fact that they contain tigroid substance and neurofibrillae characteristic of the nerve cells or **neurons** of the higher animals. Physiologically, however, they are simpler than neurosensory cells, since they transmit nervous impulses in any direction, while neurosensory cells are definitely polarized and transmit impulses in a single direction only. They are, therefore, interpreted as neurosensory cells which have lost both their primary connexion with the skin and their functional polarity. (Fig. 388)
In some coelenterates, the primitive ganglion cells form a loose subcutaneous network or plexus in which, as experiments show, nervous impulses may be carried in any direction. Morphologists incline to the opinion that the nerve net of coelenterates becomes the central nervous system of higher animals.

A final step in the evolution of the neuron is taken by the flatworms, in which the neurons, like the neurosensory cells of coelenterates, trans-

![Diagram](image_url)

**Fig. 387.**—A diagram illustrating hypothetical stages in the phylogenesis of the characteristic sensory (afferent) neuron of vertebrates. Earlier stages at the left, final stage at the right. Arrows suggest that the direction of growth of the neurite is away from the source of stimulus. The diagram assumes that the primitive neurosensory cell becomes the definitive sensory neuron and that the definitive sense receptor is secondary. It is quite possible, however, that the neuron is secondary and that the neurosensory cell becomes the definitive receptor. (Redrawn after Ariëns-Kappers modified.)

mit nervous impulses in only one direction. In contrast with neurosensory cells, however, a neuron has at least two nervous processes, of which the dendrite carries impulses toward the cell body, while the neurite (neuraxon) carries impulses away from the cell body. Each neuron has but one neurite, and may have one or many dendrites. In ontogenesis the neurite grows away from the source of stimulation and the dendrites towards the stimulus.
The differentiation of the neuron is accompanied by the appearance of two sheaths, neurolemma and medullary or myelin, which cover the nervous processes and serve to insulate and nourish them. Each neurite may be covered by a chain of neurolemma cells, or it may not; each may or may not have a fatty medullary sheath. The familiar distinction between white and gray matter in the nervous system rests on the presence or absence of medullary sheaths. Ganglia and non-medullated fibers form gray matter; medullated fibers appear white. That the medullary sheath serves at least for insulation is indicated by the fact that nervous impulses are conveyed more rapidly in medullated than in non-medullated nerves.

Within the central nervous system of vertebrates, neurites lack the neurolemma sheath, but are usually medullated. The presence of a neurolemma is, therefore, not essential to the secretion of this fatty myelin sheath. Most peripheral nerves are medullated, but the medullary sheath...
does not appear until after the neurolemma is differentiated. The nerves of amphioxus and of cyclostomes are not medullated. This primitive condition is retained by the sympathetic nerves and plexuses of higher forms. Primitive ganglion cells like those of coelenterates occur in vertebrates only in the parasympathetic plexuses associated with the alimentary canal.

The forms assumed by neurons in vertebrates are varied; and in general, the more complex the animal the more complex its neurons. Complication in form usually involves an increase in the number of dendrites, and denotes a multiplication in the number of possible func-

![Diagram of a Reflex Arc](image)

**A. DIAGRAM OF A REFLEX ARC.**

Fig. 390.—Diagram of a nervous arc. In A three neurons—afferent, intercalary, and efferent—are shown in their relations to one another and to the skin and muscle. The intercalary neuron is located in the gray matter of the spinal cord. B is an enlarged section of a nerve fiber.

tional relations. In ontogenesis, as in phylogenesis, all the processes of neurons are formed as processes of primarly simple neuroblasts.

Nerve cells manifest a tendency not only to spin out elongated protoplasmic processes so as to connect with various parts of the body and with one another, but also to form plexuses and ganglionic masses. In this way, the complex nervous systems of higher animals have been built up. The first nervous connexions appear to have been between skin and muscle, by means of neurosensory cells, so that a motor response to external stimulus is made possible. So simple an arrangement as this is, however, rarely found, even in worms and molluscs. Usually at least two nerve cells are involved in a reflex action, a neurosensory receptor and a motor ganglion cell which connects with muscle or gland. Even more frequently, a third or association cell is interpolated between the receptor and the motor cells. These association cells may multiply to form a chain of neurons within the central nervous system. Such complications were
made possible by the genesis of the central nervous systems of higher animals from the nerve net of coelenterates. (Fig. 390)

Fig. 391.—Diagram of the nervous elements in a human spinal ganglion. (From Bremer's "Text Book of Histology."

In the primitive nerve plexuses of lower animals such as the coelenterates, and also in those of the vertebrate alimentary canal, the ganglion
cells are in protoplasmic continuity with one another, and nerve impulses are carried directly from cell to cell. The differentiated neurons of higher animals appear not to be so interconnected, but have greater individuality, for the telodendria of one neuron are brought into relation with the dendrites of another only indirectly through the so-called synapse. A synapse is the region where the fine telodendria of one neuron are brought into physiological relation with the dendrites of another neuron. Nerve impulses which involve the activity of two neurons must pass through such a synapse. The transmission of a nervous impulse through the synapse is believed to involve a semipermeable membrane through which impulses pass when conveyed from one neuron to another. The physical process by which such a transfer is effected has been compared to the jump-spark action of a gasoline engine.

It should not, however, be understood that this synaptic membrane has been demonstrated beyond a reasonable doubt. Its presence is inferred chiefly because refined neurological technique has not been able to demonstrate the continuity of the neurofibrillae of adjacent neurons. The fact that each neuron arises from a neuroblastic cell which is primarily independent of other cells and that the termination of a growing neurite is free further strengthens this conclusion. Some physiological experimental evidence points in the same direction.

With the differentiation of the neuron, with neurite and dendrites which normally convey nerve impulses in one direction only, and with tigroid bodies and neurofibrillae in its cytoplasm, the evolution of the nervous unit or neuron reaches its climax.

The steps in the phylogenesis of the nervous system are, therefore, the differentiation of the neurosensory cell, the attainment of functional connexion with muscle or gland cells, the recession of the neurosensory cell from the external epithelium to form a primitive ganglion cell, the formation of an interconnected nerve-net containing association cells, the union of afferent and efferent neurites into bundles or nerves, and the concentration of nerve-cell bodies to form ganglia.

**ORGANIZATION OF THE NERVOUS SYSTEM**

When nervous units convey impulses towards and away from a subcutaneous nerve-net, as in the coelenterates, there are the beginnings of a nervous system. The nerve net forms the central nervous system, the afferent and efferent neurites the peripheral nervous system. The primitive and characteristic function of such a system is the nervous reflex. A nervous reflex or reflex action is a simple motor response to stimulus involving sensory and motor neurones and their interconnexions within a nerve-net or nerve center.
If we take the subcutaneous nerve-net of coelenterates as an early stage in the evolution of the central nervous system and the neurosensory cells as the beginnings of sensory nerves, the primitive ganglion cells are the original association and motor cells. From such beginnings it is not difficult to derive the complex nervous systems of the higher animals.

The flatworms show a distinct advance above the coelenterate stage. In them, the nerve net is partly aggregated into two or more paired longitudinal cords or connectives, which unite at the anterior end of the worm, in close association with pigmented eye-spots, to form the beginnings of a brain. (Fig. 392)

Morphologists are inclined to derive the paired lateral nerve cords of flatworms directly from the subumbrellar ganglionic ring of a medusa. Like the subumbrellar ring, the nerve cords of flatworms consist of nerve fibers associated with clusters of primitive ganglion cells. Kappers explains the concentration of nervous material in the anterior brain as a result of the great exposure of the head to stimuli. Unfortunately, such an hypothesis is unsupported by experimental evidence. (Fig. 393)

In the simple flatworm Planocera, there is a single pair of nerve cords. The number increases in other forms, and the cords may be dorsal and ventral as well as lateral. This fact is important in its bearing upon the development of the nervous systems of higher animals, which in general are assumed to have evolved from flatworm-like ancestors. For the presence of both dorsal and ventral nerve cords in flatworms makes it possible to derive annelids and arthropods from flatworms in which the ventral cords become the dominant nervous centers, and to derive vertebrates from flatworms in which the dorsal cords become predominant. The dorsal nerve cord of vertebrates therefore need not have been derived from the ventral cord of annelids by the inversion of the worm. It has
been asserted that the ventral nerve cords are larger in flatworms which crawl, while the dorsal cords are larger in free-swimming types.

As we pass from the flatworms to higher groups, two contrasting trends are noticeable. In annelids and arthropods the nerve cords become markedly metameric and are non-tubular, while that of chordates is tubular and primarily non-metameric, as in Protochordates.

The nerve cord of the primitive annelids consists of a chain of paired ganglia linked together both by longitudinal connectives and by transverse commissures. The longitudinal connectives pass around the esophagus to connect the supra- and sub-esophageal ganglia. In the higher annelids the paired ganglia tend to unite in the mid-ventral line and to lose the primitive rope-ladder arrangement. Concentration and fusion greatly reduce the number of ganglia, especially in arthropods. (Fig. 394)

These profound changes in the form of the nervous system of articulates are accompanied by histological and physiological differences. Most of the nerve cells become definitely polarized to transmit impulses in one direction only, either towards or away from the central nerve cord. Thus
the neurons become in all essentials like those of vertebrates, being differentiated either as sensory or motor, while those within the nerve-cord become association-cells. A reflex-arc pattern is thus established, in which the motor and sensory cells involved in the reflex may be either homolateral or heterolateral according as the neurons involved belong to one or to both sides of the body. In insects separate motor and sensory nerve roots appear, reversed in position as compared with vertebrates. Motor roots are dorsal and the sensory roots ventral, while in vertebrates motor roots are ventral and sensory roots dorsal. It will be noted, however, that if the insect were turned over on its back so as to bring the nerve cord on the dorsal side of the body as in vertebrates, the relations of the nerves would be similar to those of vertebrates. Giant ganglion cells and fibers, resembling those of fishes, appear in the nerve cord of annelids.

**Fig. 394.**—Invertebrate (annelid) and vertebrate nervous systems compared. In both sub-kingdoms the nervous system is derived from the ectoderm. The central nervous system of Sigalion (A) retains its original connexion with the skin. In Allolobophora (B), however, as in most annelids and in vertebrates (C) the nerve cord separates from the skin. In figure C the vertebrate spinal cord is shown in reversed position with dorsal side down. In A, B, and C the axon processes of the ganglion cells within the nerve cord are similarly directed away from the surface. D and E show the relations of afferent and efferent neurons in an annelid (D) and a vertebrate (E). (Redrawn after Parker.)

**NERVOUS SYSTEM OF CHORDATES**

**Hemichordates.** Hemichordates have a dorsal tubular nerve cord limited to the collar region, but a ventral invertebrate type of nerve cord in the gill and trunk region. The tubular portion of the dorsal cord remains open at both ends throughout life. It contains neurosensory cells of a primitive type and some giant ganglion cells, is surrounded by an outer fibrous layer as in vertebrates, and continues forward into the proboscis and backwards into the body as a non-tubular strand of nervous tissue. A circumesophageal ring connects this dorsal cord with a ventral median strand. The ventral nerve strand is simply a local thickening of a layer of nerve fibers which forms continuous network beneath the skin.
The association in hemichordates of invertebrate and vertebrate types of nervous system helps to bridge over the gulf between the two groups. (Fig. 532)

**Urochordates.** The nervous system of larval urochordates shows an advance towards that of vertebrates, for the ventral invertebrate nervous system has disappeared, and the nerve cord is tubular throughout. Three divisions may be distinguished, an expanded anterior brain or sense vesicle which encloses an unpaired eye and static organ; a short trunk portion; and, behind, a slender cord which in the larva extends into the tail. Paired nerves connect the cord with the caudal muscle. The brain is anterior to the notochord, and has therefore been considered as the homologue of the forebrain of vertebrates. (Fig. 538, A)

In most urochordates, the tail is lost during metamorphosis, and with it the associated nerves, so that only in Appendicularia do these persist throughout life.

**Cephalochordates.** Cephalochordates have a nervous system with many vertebrate characteristics. The cord extends through the entire length of the body as a tube with a slit-like lumen, which is expanded anteriorly in the region of the so-called brain. It also resembles that of vertebrates in its origin from a thickened placode of ectoderm on the dorsal side of the embryo. The neuropore persists in the larva, but closes in the adult animal to form the so-called olfactory pit. (Fig. 538, B)

Two divisions of the brain are recognized, an anterior **prosencephalon** and a posterior **deuterencephalon**. The prosencephalon is lined with ciliated columnar epithelium which shows little if any nervous differentiation. In its anterior wall is a pigment spot which, with scant justification, is called an eye. From the prosencephalon a pair of sensory nerves, the terminal nerves, extend forward towards the snout. The posterior boundary of the brain is marked by a cluster of ciliated sense cells, the **infundibular organ**.

The deuterencephalon is possibly homologous with the mid- and hindbrain of vertebrates. It differs from the spinal cord in having in its dorsal wall large neurosensory cells known as cells of Joseph. Two paired dorsal sensory nerves—numbered II and III—connect with the deuterencephalon. The first pair of motor nerves connect with its ventral wall. (Fig. 436)

In amphioxus dorsal and ventral nerves alternate with one another throughout the length of the body. Except the two anterior pairs, which are wholly sensory, the dorsal nerves of Amphioxus are mixed in function. They extend between the myotomes to the skin, where they divide into dorsal and ventral rami. Ventral nerves, on the other hand, pass from the cord directly to the myotomes opposite. Consequently, in cephalochordates, dorsal and ventral nerves do not unite. The
ganglion cells of the dorsal nerves lie either in the dorsal wall of the cord or are embedded in the nerves. The motor ganglion cells, as in vertebrates, lie within the ventro-lateral wall of the cord. (Fig. 429, A)

On the basis of their peripheral distribution, four kinds of nerve fibers are distinguished, somatic motor and somatic sensory, visceral motor and visceral sensory. Each somatic motor nerve innervates three successive myotomes, but most of its fibers pass to the middle one. Giant ganglion cells occur in the mid-dorsal line of the cord at the anterior and posterior parts of the body, but are wanting in the intermediate region. Since these connect with the sensory nerves, they are probably elements in a reflex system. Sympathetic nerve fibers connect with the blood vessels and the viscera, but there is no chain of sympathetic ganglia.

**Cyclostomes.** Compared with cephalochordates, the cyclostomes show a marked advance in the complexity of their nervous system. Instead of only two brain divisions, cyclostomes have five, telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon. Ontogenesis reveals, however, that these five vesicles of cyclostomes and higher vertebrates develop from the original three which are correlated with the three major senses, smell, sight, and hearing. The primitive forebrain, which in the opinion of most morphologists corresponds to the prosencephalon of amphioxus, becomes the telencephalon and diencephalon, the midbrain continuing as the mesencephalon, and the original hindbrain divides into metencephalon and myelencephalon. Since the cyclostome brain may be taken as the complete prototype of that of all vertebrates, and since most of its features persist in higher forms, these are worthy of mention in some detail. (Fig. 395)
The telencephalon is paired, in correlation with the development of paired olfactory lobes. Although paired eyes develop from the forebrain, they acquire sensory centers within the optic lobes of the mesencephalon. Olfactory centers arise in the diencephalon, and effect connexion with spinal motor centers to form a mechanism for olfactory reflexes. Also involved in these reflexes are paired habenular ganglia in the roof of the diencephalon, and the interpeduncular nucleus in the base of the mesencephalon. Paired epiphyses project from the roof of the diencephalon, and its lateral walls are thickened as the ganglionic masses of the thalami. A funnel-shaped infundibulum projects from the floor towards the roof of the mouth. (Fig. 396)

The roof of the mesencephalon of cyclostomes is peculiar in having a chorioid plexus, which serves as a means of nourishing the brain. Lateral to this plexus are the conspicuous paired swellings of the optic lobes, the centers of vision. The thickened lateral wall of the midbrain is largely fibrous and is known as the tegmentum. The floor of the midbrain contains the motor center of the oculomotor nerve, which innervates four of the eye muscles. The functions of the midbrain are predominantly locomotor and somatic rather than visceral.

From the roof of the metencephalon arises an inconspicuous cerebellum, which is the anterior continuation of the lateral line centers of the myelencephalon. In it are located the complex Purkinje cells, which have fiber connexions with motor cells in the medulla and cord, and are found in the cerebellum of all vertebrates. The lateral walls and base of the metencephalon consist largely of fiber tracts, most of which are ascending and descending fibers which connect brain and spinal cord. No pons, which is so prominent a feature of the base of the mammalian metencephalon, is present in cyclostomes or in any of the lower vertebrates.

The myelencephalon or medulla oblongata is a transitional region between brain and spinal cord. Its roof is largely differentiated as a chorioid plexus. The lateral walls contain the sensory centers of the lateral line nerves as well as those of other cranial nerves. The motor centers of the trigeminal, facial, glossopharyngeal, and vagus nerves are also located in the medulla.

The lumen of the brain expands into four large ventricles, two of which lie in the paired divisions of the telencephalon, the third is in the diencephalon, and the last in the myelencephalon. Three fiber tracts or commissures connect the right and left halves of the brain, the anterior in the wall of the telencephalon, the habenular in the roof of the diencephalon and the posterior in the roof of the mesencephalon. All three persist throughout the vertebrate series to man, and serve as important landmarks by which to determine homologies.
In addition to the numerous nervous structures which emerge in the cyclostome brain, the hypophysis acquires intimate relations with the infundibulum, and shows the first stages in the formation of the pituitary gland, which is represented by a cluster of vesicles derived from the hypophysis.

![Diagrams of the vertebrate brain, based upon the brain of a cyclostome. A shows the brain in median longitudinal section, with nerves as if projected upon the median plane. B is the brain viewed from above. (Redrawn from Plate, after Bütschli.)](image)

The nourishment of the brain is effected chiefly through the three chorioid plexuses in the roof of diencephalon, mesencephalon, and myelencephalon.

The spinal cord in cyclostomes has become a thick-walled tube in which three layers are differentiated, an outer **marginal** layer of fibers, a middle **mantle** layer of gray matter, and a central **ependymal** layer which lines the central canal. The gray matter has only two lateral wings or columns instead of the four characteristic of higher vertebrates. A number of giant nerve fibers like those of amphioxus extend along the spinal cord, but they do not decussate (i.e., cross to the opposite
side of the cord), and they carry impulses caudad only, an indication of the growing dominance of the anterior portion of the nervous system. A primitive trait appears in the location of sensory ganglion cells within the wall of the neural tube.

The anterior ten pairs of nerves in Cyclostomes have their exit through foramina in the cranium and hence are known as cranial nerves. It is not unlikely that all correspond to anterior nerves of amphioxus, except the optic which is a fiber tract of the brain and not a true peripheral nerve. The ten cranial nerves are the olfactory (I), optic (II), oculomotor (III), trochlearis (IV), trigeminal (V), abducens (VI), facialis (VII), auditory (VIII), glossopharyngeus (IX), and vagus (X). In lower vertebrates the hypoglossus and spinal accessory nerves are not cranial but spinal. Of the ten cranial nerves, I, II, and VIII are sensory, III, IV, and VI somatic motor, and the others mixed sensory and motor. The so-called nervus terminalis appears not to be an independent nerve, but a component of the olfactory. The remaining neurites of the olfactory are processes of neurosensory cells in the olfactory epithelium.

The optic nerve develops in correlation with the eye, the retina, from which the optic nerve fibers arise, being a segregated part of the wall of the telencephalon. Some of its fibers cross below the brain in front of the infundibulum to form the optic chiasma. The optic nerves, after entering the wall of the diencephalon, pass by way of the optic thalami to their reflex centers in the roof of the mesencephalon.

The oculomotor, a somatic motor nerve with its nucleus or motor center in the base of the midbrain, innervates four eye muscles, the

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Fig. 397.—Diagram of cranial nerves of lower vertebrate. Eye-muscle nerves omitted; central nervous system dotted, fifth nerve represented as composed of two nerves; lateralis nerves separated from the ninth and tenth nerves. I–X, cranial nerves; 1–5, gill clefts; b, buccalis nerves; c, chorda tympani; g, geniculate ganglion; h, hyoid nerve; i, intestinal (pneumogastric) nerve; j, jugal ganglion, l, lateral line nerve of X; m, mouth; md, mandibular nerve; mt, mentalis nerve; mx, maxillary nerve; op, ophthalmicus profundus nerve; opV, opVII, superficial ophthalmic nerves of V and VII; p, palatine nerve; po, posttrematic nerves; pr, pretrematic nerves; pt, petrosal ganglion; s, semilunar (Gasserian) ganglion; sp, spiracle. (From Kingsley’s “Comparative Anatomy of Vertebrates.”)
superior, inferior, and anterior recti and the inferior oblique. Sympathetic non-medullated fibers presumably occur in the oculomotor, but no distinct sympathetic ganglion is formed.

The *trochlearis* arises from a motor nucleus in the floor of the mesencephalon posterior to that of the oculomotor and supplies the superior oblique eye muscle. Its fibers emerge from the medulla near the root of the profundus. The dorsal chiasma of the trochlearis appears to be absent in cyclostomes.

The *trigeminus* is so named because, in all vertebrates, it has three chief branches, a sensory *ophthalmicus profundus* which extends above the eye to the skin on the upper side of the snout, a sensory *maxillaris* branch to the skin on the side of the snout and the region which corresponds to the upper jaw of fishes, and a mixed *mandibularis* branch which supplies the skin and muscles of the first visceral arch.

Cyclostomes are the only vertebrates in which the profundus branch arises by an independent root. This fact supports the conclusion that the profundus was once an independent segmental nerve and that its union with the trigeminus in all vertebrates above cyclostomes is secondary.

The motor center of the trigeminus is in the lateral column of the medulla. A unique feature of the trigeminus is a sensory nucleus in the roof of the mesencephalon, the fibers of which bring nerve impulses from mandibular muscles. Most of the sensory fibers of the trigeminus arise from ganglion cells in the large Gasserian ganglion near its root of origin from the medulla. With few exceptions, the sensory nerves of all vertebrates have similar ganglia near their roots of origin.

The *abducent* is a somatic motor nerve which emerges from the medulla ventral and posterior to the root of the trigeminus and innervates the posterior or external rectus eye muscle.

The *facialis* carries both special and general somatic sensory fibers, and also visceral sensory and motor fibers. The motor fibers arise from an elongated nucleus in the lateral column of the medulla, and supply muscles of the hyoid arch. There are four major branches. The sensory *ramus ophthalmicus superficialis* innervates the supraorbital series of lateral line organs. The *buccalis* supplies the infraorbital series. The deep *palatine* branch is distributed to the skin of the roof of the mouth. The *hyomandibular* innervates the muscles of the hyoid arch and the skin of the mandibular region.

The *auditory* supplies the otic capsule which in cyclostomes is chiefly an organ of equilibration. As might be expected from its origin as a branch of the facial nerve, its roots are closely associated with those of the facial. Since the otic capsule is a modified lateral line organ, the fibers of the auditory nerve belong to the group of *lateralis* or special somatic sensory components.
Fig. 398.—Diagrams of the branches and components of (A) the trigeminal, (B) facial, and (C) glossopharyngeal and vagus nerves of a lower vertebrate.  

b, buccalis nerve; ct, chorda tympani; d, dorsal rami of IX and X; g, gastric nerve; gg, in A, Gasserian ganglion, in B, geniculate ganglion; h, hyoid nerve; hm, hyomandibular trunk; j, Jacobson’s connective; jg, jugular ganglion; l, lateralis nerve; mxe, maxillaris externus nerve; op, ophthalmicus profundus nerve; os, superficial ophthalmic nerve; pal, palatine nerve; po, pr, post- and pretrematic rami; sp, spiracle; st, nerve to supratemporal lateral line organs; 1–5, gill clefts. (From Kingsley’s “Comparative Anatomy of Vertebrates.”)
The glossopharyngeal is the mixed nerve which supplies the third visceral arch. It forks over the first gill-slit and a pretrematic branch is distributed to the posterior wall of the hyoid arch. The post-trematic branch contains sensory fibers from the floor of the pharynx and motor fibers which innervate the muscles of the third arch.

The vagus is a mixed nerve formed of fibers which are distributed to the muscles and skin of the posterior visceral arches. This suggests that a number of segmental nerves are united in the vagus. A lateralis branch is the nerve of the posterior series of lateral line organs. A visceral branch goes to heart, stomach, and intestine, and carries sympathetic fibers connected with these organs. Each branchial branch divides into pre- and post-trematic rami, which contain both visceral sensory and visceral motor fibers.

In the trunk region there is a general correspondence between the number of myotomes and of spinal nerves, since for each myotome there are usually a sensory and a motor nerve. In Petromyzon these are not united; but in Myxinoids they join to form a mixed spinal nerve with two roots, a dorsal ganglionated sensory root and a ventral motor root, each neurite of which arises from a multipolar ganglion cell located in the gray matter of the cord. Synaptic connexions between sensory and motor neurones take place within the gray matter. Peripherally, each spinal nerve divides into dorsal and ventral rami which supply skin and muscles.

This simple one-to-one metameric correspondence of spinal nerves and myotomes is, however, somewhat modified in the occipital region of petromyzon where the first five post-otic myotomes are innervated by the nerves of the fourth and fifth myotomes, and the nerves of the three anterior myotomes have disappeared, at least as independent roots. The nerves of post-otic myotomes 6 to 12 unite to form the hypoglossal nerve which supplies the hypobranchial muscles. In this fusion of
occipital nerves, may be seen the beginnings of the cervical plexus which persists throughout the vertebrate series. Since paired appendages are wanting in cyclostomes, no thoracic or lumbar plexuses are formed.

Little can be said concerning the sympathetic nervous system of cyclostomes. The nerves of cyclostomes like those of Amphioxus, are not medullated, so that this means of distinguishing sympathetic from other fibers cannot be used. A number of observers claim to have found clusters of sympathetic ganglion cells associated with the vagus. Also a plexus comparable to Auerbach's plexus of higher vertebrates is found in the intestinal wall. Chromaffin cells, which have an origin in common with sympathetic cells, are found in the trunk region and have a segmental distribution as in mammals.
Elasmobranchs. The nervous system of elasmobranchs shows some advances above that of cyclostomes. The roof or pallium of the telencephalon has thickened and expanded. To the corpus striatum is added an epistriatum, both connected with olfactory fibers. The telencephalon remains predominantly an olfactory center. Elongated olfactory tracts are differentiated. A saccus vasculosus, which possibly functions as a pressure organ, is appended to the infundibulum. The midbrain has lost its chorioid plexus and its roof has become thickened and wholly nervous. With the increased importance of the lateral line organs, their centers in the lateral lobes of the medulla are more developed. Possibly for the same reason, the cerebellum, which is a static center, is greatly enlarged.
Fig. 404.—Brain and cranial nerves of *Carcharias littoralis* (Princeton 310), natural size. *bo*, olfactory bulb; *br*¹-⁴, branchial nerves; *cr*, auricle of medulla; *d*, diencephalon; *e*, epiphysial stalk, the pineal organ lacking; *ec*, external canal of ear; *cr*, external rectus; *co*, external oblique; *hm*, hyomandibular nerve; *io*, inferior oblique; *l*, lateralis nerve; *md*, mandibularis nerve; *mt*, myelencephalon; *ms*, mesencephalon, also, maxillaris superior; *ml*, metencephalon; *oo*, olfactory organ; *os*, ophthalmicus superficialis nerve; *ot*, olfactory tract; *pal*, palatine nerve; *pc*, posterior canal; *po*, posttrematic branch; *pr*, pretrematic branch; *so*, superior oblique; *sr*, superior rectus; *t*, telencephalon; *u*, utriculus; *v*, visceral branch of *X*; I–X, cranial nerves. (From Kingsley's "Comparative Anatomy of Vertebrates.")
In the spinal cord, dorsal and ventral columns of gray matter are differentiated. The dorsal column, however, remains unpaired.

The cranial nerves are identical with those of cyclostomes but relatively enlarged both in correlation with the increased size of sense organs and muscles, and by the addition to the nerve fibers of medullary and neurolemma sheaths. A cranial sympathetic ganglion, the ciliary, has developed in association with the oculomotor and profundus nerves. The profundus has now become a branch of the trigeminal. Some of the supraorbital series of lateral line organs are innervated by fibers of the superficial ophthalmic branch of the fifth nerve, while the remainder are supplied by the superficial ophthalmic of the facialis.

The somatic motor nerves of five post-otic myotomes unite to form the hypoglossal, which supplies hypobranchial muscles. A thoracic plexus is formed by the union of the nerves immediately posterior to those of the cervical plexus. But the number of nerves which participate varies greatly in different elasmobranchs. In many species the fibers of the cervical and thoracic plexuses unite as a cervico-thoracic plexus. In the region of the pelvic fin is a similar but smaller lumbo-sacral plexus.

Well developed sympathetic ganglia appear in the trunk region, in the vicinity of the dorsal aorta. Their arrangement is metameric, but the anterior and largest is formed by the union of primarily separate ganglia. Each is connected by a ramus communicans with a spinal nerve. A longitudinal sympathetic cord or connective is only imperfectly developed. An intestinal plexus occurs, as in all vertebrates.

Amphibia. Amphibia have a relatively simple brain like that of cyclostomes and dipnoi. Olfactory lobes are relatively large, and merge without constriction into the cerebral hemispheres. The pallium is thick, and cells have migrated from the gray matter into the external marginal zone of white matter. The lumen of each hemisphere is reduced by the thickening of its median and lateral walls. An inner longitudinal sulcus or groove divides these walls into dorsal and ventral halves. The dorsal half of the lateral wall is the paleocortex, the ventral half is the epistriatum, and below the epistriatum is the paleostriatum. In the median
wall, the dorsal half is the archicortex or primordium hippocampi. The medio-ventral wall forms the septum by which fibers pass to and from the hippocampus. The hemispheres are interconnected by anterior, anterior pallial and posterior pallial commissures located in the lamina terminalis. Habenular and posterior commissures persist in the roof of the diencephalon. The epiphysis forms a pineal gland. A chorioid plexus

![Diagram](image)

Fig. 406.—Side and dorsal views of brain of young alligator. *c*, cerebrum; *cl*, cerebellum; *e*, epiphysial structures; *h*, hypophysis; *i*, infundibulum; *ol*, optic lobes; II–XII, cranial nerves. (From Kingsley's "Comparative Anatomy of Vertebrates," after Herrick.)

invaginates into the third ventricle. The saccus vasculosus of fishes has disappeared. The thickened walls of the midbrain reduce the lumen to a narrow passage, the aqueduct. The cerebellum is rudimentary like that of cyclostomes. (Fig. 414)

The ten cranial nerves of fishes persist in amphibia. Urodeles have lateralis nerves, but these disappear in the anura in correlation with the loss of lateral line organs. With the loss of gills, the number of branches of the vagus is reduced.

Cervical and lumbar enlargements of the spinal cord appear in correlation with the enlargement of the appendages.
Sympathetic nerve cords or connectives unite the series of sympathetic ganglia.

**Reptiles.** The cerebral hemispheres of reptiles are larger than those of amphibia and by extension caudad have partially overgrown the diencephalon. The paired ventricles are nearly obliterated by the enlargement of the striate bodies, archistriatum and neostriatum. For the first time in the vertebrate series, a cortical layer of pyramidal cells appears in the pallium, having nervous connexions with fibers of the olfactory tract. Septum and hippocampus appear in the medial wall much as in amphibia. The dorsal wall of each hemisphere is homologized with the gyrus dentatus of the mammalian brain. The transitional region between this dorsal pallium and the neostriatum has important potentialities, since it is unconnected with olfactory fibers, and since in mammals it becomes the neopallium from which develops the greater part of the cerebral cortex on which the higher psychical activities of man depend. (Figs. 406, 414)

In the region of the diencephalon of lizards the anterior epiphysial outgrowth, the parietal organ, develops a lens, retinal and pigment layers, and nerve fibers which are connected with centers in the brain wall.
Fig. 408.—Ventral view and median section of the brain of Ornithorhynchus. AC, anterior commissure; bo, olfactory bulb; c, first cervical nerve; d, cerebellum; CM, massa intermedia; e, epiphysis; f, flocculus; fd, fasciculus dentatus (anterior part of hippocampal tract); fi, interventricular foramen; h, hypophysis; hc, habenular commissure; HC, pallial (hippocampal) commissure; lp, piriform (hippocampal) lobe; mc, mammillary bodies; mo, medulla oblongata; n, nodulus; ol, olfactory lobe; olf, olfactory tubercle; pal, pallium (temporal lobe); pc, posterior commissure; rf, rhinal fissure; tc, tuber cinereum; tV, tuberculum quinti; v, velum medullare anterius; vm, motor root of V nerve; vmd, mandibularis root of V; vmx, maxillaris root of V. (From Kingsley's "Comparative Anatomy of Vertebrates," after G. Elliot Smith.)
It is therefore, so far as its structure goes, an eye. The thalamic thickenings of the lateral wall divide the third ventricle into a dorsal and ventral cavity connected by a narrow slit-like passage. In snakes the optic lobes become corpora quadrigemina by the division of each optic lobe into anterior and posterior moieties.

The cerebellum is slightly larger in reptiles than in amphibia. The gray matter of the spinal cord as seen in cross section assumes the form of a capital H with dorsal and ventral columns, as in mammals.

In reptiles occipital vertebrae fuse with the cranium. Consequently, two nerves, the *spinal accessory* which innervates shoulder and neck muscles and the *hypoglossus* which supplies the tongue, which are spinal in lower vertebrates, now become cranial. Each arises by a series of segmentally arranged roots, and is therefore believed to be formed by the union of a number of spinal nerves. Other changes in the nervous system in reptiles are relatively unimportant.

**Mammals.** The brains of lower mammals differ little from those of reptiles. Within the mammalian group, from monotremes to man, there is an enormous enlargement of the cerebral hemispheres and of the cerebellum. The expansion of the hemispheres affects chiefly the neopallium, the beginnings of which were noted in reptiles. The archipallium of reptiles, which serves chiefly as an olfactory center, becomes in mammals the hippocampal lobe. As a result of the growth of the neopallium, the hippocampus is crowded to the lower part of the brain.
Increase in the size of mammalian brains is accompanied by complication in form and structure. The cortex becomes cellular, and consequently gray in color. The amount of cortical material increases manyfold, so that if the human cortex were spread out flat it would cover a surface eighteen inches square. The number of neurons runs into the billions, and five cell layers may be distinguished. The increase in the mass of the cerebral hemispheres as we pass from lower to higher mammals is the result, not of multiplication of layers of neurons in the cerebral cortex, but of folding of the cortex.
A notable development is that of the anterior pallial commissure, which enlarges enormously to form the corpus callosum, interconnecting the two hemispheres. The olfactory lobe degenerates and is covered by the hemispheres. The corpora striata elongate caudally and rest upon the thalami. The epiphysis forms a gland, the pineal. Cerebellum and pons enlarge. The pons is a bridge of nerve fibers, present only in birds and mammals, which extends around the brain-stem ventral to the cerebellum, and which connects the two halves of the cerebellum.

Following this brief outline of the main advances in the nervous system as represented in living chordates, it seems desirable at the risk of some repetition to present separately and in greater detail the evolution of the three major divisions of the nervous system: 1. The evolution of the Central Nervous System (Brain and Spinal Cord). 2. The Evolution of the peripheral nerves (cranial and spinal). 3. The Evolution of the Autonomic or Sympathetic System.

Evolution of the Brain

Comparison of vertebrate brains from cyclostomes to man reveals a gradual and progressive change such as would be expected if the higher forms have evolved from the lower. The cerebral hemispheres are the least conservative regions. Although the hemispheres are enormously enlarged in man, the differences between man and apes are quantitative rather than qualitative. Even the speech center in the frontal lobes, which is said to be peculiar to man, is but an enlargement of regions already developed in apes. The brains of such fossil types as the Java and Peking man are transitional between those of modern man and apes.

Nor is the gap between the brain size of mammals and reptiles formidable. In a dorsal view, all five divisions of the primitive brain are visible alike in monotremes and alligators. The overgrowth of the hemispheres, begun in reptiles, reaches its climax in man, whose domination in the animal world may be ascribed to the enlargement of his conscious control centers in the hemispheres.

The cortical enlargement in mammals, however, involves more than an increase of gray matter. Correlated with the multiplication of cells is an increase in the number of nervous interconnexions. Association fiber tracts connect all parts of the enlarging brain so that all regions, however remote from one another, are interconnected. The brain produced by these evolutionary changes is an organized and integrated whole, no part of which appears to function independently of the rest.

In primates a marked retrogression of the olfactory lobes accompanies the enlargement of the hemispheres. The olfactory centers in the hippocampus persist, but other regions of the cortex enlarge dispropor-
Fig. 411.—Brains of A, a cyclostome (Petromyzon); B, an Elasmobranch (Scymnus); C, a teleost (Cyprinus); and D, an amphibian (Rana) as seen in left lateral aspect. The main fiber tracts and nerves are shown as if projected upon the median plane. Homologous fiber tracts in all figures are given identical numbers.

Nervous Pathways of the Brain (fasciculi or tracts). 1, olfactory; 2, olfactohabenularis; 3, olfactohypothalamicus; 4, olFactocorticalis; 5, olfactoepistrialis; 6, olfactopeduncularis; 7, olfactoamygdalinius; 8, olfactoamygdalinius; 9, olfactoamygdalinius; 10, parolfactohabenularis; 11, optic; 12, opticotectalis; 13, isthmo-opticus; 14, preoptico-habenularis; 15, striohypothalamicus; 16, striothalamicus; 17, striomesencephalicus; 18, fasciculus retrolexus; 19, pallial; 20, hippocampothalamicus; 21, hippocampomammillaris; 22, bulbothalamicius; 23, bulbofrontalis; 24, tectobulbaris; 25, tectothalamicus; 26, tecto-spinalis; 27, tecto-occi-pitalis; 28, tectocerebellaris; 29, frontothalamicus; 30, frontoptopetalis; 31, corticohabenularis; 32, corticothalamicus; 33, corticomammillaris ( fornix); 34, corticobulbaris; 35, lemnisco-cerebellaris; 36, mammillothalamicius; 37, mammillothalamicius; 38, mammillothalamicius; 39, mammillothalamicius; 40, mammillothalamicius; 41, rubrothalamicius; 42, rubro-cerebellaris; 43, rubrospinalis; 44, thalamico-spinalis; 45, tegmentocerebellaris; 46, trigeminocerebellaris; 47, quadri-cerebellaris; 48, septomesencephalicus; 49, octovocerebellaris; 50, olivocerebellaris; 51, dentocerebellaris; 52, mesencephalocerebellaris; 53, vestibulocerebellaris; 54, lateralocerebellaris; 55, faciocerebellaris; 56, spinocerebellaris; 57, cerebellodiencephalicus; 58, spinotegmental; 59, spinothalamicus; 60, spinohypothalamicus; 61, octovomesencephalicus; 62, mammillopeduncularis; 63, frontobulbaris; 64, lobotectalis. (Redrawn after Plate.)
Fig. 412.—Diagrams of the brains of E, a reptile (Lacerta); F, a bird (Anas); and G, a mammal (generalized), as seen in left lateral aspect. The course of the main fiber tracts are shown as if projected upon the median plane. Homologous fiber tracts in all figures are given the same numbers. Nervous Pathways of the Brain (fasciculi or tracts). 1. olfactory; 2, olfactohabenularis; 3, olfactohypothalamicus; 4, olfactocorticais; 5, olfactoepistriatalis; 6, olfactopeduncularis; 7, olfactoammonicus; 8, olfactoammamillaris; 9, olfactoamygdalinius; 10, parolfactohabenularis; 11, optic; 12, optico-tecalis; 13, isthmoopticus; 14, preopencerebellaribus; 15, striophyothalamicus; 16, striothalamicus; 17, stromesencephalicus; 18, fasciculus retrolineus; 19, pallialis; 20, hippocamphothalamicus; 21, hippocampomammillaribus; 22, bulbothalamicus; 23, bulbocorticalis; 24, frontobulbaris; 25, tectobulbaris; 26, tectospinalis; 27, tectothalamicoepistriatalis; 28, tectocerebellaris; 29, frontothalamicus; 30, frontoepistriatalis; 31, corticobulbaris; 32, corticothalamicus; 33, corticocerebellaris; 34, corticobulbaris; 35, lobopedunculospinails; 36, habenulointerpeduncularis; 37, habenulocorticalis; 38, mammillogeniculata; 39, mammillothalamicus; 40, rubrothalamicus; 41, rubrocoeruleus; 42, rubrospinalis; 43, thalamospinalis; 44, tegmentoepistriatalis; 45, trigeminoepistriatalis; 46, quintocerebellaris; 47, septoencephalics; 48, octavocerebellaris; 49, olivocerebellaris; 50, deitervocerebellaris; 51, diencephalocerebellaris; 52, mesencephalocerebellaris; 53, vestibulocerebellaris; 54, laterocerebellaris; 55, facialecerebellaris; 56, spinoocerebellaris; 57, cerebellotegmentalis; 58, cerebellodiencephalicus; 59, spinothalamicus; 60, spinohypothalamicus; 61, octavomesencephalicus; 62, mammilopeduncularis; 63, frontobulbaris; 64, lobotalateralis. (Redrawn after Plate.)
tionately. Vision in primates is more important than smell, and brain changes express relative functional values.

Cortex. Two parts of the primitive vertebrate brain participate specially in the great enlargement of the cerebral hemispheres, the striate body and the neopallium. These two regions are not clearly differentiated in cyclostomes, but are distinguishable in fishes. Of the two, the pallium changes more. The hemispheres of teleost fishes have a thin epithelial pallium or mantle. Compared with the mantle of teleosts, that of elasmobranchs and dipnoi, which are more directly in the line of mam-

Fig. 413.—Horizontal diagrams of ichthyopsid brains. A, sturgeon; B, elasmobranch; C, teleost; D, amphibian. Primitive forebrain wall stippled; telencephalic evaginations horizontally lined; thalamus vertical lines. e, common ventricle, f, interventricular foramen; l, lateral ventricle; m, midbrain; o, olfactory bulb; t, terminal lamina; II, optic nerve; 3, third ventricle. (From Kingsley's "Comparative Anatomy of Vertebrates," after Herrick.)

malian ancestry, is relatively thick. Homologies with the pallium of higher vertebrates are difficult on account of the lack of differentiation. In the pallium of fishes the cellular gray matter is adjacent to the ventricle, while the external layer is fibrillar. Even in the pallium of fishes, however, some cells migrate from the gray into the fibrillar zone. (Fig. 413)

The pallium of amphibia, taking Rana as a type, is thick, and is differentiated into a median archicortex and a lateral paleocortex, both associated with olfactory fibers. In reptiles the number of cell layers in the pallium increases to three. The medio-dorsal region of each hemisphere forms an archicortex or hippocampus. In the lateral pallium, dorsal to the striate body, are possibly the beginnings of a neocortex.

A true many-layered neocortex appears in all mammals and enlarges so much that the paleocortex is crowded into a ventral position and the archicortex pushed dorsally toward the median plane. The number of cell layers has increased until five are distinguished in most, if not all, mammals. (Fig. 414)

The evolution of the cortex is accompanied by cellular changes. In the pallium of lower vertebrates, cell bodies lie close together. The
thickening of the cortex in mammals is correlated with separation of the cells, which, however, retain connexion with one another by means of elongated dendritic processes, the number of interconnexions with adjacent neurons increasing with the multiplication of dendrites. In general, the higher the animal, the longer and more numerous the dendrites, and consequently the greater the possible number of interrelationships between cellular elements. A correlated increase appears in the number of associational fiber tracts which connect the gyri or folds of the cortex.

In the millions of years which elapsed during the Tertiary period, there was a marked increase in the size of mammalian brains. This increase affected all parts, and was accompanied by a corresponding increase in the size of the cranium. The growth of the cerebral cortex
was, however, out of all proportion to the enlargement of the rest of the brain. This increase was made possible by the complex folding of the outer layers of the brain and resulted in the formation of the gyri and sulci which are such a characteristic feature of the surface of the human brain. (Figs. 418, 419)

Hemispheres in Man. The human cerebral hemispheres are separated in the median plane by a longitudinal fissure. Viewed from the surface, four topographic but not functional divisions are recognized, the frontal, parietal, occipital, and temporal lobes. Each is subdivided by sulci or fissures into convolutions or gyri. The gyri of the frontal lobe are the superior, middle, inferior, rectus, and orbital. Those of the
parietal lobe are the **anterior** and **posterior central**, the **superior** and **inferior parietal**, the **submarginal**, and the **angular**. The occipital lobe has **lingual**, **fusiform** in part, and **lateral** gyri; the temporal lobe **superior**, **middle** and **inferior**, **hippocampal**, and **uncus**. The **gyrus cinguli** on the median surface of the hemispheres extends through frontal and parietal lobes. Covered by the parietal, frontal, and temporal lobes on the lateral side of the hemisphere is an **insula**, the surface of which is subdivided into **short** and **long** gyri. (Figs. 418, 419)

![Diagrams of the brains of insectivores and of lower primates viewed from the left side.](image)

Each lobe contains a restricted portion of a lateral ventricle. Connection with the third ventricle is effected by an **interventricular foramen** or foramen of Monro.

**Corpus Striatum.** The second portion of the telencephalon which undergoes striking changes and enlargement in the course of phylogenesis is the corpus striatum, so-called because of its striped appearance in sections. This striate body or basal ganglion arises as a local thickening of the ventro-lateral wall of the telencephalon. Like other parts of this division of the brain, the striate body is connected primarily with olfactory fibers and is an olfactory reflex center. The organ is poorly developed in cyclostomes; but is a well-marked swelling in elasmobranchs, with a paleostriatum and an epistriatum. (Figs. 414, 415)

The amphibian brain, however, may be taken as the prototype of the vertebrate. Each hemisphere of the amphibian brain is divided
by a longitudinal groove into a dorsal and ventral half, and by the fissure-like ventricle into median and lateral walls. The septum is the ventral division of the median wall, and the primary hippocampus or archipallium the dorsal. In the lateral wall, the striatum is ventral and the paleopallium dorsal. Functionally, the septum is the intermediate station of fibers which pass to or leave the hippocampus. In the amphibian as in the elasmobranch striatum, a ventral and median paleostriatum and a dorsolateral epistriatum are differentiated. It is not believed that the
striate body is directly connected with the olfactory organ. A large fiber tract, the ventral peduncle, connects the striatum with the thalamus.

In reptiles, the striatum becomes so greatly enlarged as nearly to obliterate the ventricle of the hemisphere. Both paleostriatum and epistriatum persist, but an archistriatum is added dorsal and lateral to the paleostriatum. Anterior to the archistriatum a neostriatum
arises from the basal wall of the hemisphere. The archistriatum is presumably chiefly olfactory in function, but the neostriatum is a receptory center for fibers from the thalamus.

These divisions of the striate body persist in mammals in which the archistriatum becomes the amygdaloid nucleus, the paleostriatum is the globus pallidus, and the neostriatum divides into caudate nucleus and putamen. With the elongation of the hemispheres, the striatum is lengthened and rests upon the thalamus like a sac of meal on a packhorse. The division of the striate body is a result of the growth of fiber tracts such as the internal capsule which conveys ascending and descending
fibers to and from the cortex. The corpus striatum may be considered as a front porch or main entrance to the higher centers of the brain. Sympathetic functions are ascribed to it.

Evolution of the Diencephalon. The evolutionary potential of the diencephalon is low, and it changes little from fish to man. The founda-

![Figure 421](image)

**Fig. 421.**—Variation in human brain size. The range is from 369 grams to 2400 grams, both of these extremes being the brains of idiots. The average male brain weighs 1400 grams. (Redrawn after Kahn’s “Das Leben Des Menschens,” W. Keller & Co.)

tions of the human brain are laid in that of cyclostomes. Three regions are distinguishable in the primitive diencephalon of cyclostomes, a dorsal epithalamus, a lateral thalamus, and a ventral hypothalamus. The epithelial roof remains thin, and there is no velum transversum to divide the diencephalon from the telencephalon. Three dorsal outgrowths arise from the epithalamus, an anterior paraphysis, a parietal outgrowth or
eye, and a posterior epiphysis which in mammals becomes the pineal gland. A pair of habenular ganglia, connected by an habenular com-

![Diagram of brain outlines and association fiber tracts]

**Fig. 422.**—Outlines of the brain of modern man, fossil men, and ape showing relative sizes. As the evolution theory would lead us to expect, the brains of fossil men are intermediate in size between ape and modern man.

![Diagram of association fiber tracts]

**Fig. 423.**—A diagram of the association fiber tracts of the cerebral hemisphere as seen in lateral aspect. Through the agency of these tracts all parts of the cerebral cortex are brought into relation with one another. The integration of the activities of the various parts of the brain is, it may be assumed, effected in this way. (Redrawn from W. Howell, after Starr.)

missure, develops at the anterior border of the epithalamus. The thickened lateral walls of the cyclostome third ventricle form the thalami,
which become a pathway for fibers connecting anterior and posterior parts of the brain. From the hypothalamus, the infundibulum is formed as a ventral funnel-like outgrowth; and immediately behind this is a second depression, the saccus vasculosus, limited to fishes and supposed to be an hydrostatic pressure organ. Below the infundibulum, the hypophysis proliferates vesicular masses which are believed to be homologous with the intermediate lobe of the pituitary gland.

In elasmobranchs geniculate nuclei connected with fibers of the optic nerves develop in the lateral portion of the thalami; hence these are often called optic thalami.

The diencephalon of Amphibia differs little from that of elasmobranchs, except that some amphibia have a rudimentary parietal eye which pierces the skin or lies just beneath it. A chorioid plexus projects into the third ventricle. The pituitary gland has the three lobes found in man.

In reptiles, the chorioid plexus of the diencephalon grows forward into the lateral ventricles, also. The epiphysis is glandular. The thickened thalami nearly meet in the median plane and divide the ventricle into dorsal and ventral chambers.

The chorioid plexus of the diencephalon persists in mammals. The epiphysis becomes the pineal gland, of problematic function, and there is no parietal organ. The habenular ganglia are rudimentary. The striate body of the telencephalon rests upon the thalamus, and the two

![Diagram of the human brain](image-url)
form a pathway for fibers to and from the cerebral cortex. From the posterior walls of the infundibulum are differentiated a tuber cinereum, and also paired mammillary bodies, which have fiber connexion with the olfactory organ. Fibers are also received from the cerebral cortex and sent to the thalami. (Fig. 420)

Brain Commissures. Commissures are fiber tracts which cross the median plane of the body and bring lateral halves of the nervous system into relation with one another. Some of those in the brain persist throughout the vertebrate series, and serve as important topographic landmarks to determine homologous regions. (Fig. 425)

Commissures have not been demonstrated in Amphioxus. In the terminal lamina of the telencephalon of cyclostomes are two, a more ventral anterior and a more dorsal pallial. Both connect the olfactory lobes with the hippocampi of the opposite side. Two habenular ganglia in the roof of the diencephalon are connected by the habenular commissure. Fibers from the hemispheres and from the hypothalamus also are contained in this commissure. Another commissure in the roof of
the brain, the **posterior** commissure, marks the boundary between diencephalon and mesencephalon. A **dorsal** commissure in the roof of the midbrain connects the optic lobes.

In addition to the commissures, the fibers of two cranial nerves, to optic and the trochlearis, cross the median plane to form **chiasmas**. The optic chiasma is ventral and just anterior to the infundibulum. The trochlearis chiasma, which occurs in all vertebrates except cyclostomes, lies in the dorsal constriction which separates mes- and metencephalon.

![Diagram of the brain](image)

**Fig. 427.**—A diagram of the chief efferent tracts of the brain in relation to the spinal cord. (Redrawn after Rasmussen's "Principal Nervous Pathways." The Macmillan Co.)

The dorsal commissure is lacking in fishes. In amphibia and reptiles a **dorsal pallial** or hippocampal commissure, connecting right and left hippocampi, adds a third to those located in the terminal lamina of the brain. In monotremes and marsupials both anterior and posterior pallial or hippocampal commissures occur. The **corpus callosum** of placental mammals is a new commissure—possibly derived from the anterior pallial—which connects the two halves of the neo-cortex. Its enlargement is correlated with that of the cerebral cortex.

**Mesencephalon.** The midbrain vesicle changes in phylogenetis less than any other division.

The mesencephalon of cyclostomes is peculiar in having a chorioid plexus. In cyclostomes, as in fishes, the optic lobes of the midbrain are the reflex centers of the optic nerve, such reflexes being mediated by
efferent fibers which pass as a bundle from the **tegmentum** or lateral wall of the midbrain to the floor of the medulla and cross to the other side by way of the **ansulate commissure.** In the tegmentum are located also a number of giant cells, the large neurites of which extend along the spinal cord to tail muscles and thus form a physiological through-way. In the floor of the midbrain lies the oculomotor nucleus and the **interpeduncular ganglion.** In cyclostomes, as in higher vertebrates, the floor of the midbrain serves as a pathway for fiber tracts leading to and from the hemispheres. One of the ascending fiber tracts is the **spinothalamicus.**

The thickening of the tegmentum in amphibia constricts the lumen to a slender tube, the **aqueduct,** which connects third and fourth ventricles.

In reptiles some of the optic nerve fibers, instead of connecting with the optic lobes as in lower vertebrates, become connected, indirectly by way of synapses within the thalami, with the posterior part of the cerebral hemispheres. This shift in brain connexions begins in reptiles and reaches its climax in mammals. (Fig. 484) A new nucleus, the **nucleus ruber,** so-called because of red granules associated with it, first appears in reptiles. It is a way station or association center for fibers which carry impulses from the cerebellum to the cerebral cortex. In snakes the optic lobes or corpora bigemina become subdivided into corpora quadrigemina.

The midbrain of mammals differs little from that of reptiles. Corpora quadrigemina are present in all mammals. The sensory centers of vision shift to the occipital lobes of the hemispheres. The upper swellings or **superior colliculi** of the corpora quadrigemina are optic reflex centers. The inferior colliculi are auditory reflex centers. They correspond to the **tori** of reptiles, which are covered by the optic lobes and are thought to be derived from the roof of the brain posterior to the optic lobes of fishes.

**Metencephalon.** The metencephalon is hardly distinguishable in cyclostomes, but is represented by a rudimentary cerebellum and a transitional region connecting mesencephalon with the widely expanded medulla. The cerebellum appears to be the anterior continuation of the equilibratory centers of the medulla. Since the cerebellum receives fibers from the medulla, thalami, and optic lobes, it may correlate olfactory, visual, and static functions. A decussation of fibers in its floor may possibly be interpreted as the beginnings of a **pons.** The floor, however, serves chiefly as a pathway for ascending and descending fiber tracts which connect brain and spinal cord.

In fishes there is great variation in the size of the cerebellum. In the dipnoi it is small and covered by the optic lobes. In some elasmobranchs it becomes conspicuous and even convoluted. In teleosts it invaginates into the cavity of the midbrain to form a **valvula.** The peculiar Purkinje cells, which are such conspicuous elements in the cortex of the cerebellum of higher vertebrates, occur in fishes. The numerous sensory and motor
connexion of the cerebellum of fishes indicate that it is an important correlating and coordinating center. (Fig. 411C)

Amphibia, compared with fishes, have a degenerate cerebellum, this reduction being correlated with a loss of physical activity.

The cerebellum of reptiles differs only slightly from that of amphibia.

In mammals, the cerebellum is much enlarged. Only its median lobe or vermis corresponds to the cerebellum of lower vertebrates. The

two lateral lobes or hemispheres are mammalian novelties. Increase of the cerebellar cortex by folding results in so complicated a structure that the term arbor vitae applied to its white fiber tracts seems not inappropriate. Three paired bundles of fibers, the superior, middle and inferior peduncles, connect it with adjacent parts of the brain. The superior peduncles or brachia conjunctiva connect the cerebellum with the midbrain; the middle peduncles or brachia pontis connect with the pons; the inferior peduncles or restiform bodies connect with the medulla

**Fig. 428.**—Cross section of the lumbar enlargement of the human spinal cord. X8. (From Bremer’s “Text Book of Histology.”)
oblongata. Where the restiform bodies join the medulla, its wall projects laterally to form the cerebellar flocculi. (Fig. 424)

The cerebellar cortex consists of gray matter. Embedded in its central core of white fibrous matter is a folded layer of gray matter, the dentate nucleus. The Purkinje cells of the cerebellar cortex have synaptic connexions with ascending sensory fiber tracts. From them impulses pass to the cells of the dentate nucleus and thence by way of the brachia conjunctiva into the tegmentum of the midbrain.

A conspicuous feature of the ventral wall of the metencephalon of mammals is the pons (Varoli), which has already been described as a bridge of nerve fibers connecting the two hemispheres of the cerebellum. Each lateral half of the pons becomes a middle cerebral peduncle or brachium pontis. The fibers of the pons come largely from the cerebral hemispheres, which decussate or cross to the opposite side as they pass to the cerebellar hemispheres. The posterior boundary of the pons marks the anterior limit of the myelencephalon or medulla oblongata.

Medulla Oblongata. The non-nervous roof of the myelencephalon or medulla oblongata of cyclostomes is modified as a choroid plexus and serves as a mechanism for nourishment of the brain. A similar plexus appears in the medulla oblongata of all vertebrates. Cranial nerves V to X have their roots and their motor centers in the lateral walls of the medulla. A number of giant ganglion cells occur in the medulla of cyclostomes, and, by their neurites or Mueller’s fibers, connect with the tail muscles. The main mass of the lateral and ventral wall of the medulla consists of longitudinal fiber tracts of both ascending and descending fibers, which connect brain and spinal cord.

In Elasmobranchs, Ganoids, and Dipnoi the lateral walls of the anterior part of the medulla form conspicuous “ears,” the restiform bodies, in which are equilibratory centers, which correlate the sensory nerves of the semicircular canals with trunk muscles. With the development of lateral line organs, their nervous centers in the lateral walls of the medulla form the conspicuous paired longitudinal vagus lobes. But in amphibia and reptiles these vagus lobes disappear, in correlation with the loss of the lateral line organs.

The beginning of the medulla oblongata at the posterior boundary of the pons is marked in the human brain by the origin of the abducens nerve. Extending along the ventral surface of the medulla are the paired pyramids, formed by bundles of fibers which connect the cerebral hemispheres with the trunk. Lateral to the pyramids are two shorter swellings, the oliva, which mark the position of the inferior olivary nucleus.

Sections of the olivary nucleus show that, like the dentate nucleus of the cerebellum, it is a horse-shoe shaped and crenated mass of gray matter. Fiber tracts connect the olivary nucleus with the cerebellum.
In the human brain the medulla is largely covered by the cerebellum. To the cranial nerves connected with the medulla in the anamnia are added the spinal accessory (XI) and the hypoglossal (XII). (Fig. 437)

**EVOLUTION OF THE SPINAL CORD**

The spinal cord is a much more conservative portion of the central nervous system than the brain. Consequently, although the contrast between the so-called brain of amphioxus and that of man is so very great that their homology may be doubted, the spinal cords of these chordate

![](image1)

extremes are recognizably similar. Both are tubular and both have a central mass of gray matter and an external layer of fibrous tissue. The relations of dorsal and ventral nerve roots are similar. The differences are bridged over by intermediate conditions in lower vertebrates.

The fact that the brain of amphioxus differs from its spinal cord, not in greater size but chiefly in the expansion of its lumen, appears to support the inference that spinal cord and brain were originally undifferentiated from one another. The same columns of gray matter are recognizable in both, although because of the absence of myelin nerve sheaths, amphioxus lacks the color contrast between white and gray matter. This conclusion is substantiated by evidence from ontogenesis, which shows
that the distribution of nervous matter is essentially similar in cord and brain.

The spinal cord of amphioxus is somewhat triangular in cross section, with the apex of the triangle dorsal, the base resting upon the notochord. The small amount of gray matter lies close to the slitlike central canal. The lateral walls are much thicker than the dorsal and ventral, since fibrillar material which makes up most of the substance of the cord is wholly lateral in position. Some cellular differentiation into sensory and motor ganglion cells is visible in the gray matter, ependymal cells being the most abundant. Sensory ganglion cells connect with the dorsal nerves, and giant neurochord cells extend across the central canal. The fibers of the giant nerve cells, after decussation, extend lengthwise of the cord, some caudal and some cephalad. Since these do not form nerve fibers which leave the cord, it is supposed that the giant fibers give off collaterals to the motor centers along the cord, and serve to correlate their activities. (Fig. 429)

The spinal cord of cyclostomes is much flattened, with the cellular matter distributed in a pair of lateral wings. Ventral to the central lumen, a number of giant or Mueller's fibers extend lengthwise and carry from the brain impulses thought to be chiefly static. Dorsal to the lumen, are sensory ganglion cells like those of Amphioxus. The outer fibrous or marginal layer of the cord is divided into longitudinal bundles of fibers, the **funiculi**. Medullary sheaths are lacking, so that sympathetic fibers can not be distinguished from others. Neurone relations in the cord indicate that it is a reflex center and a pathway for intersegmental nervous connexions. Increase in descending fiber tracts demonstrates the increasing dominance of the brain. Polynuclear gland cells possibly of endocrinal function, occur in the caudal region of the cord. (Fig. 429)
In elasmobranchs nerve fibers are myelinated, so that white and gray matter show the same contrast as in the cord of higher vertebrates. Dorsal and ventral columns of gray matter are differentiated, but the dorsal columns merge together in the median plane. Somatic motor cells of the ventral column are very large, as in other fishes, amphibia, and reptiles; and the dendrites extend into the dorsal column. Sensory ganglion cells, except the embryonic and transient Rohon-Beard cells, have migrated into the spinal ganglia. Dorsal, lateral, and ventral funiculi have relations similar to those of higher vertebrates. The enlargement of the lateral walls of the cord results in the formation of a deep ventral fissure. The suggestions of the formation of a dorsal septum are, however, slight. (Fig. 429)

The spinal cord of amphibia resembles in fundamental characters that of elasmobranchs. The dorsal columns of gray matter become more distinctly paired, so that the gray matter assumes in cross section the form of a capital H characteristic of all higher animals. In the gray matter the nerve cells retain their central position surrounded by a network of fibers and their synaptic connexions. A dorsal septum has developed as a result of the increased thickness of the dorsal portion of the lateral wall of the cord. In the cervical and lumbar regions the diameter of the cord is considerably increased in correlation with the enlargement of the appendages. (Fig. 429)

The spinal cord of reptiles differs in no essentials from that of mammals. The increase in thickness of the marginal layer of longitudinal fibers indicates an increased integration of the body. The fibers which ramify through the gray matter are non-medullated, and their color is gray in contrast with the white color of the medullated fibers of the marginal zone.

Within the gray matter of the cord, sensory and motor nerves of reflex arcs usually effect their synaptic connexions by the intermediation of association neurones located in the gray matter. The intermediolateral column, which throughout the vertebrate series contains the ganglion cells of the motor nerves which supply visceral muscles, becomes more distinctly demarked than in lower vertebrates. The gray matter crosses the median plane of the cord as the gray commissure which surrounds the central canal.

A considerable increase in the amount of white matter in mammals indicates a further dominance of the brain and a greater integration of the body. The relative amount of white matter diminishes from the medulla to the filum terminale in which the spinal cord ends. In the region of the arms and legs, at the cervical and lumbar enlargements, both gray and white matter increase in quantity. The division of the white matter into funiculi, begun in cyclostomes, reaches its climax in man. Dorsal, lateral, and ventral funiculi are separated from one another not
only by dorsal and ventral nerve roots, but also by external dorso-lateral and ventro-lateral grooves or sulci, which extend lengthwise of the cord.

The medullary sheaths of the fibers which compose the funiculi develop at different times in ontogenesis as the fibers come into functional activity. By the study of the time of myelination of fibers and their degeneration after they are cut, it has been learned that fibers of similar origin and function occur in bundles or tracts. Each funiculus consists of a number of such tracts, together with groups of tracts or fasciculi. A tract or a fasciculus may contain either ascending sensory fibers or descending motor fibers. A fasciculus may contain both kinds. Fibers may have their origin or termination at any level and relatively few extend the entire length of the cord. (Fig. 430)

Among the more important ascending fiber tracts are:

The fasciculi gracilis and cuneatus, which consist chiefly of sensory fibers from the dorsal roots. Most of these sensory neurites connect with neurones in the spinal cord, chiefly with association neurones of the Golgi type II. Those which reach the brain have synaptic relations with secondary neurones in the wall of the medulla oblongata.

The fasciculus spinocerebellaris dorsalis, formed by neurites of ganglion cells in the nucleus dorsalis or Clark’s column of the cord. These fibers reach the cerebellum by way of the restiform body.

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**Fig. 431.—Diagram of the descending (pyramidal) conduction paths. (Redrawn after Morris.)**
The **ventral spinocerebellar tract**, which consists of fibers from cells of the dorsal column. These fibers reach the cerebellum by way of the pons.

The **lateral and ventral spinothalamic tracts** which include fibers from the dorsal column which cross to the opposite side and finally reach the thalamus.

The more important descending fiber tracts are:

The **lateral corticospinal** or crossed pyramidal tract, which contains fibers from pyramidal cells in the cerebral cortex of the opposite side. The telodendria end in the gray matter of the cord in relation to the somatic motor neurons, and form part of the mechanism of voluntary control.
The ventral corticospinal or direct pyramidal tract, formed of fibers from the cerebral cortex of the same side which have synaptic connexions with somatic motor cells. The size of this fasciculus is proportionate to the use of the forelimbs and to the degree of intelligence.

The rubrospinal tract, carries fibers from the red nucleus of the mid-brain which cross the median plane and connect with somatic motor cells in the ventral column of the spinal cord.

**Neuron Relations in the Cord.** The spinal cord is both the center for reflexes and the pathway for impulses towards and away from the brain.

In the simplest possible reflex action where two neurons only are involved, the synaptic connexions between the two lie in the gray matter of the cord. The cell body of the afferent neurone is in the sensory ganglion of the afferent nerve. That of the effector neuron is in the ventral column of the spinal cord, and its neurite extends by way of the ventral root to a muscle fiber or a gland.

Usually, however, more than two neurons are chained together in a reflex act, for there may be one or more association neurons located in the gray matter of the cord, which carry the impulse from the receptor neuron to the effector neuron. But it should not be understood that a somatic motor nerve cell located in the ventral column has synaptic connexions with the telodendria of only a single neurite. On the contrary, many neurites may have synaptic relations with the dendrites of each somatic motor neuron. The motor neuron is simply "the final common path."

Within the gray matter of the spinal cord, the central connexions of the neurites of an afferent neuron may be of various kinds. The telodendria may connect directly with the dendrites of a somatic motor cell. This is the simplest relation. They may connect with a neuron in Clark's column near the median line at the base of the dorsal column, and the nervous impulse be carried in the dorsal cerebellar tract; or they may pass to a commissural neuron and the impulse be carried to the opposite side of the spinal cord. There are also connexions with sympathetic neurons.

The neurites of receptor neurons, having entered the spinal cord, immediately dichotomize to give off long ascending and short descending branches and thus add to the fibers of the fasciculus cuneatus. As these fibers pass towards the brain, they are displaced inwards by the fibers which are added from higher levels. The result of this process is that, in the neck region, the neurites which enter the cord in the lower trunk region come to lie in a median fasciculus, the fasciculus gracilis. Most of the descending short fibers end in the gray matter of the cord. From both ascending and descending neurites, fine collateral branches pass
into the dorsal column of gray matter, and come into synaptic connexions with dendrites of the same or of the opposite side.

The fibers which enter the spinal cord by the dorsal root are somatic afferent or visceral afferent, depending upon their peripheral connexions.

The visceral motor fibers, which appear in the dorsal roots of lower vertebrates, are not found in the dorsal spinal nerves of mammals.

The neurites of the ventral roots are purely efferent. Of these there are two kinds, somatic motor and visceral motor. The somatic innervate skeletal muscles derived from the mesodermal somites, the visceral are connected through the sympathetic ganglia with visceral involuntary
muscles or with glands. The ganglion cells of both types lie within the gray matter of the spinal cord; but those of the somatic motor nerves lie in the ventral column, while the visceral motor fibers come from ganglion cells in the intermediolateral column.

**EVOLUTION OF THE PERIPHERAL NERVOUS SYSTEM**

The peripheral nervous system consists of two main divisions, the cerebrospinal nerves and the autonomic system. The cerebrospinal nerves are also of two kinds; cranial, which have their foramina of exit from the cranium, and spinal, which are connected with the cord and leave the vertebral column by way of intervertebral foramina.

![Neuron relations of motor and sensory nerves which have their centers in the medulla oblongata. (Redrawn from Patten, after Ranson.)](image)

**Nerve Components.** In addition to the four kinds of nerve fibers found in spinal nerves and distinguished by differences in function and distribution, some of the cranial nerves may have special fibers which supply sense organs or specialized muscles. Four special groups of nerves must therefore be added to the four general kinds which have already been mentioned, making a total of eight kinds of nerve components. (Fig. 435)

1. **General somatic efferent** fibers are relatively large neurites, formed as outgrowths from nerve cells located in the ventral column of the spinal cord and brain. Somatic motor cells are multipolar and contain numerous Nissl bodies. The neurite arises from a hillock or implantation core free from Nissl granules. As the neurite emerges from the cord or brain it is surrounded by myelin and neurilemma sheaths. Both sheaths are
interrupted at intervals by nodes of Ranvier, but the neurite continues until it terminates on the surface of one or more muscle fibers in the form of a motor end-plate. At this end-plate the neurolemma becomes continuous with the sarcolemma sheath of the muscle fiber. The granular protoplasm of the end-plate contains many nuclei as well as pad-like terminations, the telodendria of the neurite. General somatic efferent fibers supply most of the skeletal muscles of the body. They are absent from cranial nerves with the possible exception of the spinal accessory of amniotes. But this nerve is a spinal nerve in the anamnia.

2. **Special somatic efferent** fibers innervate specialized somatic muscles of the head. These muscles are the six eye muscles and some of the muscles of the tongue. The eye muscles are innervated by the oculomotor, trochlearis, and the abducens nerves. The hypoglossus nerve supplies the tongue muscles. The hypoglossus is, however, a spinal nerve in the anamnia.

3. **General somatic afferent** nerves supply the skin and skeletal muscles. They are the nerves of general exteroceptive sensibility and of deep proprioceptive sensibility. With a few exceptions already noted the cell-bodies of somatic sensory nerves lie, not in the spinal cord or brain, but in the ganglia of the dorsal roots. Two kinds of ganglion cells may be distinguished, large and small, both usually of the unipolar (disguised bipolar) type. Their fibers are mostly myelinated, and the neurolemma sheaths cover both the cell-bodies and the neurites. (Fig. 390)

As the neurite leaves a ganglion cell, it is twisted into a glomerulus. It soon divides into two branches, one of which passes into the cord, and the other to the skin or to a muscle fiber, where it terminates as a muscle spindle. The ganglion cells are frequently surrounded by a pericellular network of nerve fibers which are possibly of sympathetic origin.

Of the cranial nerves, the trigeminal, glossopharyngeal and vagus contain general somatic afferent fibers from the skin. The dorsal roots of spinal nerves consist largely of such general somatic fibers. The oculomotor, trochlearis, abducens and trigeminal nerves carry proprioceptive impulses from the muscles.

4. **Special somatic afferent** components are limited to some of the cranial nerves and are not found in spinal nerves at all. The facial, acoustic, vagus and (?) glossopharyngeus nerves contain them. These are nerves of special sense organs, the ear and lateral line organs. The fibers of the cochlear branch of the acoustic nerve carry exteroceptive impulses while those of the vestibular branch are proprioceptive. Lateralis fibers are contained in the facial and vagus nerves, and, possibly in some fishes, in the glossopharyngeus nerve. If the optic nerve were not a specialized fiber tract of the brain, it might be classed as a special somatic afferent nerve.
5. General visceral efferent nerves supply smooth muscles of the viscera, heart muscle and digestive glands. They are relatively small medullated fibers which connect by way of the white rami communicantes with the sympathetic. Their ganglion cells, located in the lateral motor column of the brain and cord, are small. Of the cranial nerves the oculomotor, facial, glossopharyngeal and vagus nerves contain these fibers. General visceral efferent nerves form the preganglionic fibers of the sympathetic system. Among peripheral nerves they are peculiar in relaying their impulses to a second set of neurones, the cells of which are located in sympathetic ganglia. In amniotes they leave the spinal cord by way of ventral roots only, but in Anamnia some of them are contained in the dorsal roots. (Fig. 442)

6. Special visceral efferent components are limited to the head where they innervate special striped muscles which develop from the mesoderm of the visceral arches. Their motor centers lie in the ventro-lateral motor column of the medulla between the somatic motor column and the general visceral efferent column. Unlike the general visceral efferent fibers they have no connexion with sympathetic ganglia. They are among the constituents of the trigeminal, facial, glossopharyngeal, vagus and accessory nerves.

7. General visceral afferent nerves carry impulses from the mucous lining of the alimentary canal, larynx and trachea. They use the sympathetic nerves as pathways but do not have nervous connexion with the cells of the sympathetic ganglia. Some of the fibers reach the medulla oblongata by way of the facial, glossopharyngeal and vagus nerves. Their sensory centers lie in the extended nucleus of the tractus solitarius within the medulla.

8. Special visceral afferent fibers are found only in cranial nerves in connexion with the senses of smell and taste. The olfactory nerve, and with it possibly the terminal nerve, has been regarded by some as a highly specialized visceral afferent nerve. Gustatory fibers pass to the medulla by way of the facial, glossopharyngeal, and vagus nerves. Like general visceral afferent components their fibers are connected with the nucleus of the tractus solitarius. The centers in the cerebral hemispheres associated with sensations of smell and taste are at present uncertain, but are usually ascribed to the gyrus cinguli.

EVOLUTION OF THE CRANIAL NERVES

The two anterior pairs of nerves of amphioxus are purely sensory, while all posterior dorsal nerves are mixed. It is customary to compare the first pair of nerves of amphioxus with the olfactory nerves, or with the "terminal" nerves of vertebrates. Since amphioxus has no eyes, no nerves are present comparable with the optic nerves of vertebrates, and
the second pair of sensory nerves of amphioxus may be the homologues of the ophthalmic nerves of craniates. The four mixed nerves posterior to the ophthalmic have been compared respectively with the trigeminal, facial, glossopharyngeal, and vagus. It is probable, however, that at least three segmental nerves are represented in the vagus nerve of vertebrates. Of the somatic motor nerves of vertebrates, the oculomotor is possibly represented in the first ventral root of amphioxus.

Fig. 436.—A diagram showing the distribution of the anterior nerves of amphioxus. The two anteriormost nerves of amphioxus lie anterior to the myotomes and are purely sensory. The remaining nerves are either mixed like those shown in the figure or are purely motor. The former alternate, the diagram shows, with the myotomes, while the latter are metameric in position. (Redrawn after Hatschek slightly modified.)

The number of cranial nerves varies in craniotes. Fishes and amphibia have ten pairs; reptiles, birds, and mammals have twelve. These, beginning with the anteriormost, are:

I. Olfactory. Special visceral afferent.
II. Optic. Sensory. A specialized fiber tract of the brain.
III. Oculomotor. Somatic efferent, with some visceral efferent fibers.
IV. Trochlearis. Somatic efferent.
V. Trigeminus. General somatic afferent and visceral efferent.
VI. Abducens. Somatic efferent.
VII. Facialis. Mixed visceral afferent and efferent. Special somatic afferent.
VIII. Acoustic. Special somatic afferent.
IX. Glossopharyngeal. General and special visceral mixed. (?) Somatic sensory.
X. Vagus. General and special visceral mixed. Special somatic afferent.
XI. Accessory. (?) Somatic efferent, and general and special visceral efferent.
XII. Hypoglossal. Somatic efferent.
Striking differences in function and distribution distinguish these twelve and set them apart from spinal nerves. These differences may be briefly summarized:

I. Olfactorius. The olfactory nerve is peculiar in the origin of its neurites, which, like the neurites of primitive neurosensory cells, develop as processes of sense cells located in the olfactory epithelium. Their terminal arborizations effect synapses with neurons located in the olfactory lobes of the brain. By means of a neuron chain, connexions are established with the cells in the hippocampus. That the "terminal nerve" of Pincus is an independent segmental nerve has not been demonstrated. That it is a ganglionic division of the olfactory nerve is supported by the evidence of its structure, development and relations.

II. Opticus. The so-called optic nerve is not a true segmental nerve comparable with other cranial nerves. Its mode of development proves that it is a specialized fiber tract of the forebrain, since the neurosensory cells which form it are originally a part of the brain wall, and their terminal arborizations lie not in the skin but in the retina which develops from the
brain wall. Like the trochlear, the optic nerve has a chiasma which lies below the brain immediately anterior to the infundibulum. Half its fibers enter the chiasma and cross to the opposite side of the brain, the other half effect central connexions with the thalamus and optic lobe of the side from which they enter. In lower vertebrates, the central connexions of the optic are with the optic lobes of the mesencephalon. But in mammals they are shifted mostly to the occipital lobes of the hemispheres, which they reach indirectly by way of the lateral geniculate body of the thalamus.

III. **Oculomotorius.** The motor nucleus of the oculomotor lies in the somatic motor column at the base of the midbrain, median to the cerebral peduncle. It contains somatic efferent and visceral efferent fibers. It is an eye muscle nerve innervating four eye muscles; it also innervates the ciliary muscle within the eye by way of the ciliary ganglion, a para-sympathetic ganglion attached to the oculomotor and ophthalmic nerves. Like the other eye muscle nerves the oculomotor nerve remains relatively unchanged from fishes to man.

IV. **Trochlearis.** The trochlear, another eye muscle nerve, has its nucleus in the base of the metencephalon, and its root of origin from the dorsal constriction which separates the optic lobes from the metencephalon. In cyclostomes its root is said to be connected with the lateral wall of the medulla between those of the ophthalmicus and trigeminal nerves, the roots of which are separate in cyclostomes. In elasmobranchs its fibers form a chiasma over the isthmus behind the midbrain. In mammals and man its chiasma lies posterior to the inferior colliculus. Although in having a chiasma, the trochlearis is unique among motor nerves, we must class it as a somatic motor nerve, since its fibers are connected with cells in the somatic motor column of the brain posterior to those of the oculomotor. Moreover, the muscle which it innervates develops from a mesodermal somite (somite 2).

V. **Trigeminalis.** In most vertebrates the trigeminal arises from the lateral wall of the oblongata by two roots, the larger sensory, the smaller motor. Its sensory ganglion, the Gasserian or semilunar, sends an ophthalmic branch to the skin of the forehead, a maxillary branch to the upper lip and the teeth of the upper jaw, and a mixed mandibular branch to the teeth of the lower jaw and to the tongue. In man and mammals all three branches have somatic afferent fibers. (Fig. 438)

The motor root is that of the masticator nerve, which supplies special visceral efferent fibers to the chewing muscles. In man, the nucleus of the masticator nerve lies in the visceral motor column in the wall of the oblongata, median to the pons. General visceral or proprioceptive fibers enter the semilunar ganglion from the chewing muscles, and pass to the mesencephalic nucleus in the roof of the midbrain. Such sensory fibers
arising from cells within the brain are unique in amniotes, although such relations are not uncommon in invertebrates and amphioxus. (Fig. 516)

In the anamnia the ophthalmic branch of the trigeminus divides into a superficial branch, which innervates the skin of the snout but not the lateral line sense organs of that region, and a deep or profundus branch which passes through the orbit to the snout. Both contain general somatic sensory fibers. As stated above, in cyclostomes the deep ophthalmic is an independent nerve with a separate ganglion and root and is therefore regarded by many morphologists as a "segmental" nerve. In most anamnia, however, the root of the profundus nerve joins that of the rest of the trigeminus and persists in amniotes as a branch of that nerve.
VI. Abduccns. The roots of the abduccns nerve in man emerge from
the ventral side of the medulla near the posterior boundary of the pons.
In lower vertebrates it is a meta-otic nerve. Its somatic efferent fibers
come from a nucleus in the somatic motor column near the midventral
line of the medulla, and innervate the external rectus eye muscle. The
eye muscle nerves (III, IV, VI) are an especially conservative group,
which, like the muscles they innervate, differ little from fishes to man.

VII. Facialis. The facial is a mixed nerve with two roots. Its major
root is purely motor, the fibers, which belong to the special visceral motor
group, innervating the superficial facial and scalp muscles, the posterior
belly of the digastric muscle, and the stylohyoid. Its motor nucleus lies
lateral and posterior to that of the abduccns, the fibers of the facial looping
around those of the abduccns to form the genu of the facial.

The minor root of the facial forms the glossopalatine or intermediate
nerve of the facial. Most of it enters the chorda tympani nerve, which
consists of special visceral sensory fibers from the anterior taste buds of the
tongue. Some general visceral efferent fibers innervate the submaxillary
and sublingual salivary glands. The sensory fibers of this nerve come
from cells in the geniculate ganglion. With the disappearance of lateral
line organs in land amphibians, the seventh nerve loses its special somatic
sensory (lateralis) components.

VIII. Acusticus. The auditory nerve is relatively short, with two
branches, cochlear and vestibular, which have their root or origin near
that of the facialis. The fibers which develop from the spiral and vesti-
bular ganglia belong to the special somatic sensory group. The cochlear
is the nerve of hearing; the vestibular, of equilibration. The dendrites
of both receive their nervous impulses from receptor hair-cells. Their
central connexions are with the cochlearis and vestibularis nuclei in the
oblongata. The centers of hearing, however, are located in the temporal
lobes. Ganglion cells of both nerves are primitive and unique among
amniote afferent neurones in being bipolar.

IX. Glossopharyngeus. The glossopharyngeal is a mixed nerve which
contains special and general visceral fibers, both sensory and motor. Its
roots are posterior to those of the acusticus and in line with those of the
vagus. The sensory fibers come from the petrosal ganglion and are
distributed to the posterior part of the tongue and to the pharynx. The
central nucleus is that of the tractus solitarius which lies between the
cochlear and vestibular nuclei. The secondary cortical connexions and
the centers of taste are unknown. In some fishes the glossopharyngeus
receives special somatic afferent fibers from the supratemporal line of
sense organs.

The motor fibers of the glossopharyngeus come from the inferior
salivatory and ambiguous nuclei in the medulla. The general visceral
fibers connect with the otic ganglion and, by postganglionic fibers, with the parotid gland. The special visceral efferent fibers innervate the stylopharyngeus muscle. In cyclostomes, fishes, and urodeles the glossopharyngeus forks over the first gill slit to form post- and pre-trematic branches. With the disappearance of gills in land amphibia, the glossopharyngeal nerve does not lose its post- and pre-trematic branches. The latter, which is the larger, persists as the pharyngeal nerve.

X. Vagus. The vagus or pneumogastric is a mixed nerve, which has the widest and most diverse distribution of any of the cranial nerves. It arises by an extended series of fine roots from the medulla posterior to the roots of the glossopharyngeus.

The sensory components arise in the ganglion jugulare and ganglion nodosum and are distributed to the larynx, trachea, lungs, esophagus, stomach, intestine, and gall bladder. Their central connexions are with the ala cinerea in the floor of the medulla. The vagus in cyclostomes, fishes and urodeles receives special somatic afferent fibers from the lateral line organs of the trunk and tail.

Some of the motor fibers come from the nucleus ambiguus and some from the dorsal motor nucleus of the vagus near the nucleus ambiguus. They innervate the muscles of the larynx, esophagus, stomach, small intestine, and part of the large intestine. Inhibitory fibers pass to the heart and secretory fibers to the gastric glands and pancreas.

The lateral line components of the vagus are lost in the land amphibia and appear in none of the higher vertebrates.

XI. Accessorius. The spinal accessory, purely motor, combines characteristics of cranial and spinal motor nerves. Some of its fibers come from the vagus and ambiguus nuclei and join vagus fibers in the innervation of thoracic and abdominal viscera. Another group of fibers of similar medullary origin innervate striated muscles of the pharynx and larynx. A third set of somatic motor fibers innervate sternocleidomastoid and trapezius muscles. The accessory nerve of amniotes is in part a somatic motor spinal nerve which has been added to the ten cranial nerves of amnmnia as a result of the union of cervical vertebrae with the occipital region of the skull, and in part visceral motor like the vagus with which it is associated.

XII. Hypoglossus. The hypoglossal is a somatic motor nerve which supplies the tongue muscles. Its roots of origin lie posterior to those of the abducens between the pyramid and the olive. The nucleus is medial and ventral to that of the vagus, and in series with the spinal division of the accessory. Like the accessory, the hypoglossus is a spinal nerve which has become cranial as the result of the extension of the occipital region of the skull.
Fig. 439.—The brain and spinal cord of man in ventral aspect shown in relation to nerve roots and the chief autonomic ganglia. (Redrawn from Morris, after Allen Thomson.)
Evolution of the Spinal Nerves. In man thirty-one pairs of nerves are connected with the spinal cord. Of these, eight are cervical, twelve thoracic, five lumbar, five sacral, and one coccygeal. Unlike cranial nerves, each spinal nerve is connected with the central nervous system by two roots, one dorsal, sensory and ganglionated; the other ventral, motor and non-ganglionated. The fibers of the dorsal root are outgrowths of the nerve cells which form the ganglion; the nerve cells of the ventral root lie in the ventral horn of the spinal cord. The two roots unite near the ganglion to form a mixed nerve which has its exit from the vertebral canal by way of intervertebral foramina. As a spinal nerve passes towards the periphery, it divides into dorsal and ventral branches, and a visceral branch, the ramus communicans, which connects with a sympathetic ganglion. (Fig. 439)

The similarity of vertebrate spinal nerves, in their metameric repetition, to the nerves of amphioxus has been one of the reasons for assuming amphioxus to be the prototype of the vertebrates. Except the first two pairs, which are in some respects peculiar, all the segmental nerves of amphioxus are similar, each having a dorsal mixed root and a ventral motor root, which do not unite. Another peculiarity of amphioxus is the absence of a ganglion on the dorsal root. The cell bodies from which sensory neurites arise lie either in the dorsal wall of the cord or scattered along the course of the nerve. It is, however, asserted that some of the cells of the dorsal nerves are neuroepithelial cells located in the skin. The general somatic afferent fibers of the dorsal nerves pass directly to the skin by way of the myocommata. The general visceral efferent fibers leave the dorsal nerve by way of intestinal branches which supply the muscles of the intestine.

The ventral nerves emerge from the cord by numerous fibrillar roots, and connect directly with the myotomes opposite. The dorsal nerves are, therefore, intermetameric, and the ventral metameric.

In myxine the dorsal and ventral nerves unite peripherally as they do in all higher vertebrates; and only in petromyzon among cyclostomes are all dorsal and ventral nerves separate. But in the head region of all vertebrates, the somatic motor nerves, oculomotor, trochlear, abducens, and hypoglossus do not unite with sensory nerves. In this regard, as in the mixed character of such nerves as V, VII, IX and X, the cranial nerves of higher vertebrates retain a primitive characteristic which is lost by the spinal nerves.

Plexuses. Although the spinal nerves of all chordates show a segmental one-to-one correspondence with myotomes and vertebrae, this regular metamericism is modified in the region of the paired appendages by the union of a number of ventral rami into an interlaced network or plexus. Four such plexuses are recognized in vertebrates, cervical,
brachial, lumbar, and sacral. Frequently the four unite in pairs to form cervico-thoracic and lumbo-sacral plexuses. In cyclostomes and fishes the group of postoccipital nerves forms a plexus which innervates the hypobranchial muscles. In many forms this cervical plexus unites with the brachial plexus. In amniotes the two plexuses become separate and the plexus of hypobranchial nerves forms the hypoglossus (XII) nerve.

![Diagram of collector nerve and a nerve plexus.](image)

In different species, and even in different individuals of the same species, there is considerable variation in the number of nerves in a plexus and in their interconnexions, so that exact homologies are impossible. The largest number of nerves in the cervico-thoracic plexus, twenty-five, occurs in skates. In higher vertebrates the number is usually reduced to four or five, and in man, the cervical plexus includes only the first four spinal nerves. The brachial plexus in man usually involves the lower four cervical and the first thoracic nerves. The first four lumbar nerves of man unite in the lumbar plexus; the fifth lumbar and the five sacral nerves form the sacral plexus. But generalization is difficult because of the large amount of variation.

Such plexuses are presumably adaptive, since by the interlacing of fibers any muscle may be innervated by more than a single nerve and a summation of stimulation effected. This does not imply, however, that
an individual muscle fiber is innervated by more than one nerve. Evidence of such plural innervation of a single muscle fiber is lacking. In fishes other than teleosts, the lumbo-sacral plexus receives fibers from a collector nerve, which unites anterior spinal nerves with the plexus.

The problem of the origin of a nerve plexus was difficult in the days when a primary and indissoluble connexion between nerve and muscle was assumed. It is simpler, now that neuro-muscular connexions are known to be secondary. Even in those regions where no plexuses are formed, each spinal nerve innervates at least three myotomes, its own and parts of the two adjacent. This tendency to muscle piracy is carried to a greater extreme in the nerve plexuses, in which fibers from one nerve may innervate more than three adjacent myotomes.

The numerous variations in plexuses, therefore, demonstrate that the peripheral distribution of a given neurite is not unalterably predetermined, though it must be admitted that the factors which determine the direction of growth of a given neurite are still uncertain. In the light of the evidence which we now possess, it does not seem necessary to explain the formation of a plexus by assuming a crowding of adjacent nerves in the formation of an appendage. The crowding is secondary, not primary.

Since both brachial and lumbosacral plexuses have their origin and meaning in relation to appendages, it is significant that both brachial and lumbo-sacral plexuses occur in snakes.

In mammals the cord ends in a terminal thread, the filum terminale, the length of which is proportional to that of the tail. The spinal cord in the fetus stops growing sooner than the vertebral column. As a result, the more posterior spinal nerves, which have their foramina of exit in

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![Diagram](https://via.placeholder.com/150)

**Fig. 441.—Motor nerve endings of intercostal muscle fibers of a rabbit. X150.**

(From Bremer's "Text Book of Histology.")
the lumbar and sacral vertebrae, are drawn out into a bundle of nerves parallel to the spinal cord and lying within the spinal canal. From its resemblance to a horse's tail, this is known as the **cauda equina**. Similar relations are found in anura and in some teleosts.

**THE AUTONOMIC NERVOUS SYSTEM**

In the higher chordates a special system of nerves, the **autonomic**, is distributed to the smooth muscles of the digestive and circulatory systems

![Diagram of neurons of the spinal cord and spinal nerves](image)

Fig. 442.—A diagram of neurons of the spinal cord and spinal nerves shown in their relations to one another and to their end-organs. Somatic sensory fibers are shown by continuous lines, somatic motor fibers by fine dots. Visceral sensory fibers are indicated by short broken lines, visceral motor by long broken lines. (Redrawn after Plate.)

and to many other organs. This autonomic system is most evident in the chain of **sympathetic ganglia** which lie along the dorsal aorta from the neck to the sacrum. These, however, are only a portion of the autonomic system, which is distinguished by functional rather than anatomical characteristics, for the cerebrospinal system is so intimately connected with autonomic nerve fibers that the two systems cannot be separated
anatomically. The vagus nerve, for example, which seems to be a part of the cerebro-spinal system, contains many autonomic fibers connected with the nervous plexuses of the viscera. Moreover, each sympathetic ganglion of the trunk has fiber connexions with a spinal nerve and with the plexuses of the intestine. (Figs. 439, 442, 443)

Autonomic nerves are connected not only with the digestive and circulatory systems but also with respiratory and urogenital systems, endocrinal and other glands, and the skin, so that there are few parts of the body which autonomic fibers do not reach. Except possibly the autonomic fibers connected with the ciliary muscle of the eye, autonomic nerves, although markedly influenced by the emotions, are not under the control of the will.

Two kinds of autonomic nerves, **sympathetic** and **parasympathetic**, may be distinguished on the basis of their antagonistic action and their different response to drugs.

A sharp distinction between the sympathetic and parasympathetic fibers cannot be drawn on the basis of function. The sympathetic fibers are usually excitatory; the parasympathetic are usually inhibitory. Most organs of the body have this double innervation and the action of the two kinds of nerves is antagonistic. But some parasympathetic fibers, as for example those in the vagus nerve, are excitatory.

The two sets of nerves differ in their reaction to atropin and adrenalin. Atropine is stimulating to parasympathetic nerves but not to sympathetic. Adrenalin stimulates sympathetic nerves but not parasympathetic. Possibly this latter reaction might be expected, since adrenalin is secreted by cells which have their origin from the sympathetic anlagen.

To the sympathetic group belong the vasomotor and secretory fibers which connect with the sympathetic ganglia of the neck and trunk, from the first thoracic to the fourth lumbar. Parasympathetic fibers are found in the oculomotor nerve connected with the ciliary ganglion, and in the chorda tympani and vagus nerves, and in the second, third, and fourth sacral nerves. In this system must also be grouped all the neurons with which these nerves have synaptic connexions.

It is evident, therefore, that there are three distinct groups of autonomic nerve fibers, a cranial group, a thoracico-lumbar group, and a sacral or pelvic group. Of these, the cranial and sacral elements are parasympathetic, and hence are grouped together as the craniosacral division of the autonomic system. The thoracico-lumbar division constitutes the sympathetic portion of the autonomic system.

Autonomic nerves may also be classified, on the basis of their distribution, into **somatic** fibers which innervate the blood vessels of the body wall and the smooth muscles of skin and sweat glands, and **visceral** fibers which supply the glands and smooth muscles of the viscera.
Fig. 443.—The autonomic nervous system in man. Autonomic ganglia are lettered, autonomic nerves given arabic numerals, cranio-spinal nerves are indicated by Roman numerals. Relations to brain and spinal cord are shown to the right by a series of cross sections taken at various levels. 1, Lacrimal nerve; 2, Oculomotor nerve; 3, Nasociliary nerve; 4, Gasserian ganglion; 5, ramus maxillaris; 6, posterior nasal nerve; 7, vidian nerve; 8, superficial petrosal n.; 9, deep petrosal n.; 10, chorda tympani n.; 11, minor superficial petrosal n.; 12, lingual nerve; 13, vagus nerve; 14, inhibiter cordis nerve; 15, broncho-dilator nerves; 16, accelerator cordis n.; 17, vertebral nerve; 18, major splanchnic nerve; 19, minor splanchnic nerve; 20, hypogastric nerve; 21, pelvic nerve; 22, nervus erigens. A, ciliary ganglion; B, sphenopalatine gang; C, otic ganglion; D, carotid ganglion; E, sublingual ganglion; F, superior cervical ganglion; G, stellate ganglion; H, celiac ganglion; I, inferior mesenteric ganglion. (Redrawn from Ariëns Kappers, after L. R. Muller.)
The somatic fibers act upon the hairs to stimulate their erection and cause "goose flesh." They also serve the important function of regulating temperature by influencing the tonus of the capillaries in the skin and thus, by changing the rate of blood flow, altering the amount of secretion of the sweat-glands. (Fig. 136)

The course followed by sympathetic and parasympathetic fibers within the central nervous system is almost unknown. Evidence is not lacking that stimulation of the cerebral cortex may be followed by reactions of the viscera.

Three kinds of autonomic fibers connect with sympathetic ganglia. **Preganglionic fibers** are visceral efferent fibers which come from ganglion cells located in the lateral column of the spinal cord and have their terminations in sympathetic ganglia. **Post-ganglionic fibers** are also visceral efferent and have their cell bodies within sympathetic ganglia and their telodendria upon smooth muscles of the intestine and of the blood vessels. The preganglionic fibers are medullated and form the **white rami communicantes** which connect spinal nerves with sympathetic ganglia. The post-ganglionic fibers are rarely medullated. They pass

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**Fig. 444.**—Diagram of the relations of the sympathetic system. The character of the different fibers is shown by conventional lines. *be,* blood-vessel; *cg,* chain ganglion; *d,* dorsal ramus; *dr,* dorsal root; *g,* gland; *gr,* gray ramus; *pc,* Pacinian corpuscle; *pg,* peripheral ganglion; *pvg,* prevertebral ganglion; *sg,* ganglion of dorsal root; *st,* sympathetic trunk; *v,* ventral ramus; *vi,* visceral ramus; *vr,* ventral root; *wr,* white ramus. (From Kingsley's "Comparative Anatomy of Vertebrates," based on Huber.)
either to the viscera by way of sympathetic nerves or to the body wall and skin by way of the spinal nerves with which they are connected through the gray rami communicantes.

Visceral afferent fibers, the third type, with cell-bodies in the dorsal ganglia, carry impulses directly from visceral muscles to the gray matter of the cord. Visceral afferent fibers having cell-bodies in the sympathetic ganglia have not been demonstrated, the cells of sympathetic ganglia being exclusively motor.

Most, if not all, actions of the autonomic system are reflexes mediated through the brain or cord. Some intestinal reactions, however, may occur after all nerve connexions with the cord and brain have been severed. It is, therefore, possible that some visceral reflexes pass through the intestinal plexuses only.

Three kinds of autonomic ganglia may be distinguished, ganglia of the sympathetic trunk, collateral ganglia such as the coeliac and mesenteric located in the wall of stomach and intestine, and terminal ganglia like the ciliary and cardiac located in the organs which they innervate.

Evolution of the Autonomic System

The nervous system of coelenterates is a plexus of primitive ganglion cells connected with neurosensory cells and smooth muscle fibers and located between the two primary body layers. This persists as an intestinal plexus in other invertebrates, from flatworms to molluscs and insects. That the intestinal plexus of vertebrates is homologous with that of invertebrates has not been demonstrated beyond a reasonable doubt, but may be assumed in the absence of evidence to the contrary. The late ontogenetic appearance of the plexus in vertebrates does not, however, harmonize with this assumption, since, in the light of the fundamental law of biogenesis, we should hardly expect the most ancient part of the nervous system to be one of the last to appear in the embryo. On the other hand, we may have here another example of retarded development, of which there are numerous examples in ontogenesis. Moreover, the relations of the myenteric and submucous plexuses of the walls of the stomach and intestine resemble those of the invertebrate intestinal plexuses, and both are equally autonomic in their functions. Finally, in elasmobranchs, sensory cells in the wall of the alimentary canal form a part of the system as in invertebrates. Evidence of similar cells in mammals is wanting.

In invertebrates and vertebrates alike the evolution of the autonomic system keeps pace with that of the digestive and circulatory systems. Sympathetic and parasympathetic systems are recognized in arthropods; but no structures are homologous with the autonomic ganglia of vertebrates.
As a system, therefore, the sympathetic of vertebrates is a new addition which arises late both ontogenetically and phylogenetically. Kappers, however, calls attention to the fact that in arthropods the intestinal plexuses, like the parasympathetic system of vertebrates, are limited to the cerebral and caudal part of the intestine.

So far as sympathetic ganglia are concerned, chordates appear to start with a clean slate, since there is no evidence of sympathetic ganglia in any of the protochordates. The autonomic system is, however, represented in protochordates, as in vertebrates, by the visceral nerves, motor and sensory. In the myxinoids the intestinal plexuses develop exclusively from the brain region, mostly from the vagus nerve. Tretjakoff has found in petromyzon autonomic fibers in all spinal nerves.

Some sympathetic and parasympathetic ganglia are found in elasmobranchs where, as in the higher vertebrates, the ciliary ganglion is parasympathetic and connected with the oculomotor and ophthalmic nerves. Several sympathetic ganglia occur in the trunk in connexion with a limited number of spinal nerves. The metameric arrangement seen in the embryos is modified in the adult through fusion. No longitudinal connectives are found in elasmobranchs. But Allis has described in the head region of teleosts segmental autonomic ganglia chained together by connectives. Nothing similar has been found in other vertebrates.

The autonomic system in tetrapods is essentially similar to that of man. A shift in the relations of the autonomic fibers occurs in phylogensis. In amniota, visceral motor fibers have their cell-bodies in the lateral horn and have their exit from the tube by way of the dorsal roots; those in the thoracico-lumbar and sacral region of amniotes, on the other hand, enter the ventral or somatic motor roots. The meaning of this shift is not clear.

In the head region, the connexion with dorsal roots is maintained throughout the vertebrate series.

**DEVELOPMENT OF THE BRAIN**

The central nervous system of vertebrates arises as a thickened placode of dorsal ectoderm anterior to the blastopore. This placode is known as
the neural plate. Next to the notochord, the nervous system is the first organ to develop. By the elevation of its edges, the neural plate is converted into a neural groove bordered by neural folds. The anterior more widely expanded portion forms the brain, and the narrower posterior portion the spinal cord. The transition between the two is, however, in most animals, gradual rather than abrupt.

As the neural folds rise, they bend towards the median plane and finally unite to form a neural tube with an anterior enlarged brain and a posterior constricted spinal cord. The closure of the neural tube begins in the neck region and proceeds cranial and caudal. But even before the neural folds in the cephalic region unite, a series of three expansions
appear, corresponding with forebrain, midbrain, and hindbrain, the forebrain differing from the other two in being anterior to the notochord. From these, by processes of local unequal growth, all the parts of the definitive brain are differentiated. Experiments demonstrate that the position of the three brain divisions is predetermined in the open neural plate. Soon after their closure and expansion as midbrain and hindbrain vesicles, the lateral walls become divided by a longitudinal sulcus into a ventral basal plate and a dorsal alar plate. Less clearly seen is a narrow floor plate in the midventral line, and a roof plate in the mid-dorsal line.

![Fig. 447.—Diagrams of the development of the brain.](image)

Since this sulcus does not develop in the forebrain, and ends where the notochord ends, it appears that the forebrain consists of alar and roof plates only. By the time a human embryo is a month old, the primitive forebrain vesicle has begun to divide into the anterior telencephalon and posterior diencephalon. In a five weeks embryo, the hindbrain has begun to divide into the anterior metencephalon and posterior myelencephalon. The undivided midbrain is the mesencephalon. These five brain regions occur in all vertebrates, and from them all the parts of the adult brain are formed.

**Brain Flexures.** While the subdivision of the primary vesicles is taking place in ontogenesis, the brain undergoes in amniote embryos three successive flexures, the cephalic or primary, the pontine, and nuchal or cervical. The cephalic flexure occurs in the midbrain region, the other two in the region of the hindbrain. All three flexures are in a vertical plane, but the bend of the pontine is the reverse of the other two. The
Fig. 448.—Human embryo of 2.4 mm. showing the neural tube partially closed. (From Ranson's "The Anatomy of the Nervous System," after Kollmann; courtesy of W. B. Saunders Company.)

Fig. 449.—Three stages—A, B, and C—in the development of the human brain, showing the brain vesicles and flexures. A is an early stage, dorsal aspect, B the brain of a three-weeks embryo in lateral aspect, C that of an eight-week embryo in lateral aspect. (Redrawn after His and Hardesty.)
bending is presumably the result of the elongation of the brain in limited space, since the brain elongates more rapidly than does the head itself. The cephalic flexure is well marked in the embryos of anamnia, but the pontine and nuchal flexures scarcely appear. They become increasingly evident as we pass from lower to higher amniotes. (Fig. 449)

**Brain Vesicles and Their Derivatives**
*(After Keibel and Mall)*

<table>
<thead>
<tr>
<th>Primary vesicles</th>
<th>Secondary vesicles</th>
<th>Derivatives</th>
<th>Ventricles</th>
</tr>
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<tbody>
<tr>
<td>Telencephalon</td>
<td>Diencephalon</td>
<td>Olfactory lobes, Corpora striata, Cerebral cortex, Optic thalami</td>
<td>Lateral (1st &amp; 2nd) ventricles, Anterior part of 3rd ventricle</td>
</tr>
<tr>
<td>Forebrain.........</td>
<td></td>
<td>Epithalamus (pineal gland, etc.), Thalamus, Hypothalamus, Infundibulum, Tuber cinereum, Mammillary bodies, Posterior lobe of pituitary</td>
<td>Posterior part of 3rd ventricle</td>
</tr>
<tr>
<td>Midbrain..........</td>
<td>Mesencephalon</td>
<td>Corpora quadrigemina, Tegmentum, Crura cerebri (peduncles)</td>
<td>Aqueduct</td>
</tr>
<tr>
<td>Hindbrain.........</td>
<td>Metencephalon</td>
<td>Cerebellum, Pons</td>
<td>Fourth ventricle</td>
</tr>
<tr>
<td></td>
<td>Myelencephalon</td>
<td>Medulla</td>
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**Telencephalon.** The division of the primary forebrain into telencephalon and diencephalon is effected by a dorsal constriction. The hemispheres develop from the telencephalon by paired lateral expansions of the alar plates. The roof plate takes no part in this, but persists between the hemispheres as the *lamina terminalis* of the adult brain. The paired hemispheric enlargements become conspicuous in a human embryo of six weeks and by the fifth month, have overgrown the cerebellum. In a six weeks embryo two chief divisions appear in each hemisphere, a dorsal expanded *pallium* and a ventro-lateral thickening, the *corpus striatum*. The pallium is indistinctly divided into a more ventral and median archipallium, and a more dorsal neopallium. (Fig. 447)
THE NERVOUS SYSTEM

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The neopallium, by great enlargement, forms most of the hemispheres; the archipallium develops into the olfactory and hippocampal lobes.

The wall of the brain consists primarily of a simple columnar epithelium, which in the region of the basal and alar plates rapidly becomes many-layered. Soon three strata may be distinguished, an inner epithelial or ependyma layer where the most rapid multiplication of cells occurs, a middle relatively thick mantle layer of compact epithelial cells, and an outer marginal layer of nerve fibers. As the hemispheres enlarge, cells migrate from the mantle layer into the marginal zone where they form the cortex, a layer which, lacking in lower vertebrates, appears first in Reptiles. The cortical cells of the definitive hemispheres become arranged in five layers of multipolar neurons.

During its early expansion, the surface of the hemisphere is smooth. In the fourth month, fissures arise, and eventually cut the hemisphere into lobes and gyri. The first to appear are those between the olfactory lobes and the pallium. Later, the hippocampal, lateral, and other fissures develop successively. These are followed during the last two months of fetal life by shallower sulci. The chief factor in forming these grooves is the more rapid increase of cortex, compared with that of the underlying white fibrous matter.

The lumen of each hemisphere persists as the lateral ventricle of the adult brain.

The corpora striata develop as local thickenings of the ventro-lateral walls of the telencephalon. As the dorsal pallium expands into the enlarged neocortex, the thickness of the corpus striatum steadily increases by cell multiplication. Consequently, in a six weeks embryo, each striate body projects into the lateral ventricle as a conspicuous swelling. Pri-
marily, the thickening of the striate body is the anterior continuation of that of the thalamus. As a result of the local enlargement of each, the two become separated by a deep groove until the end of the third month.

The growth and elongation of the hemisphere carries the corpus striatum back over the thalamus, so that it rests on the thalamus like a saddle on a horse; and the two merge into what is structurally and func-

![Diagram](image-url)

**Fig. 451.**—Diagram of median longitudinal section of four-day chick. Due to a slight bend in the embryo the section is para-sagittal in the mid-dorsal region but for the most part it passes through the embryo in the sagittal plane. (From Patten's "Embryology of the Chick.""

tionally a unified organ which becomes a pathway for fibers to and from the cerebral cortex. In the corpus striatum these fibers form the internal capsule which divides the corpus striatum into a median **caudate** nucleus and a lateral **lenticular nucleus**. At the end of the fourth month, the relations resemble those of the adult brain.

**Olfactory Lobes.** The olfactory lobes grow out from the base of the hemispheres. At first they are hollow, but as they become differentiated into bulb and tract, the cavity is lost. Fibrous connexion with that part of the pallium which becomes the hippocampus is effected by neurites from cells in the bulb.
Commissures. The morphological changes which the brain undergoes are accompanied by the development of fiber tracts which connect the various parts of the brain and effect its functional unity. Among these, none are more important than the commissures which unite the lateral halves of the brain. These are formed by bundles of neurites which grow from neuroblast cells in each side of the brain to corresponding nuclei in the other side. The anterior and hippocampal commissures develop in the lamina terminalis. Following the elongation of the cerebral hemispheres, the hippocampal commissure is carried caudad and incorporated in the posterior part of the fornix. The fibers of the anterior commissure connect the olfactory lobes with the hippocampus of the opposite side; those of the hippocampal commissure mostly connect the hippocampus with the hypothalamus of the opposite side. (Fig. 425)

In correlation with the growth of the cerebral cortex, the corpus callosum develops just above and anterior to the hippocampal commissure. When it first appears, the corpus callosum is semicircular in cross section; but as development proceeds, it assumes, in a five months embryo, the elongated sickle-shape characteristic of the adult. Between the fornix and corpus callosum, the thin median walls of the hemispheres are stretched to form the median septum pellucidum. Between the two layers of this septum there frequently develops a cavity erroneously known as the fifth ventricle. (Fig. 383)

Chorioid Plexus. From the roof of the forebrain, in the region where telencephalon and diencephalon merge into one another, a chorioid plexus, which involves numerous blood vessels as well as brain wall, grows down into the cavities of the brain. This plexus penetrates the paired ventricles of the hemispheres and the median unpaired third ventricle of the diencephalon.

Diencephalon. The wall of the posterior half of the primary forebrain differentiates four zones, roof plate, epithalamus, thalamus, and hypothalamus. The roof-plate forms a chorioid plexus, which is continuous with that of the telencephalon, and which pushes into the ventricle. An outgrowth from the epithalamus becomes the pineal gland. A sulcus divides the thickened lateral wall into thalamus and hypothalamus. The thalamus becomes a massive thickening and unites with the corpus striatum.

From the hypothalamus develop the tuber cinereum, mammillary bodies, infundibulum, and the neural lobe of the pituitary gland. The tuber cinereum and mammillary bodies, thickenings of the posterior wall of the infundibulum, become connected with the hippocampus by means of a fiber tract, and are therefore believed to have an olfactory function. The infundibulum is formed as a funnel-shaped pit with apex towards the
roof of the mouth. The pars nervosa of the pituitary is proliferated from its ventral extremity during the third month.

**Mesencephalon.** The mesencephalon undergoes relatively little change during ontogenesis. As a result of thickening the lateral walls, the central cavity is reduced to a slender *aqueduct* which connects third

![Diagram of the brain of a four-day chick](image)

**Fig. 452.**—Diagrams to show the topography of the brain of a four-day chick. *A*, plan of sagittal section. The arbitrary boundaries between the various brain vesicles (according to Kupffer) are indicated by broken lines. *B*, dextral view of a brain which has been dissected free. *C*, schematic frontal section plan of brain. The flexures of the brain are supposed to have been straightened before the section was cut. (From Patten's "Embryology of the Chick.")

and fourth ventricles. From the dorsal portion of the midbrain arise the corpora quadrigemina, which contain optic and auditory reflex centers. From the dorsal plate of the mesencephalon develop also the red *nuclei*, which receive fibers from the cerebellum and send fibers by the rubrospinal tract into the spinal cord.

The motor nucleus of the oculomotor nerve develops in the basal plate. Posterior to it at the same level is the nucleus of the trochlear nerve which belongs originally, in elasmobranchs, with the mesencephalon.
Along the ventral wall of the mesencephalon develop two parallel fiber tracts, the cerebral peduncles, visible on the ventral side of the brain stem, which contain most of the ascending and descending fibers connecting the hemispheres with the lower parts of the body. Just dorsal to these, the tegmentum is differentiated as a region of interwoven fibers interspersed with masses of nerve cells.

**Metencephalon.** The chief modifications of the vesicle of the metencephalon are the cerebellum which develops from the alar plates, and the pons which is differentiated from the basal plates.

Four anlagen are involved in the cerebellum. From a pair of small thickenings near the median line the vermis is developed, while a larger pair of lateral masses form the cerebellar hemispheres. The formation of the cerebellar cortex resembles that of the cerebral. The relatively rapid growth of the cortex results in the formation of lobules and fissures of the adult cerebellum. The dentate nucleus is a cellular mass which develops within the white matter of the cerebellum. Three large bundles of fibers grow from the cerebellum, the brachium pontis, brachium conjunctivum, and the restiform body.

The cavity of the metencephalon forms the anterior part of the fourth ventricle.

**Myelencephalon.** The fifth and last of the brain vesicles forms the medulla oblongata. Its ventricle enlarges to form the posterior part of the fourth ventricle, which is partly obliterated by a choroid plexus developed from the thin dorsal roof of the medulla. Early in development, the alar and basal plates of the medulla show a series of five expansions, the rhombomeres or neuromeres, which disappear in ontogenesis and have been interpreted as evidence of a primitive metamers corresponding to that of the trunk and possibly, it is suggested, inherited from the metameric ganglia of invertebrate ancestors. The motor fibers of the trigeminal, abducens, facial, glossopharyngeal, vagus, accessory, and hypoglossal nerves arise from nuclei located in the medulla. The growth of nerve fibers in all directions within the wall of the medulla results in the reticular formation which is strikingly shown in cross section. Among the nuclei which develop in the medulla are the nucleus cuneatus and nucleus gracilis, the sensory centers of the fibers which pass into the medulla from the spinal cord by way of the fasciculus cuneatus and fasciculus gracilis.

**DEVELOPMENT OF THE SPINAL CORD**

When the neural plate becomes the neural tube, its wall is a simple columnar epithelium. In consequence of more rapid cell proliferation, limited to a layer of germinal cells which lie near the lumen of the cord,
the lateral walls become greatly thickened, while the mid-dorsal and midventral portions remain as thin roof and floor plates.

This thickened lateral wall becomes divided by a median longitudinal sulcus into a dorsal alar plate and a ventral basal plate.

Three layers are differentiated in the lateral walls of the cord, an ependymal layer next to the lumen, a thick mantle layer of spindle-shaped cells, and an outer marginal layer of fibers free from cells. The marginal layer increases in thickness by the addition of fibers which grow lengthwise of the cord. By the addition of myelin sheaths to these fibers, the marginal zone is converted into the white matter of the cord.

As the lateral walls increase in thickness, the lumen of the cord is narrowed down so that in a cross section it appears as a slit which, how-
ever, widens out slightly at the level of the longitudinal sulcus. Finally, the lateral walls fuse together, except in the ventral region, where a portion of the lumen is left as the central canal of the cord. The plane of fusion of the ependymal cells persists in the adult as the dorsal septum. On the ventral side of the cord, however, a median fissure is formed as a result of the increase in thickness of the lateral walls and the failure of the floor-plate to grow.

The mantle layer becomes the gray matter of the cord. As a result of unequal growth of this layer, dorsal, lateral and ventral gray columns develop. By the time the embryo is three months old, the gray matter has assumed in cross section its characteristic H-shape.

In the early stages of the spinal cord, two kinds of cells are differentiated, germinal cells which become neuroblasts, and non-nervous spongioblast cells. Following the outgrowth of the neurite from a neuroblast, a number of dendrites grow in the opposite direction. According to the theory of neurobiotaxis of Kappers, the neurite is stimulofugal, that is, grows away from the source of stimulus, and the dendrites are stimulopetal, that is, they grow towards the stimulus. Nerve cells of two kinds arise, motor, which are limited to the anterior and lateral gray columns, and association cells, which may lie in the dorsal column.

Two types of supporting cells develop from the spongioblasts, ependymal cells, with elongated processes which extend radially from the central canal to the periphery of the cord, and neuroglia cells, which have shorter
and more numerous processes, and which do not extend through the entire thickness of the wall. Some of the spongioblasts form transient neurolemma cells which enclose the neurites while the myelin sheaths are formed. Most of these disappear in the adult cord. Some of the ependymal cells persist as the epithelial lining of the lumen of the cord.

The marginal layer gradually thickens by the addition of fibers, some of which grow cranial and some caudal, and most of which soon acquire a myelin sheath. With the appearance of dorsal and ventral nerve roots in connexion with the spinal cord, the marginal zone of white fibers becomes divided into dorsal, lateral, and ventral funiculi. Since the time of myelination of fibers differs in the several tracts, depending upon the time when they begin to function, some, like the pyramidal, become medullated only after birth.

DEVELOPMENT OF PERIPHERAL NERVES

The problem of how nerves become connected with their end-organs in skin, muscle, or gland has been a controversial issue down to the present. There is, however, no doubt that all nervous tissues are of ectodermal origin. Three theories of neurogenesis may be mentioned.

The Hensen Theory. According to the Hensen theory, which has been revived in this century, the connexion between nerve and muscle is primary. This hypothesis is based upon the assumption that an embryo is not a mosaic of cells but a syncytium or mass of protoplasm containing numerous nuclei but without cell boundaries. Hensen asserts that the protoplasm of a vertebrate embryo is continuous and unbroken; that when cells divide, the division is never quite complete, but connexion is retained by means of protoplasmic threads or plasmodesms. Not all of these plasmodesms, however, become nervous. Some degenerate and disappear during ontogenesis. The plasmodesms which later become nerves do so as a result of nervous activity and consequent enlargement. Within them eventually appear neurofibrillae. The mesenchyma cells
which form the neurolemma sheaths migrate into the nerve anlagen. The medullary sheaths are secreted later by the nerve fibers. The Hensen hypothesis has recently been supported by J. Graham Kerr in his text-book of vertebrate embryology.

In support of the Hensen hypothesis, Kerr advances evidence derived from the study of fish embryos. The first connexions between myotome and neural tube which he is able to discover are fine plasmodesms which, without evidence, Kerr assumes to be primary. Later, these connexions increase in length and diameter, become fibrillar, and finally are invaded by the mesenchyma cells which form the neurolemma. The elongation of nerve fibers, which has been cited by others as evidence in favor of the outgrowth theory of nerve development, Kerr interprets as evidence of stretching of the primary connexion. In favor of the theory of primary connexion of nerve and muscle, Kerr calls attention to the fact that, from the time of their first appearance in the embryo, neural tube and myotome are in close proximity to one another and hence might easily be connected by plasmodesms. As evidence in favor of the Hensen hypothesis, Kerr mentions the results of an experiment of Spemann who transplanted the limb bud of a frog to its cheek. The leg muscles became innervated by nerves from the cheek. It might appear that such an experiment proves that nerve and muscle may become secondarily interconnected, but Kerr interprets the evidence as favoring the Hensen hypothesis!

Of the presence of plasmodesms in vertebrate embryos, there can be not the slightest doubt. The fact that they are more conspicuous in some embryos than in others, and that they are exaggerated by some
methods of fixation by no means proves that they are artifacts. The evidence, however, that they are primary in origin is not convincing. Moreover, the supporters of the hypothesis have failed to show that plasmodesms become nervous.

The Balfour Hypothesis. The distinguished British embryologist, Balfour, maintained that embryonic nerves are cellular and that nerves are modified cell chains. He concluded that all nerve cells are ectodermal in origin; that sensory nerves develop from chains of cells derived from the neural crest, and motor nerves come from cells which emerge from

the brain or spinal cord. The connexions of nerve and end organ are therefore secondary.

The histogenesis of a nerve fiber, according to Balfour, involves first the arrangement of spindle-shaped ectodermal cells in a chain extending from the central nervous system to the end organ. Each spindle-shaped cell becomes differentiated into an axial thread and a peripheral protoplasmic non-nervous sheath. The axial threads unite end to end to form the neurite, while the enclosing nucleated protoplasm becomes the neurilemma sheath which is thus formed of a series or chain of cells as in the adult nerve fiber. In medullated nerve fibers, the fatty medullary sheath arises later between the neurite and the neurilemma.

The Balfour hypothesis leaves unsolved the question how the chain of cells which forms a nerve fiber is directed in its development towards
the end-organ. But this difficulty confronts any hypothesis which assumes a secondary connexion between nerve and end organ. The Balfour hypothesis had respectable standing only as long as special methods of staining embryonic nerves had not been invented, or were unused. When methods of staining which were specific for embryonic nerves were finally employed by Golgi, Cajal, Bielschowsky, Ranson, and others, the foundations of the Balfour hypothesis were gradually undermined. It was found that embryonic nerves are fibrillar from the

Fig. 458.—A portion of a section of a 7 mm. elasmobranch embryo in the trunk showing an early stage in the development of a somatic motor nerve, Bielschowsky preparation. The nervous connexion is secondary and not formed by the enlargement of a plasmodeum. The nervous character of the connexion is attested by its affinity for special nerve stains. That the nerve anlage is formed by processes of neuroblast cells in the spinal cord is further evidenced by the fact that processes of medullary neuroblasts may be traced into the nerve anlage. Moreover, deeply staining neuroblasts are differentiated in the wall before the nerve anlage appears, as would be expected if they form the nerve.

time of their first appearance, and that sheath cells are a secondary addition. Finally, the experiments of Harrison were decisive against this hypothesis and in favor of the process theory of Kupffer.

The Kupffer Theory. The German anatomist, Kupffer, was the first to suggest that a nerve fiber becomes connected with its end-organ by means of protoplasmic outflow from a neuroblast cell either in the spinal cord or in the neural crest cells. Hence his theory became known as the process theory of nerve development. Kupffer's theory of neurogenesis may be better understood by taking as an example the development of a somatic motor nerve fiber in a vertebrate embryo. The neurite of such a fiber is formed by the protoplasmic outflow from a neuroblast cell located in the ventro-lateral wall of the neural tube. Neural tube and myotome are primarily unconnected. The neuroblast cell before it forms a process is a spindle-shaped epithelial cell in the wall
of the neural tube, distinguished by its affinity for specific nerve stains, which reveal a deeply staining network within the cytoplasm of the neuroblast. Subsequently, an amoeboid process extends from the cell into the liquid-filled space between neural tube and myotome. This space is narrow and connexion between neuroblast cell and myotome is quickly effected. From the time of its first appearance, the nervous character of this process is attested by its affinity for specific nerve stains. The subsequent changes in this neurite involve its elongation along the median surface of the myotome or its penetration into the mass of the muscle fibers. Other neurites are added after the manner of the one

![Diagram](image)

Fig. 459.—A camera drawing of a portion of a cross section of a 6 mm. elasmobranch embryo showing a Rohon-Beard "giant" ganglion cell, stained by the vom Rath method. In the specimen represented the body of the Rohon-Beard cell is located in the dorsal wall of the spinal cord and its neuraxon process extends to the level of the myotome. Peripherally the neuraxon terminates in numerous amoeboid processes. Sectioned material provides no better evidence than this of the correctness of the process theory of Kupffer.

first formed, until the connexion between tube and myotome becomes a bundle of naked neurites. Cells from the surrounding mesenchyma are soon added to the nerve anlage. In Elasmobranchs, cells migrate from the wall of the neural tube to form the neurolemma of the differentiated nerve. Finally, medullary sheaths appear, apparently as a result of a reaction between neurite and neurolemma.

One of the early objections raised against the process theory was that it left unexplained the problem of how nerves find their way to their end-organs. This difficulty, however, does not appear to be serious in the case of most somatic nerves, since these are separated by a minimal distance from their end-organ, the myotome. The difficulty is more serious for such a nerve as the trochlearis, the fibers of which grow from the floor of the metencephalon, emerge from the roof of the isthmus, and grow a long distance through the mesenchyma surrounding the brain, until they reach the anlage of the superior oblique muscle. We have today no theory which satisfactorily explains this circuitous route; but such are the facts even if we cannot explain them. A similar phenomenon
is seen in the outgrowth of the neurites of the Rohon-Beard cells in the spinal cord of fishes. These transient nerve fibers extend, devoid of sheath cells, from cells in the roof of the spinal cord to the skin in the extra-embryonic blastoderm.

The decisive proof of the truth of the process theory, however, was afforded by the beautiful experiments of Harrison, who removed a piece of the spinal cord of a frog or salamander embryo before somatic motor nerves had appeared. Such a fragment, when placed in a sterile nutrient solution, produced elongated protoplasmic processes such as are formed by the Rohon-Beard cells within the normal embryo. No more convincing proof of the process theory could be asked and, as a result, this theory is all but universally accepted by students of neurogenesis.

The origin of the neurolemma and the medullary sheaths, however, presents another problem which also Harrison tried to solve by experiment. Observations of sectioned material suggested that, in amphibian embryos, the cells present in embryonic nerves are derived from the neural crest. Harrison therefore removed the skin and neural crest from the back of a salamander larva. The result was striking. Larvae from which the neural crest had been thus removed not only lacked sensory nerves, which develop from the crest, but their somatic motor nerves were wholly devoid of cells. The conclusion seems reasonable that, in amphibia at least, many, if not all, sheath cells are derived from the neural crest and that, in this group, medullary cells do not migrate from the cord into the somatic motor nerves. Later, Harrison was able to observe in the tail of living tadpoles neurolemma cells migrating along naked neurites and thus to confirm the conclusion that neurolemma cells migrate to their definitive position.

Harrison left unsolved the problem of the origin of the medullary sheath. Speidel, on the basis of observations upon the tails of living tadpoles, has made it seem likely that, in this region, the myelin sheath is formed as a result of a reaction between the neurolemma and the neurite. He has found that the myelin appears soon after the neurolemma encloses the neurite, and the naked neurite seems unable to secrete myelin unaided.

**Histogenesis of Motor Nerves.** Somatic motor nerves arise as protoplasmic processes in the manner just described. The neurites become secondarily connected with myotomes by protoplasmic outflow from neuroblast cells, located in the ventral gray column of the neural tube, which are neurofibrillar from their first appearance. The researches of Coghill and others lead to the conclusion that this protoplasmic outflow is a response to stimulus from a bundle of longitudinal nerve fibers which grow caudad along the neural tube. Following the outgrowth of the neurite to the muscle, the dendrites grow in the opposite direction towards the source of stimulus.
Neurolemma cells are added to the nerve either by migration from the neural tube or the dorsal ganglia or from the loose mesenchyma which surrounds the nerve anlage. The migration of medullary cells from the cord appears to be absent in amniote embryos. Some embryologists assume that all neurolemma cells are derived from the dorsal ganglia. The appearance of the medullary sheath is correlated with the enclosure of the neurite by the neurolemma cells. The telodendria of each neurite are associated with the end-plate on the surface of one or more muscle fibers.

Fig. 460.—Drawing showing closure of the neural tube and formation of the neural crest. From pig embryos of:—A, 8 somites; B, 10 somites; C, 11 somites; D, 13 somites. X135. (From Patten's "Embryology of the Pig."

Visceral motor fibers develop in a manner similar to that of somatic motor fibers, except that the nerve cells are located in the lateral column dorsal to the somatic motor column. Both the nerve cell in the neural tube and the peripheral fiber from it are relatively small and the myelin thin. In the trunk region, the telodendria acquire synaptic connexions with the ganglion cells of the sympathetic ganglia.

**Histogenesis of Sensory Nerves.** All sensory neurites develop as outgrowths of cells located in the dorsal ganglia which, in turn, are groups of cells derived from the neural crest.

When the neural groove closes over and its edges fuse together during the formation of the neural tube, some loose cells are left between skin and neural tube. These ectodermal cells form the neural crest. Whether by this process the neural crest cells are derived from the dorsal wall of the neural tube or from the ectoderm of the skin above matters little, since they are derived, like the neural tube itself, from the ectoderm. The neural crest cells, soon after they first appear, multiply by division,
and become concentrated into two parallel strands dorsal to the spinal cord. The crest is continuous throughout the entire length of the central nervous system, except for an interruption in the head region between the fifth and seventh nerves. As development proceeds, each strand of neural crest cells migrates en masse ventrad. In the trunk region the cells become more and more concentrated and metamERICAlly arranged as a series of ganglionic masses median to the myotomes. For each myotome, there develops both a somatic motor root and a dorsal sensory ganglion. Within the sensory ganglia, two kinds of cells become differentiated. Toward the center, most of the cells become nerve cells, from each of which processes grow in two directions, one process into the dorsal

![Diagram](attachment:image.png)

**Fig. 461.**—A, diagram of early spinal cord; B, later, showing increase in size and consequent ventral fissure. c, central canal; e, ectoderm; f, floor plate; g, anlage of spinal ganglion; mc, neural crest; r, roof plate; s, sulcus limitans; a, ventral fissure. (From Kingsley's "Comparative Anatomy of Vertebrates.")

column of the tube and the other ventrally to join the somatic motor nerves which have already formed. The resulting mixed nerve gives off dorsal and ventral rami, to skin and muscles. The relations of the fibers of the sensory roots have already been described. Most of the peripheral cells of the ganglion become neurolemma cells. Possibly all neurolemma cells of sensory nerves are so derived.

The development of the neural crest in the head region differs in some details from that of the spinal nerves just described. Olfactory nerve fibers, except those in the nervus terminalis, develop not from the neural crest but from the olfactory epithelium; and, since the optic nerve is strictly a fiber tract of the brain, its development also is not from the neural crest. The oculomotor nerve is somatic motor, like the trochlearis, abducens, and hypoglossus, and its development is like that of the ventral root of a spinal nerve. The trigeminal is a mixed nerve with visceral motor fibers and with sensory fibers developed from the neural crest. There is evidence that some of the neural crest cells of all the visceral arches enter into the formation of connective tissue of the arches. The sensory elements of the facial and acoustic come from a common ganglion. Indeed the acoustic nerve develops as a branch of the seventh and only secondarily acquires an independent root. The
glossopharyngeal and vagus nerves are mixed, like the trigeminal, and have a similar double origin. Their sensory elements come from the neural crest and skin, while their motor fibers arise as processes (neurites) of motor cells located in the lateral wall of the medulla. One peculiarity of the V, VII, IX and X nerves is that their ganglia receive cellular increments from the skin just above the visceral pouch with which the nerve is associated. The patches of thickened ectoderm which proliferate these cells are known as epibranhial placodes. They have been interpreted, perhaps erroneously, as rudiments of sense organs which have degenerated.

Fig. 462.—The autonomic system of a 16 mm. human embryo. The sympathetic trunk is shown in solid black. The intestine is stippled. (Redrawn from Bremer, after Streeter.)

Development of Sympathetic Ganglia. Before the embryological facts were known, it was assumed that the sympathetic ganglia of vertebrates represent the chain of ventral ganglia of invertebrates. Their origin in vertebrates proves that this homology is incredible. The sympathetic ganglia of vertebrates are derived, like the neurolemmal cells, from the dorsal ganglia by the migration of neural crest cells ventrally along the nerves toward the dorsal aorta. They first appear as clusters of cells, each cluster connected with the nerve from which it arose, at the level of the aorta. In the head the ciliary, sphenopalatine, otic, and submaxillary ganglia are formed in this way. In the trunk the superior and inferior cervical ganglia, and the series of vertebral and prevertebral ganglia belonging to the sympathetic are derived from the neural crest by the prolonged migration of nerve cells. In the sympathetic ganglia the nerve cells “spin” the postganglionic fibers to the blood
vessels and viscera. Connexions with the nerves from which the sympathetic ganglia arise persist as the **rami communicantes**. The metameric ganglia become secondarily connected by a sympathetic cord which runs parallel with the dorsal aorta. The prevertebral plexuses, cardiac, coeliac, and hypogastric, arise by the more extensive migration of cells from the ganglia of the vagus nerve. The most extensive cellular migration leads to the formation of the myenteric and submucous plexuses (the plexuses of Auerbach and of Meissner). But, however remote from their source such sympathetic cells may be, they retain fibrous connection with the rest of the nervous system. (Fig. 463)

The whole sympathetic system is well established in a three months human embryo.

**MENINGES**

The spinal cord of Amphioxus is surrounded by loose connective tissue. In cyclostomes this tissue shows the beginnings of differentiation into compact outer and inner layers with loose tissue between, the three representing possibly the three meningeal layers of higher vertebrates. In fishes the cranium and the vertebreal layers are lined by compact periosteum or perichondrium, between which and the brain or cord the connective tissue is loose, except where the connective tissue comes in contact with the central nervous system. There it becomes the highly vascular **meninx primitiva**. Such connective tissue membranes or **meninges** surrounding the central nervous system (brain and cord) serve both for protection and for nourishment.
Two such meninges surrounding brain and cord occur in Amphibia, a pia mater primitiva next to the brain and cord and, outside this, a dura mater. The wide space between dura mater and periosteum is bridged by connective tissue trabeculae.

In mammals, three meninges are differentiated. Innermost is the pia mater, thin and highly vascular, from which connective tissue processes grow into brain and cord carry in blood vessels, and support the nervous tissue. Outside this is the arachnoid, which as its name suggests, is a delicate web-like tissue. Only its outer layer is organized into a membrane. Outermost of the three is the dura mater, thickest and toughest of all, and more or less closely attached to the periosteum which lines the cranium and the vertebral canal, so that this periosteum is sometimes reckoned as a part of the dura mater.

Where the dura mater of mammals penetrates between the cerebral hemispheres it forms the falx cerebri. A similar fold of the dura mater grows between the hemispheres and the cerebellum to form a tentorium cerebelli.

All three meninges develop from the loose mesenchyma which surrounds the embryonic neural tube.
CHAPTER 14

THE SENSE ORGANS

The sense organs of animals consist of sensory cells or groups of cells adapted to respond to stimuli and transmit an impulse to the nerves. The essential property of sense cells is, therefore, irritability. Like nerve cells they are able to transmit impulses caused by physical and chemical changes, either in the environment or within the organism.

The receptor organ may be either the neurosensory cell itself, or a secondary sensory cell which transmits a stimulus to the nerve. In higher animals, moreover, sense organs, in addition to receptor cells, have various mechanisms for protecting and supporting the sensory cells or conveying stimuli to them so that great diversity of receptor cells and of sensory nerve terminations has arisen during the course of evolution.

The result is a considerable number of special senses. These may be classified as major or minor, according to their importance. Major senses are touch, taste, smell, hearing, and sight. Minor, in addition to the muscular and visceral senses, include heat, cold, pain, hunger, thirst, fatigue, sex, and equilibrium. It is evident that this division of the senses rests on their conscious accompaniments.

On the basis of the source of stimulus, senses are Exterior—sight, hearing, taste, smell, pressure, heat, cold; or Interior—pain, hunger, thirst, the muscular and visceral senses, equilibrium, lust.

Some physiologists recognize as many as thirty-six special senses, separated for the most part by differences in sensation. Certain it is that we have many more than the traditional five!

EVOLUTION OF SENSE CELLS

Sense organs and sensory nerves alike begin in responsiveness to stimuli, such as is manifested by amoeba, which reacts to changes in pressure, light, heat, chemical substances, and electricity.

The first sense cells differentiated are the neurosensory cells of coelenterates, which establish nervous connexion with underlying muscle cells by means of protoplasmic processes, while the body of the cell remains in the external epithelium. Each cell may have a stiff sensory bristle or hair.

An advance towards conditions in higher animals is taken when the body of the cell recedes from the surface, retaining connexion by means
Fig. 465.—A primitive vertebrate, squalus, viewed in left lateral aspect and in a series of typical sections, showing the location and relations of some of the chief sense organs.
of an elongated process. Usually the outer termination of these cells also is beset with one or more hair-like processes. Neurosensory cells of this sort have a wide distribution in the animal kingdom. Those of the olfactory epithelium of vertebrates are at this stage.

A third stage is represented by sensory neurons which have lost their connexion with the external surface, but retain "free" nerve terminations in the epidermis. Such a cell is bipolar in form with both cutaneous and central connexions. A neuron of this sort may also terminate within the underlying corium, branch freely in the connective tissue,

end between tactile cells, or become surrounded by a connective tissue capsule.

A definitive evolutionary stage is attained when a secondary sensory cell becomes the receptor element by means by which a stimulus is transferred to the dendrites of a neuron. The receptor cells of the taste-buds and the hair-cells of the cochlea represent a final stage of this sort. The substitution of a secondary sensory cell for the primary neurosensory one presents a problem which has never been satisfactorily solved. That such an evolutionary change has occurred seems indisputable, but transitional stages are wholly conjectural.

Among the factors which have led to the formation of the sense organs of higher animals, may be noted the tendency of the neurosensory
cells, which were primarily scattered and separate, to become concentrated in clusters to form the sense organs. Secondary sense cells show the same tendency, and the cephalization of the nervous system is correlated with the concentration of the sense organs in the head region. Attention has already been called to the fact that the three primary divisions of the brain are associated with three major sense organs, the nose, the eye, and the ear.

**CUTANEOUS SENSES**

At least four senses, pressure or touch, pain, warmth, and cold, are based upon nerve terminations in the skin. The experiments of Goldschneider and others demonstrate that corresponding with these four sensations are four different sorts of nerve terminations. These may be either free or encapsuled. Usually, the free nerve terminations are located in the basal layers of the epidermis, and are therefore more superficial, while the encapsuled terminations lie in the corium below.

**EVOLUTION OF CUTANEOUS SENSE ORGANS**

It may be assumed that the various cutaneous sense organs were derived from neurosensory cells of the epithelium, which by the outgrowth of a neurite become connected with the nerve net or cord. When the body of the cell gradually migrated into the underlying connective tissue and the epidermis became many-layered, all connexion with the surface was lost, and the neurosensory cell was converted into a sensory neuron, with free nerve terminations in the lower layers of the epidermis and central connexions with the nerve cord. As a last step, connexion with the epidermis was lost, and the peripheral termination of the sensory cell was buried in the corium.

All these stages are represented in chordates. The skin of amphioxus, for example, is beset with many neurosensory cells, both single and in clusters, many of which possess a stiff terminal bristle which projects above the general surface. Amphioxus also has sensory nerves with free nerve terminations branching among the epithelial cells.

The encapsuled nerve terminations have apparently followed two independent lines of evolution. On the one hand, free nerve terminations in the corium have become encapsuled by concentric layers of connective tissue cells, as represented in the corpuscles of Pacini, Krause, and Golgi-Mazzoni. On the other hand, some nerve terminations are associated with tactile cells, which primarily were located in the basal layer of the epidermis, but which later migrated into the corium. In some instances, a single lenticular tactile cell may rest upon a cup-shaped termination of a sensory neurite, or the nerve may branch among a cluster of such cells. As a final evolutionary stage, a cluster of tactile cells connected
with the dendrites of a sensory nerve may become encapsuled by connective tissue to form a Meissner’s corpuscle.

Free nerve terminations occur in the skin of all classes of chordates, usually in the form of multiple arborizations or dendrites. These may lie in the epidermis or in the corium, in either case, are located where they may respond to changes in pressure. Such free nerve terminations in the skin are found in all classes of vertebrates, and are believed to be

![Diagrams of cutaneous sense organs in Craniates with secondary sense cells.](image)

the sensory mechanism of painful sensations arising in the skin. The sense of touch is believed to depend chiefly upon the tactile cells or corpuscles in the corium, of which various forms occur.

Meissner’s corpuscles, present only in primates, are located in the corium papillae of the palms and soles, and in the external genital organs. Each corpuscle consists of a group of tactile cells surrounded by a relatively thin envelope of connective tissue and connected with one or more nerve fibers. The non-medullated nerve fibers twists spirally among the tactile cells, each of which is in contact with a reticular nerve termination.

In birds and reptiles nerve endings are connected with tactile cells of Merkel but without a connective tissue capsule. These tactile cells
are sometimes solitary, sometimes clustered. On the other hand, the Grandry's corpuscles of birds are encapsuled, and the nerve termination lies between two tactile cells.

In the relatively small corpuscles of Krause and in the large one of Pacini, both found in mammals, the nerve termination is club-shaped and encapsuled. In a Pacini corpuscle, are as many as eight concentrically arranged lamellae. A secondary or adjunct nerve fiber penetrates the capsule and forms a varicose network within the inner lamella. Pacini's corpuscles are located not only in the deeper layers of the skin, but also in the mesenteries, tendons, and periosteum. Those present in tendons give rise to sensations which serve to indicate the position of a limb. Those in the deeper parts of the body probably give rise to painful sensations associated with disease.

The Golgi-Mazzoni corpuscles are spherical or club-shaped tactile corpuscles, in which the coiled nerve termination is enclosed by, but not in contact with, the surrounding capsule. In them, both chief and adjunct nerve fibers are present. These corpuscles occur in the corium, the peritoneum, and in the conjunctiva of the eye. The genital corpuscles found in the corium of the glans penis are supposed to be the sensory mechanism associated with sexual desire.

Development of Cutaneous Sense Organs

Free nerve terminations are formed by the outgrowth of sensory nerve fibers from the sensory ganglia. Of these, some remain free, some effect connexion with tactile cells, some become enveloped by connective tissue capsules.

Lateral Line Organs

Lateral line organs are a specialized type of cutaneous sense organs limited to fishes and water-dwelling amphibia. It is believed that they respond to currents of water and to sudden changes in pressure. Although, among cutaneous sense organs, the arrangement in rows is peculiar to the lateral line organs, this linear arrangement is presumably secondary, since both invertebrates and vertebrates have, scattered over the surface of the body, sensory papillae or neuromasts similar to those of the lateral line organs.

Dorsal, lateral, and ventral rows of lateral line organs occur in vertebrates on each side of the body. Usually all three are present only in embryonic and larval stages. The lateral rows persist in the trunk region of adult fishes and urodeles. Three lines, however, are present in the head, supraorbital, infraorbital, and mandibular, innervated by branches of the facial and vagus nerves, and exceptionally by a branch
THE SENSE ORGANS

of the glossopharyngeal nerve. A supratemporal line may connect the systems of the two sides across the posterior part of the skull.

A sense organ of the lateral line consists of a cluster of pear-shaped hair cells, each of which is connected with a branch of the lateral line nerve. Usually the cluster of sense cells is encircled by a ring of columnar epithelial cells. The sensory cells of neuromasts, unlike those of taste-buds, do not extend to the base of the epithelium.

**Fig. 468.**—Head of pollack, showing lateral-line canals and nerves of the lateralis system. Lateralis nerves black, canals and brain dotted. b, buccalis ramus of VII nerve; dl, dorsal ramus of lateralis of X nerve; hm, hyomandibular line of organs; io, infraorbital line; l, lateral-line canal; n, nares; o, olfactory lobe; op, operculum; os, ophthalmicus superficialis nerve; soc, commissure connecting lines of the two sides; so, supraorbital line of organs; st, supratemporal part of lateral line; vl, ventral ramus of lateralis of X nerve; x, visceralis part of X nerve. (From Kingsley's "Comparative Anatomy of Vertebrates," after Cole.)

**Evolution of Lateral Line Organs**

It is generally assumed that neuromasts have evolved from clusters of neurosensory cells like those of lower invertebrates. Similar clusters occur in the oral tentacles of amphioxus. Later in phylogensis, however, sensory cells of the secondary type become the sensory elements of the neuromasts. How this change occurred is problematic. At present, there is no evidence adequate to settle the question whether this change involves the replacement of primary sensory cells by secondary ones, or by the retention of the cell-bodies of the primary cells and the substitution of new nervous connexions for the primary ones. Since neuromasts with secondary sense cells like those of chordates occur also in leeches of the genus Glossosiphon, it is evident that the substitution of secondary for primary neurosensory cells has occurred independently in vertebrates and invertebrates.
The stages in the evolution of neuromasts are repeated in ontogenesis and also represented in the lateral line organs of adult craniotes. Primarily, the neuromasts are scattered over the surface of the body, but appear first in the head region. Those which become components of the lateral line organs sink into grooves, which extend from the ear region both craniad and caudad. There is evidence to suggest that neuromasts originally had a metameric arrangement, but this metamerism is usually lost through the subdivision and multiplication of the primary clusters of sensory cells.

In cyclostomes and tailed amphibia each neuromast sinks into a separate pit. In the fishes lines of neuromasts sink below the surface. In chimaera the grooves remain open throughout life. In other groups of fishes, this being the definitive condition, the grooves are converted into mucus-filled canals with occasional pores opening to the surface.

Lateral line organs, although limited to the ichthyopsida, are of special interest to morphologists since the evidence leads some to believe that the nose and ear are modifications of these. The reasons for this conclusion are more convincing for the ear than for the nose, since the hair cells of the nose resemble primary neurosensory cells of the invertebrate type, not the secondary sensory neuromast cells characteristic of lateral line organs.

**Development of Lateral Line Organs**

In fish embryos, the first indication of lateral line organs is a local thickening of the ectoderm in the ear region above the first visceral pouch. By local thickening the placode becomes extended anteriorly and posteriorly. Later stages resemble those of phylogensis already described. Differentiation of the canals proceeds both craniad and caudad. Grooves are formed in the elongated placode, which later close over, leaving apertures at regular intervals. The epithelial cells at the
bottom of the groove become differentiated into clusters of neuromast cells surrounded by indifferent supporting cells. Mucus cells also develop, and fill the canal with their secretions. Nervous connexions are secondary, and are formed by neurites from neural crest cells, usually of the vagus and facial ganglia, but sometimes of the glosopharyngeal ganglion.

**MUSCLE SPINDLES**

Muscle spindles form a special set of sensory nerve terminations upon muscle fibers, by means of which we are able to sense the degree of contraction of a muscle and the position of parts of the body. Such neuromuscular spindles are found in vertebrates, beginning with the Amphibia. As their name suggests, they are spindle-shaped structures located among the fibers of a muscle, usually near where the muscle joins a tendon.

![Diagram of muscle spindle](image)

Each spindle usually consists of several striped muscle fibers attached to a tendon at one end and to intramuscular connective tissue at the other. One or more nerve fibers connect with the spindle. Each nerve fiber terminates within the spindle in the form of a spiral encircling a muscle fiber.

Neurotendinous spindles resemble muscular, but are connected with tendons. These also serve to indicate the amount of muscular work and the resistance overcome.

**OLFACTORY ORGANS**

There are two chemical senses, smell and taste, but distinction between the two is difficult to draw in lower animals in which differentiated organs are wanting. For smell and taste alike chemical substances, in order to affect sense receptors, must be dissolved in water. This response to dissolved chemicals is a fundamental property of organisms, as is shown by such facts as that an amoeba will engulf a protein particle but not a piece
of glass, and that injurious substances swept into the gullet of a paramecium cause a reversal of ciliary action. A similar sensitivity is shown by multicellular forms. A sea anemone responds differently to pieces of meat and of blotting paper, yet it has no specialized olfactory or gustatory organs.

Beginning with this fundamental property of organisms, evolutionary changes in the chemical sense have followed two paths, one leading to the differentiation of an olfactory epithelium and the other to the formation of taste-buds. Both types of sense organ occur in aquatic animals, and they become still further differentiated in land animals, one responding to chemicals suspended in the air and the other to substances dissolved in water. Of the two, smell is far more delicate. In us the two senses are much confused in experience, since much that we eat is not only tasted but also smelled. In general we do not taste flavors such as those of onion or coffee, but smell them.

We may infer that smells and tastes are not distinguished by coelenterates, since they are not attracted to food at a distance. Actinians react to food placed in the tentacles, but not to food placed near the mouth. The chemical sense receptors are therefore probably neurosensory cells located in the tentacles.

Some flatworms search for bait placed at a distance and are therefore credited with an olfactory sense. In some species, the so-called olfactory organs are located upon tentacles, while in others they take the form of ciliated pits near the anterior end of the body. Both tentacles and pits have hair cells which are connected by nerves with the brain. Some tapeworms have at the anterior end of the body a transverse ciliated groove to which an olfactory function is ascribed. In nemerteanas, a tubular pit, the cerebral organ, which is lined by ciliated epithelium and terminates near the brain, has been assumed to have a like function.

Annelids are believed to have two sorts of chemical sense organs, paired ciliated "olfactory organs" near the anterior end of the body, and sense buds formed of clusters of cells, scattered in various parts of the body, each cell terminating in a sensory bristle. These latter are of special interest, since they resemble roughly the neuromasts of vertebrates.

Both cuttle fish and snails go in search of food, guided by their sense of smell. In land snails the olfactory organs are located, not only on the tentacles, but also over the general surface of the body. The receptors
are slender neurosensory cells with swollen terminations beneath the cuticula, especially abundant at the tips of the tentacles. Some molluscs have sphradia or "false gills," which are believed to have an olfactory function.

The olfactory sense is so keen in land molluscs that snails were used as gas detectors in the trenches of the world war, the animals withdrawing into their shells in response to a quantity of poison gas so minute as to be imperceptible to man, yet dangerous when its action is prolonged.

The olfactory organs of insects and crustacea have the form of olfactory hairs or bristles on the appendages, especially in the head region.

That the olfactory organs of vertebrates have evolved from any of the many sense organs of invertebrates has not been demonstrated. It is, however, possibly significant that the olfactory receptors of chordates are neurosensory cells which, like those of invertebrates, spin their own neurites, but persist as constituent elements of the olfactory epithelium.

The olfactory epithelium of most vertebrates is of the simple columnar type, in which neurosensory cells are uniformly distributed among supporting non-nervous epithelial cells. Each receptor terminates on the surface in a brush of fine hairs, and is prolonged from its basal end in a neurite, which breaks up in numerous telodendria within the olfactory bulb. As a special modification in some fishes and amphibia, the sensory cells are aggregated into olfactory buds, separated from one another by intermediate areas of indifferent non-sensory cells. In the higher vertebrates, however, the sensory cells have their original uniform distribution in the olfactory epithelium.

Olfactory organs seem to be lacking in the protochordates, yet these respond to chemical stimulation, so that they must be assumed to have chemo-receptors.

Amphioxus also lacks a specialized olfactory organ and does not hunt for its food, but lies buried in the sand. Koelliker's pit, which was formerly assumed to be an unpaired olfactory organ, is the remnant of the larval neuropore, and is non-nervous. Hatschek's pit, in the roof of the
mouth is not nervous, as was once assumed, but glandular. A chemical sense, however, amphioxus indisputably has, since it responds to chemical stimulation. Neurosensory cells occur in clusters on the oral cirri and scattered over the surface of the body, and these may be assumed to be the chemoreceptors.

In cyclostomes, as in all the higher vertebrates, are paired olfactory pits innervated by olfactory nerves. The erroneous notion that cyclostomes are monorhinal is based upon the fact that the olfactory pits open into the median unpaired hypophysis, the external opening of which lies on the dorsal side of the snout. This evidence is, however, misleading, since the monorhinal condition in the embryo results from the fusion of primarily paired anlagen, and the olfactory pits develop as paired organs connected with paired olfactory lobes of the brain. The proximity of the olfactory pits and their connexion with the hypophysis may be explained as the result of the great enlargement of the upper lip of the sucking mouth. The connexion of the olfactory pits with the pharynx by way of the hypophysis in myxinoids is not to be compared with the paired posterior nares or choanae of air-breathing vertebrates. Paired narial passages are not present in most fishes and make their first appearance in dipnoi.

The olfactory epithelium of cyclostomes is a many-layered ciliated membrane, beset with neurosensory cells like those of worms. By the folding of this epithelium, as in fishes, the number of hair-cells is multiplied, and the sensitiveness of the organ correspondingly increased. In petromyzon the bellows-like action of the pharyngeal muscles forces water in and out of the hypophysial pit as if it were a pipette.

In elasmobranchs the olfactory organs are paired pre-oral pits, lined with plicated olfactory epithelium, and as in other fishes generally, unconnected with the mouth. In some genera such as Pristius, however, nasobuccal grooves extend from the nasal pits to the corners of the mouth. Morphologists see in these grooves the beginnings of the narial passages, which in higher vertebrates, beginning with the dipnoi, connect the nasal

![Head of human embryo](image-url)
pits with the pharynx. As a special adaptation to aquatic life the nasal pits of elasmobranchs become incompletely divided by a transverse fold of skin, so that as the fish swims, water flows into the anterior and out of the posterior opening.

The dipnoi take an important step forward in the evolution of the nose by acquiring a connexion between the olfactory pits and the mouth. True choanae opening into the pharynx first appear in this group, and thus the functions of smelling and breathing become associated. In the embryo, the narial passages are formed by the closure of the edges of paired nasobuccal grooves, such as are seen in adult elasmobranchs.

The connexion between olfactory organs and respiratory passages which was invented by dipnoi, is also found in amphibia; but the lamellated olfactory epithelium disappears as unsuited to life in the air. Narial passages enlarge in amphibia, and become divided into a more dorsal olfactory region and a more ventral respiratory passage. Olfactory hair-cells are limited to the upper region. A supplementary olfactory organ, the organ of Jacobson, arises in connexion with each narial passage and thus with the mouth. It may serve to test the food taken into the mouth. A lacrimal duct from each eye opens into the narial passage, and serves to moisten the olfactory epithelium.

Some reptiles, lizards for example, have added to the narial passage a more expanded and glandular vestibule, which is apparently a mechanism for eliminating dust from the air taken into the lungs. Novel also in this group are the paired turbinal bones or conchae, which project into the nasal passages, and serve to increase and support the olfactory membrane. A nasopharyngeal cavity distinct from the mouth cavity also first appears in this group, as the result of the ingrowth and extension of the palatine
bones. Thus a bony palate is formed, and the narial passages open by secondary choanae into the pharynx. The vomer bone, therefore, no longer lies in the roof of the mouth, but in the naso-pharyngeal passage. By the formation of the palate, the nasopharyngeal cavity is both enlarged and elongated. (Fig. 183)

In birds there are three pairs of conchae, and Jacobson’s organ disappears.

In mammals there is an enormous enlargement of the narial passages, and a corresponding multiplication of conchae, the single pair of reptilian conchae persisting as the maxillo-turbinals, and ethmo-turbinals, upper and lower, being added. Jacobson’s organ nearly disappears in the higher mammals. The contrast between the upper olfactory and the lower respiratory region persists.

That the olfactory organ of man is degenerate, is evidenced by the reduction of the conchae in size and number, and in the ontogenetic loss of three pairs of turbinal bones present in the embryo. What is left of Jacobson’s organ in man enters into the formation of the incisive canal, which connects the anterior part of the nasal passage with the mouth cavity. (Fig. 474)

Development of Olfactory Organs

In elasmobranchs, each olfactory organ develops from a placode-like thickening at the anterior termination of the series of lateral line organs: Subsequently each placode, by invagination, is converted into a pit, which lies in close apposition to the telencephalon vesicle. In man a groove similar to the nasobuccal groove of elasmobranchs connects each olfactory
pit with the corner of the mouth. The narial passages, however, are not formed by the fusion of the edges of this groove, as in some amphibians and fishes, but by the backward extension of the olfactory pits, which acquire a secondary connexion with the mouth. Hare-lip in man results from the imperfect obliteration of the nasobuccal groove. The primary openings of the narial passages into the mouth correspond with those of amphibians and reptiles. The secondary and definitive choanae rise posterior to the primary pair, when paired palatine processes unite in the middle of the roof of the mouth, and thus separate the naso-pharyngeal cavity from the mouth cavity. Palatine processes appear first in a two-months human embryo, and the formation of the palate is completed at five months.

The inferior or maxillary conchae arise early in ontogenesis. Five more pairs are formed by outgrowth from the ethmoid. Of these, three later disappear, leaving the maxillary and two ethmoid characteristic of the adult.

**TASTE ORGANS**

The second of the chemical senses is taste which, as we have seen, has a common origin with smell. All animals respond in one way or another to substances dissolved in water. Specialized taste organs in the form

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Fig. 476.—The development of the narial passages in A, Chick and B, Man. In phylogeny the narial passages are believed to have arisen through the approximation and closure of the edges of the nasobuccal grooves. Such grooves appear in ontogenesis. Failure of such grooves to close over is the best explanation of hare-lip and perforate palate shown in B. In normal growth in the human embryo, however, the narial passages are not formed by the closing over of grooves but by the backward growth of an ectodermal cord which grows from the nasal pit to the mouth cavity. (A redrawn after B. Patten, and B after Corning.)
of **taste-buds** occur in annelids, in which they are scattered over the surface of the body, but are more numerous in the mouth region; and experiment demonstrates that leeches can taste. In molluscs, neurosensory cells connected with subcutaneous ganglia surround the mouth. A few insects have gustatory hairs or bristles on the antennae, and some have them around the mouth. With the exception of the taste-buds, none of the invertebrate sense organs appears to have a genetic relation with those of chordates.

The organs of taste of chordates are taste-buds, with a core of sensory hair cells and an outer rampart of supporting cells. Unlike the cells of the neuromasts, however, both sensory and supporting cells of taste-buds are of equal length, and the sensory as well as the supporting cells rest upon the basement membrane of the epidermis. Each hair cell of a taste-bud is a secondary sense cell, which is supplied by the dendritic terminations of sensory nerves. Taste-buds differ little in lower and higher vertebrates, though tending to be less widely distributed over the bodies of higher forms. (Fig. 477)

In amphioxus, clusters of hair-cells connected with sensory nerves occur in the velum and the oral cirri. A chemical sense, whether smell or taste would be difficult to say, may therefore be ascribed to this animal. That similar sense organs are generally distributed over the surface of the body has not been demonstrated. Consequently, if the arrangement of taste-buds in amphioxus may be taken as primitive, the chordates start their phylogensis with a high degree of concentration in the distribution of their organs of taste.

Pharyngeal taste buds occur in larval cyclostomes, while in the adult they are present also on the surface of the head. In elasmobranchs the taste-buds are limited to the lining of the mouth and pharynx, chiefly on the surface of papillae. In ganoids and teleosts they are found on the
surface of the head as well as on the pharynx. A few teleosts such as amniurus have taste buds on the surface of the trunk, fins, and mouth.

In amphibia, with the assumption of a land life, taste buds become limited to the tongue and the roof of the mouth. In man, they are found on the tongue, especially on the sides of the vallate papillae, upon the soft palate, and upon the posterior surface of the epiglottis.

A taste-bud is an ovoid cluster of columnar epithelial cells, each of which extends from the basement membrane to the free surface of the epithelium. The cells of the outer layer are arranged like the sections of a melon, so that the ends of the cells are brought close together around a small pore, which opens on the surface. Two kinds of cells are differentiated, peripheral supporting cells, and sensory taste-cells, which form the core. The sensory cells stain more intensely, and are distinguished by the bristle-like process in which each cell terminates. (Fig. 99)

To stimulate the taste cells, substances must be dissolved, so that they can penetrate the pore-like opening of the bud. Only four kinds of substances can be tasted by us, sweet, sour, bitter, and salt. Other flavors are smelled, not tasted.
Development of Taste Organs in Man

The lingual papillae upon which the taste buds develop first appear in a nine weeks embryo as minute elevations on the surface of the tongue. The formation of circumvallate papillae involves not only similar elevations of the surface, but also the ingrowth of the epidermis around each papilla. By the subsequent splitting of this ring of epidermis into an inner and outer layer separated by a circular groove, the papilla becomes vallate. The taste buds are differentiated on the sides of the papillae, which are covered by a stratified epidermis of endodermal origin. Each taste bud appears primarily as a local thickening of the epidermis, due to the elongation of the cells which are to become the sensory and supporting cells. During the fifth to the seventh month of fetal life, taste buds are more numerous than later, and occur very generally over the surface of the mouth and pharynx. Later the number diminishes and each taste bud requires an external pore opening to the surface.

Visual Organs

Sensitivity to light is a wide-spread, if not a universal, property of living cells. An amoeba will not enter strong light; and sea anemones, among other creatures, react to light, although they have no specialized photoreceptors. All flagellates which are phototropic have a red pigment spot or stigma like that of Euglena; and in general, in multicellular creatures, only those cells respond to light which contain some such pigment as visual purple, which is altered by light.

The so-called eye-spots of coelenterates are pigment cells which respond to changes in intensity of light. Many medusae have clusters of pigmented columnar epithelial cells on the margin of the umbrella, which are interpreted as photic organs, since the animal ceases to be phototropic when these are removed. The jelly-fish Nausithoe has a lens associated with each of these pigment spots.

Many species of flatworms have paired pigment spots closely associated with the brain, which are interpreted as eyes. In some species, beaker-like clusters of pigmented cells surround the terminations of sensory nerves, and may, therefore, be regarded as among the most primitive of true eyes.

While, however, photoreceptors occur in coelenterates and all phyla above, true vision is limited to those forms in which the photoreceptors are aggregated into eyes capable of forming an image on a retina. Among invertebrates two types of eyes predominate, beaker eyes and vesicular eyes. Beaker eyes get their name from their shape. They usually have a core or plug of cuticula. Vesicular eyes, however, have a liquid-filled cavity around which the photoreceptor cells are arranged.

The eyes of annelids are varied. Some free-swimming forms have beaker-eyes with spherical lenses and a layer of retinal cells connected by
nerve fibers with the brain. In some, the beaker-like eyes are connected with the epidermis; in others the eye sinks below the skin. Nereis has vesicular eyes. The differences between the various types of annelid eyes are so great that it is impossible to believe that they are genetically related to one another.

The eyes of molluscs are sometimes beaker-eyes, sometimes vesicular eyes with a lens. On the edge of the mantle of pecten, are complex vesicular eyes, which have many features in common with those of vertebrates. Each eye is partly surrounded by a layer of opaque pigmented epithelium, which in front of the eye becomes a translucent cornea. Beneath the cornea and adherent to it, is a biconvex lens. Like the vertebrate eye, that of Pecten has a liquid-filled chamber. But the retina of Pecten, unlike that of vertebrates, has two layers of photoreceptors, each photoreceptor connected with a nerve fiber. Back of the retina lies an inner layer of pigment epithelium. There is no reason to doubt that such an eye is able to form an image.

The eyes of cephalopods, especially those of sepia and loligo, bear a striking resemblance to those of vertebrates. But the fact that the retina is not inverted as in vertebrates, proves that the two cannot be genetically related. Bergson has cited this instance of similar results, notwithstanding diverse conditions, as proof of the existence of a vital factor or "elan vital" which distinguishes the living from the lifeless. Since Bergson appears to be substituting one mystery for another, the elan vital hypothesis has not made a very strong appeal to biologists. Nevertheless, it is equally difficult to accept the assumption that eyes so alike could have been independently produced merely by the selection of random variations of so many elements as enter into the composition of cephalopod and vertebrate eyes.
Urochordates have pigment spots and an unpaired eye, neither of which can be compared with those of vertebrates. Such forms as salpa have a median vesiculated eye derived from the brain and usually pigmented. Only in their origin from the brain do such eyes resemble those of vertebrates.

Among cephalochordates the so-called eye of amphioxus is a pigment spot located at the anterior end of the nerve cord. There is obviously very little resemblance between such a structure and the eye of a vertebrate. The reasons for calling it an eye are that pigment is associated with eyes, and that this special pigment spot is associated with the anterior expansion of the nerve cord, which is generally homologized with the forebrain of vertebrates. On the basis of such slight resemblance, it is scarcely possible to derive the paired vertebrate eyes from this unpaired pigment spot.

In the floor of the nerve cord of amphioxus, throughout its length, are photoreceptors partially enclosed by pigment capsules. Since removal of the pigment spot from the so-called brain of amphioxus does not affect its response to light, it is assumed that the true light-recipient organs of this animal are these photoreceptors of the nerve-cord.

The study of invertebrates reveals that their eyes have all the histological elements of the paired eyes of vertebrates, but never in the same combinations. Some invertebrates have photoreceptors in the form of rods and cones associated with pigment spots and with the brain. But vertebrates alone have eyes with an inverted retina formed as an outgrowth of the brain wall, and surrounded by a mesenchymatous capsule. Comparative anatomy throws little, if any, light upon the past history and origin of paired eyes, since the eyes of the cyclostomes are in all essentials like those of the highest vertebrates. Eyes, therefore, appear to spring into existence full-formed, and we are compelled to draw phylogenetic conclusions from the facts of ontogenesis.

These facts appear to justify the conclusion of Ray Lankester (1880) that paired eyes of vertebrates are paired pigmented depressions in the anterior part of the neural plate. It has been asserted that the parietal eye has a similar paired origin, from pits anterior and lateral to those which form the paired eyes; and the conclusion has been drawn that, when the neural plate was converted into a neural tube, the unpaired eye was formed by the fusion of the lateral paired pits, which subsequently grew out as a stalked vesicle. Thus the parietal eye looks upwards, while the paired eyes, bulging laterally from the brain wall are receptors of light from the sides and below. In most vertebrates, the median eye degenerates; but the paired eyes enlarge and become the definitive organs of vision.

It is fairly easy to imagine the conditions which led to the lateral outgrowth of the paired eyes. Among the factors involved was presum-
ably the enlargement of the head and the recession of the brain from the surface. Less light, consequently, would reach the photoreceptors in the brain wall. When the skin became pigmented, eyes in the brain wall would become useless.

On the other hand, we are still painfully ignorant as to the factors which would start the growth of the eyes towards the skin and convert the skin into a lens. Possibly the invagination of the optic cup was primarily determined by the enlargement and ingrowth of the lens. Yet experiment shows that lens formation in the embryo is stimulated by the optic vesicle, in the absence of which no lens develops, and that if the optic vesicle is removed from the brain and grafted under the skin of the trunk, it will cause a lens to develop there.

As the eye became a two-layered cup enclosing a lens and surrounded by a connective tissue capsule, the sclerotic, it acquired nerve connexion with other parts of the brain. The eye muscles became attached to the eyeball and were preserved, while other pre-otic muscles disappeared. That the lens is a modified lateral line organ has been plausibly urged both from its position of origin and from its mode of development.

The phylogensis of the paired eyes of vertebrates may be briefly summarized. First these were open beaker eyes, like those of such invertebrates as nautilus, with photoreceptors towards the source of light and with pigment, but without lens. Later by invagination the eyes were

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**Fig. 480.**—Diagrams illustrating Boveri's theory that the paired eyes of vertebrates have evolved from lateral outgrowths of the brain-wall. The theory accords well with embryological evidence.
carried into the anterior brain vesicle, so that the retina became inverted and each eye grew in the form of a hollow ball towards the skin and the source of light. The photoreceptors, however, come to lie on the side of the retina farthest from the source of light, and hence are “inverted” in position. Possibly a lateral line organ was converted into a lens, which by enlarging and pushing into the optic vesicle, converted this into a two-layered cup with an inner retinal, and an outer pigment layer. Finally, the surrounding mesenchyma was converted into a sclerotic layer and the eye-ball thus formed became connected with the eye muscles.

The paired eyes of all vertebrates are essentially similar. Except in size, the eye of petromyzon is like that of mammals. Having once invented a camera-like eye in cyclostomes, “nature” has pursued the policy of letting well enough alone. A description of the human eye will, therefore, serve for vertebrates generally.

Fig. 481.—A diagram of a median section of the eye. (Redrawn after Sobotta.)

**The Eye of Man**

Comparison of the eye with a camera holds for many details. Both are mechanisms by which an image is focused upon a sensitive layer, the film or the retina, the opaque sclerotic corresponding with the box of the camera. Each has a lens to form the image, and an iris diaphragm to regulate the amount of light. The eye, however, is filled with liquid, the **humors** of the eye. That between the translucent cornea and the lens is the **aqueous humor**; the semisolid material between lens and retina is the **vitreous humor**. A ray of light entering the eye passes first through the cornea, then successively through aqueous humor, pupil, lens, vitreous
humor, and retina. The curved cornea serves to converge rays of light, and the lens increases the convergence.

The lens is a biconvex translucent and elastic body surrounded by an elastic capsule. Fibers which extend from the periphery of the lens to the ciliary body form a suspensory ligament which holds the lens in position back of the iris. The ciliary body is a ring of vascular and muscular tissue, wedge-shaped in cross section, which projects into the cavity of the eye-ball, just back of the iris. The ciliary muscles, circular and meridional, act on the suspensory ligament of the lens, and accommodate the eye for near or far vision. When the meridional fibers contract, the suspensory ligament tightens, and flattens the lens for distant vision. When the circular muscle contracts, the ligament is loosened, and the lens by its own elasticity becomes more nearly spherical. When, in later life, this elasticity is lost, we put on convex glasses.

The iris is a muscular diaphragm, usually pigmented, which projects from the ciliary body into the cavity of the eye, between lens and cornea, and is perforated at its center by the pupil. It has two sets of muscles, a radial and a circular, which are controlled by the sympathetic system. In dim light, the radial muscles contract and the pupil enlarges. In strong light, the circular muscles contract and reduce the opening.

![Diagram illustrating the mechanism of accommodation of the eye by means of the change of shape of the lens.](image-url)
The retina lines the posterior chamber, but thins out where it covers the ciliary body. In the region where light strikes the retina, at least eight layers are distinguishable. Beginning with the innermost, these are: a layer of nerve fibers, a ganglion cell layer, an inner reticular layer, an inner nuclear layer, an outer reticular layer, an outer nuclear layer, a layer of rods and cones, and a pigment epithelium. (Fig. 483)

By using special nerve stains, such as that of Golgi, the retina has been found to consist of three layers of neurones chained together and connected with the brain by the optic nerve. One set of neurones, the rods and cones, is the true sensory layer. The rods are sensitive to light of low intensity; the cones are affected by light waves of different lengths, and are regarded as the mechanism of color vision. There are in the human retina four times as many rods as cones. Both rods and cones have synaptic connexions with the neurones which form the inner nuclear layer, and these in turn are connected with the dendrites of the ganglion cell layer, the neurites of which form the optic nerve.

When the retina is flooded by intense light processes of the cells of the pigment epithelium penetrate between the rods and cones. In the dark these processes are withdrawn. When the eye is focussed upon an object, the region of sharpest vision is a small spot near the center of the retina, the yellow spot, or macula lutea. At its center, is a depression, the fovea centralis, where the nuclear and reticular layers are absent and the retina is thin. The greater sensitivity of this area is, therefore, due to the fact that light strikes the rods and cones without passing through the other layers.

A vascular chorioid layer surrounds retina and pigment epithelium. Besides many pigment cells, this layer contains many blood vessels.
branches of the central retinal and of the anterior and posterior ciliary arteries, and veins. The retina, however, is supplied by its central vessels. Most of the blood leaves the eye ball by way of four to six vorticose veins.

The ganglion cells of the retina give off neurites which converge towards the "blind spot," where the optic nerve fibers leave the retina, and rods and cones are absent. Of the fibers of the optic nerve, half pass to the

 Fig. 484.—A diagram illustrating the course of optic nerve fibers in A, a fish, B, a reptile, and C, a mammal. The definitive centers of vision lie in the occipital lobes of the cerebral hemispheres. The primitive centers in the optic lobes persist in mammals as reflex centers located in the superior colliculi. (Redrawn after Monakow.)
thalamus of the opposite side of the brain and half to that of the same side. The sensory centers of vision are located in the occipital lobes.

The outer layer of the eyeball is the sclerotic or tunica fibrosa, composed of interwoven bundles of compact connective tissue fibers. This layer is opaque, except the portion which forms the cornea. A many-layered epithelium or conjunctiva covers that part of the cornea which is exposed to the air, and also lines the eyelids.

Eyelids occur only in land forms, as an adaptive device for protecting the eyeball. They are folds of skin above and below the eyes, movable except in serpents. They are opened by levator and closed by the orbicularis muscle. The upper lid is more movable than the lower. Along the edges of both lids, a series of sebaceous Meibomian or tarsal glands form a film of oil, which keeps the tears from flowing over the lower lids.

The lacrimal glands are compound tubular glands, located at the upper border of the upper eyelid. Their secretions are poured into the conjunctival sac, and are carried over the surface of the eyeball to the lacrymal ducts, one in each eyelid, near the nose. The two lacrimal ducts of each side unite to form the nasolacrimal duct, which opens into the nasal passage below the inferior concha of the same side.

Development of the Vertebrate Eye

The vertebrate eye has a twofold origin. The retina, optic nerve and pigment epithelium are derived from the brain, and therefore from the ectoderm. The lens and conjunctiva are also ectodermal. On the other hand, the sclerotic, the cornea, the aqueous humor, possibly the vitreous humor, the choriod, the ciliary body, the iris, the eye muscles, and the connective tissue surrounding the eye-ball, all come from the mesenchyma. The tarsal and lacrimal glands associated with the eyelids are ectodermal.

The optic vesicles arise as lateral outpocketings of the forebrain. In some animals, however, such as the elasmobranchs and amphibia, the anlagen of the optic vesicles appear as paired depressions of the neural plate. As the optic vesicles continue their lateral expansion, the connexion with the brain becomes constricted to an optic stalk, which later is converted into a shallow trough to guide the fibers of the optic nerve as they grow from the retina to the brain wall.
Where the optic vesicle, as it expands, comes into contact with the ectoderm, a local thickening of the ectoderm forms as the anlage of the lens. This placode thickens, invaginates, and sinks below the surface to form a small hollow vesicle, which eventually loses connexion with the skin. The lens vesicle is finally converted into a solid lens by the thickening of its medial wall, the epithelial cells of which become elongated into fibers and arranged in layers like the coats of an onion.

While the lens is undergoing these changes, it becomes enclosed by the optic cup, formed by invagination of the optic vesicle. Possibly the ingrowth and enlargement of the lens is a factor in this invagination. The optic vesicle is thus converted into a two-layered optic cup, attached to the brain by the optic stalk. The cup is, however, incomplete, for a fissure divides it along its lower side, and extends as a groove along the lower side of the optic stalk.

Of the two layers of the optic cup, the outer persists as the single-layered pigment epithelium, and the inner thickens to form the three layers of neurons of the definitive retina. Neurites from the inner ganglion cell layer grow along the optic stalk and gradually fill its groove. Half of these fibers cross to the opposite side of the brain to form the chiasma of the optic nerve. The cells of the optic stalk are converted into neuroglia cells.
The remaining parts of the adult eye are derived from mesenchyma. The cellular elements of the aqueous humor, and possibly also some of those of the vitreous body are mesenchyme cells which enter the optic cup by way of the optic fissure. But the fact that fibers connect the lens and retina has led some investigators to infer that the vitreous body is derived from the retina and therefore is ectodermal. On the outside of the eye, the chorioid and fibrous tunics are added from the surrounding mesenchyma. The eye muscles of man have a like origin, although in lower vertebrates they arise from the walls of the head "cavities." Folds of skin form the eyelids, which unite temporarily but in man separate again before birth.

Unpaired Eyes

Two kinds of median eyes are recognized, the parietal and the pineal. Each, when present, arises from the roof of the diencephalon, and lies beneath an unpigmented "apical spot" on the upper surface of the head.

That parietal and pineal eyes are light-recipient organs is indicated by the presence of a retina with photoreceptors, pigment, ganglion cells, nervous connexions with the brain, and sometimes a lens. Experimental evidence is somewhat conflicting. But lizards show a muscular response to photic stimulation of the parietal organ, and teleosts react to stimulation of the pineal organ.

The history of the median eyes of vertebrates is one of reduction and of functional change. Among the possible factors in the degeneration of these organs may be the increased importance of the lateral eyes and the great enlargement of the cerebral hemisphere, which in mammals overlie the diencephalon.

Cyclostomes have both parietal and pineal organs, in the form of epithelial vesicles immediately below an unpigmented "apical spot" between the lateral eyes. The pineal vesicle, which lies above the parietal, is considerably larger, and its upper epithelium is thin and translucent, while its lower layer is thickened, and consists of columnar epithelial cells, some of which contain pigment. For this reason, the lower layer is regarded as a retina. This inference is supported by the fact that the photoreceptors of the retina are supplied with nerve fibers from adjacent ganglion cells. Neurites of these ganglion cells unite to form a pineal nerve, the fibers of which may be traced by way of the posterior commissure to the mesencephalon.

The lower or parietal vesicle resembles the pineal vesicle in essentials, but rests upon a segregated portion of the left habenular ganglion. The nerve fibers of the parietal nerve connect with the left habenular ganglion. Whether parietal and pineal organs are serially homologous, one anterior and the other posterior, or whether they are members of a pair which
have in time shifted their position to the present antero-posterior arrangement, remains a disputed question. That they were formerly paired organs is suggested by the fact that in geotria, a cyclostome, each has a lateral position in relation to the other; and the parietal organ has nervous connexion with the left habenular ganglion, while the pineal organ is connected with the right habenular ganglion; and also by the fact that the anlagen of the two in the embryos of fishes, amphibia, and reptiles lie in
the same cross section. On the whole, these facts tend to suggest that cyclostomes have a right pineal eye and a left parietal eye. In myxine, however, the pineal organ is wanting.

The median eyes of fishes are degenerate. The parietal organ is lacking, and the pineal does not perforate the skull. A tendency for the organ to become glandular is shown by the folding of the wall of the vesicle. In the elasmobranch embryos, the anlage of the parietal organ appears but later degenerates.

Among the amphibia, the anura have a translucent "apical" spot like that of cyclostomes. Beneath this spot, lies the vesicle of the pineal eye, connected by a nerve with the brain. The basal layer of the vesicle forms a thickened retina. A parietal organ is wanting. In the fossil stegocephala, the roof of the cranium is perforate between the two parietal bones and from this a functional pineal eye in these animals is inferred.

In reptiles the tendency of the epiphysis to become glandular is evident. But in crocodiles, the pineal organ wholly disappears. The parietal organ of this group assumes even more markedly than in the lower vertebrates the characteristics of the vesicular eye of invertebrates. In sphenodon and many lizards, the upper layer of cells of the vesicle forms a lens-like thickening, which focusses light upon the retina. The skull is perforate.

Among the reptiles the parietal eye of anguis fragilis is most highly differentiated. The terminal vesicle in this animal lies immediately below a translucent apical spot, and is connected with the left habenular ganglion by a ganglionated parietal nerve. The vesicle is lined by columnar epithelial cells, which become locally thickened on the upper

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**Fig. 490.**—Parietal eye of Anguis fragilis. ct, connective-tissue cells around nerve; gc, ganglion cells; l, lens; n, nerve fibers; pn, parietal nerve; pc, pigment cells; r, retinal cells; vb, vitreous body. (From Kingsley's "Comparative Anatomy of Vertebrates" after Nowikoff.)
side to form a biconvex lens, which concentrates light upon the retinal layer below. Three kinds of cells are distinguishable in this retinal layer, sensory flagellated cells, pigment cells alternating with the sensory cells, and ganglion cells connected with the brain by the parietal nerve. Except in the region of the lens, the entire vesicle is surrounded by a single layer of pigment epithelium. The lumen of the vesicle is filled with translucent processes of the surrounding epithelial cells, and thus is analogous with the vitreous body of the lateral eyes.

In mammals a parietal organ is wanting. The pineal organ is glandular. Its function is problematic, but is commonly assumed to be endocrinal. The rich vascular supply of the organ suggests this, but experiments to demonstrate the secretion of hormones have failed, and the removal of the gland does not cause death or affect health.

**DEVELOPMENT OF THE PINEAL ORGAN IN MAN**

The pineal organ arises in a four-months embryo as a hollow tubular outgrowth from the roof of the diencephalon. By the formation of secondary lateral outgrowths, the anlage is converted into a compound vesiculated structure richly supplied with blood vessels. The vesicular structure later disappears, and the adult organ consists of solid masses of polygonal epithelial cells of which various sorts may be distinguished by their different staining properties. No ganglionic or nervous elements can be recognized. Mulberry-like concretions sometimes occur.
A wide-spread and remarkable trait of animals is the ability to respond to gravitation, and thus to orient their bodies in space. The long axis of the body is usually kept horizontal, but occasionally, as in man, vertical. With few exceptions, animals have dorsal and ventral sides. But the ventral side does not lie nearer the earth because it is heavier, for when a fish dies in the water it turns ventral side up. Orientation in relation to gravity is a reflex act, which involves nervous and muscular mechanisms and special sense organs. Such organs are known as static organs.

Some microscopic floating plankton organisms are indifferent to gravity. When these maintain a constant position the stable balance is due to the greater weight of one side. Where special static organs are lacking, orientation may be maintained through eyes or tactile organs or both. Some crustacea, for example, will swim upside down when the body is illuminated from below. Although static organs are generally absent in insects, most insects, placed on the back, will right themselves, probably through the action of nerves connected with tactile hairs.

The normal position of many animals such as worms brings the ventral side of the body in contact with the bottom. When this contact is lost, reactions tending to restore it take place. The sensory basis of this orientation is the sense of touch. In the orientation of the mammalian body, tactile organs, muscular spindles, and the semicircular canals of the ear are all involved.

Among invertebrates most static organs have a hollow sac or statocyst which contains one or more statoliths, which are granules of calcium carbonate or sulphate mixed with organic matter. Frequently, loose crystals or otoconia occur in statocysts, and serve by their motion to

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**Fig. 402.—Diagram of the membranous labyrinth of a vertebrate, the sensory areas dotted.**

- ac, anterior semicircular canal;
- ap, ampulla;
- ca, cristae acusticae in the ampullae;
- de, ductus endolymphaticus;
- hc, horizontal (external) canal;
- l, lagena;
- ml, mn, ms, mu, maculae (of lagena, neglecta, sacculi and utriculi);
- pc, posterior semicircular canal;
- s, saccus;
- se, saccus endolymphaticus;
- suc, sacculo-utricular canal;
- u, utriculus. (From Kingsley’s “Comparative Anatomy of Vertebrates.”)
stimulate the hair cells which are the sensory elements of the organ. Grains of sand occasionally replace the otoliths.

The diversity of static organs in invertebrates is, however, so great that we must conclude that they have been independently acquired in the different groups. The fact that similar statocysts occur in such diverse forms as echinoderms, annelids, and mollusces points in the same direction.

Auditory organs have not been demonstrated in aquatic invertebrates. Indeed, it has not been demonstrated that any fishes can hear. Fishes respond to blows upon the surface of the water, but this may involve the lateral line organs or the sense of touch, not the ear. Auditory organs may be unnecessary among animals which are themselves unable to produce sounds.

Among invertebrates, true auditory structures are represented by the chordotonal and tympanic organs of insects. But neither these nor any other organs of invertebrates have a genetic relation to the ears of vertebrates.

Static organs occur in the free-swimming urochordates. In the larvae of ascidia and phallusia, a static organ with ciliated sensory epithelium, statolith, and nervous connexions projects into the brain cavity. Nothing similar is found in vertebrates. Amphioxus lacks a static organ, and is
quite unable to maintain its balance in swimming. Plate's suggestion that the ciliated infundibular organ of amphioxus is a static organ has little in its favor.

All vertebrates have a static organ, which is a novelty in this group and not a structure inherited from invertebrate forbears. In fishes and aquatic urodeles, the membranous labyrinth of the ear appears to be exclusively a static organ. But in land forms, beginning with the amphibia, the ear has the double function of equilibration and hearing.

Of vertebrates, the cyclostome myxine has the simplest static organ, which in shape is not unlike an inflated inner tube of an automobile tire with some inequalities of expansion. From its nerve supply, it is thought to correspond to the utriculus and the two vertical semicircular canals of the higher vertebrates. Homology with two semicircular canals of vertebrates rests on the presence of two ampullae, each of which contains an elongated cluster of hair cells, the crista, innervated by branches of the auditory nerve. Each of the semicircular canals of higher vertebrates has, however, only a single crista and ampulla, with three sensory maculae representing the single macula of myxine. A macula is a cluster of sensory cells with short hairs located either in the utriculus or sacculus. A rudimentary endolympathic duct which extends dorsally towards the skin is present.

The statocyst of petromyzon is slightly more complex than that of myxine. A ventral sacculus is partly separated from the utriculus by a circular constriction. There are three maculae instead of one. The statolith is represented by a mass of calcareous particles encased in a mucous matrix, and lying in contact with the hairs of the sensory cells of the maculae. None of the cyclostomes has a horizontal semicircular canal.

In elasmobranchs, the cavity of the statocyst retains its primary connexion with the outside, through the persistent invagination canal, which is sometimes erroneously homologized with the endolympathic duct of higher vertebrates. The statocyst is filled with sea water, instead of endolymph secreted by its own cells; and, in some species of sharks and rays, grains of sand replace calcareous statoliths. All three semicircular canals are present, as in higher vertebrates. The sacculus becomes further separated from the utriculus, and connexion between the two is effected by a canalis reuniens. The lagena is formed as an outgrowth of the sacculus, but it has not been demonstrated that it has an auditory function. The entire membranous labyrinth is enclosed in a cartilaginous capsule, which fuses with the cranium.

In teleosts, the invagination canal degenerates, and is replaced by an endolympathic duct, which grows out from the sacculus. The cavity of the bony auditory capsule opens into that of the cranium, and the perilymph surrounding the statocyst is identical with the cerebrospinal fluid.
The cavity of the otic capsule in amphibia becomes closed and independent of that of the cranium. Near the lagena, another outgrowth of the sacculus, the basilar papilla, is formed. From this and the lagena, arises the cochlea of the higher vertebrates. To its static function, the ear of the amphibia now adds an auditory one. (Fig. 494)

The loss of gills in land amphibia is associated with important changes in the visceral arches. The hyomandibular cartilage ceases to be a suspensory apparatus of the jaw, and slips into the spiracular passage as the stapes or columella. Amphibia are, therefore, the first animals to add to

the inner membranous ear structures corresponding to the middle ear of mammals. (Fig. 501)

In reptiles the lagena and basilar papilla unite in an elongated cochlea, which in crocodiles becomes spirally wound. By the attachment of the cochlear duct to the bony labyrinth along two sides, the perilymphatic cavity is divided into two portions, the scala vestibuli and the scala tympani. Further advance towards the mammalian ear is seen in the appearance of a membrane-covered window, the fenestra vestibuli, to which the stapes is attached. As a result of these advances, the hearing of reptiles is noticeably keener than that of creatures lower in the scale.

In mammals, the length of the cochlea varies from a half-turn in echidna to three and a half turns in the deer. The keenness and range of the sense of hearing differ correspondingly in the two animals. In correlation with the elongation of the cochlea, the length of Corti’s organ
is increased and, with it, the range of audible sounds. A second membrane-covered window, the fenestra cochleae, is added to the inner ear. The malleus and incus are added to the stapes, to form a chain of bones so arranged that the amplitude of the vibrations of the ear drum is reduced and their intensity increased as they pass from the drum to the fenestra vestibuli. The efficiency of the apparatus is increased by the addition of two muscles, the stapedial, the smallest of skeletal muscles, and the tensor tympani whichtightens the drum. (Fig. 501)

The conclusion of morphologists that the vertebrate membranous ear is a modified lateral line organ, or a group of such organs, seems justified by the fact that the membranous ear develops, like a lateral line organ, from a thickened placode of ectoderm on the side of the head, and that its later ontogenetic changes resemble those of a lateral line organ. In both cases, the skin sinks below the surface, and patches of sensory cells are differentiated. Moreover, the eighth nerve develops as a branch of the facial, a nerve which supplies lateral line organs. In the elasmobranchs, the external apertures of the invagination canal of the statocyst lies near the openings of the occipital row of lateral line organs. A similar separation of lateral line organs also occurs in the case of the ampullae of Lorenzini and the vesicles of Savi in elasmobranchs. Both from their development and nerve relations these organs are obviously differentiated lateral line organs. The ear, it is believed, has had a similar history.

THE HUMAN EAR

The ear consists of three parts, external, middle, and internal. The last is the true sensory organ, which has the double function of equilibration and hearing.

The External Ear. The external ear has two parts, an auricle or pinna, supported by cartilages, and an auditory meatus, which extends to the ear drum. Sound waves are collected by the pinna, and conveyed by the meatus to the ear-drum which lies about an inch below the surface of the head. The deeper portion of the auricle, which forms a vestibule to
the meatus, is the concha. The opening of the meatus is guarded by two processes, a ventral tragus next the cheek and a dorsal antitragus opposite. The incurved outer rim of the auricle is the helix. The antihelix is a smaller ridge which bounds the concha dorsally. The walls of the meatus are supported laterally by fibro-cartilage and medially by bone and lined by skin. The meatus is beset with hairs, and contains many tubular glands, which secrete the ear-wax.

The Middle Ear. A tympanic membrane or ear-drum separates the external meatus from the tympanic cavity or middle ear, within which lie the ear bones. Leading from the tympanic cavity to the pharynx, is the auditory or Eustachian tube, which serves to equalize the atmospheric pressure on the two sides of the tympanic membrane, so that this may vibrate freely. Temporary deafness occurs when the auditory tube is closed because of inflammation caused by a cold. Functionally, however, the most important elements of the middle ear are the three ear bones.

The Internal Ear. The membranous sac or true organ of equilibration and hearing is so complex that it is frequently called the membranous labyrinth. The otic bone in which it is embedded takes on its shape and is equally complex, and hence is known as the bony labyrinth. Except in the region where the membranous labyrinth is attached to the bone, it is surrounded by a cavity filled with the perilymph. The sac itself is filled with endolymph. (Fig. 495)

The Organ of Equilibration. The function of equilibration in man is served, as in lower vertebrates, by the utriculus and the three semicircular canals connected with it. All three are hollow membranous canals lined
by columnar epithelium and loosely attached by connective tissue to the periosteum of the otic bone. Connected at both ends with the utriculus, each canal swells at one end into an **ampulla**. On one side of each ampulla, an elongated cluster of hair-cells forms a **crista**, which is innervated by a branch of the vestibular nerve.

The elongated hairs of the sensory cells of the crista extend into the endolymph, the movements of which are communicated to the hairs, and thus indirectly to the nerves connected with the hair-cells. Similar patches of hair cells, the maculae, with shorter hairs, occur on the sides of the utriculus and saccus and, like the cristae, have a static function.

![Diagram of the organ of Corti](image)

**Fig. 497.**—A stereogram of a portion of the organ of Corti (spiral organ) of man. The precise function of the tectorial membrane is uncertain. It may serve as a dampener or it may intensify the action of the "sound waves" upon the sensory hair cells. (Redrawn after Kahn's "Das Leben Des Menschen," W. Keller & Co.)

Proof of the static function of utriculus, saccus, and semicircular canals has been obtained by extirpation experiments upon lower animals. An animal without these parts of the ear is unable to orient its body in space. The centers of equilibration in the brain are closely associated with those of the vagus nerve; so that the sea sickness which follows continuous and violent disturbance of the static organ results from its relation to the nerve which innervates the stomach. The action of the endolymph upon the hairs of the cristae and maculae is intensified by the presence of small calcareous crystals or **otoconia** in the endolymph.

**The Organ of Hearing.** The organ of hearing is the **cochlear duct**; otherwise known as the scala media, which is attached to the outer side of the spiral bony cochlea. The cochlear duct is connected with the saccus by means of a narrow tubular **ductus reuniens**. The saccus is
also connected with a slender endolymphatic duct, which terminates in a
swollen saccus endolymphaticus near the dura. The utriculus connects
with the saccus through the utriculosaccular duct by means of the
endolymphatic duct. (Fig. 494, G)

Throughout the two and a half turns of its extent, the membranous
duct of the cochlea is triangular in cross section, and is attached at its

![Diagram of the cochlea with labels for Scala Vestibuli, Membrana Tectoria, Cochlear Duct, Basilar Membrane, Inner Hair Cells, Outer Hair Cells, Pillar Cells, Scala Tympani, Cochlear Nerve, Organ of Corti.]

Fig. 498.—A stereogram of a portion of the cochlear duct of man. The figure
suggests how "sound waves" are conveyed to the hair cells of the organ of Corti.
(Redrawn after Kahn's "Das Leben Des Menschen," W. Keller & Co.)

apex and base to the surrounding bone. The side lying towards the
greater curvature of the cochlea consists of a much thickened periosteum,
the spiral ligament. The upper side, the vestibular membrane, consists
of a thin sheet of connective tissue, covered on both sides by flattened
epithelium. As in reptiles, the apex of the triangle is fastened to the thin
bony lamina which projects into the perilymphatic cavity, and partly
divides this into a dorsal cavity, the scala vestibuli, and a ventral cavity,
the scala tympani, both of which are filled with perilymph and connected
with one another at the apex of the cochlea. (Fig. 498)

The third and lower side of the cochlear duct is the essential auditory
organ, the spiral organ of Corti, which rests upon a connective tissue
basilar membrane. In the region of the spiral organ, the epithelial lining of the cochlear duct becomes a much thickened columnar epithelium, in which are sensory hair-cells and supporting cells. Two kinds of supporting cells occur, pillar cells arranged like the rafters of a house, and Deiter's cells, which support the sensory hair cells. Between them, is a liquid-filled cavity, the tunnel. (Fig. 497)

The hair cells do not extend through the entire thickness of the epithelium, but are suspended with their rounded bases hanging between the supporting cells. Four to six rows of hair cells extend through the entire length of the cochlea. An inner row is separated by the pillar cells from the outer rows.

These hair-cells are estimated to be sixteen thousand in number. Each has on its free surface about forty stiff hairs which project into the endolymph. The base of each hair cell is supplied with the dendritic terminations of a nerve fiber from the cochlear nerve.

Suspended in the endolymph above, and possibly in contact with the hair, is the fibrous membrana tectoria, the function of which is problematic. It has been suggested that its vibrations are communicated to the hairs. Others believe that like a soft pedal it acts as a dampener to reduce vibration.

Between the liquid-filled cavity of the internal ear and the air-filled tympanic cavity, are the two membrane-covered openings, the fenestra vestibuli or fenestra ovalis, to which the stapes bone is attached, and the fenestra cochleae or rotunda. By means of the stapes, vibrations are transmitted through the fenestra vestibuli to the perilymph and to the top of the scala vestibuli. These vibrations, passing down the scala tympani cause similar vibrations of the fenestra cochleae. It is still a disputed question, whether the vibrations are communicated to the hair-cells through the endolymph and the tectorial membrane, or through the vibrations of the basilar membrane of the spiral organ.

The auditory centers of the brain are located in the temporal lobes of the cerebral hemispheres.

Development of the Human Ear

The membranous sac of the ear begins in the two-somite embryo as a thickened patch of ectoderm lateral to the hindbrain. By the time the embryo has acquired eleven somites, this placode has begun to bend in towards the brain wall to form a pit. In a five-weeks embryo, the otic pit is converted into a spherical liquid-filled otic vesicle, which has lost its original connexion with the ectoderm. This vesicle elongates dorsoventrally, and an endolymphatic duct grows from the dorsal side, not as a remnant of the primitive invagination canal, but as a new formation.
By the elongation and spiral twisting of the ventral part of the vesicle, the cochlear duct is formed.

The dorsal portion of the vesicle, following the outgrowth of the endolymphatic duct, becomes the utriculus. The two vertical canals develop from a single dorsal hollow outpocketing of the utriculus; but the lateral hollow outgrowth from which the horizontal semicircular duct develops arises later, as might be expected from its phylogenetic history. Each semicircular duct is formed by a partial fusion of the lateral walls of its hollow anlage, by which the cavity is obliterated except in its periphery, where it persists as the cavity of the definitive duct connected with the utriculus at each end. At one of these ends the duct swells out into an ampulla.

That portion of the membranous sac which is intermediate between the utriculus and the cochlea is converted into the sacculus. Its separation from the utriculus is initiated by a horizontal constriction, which finally reduces the connexion to the slender utriculosaccular duct. By a similar constriction, the connexion between the cochlear duct and the sacculus becomes a ductus reuniens.

From the beginning, the otic vesicle is directly attached to that part of the neural crest which forms the ganglion of the facial nerve. This connexion is retained by the auditory nerve, which arises as a branch of the facial, although the roots of the two subsequently become separated. Throughout the changes which convert the otic vesicle into the membranous labyrinth, the connexions of the auditory nerve are retained. Two main branches are differentiated, the vestibular, connected with utriculus
and semicircular canals, and the **cochlear**, which innervates the hair-cells of Corti’s organ.

Most of the membranous labyrinth retains throughout life its primitive epithelial character. In local patches, however, it is converted into sensory columnar epithelium, the cells of which are connected with branches of the auditory nerve. Each ampulla develops a ridge-like **crista** composed of hair cells. The utriculus and sacculus develop larger cushion-like maculae. One side of the cochlear duct is modified as the spiral organ of Corti.

The development of the tectorial membrane, like its function, has long been a controversial question. Primarily, this membrane is closely attached to the columnar epithelium from which the organ of Corti arises. The intimacy of the connexion is gradually reduced during ontogenesis, so that eventually the membrane loses its connexion with the cells of the spiral organ and floats above them in the endolymphatic fluid.

The differentiation of the elements of the spiral organ is not completed at the time of birth, so that an infant is stone deaf until it is some weeks old.

The mesenchyma surrounding the membranous labyrinth becomes differentiated into an inner connective tissue membrane which lies in contact with the epithelium of the sac, and an outer cartilaginous capsule which encloses the membranous ear. Later, the portion of the cartilage near the membranous sac disappears and is replaced by liquid perilymph around the sac. As the cochlear duct develops, it becomes triangular in cross section.

![Diagram of developing human labyrinth from 6 to 30 mm. long.](image)
In the higher vertebrates the cartilaginous otic capsule is subsequently converted into bone by the process of endochondral bone formation. But in the axis of the spiral cochlea the connective tissue is converted directly into bone, after the manner of membrane bone formation. The contrast between the modes of formation of the inner and outer portions of the bony part of the cochlea seems to have no phylogenetic significance.

The middle ear and the Eustachian tube which leads from it to the pharynx are both derived directly from the spiracular pouch, a diverticulum of the pharynx. Consequently, both, like the pharynx from which they evaginate, are lined by endoderm. To meet this endodermic diverticulum, the ectoderm invaginates to form the external auditory meatus. The two-layered membrane between the two invaginations,
strengthened secondarily by the ingrowth of mesenchyme between the two layers, forms the ear-drum.

The three ear bones are primarily embedded in the connective tissue dorsal to the tympanic cavity in which the spiracular pouch terminates. This connective tissue subsequently disappears, and the tympanic cavity is correspondingly enlarged and surrounds the earbones. The bones thus become enclosed by the endodermic epithelium, which persists throughout life. The origin of the three ear bones from elements of the visceral skeleton is clearly evidenced by the facts of ontogenesis.

The external auricle develops from materials supplied by the mandibular and hyoid arches. Three small hillocks arise on each of these arches, and each hillock acquires a cartilaginous support. By the enlargement and fusion of these six hillocks and their cartilaginous supports, the external ear develops. The three nodules of the mandibular arch form tragus and helix; those of the hyoid arch become antitragus and antihelix. The claim that the cartilages of the ear are derived from those of the hyoid arch has not been confirmed.
CHAPTER 15

THE HEAD PROBLEM

The striking contrast between head and trunk has not prevented morphologists from comparing the two regions. To those who assumed the origin of vertebrates from annelid ancestors, the fundamental similarity seemed self-evident. Curiously enough, the first attempt to demonstrate that the head contains segments like those of the trunk was made in pre-Darwinian days, even by those who denied evolution. Now, however, for more than a century, it has been assumed that the present differences between head and trunk are coenogenetic, and that the two regions were differentiated from one another in the immediate ancestors of vertebrates.

The "head problem" is a threefold one. First, is the head, like the trunk, metameric? Second, if metameric, are segments of head and trunk fundamentally similar? Third, how many segments are contained in the head? The complexity of this inquiry and diversity of answers have combined to make it one of the persistent problems of vertebrate morphology.

The problem is not identical with that of the ancestry of vertebrates, although its elucidation may throw light upon the latter. Even if it were demonstrated that metamerism characterizes both head and trunk of vertebrates, this would by no means prove that vertebrates are derived from metameric ancestors. For metamerism, like any other animal characteristic, may be a convergent trait acquired de novo within the chordate group.

Historically, the head problem has passed through three phases, which may be called the transcendental, the anatomical, and the embryological.

Transcendental Phase. In its first phase, the head problem was limited to the skeleton, and the rest of the head region was ignored. The distinguished German poet Goethe was the first to conceive that the skull consists of a number of enlarged and united vertebrae. In 1790, Goethe wrote to his friend Karoline Herder that the study of a sheep's skull found in the Jewish cemetery near Venice had given him a new notion in regard to the structure of the head. Goethe was familiar with Greek authors and, through them, with the evolution theory. In fact, he had already suggested that a flower is a shortened and modified branch, a theory now universally accepted by botanists. Goethe, however, did not publish
his vertebral theory of the skull until 1823. In the meanwhile a German naturalist Oken published, in 1807, a similar conception of the skull as a composite of enlarged vertebrae. Quite unrestrained by sound morphological principles, Oken compared the upper jaw with the arms, the lower jaw with the legs, and the fingers and toes with the teeth.

In England, the distinguished anatomist Owen adopted Oken's conception and attempted to demonstrate in the bones of the skull all the typical elements of a trunk vertebra. Owen's familiar figure of an "archetypal vertebrate," with four vertebrae in the skull and each cranial vertebra with typical vertebral elements, is shown in Fig. 503. During
the first half of the nineteenth century, the vertebral theory formed an essential part of the orthodox creed of biologists. The brilliant morphologist Johannes Mueller defended it in Germany, while Carl Vogt opposed it. Rathke and Reichert supported it on embryological grounds. In France, Cuvier was coolly indifferent. In America, Louis Agassiz opposed it.

It was Thomas Huxley who, in 1858, a year before the publication of the *Origin of Species*, dealt the vertebral theory of the skull its death blow. In his famous Croonian lecture, Huxley pointed out that the fish skull develops primarily as a cartilaginous box, and not as a series of vertebral elements. He thus turned against the vertebral theory embryological evidence which Rathke and Reichert had interpreted in its favor. No vertebra-like structures are present in the cartilaginous skull of elasmobranch fishes, in which, according to hypothesis, vertebrae ought to be more evident than in higher forms. Although the vertebral theory of the skull never recovered from Huxley’s attack, it was Huxley who converted the head problem from a problem of the morphology of the skull only, to one of the structure of the entire head.

**Anatomical Phase.** In 1869, Huxley, abandoning the vertebral theory, demonstrated that evidence of head metamerism is found in the series of cranial nerves and the gill-slits with which they are associated. The facial nerve forks over the spiracular cleft, the glossopharyngeus over the first branchial, and the vagus over the more posterior clefts. Huxley assumed that the gill-slit proper to the trigeminal nerve is the mouth which, in his opinion, might have been formed by the coalescence of a pair of gill-slits. He also suggested that the ophthalmicus profundus nerve represents a pre-oral segment, and that the embryonic orbito-nasal groove to which it is related is the remnant of a gill slit. Huxley recognized altogether nine head segments, four in front of the ear and five behind.

Two years later, Gegenbaur confirmed the conclusions of Huxley and added the cartilaginous visceral arches as criteria of metamerism. To supply skeletal elements for pre-oral segments, he used the labial cartilages of the elasmobranchs. Gegenbaur, however, erroneously compared visceral arch cartilages with trunk ribs and consequently regarded head
and trunk segments as serially homologous. It has since been demonstrated that visceral arches differ from ribs, both in development and in relations to other parts, and hence are not homologous. Gegenbaur called attention to the fact that the presence of membrane bones in the skull makes it impossible to compare the skull with a vertebra. Like Huxley, Gegenbaur counted nine segments in the head. These he regarded as serially homologous with those of the trunk.

**Head Segments According to Gegenbaur**

<table>
<thead>
<tr>
<th>Primary visceral skeleton</th>
<th>Modified visceral skeleton</th>
<th>Nerve</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st arch</td>
<td>1st upper labial cartilage</td>
<td>Ramus 2</td>
</tr>
<tr>
<td>2nd arch</td>
<td>2nd upper and 1st lower labial cartilages</td>
<td>Trigemini</td>
</tr>
<tr>
<td>3rd arch</td>
<td>Mandibular arch</td>
<td>Ramus 3</td>
</tr>
<tr>
<td>4th arch</td>
<td>Hyoid arch</td>
<td>Facial</td>
</tr>
<tr>
<td>5th arch</td>
<td>1st gill arch</td>
<td>Glossopharyngeal</td>
</tr>
<tr>
<td>6th arch</td>
<td>2nd gill arch</td>
<td>Ramus, 1 vagi</td>
</tr>
<tr>
<td>7th arch</td>
<td>3rd gill arch</td>
<td>Ramus, 2 vagi</td>
</tr>
<tr>
<td>8th arch</td>
<td>4th gill arch</td>
<td>Ramus, 3 vagi</td>
</tr>
<tr>
<td>9th arch</td>
<td>5th gill arch</td>
<td>Ramus, 4 vagi</td>
</tr>
</tbody>
</table>

**Embryological Phase.** With the rise of the science of embryology during the latter part of the nineteenth century, the head problem entered its third and last phase. The assumption which underlies the interpretation of embryological evidence, as applied to the head problem, is von Baer's law, the fundamental law of biogenesis, that the development of the individual recapitulates briefly the past history of the race. The truth
of this assumption has been persistently challenged, and experience has demonstrated that it should not be pressed too far. In a very general way, however, the law has proved helpful, especially in relation to the head problem.

In 1878 Francis Balfour made the important discovery that in elasmobranch embryos the coelom extends continuously throughout head and trunk. He thus demonstrated that in this fundamental respect head and trunk are similar to a degree not previously realized. Balfour also stressed the fact that, by the formation of gill-pouches, the cephalic coelom is divided into a series of mesodermal "cavities," which Balfour erroneously compared with trunk somites. The falsity of this comparison was subsequently recognized when it was demonstrated that the trunk somites develop from the epimere, while the mesoderm of the visceral arches comes from the hypomere.

In 1881, Balfour's pupil, Marshall, emphasized the distinction between the segmentation of the somites and that of the mesoderm of the visceral arches, and asserted the independence of the two. Only segmentation of the dorsal somites of head and trunk are comparable. The mesodermal cavities within the visceral arches are peculiar to the head. This contrast between "mesomerism" and "branchiomerism" has been recognized by later morphologists. Whether or not these two kinds of segmentation originally corresponded has remained a controverted issue to this day. Marshall also showed that the first or premandibular "cavity" gives rise to the four eye muscles innervated by the oculomotor nerve, while the external rectus muscle comes from the third somite.
Fig. 506.—Diagrams of the mesodermal segmentation in the head region of chordate embryos. The somites are stippled and nerve ganglia shown in solid black, visceral pouches cross-hatched. A, Larval Amphioxus; B, Petromyzon (cyclostome); C, Squalus (elasmobranch). The neuromeres are numbered with Roman numerals.
### HEAD SEGMENTS ACCORDING TO MARSHALL

<table>
<thead>
<tr>
<th>Segment</th>
<th>Nerve</th>
<th>Visceral cleft</th>
<th>Visceral arch</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Preoral</td>
<td>I. Olfactory</td>
<td>Olfactory</td>
<td></td>
</tr>
<tr>
<td>2. Preoral</td>
<td>III. Oculomotor</td>
<td>Lacrimal</td>
<td>Maxillary</td>
</tr>
<tr>
<td>3. Oral</td>
<td>IV. Trochlearis</td>
<td>Buccal</td>
<td>Mandibular</td>
</tr>
<tr>
<td>4. Postoral</td>
<td>V. Trigeminal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Postoral</td>
<td>VII. Facial</td>
<td>Spiralacular</td>
<td>Hyoid</td>
</tr>
<tr>
<td>6. Postoral</td>
<td>VI. Abducens</td>
<td>1st branchial</td>
<td>1st branchial</td>
</tr>
<tr>
<td>7. Postoral</td>
<td>IX. Glossopharyngeal</td>
<td>2nd branchial</td>
<td>2nd branchial</td>
</tr>
<tr>
<td>8. Postoral</td>
<td>X. Vagus, 1st branch</td>
<td>3rd branchial</td>
<td>3rd branchial</td>
</tr>
<tr>
<td>9. Postoral</td>
<td>X. Vagus, 2nd branch</td>
<td>4th branchial</td>
<td>4th branchial</td>
</tr>
<tr>
<td>10. Postoral</td>
<td>X. Vagus, 3rd branch</td>
<td>5th branchial</td>
<td>5th branchial</td>
</tr>
<tr>
<td>11. Postoral</td>
<td>X. Vagus, 6th branch</td>
<td>6th branchial</td>
<td>6th branchial</td>
</tr>
</tbody>
</table>

The year following the publication of Marshall’s paper, van Wijhe discovered in elasmobranch embryos an unbroken series of somites beginning with the premandibular and extending throughout head and trunk. He was thus able to demonstrate an “acraniote stage” of the vertebrate embryo, which, so far as the mesodermal segmentation is concerned, resembles the acraniote amphioxus. While all the myotomes of amphioxus persist throughout life, in elasmobranchs some of those in the region of the ear degenerate. As a result, the three anterior somites, which form eye muscles, become separated from the metaotic. In cyclostomes, however, according to Koltzoff (’02), all the embryonic myotomes form muscles, which persist in the adult lamprey as in amphioxus. There is, therefore, in the lamprey no hiatus between prootic and metaotic muscles. (Figs. 507, 508)

### HEAD SEGMENTS ACCORDING TO VAN WIJHE

<table>
<thead>
<tr>
<th>Somite</th>
<th>Muscles from the somite</th>
<th>Ventral nerve root</th>
<th>Dorsal nerve root</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Rect. sup., inf., int., and inf. oblique</td>
<td>Oculomotor</td>
<td>Ophthalmicus profundus</td>
</tr>
<tr>
<td>2</td>
<td>Superior oblique</td>
<td>Trochlearis</td>
<td>Trigeminus less ophth. prof.</td>
</tr>
<tr>
<td>3</td>
<td>Rectus externus</td>
<td>Abducens</td>
<td>Acusticofacialis</td>
</tr>
<tr>
<td>4</td>
<td>None</td>
<td>None</td>
<td>Glossopharyngeal</td>
</tr>
<tr>
<td>5</td>
<td>None</td>
<td>Not recognizable</td>
<td>Vagus</td>
</tr>
<tr>
<td>6</td>
<td>Very rudimentary</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Muscles from skull to shoulder girdle, with anterior part of sternohyoid</td>
<td>Hypoglossus</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Van Wijhe confirmed the conclusions of Marshall in regard to the fate of the first and third somites, and also asserted that the superior oblique muscle is derived from the second somite. In the metaotic region the first permanent myotome develops from the seventh somite, and van Wijhe concludes that altogether nine segments enter into the formation of the head, a conclusion very similar to that reached by Huxley and Gegenbaur on anatomical grounds. In a later paper, van Wijhe ('22) adds another metaotic segment, making a total of ten in the head of elasmobranchs.

Since van Wijhe's first paper, many embryologists have investigated the mesodermal segmentation of embryos in all classes of vertebrates.

While their observations and conclusions have not been wholly consistent, it may be said that van Wijhe's general results have been confirmed. Somites like those of elasmobranchs have been found in cyclostomes and amphibia. Their presence indicates that the ancestors of vertebrates, like the living amphioxus, were segmented throughout the length of the body, that the metamerism was primarily muscular, and that head segments were like those of the trunk.

The conclusion that the mesodermal segments in the head region are comparable with those of the trunk has by no means been accepted by morphologists without opposition. Among the objections raised are that the head segments are due to the mechanical influence of surrounding parts such as the gill-pouches; that the head somites are irregular in size; that the continuity of trunk and head segments does not prove their serial homology; that the head segments do not develop in succession.
with those of the trunk, as would be expected if they were members of a continuous series; that the prootic segments do not become differentiated into myotome and sclerotome as do trunk somites; that the muscles in the trunk region are differentiated from the median wall of the somite, while the musculature of the pre-otic segments arises in large part from the lateral wall; that the mesenchyma of trunk somites comes from a constricted region of the somite, while in the head segments it comes from the entire median wall; that relations of the nerves to the head segments differ from those of spinal nerves to the trunk somites. In addition to these general objections, special objections have been raised against the inclusion of the first and second pro-otic segments as true somites. Most of these assertions have proved to be erroneous.

![Diagram of mesodermal somites](image)

**Fig. 508.**—A parasagittal section of an eight-day Petromyzon embryo viewed from the left side showing the mesodermal somites. The first somite is shown in an adjacent section, not in the figure. According to Koltzoff all of the head somites of Petromyzon form permanent muscles. The first three form the eye muscles, while the fourth is the first myotome of the lateral trunk muscles. (Redrawn after Koltzoff.)

That the segments discovered by van Wijhe in elasmobranch embryos are true somites homologous with those of the trunk, now seems sufficiently established by the fact that their presence in diverse groups of vertebrates has been repeatedly confirmed; that their segmentation is independent of the visceral segmentation represented in the visceral arches; that they form a series continuous with that of the trunk; that they are dorsal in relation to the dorsal aorta and notochord; that they develop consecutively, beginning in the neck region; that they become differentiated like trunk somites into myotome and sclerotome; that their muscles develop from the median wall; and that they correspond numerically with the neuromeric segments. Consequently, the conclusion that they form the most convincing evidence of the fundamental similarity of the segmentation in head and trunk seems warranted.

Van Wijhe noticed in the embryo of Galeus, an elasmobranch, a pair of mesodermal segments or "cavities" which he interpreted as an anterior
prolongation of the premandibular cavity. Later, Julia Platt found these segments in squalus embryos, and observed that they develop anterior to the premandibular cavities and independent of them. Finding rudimentary muscle fibers in the walls of these cavities, she concludes that they are serially homologous with mesodermal somites, and named them **anterior cavities** (somites). If her interpretation of the anterior cavities as somites is correct, this adds another segment to the series discovered by van Wijhe.

The existence of the anterior somites has been repeatedly confirmed by subsequent investigators, but opinion is divided as to their significance. Van Wijhe, Dohrn, and Goodrich doubt their segmental value and assume that they are derivatives of the premandibular somites. Goodrich urges that in any scheme of cephalic metamersim the anterior cavities should be ignored, since "they soon disappear and form no permanent structure, are scarcely or not at all developed in other elasmobranchs, have not been found at all in other gnathostomes, and are absent in petromyzon."

None of these objections, however, appears to invalidate Miss Platt's interpretation. In making them, Goodrich seems to have overstrained his point. If, for example, every embryonic feature should be ignored if it "soon disappears and forms no permanent structure," we should have to ignore also van Wijhe's fifth and sixth somites which, like the anterior somite, break up into mesenchyma. If we are to ignore the anterior somites because they are "scarcely or not at all developed in other elasmobranchs," to be consistent, we should have to ignore also the tubular
connexion between the premandibular cavity and the hypophysis discovered by Goodrich ('17) in Torpedo. The fact is that in the development of the anterior cavities, as in many other respects, Squalus and Galeus present more primitive characteristics than do most elasmobranch embryos. While petromyzon, as Goodrich says, does not have anterior

cavities, there are mesenchyma cells anterior to the premandibular somite which may represent the anterior cavities.

The assertion that the anterior cavities "have not been found at all in other gnathostomes" may be questioned, since Reighard ('02) has shown that the adhesive organs of amia, a ganoid fish, resemble the anterior cavities both in development and in their relations to the preoral gut and to the premandibular somite, and must therefore be considered

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**Fig. 510.**—Diagrams of frontal and cross sections of Amphioxus (cephalochordate), Amia (ganoid), and Squalus (elasmobranch) embryos, showing the exact homology of the anterior endodermic diverticula of Amphioxus, the adhesive organs of Amia, and the anterior somites of Squalus. A, A', A², A³ sections of amphioxus; B, B' sections of Amia; C, C' sections of Squalus.
to be homologous with them. There is evidence also that they are possibly homologous with the pit-organs of vipers.

The facts of development do not bear out the assertion that the anterior cavities are segregated portions of the premandibular cavities. It would be equally misleading to state that the premandibular cavity is a segregated portion of the mandibular cavity. The three structures

FIG. 511.—Parasagittal sections showing the similarity of the relations of the anterior endodermic diverticula of Amphioxus (A) to those of the adhesive organ of Amia (B) and of the anterior somites of Squalus (C). Each of these "cavities" arises immediately in front of the first permanent myotome (somite 1).

are, in fact, serially homologous—at least in part—and have equal segmental value. This conclusion is supported by the resemblance of the anterior cavities to the anterior endodermic diverticula of amphioxus. Like the latter they are the anteriormost cavities of the body and develop immediately anterior to the first permanent myotomes. The resemblance of the adhesive organs of amia to the anterior endodermic diverticula of amphioxus is even more striking. Both arise as paired endodermic diverticula of the anterior end of the preoral intestine. Both open by pores to the exterior, the left cavity in amphioxus forming the preoral pit.
In the light of the evidence we are compelled to add another segment to those enumerated by van Wijhe, so as to make eleven segments in the elasmobranch head, instead of the ten recognized by Goodrich.

Fig. 512.—A parasagittal section of a 33-hour chick embryo showing the brain neuromeres. The neuromeres are indicated by Roman numerals.

Among the criteria used to determine head segmentation, some morphologists have leaned heavily upon the so-called neuromeres or segments of the central nervous system. Neuromeres are evanescent embryonic structures, first described by Bischoff ('42) in the medulla of mammal embryos. The assumption that neuromeres are reliable criteria of segmentation has been based partly upon the belief that vertebrates are the descendents of annelids which have a segmented
nervous system. In annelids and arthropods each metamere typically contains a well-marked ganglion which serves as a nerve center for the segment. In some arthropods in which the metameres have been telescoped together, the original segmentation is still represented in a series of metamERICally arranged ganglia. Here the neuromeric segmentation persists when other signs of metamerism are all lost. The fact of the transiency of vertebrate neuromeres has not counted against their value as criteria of segmentation, but in their favor, as vanishing remnants of the metamerism of invertebrate ancestors.

Compared, however, with the results based upon mesomeres (somites), the study of neuromeres has proved disappointing. Students of neuromeric segmentation agree as to the existence of hindbrain neuromeres or rhombomeres, but as to little else. The discrepancies in their results, combined with the increasing distrust of the theory of the annelid ancestry of vertebrates, have served to weaken confidence in conclusions based upon the study of neuromeres. Moreover, most morphologists are convinced that metamerism began in the muscular, not in the nervous system. Nervous metamerism is, in their judgment, a secondary adaptation to muscular segmentation.

Locy ('94) and his pupil Hill ('oo) claim to have found a uniformly beaded segmentation throughout the length of the brain and spinal cord. Their highly diagrammatic figures have found their way into recent textbooks, in spite of the fact that the majority of investigators have failed to confirm their results. As a matter of fact, the serial homology

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**Fig. 514.**—Diagrams of the neuromeres in chordate embryos. Wanting in Amphioxus (A), they appear with increasing distinctness in Petromyzon (B), Squalus (C), and Chick (D). This evidence does not accord with the assumption that they are pre-chordate structures which appear transiently in vertebrate embryos.
of neural divisions anterior and posterior to the neuromeres of the medulla has not been demonstrated.

A number of facts appear to invalidate the assumption that neuromeres are reliable criteria of the primitive segmentation of the head. Neuromeres are more conspicuous in the embryos of higher than in those of lower vertebrates, and it was evidence similar to this that led to the abandonment of the vertebral theory of the skull. Neuromeres in cyclostomes appear to be limited to the medulla and even there are identified with difficulty; but they become increasingly prominent as we pass in the vertebrate series from fishes to mammals. Such evidence does not accord with the assumption that neuromeres have phylogenetic significance.

As stated above, little resemblance is seen between rhombomeres (neuromeres of the medulla oblongata) and the neural segments anterior and posterior to them. Since rhombomeres appear chiefly in the lateral plates of the medulla, the only structures comparable anteriorly are the forebrain and midbrain vesicles, not secondary subdivisions of these. The so-called neuromeres in the trunk region are transient effects produced by the pressure of the mesodermal somites in early stages of their development, and affect only the ventro-lateral portions of the spinal cord. Such evidence leads to the conclusion that a rhombomere is a new structure, possibly developed in relation to the visceral arches and clefts.

Furthermore, the cranial nerves do not have simple one-to-one relations with neuromeres, as might be expected if they are metameric
structures. If, for example, each rhombomere were metameric, it should be connected with a visceral arch by such a cranial nerve as V, VII, IX or X. At least the motor fibers of each nerve should have a center in a single neuromere. It is found, however, that the mandibular branch of the fifth nerve has its motor centers in two rhombomeres, the second and third; that the centers of the seventh nerve lie in four rhombomeres, the fourth to seventh inclusive, and that those of the ninth have their nucleus in the sixth and seventh rhombomeres. Of the somatic motor nerves, the relations of the abducens (VI) are even less clearly metameric.

Although the abducens innervates a single myotome, that of the third head cavity, the motor nucleus stretches through three rhombomeres, the fifth, sixth, and seventh. Since these relations occur both in elasmobranchs and in mammals, it may be assumed that they occur in all other vertebrates. While these confused nerve relations by no means prove that the neuromeres are without metameric value, they are certainly not the relations which would be expected in metameric structures. If the relations of cranial nerves to muscles and visceral arches were originally metameric, they have obviously been profoundly modified in the course of phylogenesis.

Doubt as to the value of neuromeres as criteria of metamericism also arises out of the failure of students of neuromerism to agree on the number of neuromeres in the head. This divergence of opinion is partly based upon disagreement in regard to what structures may be counted as
neuromeres. While some hold that the segmentation visible in the open neural plate is the true neural segmentation, others assume that the secondary subdivisions of the brain vesicles are to be counted.

Opinions differ also as to the criteria of neuromeres. Some observers find the neural segments inconstant and asymmetrical. It is, therefore, not surprising that the majority of those who have studied neuromeric segmentation are skeptical of their metameric value, those of the hindbrain possibly excepted. If any brain divisions anterior to those of the hindbrain may be counted as neuromeres, they are the primary forebrain and midbrain vesicles, which owe their primary appearance to their functional association with the olfactory organs and the paired eyes. It is possibly significant that these two vesicles, like the neuromeres of the hindbrain show a numerical correspondence with mesodermal somites, including Miss Platt’s anterior somites. If this numerical correspondence seen in elasmobranch embryos is not wholly accidental, the neuromeres, like the mesodermal somites, may have a metameric value. (Fig. 517)

In 1885 Beard and Froriep independently discovered that the ganglia of the cranial nerves receive cellular accessions from epidermal placodes above the gill-pouches. To these placodes Beard gave the name epi-branchial sense-organs. Since they may be assumed to have a primary numerical correspondence with gills, they were used by Beard as criteria of the primitive segmentation of the head. (Fig. 518)
In cyclostome embryos, Kupffer ('95) found thirteen such epibranchial sense organs, five anterior to the facial ganglion and seven posterior. Six of these are associated with the visceral branches of the vagus nerve. Kupffer's results, however, have never been confirmed, and relatively few schemes of cephalic segmentation make use of epibranchial ganglia as criteria of metamerism.

In the attempt to compare a head segment with a trunk segment, a number of mistakes have been made. Gegenbaur's homology of a skeletal visceral arch with a rib is invalidated by the fact that the two
resemble one another neither in development nor in relations. The same objection may be made against the attempt to compare one of the aortic arches with one of the intercostal arteries. Balfour’s failure to distinguish between the mesoderm of the visceral arches and that of the somites has misled many, and this error has been perpetuated by H. E. Ziegler (‘15). Van Wijhe’s head somites develop from the epimere, while the mesoderm of the visceral arches comes from the hypomere. The segmentation of the somites has been shown to be independent of that of the visceral arches. There is nothing in the trunk region comparable with a visceral arch. Branchiomericism is confined to the head. If branchiomeric segmentation were the only evidence of head metamerism, we should have to conclude that the head is a region sui generis. Whether or not there was, or is, a correspondence between mesomerism and branchiomerism remains today an open question. Their topographic relations in amphioxus and cyclostome embryos justify the assumption of a primitive correspondence, but the tendency of visceral arches and pouches to be reduced and modified, makes them less satisfactory criteria of the primitive segmentation than the somites.

A number of objections have been made against the use of cranial nerves as criteria of head segmentation and against the attempt to compare them with spinal nerves. The dissimilarities of the two have been emphasized. It has been asserted that cranial nerves, such as V, VII, IX and X, are mixed motor and sensory, while the dorsal spinal nerves are purely sensory; that the cranial nerves mentioned receive cellular contributions from epibranchial ganglia, while spinal nerves do not; that the ganglia of cranial nerves lie lateral to the somites, while those of spinal nerves are medial; that spinal nerves have a metameric distribution, while cranial nerves have an extensive polymeric distribution.

To meet these objections, it has been pointed out that the dorsal nerves of amphioxus are mixed in function, and that in this respect cranial nerves retain an ancestral trait which has been lost by the dorsal roots of spinal nerves. As a matter of fact visceral motor fibers occur in the dorsal roots of spinal nerves of fishes and amphibians. They disappear from these roots in amniotes. The difference in the relations of dorsal nerves to the somites and to epibranchial ganglia may be explained as a result of the reduction in size of cranial as compared with trunk somites, and the limitation of gills, with which epibranchial ganglia are associated, to the head region. The wide peripheral distribution of cranial nerves is regarded as a coenogenetic adaptation. There is some evidence of metamerism in cranial nerves, however, in the relations of the visceral branches of cranial nerves to the series of gill-clefts.

The relations of the somatic motor cranial nerves, the oculomotor, trochlearis, and abducens, resemble those of spinal somatic motor nerves.
The hypoglossus is evidently a spinal nerve which has become cranial in amniotes. It is a reasonable conclusion that originally cranial and spinal nerves were similar and serially homologous. Amphioxus presents the living evidence that a serially homologous segmentation extended throughout the entire length of the chordate ancestor from which vertebrates evolved. The differences between head and trunk, therefore, are coenogenetic, and are due largely to the concentration of the major senses in the head and the high degree of differentiation of cranial organs.

All who have studied head metamerism agree that the head is segmented. Some, however, have concluded that the prootic region is a region *sui generis*. Yet the great majority compare prootic and metaotic segments with those of the trunk. Some disagreement appears in estimates of the total number of segments. This is not surprising, since the number of occipital segments varies in different classes. That vertebrae have been added to the skull is shown by the fact that the accessory and hypoglossal nerves are cranial in amniotes but spinal in anamnia.

**SUMMARY OF THE EVIDENCE**

The resemblances and differences between head and trunk metameres may be summarized thus:

<table>
<thead>
<tr>
<th>Head</th>
<th>Trunk</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>I. Resemblances</strong></td>
<td></td>
</tr>
<tr>
<td>Coelom</td>
<td>Coelom</td>
</tr>
<tr>
<td>Myotome</td>
<td>Myotome</td>
</tr>
<tr>
<td>Sclerotome</td>
<td>Sclerotome</td>
</tr>
<tr>
<td>Somatic efferent nerve</td>
<td>Somatic efferent nerve</td>
</tr>
<tr>
<td>Visceral efferent nerve</td>
<td>Visceral efferent nerve</td>
</tr>
<tr>
<td>Somatic afferent nerve</td>
<td>Somatic afferent nerve</td>
</tr>
<tr>
<td>Visceral afferent nerve</td>
<td>Visceral afferent nerve</td>
</tr>
<tr>
<td>Sympathetic</td>
<td>Sympathetic</td>
</tr>
<tr>
<td>Neuromere</td>
<td>Neuromere</td>
</tr>
<tr>
<td>Vertebrae (occipital)</td>
<td>Vertebrae</td>
</tr>
<tr>
<td><strong>II. Differences</strong></td>
<td></td>
</tr>
<tr>
<td>Aortic arch</td>
<td>None</td>
</tr>
<tr>
<td>Visceral cleft</td>
<td>None</td>
</tr>
<tr>
<td>Epibranchial sense organ</td>
<td>None</td>
</tr>
<tr>
<td>Visceral skeleton</td>
<td>None</td>
</tr>
<tr>
<td>None</td>
<td>Kidney tubule</td>
</tr>
</tbody>
</table>

It is, therefore, evident that head and trunk segments in vertebrates are fundamentally similar. To prove this comparability it is not necessary to demonstrate that there are no differences in regions which are so highly specialized, since the observed differences might arise through adaptive modification of parts originally alike. The most convincing evidence of head metamerism is that manifested in the mesodermal somites of anamniote embryos.
There appear to be four or five prootic metameres. The number of metaotic segments varies in different vertebrates, depending on the number of occipital vertebrae added. In elasmobranchs five or six have been counted. From this evidence of metamerism in both head and trunk region of vertebrates, most morphologists conclude that vertebrates have evolved from metameric ancestors. Such a metameric ancestor is best represented today by amphioxus. But, like vertebrates, amphioxus is a chordate. Were the ancestors of chordates metameric animals? Does the metamerism of amphioxus warrant the inference that chordates have evolved from metameric ancestors like the annelids? Or is the metamerism of chordates and annelids a convergent character? The discussion of the head problem thus leads to that of the ancestry of vertebrates.
CHAPTER 16

THE ANCESTRY OF THE VERTEBRATES

The histories of the various vertebrate organs, as set forth in this text, may seem to involve certain inconsistencies. Nematodes, for example, appear in the account of the digestive system, but are not mentioned in describing the phylogenesis of the nervous system. Similarly, in discussing the excretory system of vertebrates, that of annelids is significant, while for the phylogenesis of the nervous system that of annelids may have no meaning. The gonadic sacs of nemerteans may be genetically related to the coelomic segments of vertebrates while it is difficult, if not impossible, to compare their muscles with those of chordates.

Clearly then, for the genesis of one system of vertebrate organs, the condition in one group of invertebrates may be most enlightening, while for another system some quite different group may reveal the ancestral relations. This implies the paradoxical notion that a particular vertebrate phylum may be "ancestral" to the vertebrates for one set of organs but not for another. It is as if each set of organs were an independent variable in the evolution of the various phyla. For this reason, morphologists have ceased searching for a single common ancestor of all chordates.

None of the several species of prehistoric men—Java, Sussex, Peking, Neanderthal—appears to be directly in the line of ancestry of Homo sapiens. None is "the missing link." None the less they serve to bridge the gulf which separates man from his mammalian relatives. One fossil type has retained certain characteristics possessed by the common ancestor of both itself and Homo sapiens, which Homo sapiens has lost. Another fossil type has retained a different feature. All throw some light on the hypothetical course of evolution of modern man. All are near the ancestral line. None is completely on it. Their relations must, therefore, be expressed graphically by a branching diagram.

One may, then, in considering both human origins and the larger problem of vertebrate ancestry, draw quite wrong conclusions, unless one keeps always in mind what is meant by "ancestor" or "ancestral stage," noting always that a group may become greatly specialized along one or more lines, while it retains in other organs primitive and ancestral traits. When, therefore, one speaks, for example, of an annelid stage of vertebrate ancestry, this should not be understood to mean that any vertebrate ancestor ever was, in all respects, a typical annelid, or that any annelid stands in the direct line of vertebrate descent. All that is
meant is that annelids retain certain traits which more or less closely match those which the ancestors of vertebrates are thought to have possessed. Since, then, a group treated as ancestral may resemble an ancestor in one respect, but depart widely from the ancestral condition in others, the conventional family tree may be misleading, unless it is
clearly understood that the so-called ancestors are near, not on, the family line.

In such a phylogenetic series or family tree for vertebrates, morphologists agree that protozoa and coelenterates are near the root. In addition nearly all are convinced that in many respects flatworms lie near the main line of ancestry. Great diversity of opinion, however, prevails in regard to the groups which may be thought to link flatworms to vertebrates. There is great uncertainty, even, as to the group which may be considered as immediately ancestral to vertebrates.

Among the immediate precursors of vertebrates have been included arthropods, annelids, urochordates, hemichordates, cephalochordates, and even the trochophore larva of annelids. The evidence which has been advanced by the proponents of these various theories may be briefly summarized.

**ANNELID THEORY**

Since vertebrates are strikingly metameric, it is not surprising that early speculations generally assumed that vertebrates have descended from metameric invertebrate ancestors. Saint Hilaire (1822) sought to derive vertebrates from insects. The necessity of reversing the upper and lower sides of the arthropod in order to bring the nervous system on the dorsal side as in vertebrates has not deterred morphologists from making such comparisons.

As phylogenetic speculation became more restrained, however, the origin of vertebrates from such highly specialized forms as insects began to seem less probable. Biologists, therefore, sought for more generalized invertebrates as hypothetical ancestors. To some, annelids seemed to meet the necessary requirements. Delsman, a recent supporter of the annelid hypothesis of vertebrate ancestry writes, (1922) “Hardly two of the great subdivisions or phyla of the animal kingdom show such a close agreement, even in the details of their structure, as annelids and vertebrates, and in no other case can the structure of one be derived so completely from that of the other.”

In 1875, Semper and Dohrn attempted independently to demonstrate the origin of chordates from annelids.

Both annelids and chordates are coelomate and metameric; both elongate by means of terminal growth; circulatory and urogenital systems are fundamentally similar; resemblances of nervous and muscular systems may be found; and the differences between annelids and chordates may be interpreted as coenogenetic.

The reversal of upper and lower sides necessary to convert an annelid into a vertebrate is not regarded by supporters of the theory as a serious difficulty. They point to the fact that some animals swim either side
up indifferently, and that dorsal and ventral sides may be reversed in
relation to the earth in different genera of the same phylum. Among
crustaceae for example many phyllopods swim with the neural side upper-
most. This is the normal position of most adult cirripeds. Amphioxus
in swimming maintains no fixed orientation of its body in relation to
gravitation.

The main supports of the annelid hypothesis are found in metamerism,
terminal growth, and the circulatory and urogenital systems. Both
annelids and vertebrates have dorsal and ventral longitudinal blood
vessels, interconnected around the pharynx by aortic arches. If the
dorsal and ventral sides of the annelid are reversed, the flow of blood is
similar, and the contractile dorsal vessel of the worm becomes the heart
of the vertebrate. The heart of amphioxus and that of vertebrate
embryos is, as would be expected from the annelid theory, a median
longitudinal tube. In both phyla, similar visceral and somatic vessels
occur. The cardinal veins of chordates, however, are wanting in annelids.

Semper, in supporting the annelid theory, laid great stress upon the
similarity of segmental tubules in annelids and chordates. The pro-
tonephridia of amphioxus are identical with those of annelids, and the
coelemoducts of annelids resemble the renal tubules of vertebrates
both in development and in metameric relations. Some annelids have
both nephridia and coelemoducts in the same metamere. Apparently,
nephridia have persisted in cephalochordates and coelemoducts in verte-
brates. The failure of earlier morphologists to recognize the difference
between nephridia and coelemoducts should, therefore, not prejudice
the case against the annelid theory.

The presence of a longitudinal collecting duct, into which the nephridia
open in such annelids as allolobophora, has been cited as evidence in
support of the annelid theory. Superficially this collecting duct might
seem to resemble the primitive duct of vertebrates. But the resemblance
is misleading, since the collecting duct of annelids is ectodermal in origin,
while the primitive duct of vertebrates is mesodermal. The two ducts,
therefore, cannot be homologous. The evidence, instead of supporting
the annelid theory, actually weakens it, since it shows that structures not
genetically related may closely resemble one another. In other words,
this evidence appears to favor the alternative theory that the resemblances
between annelids and chordates illustrate the principle of convergence.
If the ectoderm of annelids and the mesoderm of vertebrates can produce
organs so similar in form and function, we are impressed more by the
plasticity of organisms than by their genetic relationship.

On the other hand, the gonads of annelids and chordates appear to be
comparable. But there are no facts which invalidate the assumption
that the gonads of annelids and chordates have evolved independently
from the gonadic sacs of flatworms. The metamerism which is so characteristic of the gonads of amphioxus is lost in vertebrates.

The attempt has been made to compare the mesodermal bands of annelids and chordates. These in annelids arise from a pair of teloblastic cells located in the posterior end of the body. In amphioxus, which is usually taken as the prototype of chordate development, the anterior portion of the mesoderm arises as an outpocketing of the primary endoderm. A similarity of origin is, therefore, not easily demonstrated. It is true, however, that the mesoderm of annelids and of amphioxus undergoes a similar total segmentation into a series of metameric divisions. The coelomic cavity of amphioxus is primarily connected with the enteron and is therefore an enterocoele, while that of annelids is not. It must be admitted that the case for the annelid theory is not greatly strengthened by the study of the mesoderm.

One of the most striking contrasts between annelids and chordates is afforded by the notochord. If chordates are the descendants of annelids, it is necessary to assume either that the notochord is a novelty or that an homologous structure is present in annelids. Some morphologists prefer the first alternative. Others assume that the notochord has developed from the "Faserstrang" of annelids, which is a bundle of connective tissue fibers extending along the ventral nerve cord. Both nerve cord and faserstrang are enclosed in a common connective tissue sheath. Histologically, however, there is little resemblance between faserstrang and notochord, and there is no evidence of similarity in development.

The annelid theory throws no light upon the origin of either the cartilaginous or the bony skeleton of vertebrates.

The absence of gill-slits in annelids and their presence in chordates has led to considerable speculation on the part of supporters of the annelid hypothesis. The most plausible guess as to their origin has been that gill apertures have arisen from paired diverticula of the pharynx, which reached the skin and became perforated. It has also been suggested by Dohrn that nephridia have been converted into gill-slits by the attachment of their inner ends to the pharynx, and subsequent shortening. The elongated tubular ectodermal passages of the gills of myxinoids have been mentioned as evidence in support of this assumption. Since, however, the gills of cyclostomes are wholly endodermal, and since in all vertebrates the development of gills is initiated by endodermal pouches, the suggestion that ectodermal nephridia have been converted into gill-slits seems quite incredible. It is true, however, that the ectoderm is not wholly passive in the development of gills, and that in fishes the ectoderm participates in the formation of internal and external gills, but this evidence by no means justifies the supposition that nephridia have been converted into gills.
Some supporters of the annelid hypothesis compare the external gills of fishes and amphibia with the filamentous gills attached to the parapodia of annelids. To convert these into internal gills, it is assumed that they wander into the openings of the nephridia. Most suggestions of this sort are couched in Lamarckian terms which make little appeal to the morphologists of this generation.

Dohrn (‘75) and Marshall (‘79) regard the olfactory pits of vertebrates as the anteriormost pair of pre-oral gill-pouches, and hence unlike any structures in annelids. Balfour (‘81) and Gegenbaur (‘87), however, opposed the assumption that olfactory pits are gill-pouches, on the ground that olfactory pits are ectodermal, while gill-pouches are endodermal. Advocates of the annelid hypothesis are inclined to compare the olfactory pits of vertebrates with a pair of ciliated pits located in the dorsal half of the prostomium of annelids. With a reversal of surfaces, the pits would be brought into their definitive position on the ventral side of the snout of fishes.

Eisig (‘87) believed that the lateral line organs of vertebrates are represented in annelids by certain sense-buds found in capitellid worms. These sense-organs are metamERICALLY arranged in annelids as are the lateral line organs of teleost embryos. Their structure is also similar. Their innervation, however, is different, for lateral line organs are innervated by cranial nerves which extend through many metameres, the segmental sense organs of annelids by segmental nerves. To explain this difference, it is assumed that a collector nerve, which originally connected the segmental nerves of the trunk, has become the lateralis branch of the vagus nerve. The epibranchial ganglia of vertebrates are supposed to be comparable with the lateral or parapodial ganglia of annelids, which have been preserved only in the head region of vertebrates.

The intestinal muscles of annelids are arranged like those of chordates in circular and longitudinal layers. The resemblances of the somatic muscles is not so striking. Except possibly in the gill region, the circular muscles of annelids are lacking in chordates. Annelids have longitudinal metameric muscles on both dorsal and ventral sides of the body. In the trunk region of chordates, muscles are primarily lacking in the ventral half of the body; but are secondarily supplied by migration from the dorsal side. Acceptance of the annelid theory, therefore, makes it necessary to assume that the dorsal muscles of annelids have disappeared in the course of phylogenesis.

Some morphologists regard the transient neuromeres of vertebrate embryos as evidence in favor of the annelid theory, and interpret neuromeres as remnants of the segmental ganglia of the annelid nerve-cord. It has, however, not been demonstrated that neuromeres are metameric structures. Serial repetition of structures does not demonstrate that
they are metameric in the strict sense of the word metameric. The reliability of neuromeres as criteria of metamericism rests upon the assumption that vertebrates come from metameric ancestors like the annelids. Those who hold this view explain the absence of neuromeres in amphioxus as the result of degeneration. There is, however, a suspicion that we have here another instance of reasoning in a circle. Until we have a more general agreement among students of neuromerism in regard to the existence of neuromeres in the trunk region, their presence in the hind-brain region does little to strengthen the belief in the annelid ancestry of vertebrates.

It has generally been assumed by advocates of the annelid hypothesis that annelids are derived from non-metameric ancestors like the flatworms and actinians. The protonephridia of annelids resemble those of flatworms. In some ways the trochophore larva of annelids resembles a flatworm. The mesenchyme of the larva is comparable with that of the flatworm, and the coelomic cavities of the adult may be compared with the gonadic sacs of nemerteans. The flatworms in turn may be derived from the actinian by the partial union of the borders of its slit-like mouth. By the persistence of the anterior and posterior portions of the actinian mouth after the intermediate region had united, the mouth and anus of the ancestor of annelids, it is assumed, were formed. In this way, the nerve-ring which surrounded the mouth of the actinian would be brought into the relations characteristic of annelids.

Objections to the Annelid Theory. One of the fundamental difficulties which has turned some biologists away from the annelid theory is the difference in the fate of the blastopore in annelids and chordates. Indeed, had this difference been known when the annelid hypothesis was first promulgated, it is doubtful whether the theory would have seemed so plausible. It was Goette who, in 1895, first found the difference in the fate of the blastopore an insuperable objection to the annelid theory. Comparison of annelid and chordate is difficult, if not impossible, Goette says, since in annelids the blastopore becomes, at least in part, the mouth, while in chordates it becomes the anus, or lies near the anus. It was this difference which led Grobben to classify animals into two great groups, Protostomians and Deuterostomians. If this evidence has the weight which it seems to have, the separation of annelids and chordates occurred long before either of their adult types of organization had appeared, possibly even before such an organism as a trochophore larva emerged from a coelenterate ancestor.

To meet this objection, supporters of the annelid hypothesis minimize the importance of the fate of the blastopore and assert that even in different genera of the same phylum the fate of the blastopore may differ, so that its fate cannot have a phylogenetic significance.
Another objection raised against the annelid hypothesis has been the impossibility of comparing the mouth of the annelid with that of the vertebrate. The acceptance of the annelid hypothesis makes it necessary to assume that the transformation of the annelid into the vertebrate has involved the loss of the annelid mouth and the formation of a new mouth ventral to the nervous system.

Leydig, in 1864, was the first to suggest that the esophagus formerly passed through the vertebrate brain in the region of the fourth ventricle, between the crura cerebri. The late appearance of the mouth in the vertebrate embryo has been interpreted as supporting this assumption. Dohrn (1875) pointed out the fact that the embryo of a vertebrate is almost completely formed, that all other organ systems are developed, and that circulation has begun before the mouth opens, while in invertebrates the mouth is one of the first organs formed. To some morphologists, however, there appears to be insurmountable difficulty in assuming that the gut of vertebrates once pierced the brain, either in the region of the infundibulum or between the crura cerebelli. Of such a relation, ontogenesis affords not the slightest evidence.

To meet this difficulty, Beard 1888 assumed that when the annelid became a vertebrate the supra-esophageal ganglion disappeared, so that the nerve cord came wholly from the ventral cord of annelids. The assumption that the esophagus of vertebrates once pierced the nerve cord was thus rendered unnecessary.

Speaking of the annelid hypothesis, Minot (1897) says, "As regards the head, however, even theories have hitherto failed us, and no hypothesis as to the evolution of the vertebrate head from the annelidan type has been brought forward, which could not be shown to encounter insuperable objections, or at least which appeared insuperable to those who were opposed to the annelid theory."

As his contribution of the solution of this problem, Minot suggested that, in the evolution of a vertebrate, the paired lobes of the supra-esophageal ganglion of the annelid failed to unite in the median plane, and were converted into the lateral eyes of vertebrates. "We are thus led to the supposition that eyes and optic nerves represent in vertebrates the supraesophageal ganglia and the esophageal commissures of the articulates." Thus, according to Minot, the brain of vertebrates arose from the subesophageal and adjacent ventral ganglia of the annelid. Its enlargement would cause the brain to expand forward and carry the mouth to a new position on the hemal or heart side, and at the same time prevent the eyes and preoral ganglia from meeting in the median line and force the visual organs into lateral positions. "We thus reach a natural and simple explanation of the difference between the annelid and vertebrate head." Minot stresses the similarity of the ectodermal invagi-
nation which forms the mouth in annelids to the ectodermal hypophysis in cyclostomes.

Minot’s hypothesis involves three assumptions:
1. The preservation of the ectodermal stomodeum of annelids as the naso-hypophysial invagination of vertebrates.
2. The formation of the vertebrate brain from several of the post-oral ganglia of the ventral chain.
3. The conversion of the visual apparatus and supra-esophageal ganglia, which are prevented from fusing in the median line by the enlargement of the vertebrate brain, into the vertebrate retina, the esophageal commissures persisting as optic nerves. In Minot’s opinion, this hypothesis obviates those difficulties of the Dohrn-Semper annelid theory which at present are the most serious. He explains the absence of eyes in amphioxus as the result of degeneration. Concerning the failure of embryology to confirm his speculations Minot is silent.

Fig. 521.—Diagrams of A, Annelid, B, Acraniote, C, Craniote. According to Delsman the ectodermal stomodeum of annelids is converted in vertebrates into the neural tube. Amphioxus is a transitional form between annelids and vertebrates. The blastopore of annelids becomes the neurenteric canal of chordate embryos. (Redrawn after Delsman slightly modified in lettering.)

DELSMAN’S THEORY

A modified annelid hypothesis has been advanced by Delsman (1913), not, however, as an attempt to render the views of Dohrn and Semper acceptable, but as an entirely new theory which grew out of embryological researches on invertebrates. The gist of Delsman’s theory is that the neural tube of vertebrates was originally a part of the alimentary canal of invertebrates and that it corresponds to the ectodermal stomodeum of invertebrates such as the annelids.

Kowalewsky (1877) was the first to suggest that the neural tube may originally have functioned as a part of the digestive system. Sedgwick
(1884) accepting this hypothesis assumed that the neural tube originated in animals as a dorsal groove which secondarily became converted into a canal opening into the archenteron. Van Wijhe (1884) reached independently the same conclusion, but assumed that the neural tube may have functioned as an ingress for food and as an outlet for wastes. T. H. Morgan (1890) has supported this view.

Delsman finds many points of agreement between the medullary tube of chordate embryos and the stomodeum of Protostomians. In the development of both groups, the border of the blastopore, originally wide and large, contracts to a very narrow opening, the definitive blastopore. In both annelids and chordates, there is formed, in connexion with the blastopore, a tube of ectodermal origin, which at one end opens to the exterior, and at the other end leads to the archenteron. In annelids this ectodermal tube is the stomodeum, the outer opening being the mouth, the inner the "cardiac pore" which is the opening of the stomodeum into the annelid stomach. In chordates the ectodermal tube is the neural tube with its neuropore and neurenteric canal. The fundamental similarity of the relations in the two groups is obscured by the fact that the "cardiopore" of the annelid lies at the anterior end of the enteron, while the neurenteric canal of chordates lies at the posterior end.

As additional proof of the comparability of chordates and annelids, Delsman calls attention to the fact that the stomodeum of annelids, like the neural tube of a young amphioxus, is ciliated. Morgan ('90) has found that the neural tube of frogs is ciliated. Delsman sees significance in the fact that "while all other developmental processes of segmented animals proceed from in front backwards, the formation of the neural tube in lower chordates has its starting point at the blastopore and proceeds in a forward direction."

If we assume that in chordates the stomodeum of invertebrates has become elongated so as to carry the "cardiac pore" backwards to the hinder-end of the body, the agreement between stomodeum and the embryonic neural tube becomes almost complete. Delsman asserts that in ontogenesis of vertebrates the backward shifting of the blastopore is quite evident. Thus the conditions arise which necessitate the formation of a new mouth. That the definitive vertebrate mouth is a new mouth is almost universally agreed.

"The primary mouth, being that of annelids," says Delsman, "is represented by the neuropore of amphioxus, and this itself again is phylogenetically secondary in respect to the "Urmund," the mouth of the hydroid polyps, which in annelids we find again in the cardiac pore, and in chordates in the neurenteric canal, both representing the former blastopore. Thus in the ontogeny of vertebrates we see the three successive mouths appear in the same succession as they appeared in phylo-
geny: the blastopore (‘Urmund’), the neuropore (the Annelidan mouth), and finally the definitive vertebrate mouth.”

In deriving the neural tube of vertebrates from a part of the alimentary canal of pre-chordates, Delsman’s theory may appear to resemble that of Gaskell, which derives the ependymal lining of the neural tube from the intestine of arthropods. The similarity, however, is superficial. Gaskell’s theory assumes that the entire alimentary canal of the arthropod becomes the lining of the neural tube, so that an endodermal structure is converted into an ectodermal one. Delsman’s hypothesis holds that only a part, and that an ectodermal part, of the invertebrate intestine becomes the chordate neural tube.

The conditions under which an ectodermal stomodeum might be converted into a neural tube have been stated by H. E. Ziegler (1908). If we start with a gastrula, he says, we must assume that it was primarily nourished through the blastopore. The ciliated dorsal or neural plate swept the food towards the blastopore, and consequently might have acquired the function of a sensory epithelium. As the sensory plate was converted into a neural tube, the stream of water entered the neuropore and was carried through the neurenteric canal to the enteron. Then came the formation of an anus, and later that of the definitive mouth and gill slits. The neuropore and neurenteric canal became superfluous and disappeared. Thus the neural tube, which had acquired a sensory function, became exclusively nervous and served as the central nerve cord.

In support of this speculation of Ziegler, Delsman calls attention to the fact that in some gastropods the buccal ganglia of the nervous system are derived as a proliferation of the stomodeum.

Others also have been impressed by the evidence that the neural tube was formerly a part of the digestive system. Huntsman (1913) writes, “It may be noticed that the condition in the tunicate strongly supports the view that the neural tube was originally not nervous but a part of the digestive system.”

In agreement with most supporters of the annelid hypothesis, Delsman compares the ventral side of the annelid with the dorsal side of the chordate. But, if the stomodeum of the annelid forms the nerve cord of chordates, then what becomes of the chain of nerve ganglia of the annelid when transformed into a chordate? According to Delsman, the annelid ganglia are represented in the dorsal ganglia of vertebrates. These are formed, as would be expected, between the stomodeum and the skin in annelids, and in chordates from the neural crest. The fact that the ganglia of chordates are purely sensory, while those of annelids contain motor cells, is an objection to this homology which Delsman has attempted to meet. He points out that dorsal nerves in chordates are primarily mixed in function, and that the motor cells of the sympathetic ganglia are
mostly, if not exclusively, derived from the dorsal ganglia. Hence the possibility should not be denied that the ganglia of annelids and chordates are homologous.

The fact remains, however, that the chordate basis for a reflex action is the spinal cord and not the spinal ganglia. Consequently, the acceptance of the Delsman hypothesis compels us to assume that the reflex system of invertebrates has been lost, and a new reflex system invented when annelids became chordates. The seriousness of this difficulty seems not to have been fully appreciated by Delsman.

With Hatschek (1878), Delsman suggests that both the dorsal longitudinal musculature and the circular muscles of annelids have disappeared in the metamorphosis of the annelid into the chordate. But he thinks that the transverse muscle of amphioxus may correspond to the circular muscle of annelids, although their position is not similar.

The double muscular innervation, sensory and motor, demonstrated by Boeke (1911) in vertebrates is also found in annelids (Fraipont 1884).

The absence of an ectodermal foregut in vertebrates, Delsman takes to accord with expectation, if his theory is a correct one.

Delsman derives the lateral eyes of vertebrates from the pit-eyes of the preoral lobe of annelids. This conclusion, he thinks, is supported by the embryological evidence that vertebrate eyes appear as pigmented depressions of the neural plate in the region of the forebrain previous to its closure. He assumes with Balfour (1881) that the forebrain of vertebrates originates from the preoral lobe of annelids and amphioxus. The preoral lobe or episphere of the trochophore larva contains paired pigment spots which Delsman thinks can be traced into the paired eyes of vertebrates. A step in the vertebrate direction is taken by those annelids in which the pit-eyes become vesicular eyes. The absence of eyes in amphioxus is interpreted, in agreement with Ray Lankester (1880) and many others, as a result of degeneration. Delsman holds that vertebrate eyes became secondarily included within the brain and, as the animal became more opaque, grew out towards the skin. If, then, the prechordal part of the vertebrate embryo is the homolog of the preoral lobe of amphioxus, the prechordal forebrain and the eyes, would, according to Delsman, be derived from the same source which in annelids gives rise to the cerebral ganglia and the eyes. The otic vesicles of some annelids are paired organs lying just behind the mouth, in a position which corresponds to that of the otic vesicles of vertebrate embryos.

Hatschek (1908) defended the assumption that the infundibulum of craniotes represents the anterior boundary of the acraniote brain. But Hatschek thought that the prechordal portion of the vertebrate brain is an outgrowth from the epichordal region. This is not Delsman's view. Delsman assumes a forward extension and incorporation of ecto-
derm in front of the notochord. Consequently, Delsman stresses the contrast between a prechordal archencephalon and an epichordal deuterenencephalon. In early stages of vertebrate ontogenesis, the contrast between the two regions is very evident. The line of demarcation between the two is the plica ventralis which, according to Gegenbaur ('72), indicates the limit between the segmented "vertebral" and the unsegmented "prevertebral" part of the skull. Thus it follows, thinks Delsman, that the brain vesicle of Amphioxus is to be compared with the deuterenencephalon of the vertebrate brain.

The similarity of larval amphioxus and annelid is seen in the relations of the mouth of the annelid and the neuropore of larval amphioxus. Both openings lie just posterior to the preoral lobe and just in front of the first mesodermal segment.

Delsman regards the anterior endodermal diverticula of amphioxus as the anteriormost pair of gill pouches, and assumes that the mesoderm of the preoral lobe, like that in annelids, is formed by the forward extension of the first myotome. Thus the mesoderm of the preoral lobe is, he concludes, secondary.

The notochord of amphioxus ends primarily at the level of the neuropore, while in vertebrates the forebrain lies anterior to the notochord. Hence it follows, according to Delsman, that the forebrain of vertebrates has been formed from the ectoderm of the preoral lobe of amphioxus.

Delsman appears to think that comparison of annelid with vertebrate, and more particularly the homology of the annelid mouth with the neuropore of amphioxus, compels him to deny metameric in the preoral region and to assume that the mandibular segment with the prostomium form not two segments but a single segment. Thus the anterior endodermic diverticula of amphioxus become gill-pouches and not mesodermal somites. Consequently, the series of three divisions which form the "brain" of annelids have not the value of segmental ganglia and do not represent as many segments. The trigeminus to him becomes a single nerve, the first somatic, which belongs with the mandibular segment. The definitive vertebrate mouth is assumed to be a fused pair of gill-slits.

Objections to the Delsman Hypothesis. Since Delsman assumes that amphioxus is intermediate between annelids and vertebrates, he is confronted with the difficulty of explaining the absence of well-marked spinal ganglia in amphioxus, in which they should be more evident than in vertebrates. He attempts to meet this difficulty by assuming that either the ganglia of amphioxus have fused with the neural tube, or have been lost by degeneration, as the cerebral ganglia have been lost.

Another difficulty arises out of the development of the neural tube. From the standpoint of the Delsman hypothesis, we might expect the neural tube to arise as a tubular invagination of the ectoderm, afterwards
lengthening from in front backwards, and thus pushing its inner end and the former blastopore under the neural body-wall to the caudal end of the embryo. This is not the case, as Delsman himself points out. But, he claims, processes which occur in early development serve to explain why the neural tube does not elongate in this fashion. The backward growth of the blastopore in vertebrate embryos involves the extension of the neural plate caudad. According to Delsman this is not a process of concrescence, as is sometimes assumed, but a true process of backward growth. This precocious backward growth takes the place of the backward elongation of the neural tube. The result is the same as if there had been an elongation of the neural tube—the blastopore is carried to the posterior end of the body, where it persists for a while as the
neurenteric canal of the embryo. The facts of ontogenesis, therefore, according to Delsman, support his theory that the neural tube is the homolog of the stomodeum of annelids. (Fig. 55)

In one of his preliminary papers, Delsman (1913) makes a suggestion of vertebrate ancestry which will appeal to some who remain unconvinced by the theory just outlined. This suggestion is that the characteristic differences which separate phyla, such as the chordates, annelids, and molluscs, may have arisen by changes in the region of growth by which a larval form like the trochophore is converted into an adult. Morphology has tended to lean heavily upon evidence from comparative anatomy for phylogenetic conclusions, especially in the absence of decisive paleontological evidence. But the growing conviction that evolutionary progress has been dependent primarily upon changes in the chromatin of germ cells has made speculations which assume the evolution of one phylum from another by the transformation of highly differentiated adults seem less probable than they did to earlier morphologists. The suggestion that three great phyla may have arisen from a simple larval form like a trochophore, therefore, sounds attractive. Delsman suggests that, just as the elongated annelid develops from the trochophore by the elongation of the region posterior to the blastopore separating mouth and anus as far as possible from one another at opposite ends of the body, precisely so molluscs and chordates may have originated from a trochophore-like ancestor by change of the growth center. Most molluscs grow, not antero-posteriorly, but dorsally. In them, the mouth and anus remain relatively near one another, while an elongated dorsal sac is formed, in which the intestine and liver are bent into a U-shaped tract. Again, by the elongation of the region anterior to the blastopore so as to separate this from the anterior end of the body, a chordate form like the larval amphioxus is produced. Such assumptions as these avoid the pitfalls which are met in attempts to convert a complex adult of one phylum into that of a different phylum. Furthermore, they seem to accord with recent discoveries in genetics and embryology. If, then, this suggestion of Delsman is actually in accordance with the facts of ontogenesis, it follows that the divergence of the chordate phylum from the other invertebrate phyla, occurred before the annelid phylum made its appearance. But Delsman himself appears to have abandoned his attempt to derive chordates and other phyla from a trochophore larva and to favor the opinion that the adult annelid is in the direct line of chordate ancestry. (Figs. 521, 523)

THE ARTHROPOD THEORY

The old theory of Geoffrey St. Hilaire (1822) that an arthropod might be converted into a vertebrate by reversing dorsal and ventral sides and
acquiring a new mouth has, in more recent years, been espoused by two distinguished biologists, Gaskell (1908) and W. Patten (1912), who have followed the comparison of arthropods and vertebrates into greater detail than has been done by other students of vertebrate phylogensis. Both lean heavily upon paleontological evidence. Both assume that evolutionary change occurs through the transformation of one dominant group into a higher dominant group. Both authors assume that the most highly differentiated types of invertebrates such as the arachnids are the progenitors of the vertebrates, contrary to prevalent opinion which assumes that evolutionary change has affected chiefly generalized types.

It is significant that the two reach fundamentally different conclusions as to the most primitive types of vertebrates. These, according to Gaskell, are the cyclostomes, while Patten regards the ostracoderms as the immediate descendents of the sea scorpions. Both succeed in finding an amazing degree of resemblance between limulus and a fish, and present a great mass of evidence to prove this similarity. This resemblance, however, seems to be more for the details of anatomical structure than for fundamental characteristics.

Both authors agree that hemichordates, urochordates, and cephalochordates are degenerate, not ancestral types. Both assert that the comparative anatomy of the central nervous system affords the strongest structural evidence of the similarity of arthropods, and more especially arachnids, with vertebrates.

**Gaskell's Hypothesis**

According to Gaskell the neural tube of chordates is derived directly from the alimentary canal of arthropod ancestors. The ventricles of the vertebrate brain, Gaskell asserts, have evolved from the cavity of the cephalic portion of the arachnid stomach. Their ependymal lining corresponds to the mucous lining of the arthropod stomach. Differences in their germ-layer origin do not disturb Gaskell, who is a physiologist! Gaskell finds the brain of both scorpions and vertebrates to consist of three chief divisions, forebrain, midbrain, and hindbrain. The constrictions which separate these represent ontogenetically two nerve commissures, which cross the cephalic stomach in the prevertebrate stage, as the result of the mid-dorsal position of the pineal eyes and of the insertion of the superior oblique muscle. The anterior of the two is the commissure between the two supra-esophageal ganglia. The anterior end of the cephalic stomach of the arthropod becomes the lamina terminalis of the vertebrate brain. The evolution of the vertebrate brain from that of the arthropod is the result of the growth and extension of nervous material, which was originally ventral to the stomach, around
and over the epithelial wall of the cephalic stomach. (See Fig. 524.) The presence of neuromeres in the brains of embryonic arthropods and vertebrates is taken as another point of similarity between the two phyla.

According to Gaskell, the great enlargement of the brain in arthropods made necessary a new mouth. Just before vertebrates appeared, the arthropods were in a "terrible dilemma." They were compelled to choose between the capacity for taking in food without intelligence to capture it, or intelligence sufficient to capture food and no power to consume it. The enlargement of the brain, through which the esophagus passed, meant the strangulation of the esophagus, while the atrophy of the brain meant degeneration. Only a new intestine would solve the problem. But since the skin cells of arthropods and cyclostomes have been shown to have digestive powers, there is to Gaskell no more difficulty in getting a new digestive system from the skin than there is for an animal to gain a new respiratory or circulatory system. All of this sounds teleological, but is probably not intended to imply conscious purpose on the part of the animal.

As the result of the changes which occurred, the anterior ganglia of the arthropod formed the cyclostome brain and their cephalic stomach became the ventricles and ependymal lining of the brain, while the intestine and nerve cord became the tubular spinal cord.

Gaskell believes that the assumption that cyclostomes are degenerate forms is not substantiated by the evidence. The transformation of the
Fig. 525.—Diagrams illustrating the hypothetical evolution of the vertebrate brain from the nerve cord of a primitive arthropod such as Branchippus (fairy shrimp). Supraoesophageal ganglia are shown in solid black, prosomatic ganglia stippled, mesosomatic cross-hatched. A, olfactory nerve; B, optic nerve; C, nerve to median eye; P, prosomatic nerves; M, mesosomatic nerves. (Redrawn after Gaskell.)
ammocoetes larva into petromyzon proves that the animal is not degenerate. The resemblance of limulus and ammocoetes is attested by many anatomical details. Both, for example, have two lateral and two median eyes.

In agreement with many morphologists, Gaskell traces arthropods back to an original coelenterate stock in which the central nerve cord consists of a ring of nervous material which surrounds the mouth or the umbrella. By the union of the two halves of the coelenterate umbrella along a median line, the bilaterally symmetrical worm is formed. The phylogenetic series then leads through annelids to arthropods. But, as a consequence, the arthropod esophagus pierces the central nerve cord, and divides it into a supraesophageal and a subesophageal ganglion. Certain details of resemblance between annelids and vertebrates, such as coelom, metamerism, coelomoducts, aortic arches, etc., have led to the attempt to derive vertebrates directly from annelids. Since, however, the central nerve cord of annelids is ventral while that of vertebrates is dorsal, the annelid hypothesis of vertebrate ancestry necessitates the reversal of dorsal and ventral sides of the body, and a new ventral mouth to replace the old one which by reversal has been carried to the dorsal side. In Gaskell's opinion "the difficulties in the way of accepting such reversal of surfaces have proved insuperable." By imagining the enclosure of the arthropod stomach and intestine by the nerve cord and the migration of the two towards the dorsal side, Gaskell seeks to avoid the necessity for such reversal of surfaces. The necessity for a new mouth, however, cannot be escaped, and his solution of that problem will be stated later.

It is, however, obvious that changes such as are postulated by Gaskell might quite as readily take place in annelids as in arthropods. Gaskell's reason for deriving vertebrates from arthropods is the higher development of the arthropod brain.

Gaskell writes: "If there is one organ more than another which increases in complexity as evolution proceeds, which is the most essential organ for upward progress, surely it is the central nervous system, especially that portion of it called the brain. This consideration points directly to the origin of vertebrates from the most highly organized invertebrate group—the Arthropods—for among all the groups of animals living on the earth in the present day they alone possess a central nervous system closely comparable with that of vertebrates. Not only has an upward progress taken place in animals as a whole, but also in the tissues themselves a similar evolution is apparent, and the evidence shows that the vertebrate tissues resemble more closely those of the arthropod than of any other invertebrate group."
"The evidence of geology points to the same conclusion. Evolution takes place from one dominant stock to another dominant stock—man from mammals, mammals from reptiles, reptiles from amphibia, amphibia from fishes. We are therefore forced to conclude that fishes came from pre-Devonian paleostracan arthropods, the ancestors of crustacea and arachnids. These in turn came from trilobites. The earliest fishes
strongly resemble the paleostracan forms. The limulus or king-crab is a living representative of the paleostracan ancestors of fishes. From such a form vertebrates may have evolved without the necessity of reversal of dorsal and ventral sides. This is possible if we assume that the infundibular tube of the vertebrate brain represents the esophagus of the arachnid, that the vertebrate forebrain is the supraesophageal ganglion, the crura cerebri the esophageal commissures, the remainder of the brain the subesophageal ganglia. The ventricles of the brain correspond to the cephalic stomach of the arthropod. In the arthropod, the cephalic stomach leads directly into the straight narrow intestine; in the vertebrate the fourth ventricle leads into the straight narrow canal of the spinal cord.

"In the arthropod the intestine terminates in the anus; in the vertebrate embryo the canal of the spinal cord terminates in the anus by way of the neurenteric canal. Keep the animal unreversed, and immediately the whole mystery of the tubular nature of the central nervous system is revealed, for it is seen that the nervous matter, which corresponds bit by bit with that of the arthropod, has surrounded to a greater or less extent and amalgamated with the tube of the arthropod alimentary canal, and thus formed the so-called central nervous system of the vertebrate.

"The manner in which the nervous material has invaded the walls of the tube is clearly shown both by the study of the comparative anatomy of the central nervous system in the vertebrate, and also by its development in the embryo.

"This theory implies that the vertebrate alimentary canal is a new formation necessitated by the urgency of the case, and, indeed, there was cause for urgency, for the general plan of the evolution of the invertebrate from the coelenterate involved the piercing of the anterior portion of the central nervous system by the esophagus, while, at the same time, upward progress meant their development; brain development meant concentration of nervous matter at the anterior end of the animal, with the result that in the highest scorpion and spider-like animals, the brain mass has so grown round and compressed the food-tube that nothing but fluid pabulum can pass through into the stomach; the whole group have become blood-suckers. These kinds of animals, the sea scorpions, were the dominant race when vertebrates first appeared; here in the natural competition among members of the dominant race the difficulty must have become acute. Further upward evolution demanded a larger and larger brain with the ensuing consequence of a greater and greater difficulty of food-supply. Nature's mistake was rectified and further evolution secured, not by degeneration in the brain region, for that means degradation and not upward progress, but by the formation of a new food-channel, in consequence of which the brain was free to develop to its fullest extent. Thus the great and mighty kingdom of the verte-
brates was evolved with its culminating organism—man—whose massive brain with all its possibilities could never have been evolved if he had still been compelled to pass the whole of his food through the narrow esophageal tube, still existent in him as the infundibular tube."

As further evidence of the genetic relationships of arthropods and vertebrates, Gaskell points out that eurypterids and limulus, like ostracoderms, have both median and lateral eyes. Furthermore, arachnids, like vertebrates, have an inverted retina, while other invertebrates have
a simple upright retina. The resemblance holds, it is asserted, for the finer histological details of the retina.

Gaskell is much impressed by the evidence of the similarity of the skeletal elements of limulus and ammocoetes. "The evidence of the origin of the cartilaginous skeleton of the vertebrate points directly to the origin of the vertebrate from the Palaeostraca, and is of so strong a character that, taken alone, it may almost be considered as proof of such origin." Branchial cartilaginous bars are found in both. The branchial skeleton of ammocoetes begins where that of the arachnids, represented by limulus, leaves off.

The branchiae of ammocoetes are homologized with the branchial appendages of limulus, which are "sunk-in" during ontogenesis. Since, as a matter of fact, the branchial appendages of limulus are covered with ectoderm, while the epithelial covering of the gills of cyclostomes is endodermal, morphologists find it difficult to accept this homology. Germ layers, however, mean little to Gaskell.

The cranial nerves of vertebrates are identified with those which innervate the branchial appendages.

Gaskell has more difficulty in finding in vertebrates a homologue of the limulus heart. Since the heart of limulus is dorsal, a new heart has to be formed when arachnids become vertebrates. Gaskell assumes, therefore, that a pair of ventral venous sinuses in limulus unite to form a median ventral heart in vertebrates. This change is recapitulated in the ontogenesis of the vertebrate heart. The remnants of the limulus heart are found by Gaskell in the so-called fat-column, which lies dorsal to the spinal cord in ammocoetes but is lacking in higher vertebrates.

Gaskell appreciates the difficulty involved in attempting to derive the heart and circulatory system of a vertebrate from that of an arthropod. He calls attention to the fact that the invertebrate heart is systemic and drives the arterial blood directly to the different organs of the body. But the vertebrate heart is branchial and drives the blood to a ventral aorta from which it is carried to the gills. The distributing systemic vessel of vertebrates is the dorsal aorta, not the heart, which belongs essentially to the ventral venous system. The invertebrate heart is, therefore, not homologous with the vertebrate heart and the vertebrate heart is new.

Gaskell derives the vertebrate thyroid gland from the uterus of the paleostracan ancestor. This homology is made without regard to the fact that the thyroid is endodermal in origin while the crustacean uterus is ectodermal. The endocrinal influence of the thyroid upon the gonads is cited as evidence in favor of this homology.

The hypophysis of petromyzon, with its associated olfactory pits, is compared by Gaskell with the olfactory tube of scorpions. Coelomic
cavities resembling those of vertebrate embryos are found in limulus. Limulus has seven prootic segments, and a similar number should be found in vertebrates—all supplied by the trigeminal nerve. Of these seven segments, the first is represented in vertebrates by Miss Platt’s anterior somite, segments 2 to 5 by the pre-mandibular cavity, 6 and 7 by the mandibular cavity. The chiasma of the trochlearis nerve is explained by the fact that, in scorpions, the homologue of the superior oblique muscle, alone of all the head muscles, crosses the mid-dorsal line to be attached to the other side, carrying its nerve with it.

The tentacles of ammocoetes are assumed to be remnants of the prosomatic appendages of the paleostracan ancestor. The mucocartilage head-shield of ammocoetes is considered to be the exact counterpart of the head-shield of cephalaspid.

Gaskell interprets the flabellum of limulus and the pectens of scorpions as homologues of the auditory organ of vertebrates. The various endocrinal organs of vertebrates—pituitary, thymus, etc.—are assumed to come from the coxal glands of Protostraca, or primitive arthropods, which were the common ancestors of arachnids and crustacea.

Gaskell’s speculations necessitate the invention of a notochord and a new alimentary canal to replace the old one which formed the neural tube. He imagines that among the Protostraca were forms somewhat resembling trilobites but with annelid affinities, which, like Apus, possessed a deep ventral groove extending from one end of the body to the other, and also pleural fingers, as in many trilobites. This groove on the ventral side of the body was converted into a tube, and so gave rise to the notochord, while the appendages were still free and the pleurae had not met to form a new ventral surface. (See Fig. 527.)

Passing from this protostracan to a paleostracan stage, oral and respiratory chambers were formed, not communicating with each other. A ventral groove, however, connected the respiratory chamber and cloaca. Finally, with the conversion of this groove into a tube to form an alimentary canal, the opening of the oral into the respiratory chamber, and the formation of an atrium by the ventralward growth of the pleural folds, the vertebrate was completed. The pharynx was formed by the fusion and concrescence of the crustacean legs, the spaces between the legs becoming gill slits. Because of the digestive power of the epidermis, Gaskell sees no difficulty in converting skin into a digestive canal.

The suggestion that the notochord may have originated as an accessory digestive tube accords with the evidence that it is formed in some vertebrates in connexion with the alimentary canal.

Gaskell asserts that since the germ-layer theory is discredited by embryologists themselves, it may not properly be raised against his theory, which ignores it. Gaskell attacks the germ-layer theory as fallacious.
It asserts that the alimentary canal is homologous in metazoa because it is formed of endoderm. But there is no definition of endoderm except that it is always the layer which forms the definitive alimentary canal. He therefore concludes that the guts of vertebrates and crustacea are not homologous.

There appear to be two fatal objections to the Gaskell arachnid hypothesis of vertebrate ancestry. First, the theory ignores the evidence of the homology of the germ layers, by deriving the neural tube from the alimentary canal. Second, the theory leaves a heart between the pharynx and the nervous system, so that in order to meet this difficulty it is necessary to assume that the crustacean heart disappears and that a new one takes its place. There is, however, no embryological evidence to support this assumption.

It may be further urged against the theory that it pictures the ependyma of the vertebrate neural tube as receiving cellular increments from adjacent tissue to form the nervous tissue of the brain and cord. In ontogenesis, however, the mantle and marginal layers of the neural tube are not formed by additions from without, but by the proliferation of cells of the ependymal layer itself.

Of Gaskell’s theory, Patten, who has an arachnid theory of his own, says: “Gaskell at least makes a valiant fight to save the pieces of the invertebrate nervous system, even if he does annihilate the rest of the animal in the attempt.”

**Patten’s Arachnid Hypothesis**

According to Patten (1912), the structural plan of an arachnid such as limulus and a primitive vertebrate such as an ostracoderm is “all the same,” but the arachnid head and body correspond to the vertebrate head only. Nearly all of the vertebrate body consists of a new generation of metameres, not represented in arachnids. (Figs. 10, 17)

Patten, although agreeing with Gaskell that the vertebrate mouth is new, differs in his explanation of the closure of the old mouth. In Patten’s view, the closure of the old mouth is due to the “conditions created by apical growth, by cephalization, and by the increase in the volume of the yolk sphere.” The new mouth is derived from an ancient arthropod organ known as the “dorsal organ,” which in limulus becomes the “cephalic navel.” What its original significance may be is not apparent.

Patten sees no difficulty in converting the nerve cord of arachnids into the tubular cord of vertebrates. In the brains of both he finds the same five divisions. The resemblance holds good even for their subdivisions and their histological details. He lays much stress upon the numerical correspondence between the neuromeric divisions of the brain described by Locy and Hill and those which he finds in limulus. There are, he
says, thirteen neuromeres in the arachnid brain, but these do not correspond with the number of metameres in the head. Arachnid and vertebrate brains are also in essential agreement in the distribution of the main fiber tracts. The fact that the arachnid has nothing comparable with the vertebrate trunk makes it seem to Patten impossible to compare the

Fig. 528.—Diagrams "showing the five characteristic body regions of arthropods, and their progressive concentration to form the head of a vertebrate." A and B, Insects; C, Arachnid; D, Vertebrate. The principal points illustrated are: The enlargement and concentration of the anterior cephalic neuromeres; the closure of the old mouth and the formation of a new one; the transfer of locomotor organs from the mesocephalon to the postbranchial metameres. (From Patten's "Evolution of Vertebrates and Their Kin."
cranial and spinal nerves, since they have diverse origins. In the head, however, he recognizes in arachnids the twelve cranial nerves of vertebrates from the olfactory to the hypoglossal.

The peripheral nervous system of arachnids attains a condition similar to that in vertebrates. The neural (ventral) nerves of arachnids like the dorsal nerves of vertebrates, are ganglionated, and the hemal (dorsal) nerves are non-ganglionated, like the ventral nerves of vertebrates.

In order to compare arachnid and vertebrate hearts, Patten assumes that the arachnid heart represents the ventricular portion of vertebrates, and that the posterior portion of the pericardial cavity of arachnids corresponds with the atrium and sinus venosus of vertebrates.

But even Patten, who is so impressed by the resemblances of scorpions and vertebrates, is compelled to admit that comparison of arachnid with vertebrate circulation is difficult. He is, however, curiously reticent in regard to the fact that the blood in limulus flows to the heart from the gills, and not the reverse as in vertebrates. In limulus five veins bring blood from the gills to the pericardial cavity. It is difficult to understand why Patten should label the last of these, and only the last, the ductus Cuvieri.

According to Patten, the auditory organ of vertebrates is represented in the limulus embryo by a large discoidal placode which lies opposite the fourth pair of legs. There is, however, no evidence that this is auditory, or even sensory, and it disappears early in development.

Both parietal and lateral eyes of vertebrates are homologous with those of arachnids. During the evolution of vertebrates from arachnids, Patten assumes, there was a considerable period during which the lateral eyes were adjusting themselves to their new position inside the brain chamber, and when they were in functional abeyance. When the lateral eyes again became functional, the parietal eye began to decrease in size and effectiveness.

"The characteristic shape of the arthropod eye and the arrangement of its retinal cells is retained in an exaggerated form in the vertebrate retina, and affords us the only satisfactory explanation of its inversion, its contour and mode of growth, its choroid fissure, its arrangement of rod and cone cells, and its centrally located optic nerve.

"The agreement between the olfactory organ of limulus and that of vertebrates may be traced in respect to so many different characters that the existence of a genetic relationship between the marine arachnids and the vertebrates is placed beyond a reasonable doubt. Indeed, there is a greater difference in respect to this organ, between limulus and other invertebrates than there is between limulus and vertebrates."

The olfactory apparatus arose in the higher arachnids through the secondary modifications of pre-existing organs which had some other function or meaning.
THE ANCESTRY OF THE VERTEBRATES

Fig. 530.—Diagrams illustrating the principal stages in the evolution of segmented animals. They illustrate "the substitution of one organ for another. The most striking illustration is the closing of the old mouth and stomodeum and the formation of a new opening into the mesenteron in the region of the 'dorsal organ'; the substitution of lungs for gills. The most striking innovation is the perforation of the walls separating gill sacs and enteric diverticula; the rise and decline of metamerism." (From Patten's "Evolution of Vertebrates and Their Kin.")
The segmental taste organs and slime buds of the arachnids are the forerunners of the special cutaneous organs of vertebrates, the taste organs of the arachnids corresponding with the taste-buds of the vertebrates, and the slime buds probably in part with the neuromasts of lateral line organs.

Nothing resembling the dermal skeleton of limulus occur in any other invertebrate. But this skeleton resembles that of the ostracoderm, Pteraspis, more than does the skeleton of any other known animal, vertebrate or invertebrate. Since ostracoderms are vertebrates, the close affinity of limulus to vertebrates is thus attested. The ostracoderm skeleton is a highly specialized one, produced by an exaggeration of the type of skeleton seen in limulus. Patten, however, admits the possibility that the exoskeleton of ostracoderms may be mesodermal and not, like that of limulus, ectodermal. But in his opinion, very slight changes would be necessary to convert the skeleton of limulus into that of vertebrates. He is inclined to assume that the mesenchyme which forms dermal bone in vertebrates is of ectodermal origin. The fact that the ectodermal part of the skeleton of limulus is chitinous while that of vertebrates is enamel does not disturb Patten, since in his opinion they "have essentially the same structure and mode of growth."

Patten also finds a cartilaginous endocranium characteristic of the arachnid-vertebrate stock. "The fully developed arachnid endocranium is in every essential respect a duplicate of the primordial cranium of a primitive vertebrate embryo." They agree, he says, in position, general form, mesodermal origin and histological structure, absence of metamersm, and in their planes of growth.

The resemblance also holds for the branchial skeleton. In limulus, as in vertebrates, the "branchial bars" are post-cranial, and may be united by longitudinal bands. The gill-bars of both consist of mucocartilage and not, like the cranium, of fibro-cartilage. The pre-auditory region is without gills and gill bars.

The neural arches of limulus represent the initial stages in the formation of a vertebral column. They agree in general form and in the direction of their processes, with the neural arches of vertebrates. The homologue in arachnids of the notochord of vertebrates is the bothroidal cord or lemmatochord. Lemmatochond and notochord have according to Patten a similar embryonic origin and similar relations to the nerve cord in the adult.

**Objections to the Arachnid Hypothesis of Patten.** It is customary to object to the arachnid hypothesis on the ground that arachnids, such as limulus, are highly specialized animals, while evolution proceeds by the transformation of generalized forms. The very fact that limulus has changed little, if at all, in millions of years might seem to weaken the
case based upon the assumption that vertebrates are descendants of a limulus-like arachnid ancestor.

Patten's hypothesis is based upon the assumption that ostracoderms are primitive vertebrates. But morphologists are generally of the opinion that ostracoderms are highly specialized descendants of elasmobranchs, more closely related to teleosts than to cyclostomes.

In order to reconcile his homologies of arthropod and hemichordate embryos, Patten is obliged to ignore the fact that the primary blastopore in hemichordates becomes anus and not mouth. He assumes that the water pore of hemichordates is the primitive mouth or "neurostoma," and that the blastopore is a "telopore." Likewise, in spite of the evidence of the origin of the notochord from the primary endoderm of amphioxus, Patten asserts that the notochord is ectodermal in origin, apparently because the lemmatochord of limulus is ectodermal.

Patten's theory compels him to locate the primitive mouth in the floor of the neural plate, at the place where later the infundibulum develops. That this is a late and secondary development seems not to matter to him. Neither does the fact that embryology presents not the slightest evidence that the foregut was ever open to the exterior at this point. Also, in order to substantiate his hypothesis, Patten is compelled to assume that echinoderms, urochordates, balanoglossus, and cephalodiscus are degenerate offshoots of a common arthropod-vertebrate stock. The evidence of this degeneration is, to say the least, not convincing.

Patten's argument for the close blood relationship of arachnids and vertebrates is based largely, if not exclusively, upon details of anatomical structure rather than upon fundamental resemblances. The striking contrast in basic features of the two groups does not accord with expectation, if arachnids and vertebrates are closely related phyla. This difficulty has left biologists unimpressed by the mass of evidence of detailed resemblance gathered by Patten.

Consequently, the evidence of similarity in some, or even many, details of structure fails to convince zoologists of their genetic affinities. Furthermore, the argument that one dominant group of vertebrates has succeeded another dominant vertebrate group does not justify the conclusion that fishes have come from a dominant group of invertebrates. When two able biologists such as Gaskell and Patten, on the basis of identical material, reach diametrically opposite conclusions, it is not surprising that a skeptical attitude toward phylogenetic speculation characterizes this generation of zoologists.

The Nemertean Hypothesis

In 1883, Hubrecht advanced the hypothesis that nemerteans are the long-sought ancestors of vertebrates. Among advantages of this
theory is that it derives vertebrate from invertebrate without reversing dorsal and ventral sides. Hubrecht assumes that the paired nerve cords of the Nemertean unite in the mid-dorsal line to form the nerve cord of vertebrates. The paired cerebral lobes of the nemertean become the brain of the vertebrate. Hubrecht compares the intestinal diverticula of the flatworm with the coelomic outpocketings of the amphioxus embryo. The more anterior diverticula are possibly the homologues of the gill pouches of chordates.

One of the chief difficulties in making comparison between vertebrates and invertebrates has been the absence in invertebrates of any structure similar to the notochord. By comparing the proboscis sheath of nemertean with the notochord, Hubrecht thinks that he has removed this obstacle

and has thus demonstrated that nemertean are the connecting link. The nemertean proboscis, which is of ectodermal origin, is homologized with the vertebrate hypophysis. Hubrecht points out that the
hypophysial ingrowth is directed towards the anterior termination of the notochord. If it were to grow into the notochord, its relations would be similar to those of the proboscis to its sheath.

Hubrecht, however, fails to show that the proboscis sheath is endodermal. It is in fact mesodermal, while the notochord is endodermal. The two structures are, therefore, not comparable. This objection remains, even if the notochord sometimes arises as a hollow outgrowth and therefore may have been, like the proboscis sheath, originally hollow. Two hollow structures may be compared, but only if derived from the same germ layer. Further difficulty appears in the fact that in the lowest vertebrates, the myxinoids, the hypophysis connects posteriorly with the pharynx, not with the notochord.

Nemerteans certainly do resemble vertebrates in having paired segmentally arranged nerves connected with the paired nerve-cord, and with a dorsal nerve-cord, when this is also present. There is, however, not a regular alternation of sensory and motor nerves in nemerteans as in amphioxus and vertebrates.

The case which Hubrecht is able to make in favor of the nemertean ancestry of vertebrates is obviously not very convincing. This, however, should not blind us to the fact that, in some ways, such as the presence of gonadic sacs, the flatworms exhibit traits which may be considered ancestral to those of vertebrates.

**Balanoglossus Theory**

Bateson (1886) was the first to suggest that bilaterally segmented animals have evolved in two directions. In one group, the alimentary canal pierced the nervous system, leading to annelids and arthropods;
in the other, the nervous system was dorsal to the alimentary canal, leading to chordates. Balanoglossus, the representative genus of hemichordates, belongs in the latter group and exhibits many traits which are transitional between those of non-chordates and vertebrates. The found-

![Diagram of Balanoglossus embryos](image1)

**Fig. 533.**—Balanoglossus embryos. *A.* A horizontal section of a young embryo, showing the origin of mesodermal pouches. MacBride and others have noted the similarity of this section to that of a young amphioxus embryo as evidence of the close affinity of these two forms. *B.* A young Balanoglossus larva with five pairs of gill slits viewed from the left side. The gill slits of Balanoglossus bear a striking resemblance to those of Amphioxus. On the other hand the young larva of Balanoglossus is strikingly like the larva of echinoderms. (Redrawn after Bateson.)

ations of the balanoglossus theory of vertebrate ancestry are found by Bateson in the presence of a rudimentary notochord, gill slits resembling those of amphioxus, a dorsal nerve cord which is tubular in the anterior portion, a preoral lobe with epithelial cavities resembling those of the pre-oral lobe of amphioxus, segmentally arranged gonads like those of amphioxus, three pairs of enterocoelic cavities, and the resemblance of the tornaria larva of balanoglossus to the early embryo of amphioxus. All of these features show that the affinities of balanoglossus are with

![Diagram of Harrimania, Hemichordate](image2)

**Fig. 534.**—Harrimania, a Hemichordate. *A.* The dorsal portion of a cross section of Harrimania in the region of the esophagus. The resemblance of this cross section to one of amphioxus is striking and serves to demonstrate the close genetic affinities of these two chordates. In Harrimania the notochord is present not only in the preoral lobe as in other hemichordates but also in the collar and anterior pharyngeal regions. *B.* A stereogram of Harrimania in the collar and anterior pharyngeal region, showing the presence of the notochord in these regions. Such evidence tends to remove the doubt that a true notochord exists in Hemichordates. (Redrawn after Ritter.)
chordates, but, unfortunately, do not connect it with any phylum of invertebrates.

That the so-called notochord of balanoglossus is a true chorda dorsalis like that of other chordates has been doubted. But Ritter (1900), on the basis of his studies on Harrimania, a close relative of balanoglossus, says that "there can be no serious doubt that we have in this organ the immediate genetic forerunner of the vertebrate notochord." Its peculiarities, in Ritter's opinion, do not warrant giving it another name, as has been suggested. In Harrimania, two regions of the notochord are distinguishable, an anterior nuchal and a posterior esophageal. The poste-

rior is embryonic and transient in other genera of hemichordates, but persists in Harrimania, which must therefore be regarded as a more primitive type. In the possession of a lumen, the notochord of balanoglossus is peculiar; but in some chordate embryos as in Harrimania the notochord arise as a grooved outpocketing of the median dorsal wall of the endoderm. (Fig. 534)

While the connexion of balanoglossus with lower vertebrates is obscure, the affinities of its tornaria larva with the larvae of echinoderms and with such primitive types as Cephalodiscus and Rhabdopleura are suggestive of relationship with lower invertebrates.

APPENDICULARIA THEORY

Following Kowalewsky's (1868) researches upon the embryology of urochordates and amphioxus, it was supposed that the long-sought ancestor of vertebrates had been found, and the tunicate larva was pro-
claimed to be the missing link. The pendulum of opinion, however, later swung away from this view, when Dohrn and Ray Lankester made it seem probable that tunicates are degenerate vertebrates. But... (1893), after a thorough investigation of the anatomy and development of pelagic tunicates, stated that he was unable to find any degeneration in Appendicularia, a pelagic larval type of Ur.

Fig. 536.—A diagram of Cephalodiscus viewed from the left side as if in median optical section. The presence of a notochord in the pre-oral lobe is one of the reasons for placing this animal among hemichordates. While not regarded as a form "ancestral" to vertebrates, cephalodiscus interests morphologists as a primitive chordate. (Redrawn after W. Patten.)

As a result, Brooks totally rejected the dogma that vertebrates are modified annelids and the assumption that tunicates are degenerate vertebrates. He regards the free-swimming appendicularia as the type from which chordates have evolved, and thus revives the tunicate theory of vertebrate ancestry. The many points of resemblance of appendicularia to amphioxus, and the similarity of their development, give a strong foundation to this hypothesis. Appendicularia, like the larvae of other tunicates, is obviously a chordate with fundamental chordate traits—notochord, hollow dorsal nerve cord, expanded "brain" vesicle, gill-slits, endostyle, and ventral heart. Indeed, the resemblances between tunicates and amphioxus led Minot to suggest that the urochordates and cephalochordates should be grouped together as Atriozoa.

Fig. 537.—Diagram of a larval urochordate. The similarity of the larval urochordate to the embryo of a cephalochordate (amphioxus) suggests that a form like this lies near the main line of vertebrate ancestry. (Redrawn after von Beneden and Julin modified.)
The relations of the thyroid gland in cyclostomes, and its derivation from a hypostyle-like structure in the embryo, strongly suggest that vertebrates came from an animal like the cephalochordates and urochordates, in which food was drawn by ciliary action into an enlarged and elongated pharynx and collected by the mucus-secreting endostyle.

Appendicularia meets all the requirements of such a hypothetical ancestor of chordates.

Brooks suggests that gill slits originated in tunicates, not as respiratory organs, but to allow water to escape from the pharynx, so that food which passes to the stomach and intestine can be more concentrated. Dohrn's hypothesis that gill slits are modified segmental nephridia lacks proof. Dohrn himself admits that he is unable to "assign any reason (sic) why segmental organs should unite with the gut." The suggestion obviously is based on the assumption that vertebrates are derived from annelid
ancestors and that urochordates are degenerate vertebrates. Brooks denies the truth of both of these assumptions.

The objection most frequently raised against the appendicularia theory is that tunicates are chordates, and that this theory does not carry us beyond the limit of the phylum. The purpose of a theory of vertebrate ancestry, however, is to reveal the non-chordate predecessors of chordates. But there appear to be no invertebrates which can be considered the immediate predecessors of chordates—no forms transitional between chordates and the much simpler coelenterates.

**CONCLUSION**

A survey of these various attempts to solve the problem of the ancestry of vertebrates seems to suggest that the most promising clue to the solution is to be found in the lower chordates. Cyclostomes, more especially their larval stages, lead us in the direction of Amphioxus, which “if it hadn’t existed, would have had to be invented.” The similarity of amphioxus embryos to larval tunicates strongly suggests their common origin. Since this seems the most reasonable interpretation of the facts, we may conclude that metamerism has been attained de novo by chor-
dates, and not inherited from metameric invertebrates. Hesitation to accept this conclusion seems to be due chiefly to the fact that no pre-

chordates can be found which resemble larval chordates. Thus the chordate clue seems to lead us into a blind alley out of which the most promising exit is the way back.

Fig. 540.—A diagram of the phylogenesis of man, based on the assumption that the Protochordates resemble vertebrate ancestors more closely than do the annelids. Annelids and other Proterostomians have, it is assumed, diverged from the main line of vertebrate ancestry very early in animal phylogenesis. Before man emerged in the late Tertiary transitional forms between man and the lower Primates made their appearance. Among these the best known are Propliopithecus, Dryopithecus and Australopithecus, which are true "connecting links."
The absence of bony skeletal structures in the simpler chordates makes it appear unlikely that paleontological evidence can be used in the solution of the problem. Students in the past have possibly depended too much upon comparative anatomy. The study of genetics has not tended to support the orthodox assumption of the transformation into chordates of adult invertebrates of the types now extant. Future students of phylogenesis will turn to embryological evidence more than has been done in the past. Delsman’s suggestion of a common origin of annelids, molluscs, and chordates by alteration in the growth centers of a trochophore-like ancestor sounds plausible.

For the present, morphologists must resort to the eclectic method used in this text, and select the hypothetical stages in the evolution of the various organ systems in whatever invertebrate types they may be found. However, in view of the evidence of the convergent and independent appearance of similar structures in different phyla, phylogenetic “series” are necessarily speculative and tentative.

Among the invertebrate groups with traits resembling those of the hypothetical ancestors of vertebrates this text has mentioned Protozoa, Coelenterates, Platyhelminths (including Nemerteans), Nematodes, and Annelids. More closely related to vertebrates than any of these are Hemichordates, Urochordates, and the Cephalochordates, which may therefore be regarded as having some of the ancestral traits. None of these, however, lies in the main line of vertebrate descent, as is indicated by the phylogenetic tree of the animal kingdom shown in Fig. 540. The main line of vertebrate phylogenesis is today better represented in larval stages like the trophophore than in any adult forms. On the whole, the evidence supports the conclusion that the separation of animal phyla occurred farther down in the phylogenetic series than has hitherto been assumed. See Fig. 520.
GLOSSARY

abdomen. The portion of the body between thorax and pelvis.
abducens. The sixth cranial nerve.
abduction. The withdrawal of a part from the median plane.
aberrant. Wandering from the usual.
abnormality. Deviation from the normal.
abomasum. The fourth stomach of a ruminant.
aboral. Opposite to the mouth.
abortion. Expulsion of a fetus before it can live.
acetabulum. The socket in the coxal bone in which the head of the femur articulates.
acidophilic. Easily stained with acid dyes.
acidosis. Reduction of alkali reserves in the body.
acinus. A grape-like terminal subdivision of a gland or lung.
acrania. Chordate animals without a brain-case.
acrodont. With teeth fastened to edge of jaw and not lodged in sockets.
acromegaly. A disease which involves an enlargement of bones due to over-functioning of pituitary gland.
acromion. The lateral extension of the spine of the scapula.
adduction. The act of drawing a part towards the median plane.
adrenin. The suprarenal medullary hormone.
afferent. Centripetal, conveying towards the center.
afterbirth. Extra-embryonic membranes discharged from uterus after the child is born.
air bladder (sac). Respiratory or hydrostatic organ in fishes.
ala cinerea. The vagal eminence which projects into the fourth ventricle.
alar plate. The dorso-lateral portion of the embryonic neural tube.
alisphenoid. That part of the embryonic cartilage cranium which forms most of the great wing of the sphenoid.
allantois. A hollow outgrowth of the embryonic hind-gut.
ameloblast (adamantoblast). A cell which secretes enamel.
ammocoetes. The larval stage of Petromyzon.
amnion. The liquid-filled sac which encloses the embryos of reptiles, birds and mammals.
amniota. The animals the embryos of which are enclosed in an amnion.
amphicoelous. Biconcave like the centrum of a fish vertebra.
ampulla. A flask-like dilatation.
amylopsin. A starch-splitting enzyme secreted by the pancreas.
analogy. Resemblance based on similarity of function.
anamnia. Vertebrates the embryos of which lack an amnion.
anastomosis. The communication of two vessels or connexion of two nerves.
angioblast. One of the cells from which blood and blood vessels develop.
angular (e). A membrane bone of the lower jaw.
anisotropic. Doubly refracting or polarizing.
ankylosis. Consolidation or fusion of the bones of a joint or suture.
anlage. The embryonic fundament of an organ.
anterior. Toward the head. In human anatomy toward the ventral side.
anthropoids. The man-like apes.
antibodies. Chemical substances formed by a body in reaction to foreign substances introduced.
anchilis. The inner curved edge of the external ear.
antithrombin. A substance in the blood which prevents clotting.
antitoxin. A substance in the blood serum antagonistic to a poisonous substance or toxin.
antitragus. An ear prominence opposite the tragus.
antrum. A bone cavity.
anus. The egestive opening of the intestine.
aorta. The chief artery which leaves the heart.
aponeurosis. A connective tissue membrane or fascia which surrounds or attaches a muscle.
appendices epiploicae. Fatty pouches attached to the colon.
appendicularia. A free-swimming pelagic genus of urochordates.
aqueous humor. The refractive liquid between cornea and lens of the eye.
arachnoid. A web-like membrane between the dura mater and pia mater of brain and spinal cord.
arbor vitae. The tree-like arrangement of fiber tracts seen in section of the cerebellum.
arch. A bent or curved structure.
arhenteron. The primitive digestive cavity.
arhencephalon. The primitive forebrain of chordates.
arhetype. An ideal original form.
arhicortex (archipallium). The olfactory cerebral cortex including the hippocampus.
arhinephros. The primitive kidney or mesonephros (Wolffian body).
arhipterygium. The original appendicular skeleton of vertebrates.
arheolar tissue. A fibrous tissue containing minute interspaces.
arrectores pilorum. Cutaneous muscles attached to hairs.
ariculare. The bony articular element of the lower jaw of lower vertebrates.
arhythnoi. A pitch-like cartilage of the larynx or voice-box.
assimilation. Constructive metabolism.
aragalas. The ankle bone which articulates with the tibia.
ateiotic dwarf. A normal dwarf or midget.
atlas. The first cervical vertebra.
atrium. 1. An auricle of the heart. 2. The chamber surrounding the gills of lower chordates.
atrioventricular bundle. A muscle which connects auricle and ventricle.
atrophy. The wasting of a part or organ.
atropine. A poisonous alkaloid which stimulates the sympathetic.
adiliary bulba. A capsule-like portion of the tympanic bone.
adiliary meatus. The external meatus extends from the drum to the outside.
adiliary tube. A passage from the middle ear to the pharynx.
Auerbach's plexus. A sympathetic plexus in the wall of the intestine.
auricle, external. The pinna of the ear.
auricularis magnus nerve. A sensory nerve distributed to face, ear, and neck.
autonomic system. The sympathetic and parasympathetic nervous systems.
**GLOSSARY**

**axilla.** The arm-pit.

**axis** (epistropheus). The second cervical vertebra.

**axolotyl.** The larval, and sometimes permanent, stage of the salamander *Ambystoma*.

**Bartholin, glands of.** The vulvo-vaginal glands.

**basalia.** The proximal elements of the cartilaginous skeleton of the extremity.

**basihyal.** The ventral element of the hyoid skeletal arch.

**basilar membrane.** The basal membrane of the organ of Corti.

**basilar plexus.** A venous plexus in the dura mater which lines the occipital bone.

**basioccipital.** The basal portion of the occipital ring.

**basophilic.** With affinity for basic dyes.

**Bell’s law.** The dorsal roots of spinal nerves are sensory, the ventral motor.

**biceps brachii.** The arm muscle which flexes the forearm.

**bicuspid.** A tooth (premolar) with two cusps. The left atrioventricular valve of the heart.

**bilateral.** A type of symmetry such that one plane, and only one, will divide a body into equal halves.

**biogenesis.** Life comes from life, not from the lifeless.

**biogenesis, fundamental law of.** Ontogenesis repeats phylogenesis.

**blastocoele.** The cavity of the blastula.

**blastoderm.** The membrane from which the embryo develops.

**blastopore.** The external orifice of the gastrula.

**blastula.** The one-layered stage of ontogenesis.

**body-stalk.** The mesodermal bridge which connects the embryo with the chorion.

**Bowman’s capsule.** The globular dilatation of an uriniferous tubule enclosing a glomerulus.

**brachium conjunctivum.** The superior peduncle of the cerebellum.

**brachium pontis.** The middle peduncle of the cerebellum.

**branchial bars.** The gill or visceral skeletal arches.

**branchiomerism.** The metamericism represented in the visceral arches and pharyngeal pouches.

**broad ligament.** The peritoneal fold which supports uterus and ovary.

**bronchiolus.** One of the branches of a bronchus.

**bronchus.** One of the two branches of the trachea.

**Brunner’s glands.** Submucous glands of the duodenum.

**bulbus.** The enlarged origin of the aorta.

**bulbo-urethral glands.** Cowper’s glands of the urethra.

**bulbus urethrae.** An elongated swelling of the urethra.

**bursa.** A sac-like cavity.

**buttock.** The prominence formed by the gluteus muscle.

**calcaneum.** The heel bone.

**calcareous.** Composed of lime (calcium) salts.

**callosity.** A local thickening of the horny layer of the skin.

**calyx** (pl. calyces). One of the recesses of the renal pelvis which encloses the pyramids.

**canaliculus.** One of the fine canals which connects bone lacunae.

**canalis reuniens.** The duct which connects the cochlear duct with the sacculus.

**cancellous bone.** Spongy bone.

**canine tooth.** The single cuspid tooth between lateral incisor and first premolar.

**capillaries.** The minute vessels which connect arteries and veins.

**capitiate.** The os magnum of the carpus.

**capitulum costae.** The head of a rib.

**cardinal veins.** The paired veins which drain head and trunk in lower vertebrates.
carnassial teeth. The last upper premolar and the first lower molar tooth of carnivora.
carnivorous. Flesh-eating animals.
carpus. The wrist.
cartilage. An elastic connective tissue with cells embedded in a homogeneous matrix.
castrate. To remove the testes.
catalyzer. A substance which by its presence changes the velocity of a chemical reaction.
caudad. Toward the tail.
cecum. That diverticulum of the colon into which the vermiform appendix opens.
centrogenetic. Of recent, as contrasted with ancestral, origin.
centrum. The body of a vertebra.
cephalic. Pertaining to the head.
cerebellum. The little brain, a coordinating center above the fourth brain ventricle.
cerebrum. The chief division of the brain.
cheiropygium. The skeleton of the fingered appendage.
chemoreceptor. A sensory cell which responds to chemical stimulation.
chiasma. A decussation or x-shaped crossing of nerve fibers within the central nervous system.
chief cells. The pepsinogen secreting cells of the gastric glands.
chitin. The horny nitrogenous substance which forms most of the skeletons of arthropods.
choana. A funnel-shaped opening.
cholesterol. A fat-like substance which forms the usual type of gallstones.
chondrin. A gelatin-like protein found in cartilage.
chorda dorsalis. The notochord, the primary chordate axial skeleton.
chorda tympani. A mixed branch of the facial nerve.
chordae tendineae. The tendons of the heart-valves.
chorio-allantois. The fused membranes of the allantois and chorion.
chorioid (choroidal). A chorion-like vascular membrane. In the eye a layer between retina and sclera.
chorioid fissure. A defect in the optic cup and a groove along the optic stalk.
chorion. The outer protective extra-embryonic membrane of amniotes.
chromaffin cells. Cells of sympathetic origin having an affinity for chrome salts.
chromatophore. A pigment cell.
chyme. The partly digested material which passes from the stomach to the duodenum.
ciliary body. A local thickening of the choroid layer of the eye to which the lens is attached.
cingulum. An association fiber tract which encircles the corpus callosum near the median plane.
cisterna chyli. A receptacle or enlargement at the lower extremity of the thoracic duct.
Clarke's column. A tract of nerve cells in the dorsal column of gray matter of the cord.
cleft palate. Congenital fissure in the roof of the mouth.
cleithrum. A membrane bone of the shoulder girdle of fishes and amphibia.
clitoris. An erectile organ of the female homologous with the penis.
cloaca. The cavity into which digestive and urogenital organs open.
cochlea. The spiral tube of the inner sensory ear.
celiac (solar) plexus. A large sympathetic plexus in the epigastric region.
coelom. The chordate body-cavity.
coelomoducts. Paired segmental reproductive ducts of annelids.
collagen. The chief organic constituent of bone and connective tissue.
collateral. A side branch of an axon.
GLOSSARY

colliculus. One of the divisions of the corpora quadrigemina.
colloid. Glue-like.
colon. The large intestine to the rectum.
columella auris. The ear bone of amphibia and sauropsida.
commissure. A bundle of nerve fibers which connect right and left halves of central nervous system.

Concrescence Theory. 1. The theory that separate primordia unite in the median plane to form the right and left halves of the embryo. 2. The theory that compound teeth are formed by the fusion of simple conical teeth.

condyle. A rounded articular surface of a bone.
congenital. Existing at or before birth.
conjunctiva. The delicate membrane which covers the eyeball and lines the eyelid.
conus arteriosus. 1. The conical portion of the right ventricle which joins the pulmonary artery. 2. The valvular region of the ventral aorta.
copulation. Sexual congress.
coracid. The posterior of the two ventral elements of the pectoral girdle.
corium. The deeper mesodermal layer of the skin.
cornea. The translucent anterior portion of the sclera of the eyeball.
corneified. Converted into horny tissue.
corona radiata. The projection fibers which radiate from the internal capsule to the cerebral cortex.
coronal. Encircling like a crown.
coronoid bone. A membrane bone of the lower jaw.
corpora bigemina (quadrigemina). The midbrain centers of optic reflexes.
corpora cavernosa penis. The paired masses of erectile tissue of the penis.
corpus albicans. The fibrous tissue formed after the discharge of the ovum.
corpus callosum. A group of commissural fibers which connect the two cerebral hemispheres.
corpus cavernosum urethrae. The spongy tissue surrounding the urethra.
corpus luteum. The yellowish tissue formed in the Graafian follicle when an ovum is discharged and fertilized.
corpus striatum. The basal ganglion of the cerebral hemisphere.
cortin. The hormone secreted by the adrenal cortex.
coxal bone. The hip bone.
cranium. The brain case.
cretin. A type of idiotic dwarf supposedly caused by deficient thyroxin secretion.
cribiform plate. A sieve-like portion of the ethmoid bone.
cricoid. One of the laryngeal cartilages which resembles a seal ring.
crista. A crest or ridge of sensory hair-cells.
crura cerebri. The brain peduncles formed by descending fiber tracts from the hemispheres.
crypt. A pit or follicle.
cryptorchism. The condition of undescended testicles.
cuboid. The most lateral distal tarsal bone of the foot.
cuneiform bones. Three wedge-shaped bones of the distal tarsals.
cusp. A conical projection of a tooth.
cutaneous. Pertaining to the skin.
cuticle. The epidermis or outer layer of the skin.
cystic duct. The duct from the gall bladder to the common bile duct.

deciduous placenta. The primitive placenta in which chorion and uterine mucosa are loosely associated.
decussation. A decussation of nerve fibers occurs when they cross the median plane to connect unlike centers on the two sides.

Deiter's cells. The cells in Corti's organ which support the outer hair cells.

delamination. The splitting of a cell layer into two or more layers of cells.

demersal eggs. Eggs (of fishes) which sink to the bottom of the water.

demilunes. Crescent-shaped cells of mucus-secreting acini.

dendrite. One of the branched processes of a neuron which carries impulses towards the cell body.

dentary. The membrane bone of the lower jaw to which teeth are attached.

dentine. The bone-like substance which forms most of the material of a tooth.

dentition. The kind, number, and arrangement of the teeth.

depressor. A muscle which lowers an organ. A nerve which inhibits action.

dermatome. That portion of the epimere which forms corium.

deuterencephalon. That part of the embryonic brain which includes mid- and hind-brain.

deuterostomia. Animals in which the blastopore forms the anus or lies near the anus.

deutoplasm. The passive nutritive portion of the germ-cell.

development. The process by which an egg changes into an adult.

diabetes. A disease which is marked by excessive excretion of urine.

diapragm. The muscular partition which in mammals separates thorax and abdomen.

diapophysis. A process of the neural arch which articulates with the tubercle of a rib.

diastema. A space between the teeth, especially between the canine and the lateral teeth.

diencephalon. The second of the five successive divisions of the brain.

differentiation theory. The theory that compound teeth have evolved by differentiation from simple conical teeth.

digestion. The process by which foods are made soluble.

dioecious. Having sexes separated in two individuals.

diphyodont. Having two sets of teeth.

diploë. The cancellous bone between the two layers of compact bone of the cranium.

diploid. The double number of chromosomes characteristic of body cells.

diplopondyly. The condition of double centra in vertebrae.

distal. Opposed to proximal.

dorsal. Pertaining to the back or dorsum.

duodenum. The anterior portion of the small intestine.

dura mater. The tough outermost membrane which surrounds the central nervous system.

ectoderm. The outermost germ layer.

ectosarc. The outer layer of the Protozoon cell.
effector. The end-organ, muscle or gland, which responds to nervous stimulation.
efferent. Away from a center or organ.
egg. The animal ovum.
ejaculatory duct. The duct which unites the seminal vesicle and ductus deferens with the urethra.

“elan vital.” Bergson’s name for the “vital factor.”

endobranchiate. Forms with endodermal gills.

endocardium. The epithelial membrane which lines the heart.

endochondral bone. Bone which develops within cartilage.

endocranium. The dura mater of the brain.

endocrine gland. A gland which secretes internally into the blood.
GLOSSARY

endoderm. The innermost germ layer.
endolymph. The liquid contained in the membranous sac of the inner ear.
dermatium. The mucous lining of the uterus.
doneurium. The connective tissue which subdivides a nerve into funiculi.
doskeleton. The internal skeleton as distinguished from the dermal skeleton.
dostyle. A ciliated groove in the floor of the pharynx of lower chordates.
dothelium. The thin membrane which lines blood vessels and lymphatics.
der-plate. The expanded termination of a motor nerve on a muscle fiber.
ensiform. Shaped like a sword.
enterocoele. A mesodermal cavity formed as an outpocketing of the endoderm.
teron. The cavity of the alimentary canal.
terokinase. An enzyme secreted by the small intestine which converts trypsinogen into trypsin.
enzyme. A catalytic organic compound which facilitates chemical changes such as the splitting of foods into simpler substances in the alimentary canal.
eosinophile. A leucocyte with an affinity for eosin.
epalial. Dorsal to the vertebrate axis.
ependyma. The lining membrane of the central nervous system.
epibranchial organs (ganglia or placodes). Ectodermal masses above the gill-pouches of vertebrate embryos.
epicardium. The outer covering of the heart.
epidermis. The outer ectodermal layer of the skin.
epididymis. The mass of convoluted tubules and duct attached to the testis.
epiglottis. The lidlike structure which covers the entrance to the larynx.
epimere. The dorsal portion of the mesoderm.
epinephrine (adrenin). The hormone secreted by the medulla of the suprarenal.
epineurium. The connective tissue covering of a nerve.
epiphrax. The nasal portion of the pharynx.
epiphysis. The terminal portion of a long bone. The pineal organ.
epithalamus. The dorsal portion of the diencephalon.
epithelium. The tissue which covers a surface.
epitrichium. The outer layer of the fetal epidermis.
epoophoron. A rudiment of the mesonephros near the ovary.
ereptose (erepsin). A peptone-splitting enzyme secreted by the intestinal mucosa.
erthrocytopoietic tissue. Tissue forming red blood corpuscles.
esophagus. The portion of the alimentary canal between pharynx and stomach.
esothmotubinals. The superior and middle turbinated bones.
ethmoid. The sieve-like bone at the front of the skull.
eunuch. A castrated individual.
eustachian tube. The passage which connects the tympanic cavity with the pharynx.
excrtion. The elimination of liquid wastes.
exoskeleton. That part of the skeleton which is derived from the skin.
enteroceptive. Receptive to external stimuli.
exirpation. The complete removal of a part.
extravasation. The escape of blood from a vessel into surrounding tissues.
extremity. A limb.
extrinsic. Originating outside an organ.

falciform ligament. A fold of peritoneum between liver and diaphragm.
Fallopian tube. The uterine tube or anterior portion of Muellerian duct.
falx cerebri. That portion of the dura mater between the hemispheres.
fasciculate layer. The middle layer of the suprarenal cortex.
fasciculus. One of the divisions of a funiculus of the spinal cord.
femur. The thigh bone.
fenestra cochleae. The round window of the internal ear.
fenestra vestibuli. The oval window to which the stapes bone is attached.
fertilization. The union of sperm and egg nuclei within the ovum.
fetus. The child in the womb after the end of the third month.
fibril. A cytoplasmic thread.
fibrin. The clot-forming substance of the blood.
fibrocyte. A flat elongated connective tissue cell.
fibula. The outer shin bone.
filum terminale. The thread-like termination of the spinal cord.
fimbriae tubae. The fringe-like end of the uterine tube.
fission. Asexual division into equal parts.
fissure. A deep fold of the cerebral cortex which involves the entire thickness of
the brain wall.
fistula. A deep ulcer-like opening, usually into a hollow organ.
flabellum. A fan-like set of radiating fibers in the corpus striatum.
flagellum. A whip-like protoplasmic process of a cell.
flame-cell. An excretory cell having one or more flagellae.
flexion. The condition of being bent.
flexure. A bend or fold.
flocculus. A small lobe on the lower side of the cerebellum.
floor plate. The floor of the neural tube.
foliate papillae. Leaf-like folds on the sides of the tongue.
follicle. A small secretory sac or gland. The integumentary sac enclosing the base
of a hair or feather.
fontanelle. One of the unossified regions in the skull of the infant.
foramen. A small opening, usually in a bone.
ornix. A band of commissural fibers ventral to the corpus callosum.
fossa. A pit or depression.
fovea centralis. A pit in the macula lutea of the retina where the layer of nerve fibers
is lacking.
freemartin. The sterile female twin of a male calf.
frenulum linguae. A median fold between tongue and mandible.
friction-ridge pattern. A concentric arrangement of fine ridges on the hands and
feet.
frontal. The bone of the forehead. A sectional plane which divides a bilateral body
into dorsal and ventral divisions.
function. The normal activity of an organ.
fundus. The part of a hollow organ opposite its opening.
fungiform. Mushroom-shaped.
funiculus. One of the three chief divisions of white matter on the sides of the cord.
gall bladder. The pear-shaped sac which stores the bile secreted by the liver.
gamete. A sexual cell—ovum or spermatozoon.
ganglion. A functional group of nerve cells outside of the central nervous system.
Gartner’s duct. The rudiment of the Wolfian duct in the female mammal.
Gasserian ganglion. The semilunar ganglion of the trigeminal nerve.
“gastraea” theory. The theory that the gastrula stage represents a coelenterate stage
in vertebrate phylogenesis.
gastric glands. The glands of the stomach wall.
gastrula. The two-layered stage of ontogenesis.
gelatin. The translucent protein which forms jelly and glue.
generic. Pertaining to origin or birth.
geniculate body. A tubercle-like body in the lower part of the optic thalamus.
geniculate ganglion. The ganglion of the facial nerve.
genital. Pertaining to the organs of reproduction.
gestation. Pregnancy. The condition of being with child.
gigantism. Excessive growth sometimes due to disease of the anterior lobe of the pituitary.
gingiva. The gum. The tissue which covers the jaw and surrounds the necks of the teeth.
gizzard. The muscular grinding stomach of birds and reptiles.
gladiolus. The middle chief portion of the sternum.
glan penis. The swollen terminal portion of the penis.
glenoid. The concave depression in the scapula in which the head of the humerus articulates.
globus pallidus. The pale interior of the lenticular nucleus of the corpus striatum.
glomerulus. The knot of capillaries of a renal corpuscle.
glottis. The pharyngeal opening of the larynx.
glycogen. Animal starch, a carbohydrate stored in the liver and other tissues.
gnathostomes. Fishes with biting jaws in contrast with cyclostomes.
goblet-cells. Mucus-secreting cells of the intestine.
groat. Enlarged thyroid gland.
Golgi-Mazzoni corpuscles. Special tactile corpuscles of the finger-tips.
gonad. A gamete-producing gland.
gonotome. That part of the mesoderm which forms the gonad or germ-gland.
goose flesh. The formation of skin papillae due to the action of cutaneous muscles on hairs.
Graafian follicle. An ovarian vesicular sac containing an ovum and secreting an hormone (estrin).
Grandry's corpuscles. Special tactile corpuscles of tongue and mouth. The same as Merkel's corpuscles.
granulocyte. A leucocyte which contains coarse granules.
gray matter. That portion, mostly cellular, of the central nervous system which lacks the white myelin.
groin. The part of the abdominal wall adjacent to the thigh.
gubernaculum testis. The fetal cord which attaches the testis to the scrotal sac.
gullet. The esophagus.
gustatory. Pertaining to the sense of taste.
gynandromorph. An organism having both male and female characteristics.
gyrus. A fold or convolution of the brain cortex.
hagfish. The cyclostome myxine.
habenular commissure. The “superior” commissure which connects the habenular ganglia in the roof of the diencephalon.
habenular ganglia. Olfactory centers anterior to the pineal body.
hamate. The distal carpal bone adjacent to the fifth metacarpal.
haploid. The reduced number of chromosomes found in mature germ-cells.
harelip. A congenital cleft in the upper lip, rarely double.
Harrimania. A genus of hemichordates.
harvest men. Long-legged spiders or “daddy-long-legs.”
Hassall's corpuscles. Clusters of concentrically arranged epithelial cells of the thymus.
Hatschek's pit. A preoral pore in amphioxus which opens into the left anterior cavity. 

haustra. Sacculations of the wall of the colon.

Haversian canal. A bone canal which contains a blood vessel and nerves.

“heat.” Estrus or sex ardor in animals.

helix. The margin of the pinna of the ear.

ehemal. Pertaining to the blood.

hemibranch. The anterior or posterior half of the respiratory portion of a visceral arch.

hemoblast. A primitive blood cell.

hemoglobin. The coloring matter of a red blood cell.


Henle's loop. A loop of a uriniferous tubule.

Hensen theory. The theory that nerve fibers are enlarged plasmodesms.

hepatic. Pertaining to the liver.

hermaphrodite. An individual with both male and female characteristics.

hermia. The protrusion of an organ through an abnormal opening.

heterodont. Having specialized kinds of teeth.

heterogamy. Reproduction which involves the union of unlike gametes.

heterolateral. Relating to opposite sides.

Highmore's antrum. A cavity or sinus of the maxillary bone.

hilus (hilum). The pit of an organ where blood vessels and nerves enter.

hindbrain. The posterior of the three primary embryonic brain vesicles.

hippocampus. A gyrus in the floor of the lateral ventricle which constitutes the greater portion of the olfactory centers.

histogenesis. The ontogenetic differentiation of a tissue.

holobranch. An entire fish gill.

homodont. Having teeth all alike.

homolateral. On the same side.

homologous. Having the same structure, development, and relations.

hormone. The secretion of an endocrine gland which affects the activity of one or more other organs.

hyaline. Translucent.

hydatid of Morgagni. The rudiment of the Müllerian duct attached to the oviduct or testis.

hydrostatic organ. An organ of aquatic organisms which serves to adjust internal to external pressure.

hymen. The membrane which more or less completely closes the external opening of the vagina.

hyoid. The second visceral arch of vertebrates. The hyoid bone of mammals develops from skeletal elements of the second and third visceral arches.

hyomandibula. The dorsal element of the hyoid skeletal arch.

hypaxial. Ventral to the chief axis.

hypertrophy. The abnormal enlargement of an organ.

hypobranchial muscles. The muscles ventral to the gills.

hypochorda. A transient cord of cells ventral to the notochord.

hypocone. A fourth tubercle of a compound tooth.

hypodermic. Administered beneath the skin.

hypomere. The ventral portion of the mesoderm.

hypoparathyroidism. Insufficient secretion of the parathyroid glands.

hypophysis. Usually identified with the pituitary gland but strictly forming only the anterior lobe of the latter.

hypothalamus. The ventral portion of the diencephalon.

hypothenar. The ridge on the ulnar side of the palm.
GLOSSARY

hypothesis. An attempted explanation.

ichthyopsida. The sub-phylum which includes the fish-like forms—Fishes and Amphibia.

ichthyopterygium. The skeleton of the extremity of fishes.

ileum. The posterior portion of the small intestine.

ilium. The dorsal element of the pelvic girdle.

imbricate. A tile- or shingle-like arrangement of alternating parts.

immunity. The condition of resistance to infection.

impulse, nervous. The change transmitted along an active nerve fiber.

incisive canal. The passage in the maxillary bone from the nasal fossa to the mouth cavity.

incisor. One of the four front teeth of either jaw.

incus. The anvil-like middle ear bone.

infundibulum. The funnel-like portion of the hypothalamus which connects with the pituitary gland.

inguinal canal. The passage in the groin which contains the spermatic cord.

inscriptiones tendineae. Fibrous bands which partially divide the belly of a muscle.

insertion. The attachment of a muscle to the bone which it moves.

insula. A triangular portion of the cerebral hemisphere covered by the temporal lobe.

insulin. The hormone secreted by the islands of Langerhans in the pancreas.

integration. The coordination of functions.

intercalated. Placed between or interposed.

intercostal. Between the ribs.

intergrade, sex. An individual with characteristics intermediate between those of the sexes.

interceptors. Sense organs in the lining of the alimentary canal.

interrenal body. The tissue which in higher vertebrates forms the adrenal cortex.

interstitial tissue. The endocrinal tissue of the testis.

intestinal portal. The transient embryonic anterior opening of the hindgut and the posterior opening of the foregut which appear during the formation of the floor of the intestine.

intima. The innermost lining of an artery.

intrinsic. Situated within a part or organ.

invaginate. The enclosure of a part by another portion of the same thing.

iris. The circular pigmented membrane between the cornea and lens of the eye.

ischium. The posterior of the two ventral elements of the pelvic girdle.

islands of Langerhans. Endocrinal organs embedded in the substance of the pancreas which secrete the hormone insulin.

isogamy. The union of similar gametes.

Jacobson's organ. An accessory olfactory organ which opens into the nasal cavity.

jejunum. The middle of the three divisions of the small intestine.

jugular ganglion. The "root" ganglion of the vagus nerve.

keratin. An insoluble protein which forms the base of horny structures.

kidney. The chief excretory organ of amniotes.

Koelliker's pit. The rudiment of the embryonic neuropore of Amphioxus.

Krause's corpuscles. Rounded sensory corpuscles located in mucous membranes.

labial cartilages. Rudimentary cartilages of elasmobranchs.

labium. A lip or lip-like structure.
labyrinth. The internal ear of vertebrates.
lacrimai. Pertaining to the tears.
lactal. Pertaining to milk. An intestinal lymphatic.
lacuna. A pit or hollow. In bone the cavity filled by a bone cell.
lagena. An outgrowth of the sacculus of the ear.
lamella. A thin leaf or plate as of bone.
lamina terminalis. The thin membrane which forms the anterior wall of the third brain ventricle.
lanugo. The fine hairy covering of the fetus of man.
larva. An immature but active stage in the development of an organism.
larynx. The cartilaginous organ which encloses the vocal cords.
lateral line. A series of sense organs which extends along the sides of the body of fishes and some amphibia.
lemmatochord or bothriochord. An arthropod structure which W. Patten has compared with the notochord.
leucocyte. A "white" blood corpuscle.
Lieberkuehn's glands or crypts. Tubular mucous glands of the intestine.
linea alba. The tendon in the median line of the abdomen.
lingual. Pertaining to the tongue.
lipase (stcapsin). A fat-splitting enzyme secreted by the pancreas and some other digestive organs.
lipoids. Fat-like cell constituents soluble in alcohol and ether.
lobule. A normal small division of a lobe.
Lorenzini's ampullae. Tubular sensory organs of Elasmobranchs.
luciferin. A substance which combined with luciferase in luminous animals produces light.
lumen. The cavity of a hollow organ.
lunula. The whitish crescent at the root of a nail.
luteal hormone. The hormone progestin secreted by a corpus luteum.
lymph. The coagulable liquid of the lymphatic vessels.

maculae acusticae. The sensory patches of the sacculus and utriculus.
macula lutea. The point of clearest vision at the center of the retina.
malar bone. The zygomatic or cheek bone.
malleolus. The hammer-headed process of a bone (tibia and fibula).
malleus. The ear ossicle which is attached to the drum.
maltase. The enzyme which splits maltose into dextrose.
mamma. The breast or mammary gland.
mammillary bodies. Paired rounded bodies posterior to the tuber cinereum.
mandible. The horseshoe-shaped lower jaw.
mandibular arch. The anteriormost visceral arch.
mantle. The body wall of urochordates. The shell-secreting organ of molluscs.
manubrium. The anterior division of the sternum.
marsupial pouch. The abdominal pouch of marsupials in which the young are carried after birth.
mastoid. A process of the temporal bone.
maturity. The process by which homologous chromosomes are segregated.
maxilla. The upper jaw bone.
maxillo-turbinals. The inferior turbinated bones.
meatus. A passage or opening.
Meckel's cartilage. The lower jaw of cartilaginous fishes.
mediastinum. The thick partition which divides the two pleural cavities.
meadulla. The marrow or core of an organ.
medulla oblongata. The posterior brain division which contains the fourth ventricle.
Meibomian glands. Sebaceous glands of the eye lids.
Meissner's corpuscles. Tactile corpuscles with thick capsule and brush of nerve terminations.
melanophore. A pigment cell containing melanin.
membrane bones. Bones which are not preformed in cartilage.
meninges. The three membranes which enclose the brain and spinal cord.
menopause. The time in life when menstruation normally ends.
menstruation. The monthly flow of women.
mentum. The chin.
Merkel's corpuscles. Tactile corpuscles of the tongue and mouth.
mesencephalon. The third or mid-brain vesicle.
mesenchyme. The embryonic connective tissue.
mesentery. The peritoneal membrane which attaches the intestine to the body wall.
mesethmoid. The median cribriform portion of the ethmoid bone.
mesocardium. The membrane which connects the embryonic heart with the body wall.
mesoderm. The middle germ layer.
mesogaster. The peritoneal membrane which attaches the stomach to the body wall.
mesoglea. The gelatinous middle tissue of sponges and coelenterates.
mesomere (nephrotome). That portion of the trunk mesoderm which connects each somite (epimere) with the ventral mesoderm or hypomere.
mesomerism. The segmentation of the epimeric or dorsal mesoderm into somites.
mesonephros. The middle kidney or Wolfian body, the functional kidney of amniota.
mesopterygium. The middle basal cartilage of the elasmobranch pectoral fin.
mesorhynch. The peritoneal membrane which attaches the testis to the dorsal body wall.
mesorectum. The mesentery of the rectum.
mesothelium. The cellular layer which encloses the coelom.
mesovarium. The peritoneal membrane which connects the ovary to the body wall.
Mesozoic. The middle life era of geologic time.
muscle. The chemical cycle of matter in living organisms.
muscle apparatus. The group of five bones between the wrist and the fingers.
muscle cone. The postero-external cusp of the upper molar teeth of mammals.
muscle conid. The postero-internal cusp of the lower molar teeth of mammals.
muscle. One of the serial divisions of the body of a segmented animal.
muscle. A striking change of form during development, as seen in the transformation of the tadpole into a frog.
muscle. The definitive kidney of the amniotes.
muscle. Posterior to the ear vesicle.
muscle. Paired folds on the ventral side of the body of Amphioxus.
muscle. The posterior basal cartilage of the pectoral fin of elasmobranchs and some ganoids.
muscle. The posterior or xiphoid process of the breast bone.
muscle. The five bones between the ankle and the toes.
muscle. Many-celled animals.
muscle. The fourth brain division which forms cerebellum and pons.
muscle. The third or mesencephalon division of the brain.
muscle. The left atrioventricular valve of the heart.
muscle. An extinct running bird of New Zealand.
muscle. The three grinding teeth of each half jaw.
monocytes. Large mononuclear leucocytes with kidney-shaped nuclei.
monoeocious. Having male and female flowers separated on the same plant.
monophyletic theory. The theory that all forms of blood cells arise from a common primitive type of cell or hemoblast.
monophyodont. Having a single permanent set of teeth.
monorhine. Having a single nares.
myocoele. The connective tissue between two myotomes.
myotome. The muscular portion of a somite.
myxine. The hagfish, a genus of cyclostomes.
nail wall. The skin which covers the base of the nail.
nasal. The nostrils.
nascial. The scaphoid bone of the carpus and tarsus.
Neanderthal. A gorilla-like type of fossil man.
necrobiotic. Dying as a result of functional activity.
neocortex. The major portion of the cerebral hemispheres.
neostoma. The definitive mouth of vertebrates.
neostriatum. An olfactory center, near the corpus striatum, which becomes in mammals the nucleus amygdalae.
nephridium. The ectodermal excretory tubule of annelids and amphioxus.
nephrostome. The opening of a nephridium into the body cavity.
nephrotome. The intermediate portion of the mesodermal somite which gives rise to a renal tubule.
nerve. A bundle of nerve fibers which connect the central nervous system with some part of the body.
nerve fiber. The axon process of a neuron plus sheaths when such occur.
nerve nucleus (nidulus). A group of nerve cells within the central nervous system.
nerve tract. A bundle of nerve fibers of similar origin and function within the central nervous system.
nervus terminalis. A sensory nerve associated with the olfactory.
neuraxon. The nerve fiber or axon process of a nerve cell.
nieurenteric canal. The blastoporic opening which in chordate embryos connects the neural tube with the enteron at the posterior end of the body.
neurolemma. The cellular sheath of an axon.
neurite. The axon process of a neuron which carries impulses away from the cell body.
GLOSSARY

neurobiotaxis. The migration of the cell bodies of neurons towards the source of stimulation.

neuroblast. The embryonic neural cell which forms an axon process.

neuro-epithelial cell. A sensory receptor cell the body of which is located in an epithelium.

neurofibrillae. The fine fibrils within a neuron.

neurogenesis. The differentiation of nervous tissue in ontogenesis.

neuroglia. The ectodermal supporting tissue of the central nervous system.

eurohumor. A nerve secretion which stimulates an effector cell.

neuromast. A cluster of sensory cells in the skin such as is represented in a lateral line organ.

neuromere. An embryonic segmental division of the central nervous system.

neuromuscular spindle. Specialized sense organs located in muscles.

neuron. The functional unit of the nervous system.

neuropore. The anterior opening of the embryonic neural tube.

neurosensorial cell. A sensory or receptor cell the cell body of which lies in an epithelium.

neurostoma. The hypothetical mouth (Delsman) of vertebrate ancestors, 'which is represented in the neuropore of chordate embryos.

neurotendinous spindle. A special type of sensory nerve termination connected with a tendon.

neutrophile. A blood cell with an affinity for neutral stains.

Nissl bodies. Large protein granules with an affinity for basic dyes found in nerve cells.

nodosum ganglion. The ganglion of the vagus below the jugular ganglion.

non-deciduate placenta. The type of mammalian placenta which does not involve the uterine mucosa at birth.

non-medulated. Devoid of myelin sheath.

Nordic. The blond teutonic type of man of northern Europe and Africa.

normoblast. A nucleated stage in the histogenesis of a red blood corpuscle.

notochord. The axial rod between the chordate nervous system and the dorsal aorta.

nuchal. Pertaining to the nape of the neck.

obturator foramen. The opening between the pubis and ischium.

occipital lobe. The posterior lobe of the cerebral hemispheres.

occlusion. The state of being closed.

odontoblast. One of the dentine-secreting cells.

odontoid process. The tooth-like process of the axis (epistropheus) vertebra.

oestrus (estrus). The period of "heat" or receptivity in the female.

olecranon process. The process of the ulna at the elbow.

oliva. A prominence of the medulla oblongata lateral to the pyramid.

omasum (psalterium). The third division of the ruminant stomach.

omentum. A sac formed by the doubling of the mesentery.

ontogenesis. The development of the individual from the egg.

oocyte. The immature egg.

operculum. The gill-cover of fishes.

opisthonephros. The posterior metanephros-like portion of the mesonephros of anamnia.

optic vesicle. The hollow lateral outpocketing of the forebrain which forms the retinal and pigment layers of the eye.

oral hood. The funnel-like membrane which in Amphioxus bears the tentacles.

orbit. The bony socket which surrounds the eye.

os uteri. The orifice of the uterus.
osculum. A minute aperture.
osmosis. The passage of dissolved substances of different concentration through a semipermeable membrane which separates them.
ossification. The formation of bone.
osteoblast. A bone-secreting cell.
ostium tubae. The opening of the oviduct or uterine tube into the body cavity.
otic. Pertaining to the ear.
otoconia (or otoliths). Crystals of calcium carbonate contained in the endolymph of the membranous ear.
ovariotomize. To remove an ovary or ovarian tumor.
oviduct. The egg duct or uterine tube.
oviparous. Egg-laying.
avulation. The discharge of an egg from the ovary.
oxotocin. A pituitary hormone which affects the uterine muscle.

pabulum. Food.
Pacini's corpuscles. Large tactile corpuscles with single dendrite and many-layered capsule.
 palate. The roof of the mouth—hard and soft.
 palatine. The membrane bone which forms the posterior part of the hard palate.
 paleocortex. The primitive cortex, or olfactory portion of the hemispheres.
 paleontology. The science which treats of fossils.
 paleostoma. The hypothetical primitive mouth of vertebrates—possibly represented in the hypophysial duct.
 paleostriatum. The primitive corpus striatum (basal ganglion) as distinguished from the Epi- and Neostriatum.
 paleozoic. The ancient life era from the Cambrian to the Permian period.
 pallium. The cerebral cortex or layer of gray matter which covers the cerebral hemispheres.
 pancreas. A combined digestive and endocrinial gland between stomach and duodenum.
 panniculus carnosus. A layer of integumentary muscles represented in man by the platysma of the neck.
 papilla. A small nipple-shaped elevation.
 parachordal. A cartilage which lies along the anterior end of the notochord.
 paracone. The anterior external cusp of an upper molar tooth.
 paraconid. The anterior cusp of a lower molar tooth.
 paradidymis. A rudiment of the mesonephros near the testis.
 paraphysis. A hollow outgrowth of the anterior dorsal roof of the diencephalon.
 parapodium. One of the paired appendages of annelids.
 parapophysis. A transverse process from the centrum of a vertebra.
 parasite. An organism which depends upon another for its living without paying board.
 parasphenoid. A membrane bone of the roof of the mouth of fishes and amphibia.
 parasympathetic. The craniosacral portion of the autonomic nervous system.
 parathyroid glands. Ductless glands, usually four, which lie near the thyroids.
 parietal organ (eye). The anterior epiphysial outgrowth from the diencephalon.
 paroöphoron. A rudiment of the mesonephros near the mammalian ovary.
 parotid. The serous salivary gland below the ear.
 patella. The knee-pan.
 pecten. A comb-like structure in the vitreous body of the eyes of reptiles and birds.
 pectoral. Pertaining to the chest.
 pedal. Pertaining to the foot.
GLOSSARY

pedicle. The bony connexion between the lamina and centrum of a vertebra.

peduncle. A fiber tract which connects the cerebellum with the brain stem.

Peking man. A fossil species of man intermediate between the Java man and the Neanderthal.

pelvis. The basin-shaped ring of bone which connects back and leg bones.

penis. The male intromittent organ.

pepsinogen. A zymogen which when combined with hydrochloric acid forms pepsin.

peptone. A soluble derived protein formed by the hydrolysis of protein.

perennibranch. With persistent gills.

pericyon. The membranous sac which encloses the heart.

perichondrium. The connective tissue membrane which surrounds cartilage.

periderm. The transient external layer of the mammalian embryonic epidermis.

perilymph. The liquid in the space between the membranous and the skeletal labyrinth of the internal ear.

perimysium. The delicate connective tissue membrane which surrounds a bundle of muscle fibers.

perineum. The floor of the pelvic outlet.

perineurium. The connective tissue covering a nerve cord.

peristalsis. The wave of contraction which passes along the intestine.

peritoneum. The serous membrane which lines the body cavity and covers the viscera.

petrosal. The petrous portion of the temporal bone.

Pflueger's egg tubes. Cords of peritoneal cells which are said to grow into the stroma of the ovary.

phagocyte. A cell which ingests bacteria.

phalanx. One of the finger or toe bones.

phallus. The penis.

pharynx. That part of the alimentary canal which connects mouth and esophagus.

photophore. A luminous organ.

photoreceptor. A sensory cell sensitive to light.

phylogenetesis. Racial history. The evolution of higher from lower animals.

pia mater. The innermost and most vascular of the three coverings of the central nervous system.

pilaster cells. Columnar supporting cells peculiar to fish gills.

pillar cells. Special columnar cells of Corti's organ located between the inner and outer rows of hair cells.

pineal body. The posterior epiphysis of the diencephalon.

pinna. The projecting portion of the external ear.

pisiform. A pea-shaped proximal carpal bone on the ulnar side of the wrist.

pit organs. A pair of sensory pits anterior to the eyes of vipers.

pituitary gland. An endocrine organ attached to the infundibulum.

pituitrin. Extract of posterior lobe of pituitary gland, used to stimulate contraction of smooth muscle (uterus, etc.).

placenta. The mammalian organ of attachment and nutrition of the embryo.

placode. A local disc-like thickening formed as an anlage of an organ.

placoid scale. The typical clasmobranch scale with enamel and dentine layers.

plankton. Floating organisms which may be collected with a tow-net.

plantigrade. Flat-footed.

plasma. The liquid portion of the blood, the serum and fibrinogen.

plasmodesm. A fine protoplasmic thread which connects two cells.

plastraon. The ventral bony shield of the turtle.
platysma. The integumentary muscle of the neck.
pleura. The serous membrane which lines the chest and covers the lungs.
plexus. A network of nerves or blood vessels.
plica. A fold or pleat.
polymerization. The chemical synthesis of two or more molecules to form a new compound without the production of a secondary compound.
polymorphonuclear leucocyte. A white blood corpuscle which has a nucleus with irregular constrictions.
polyp. The sessile or attached stage of a coelenterate.
polyphyletic theory. The theory that the various blood cells have had a multiple origin.
polyphyodont. Having more than two sets of teeth.
pont. A bridge of fibers below the cerebellum which connects cerebrum, cerebellum and medulla oblongata.
postanal gut. That part of the embryonic digestive tract posterior to the anus.
postfrontal. A roofing bone of the skull posterior to the frontal.
posttrematic branch. That division of a cranial nerve which forks behind a gill-slit.
precoracoid. The anterior of the two ventral elements of the pectoral girdle.
pregnancy. The condition of being with child. Gestation.
preamandibular cavity. The second somite which forms the superior oblique eye muscle and—it is asserted—a part of the external rectus.
premolar. A bicuspid tooth.
preoral gut. That part of the embryonic intestine which is anterior to the mouth.
prepuce. The skin fold which covers the glans penis or the clitoris.
pretrematic branch. The nerve branch which forks in front of a gill-slit.
primitive duct. The pronephric duct.
primitive streak. The elongated and closed blastopore of amniote embryos.
process theory. The theory that nerve fibers (axons) develop as processes of neuroblast cells.
proctodeum. That portion of the hindgut which is lined by ectoderm.
progesterone. A luteal hormone which affects the endometrium of the uterus.
progon. A proprietary name for the female sex hormone.
pronation. The act of turning the palm of the hand downwards.
pronephroi. The primitive vertebrate kidneys.
proprioreceptors. The mechanisms for receiving stimuli from within the body.
propterygium. The anterior basal element of the fish extremity.
promencephalon. The anterior division of the embryonic brain which forms the cerebral hemispheres.
prosimian. Pertaining to primitive apes.
prostate gland. A muscular gland which surrounds the urethra where it leaves the bladder.
prostomium. The preoral lobe of Annelids.
proterostomia. Those animals in which the blastopore becomes the mouth or lies near the mouth.
proteose. A soluble protein formed by hydrolytic cleavage of a protein.
protochordate. The primitive chordates which do not acquire a vertebral column.
protocone. The inner cusp of an upper molar.
protoconid. The outer cusp of a lower molar.
protonephridia. Primitive excretory tubules without nephrostomes and with solenocytes.
prototype. The original form or type from which others evolve.
proximal. Towards the body.
pseudocoelom. A false body cavity not lined by peritoneum.
pterygoid. A portion of the mandibular arch which doubtfully becomes the pterygoid process of the mammalian sphenoid.

ptyalin. The starch-splitting enzyme found in the saliva.

puberty. The age at which reproductive organs start to function.

pubis. The anterior of the two ventral arms of the pelvic girdle.

Purkinje cells. Large much-branched neurons of the cerebellar cortex.

putamen. The outer darker portion of the lenticular nucleus of the corpus striatum.

pylorus. The aperture at the posterior end of the stomach.

pyramids, renal. The conical masses present in the medulla of the kidney.

pyramids of the medulla. Paired eminences on the ventral side of the medulla.

pyramidal cells. Neurons with pyramid-shaped cell-bodies in the cerebral cortex.

Rathke’s pouch. The hypophysis of amniote embryos.

ray-finned fishes. Fishes with bony and horny rays—includes most fishes.

recapitulation theory. The theory that individual development repeats briefly the evolutionary history of the race.

receptaculum (cisterna) chyli. A chamber for the storage of lymph at the lower end of the thoracic duct.

receptor. A sensory cell.

rectum. The lower six to eight inches of the large intestine.

red nucleus. A nervous center in the tegmentum of the midbrain. Its cells contain a red pigment.

reduction. Meiosis. The process by which the haploid number of chromosomes is attained.

reflex action. An action which involves a reflex arc, i.e., a sensory and a motor neuron connected within a central nervous system.

renal corpuscle. The expanded termination of an excretory tubule containing a glomerulus.

respiration. The regulated burning of carbon compounds within living cells.

restiform bodies (inferior peduncles). A fiber tract which connects sensory spinal nerves with the cerebellum.

rete testis. A network of fine ductules between the seminiferous tubules and the ductuli efferentes.

retina. The sensory innermost layer of the eye.

Rhodesian man. A prehistoric type of man having affinities with the Neanderthal man.

“rhomboid.” A kite-shaped area where four hair currents meet.

rhombomere. A hindbrain neuromere.

roof plate. The median dorsal wall of the embryonic neural tube.

rods and cones. The receptor cells of the retina.

rubrospinal tract. A longitudinal fiber tract which connects the red nucleus with the somatic motor cells of the spinal cord.

rumen. The anteriormost stomach of a ruminant.

saccus. The membranous sac connected with the cochlear duct of the ear.

sacrum. The five fused vertebrae to which the ilium is attached.

sagittal plane. A median longitudinal vertical section.

Santorini’s duct. The accessory duct of the pancreas.

sarcotubule. The delicate elastic membrane which surrounds a muscle fiber.

sarcolemma. The intercellular substance of a striped muscle fiber.

Savi’s vesicles. Cranial sensory vesicles of Torpedo without external openings.

scala media. The cochlear duct.
scala tympani. The ventral or descending staircase of the cochlea.
scala vestibuli. The dorsal or ascending staircase of the cochlea.
scapula. The shoulder blade. The dorsal arm of the pectoral girdle.
Schwann’s sheath. The neurilemma of a nerve fiber.
sclerotic (sclera). The tough white outer covering of the eye-ball.
sclerotome. The part of the somite which forms the vertebral column.
scrotum. The integumentary sac in which the testes of mammals are lodged.
scute. A scale-like skeletal structure.
sebaceous gland. A gland which produces a greasy secretion.
secretin. An intestinal hormone which activates the pancreas.
secretion. A product of cell metabolism which is thrown out as waste or used by the organism in its normal activity.
sella turcica. The pituitary fossa in the sphenoid bone.
semen. The external secretion produced by the male in coitus.
semicircular canal. One of the ducts of the membranous ear used in equilibration.
semilunar valves. Crescentic valves at the root of the aorta and pulmonary artery which prevent blood from returning to the ventricles.
seminal vesicle. A secretory gland and reservoir for spermatozoa connected with the ductus deferens.
seminiferous tubule. One of the secretory tubules of the testis.
septum testis. The connective tissue partitions which divide the testes into compartments.
septum pellucidum. A double membrane which lies in the median plane of the brain, between the corpus callosum and the fornix.
septum transversum. A transverse partition which separates pericardial and peritoneal cavities of vertebrates.
serous gland. A gland which secretes a thin watery secretion (serum).
Sertoli cells. Columnar cells of the seminiferous tubules, which serve as a base of attachment for spermatozoa.
serum. The clear liquid portion of the blood devoid of cells and of fibrinogen.
 sessile. Fixed or attached.
sex. The differentiation of two kinds of reproductive cells and of the individuals which produce them.
shell membrane. A tough double membrane attached to the shell of the hen’s egg.
sigmoid flexure. The bent lower part of the colon to the rectum.
Sinanthropus. The Peking species of fossil man.
sino-auricular node. A group of fibers at the root of the precava which in contraction serves as “pace-maker of the heart” beat.
sinus. A cavity or hollow space.
sinusoid. Relatively large anastomosing blood spaces lined by endothelium without adventitia.
solenocyte. An elongated flagellated excretory cell associated with the protonephridia of annelids.
somatic muscle. Derived from the somite or epimere in contrast with the visceral muscle which is derived from the hypomere.
somatopleure. The combined layers of ectoderm and parietal mesoderm.
somite. A segment of the dorsal or epimeric mesoderm.
spermatogonia. Immature germ-cells which by enlargement form the primary spermatocytes.
sphenopalatine ganglion. Meckel’s ganglion of the autonomic and facial nerves.
splanchnopleure. The double embryonic layer formed by the visceral layer of mesoderm and the endoderm.
spongioblast cells. The cells of the neural tube which form ependyma and glia cells.
squamosal. The bone which forms the thin vertical element of the temporal.
stapes. The innermost ear bone which is attached to the foramen vestibuli.
static organ. An organ of equilibration, a statocyst.
status thymicolympathicus. A edematous condition associated with enlarged thymus.
steapsin (lipase). A fat-splitting enzyme secreted by the pancreas.
Steno's (Stensen's) duct. The duct of the parotid gland.
sternebra. One of the segments of the sternum.
stimulofugal. Reacting by motion or growth away from a stimulus.
stomodeum. The ectodermal invagination which leads to the formation of the mouth.
stratum corneum. The outer horny layer of the epidermis.
stratum germinativum. The lowest layer of the epidermis from which the other layers are derived.
stroma. The connective tissue matrix of an organ.
styloid. Long and pointed.
sublingual gland. A salivary gland below the tongue.
submaxillary gland. A mixed salivary gland below the angle of the lower jaw.
submucosa. The connective tissue layer below the mucous lining of the intestine.
sulcus. A groove or fissure especially of the brain.
superciliary. Pertaining to the region of the eyebrows.
superior colliculi. The anterior larger pair of swellings of the corpora quadrigemina.
supination. Turning the palm upwards.
Sussex man. A prehistoric type of man the remains of which were found at Piltdown, Sussex, England.
suture. The line of junction of two cranial bones.
sympathin. A neurohumor secreted by sympathetic nerves.
symphysis. The line of junction of primarily separate bones.
synapse. The histological connexion between two neurons.
synarthrosis. The fusion of two bones with resultant elimination of a joint.
synctium. A multinucleate mass of protoplasm.
systole. The contraction of the heart.
talus (astragalus). The ankle bone which articulates with the tibia.
tarsal (Meibomian) glands. Sebaceous glands of the eyelid.
tarsus. The ankle or instep with its seven bones.
taste-bud. A cluster of chemoreceptors which form a taste-organ.
Taungs man-ape. A fossil ape skull discovered in South Africa.
taurodont. Having a small pulp-cavity and thus resembling a human tooth.
tectorial membrane. The colloidal membrane which covers Corti's organ of the cochlear duct.
tectum. The roof of the midbrain.
tegmentum. The gray matter which covers each of the brain peduncles.
telencephalon. The anteriormost of the five brain vesicles which forms the cerebral hemispheres.
teloblast cells. The posterior pair of cells which in annelids forms the mesodermal bands.
telodendria. The motor end-plates or terminations of a neurite.
tendon. The fibrous attachment which connects a muscle with a bone or other structure.
teniae coli. Three longitudinal muscle bands of the colon.
tentorium cerebelli. The dura mater partition between cerebrum and cerebellum.
terminal nerve. A ganglionated portion of the olfactory nerve.
tetany. Painful muscular spasms associated with calcium deficiency.
thalamus. Gray matter located in the lateral walls of the diencephalon.
thecodont. That type of dentition in which the teeth are lodged in sockets.
thelin. The female sex hormone.
thoracic duct. The main lymph channel which conveys lymph from the lower half of
the body to the left jugular vein.
thrombin (fibrinogen). A hypothetical enzyme in clotted blood which converts
fibrinogen into fibrin.
thymus. A ductless gland, largest in infancy, which lies below the sternum in the
mediastinum.
thyroglossal duct. A rudiment of the connexion of the thyroid gland with the pharynx.
thyroid gland. An endocrine organ located on the sides of the trachea.
thyroxine. The iodine-containing hormone secreted by the thyroid gland.
tibia. The shin bone which carries the weight of the body to the ankle.
tigroid substance. The deeply-staining granular substance which forms the Nissl
bodies.
tonus. The normal condition of tension of a muscle.
Tornaria. The free-swimming larva of Balanoglossus (Hemichordate).
trabeculæ. The embryonic prechordal cartilages which enter into the formation of
the basicranium.
trachea. The cartilaginous tube which connects the larynx with bronchial tubes.
tragus. The cartilaginous projection before the opening of the auditory meatus.
transverse septum. The connective tissue partition which separates the pericardial
cavity from the abdominal cavity.
triconodont. A primitive type of dentition in which three cusps in line occur.
tricuspid valve. The right atrio-ventricular valve.
trigone. A triangular area as of the bladder.
trilobite. A fossil crustacean extinct since the Carboniferous.
triquetrum. A proximal carpal bone between the lunate and the pisiform.
trochanter. One of the two processes below the head of the femur.
trochea. A pulley-like structure.
trochophore. The swimming larval stage of some annelids.
trophoblast. The ectodermal portion of the fetal villi of mammalian embryos.
trypsin. The protein-splitting enzyme secreted by the pancreas.
tuber cinereum. A conical process of the subthalamus between the mammillary bodies
and the infundibulum.
tuberculum impar. The anlage of the apex of the tongue.
tuberosity. A tuber-like process of a bone.
tunica. A covering tissue or coat.

ultimobranchial (postbranchial) bodies. Glands of unknown function derived from
the last pair of pharyngeal pouches.
umbilicus. The scar which marks the abdominal connexion of the umbilical cord.
uncinate. Hooked.
un cusus. The backward-bent anterior portion of the hippocampal gyrus.
ungenulate. Hoofed.
urachus. The canal which leads to the allantois and which becomes the median
umbilical ligament.
ureter. The duct which connects the metanephros (kidney) with the bladder.
urethra. The outlet of the bladder. In the male the urinogenital passage.
uterus. The "womb" in which the fetus develops.
utriculus. That part of the static organ with which the semicircular canals connect.
uvula. The median posterior pendulous process of the soft palate.
vagina. The tubular passage from the uterus to the outside.
valvulae conniventes. Transverse folds of the lining of the small intestine.
varicose. Tortuous and swollen.
vas deferens. The efferent duct of the testis.
vasa efferentia. The ductules which connect the testis with the ductus (vas) deferens.
vasopressin. An hormone secreted by the posterior lobe of the pituitary, which stimulates contraction of smooth muscle.
veliger. The trochophore larva of molluscs.
ventricle. A small cavity such as is found in the brain and heart.
vermis. The median lobe of the cerebellum.
vernix caseosa. The waxy covering of the fetal skin.
vesicle. A liquid-filled sac or cavity.
vitamin. A food substance of unknown composition necessary for growth and health.
vitelline. Pertaining to vitellus or yolk.
vitreous humor. The translucent semisolid substance between retina and lens.
viviparous. Giving birth to living young.
volvox. A genus of flagellate algae.

Wharton’s duct. The duct of the submaxillary.
Wirsung’s duct. The duct of the pancreas.
Wolffian ducts. The ducts of the mesonephros. In the male the ductus deferentes.
Wolffian folds or ridges. Paired longitudinal ridges of the embryo from which the paired appendages are differentiated.

xiphisternum. The xiphoid cartilage of the sternum.

zygapophysis. An articular process of a vertebra.
zygomatic bone. The malar bone.
zymogen. An enzyme-forming substance.
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