CHORDATE ANATOMY

Neal AND *Rand*

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WITH 378 ILLUSTRATIONS

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PREFACE

Comparative anatomy has both practical and theoretical interest. Courses in it based, like other science courses, upon laboratory work give the student first-hand acquaintance with the structure of fishes, amphibians, reptiles, birds and mammals. If, as psychologists assert, all our ideas derive from sense impressions, all real knowledge of animal structure must be based upon such laboratory experience. "Starve the senses and you starve the soul." In the laboratory, as the student increases his acquaintance with animals, he gains also in resourcefulness and independence. Many biologists believe that comparative anatomy affords the best approach to the understanding of human structure and function. In many American colleges and universities the course in comparative anatomy is a prerequisite to advanced courses in histology, embryology and physiology. In this way the student passes in his analysis from the general to the particular, from the gross to the microscopic.

To many persons, however, the theoretical interest of comparative anatomy makes stronger appeal than does practical familiarity with animals. The major problem which faces the student of comparative anatomy is that of the genesis of the human body. The clue which gives meaning to many of the details of anatomy is found in the evolution theory. Most teachers of biology are so convinced of the truth of that theory that the issue is no longer debated by them. Each generation, however, must examine for itself the evidence which has led to the general acceptance of evolution by experts. While the record of the rocks is probably the most convincing evidence of evolution, the facts of comparative anatomy greatly strengthen the case for evolution. As a result of the researches of several generations of comparative anatomists, it is now possible to sketch in fairly firm outlines the hypothetical past history of the human body. One of the purposes of this book is to summarize some of this evidence.

To meet the laboratory needs of students, a number of excellent laboratory guides have been written, some dealing with the dissection of a single animal, others with several animals. Most of them, however, make no attempt to deal with animals comparatively. They let the student make his own comparisons, which is possibly more than may be expected of him. The present book is intended to help him in these comparisons and to correlate and interpret the facts gathered in the laboratory. The material presented has been selected for the light it throws on the phylogenesis (racial history) and the physiology of the human body.

The present text has been written to meet the needs of students in semester courses in comparative anatomy. It is an abbreviation of the Comparative Anatomy written by the same authors and published in 1936. In the condensation, however, no material essential to the proper understanding of the physiology and phylogenesis of the human body has been omitted. Due acknowledgment of assistance in the preparation of the book has been made in the earlier work, to which the reader is referred.

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CHORDATE ANATOMY

CHAPTER I

THE ANIMAL KINGDOM

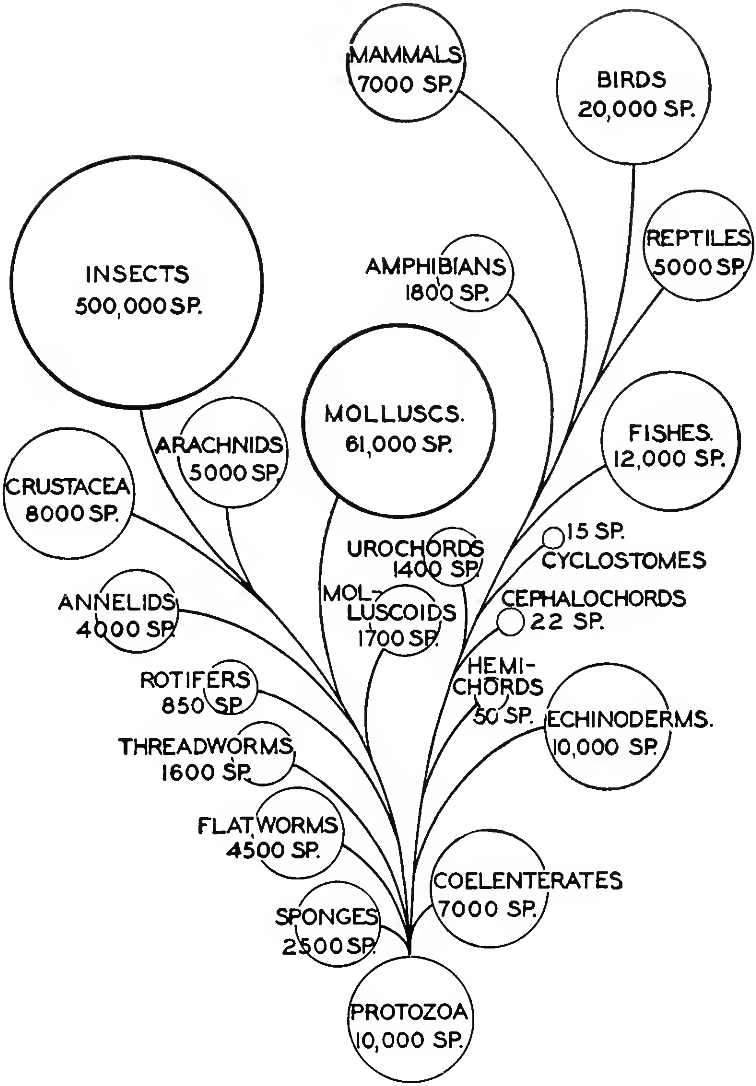
Since some of the so-called lower animals, living or extinct, more or less resemble hypothetical ancestors of man, some knowledge of them is necessary for a proper understanding of the history of the human body. Moreover, certain highly complex and obscure organs of man are most easily understood in 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's fly-trap, catch and devour insects; and also some of the unicellular algae 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,



A PHYLOGENETIC TREE OF THE ANIMAL KINGDOM.

FIG. 1.—A phylogenetic tree of the animal kingdom, showing the dichotomy of animals into Proterostomians and Deuterostomians.

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.

On the basis of the number of cells in the body animals are divided into the two **Sub-Kingdoms**—(1) the unicellular **Protozoa,** (2) multicellular **Metazoa.** Since the Protozoa are the simpler organisms, it may be assumed that the first animals on earth were protozoans.

The division of animals into the two phylogenetic series graphically represented in Fig. 1 is based upon differences in the fate of the embryonic mouth or **"blastopore."** The left-hand branch includes the **Proterostomians,** which are the Metazoa in which the blastopore becomes the mouth or lies near the adult mouth. Most animal phyla are Proterostomians, which include such diverse forms as the **Porifera, Coelenterates, Platyhelminths, Molluscoids, Rotifers, Annelids, Molluscs** and **Arthropods.** This branch of the animal kingdom reaches its climax in the arthropods and molluscs.

The **Deuterostomians** are the animals in which the blastopore becomes the anus or lies near the anus. The group includes the **Echinoderms** and the **Chordates.** The branch reaches its climax in the vertebrates and man.

Since our present interest centers in man and chordates, and since none of the non-chordate phyla are believed to lie in the direct line of human ancestry, the non-chordate phyla will be mentioned only when they possess structures resembling those of the hypothetical ancestors of man. It may be assumed that students in a comparative anatomy course have some acquaintance with non-chordates. Consequently no detailed description of them is needed here. We may therefore turn our attention directly to the sub-phyla and classes of chordates.

Phylum CHORDATA

The chordates are animals which, at least early in life, have a supporting 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—**Hemichorda, Urochorda, Cephalochorda,** and **Vertebrata.**

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, enteric coelomic pouches, a notochord-like diverticulum of the fore-gut in the preoral lobe, and upon the relations of the blood-vessels and nerves. Segmental excretory organs are, however, absent.

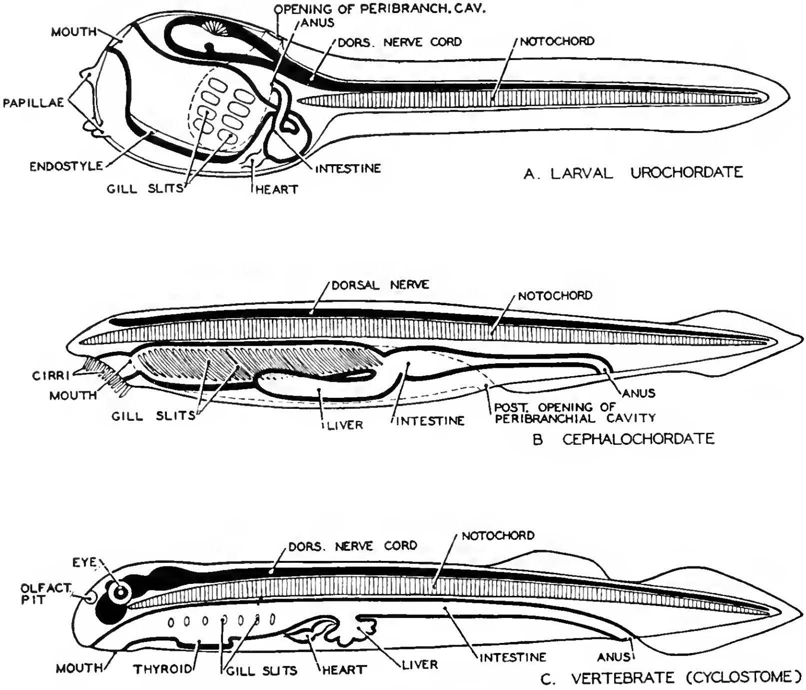


FIG. 2.—Diagrams of *A*, larval urochordate, *B*, cephalochordate (Amphioxus), and *C*, vertebrate (Petromyzon), illustrating the fundamental characteristics of chordates; redrawn after Hesse-Doflein.

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.

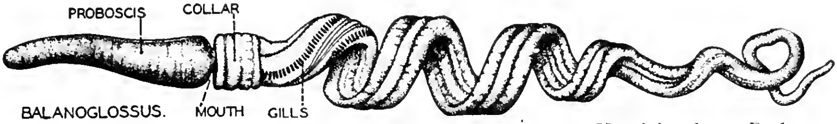


FIG. 3.—Balanoglossus, a typical genus of the sub-phylum Hemichorda. (Redrawn after Bateson.)

The pharynx is divided into a dorsal portion which 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.

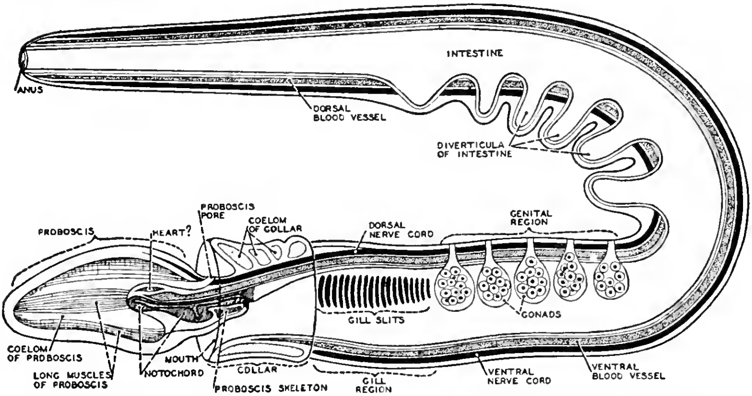


FIG. 4.—Balanoglossus, the typical genus of the hemichordates, seen in left lateral aspect. The possession of both dorsal and ventral nerve-cords links hemichordates on the one hand with invertebrates and on the other with vertebrates. (Redrawn after Stempell.) For the purposes of the diagram, the body of the animal is bent upon itself.

The nervous system consists of dorsal and ventral nerve strands containing occasional giant nerve cells. There are no special sense organs.

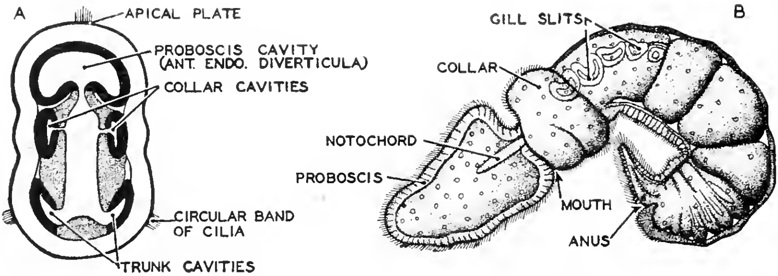
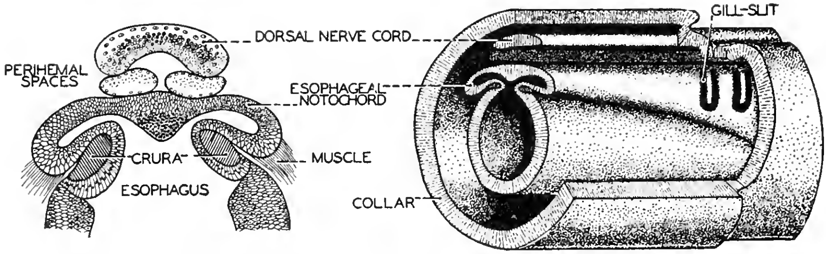


FIG. 5.—Balanoglossus embryos. *A*. A horizontal section of a young embryo, showing the origin of mesodermal pouches. McBride and others have noted the similarity of this section to that of a young Amphioxus embryo as evidence of the close affinity of these two forms. *B*. A young Balanoglossus larva 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.)



A ESOPHAGEAL REGION – X.S. B. HARRIMANIA – STEREOGRAM OF COLLAR REGION.

FIG. 6.—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.)

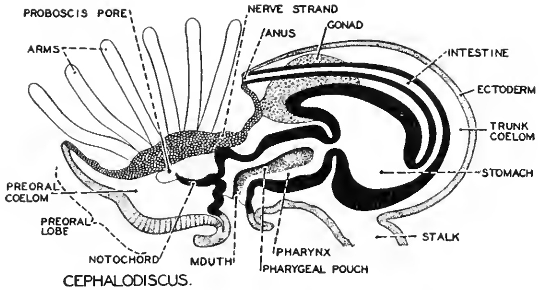


FIG. 7.—A diagram of Cephalodiscus viewed from the left side as if in median optical section. The presence of a notochord in the pre-oral lobe is one of the reasons for placing this animal among hemichordates. While not regarded as a form "ancestral" to vertebrates, Cephalodiscus interests morphologists as a primitive chordate. (Redrawn after W. Patten.)

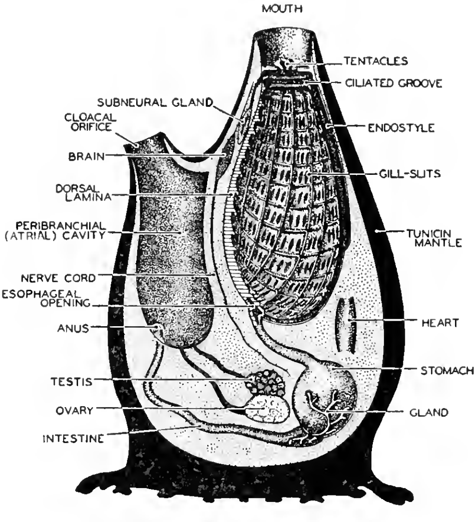
The so-called notochord is a diverticulum of the intestine which extends with a narrow lumen into the proboscis from a point just behind the mouth.

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.

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 metamor-



ASCIDIA - A UROCHORDATE

FIG. 8.—Ascidia, a urochordate. The animal is viewed as if cut in median longitudinal section and as seen from the right side. (Redrawn from Sewertzoff, after Boas.)

phosis. 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.

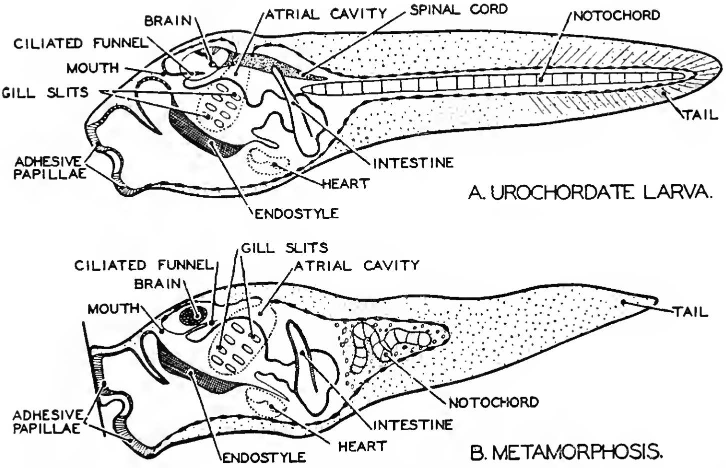


FIG. 9.—Diagrams of stages in the metamorphosis of a urochordate larva. When the larva settles down and becomes fixed by its adhesive papillae, the tail is lost and the notochord disappears. Thus the chordate characters which are so evident in the larva are partly lost in the mature organism. (Redrawn from Korscheldt and Heider, after Seeliger.)

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.

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 pituitary gland of vertebrates. The unpaired eye and static organ contained in the brain vesicle of the larva degenerate in the metamorphosis.

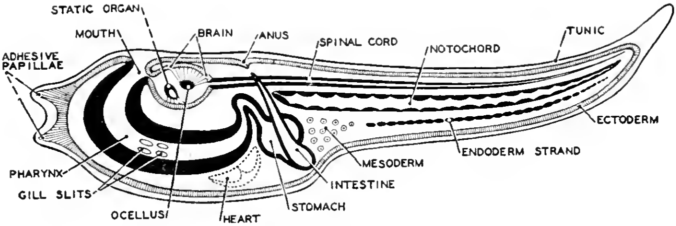


Fig. 10.—Diagram of a larval urochordate. The similarity of the larval urochordate to the embryo of a cephalochordate (Amphioxus) suggests that a form like this lies near the main line of vertebrate ancestry. (Redrawn after von Beneden and Julin modified.)

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.

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. Its resemblance to the larva of cyclostomes is impressive. (Fig. 11)

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 atriopore just behind the pharynx. In the region of the pharynx, a pair of ventro-lateral **metapleural folds** extend as far back as the atriopore.

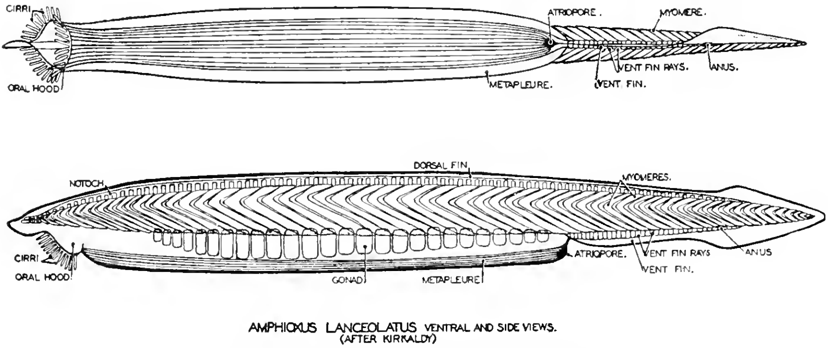
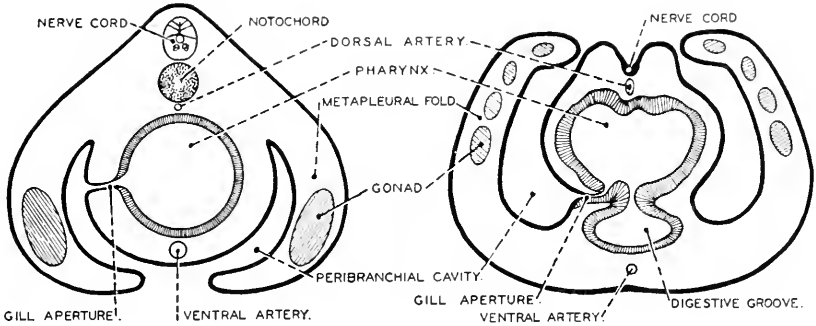


FIG. 11.—Amphioxus, in ventral and side views. Metamerism, lacking in urochordates, and scarcely evident in hemichordates, is strikingly shown by Amphioxus. Whether this metamerism is inherited from annelid-like ancestors or is a convergent trait independently acquired, is a moot question in morphology. (Redrawn after Kirkaldy.)

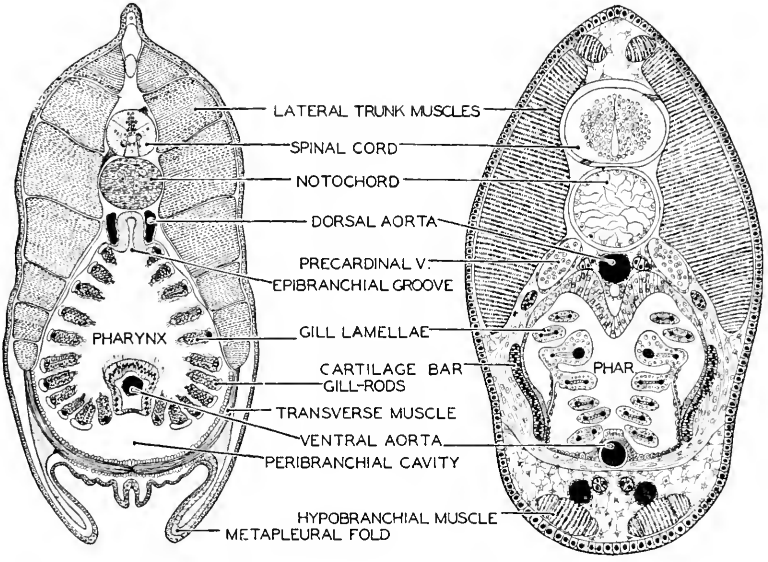
The body is covered by a thin external cuticula secreted by the simple epithelial epidermis. Beneath the skin and visible through it are sixty pairs of myotomes which alternate with one another along the two sides of the body. As in the vertebrates generally, these myotomes are greatly thickened along 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 to the endostyle of urochords, extends the entire length of the pharynx.



A. AMPHIOXUS. B. PTYCHODERA.

FIG. 12.—Diagrams illustrating divergent methods by which the peribranchial cavity is formed. In Amphioxus (*A*) the pleural folds are separated from the pharynx by paired folds which extend dorsally from the ventral side. In the hemichordate Ptychodera (*B*), on the other hand, the paired folds begin to form at the dorsal side of the worm and extend ventrally. The peribranchial cavity in urochordates arises in a similar manner. As frequently happens in animals, a similar end-result is attained by divergent means. (Redrawn after Gaskell.)



A. AMPHIOXUS B AMMOCOETES.

FIG. 13.—Cross sections of *A*, Amphioxus and *B*, Ammocoetes (larval Petromyzon) through the pharyngeal region showing their fundamental resemblance.

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. 263)

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, but 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 fore-brain 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 may be 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. There are no scales in the skin, and the teeth are horny. Some species are hermaphroditic. Paired appendages are absent.

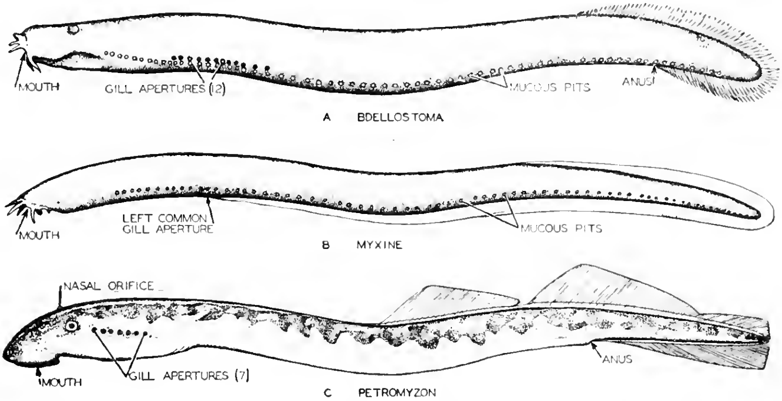


Fig. 14.—Three characteristic genera of cyclostomes—Bdellostoma, Myxine, and Petromyzon. That they are the most primitive vertebrates is shown in many traits, such as a permanent notochord, absence of paired appendages and jaws, etc. (Redrawn after Dean.)

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.

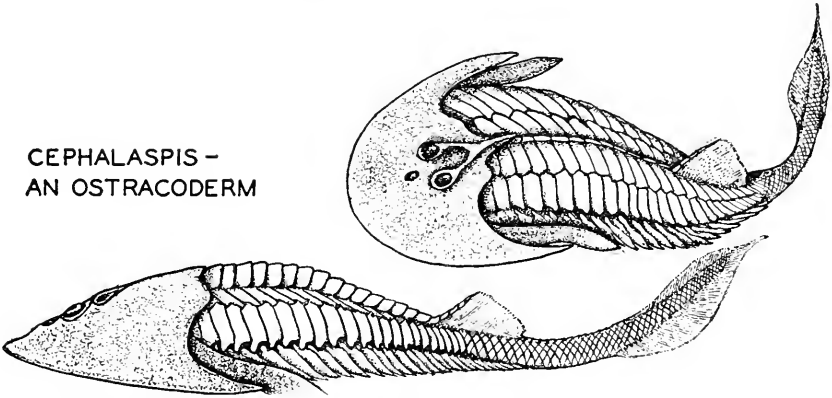


Fig. 15.—Cephalaspis, an ostracoderm, appears to have affinities with cyclostomes and has been thought by W. Patten to connect vertebrates with arachnids.

Class Ostracodermi

The ostracoderms are fossil forms which, as Stensiö and others have shown, resemble cyclostomes in some striking respects. Unlike the latter,

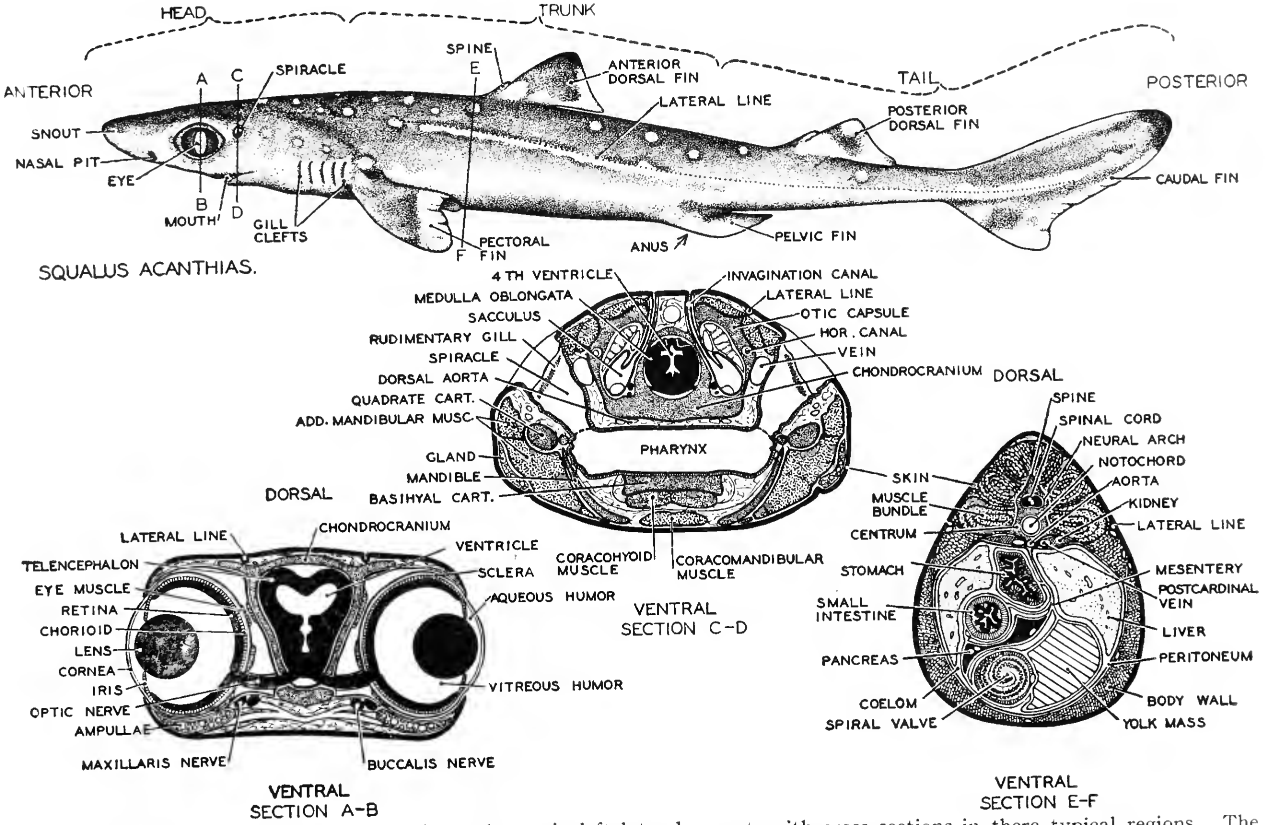


FIG. 16.—Squalus acanthias, a typical vertebrate, in left lateral aspect, with cross sections in there typical regions. The figure illustrates the chief features of vertebrate topographic anatomy. Section *A-B* is taken through the eyes; section *C-D* through the spiracles; section *E-F* through the trunk immediately anterior to the anterior dorsal fin.

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.

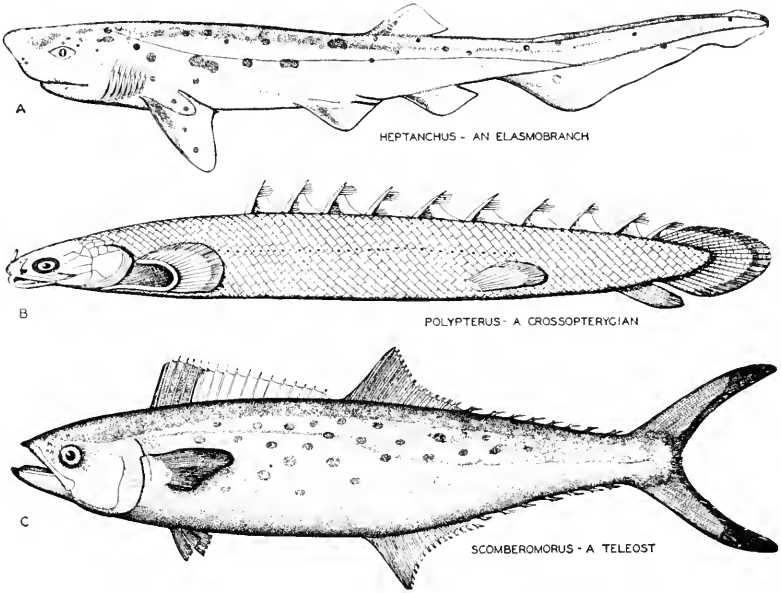


FIG. 17.—Types of three sub-classes of fishes—Heptanchus, an elasmobranch; Polypterus, a crossopterygian ganoid; and Scomberomorus, a teleost. (Redrawn after Dean.)

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 near the line of ancestry of land animals. Probably cartilaginous forms like the **Elasmobranchs** (sharks and skates) were the common stock from which the remaining orders of fishes were evolved. Their gills are not covered by an operculum; their skull is devoid of covering membrane bones; their intestine has a spiral valve. The dogfish **Squalus** (Fig. 16) is a familiar example.

Ganoids are "ray-finned" forms with either cartilaginous or bony skeletons. Their gills are covered with an operculum; they have a spiral valve; the tail is heterocercal; their air-bladder is connected with the pharynx or esophagus by means of an open duct; their skin has ganoid scales, or sometimes, bony scutes, or it may be naked. The order of **Crossopterygii,** "lobe-finned" ganoids, which make their first appearance in the Devonian period, were air-breathers and possibly the direct ancestors of land animals. The Nile "bichir," **Polypterus,** is a living representative of this largely extinct group. The sturgeon is a familiar example of the ganoid group.

Teleosts are "ray-finned" forms with a wholly bony skeleton. Unlike the ganoids their tail is never heterocercal. They are usually scaly but may be scaleless. The air-bladder when present does not have an open duct; they lack a spiral valve. Teleosts are the most abundant of fishes. The cod and salmon are familiar types.

Arthrodires are fossil fishes possibly related to the modern lung-fishes or Dipnoi. The **Dipnoi** are not believed to be the ancestors of land forms, but they are in many ways transitional in structure between fishes and amphibia. They may have either one or two lungs. The Dipnoi are represented by the **Ceratodus** of Australia.

Class Amphibia

Amphibians bridge the gap between land and water vertebrates. Either permanent or temporary gills occur. Lungs are usually present, but some are lungless. 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.

FIG. 18.—Necturus, a urodele amphibian, interests zoologists because more than any other living amphibian it resembles the fossil Stegocephala, another "ancestral" group.

Amphibia are subdivided into **Urodela** 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 fossil 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 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** (Serpentes), **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.

Rhynchocephalia are mostly fossil reptiles having very primitive characteristics. Like some primitive amphibians they have only two sacral vertebrae. **Sphenodon** (Hatteria), the only living representative, lacks the external copulatory organs present in all other reptiles.

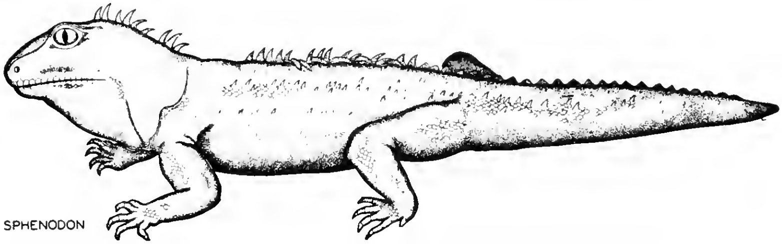


FIG. 19.—Sphenodon has been characterized as a "living fossil." As a "primitive" type of reptile it interests the student of phylogenesis. It belongs to the Order Rhynchocephalia.

The **Lacertilia** are the lizards. They usually have two pairs of limbs; the anus is a transverse slit; eyelids and an external ear opening are usually present.

Ophidia (Serpentes) are limbless reptiles devoid of movable eyelids and external ear-opening; the tongue is forked; the scales along the ventral side of the body are specially modified to assist in locomotion. Snakes.

Chelonia (Testudinata) are toothless reptiles, the broad bodies of which are enclosed by a "shell" which consists of a dorsal **carapace** and a ventral **plastron.** The eyes have lids and nictitating membrane. Turtles and tortoises.

Crocodilia have their teeth set in alveoli; the anus is a longitudinal slit; the tail is laterally compressed; the bodies are large. Alligators and Crocodiles.

Theromorpha are fossil reptiles which may have been the progenitors of mammals; in some the teeth are differentiated as in mammals; the quadrate bone is attached to the cranium as in mammals; the zygomatic arch of the skull resembles that of mammals.

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.

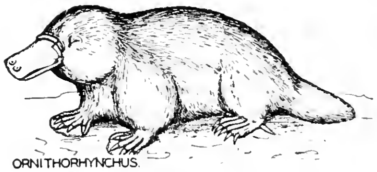


Fig. 20.—Ornithorhynchus is a representative of the most primitive group of mammals, the monotremes. As an egg-laying mammal it bridges over the gulf separating reptiles and mammals.

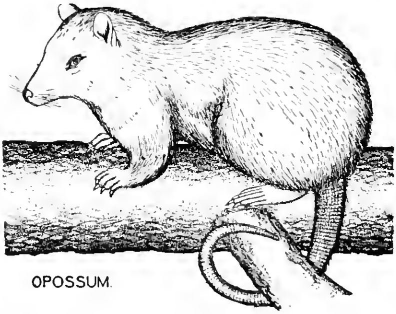


Fig. 21.—Opossum, the typical genus of didelphians. (Redrawn after Newman.)

Sub-Class Monotremata (Prototheria)

The monotremes or ornithodelphians 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 didelphians 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 PLACENTALS

The placentals or monodelphians 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 unspecialized, so that they are apparently nearest of surviving forms to the original placental.

ORDER 2. XENARTHRA. The Xenarthra 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.

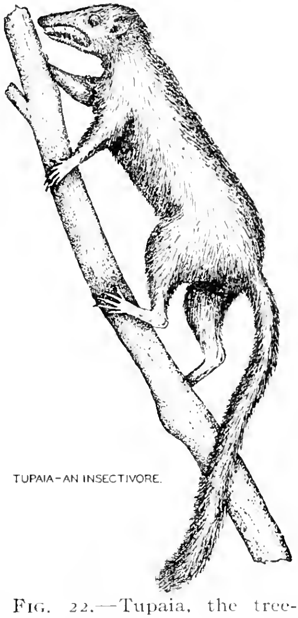


FIG. 22.—Tupaia, the tree-shrew, an insectivore.

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.

ORDER 5. ARTIODACTYLA. Artiodactyls are such hoofed forms as cattle, deer, swine, sheep, goats, camels, llamas, hippopotamuses, and giraffes, which usually 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 usually have an uneven number of hoofs on each foot. They include the horse, ass, zebra, tapir, and 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 on each foot 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.

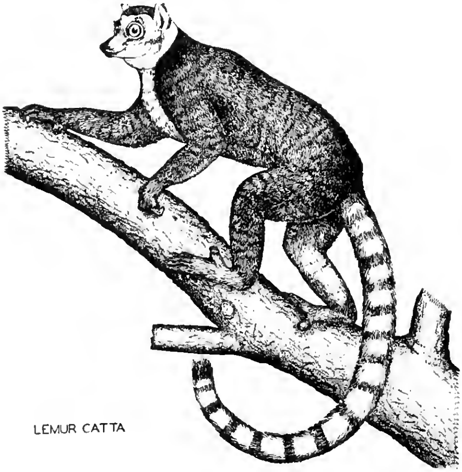


FIG. 23.—Lemur, a primitive Primate. (Redrawn after Shipley and McBride.)

ORDER 9. CHIROPTERA. Chiroptera are the bats and flying foxes. Their anterior limbs are modified to support the 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. 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.

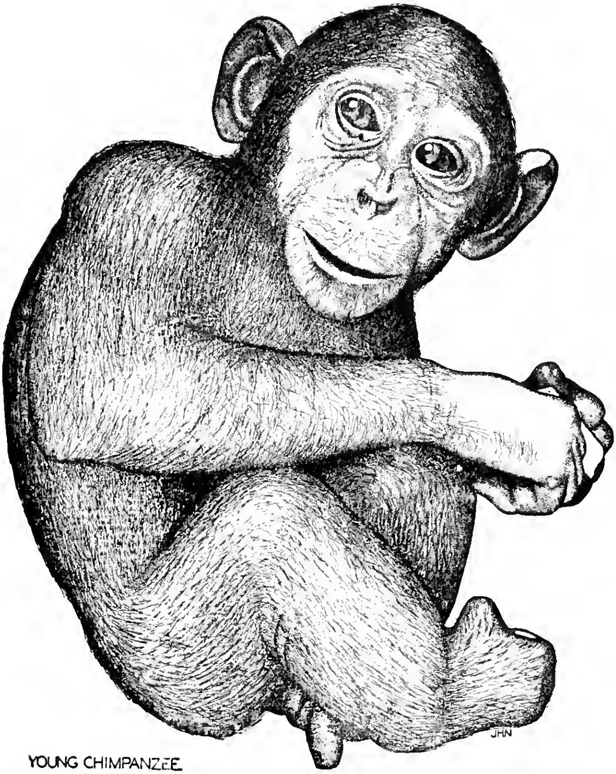


Fig. 24.—Young chimpanzee, a type of anthropoid. (From photograph by Fred Johnson.)

Three chief sections of anthropoids are recognized:

Platyrhina. 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 in each half jaw, 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.

2. PORIFERA. Multicellular. Acoelomate. Pores in body-wall.

3. COELENTERATA. Multicellular. Acoelomate. Radial symmetry may possibly disguise primitive bilateral symmetry. Two-layered body-wall. Nettling-cells. Enteron with single opening.

4. PLATYHELMINTHES. Bilateral. Flat-bodied. Without coelom. Anus in a few genera.

5. NEMATHELMINTHES. Pseudocoelomate. Cylindrical. Anus.

6. MOLLUSCOIDA. Usually coelomate. U-shaped alimentary canal. Lophophore.

7. ROTIFERA. Pseudocoelomate. Trochophore-like worms. Cilia around mouth.

8. ECHINODERMATA. Coelomate. Spiny-skinned. Water-vascular system. Bilateral symmetry disguised.

9. ANNELIDA. Coelomate. Metameric. Appendages, when present, without joints.

10. MOLLUSCA. Coelomate. Non-metameric. Mantle, mantle-cavity, foot.

11. ARTHROPODA. Pseudocoelomate. Metameric. Jointed appendages.

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. **Appendicularia, Ascidia.**

CEPHALOCHORDA. Notochord in head, trunk, and tail throughout life. Metameric. **Amphioxus.**

Hemichorda, Urochorda and Cephalochorda together are often called protochordates.

VERTEBRATA. Chordates with brain case and vertebrae. **Squalus.**

CLASSES OF VERTEBRATES (**Craniota**)

1. CYCLOSTOMATA. Without paired appendages or biting jaw. Usually hermaphroditic. Petromyzon, Myxine, Bdellostoma.

2. OSTRACODERMI. Fossil monorhine fishes related to the cyclostomes.

3. PISCES. With paired appendages and movable lower jaw. Skin usually scaly. Permanent gills. Fishes are subdivided into five subclasses:

Elasmobranchii. Gills lack operculum. 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. Claws or nails lacking.

The **Stegocephala** are a group of fossil amphibians.

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—no gills. Aortic arch on both sides. The **Theromorpha** are fossil reptiles.

6. AVES. Feathered. Modern forms toothless. Aortic arch on the right side only.

Reptiles and birds grouped together as **Sauropsida.**

7. MAMMALIA. With mammary glands and hair.

Sub-Classes of MAMMALS

1. MONOTREMATA.	Egg-laying mammals.
2. MARSUPIALIA.	Pouched mammals.
3. PLACENTALIA.	Mammals with a placenta.

ORDERS OF PLACENTALIA

1. INSECTIVORA. Insect eaters.
2. XENARTHRA. Toothless or teeth without enamel.
3. RODENTIA. Incisors specialized for gnawing.
4. CARNIVORA. Flesh eaters.
5. ARTIODACTYLA. Generally even number of hoofs.
6. PERISSODACTYLA. Generally odd number of hoofs.
7. SUBUNGULATA. Proboscidians, hyrax, and sirenians.
8. CETACEA. Whales.
9. CHIROPTERA. Winged mammals.
10. PRIMATES. Usually a single pair of thoracic mammae. Thumb usually opposable.

Lemuroidea. "Half-apes." Thumb not fully opposable.

Anthropoidea. Thumb or great toe, except in New World monkeys, opposable.

Sub-Orders of ANTHROPOIDEA

PLATYRHINA. With broad nasal septum. New World.

CATARRHINA. With narrow nasal septum. Old World.

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.)

SEQUENCE OF ORGANISMS IN GEOLOGIC TIME

Eras	Periods	Years (Barrell)	Characteristic Organisms
Cenozoic	Recent	1,000,000 to 1,500,000	Modern races of men. Recent plants and animals.
	Pleistocene (Glacial)		Early species of men and primates. Mammals dominant life. "Age of man."
	Tertiary	95,000,000 to 115,000,000	"Age of mammals." Lemuroids and insectivores appear. First placentals.
Mesozoic	Cretaceous	116,000,000 to 136,000,000	Mammals mostly marsupials. Reptiles highly specialized.
	Comanchean	120,000,000 to 150,000,000	Bony fishes abundant. Flowering plants appear.
	Jurassic	155,000,000 to 195,000,000	Diverse reptiles. Ganoid fishes. First birds.
	Triassic	190,000,000 to 240,000,000	Crocodiles and dinosaurs. Reptiles dominant. First mammals.
Paleozoic	Permian	215,000,000 to 280,000,000	Mammal-like reptiles. Trilobites disappear.
	Pennsylvanian	250,000,000 to 330,000,000	Primitive amphibians and reptiles. Coniferous plants.
	Mississippian	300,000,000 to 370,000,000	Earliest amphibian fossils. Horse-tails and club-mosses.
	Devonian	360,000,000 to 420,000,000	Amphibian foot-prints. Lungfishes. Earliest land plants.
	Silurian	390,000,000 to 460,000,000	Ostracoderm (armored) fishes. Elasmobranchs. Land plants begin.
	Ordovician	480,000,000 to 590,000,000	Vertebrates appear. First fishes. First insects.
	Cambrian	550,000,000 to 700,000,000	Invertebrate phyla abundant. First trilobites.

CHAPTER 2

REPRODUCTION

Anatomy, broadly defined, includes embryology which deals with the progressively changing anatomy of the animal in the course of its development from egg to adult. Many anatomical peculiarities of animals are unintelligible so long as only the adult is studied. Embryology gives some reason for such facts as that the chief artery emerging from the heart turns to the right in a bird but to the left in a mammal and that the diaphragm of a mammal is supplied by nerves from the neck region instead of from the neighboring trunk region of the spinal cord. The theory of evolution rests to an important extent on facts derived from the comparative embryology of vertebrates.

Sexes. Reproduction in the vertebrates always involves gonads of two types, the ovary which produces eggs (ova) and the testis which produces sperm (spermatozoa). In some tunicates (Urochorda), presumably remote allies of vertebrates, alternation of sexual and asexual generations occurs. A fertilized egg becomes an asexual individual from which arise buds. These become sexual adults which are hermaphrodite, that is, they produce both eggs and sperm.

In all vertebrates except a few fishes the individual is either male or female—the **dioecious** condition. The eel-like hag, Myxine (a cyclostome), and several of the bony fishes (Teleostei) are normally hermaphrodite (**monoecious**). Among vertebrates which are normally dioecious many abnormal cases have been reported, especially in fishes and amphibians, in which germ cells of both sexes were found in one individual.

The Germinal Bodies. The spermatozoa are derived from cells in the walls of delicate tubules which are the essential part of the testis. The ova come from primordial germ cells contained within the tissues of the usually solid ovary. (Fig. 274)

The "head" of the spermatozoön (Fig. 25) consists of compacted nuclear material (chromatin) derived from the primordial germ cell. A locomotor "tail" is formed from the cytoplasm (extranuclear protoplasm) of the original cell. The "ripe" spermatozoön is essentially a motile nucleus.

The egg in the course of its differentiation acquires a greatly increased body of cytoplasm within which is deposited more or less food material, the **yolk** or **deutoplasm**. The egg may become invested by membranes or envelopes, either protective (*e.g.*, the vitelline or yolk membrane; the hard calcareous shell of a bird's egg; see Fig. 28) or nutritive (*e.g.*, the albumen or "white" of a bird's egg).

Eggs differ most remarkably as to the amount of contained yolk and as to their outer coverings. The microscopic egg of a mammal and the gigantic ostrich egg encased in its hard shell would seem to be hardly comparable objects. The thing referred to in kitchen and market as an "egg" consists of the egg in strict sense, or ovum, plus various extraneous substances and structures. The hen's ovum, corresponding to the small egg of some fish, is merely the yellow sphere commonly called the "yolk" of the "egg," enclosed in its vitelline membrane (Fig. 28). The following data illustrate the differences in eggs in regard to size and content of yolk:

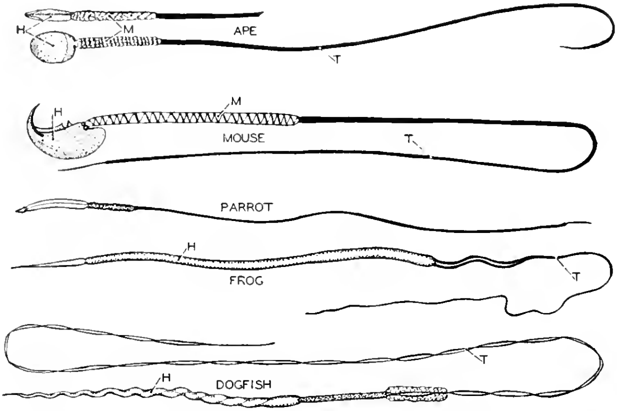


FIG. 25.—Spermatozoa of dogfish (Squalus), frog (Rana), parrot (Psittacus), mouse (Mus) and ape (Inuus). *H*, head; *M*, middle piece; *T*, tail. The spermatozoön of the frog is about 0.1 mm. long. (Redrawn from Retzius.)

Egg	Approximate diameter, mm.	Relative volumes
Amphioxus	0.1	1
Some frogs	2.0	8,000
Domestic fowl (ovum or "yolk")	30.0	27,000,000

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. Size of eggs is correlated primarily with the method of development. Correlation with size of body may appear when the developmental methods of the animals are similar, *e.g.*, in reptiles and birds.

The **eggs of fishes** are usually relatively small, less than 5 mm. in diameter. Eggs of sharks and skates, however, contain much yolk and rival in size the eggs of birds. These large eggs are enclosed in shells consisting of a horn-like material secreted by the anterior part of the oviduct. In oviparous sharks and skates the shell is usually flat and quadrangular and has long tendrils which serve to anchor it to seaweed or other objects. (Fig. 26)

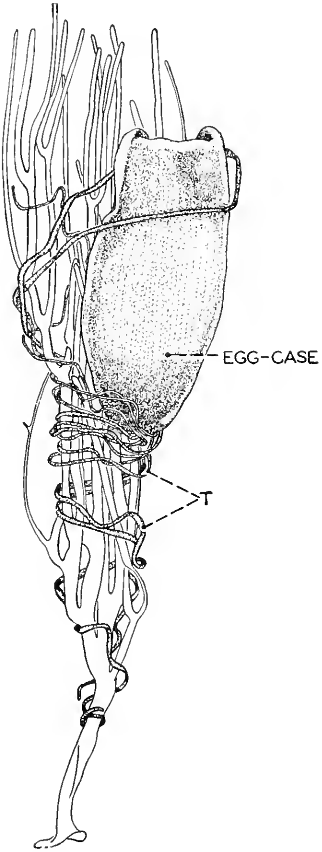


FIG. 26.—Egg-case of small shark. *T*, tendrils coiled around branches of a horny (gorgonian) coral. About half actual size. (Drawn from specimen in the anatomical collection of the Biological Laboratories, Harvard University.)

The **eggs of amphibians,** which always contain considerable yolk, are larger than the eggs of many fishes, but smaller than the average for reptiles and birds. Eggs of various frogs range from 1.5 to 3 mm. in diameter. Eggs of large salamanders (Necturus, Cryptobranchus) are 5 or 6 mm. in diameter. The amphibian oviduct deposits upon the egg a layer of gelatinous substance which, after the egg has been extruded into the water, swells to form a thick jelly-like envelope. (Fig. 27)

Reptiles and **birds** produce eggs containing an enormous amount of yolk (Figs. 28, 36). The protoplasm in these great eggs is aggregated at one spot on the surface of the egg, marking the **animal pole,** while the remainder of the egg is yolk nearly, if not quite, devoid of protoplasm. The localized protoplasm (**germ-disc**; Fig. 36) appears as a small white fleck on the surface of the yellow yolk. Before the egg is fertilized the germ-disc contains a single nucleus. These large eggs are invested by a tough **vitelline membrane** external to which may be more or less nutritive albumen (the "white" of a hen's egg) and an outer shell which in most reptiles is of a leathery texture, but in crocodiles, alligators and birds is highly calcified and therefore hard and brittle.

Eggs of mammals, with two exceptions, are minute, containing a minimum of yolk. The exceptions are the duck-bill (Ornithorhynchus) and the spiny ant-eater (Echidna) of the Australian region. These two mammals, presumably of primitive type, lay large eggs encased in tough shells. In general these mammals are reptilian in their methods of reproduction. Otherwise mammalian eggs are of microscopic dimensions (0.06 to 0.3 mm. in diameter). The egg (Fig. 29) is covered by a delicate membrane (**zona pellucida**) external to which may be a cellular membrane (**corona radiata**), both contributed by the ovary.

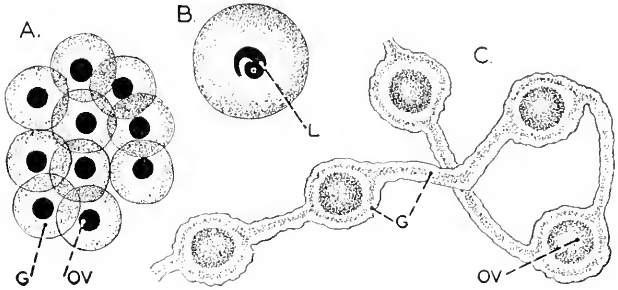


Fig. 27.—Amphibian eggs. *A*, of frog, soon after laying; *B*, early larva of frog, just before hatching; *C*, of the salamander, Cryptobranchus allegheniensis. *A* and *C*, approximately actual size; *B*, enlarged. *G*, gelatinous layer; *L*, larva; *OV*, ovum. (*A* and *B*, redrawn from Marshall, "Vertebrate Embryology"; *C*, after A. M. Reese.)

Fertilization. Development is initiated by the "fertilization" of the egg. A spermatozoön penetrates the egg (impregnation) and the sperm chromatin becomes joined with the chromatin of the egg nucleus.

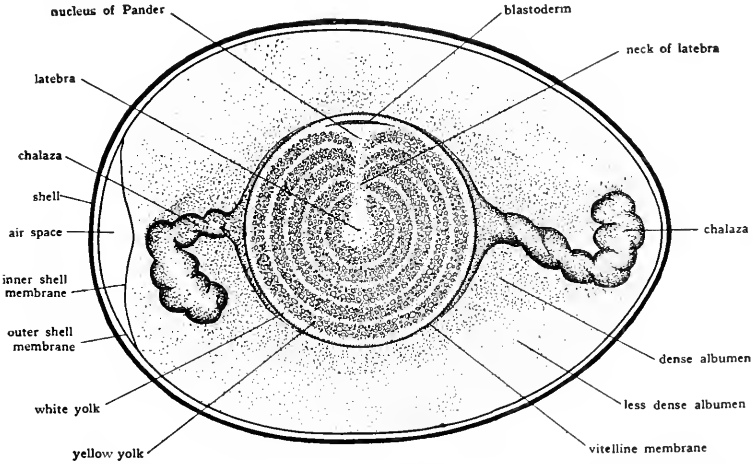


Fig. 28.—Diagram representing a section of a hen's egg cut in a plane including the long axis of the egg and passing through the blastoderm. (From Patten, "Embryology of the Chick"; after Lillie.)

The "maturation" process through which all germ cells pass reduces their chromatin to approximately half that contained in body cells, so that the union of sperm chromatin and egg chromatin provides the fertilized egg with a nucleus containing the full complement of chromatic bodies (chromosomes) characteristic of all body cells of the animal.

Therefore the fertilized egg, although the product of two cells, possesses the mechanism of a single cell. It possesses no visible structures which would adequately account for its development into a large complex animal like the parent animals. Compared to such cells as those of muscle and nervous tissue, it is strikingly devoid of visible special mechanism. Yolk is characteristic of eggs, but yolk is an inert food substance, not a mechanism.

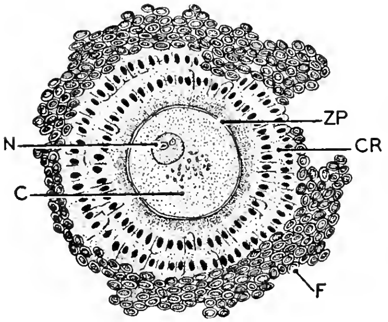


FIG. 29.—Human ovum surrounded by follicular cells. Actual diameter of ovum about 0.25 mm. *C*, cytoplasm containing some yolk; *CR*, corona radiata; *F*, follicular cells; *N*, nucleus; *ZP*, zona pellucida. (After Nagel.)

The motile and aggressive spermatozoön might seem to be the essentially "animal" body in development while the relatively large unfertilized egg, burdened with inert yolk, would appear rather as a passive and vegetative thing. But in normal development the spermatozoön merely imparts the stimulus which initiates development and provides for inheritance from a male parent. Experimentation has proved that the egg is fully capable of producing a characteristic adult without the assistance of a spermatozoön. Obviously, however, such an adult inherits only from a mother.

Exit of Sperm and Eggs. The sperm is usually carried by ducts which lead from the testis to the exterior, but in cyclostomes and some bony fishes it is discharged from the testes into the body-cavity and finds exit through abdominal or genital pores which pierce the body-wall.

Ova are usually liberated from the surface of a solid ovary (Fig. 274) into the body-cavity whence they pass into oviducts which lead to the exterior. In cyclostomes and some bony fishes the eggs pass out through abdominal pores. In other bony fishes the ovary is hollow, eggs are liberated into its lumen and pass out by way of a duct which is an extension of the wall of the ovary.

The genital ducts are usually closely associated with the duct system of the kidneys. Exceptional conditions occur in bony fishes.

Oviparity, Viviparity, Impregnation. The means whereby ovum and spermatozoön are brought together depends on whether the animal is oviparous or viviparous; also on whether the outer envelopes of the egg can be penetrated by a spermatozoön.

In most oviparous **fishes** the eggs are impregnated after the genital products have been discharged into the water ("external fertilization"). But oviparous sharks and skates produce eggs whose shells are impenetrable by sperm. Therefore copulation must occur and the egg must be reached by the sperm before the shell is deposited. Some sharks and a few teleosts are viviparous; copulation and "internal fertilization" are therefore necessary.

Among **amphibians** there is much diversity. In most frogs and toads impregnation is external. In tailed amphibians (Urodela) it is commonly internal, in oviparous as well as in viviparous species, and in many cases is effected by means of a **spermatophore,** a mass of sperm agglutinated together by a secretion from cloacal glands of the male. The spermatophore may be introduced into the cloaca of the female or else attached to the external surface of the female. In some cases it is merely discharged and picked up later by the female.

Some **reptiles** are viviparous. All **birds** are oviparous. But in all reptiles and birds the egg-shell necessitates copulation and internal impregnation.

Modern **mammals,** except Ornithorhynchus and Echidna, are viviparous. The two exceptional animals lay eggs of reptilian sort. Therefore in all mammals impregnation must be internal.

In general, eggs which acquire such envelopes as a layer of albumen or a hard shell must be impregnated while in the anterior region of the oviduct and before these external coverings have been deposited. Development begins immediately after fertilization. Therefore, if fertilization has actually occurred, the "egg" which is "laid" by the reptile or bird contains not an ovum but an embryo at an early stage of development.

Provisions for protection, nutrition and respiration during the period of development are most diverse. In most **fishes** the eggs are abandoned to the hazards of the environment. Some fishes, especially those of fresh water, arrange crude nests in gravel, sand or mud. Some fishes guard their eggs. In the sea-horse (Fig. 30) and pipe-fish, the male carries the developing eggs in a brood-pouch on the ventral surface of the body or tail—an arrangement suggestive of the marsupial pouch of a female kangaroo. The smaller fish eggs, scantily endowed with yolk. develop rapidly and soon become free-living and self-supporting while still very minute. The miniature fish then enters upon a long period concerned mainly with feeding and growth. Eggs containing larger quantities of yolk pass through a longer period of development and the young fish attains relatively large size before it is obliged to obtain food from an

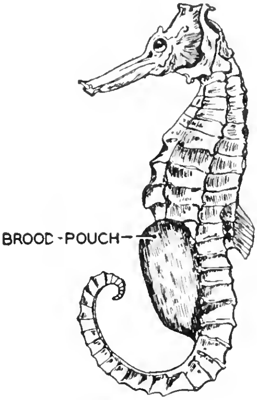


Fig. 30.—Sea-horse (Hippocampus.); male, with brood-pouch. (Redrawn after Boulenger in The Cambridge Natural History.)

external source. The embryo and young of the viviparous fish not only receive maximum protection, but may obtain from the mother some food in addition to the initial supply of yolk. In so-called "placental" sharks the wall of the oviduct develops highly vascular folds or processes and similar folds arise on the abdominal wall of the embryo. The two sets of projecting structures, maternal and embryonic, become closely approximated, thus providing for diffusion of substances from the blood of one to that of the other.

Among **amphibians** there is, in general, better provision for protection of eggs and young than in fishes. Nests and guarding of eggs are common. Among frogs and toads occur various peculiar ways of caring for eggs and young. The male of the European "obstetric" toad carries the long strings of eggs wound about his body and legs until the tadpoles emerge. In some cases eggs are carried in the mouth or vocal pouch of the male. In the South American "marsupial" frog the eggs develop in a capacious pouch formed in the skin on the back of the female. The eggs of the toad, Pipa americana, develop in individual vesicles in the skin on the back of the mother. Viviparity, affording a maximum of protection, occurs in a few amphibians, including representatives of each of the three orders, Urodela, Anura, and Gymnophiona.

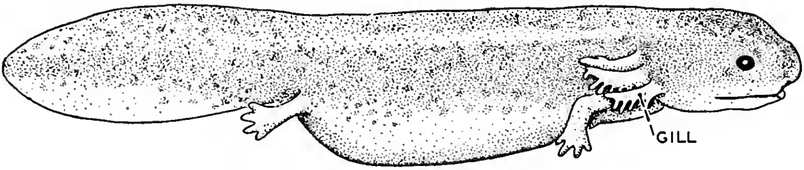


FIG. 31.—Necturus larva of about 25 mm. length. (After Eycleshymer.)

The amphibian egg, whether laid in the open or enclosed in some protective way, develops rapidly into a highly characteristic **larva,** the tadpole or "polliwog" (Fig. 31) which, with its functional gills and 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 the life of a fish. The larval period, ranging from a few weeks in some salamanders to a year or more in some frogs, is devoted mainly to feeding and growth. It terminates in a metamorphosis in the course of which the animal acquires the adult characteristics. The transformation is most radical in frogs and toads; legs and lungs develop, tail and gills are absorbed, gill clefts close, and other changes occur. In certain exceptional species of frog, especially large eggs are laid on land and develop to 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. Adult Necturus, with its tail and functional gills, is sometimes called a "permanent larva." Sexual maturity is ordinarily not attained during the larval state. But the Mexican axolotyl, the larva of the salamander, Ambystoma tigrinum, regularly breeds in the larval state.

The diversity of reproductive arrangements in amphibians is in marked contrast to the uniformity which prevails in **reptiles** and **birds.** The large yolk-mass of the eggs of these animals makes possible a long developmental period during which the young can attain relatively great size. A newly hatched alligator is gigantic compared to a newly hatched salmon. These circumstances, together with the fact that development takes place within a thick shell, make necessary some special provision whereby food derived from the yolk may be made accessible to all parts of the large embryo and an adequate supply of oxygen obtained from some external source.

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. 74), 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 (serosa).** 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 (Fig. 74) 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 (Fig. 74) 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 spreads out so that the greater part of its outer surface is, in conjunction with the chorion, in close relation to an extensive area of 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**; Fig. 74) 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 reptiles and birds building of nests and parental care of young are much more prevalent than in fishes and amphibians, reaching high specialization and efficiency in birds. Correlated with the greatly increased protection afforded during development, relatively few eggs are produced.

Primitive mammals, as indicated by such surviving examples as Ornithorhynchus and Echidna, must have retained reptilian methods of reproduction. 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 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 127) developed in and by the abdominal skin serves to prolong the period of dependence on the maternal food.

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 amount of yolk, 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. 75). 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 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 means of this **placenta,** intervening 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 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 such that, as a whole, it 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.

Fishes and amphibians show this reproductive 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, have tried (so to speak) a variety of methods. From the many reproductive "experiments" of the lower vertebrates finally emerge 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 32) suggestive of the mammalian 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—practically 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, toward the guarantee of the survival of every potential adult. This tendency bifurcates and culminates in two very differently specialized methods, one in birds, the other in mammals. 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.

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.

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 ovum increases its surfaces by dividing into small cells—the process called **cleavage.** 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. 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 (Fig. 11). The egg is correspondingly small, about 0.1 mm. in diameter, and contains very little yolk. (Fig. 32)

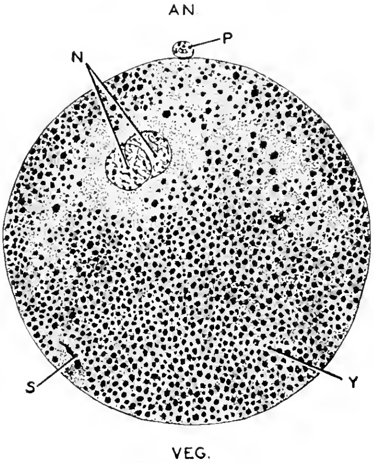


FIG. 32.—Median section of a fertilized egg of AMPHIOXUS. Diameter of egg about 0.1 mm. *AN*, animal pole; *N*, male and female pronuclei; *P*, polar body; *S*, remnant of spermatozoön; *VEG*, vegetal pole; *Y*, region of cytoplasm occupied by coarse granules of yolk. (After Cerfontaine.)

The plane of the first cleavage (Fig. 33) 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. 33 *G-I*) until between two hundred and three hundred cells have been formed. This stage of the embryo is called the **blastula.** The name, **blastocoele,** 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.

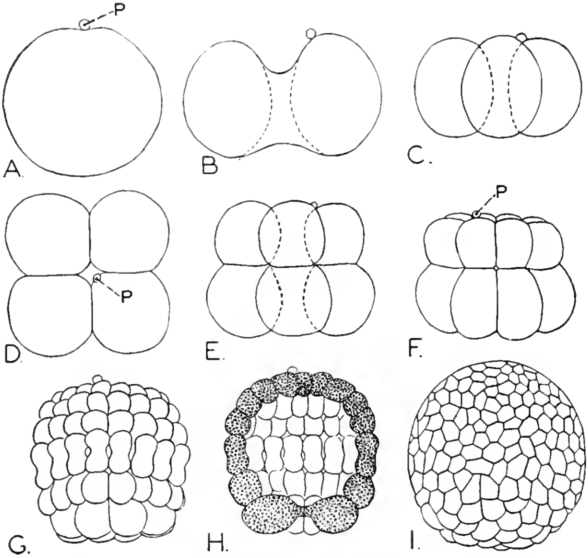


Fig. 33.—Cleavage of egg of AMPHIOXUS. *A*, undivided egg; *B*, in process of first cleavage; *C*, four-cell stage, lateral view; *D*, four-cell stage, polar view; *E*, eight-cell stage, lateral view; *F*, sixteen-cell stage, lateral view; *G*, eighty-eight cells, lateral view; *H*, same stage as *G*, median section; *I*, later stage, lateral view. *P*, polar body. (After Hatschek.)

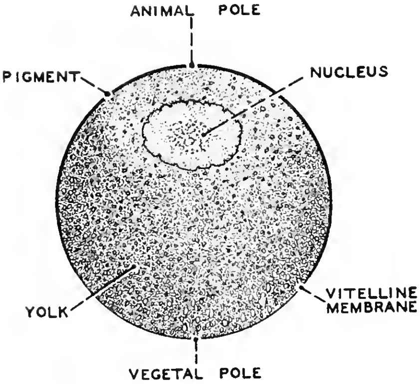


Fig. 34.—Ovarian egg of frog; median section. (Redrawn from Morgan, "The Development of the Frog's Egg"; The Macmillan Co.)

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. 34) 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 supplies may impede the progress of a company of explorers.

Figure 35 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 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.

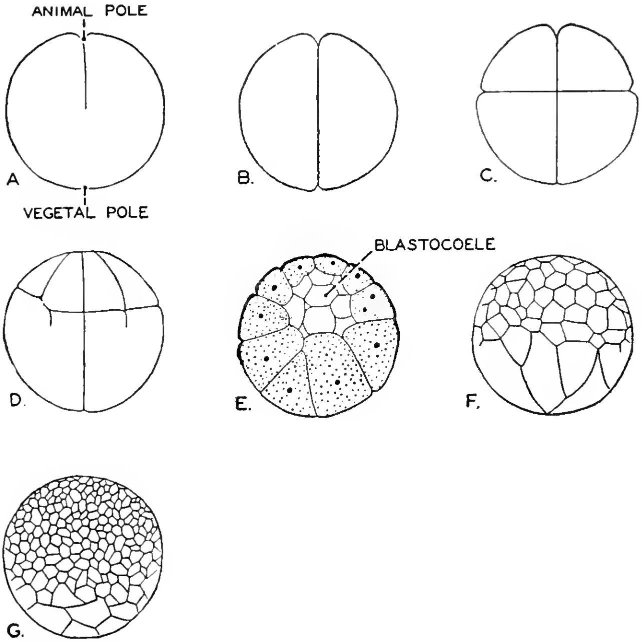


FIG. 35.—Cleavage of the frog's egg. *A*, first cleavage in process; *B*, two cells; *C*, eight cells; *D*, fourth cleavage complete in animal hemisphere but just beginning in the four cells at the vegetal pole; *E*, early blastula, median section; *F*, *G*, successively later stages, lateral view. (*D*, *F*, *G*, redrawn from Morgan, "The Development of the Frog's Egg"; *E*, redrawn from Marshall, "Vertebrate Embryology.")

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. 35*E*). 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 blastocele are obviously due to the yolk.

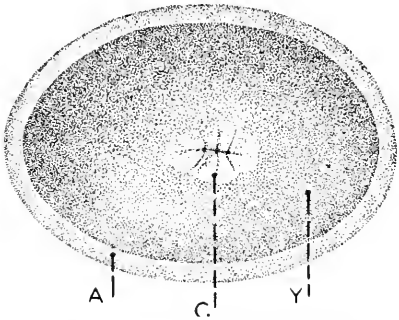


Fig. 36.—Cleavage of the germ-disc of the egg of a turtle (Glyptemys insculpta); eight-cell stage. The egg-shell is not shown. About twice natural size. *A*, albumen; *C*, the eight-cell blastoderm; *Y*, yolk. (Redrawn from Louis Agassiz, "Embryology of the Turtle.")

In Reptiles and Birds. In eggs whose yolk-mass greatly exceeds that of the amphibian egg all the protoplasm is segregated into a thin plate, the **germ-disc,** lying on the surface of the relatively enormous mass of yolk (Fig. 36). 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. 36 and 37). 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. 37).

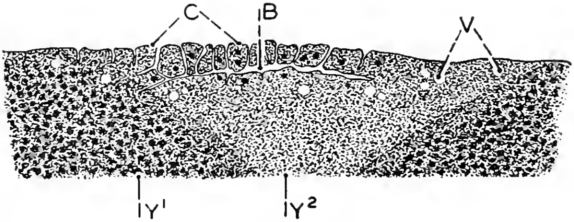


Fig. 37.—Early blastoderm of chick; plane of section passes through center of egg. *B*, blastocoele (subgerminal or cleavage cavity); *C*, cells of blastoderm; *V*, fluid-filled vesicles; Y^1, yellow yolk, Y^2, white yolk. Magnified nearly twenty diameters. (Redrawn from Duval, "Atlas d'Embryologie.")

Comparing this embryo with the blastula stages of Amphioxus and frog, it seems reasonable to interpret it as a blastula whose blastocoele is the subgerminal cavity, while its blastoderm is the animal region and the yolk-mass is the vegetal region of the embryo. 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 an essentially one-layer 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 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. 38). The vegetal hemisphere first flattens, then becomes curved inward. 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. 38*C*). As the process goes on the blastocoele 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. This region is marked by very rapid proliferation of cells, especially at the dorsal edge of the blastopore (Fig. 38*D*). 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 result of the primary invagination but by the secondary growth process.

At the close of the gastrula period (Fig. 38*D*) 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. The gastrula is the animal in its bare essentials. The outer layer, **ectoderm,** is potentially protective and nervous. It gives rise to the essential outer 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 blastopore never becomes mouth and

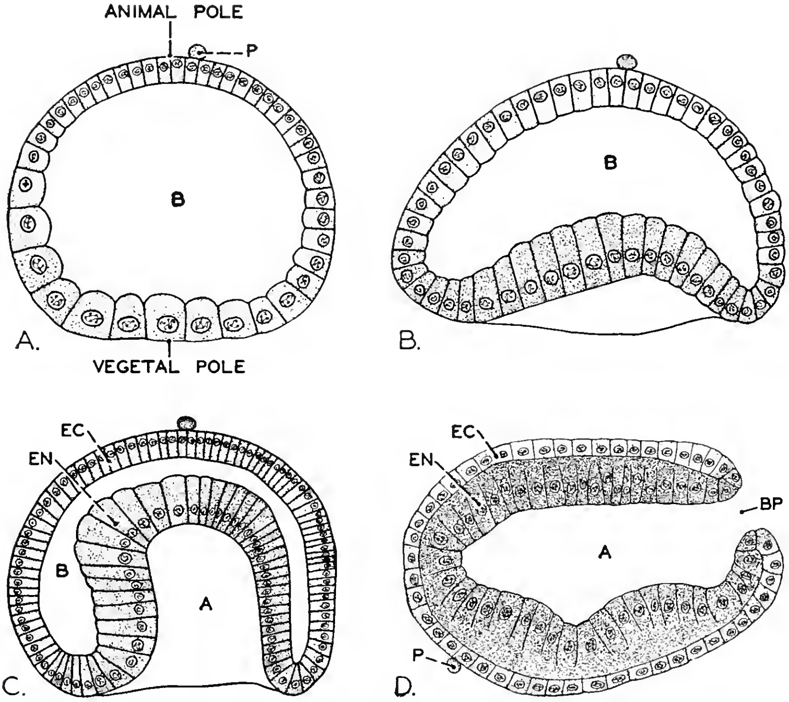


FIG. 38.—Gastrulation in AMPHIOXUS. The figures represent sections through the polar axis of the embryo. *A*, blastula with vegetal region flattened; *B* and *C*, earlier and later stages of invagination of vegetal hemisphere; *D*, gastrulation completed; with elongation of the gastrula, its long axis becomes the horizontal antero-posterior axis of the embryo. *A*, archenteron; *B*, blastocoele; *BP*, blastopore· *EC*, ectoderm; *EN*, endoderm; *P*, polar body. (After Cerfontaine.)

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. 39). 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 necessary precursor of any adult metazoan which has a skin (ectoderm) and a digestive tube (endoderm).

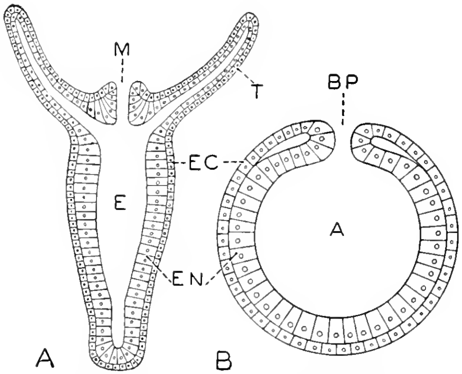


FIG. 39.—Diagrams showing structural similarity of a coelenterate and a gastrula. *A*, Hydra, longitudinal section; *B*, gastrula, axial section. *A*, archenteron, prospective digestive cavity; *BP*, blastopore; *E*, enteric (digestive) cavity; *EC*, ectoderm; *EN*, endoderm; *M*, mouth; *T*, tentacle.

In Amphibians. In the amphibian the vegetal wall of the blastula (Fig. 35*E-G*) is so thick that the vegetal hemisphere is, in effect, solid. It consists of large cells heavily laden with inert yolk. Such a wall cannot 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. 40*A*, *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

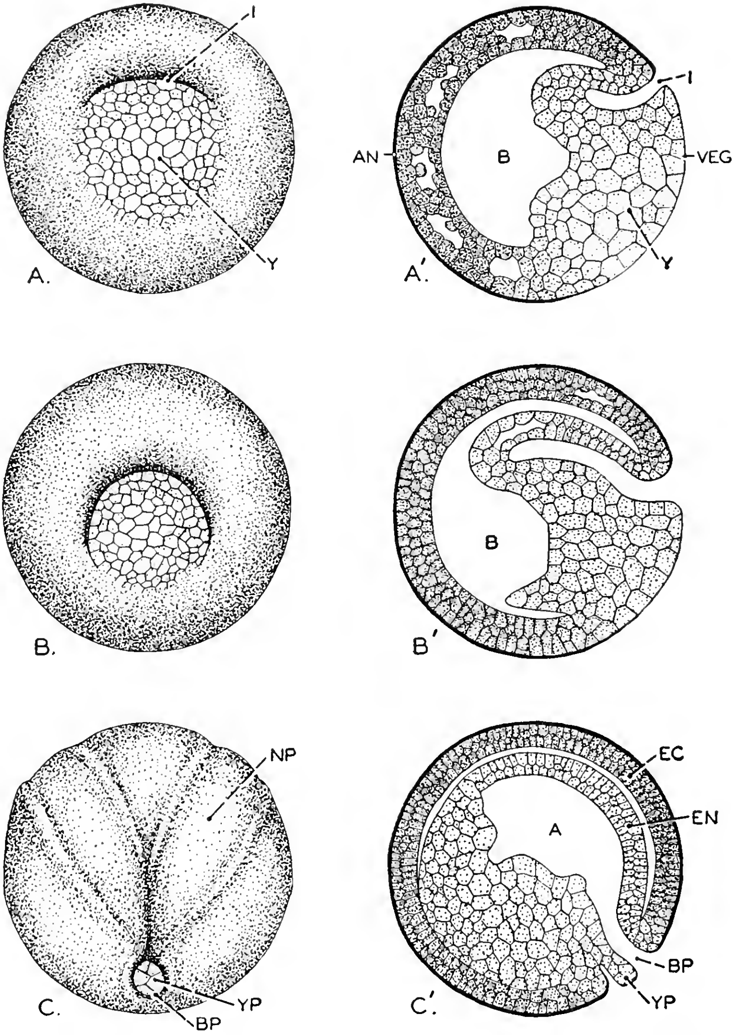


FIG. 40.—Gastrulation in the frog. *A*, *B*, *C*, the whole embryo at successively later stages; viewed toward the vegetal pole. *A′*, *B′* and *C′* represent, in somewhat diagrammatic way, sections of corresponding stages cut in the plane including the polar axis and bisecting the gastrular invagination, *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. 44*A*). *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.

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 40.I′ 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 the superficial germ-ring region; the deeper wall of the invagination consists of yolk cells. The groove, initiated as a slight invagination, rapidly deepens (Fig. 40*B*-*B*′), **not by continued invagination,** but by active growth of the 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. 40*B*) 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, grows 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. 40*C*-*C*′).

The result of the processes just described is 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 partly 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 40*C*′ 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.

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 due mainly to the enclosing of the yolk-mass by overgrowth (**epiboly**) carried out by the fold which was initiated by invagination. 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.

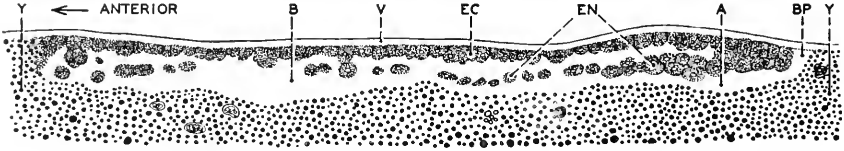


FIG. 41.—Gastrulation in the pigeon. Section approximately median, showing formation of endoderm by invagination at posterior edge of blastoderm. *A*, archenteron; *B*, blastocoele (cleavage cavity); *BP*, blastopore; *EC*, ectoderm; *EN*, endoderm; *V*, vitelline membrane; *Y*, yolk. Magnified about 100 diameters. (After J. T. Patterson.)

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. 36, 37), 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. The significant fact is that 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. 41). 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 posterior edge of the blastoderm. 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. 40*A′*, *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.

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 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.

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 38*D* shows a sagittal section of the embryo at this stage. Figure 42*A* shows a section cutting the embryo transversely and within the anterior third of its length. Except for the dorsal flattening, the configuration of layers is as simple as possible. Figures *B-G* show transverse sections at stages successively later than that of Fig. 42*A*. 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. 42*D-F*) it becomes convoluted along three lines extending lengthwise of the embryo. Its median slightly thicker region becomes sharply folded upward. On 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

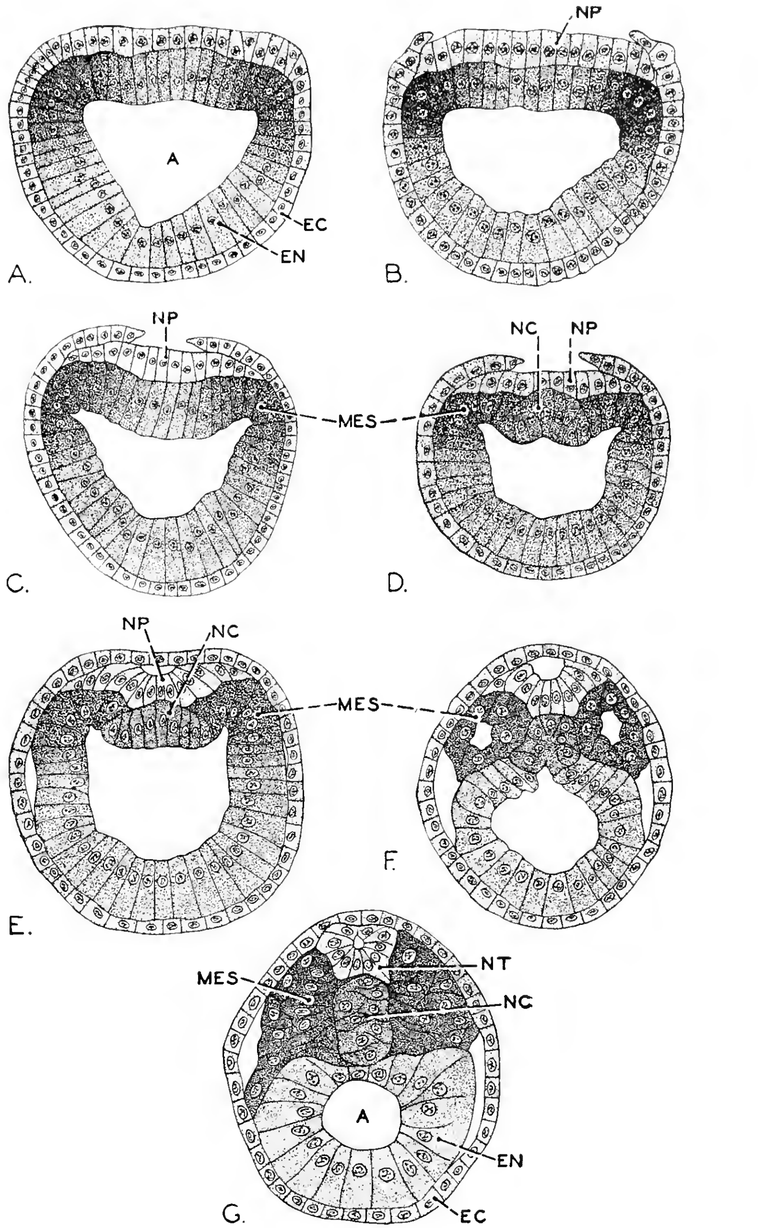


FIG. 42.—AMPHIOXUS. Transverse sections of embryos at successively later stages, showing origin of notochord, neural tube and mesoderm. *A*, section somewhat anterior to the middle of the length of an embryo slightly older than that represented in Fig. 38*D*. *E*, from embryo having two pairs of mesodermal 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.)

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. 42*F*) from the archenteric wall which, at the place where the pouch had formed, closes so that nothing is left to mark the spot.

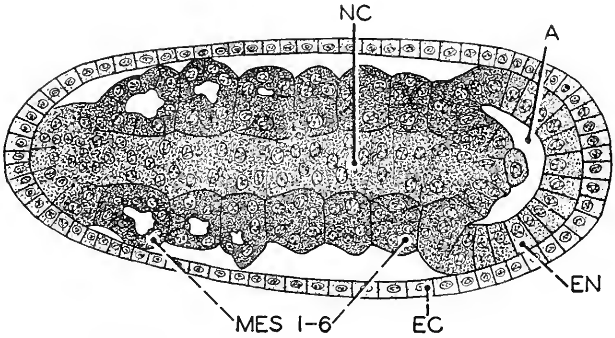


FIG. 43.—AMPHIOXUS. Frontal (horizontal) section of an embryo having six pairs of mesodermal somites. The section is through the notochord and just below the blastopore. At the posterior end of the section may be seen a region where the notochord, endoderm and mesoderm merge indistinguishably. *A*, archenteron near the blastopore; *EC*, ectoderm; *EN*, endoderm; *MES* 1–6, mesodermal somites; *NC*, notochord. (After Cerfontaine.)

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. 42, *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. (Fig. 42*G*)

In the formation of these fourteen pairs of mesodermal pouches the material of the original mesodermal folds is completely utilized. Later 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 (Fig. 43). By this means the number of pairs of mesodermal segments is increased to the adult total, usually sixty-one.

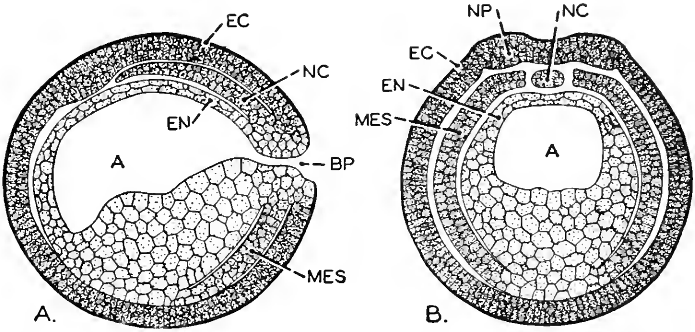


FIG. 44.—Sections of an amphibian embryo at an early stage in the development of the notochord and mesoderm. Semi-diagrammatic. *A*, median longitudinal section. *B*, transverse section near the middle of the longitudinal axis. *A*, archenteron; *BP*, blastopore; *EC*, ectoderm; *EN*, endoderm; *MES*, mesoderm; *NC*, notochord; *NP*, neural plate.

In Amphibians. In amphibians, as in Amphioxus, the blastoporal rim or germ-ring is the all-important source of mesoderm. The amphibian, however, gives little evidence of anything comparable to the paired mesodermal pouches which push out from the dorso-lateral endoderm of Amphioxus.

During the process of gastrulation in the amphibian the material destined to become mesoderm lies within the advancing edge of the overgrowing fold (Fig. 40) 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. 40*C′*, *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. 44*B*). 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. 44*A*). 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.

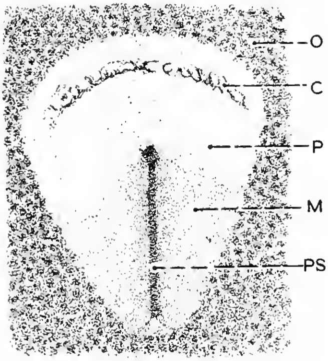


FIG. 45.—Surface view of blastoderm of chick after 15 hours incubation. *C*, "anterior crescent," occasioned by an irregular fold of underlying endoderm; *M*, region occupied by mesoderm; *O*, area opaca whose opacity is caused by adherence of yolk to the blastoderm; *P*, area pellucida —transparent in absence of adhering yolk (see Fig. 41); *PS*, primitive streak. × 14. (After Duval, "Atlas d'Embryologie.")

In Reptiles and Birds. In reptiles and birds endoderm is initiated by a small invagination or infolding at the posterior edge of the early blastoderm (see page 48). 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. 41). 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. 45). 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 walls (Fig. 46).

This primitive streak is the primary seat of mesoderm formation. Rapid proliferation of cells within the substance of the thickened streak gives rise to masses of cells which move out into the space between ectoderm and endoderm (Fig. 46, *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 and forward from the primitive streak and always in the space between ectoderm and endoderm. This layer, like the early mesoderm of amphibians, is at first unsegmented and devoid of cavity.

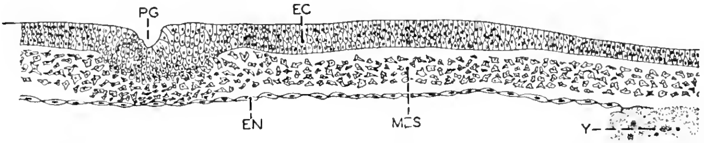


FIG. 46.—Section transverse to the primitive streak of a chick embryo of about 15 hours incubation. The section is taken near the middle of the length of the streak. *EC*, ectoderm; *EN*, endoderm; *MES*, mesoderm; *PG*, primitive groove of primitive streak; *Y*, yolk at inner margin of area opaca. × 100. (After Duval, "Atlas d'Embryologie.")

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 (Fig. 29) 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. 47*A*). 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. 47*B-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

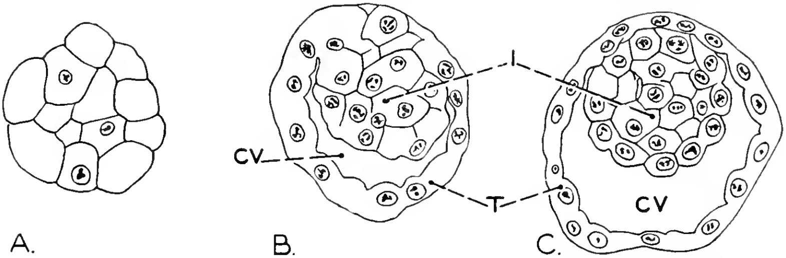


FIG. 47.—Early stages in development of a rabbit. *A*, morula stage, 47 hours after coitus; *B*, early blastodermic vesicle, 80 hours; *C*, blastodermic vesicle at 83 hours. The investing layers of the embryo are not shown. *CV*, cavity of blastodermic vesicle; *I*, inner cell-mass; *T*, trophoblast. Magnified about 285 diameters. (After Assheton.)

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. 47,*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. 48). 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.

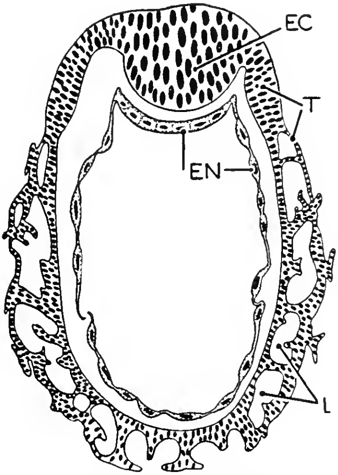


Fig. 48.—Early stage of the blastodermic vesicle of the hedgehog. *EC*, ectoderm; *EN*, endoderm; *L*, lacunae, spaces occupied by maternal blood; *T*, trophoblast (trophoderm). (After Hubrecht.)

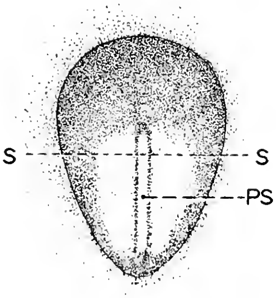


Fig. 49.—Embryonic area or "shield" of the blastodermic vesicle of the rabbit after about 172 hours development. *PS*, primitive streak; *S-S*, position of section represented in Fig. 50. (After Assheton.)

As stated above, the material which constitutes the definitive embryo is within the thick and solid cell-mass (Fig. 47, *I*) 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. 49) 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 proliferation of cells produces a mesoderm (Fig. 50) 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.

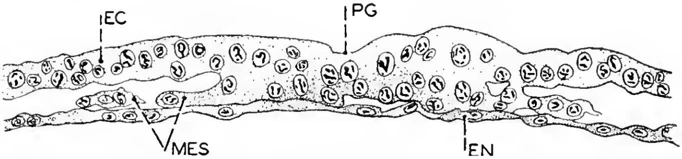


Fig. 50.—Transverse section of the embryonic shield of a rabbit at the stage represented in Fig. 49. The section is taken at the position indicated by the line *S-S* in Fig. 49. *EC*, ectoderm; *EN*, endoderm; *MES*, mesoderm; *PG*, primitive groove of primitive streak. ×175. (After Assheton.)

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 point to the conclusion that 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.

Unquestionably the yolk content of the chordate egg is much more readily subject to evolutionary change than is the developmental mechanism of the germinal protoplasm. That mechanism **can** be changed, but there is a high degree of inertia about it. The initiation of evolutionary change is evidently not within the embryo itself. Its inertia is such that it tends always to follow the old methods and it changes only as it must.

ORGANOGENESIS

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. 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 the organs in chordates.

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 in successively more posterior positions. (Figs. 42 and 43)

In the course of further development the thickened ectodermal **neural plate** becomes depressed slightly below the level of the neighboring lateral ectoderm (Fig. 42*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. 42*E*). 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. 42*F-G*)

The neural plate originally extends back to the blastopore. The over-arching process whereby the neural plate is covered proceeds 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 relation of layers and cavities are shown in Fig. 51, 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 thence to the outside by the anterior neuropore (Fig. 51,*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.

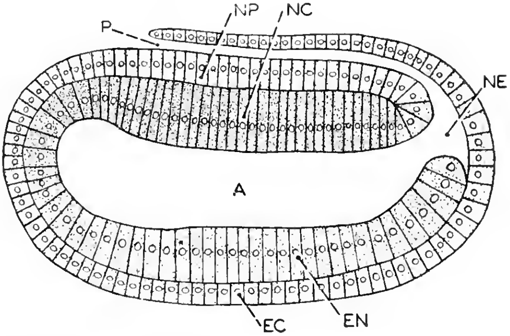


FIG. 51.—AMPHIOXUS. Median longitudinal section of an embryo having two mesodermal pouches, a stage approximately like that of the transverse section in Fig. 42*E*. The blastopore, roofed over by ectoderm, has become the neurenteric canal. *A*, archenteron; *EC*, ectoderm; *EN*, endoderm; *NC*, endoderm destined to become notochord; *NE*, neurenteric canal; *NP*, neural plate; *P*, neuropore. ×350. (Based on a figure by Hatschek.)

The **notochord,** whose development is initiated by an upward folding of mid-dorsal endoderm (Fig. 42*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. 42*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 (Fig. 43).

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 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 to the ectoderm; and an inner thin layer similarly contiguous to the endoderm. The thick part is destined to form a segment of body-muscle and is therefore called the **myotome** (Fig. 52,*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. 52). 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 segments of muscle.

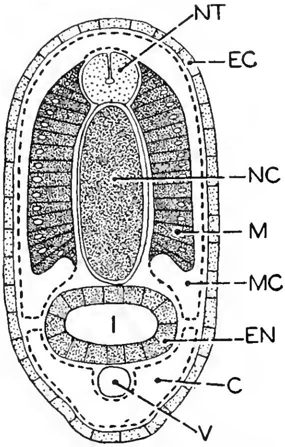


FIG. 52.—AMPHIOXUS. Transverse section midway of the length of the body of a larva with five gill clefts. *C*, coelom; *EC*, ectoderm; *EN*, endoderm; *I*, intestine; *M*, myotome; *MC*, myocoel; *NC*, notochord; *NT*, neural tube; *V*, subintestinal vein. (Modified from a figure by Hatschek.)

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.

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 anterior end (Fig. 53). 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 neurenteric canal (*NE*), at this stage, has ordinarily become closed. In the anterior region, where the differentiation of the mesoderm is most advanced, a coelom intervenes between the enteric tube and the outer body-wall (Fig. 52, *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.

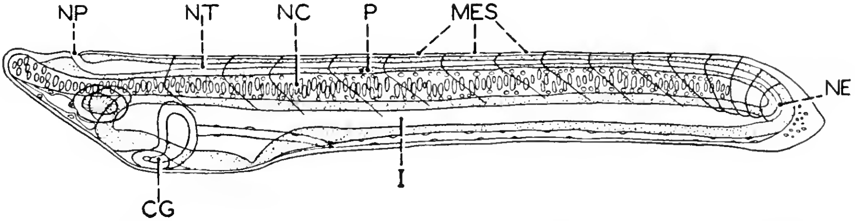


FIG. 53.—Amphioxus at beginning of larval period; 14 or 15 pairs of mesodermal somites. Actual length of larva about 1.0 mm. *CG*, club-shaped gland; *I*, intestine; *MES*, mesodermal somites; *NC*, notochord; *NE*, neurenteric canal; *NP*, neuropore; *NT*, neural tube; *P*, pigment spot in neural tube. (After Hatschek.)

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 in the study and interpretation of the processes.

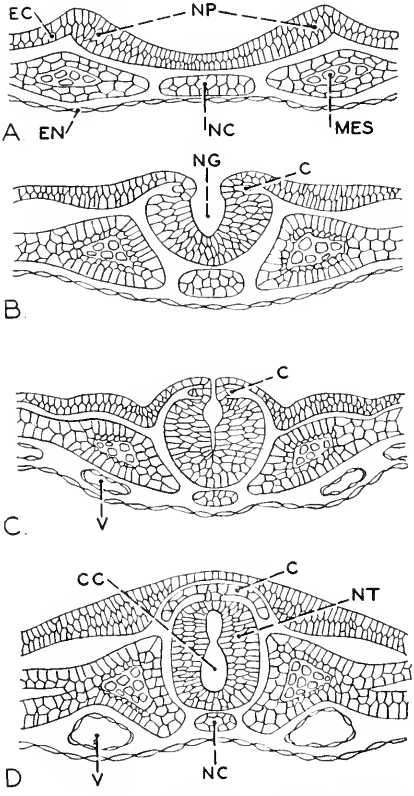


FIG. 54.—Diagrams illustrating method of origin of the neural tube of vertebrates. Transverse sections in the mid-trunk region of embryos at successively (*A* to *D*) later stages. *C*, neural crest; *CC*, canalis centralis of neural tube; *EC*, ectoderm; *EN*, endoderm; *MES*, mesoderm; *NC*, notochord; *NG*, neural groove; *NP*, neural plate; *NT*, neural tube; *V*, blood-vessel (paired dorsal aorta).

Organogenesis in the Vertebrates

In the late embryo of Amphioxus the main lines of the body plan of a vertebrate are drawn. Brief statements concerning the embryonic origin of the major organs of vertebrates follow.

Neural Tube. In Amphioxus the neural plate becomes detached from the adjacent lateral ectoderm (Fig. 42) 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. 54). Not until the tubular form is attained does the neural ectoderm of vertebrates become detached from the overlying superficial ectoderm. Figure 55 shows, in a diagrammatic way, the characteristic appearance of a recently formed neural tube with its **neural crests,** dorso-lateral 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** (Fig. 345). 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 ("sympathetic"; Fig. 345) and nerves of the autonomic system.

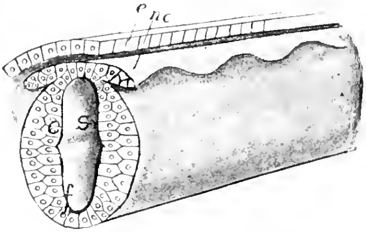


FIG. 55.—Stereogram of embryonic neural tube showing the segmenting neural crest. *e*, superficial ectoderm; *nc*, neural crest; *s*, central canal. (From Kingsley, "Comparative Anatomy of Vertebrates.")

The anterior region of the tube expands to form the brain. Three enlargements, the primary brain vesicles—**fore-brain, mid-brain** and **hind-brain** (Figs. 57, 58)—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 the front) region but the lens of the eye is derived from neighboring superficial ectoderm (Fig. 56). 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. The notochord in the several classes of vertebrates exhibits many variations in details of its mode of origin. The essential fact is that, in vertebrates as in Amphioxus, its material is derived from mid-dorsal endoderm and from the actively growing region about the blastopore. In amniotes the origin of the notochord is closely related to that of the mesoderm. Its material, like that of the mesoderm, usually seems to be derived from the primitive streak (see page 54), 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.

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.

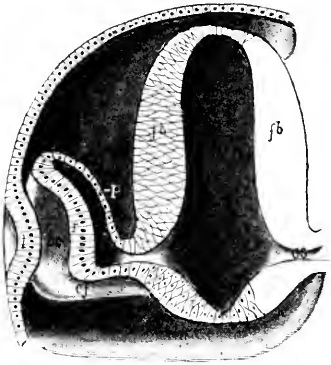


FIG. 56.—Stereogram of the developing eye. The head of the embryo is cut transversely in the region of the fore-brain. *cf*, choroid fissure; *fb*, wall of fore-brain; *l*, ectodermal thickening which invaginates to form lens; *oc*, optic cup; *os*, optic stalk; *p*, outer thin wall of optic cup, becoming 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.")

In the early embryo the ectoderm at a median anteroventral 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** (Figs. 57, *O* and *72D*) separating the external stomodeal cavity from the enteric cavity. Soon a perforation appears at the center of the membrane 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 "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. 57) connecting the hind ends of neural tube and enteric cavity. 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. 57). 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 constitutes the digestive epithelium, the essential secreting and absorbing layer of the tube.

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. In amniotes the pharyngeal pouches are merely temporary

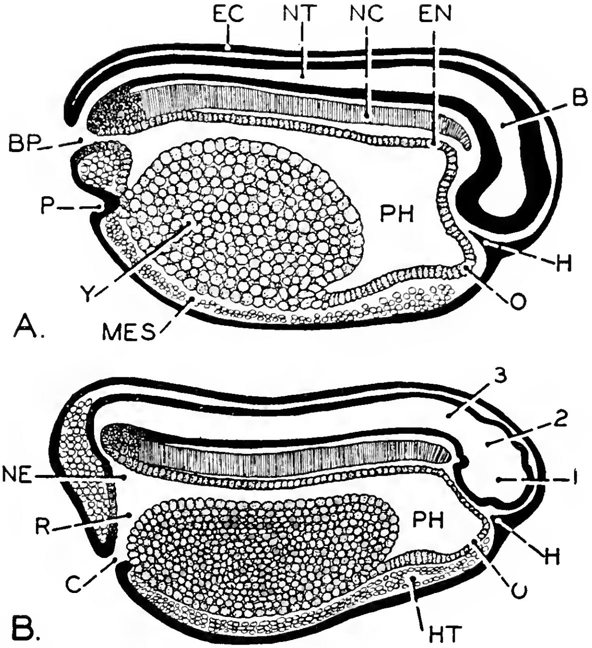


FIG. 57.—Frog: median longitudinal sections of embryos; *A*, just before conversion of blastopore into neurenteric canal; *B*, just after formation of neurenteric canal and perforation of proctodeum to form cloacal aperture. *B*, brain; *BP*, blastopore; *C*, cloacal aperture; *EC*, ectoderm; *EN*, endoderm; *H*, hypophysis; *HT*, heart; *MES*, mesoderm; *NC*, notochord; *NE*, neurenteric canal; *NT*, neural tube; *O*, region where mouth will perforate; *P*, proctodeum; *PH*, pharynx; *R*, rectal region of enteron; *Y*, yolk cells of endoderm; 1, fore-brain; 2, mid-brain; 3, hind-brain. *A*, ×24; *B*, ×19. (Redrawn from Marshall, "Vertebrate Embryology.")

embryonic features except as those of the first pair are, in a modified way, represented in the auditory passages.

Lungs develop by outgrowth from the endoderm of the pharynx (Figs. 235, 238). 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.

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. (Fig. 235)

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 develops as a mid-ventral outgrowth, sometimes more than one, from the anterior region of the prospective intestinal portion of the enteron. The pancreas arises similarly and in close relation to the liver. Vascular and connective tissues make up a large part of the bulk of the adult organs but the essential hepatic cells and the secretory tissue of the pancreas are endodermal. The position of the opening of the bile duct into the intestine marks the point of origin of the embryonic liver.

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. It is derived from the extreme hind end of the embryonic enteron. 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, the latter being the more ventral. 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.

The Mesoderm. The vertebrate mesoderm is at first devoid of segmentation and ordinarily contains no definite cavity (Fig. 44). 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. 58, 59*A*). 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. 58). 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.

The process of segmentation involves only the upper part of the mesoderm. As segmentation goes on, the space between the lower thin and unsegmented layers on either side 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. 58)

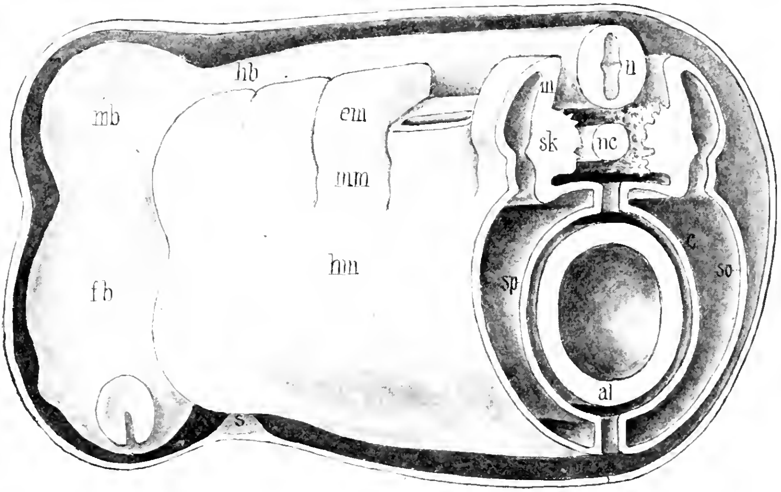


FIG. 58.—Stereogram of the anterior region of a vertebrate embryo showing the segmentation of the mesoderm. The ectoderm has been removed from the left side of the embryo. *al*, endoderm of alimentary tube; *c*, coelom; *em*, epimere; *fb*, fore-brain; *hb*, hind-brain; *hm*, hypomere; *m*, myotome; *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 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 **myocoele**—"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. 59*B*). Eventually, as the somite differentiates, the myocoele is obliterated.

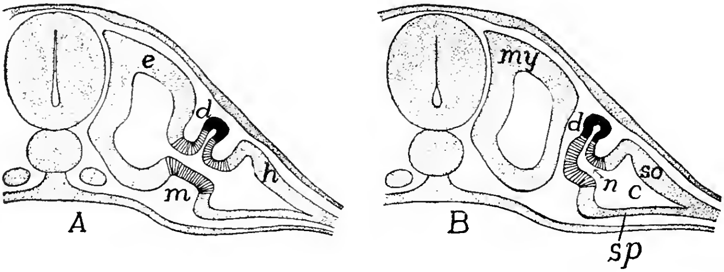


FIG. 59.—Diagrams, (transverse sections) showing embryonic origin of pronephric tubules. *A*, earlier stage; *B*, later. *c*, coelom; *d*, pronephric tubule and duct; *e*, epimere; *h*, hypomere; *m*, mesomere (cross-lined); *my*, myotome; *n*, nephrostome; *so*, somatic layer of hypomere; *sp*, visceral (splanchnic) layer of hypomere. (From Kingsley, after Felix.)

The differentiation of the vertebrate mesoderm is more elaborate than that of Amphioxus, especially in the prospective trunk region. Here, upon each side, early arise three zones of differentiation: the **epimere,** a dorsal mainly 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. 58 and 59*A*).

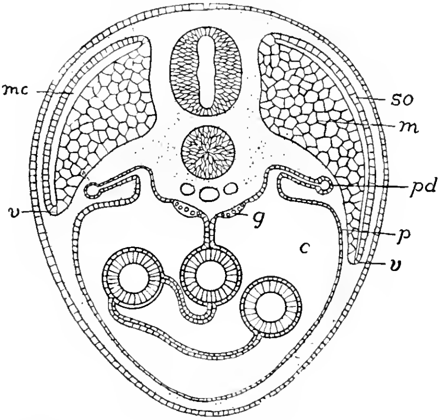


FIG. 60.—Diagrammatic transverse section of the body of a vertebrate embryo at an advanced stage. The muscle-forming myotome is beginning to extend into the ventral body-wall of the embryo. *c*, coelom; *g*, genital ridge; *m*, muscle derived from myotome; *mc*, myocoele; *p*, peritoneum; *pd*, pronephric duct; *so*, somatic layer (dermatome) of somite; *v*, advancing ventral border of myotome; the finely dotted areas are occupied by mesenchyme. (From Kingsley.)

The **epimere** undergoes three kinds of differentiation. Its heavier inner wall is mainly converted into striated body-muscle, not only the dorsal but the ventral muscle. The myotome material grows ventralwards, pushing its way between the ectoderm and the somatic mesoderm, until it reaches the mid-ventral plane (compare Figs. 60 and 61). The medial region of the epimere gives rise to loosely aggregated cellular masses (**mesenchyme**) surrounding the notochord and neural tube (Figs. 58, 60). This material produces such supporting structures—connective tissue, cartilage and bone—as may later be developed around these two axial organs. The thin outer wall of the epimere breaks up to form loose cellular masses, mesenchyme, which give rise to the **dermis,** the deeper fibrous and vascular layer of the skin.

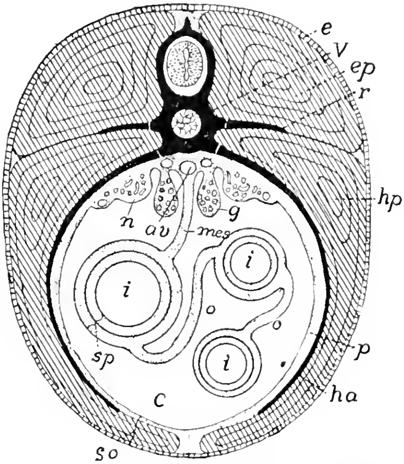


FIG. 61.—Diagrammatic transverse section of the body of a vertebrate. *av*, aorta; *c*, coelom; *e*, ectoderm; *ep*, epaxial (dorsal) muscle; *g*, gonad; *ha*, hemal rib; *hp*, hypaxial (ventral) muscle; *i*, intestine; *mes*, mesentery; *n*, nephridium; *o*, omentum; *r*, rib; *p*, somatopleure; *sp*, splanchnopleure; *v*, centrum of vertebra and, above it, neural arch containing spinal cord. (From Kingsley.)

The terms **myotome, sclerotome** and **dermatome** are applied respectively to the muscle-forming, skeleton-forming and dermis-forming regions of the epimere. (Fig. 58)

The **mesomeres** give rise to the tubular structures of the kidneys. 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** (Figs. 59, 62), and a later more posterior and more extensive 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, 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.

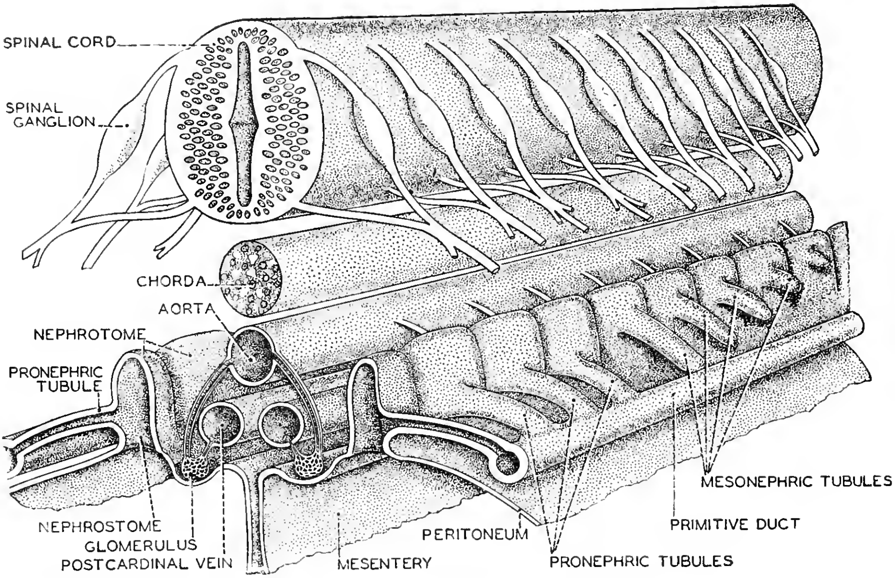


FIG. 62.—Stereogram of the developing pronephros and mesonephros. (After Kingsley modified.)

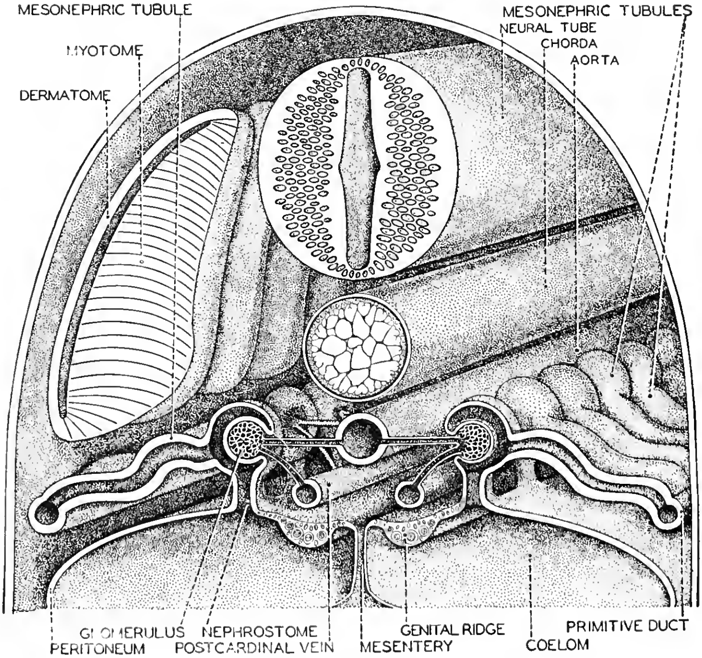


FIG. 63.—Stereogram of the developing mesonephros; stage later than that of Fig. 62. (After Kingsley modified.)

Meanwhile, as the pronephric tubules form, the mesomere material on each side of the embryo gives rise to a longitudinal tube (Fig. 59) which extends from the pronephric region to the cloaca into which it finally opens. The pronephric tubules of each side join the corresponding longitudinal **pronephric duct** (Fig. 62) thus putting the coelom into communication with the exterior by way of the cloaca. The coelomic openings or **nephrostomes** (Figs. 59*B*, *n* and 62) of the pronephros are ciliated. The arrangement apparently serves for drainage from the coelom to the exterior.

The mesonephric tubules acquire connection with the already-formed longitudinal duct which, as the pronephros degenerates, then serves, at least in part, as the **mesonephric** or **Wolffian duct.** In Anamnia usually each mesonephric tubule has a ciliated nephrostome opening into the coelom. In the kidneys of amniotes, nephrostomes rarely appear.

Mesonephric and metanephric tubules usually form specialized excretory structures. The tubule (Figs. 63, 64) 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**) **corpuscle.** The part of the tubule between the corpuscle and the mesonephric duct eventually becomes much elongated, coiled and locally differentiated.

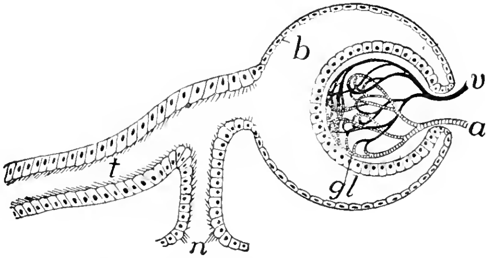


FIG. 64.—Diagram of renal (Malpighian) corpuscle. *a*, artery; *b*, Bowman's capsule; *gl*, glomerulus; *n*, nephrostome; *t*, nephridial tubule; *v*, vein. (From Kingsley, "Comparative Anatomy of Vertebrates.")

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 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 largely by outgrowth from the anterior end of the ureter.

The adult kidney (Fig. 271) consists of the entire system of tubules—mesonephric or metanephric—of one side of the embryo, increased to great number by formation of secondary tubules from the primary tubules, 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 and of all other organs which occupy the coelom. In the median plane at all regions not occupied by median organs (Fig. 58) the right and left visceral layers of the hypomere meet one another to coalesce and become membranes or **mesenteries** which connect and support the viscera. In later stages of development the mesenteries undergo considerable reduction, especially those between the digestive tube and the ventral body wall (Fig. 60). Figure 65 shows the ideal relations of

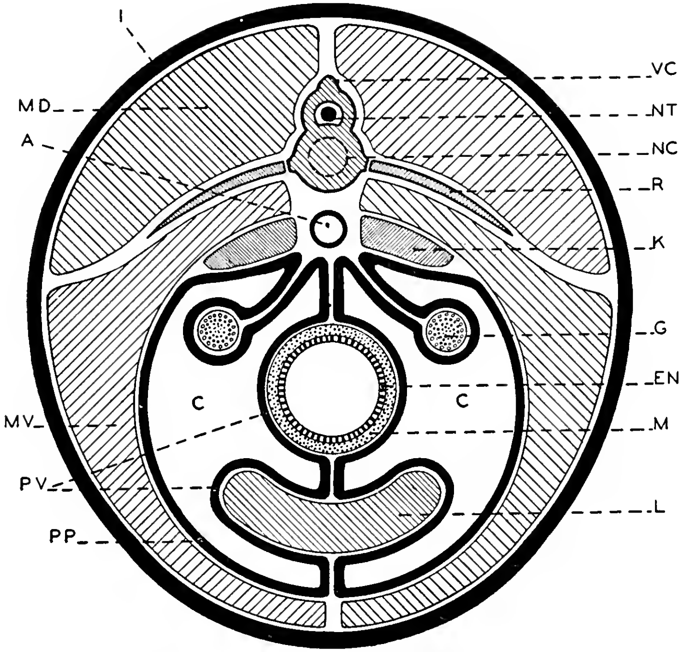


FIG. 65.—Diagrammatic transverse section of the body of a vertebrate showing relations of organs to the peritoneum and coelom. *A*, dorsal aorta; *C*, coelom; *EN*, endodermal epithelium of digestive tube; *G*, gonad; *I*, integument; *K*, kidney; *L*, liver; *M*, muscle layer of digestive tube; *MD*, dorsal muscle of body-wall; *MV*, ventral muscle of body-wall; *NC*, position of embryonic notochord; *NT*, neural tube (spinal cord); *PP*, parietal peritoneum; *PV*, visceral peritoneum; *R*, rib; *VC*, vertebral column.

the **peritoneum** and **mesenteries** to the coelomic organs. It is clear 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 sense, median organs lie **between** the peritoneal sheets of the right and left halves of the body.

The peritoneum plays a part in the development of the **gonads** although it is not necessarily the source of the germ cells. The prospective gonads first appear as longitudinal thickenings or **genital ridges** in the dorsal peritoneum, one on each side and between the dorsal mesentery and the mesonephros (Figs. 60, 61 and 66). The earlier belief that the germ cells are derived from the peritoneal layer has been shaken by evidence that the primordial germ cells first appear in the mid-dorsal enteric endoderm whence they migrate into the genital ridge. 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.

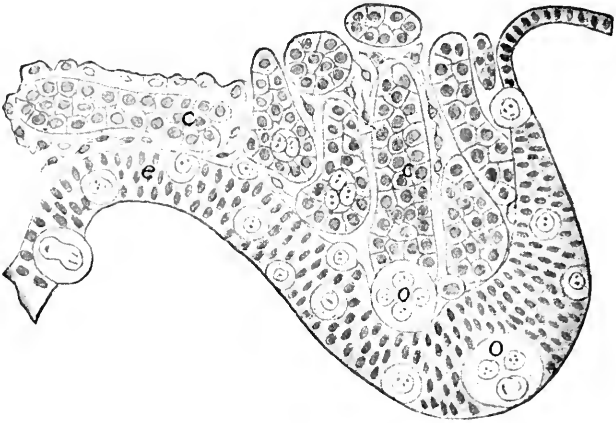


FIG. 66.—Section of genital ridge of a chick of five days incubation. *e*, peritoneal epithelium of ridge; *c*, genital cords; *o*, primordial germ cells. (From Kingsley, after Semon.)

The gonads find outlet by way of ducts which arise in relation to the kidneys. The seminiferous tubules of the testis acquire connection with the neighboring mesonephric tubules and thereby gain exit by way of the Wolffian duct which therefore, in Anamnia, serves as a urinogenital duct. In amniotes the adult male retains, in the epididymis, that part of the embryonic mesonephros which provided connection 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** in elasmobranchs and probably some amphibians arise by longitudinal splitting of the pronephric duct, one portion of it serving thereafter as the mesonephric duct while the other portion acquires, by fusion of several pronephric nephrostomes, a wide anterior opening into the coelom in the vicinity of the ovary. In other vertebrates, the oviduct develops as a fold of peritoneum (Fig. 67, *m*) closely parallel to the Wolffian duct but independent of it.

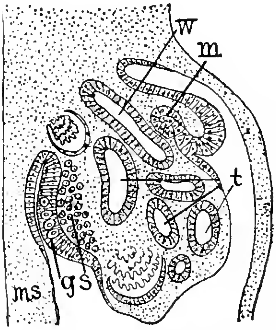


Fig. 67.—Transverse section through the urinogenital region of a four-day chick embryo. *g*, mesodermal epithelium (peritoneum) of genital ridge; *m*, infolding of peritoneum to form Müllerian duct; *ms*, mesentery; *s*, mesenchyme cells which give rise to the stroma (non-genital tissue) of gonad; *t*, mesonephric tubules; *W*, Wolffian duct. (From Kingsley, after Waldeyer.)

The Mesenchyme. Reference has been made (page 69) 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 aggregates in the spaces between the somite and neighboring organs or layers where it produces 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.

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 mesenchyme which accumulates between the enteric wall and the adjacent layers of mesoderm. The ectoderm plays a minor part but evidence has been found indicating that mesenchyme of ectodermal origin, "mesectoderm," participates in the development of parts of the skeleton of the pharyngeal region.

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

Fibrous **connective tissue** is omnipresent in the adult vertebrate. It invests, supports, connects, separates or cushions parts of the body.

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. 68) 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 (Fig. 178) 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-producing cells, **osteoblasts,** build up bone.

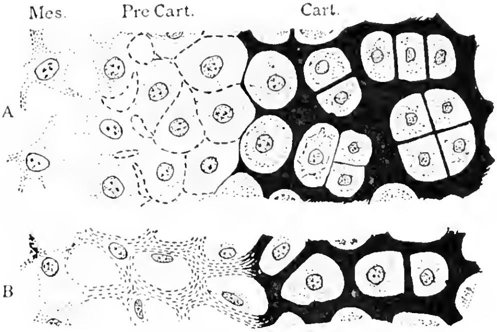


Fig. 68.—Diagrams illustrating formation of cartilage by mesenchyme. *A*, in fishes, according to Studnicka; *B*, in mammals, according to Mall. *Cart.*, cartilage; *Mes.*, mesenchyme; *Pre. Cart.*, precartilage. (From Bremer, "Text-book of Histology.")

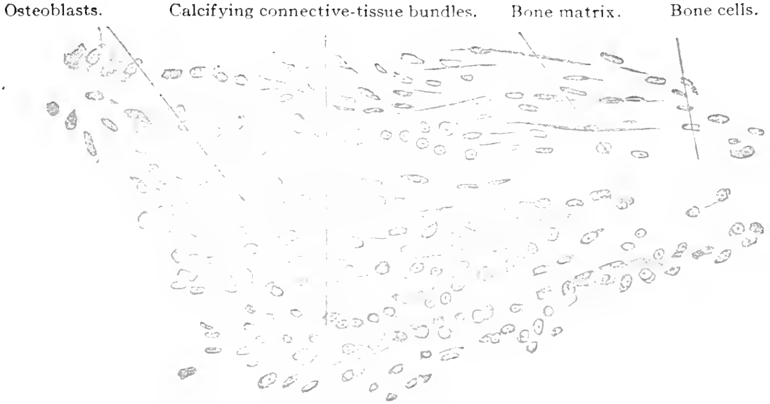


Fig. 69.—Development of dermal (secondary) bone from mesenchyme. From a section of the mandible of a human embryo of four months. ×240. (From Bremer, "Text-book of Histology.")

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. Mesenchyme cells, becoming osteoblasts, build up bone directly on the surfaces of strands of calcified connective tissue (Fig. 69). Most of the bones which develop in this manner are derived from the embryonic mesenchyme of that same general superficial layer which otherwise gives rise to the dermis of the skin. They are accordingly called **dermal bones.** Bone resulting from replacement of cartilage is called **cartilage bone.**

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 of these organs are differentiated from cells of the adjacent mesenchyme. Unstriated muscle fibers occur in the walls of larger blood-vessels and of some integumentary glands where they serve to expel the contents of the gland. Hairs and feathers are erected by contraction of delicate muscles, usually unstriated. The dilators fibers in the iris of the human eye, however, are apparently of ectodermal origin.

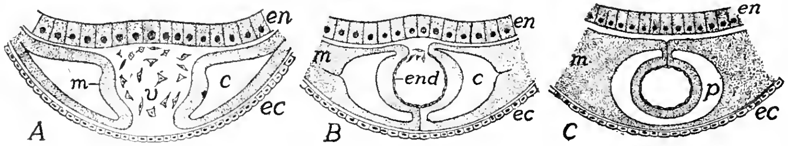


FIG. 70.—Diagrammatic transverse sections of developing heart. In *A* the descending right and left mesodermal hypomeres have nearly met; mesenchyme cells appear between them. In *B* the layers have met ventrally forming the ventral mesocardium; the enclosed mesenchyme has formed the endocardium. In *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.")

The statement that **blood-vessels** are derived from mesenchyme is probably admissible although some vessels seem to arise fairly directly from the mesoderm. They may arise as solid cords of cells, later becoming hollow, or 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 in the region just behind that where the pharyngeal clefts are forming. The right and left hypomeres of the mesoderm push ventralwards and in the median ventral space between them (Fig. 70) accumulate cells derived from the adjacent hypomeres, therefore essentially mesenchymal. These cells arrange themselves to form a very thin layer which becomes 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**) and the outer layer (**epicardium**) of the wall of the heart, also the **pericardium** lining the pericardial cavity, are derived from the adjacent hypomeric mesoderm. The heart muscle, however, unlike that of blood-vessels, is striated.

The **transverse septum,** separating pericardial from abdominal cavity, consists of pericardium in front and peritoneum behind, with connective tissue between. The **diaphragm** of the mammal is not the exact equivalent of the transverse septum of other vertebrates (Fig. 71). 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 diaphragm is muscular. Its muscle is striated and, like body-wall muscle, is derived from epimere mesoderm. Strangely, however, it is mesoderm which shifts backward from somites of the neck region. This accounts for the innervation of the diaphragm by cervical spinal nerves.

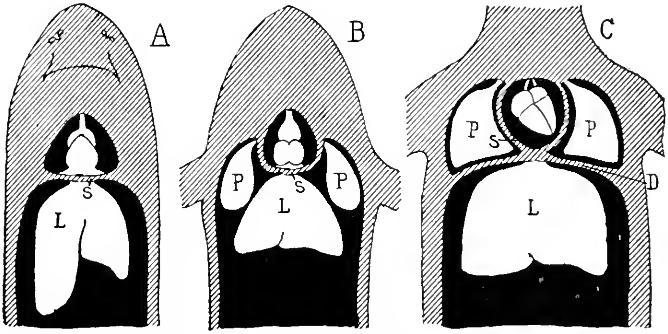


Fig. 71.—Diagrams showing the relations of the coelomic cavities (black) in fishes (*A*), amphibians and sauropsida (*B*), and mammals (*C*). *L*, liver; *P*, lungs; *S*, septum transversum; *D*, diaphragm. In *B* the lungs lie in the peritoneal (or pleuroperitoneal) cavity; in *C* they occupy special pleural subdivisions of the coelom. (From Kingsley.)

Head, Neck, Tail. The mesoderm of the head is less definitely segmented than that of the trunk. 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. 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 the dorsal mesoderm forms epimeres which give rise to neck muscles. The lateral mesoderm, remaining unsegmented; corresponds to the hypomere of the trunk. Whereas the trunk hypomere forms only the **unstriated** muscle of the digestive tube and other visceral parts, the pharyngeal hypomeric mesoderm produces **striated** muscle which differentiates into an elaborate system of muscles (**branchiomeric muscles**) related to the skeleton of the jaws and gill region (Fig. 189).

The tail is produced by growth of ectodermal and mesodermal parts backward from the region of the blastopore. Growth of the mesoderm keeps pace with that of the neural tube and notochord. The mesoderm forms somites which produce the segmental striated caudal muscle and the mesenchyme which gives rise to skeletal, vascular and connective-tissue structures of the tail.

Relation of Yolk to Organogenesis

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. 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. 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.

Yolk is food. The appropriate place for food is in the enteron. In an amphibian embryo the yolk is contained **within** cells. 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 shark, 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 until eventually it is entirely enclosed (Fig. 74) by splanchnopleure and somatopleure with coelom between them. The embryo is put to the necessity of building not only its enteron but its body-wall around its prospective food.

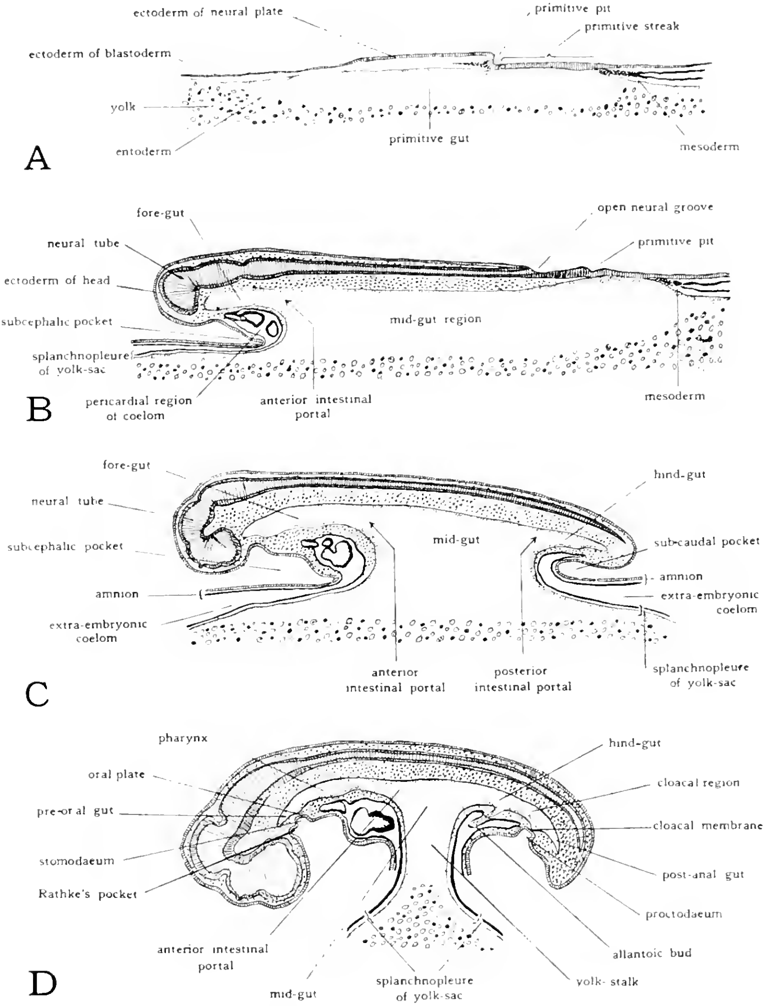


Fig. 72.—Diagrams representing median longitudinal sections of chick embryos after incubation for approximately one day, *A*; two days, *B*; three days, *C*; four days, *D*. The four stages show progressive differentiation of the regions of the enteron and progressive constriction between the yolk-sac and the shaping body of the embryo. (From Patten, "Embryology of the Chick.")

In course of development 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 (Figs. 72, 74) appears between the yolk-sac and the remainder of the embryo. 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 (Figs. 72*D*, 73). In amniotes the amnion is concerned in this constriction (Fig. 74). 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 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.

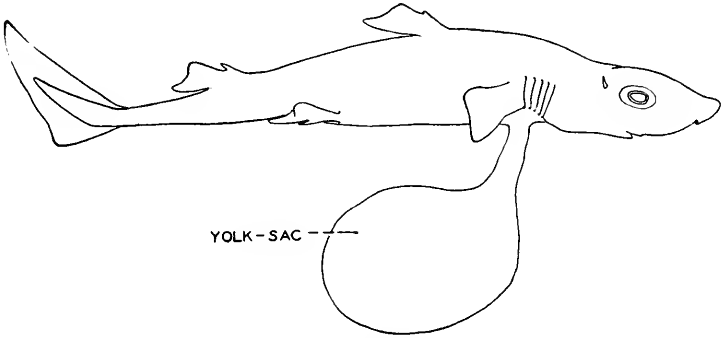


FIG. 73.—Young dogfish shortly before birth. The yolk-sac, containing a remnant of the yolk of the egg, protrudes from the ventral body-wall.

Embryonic and Fetal Membranes

In the description (pages 33–36) of the reproductive arrangements in vertebrates a general account of the embryonic membranes, amnion, chorion and allantois, of reptiles, birds and mammals was given. The foregoing account of the origin of the germ layers and the shaping up of the embryonic body now makes it possible to appreciate the manner of formation of these membranes in terms of germ layers.

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

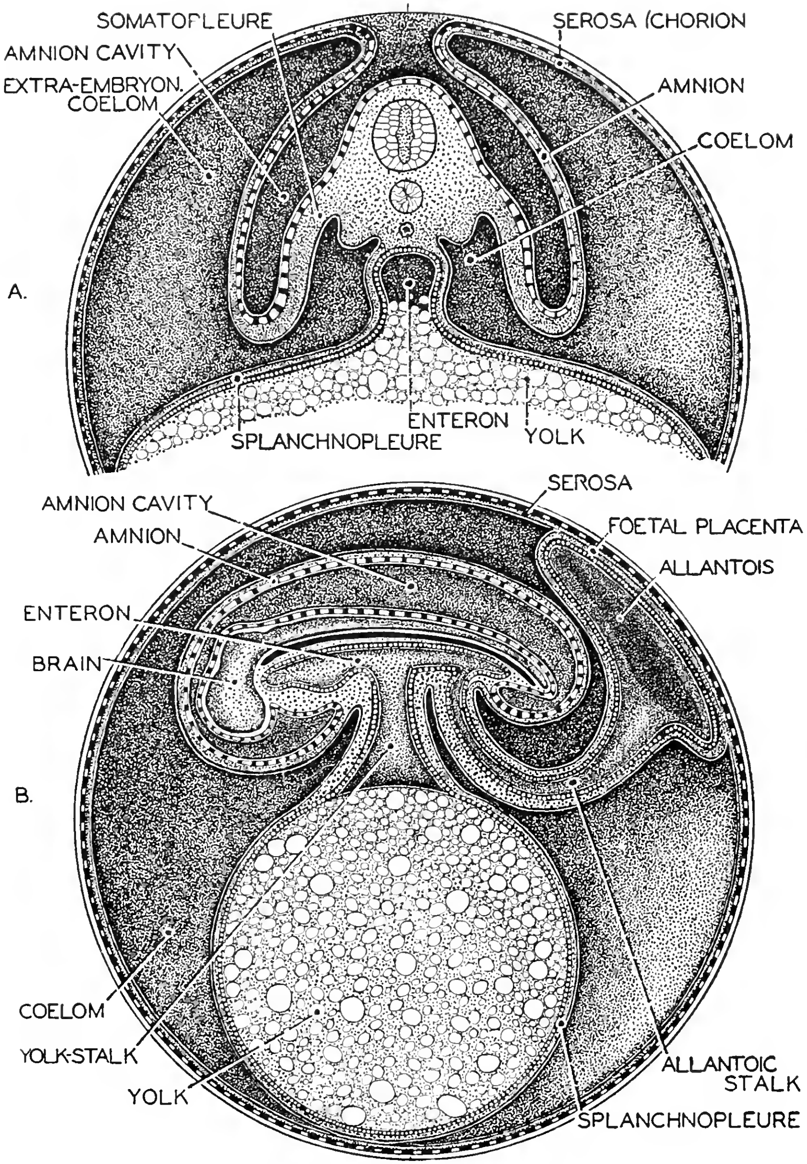


Fig. 74.—Diagrams illustrating the development of the amnion and allantois. Upper figure, earlier stage; section transverse to long axis of embryo. Lower figure, later stage; longitudinal section of embryo. (After Kingsley, modified).

The **amnion** and **chorion** are simultaneously produced by an up-rising fold of the somatopleure (ectoderm accompanied by mesoderm) or embryonic body-wall (Fig. 74). The embryo becomes completely surrounded by such a fold which then grows in centripetally from all directions and finally encloses the embryo. Where opposite edges of the fold meet above the embryo they coalesce. Reference to Figs. 74 and 75 will serve better than description to make clear the resulting relations of layers and spaces.

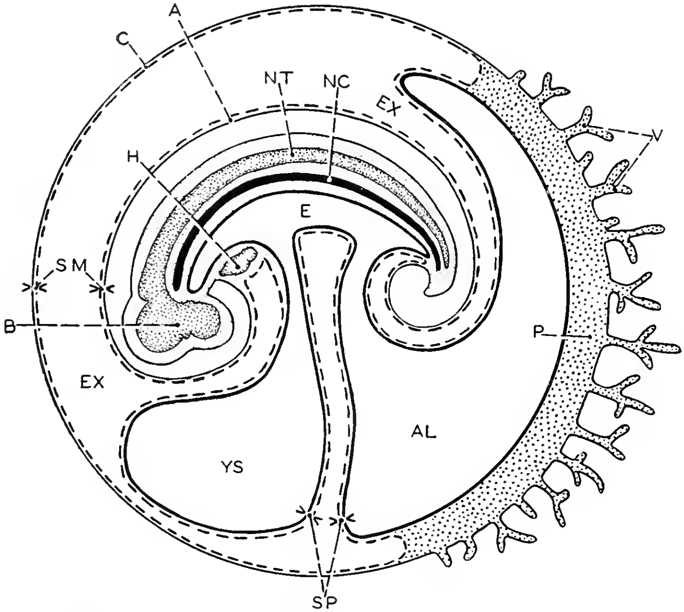


FIG. 75.—Diagram of the fetal structures of a mammal. (The broken lines represent mesoderm.) *A*, amnion; *AL*, cavity of allantois; *B*, brain; *C*, chorion; *E*, enteron; *EX*, extra-embryonic coelom; *H*, heart; *NC*, notochord; *NT*, neural tube; *P*, placental region of allantois and chorion; *SM*, somatopleure; *SP*, splanchnopleure; *V*, chorionic villi; *YS*, cavity of yolk-sac.

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.

The **allantois,** an outgrowth from the hind region of the enteron (Figs. 72*D*, 74, 75), is a product of the splanchnopleure and is lined by endoderm. In the region of its fusion with the chorion the apposed mesodermal layers of the two membranes develop a rich network of fine blood-vessels which are connected by the allantoic arteries and veins to the main blood-vessels of the embryo. This allantoic circulation in a reptile or bird provides for respiration (see pages 33, 34).

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 connexions 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, 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 possesses that organ. In birds, the adult having no urinary bladder, the proximal remnant of the allantois degenerates.

Among mammals there is some 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 main facts concerning the development of a **placenta**, by the chorio-allantoic membrane have already been stated (see page 35). The highly vascular **villi** produced by the chorio-allantoic membrane (Fig. 75) may be merely lodged in depressions in the uterine wall or they may pierce more or less deeply into its tissues. In extreme cases (*e.g.*, in man) there is destruction of walls of uterine blood-vessels and the extravasated blood fills large sinuses in the uterine wall. The 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.

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 other ungulates, the placenta is called **diffuse.** In most 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. 76). 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.

A fetal placenta whose villi do not penetrate deeply into the uterine wall separates from it readily and without loss 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 occurs in carnivores, in the elephant, and commonly in animals having a discoidal placenta.

In certain marsupials (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. Possibly in early mammals both the yolk-sac and the allantois were potentially placenta-forming. In higher primates, 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 connexion with the chorionic vessels of the placenta.

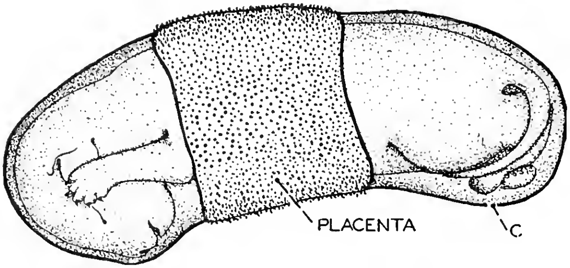


FIG. 76.—Fetus of cat, removed from uterus without rupturing chorionic sac (*C*), showing zonary distribution of placental villi.

The **umbilical cord** is the much elongated and attenuated connexion between the body of the fetus and the extra-fetal membranes.

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 severed. That portion of the allantois remaining within the body becomes the urinary bladder.

CHAPTER 3

HISTOLOGY

Animals are constituted of "living substance" or **protoplasm** together with various non-living materials which are produced by protoplasm. It is chemically complex and possesses a definite, elaborate and minute physical structure. Its basic activities as "living" substance are nutrition, respiration and excretion. For the adequate carrying on of these processes, every particle of protoplasm must be in close relation to an environment containing food and oxygen and providing for removal of wastes. Therefore protoplasm cannot exist in indefinitely large continuous masses. The protoplasm of larger animals is subdivided into minute (usually microscopic) structural and physiological units called **cells.** Circulation of fluid in intercellular spaces provides for the metabolic requirements of the individual cell. Animals, *e.g.*, most of the Protozoa, may be so small as to be organized as single cells.

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.** These organs, in contrast to the 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. In a stomach the primary tissue is the lining layer or 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.

Anatomy deals with organs as such. **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 them. **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.

Most vital functions involve **the surface between protoplasm and the medium immediately 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. Further, 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. Muscles, however, 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 contain cavities, but these cavities 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.

Every surface of the animal, whether apposed directly to the external medium or to some internal cavity, is a critical region. 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 protective non-living substance.

Provision for the adequate carrying on of these essential and diverse 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. 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

Epithelia are tissues of primary importance. They are, in double sense, the most primitive of tissues. The smaller simpler coelenterates consist merely of an outer and an inner epithelium. The gastrula of animal embryos consists of two epithelia. It is evident, then, that epithelium provides for all animal needs, and therefore all-epithelial animals may and do exist.

The outer layer of the vertebrate gastrula, while it is the source of various 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, giving 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. By far the greater part of the massive adult has been inserted between the two primary layers.

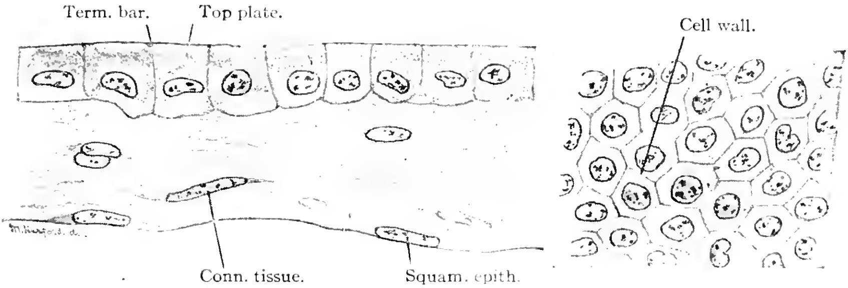
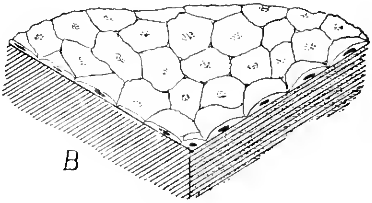


FIG. 77.—At left, section of the allantois and amnion of a pig embryo at a region where the mesodermal layers of the two membranes have coalesced. The section is perpendicular to the surfaces of the allantois (above) and the amnion (below). At right, surface view of allantois. The allantoic epithelium is cuboidal, the amnionic epithelium is squamous. The "top plate" is a superficial denser layer of the cell; "terminal bars" are thickenings of intercellular substance just beneath the surface of the epithelium. (From Bremer, "Text-book of Histology.")

The term **endothelium** is commonly applied to the lining layer of blood-vessels and lymphatics. **Mesothelium** may be used for the peritoneal epithelium. Cells may form a layer resembling an epithelium but not abutting upon a cavity. The tissues of some endocrine glands are of this nature. To such tissues is applied the adjective **epithelioid.**



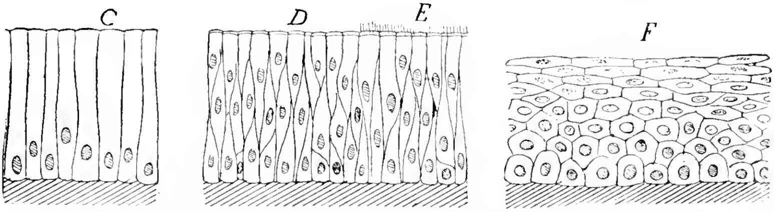


FIG. 78.—Types of epithelia. *B*, simple squamous; *C*, simple columnar; *D*, stratified columnar, ciliated at *E*; *F*, stratified polyhedral, upper cells squamous. (From Kingsley.)

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. An epithelium only one cell in thickness is termed **simple.** There is, however, great variation in the thickness of simple epithelia. The cells, seen in sections perpendicular to the surface, may be approximately square in outline. Such an epithelium is called **cuboidal** (Fig. 77), but incorrectly for the cells are usually hexagonal prisms. A simple epithelium consisting of tall prismatic cells (Fig. 78*C*) is called **columnar.** At the extreme of thinness are epithelia (**flat** or **squamous**) each of whose cells is a broad flat plate, hexagonal in outline. (Figs. 77, 78*B*)

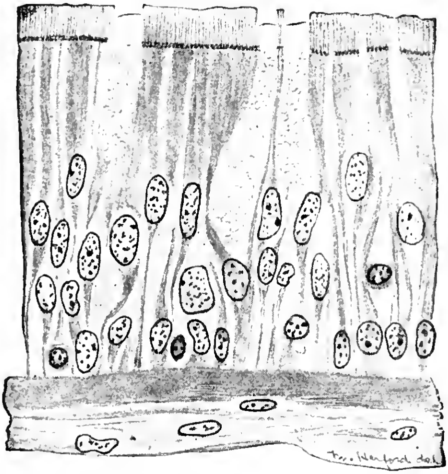


FIG. 79.—Columnar ciliated epithelium from human trachea. Most of the cells are slender, with axes more or less curved, and extend from the basement membrane to the free surface of the epithelium. Occasional short cells, basal cells, lie at or near the basement membrane and do not extend to the free surface. Several swollen mucous cells ("goblet" cells) are shown. (From Bremer, "Text-book of Histology.")

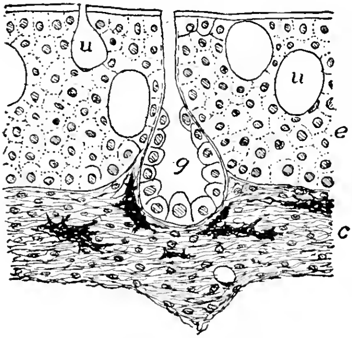


FIG. 80.—Skin of lung-fish, Protopterus; section perpendicular to surface; much enlarged. *c*, dermis (corium); *e*, epidermis; *g*, multicellular gland; *u*, unicellular gland. (From Kingsley.)

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. Surfaces of large heavy animals are exposed to excessive mechanical friction and impact. 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. 78*D-F*). In all vertebrates the epidermis is stratified (Fig. 80).

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.

In a thick stratified epithelium the cells of the bottom layer are usually columnar and those of the outer layers are more or less flattened. The intermediate cells have a form such as would result from crowding tightly together a mass of compressible spheres, that is, polyhedral. 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 delicate strands of solid, or at least dense, substance. Presumably protoplasmic, the strands are called **protoplasmic bridges** or **plasmodesms.**

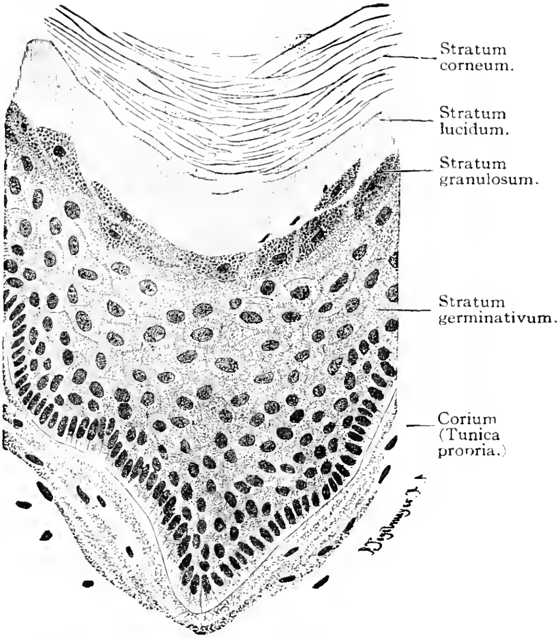


FIG. 81.—Epidermis from the sole of the foot of an adult man. Section perpendicular to surface of skin. External to the *stratum germinativum*, the strata show successive stages in the production of the *stratum corneum*. ×360. (From Bremer, "Text-book of Histology.")

Many epithelia, although "simple" in the sense of being only one cell thick, are not the ideally simple tissue of the definition (page 85), constituted of cells all "alike in their internal differentiation." Among the special functions of an epithelium are the following: (1) production of a superficial covering of non-living, mechanically protective 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.

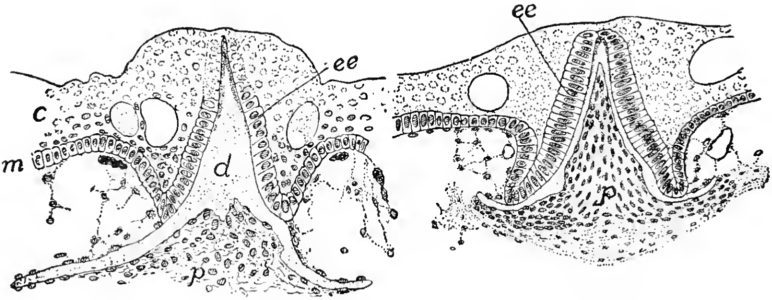


FIG. 82.—Developing scales of dogfish, Squalus; sections perpendicular to surface of skin; much enlarged. *c*, upper layers of epidermis; *d*, dentine of scale, deposited by dermal cells beneath it; *ee*, enamel-forming organ of scale—a specialized region of the germinative layer (*m*) of the epidermis; *p*, "pulp", the dentine-forming organ. (From Kingsley.)

(1) Most epithelia produce a protective covering at the free surface.

A **cuticula** is a dense, tough or hard nitrogenous material deposited on the exposed surface of an epithelium. The cells which produce it and underlie it remain alive.

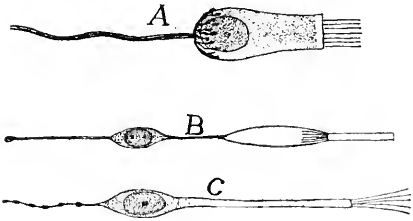


FIG. 83.—Sensory cells. *A*, cell from the sense organ (crista acustica) of an ampulla of the ear; *B*, rod cell from the retina; *C*, cell from the olfactory epithelium. (From Kingsley, After Fürbringer.)

Keratin is a nitrogenous organic substance which is formed within some epithelial cells. It is the basis of the **horny** structures of the vertebrate skin.

The "horny layer" (**stratum corneum**; Fig. 81) developed on the skin of vertebrates other than fishes, consists of one or more of the outer strata of the epidermis, the cells more or less filled with keratin and strongly adherent to one another so that the whole layer acquires a high degree of mechanical resistance. Completely keratinized cells are dead. Hair, feathers, reptilian scales, claws, nails and hoofs are horny structures.

Calcareous material may be deposited by an epithelium, either at its outer surface (*e.g.*, shell of a mollusk) or, exceptionally, at its inner surface (*e.g.*, enamel of teeth; Figs. 82, 129).

(2) A **glandular epithelium** is one in which secreting cells are scattered more or less abundantly throughout the layer. (Fig. 80, *u*)

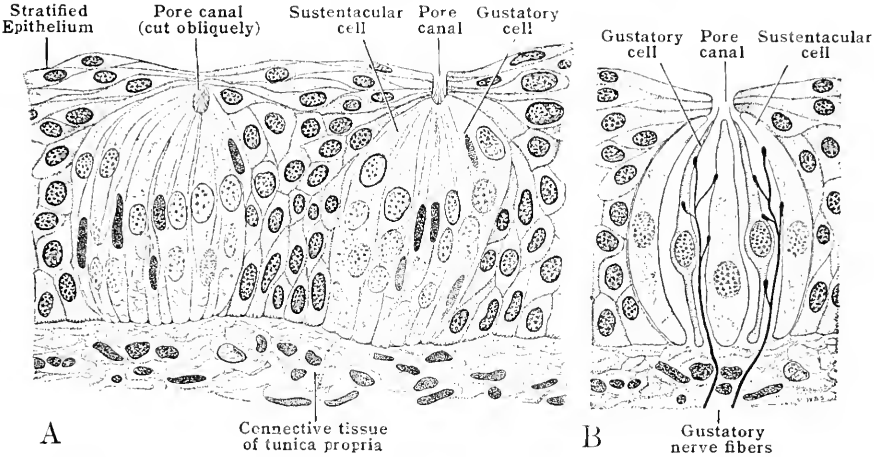


FIG. 84.—Taste-buds from a vallate papilla of the human tongue; as seen in section perpendicular to the surface of the epithelium. *B* is a diagrammatic representation of the structure of one "bud." ×475. (From Morris, "Human Anatomy.")

(3) In a **sensory** (or **neuro-**) **epithelium** certain cells are specialized for reception of stimulation by some agency in the cell's environment (Fig. 83). Epithelial sensory cells may be grouped in clusters to form sense organs (Fig. 84). An epithelium may be rendered sensory by **free nerve termination,** that is, the terminal twigs of a nerve fiber ramifying amongst the epithelial cells (Fig. 85). These nerve fibers, however, are not produced by the epithelium itself but invade it from adjacent tissue.

(4) **Cilia** are extremely delicate motile filaments borne by the free ends of epithelial cells. A single cell may carry from one to over a hundred. A **ciliated epithelium** is one in which some or all of the cells carry cilia. (Figs. 78*E*, 79)

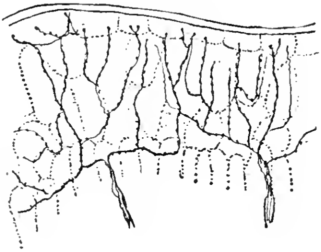


FIG. 85.—Free nerve termination in the epidermis of Salamandra. (From Kingsley, after Retzius.)

Cilia and mucous glands commonly occur in the same epithelium. The simple external epithelium of an earthworm and the stratified epidermis of a fish combine cuticular, glandular and sensory specializations.

GLANDS

"Glands" whose products are as different as are sweat, eggs and blood-cells hardly merit the same name. Accepting the name, it is necessary to distinguish different types of gland: (1) **secretory glands** whose products are retained at least temporarily and serve some useful purpose—*e.g.*, mucous, salivary and thyroid glands; (2) **excretory glands** which eliminate waste—*e.g.*, kidneys; (3) **cytogenic glands** which produce living cells—*e.g.*, reproductive glands producing eggs or sperm, various lymph and blood glands in which white blood-cells are produced.

Secretory glands may be unicellular (Figs. 79, 80, *u*) or **multicellular** (Fig. 80, *g*). Nearly all multicellular glands develop directly from epithelia and retain their epithelial character. Some endocrine glands are epithelioid.

Most secretory glands develop from either the ectodermal or the endodermal epithelium and discharge at the surface of their native epithelium. Such are the many kinds of skin glands and digestive glands. The mesoderm gives rise to some secretory glands, especially in connexion with the reproductive system—*e.g.*, the albumen glands and shell glands of oviducts and the mucous glands of the mammalian uterus.

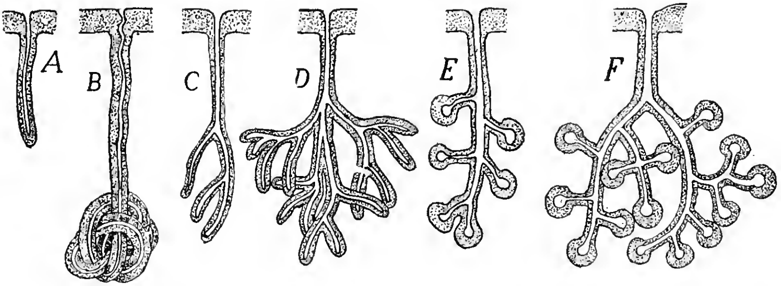


FIG. 86.—Types of multicellular glands. *A–D*, tubular; *E, F*, alveolar or acinous. A, simple; *B*, coiled; *C–F*, branched. The duct pierces the epithelium from which the gland has been produced. (From Kingsley.)

Multicellular glands may be **tubular** (Fig. 86*A-D*) , or **alveolar** (**acinous**; Fig. 86*E,F*). Glands of either type, complicated by branching, are called **compound** (Fig. 86*C-F*).

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.

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.

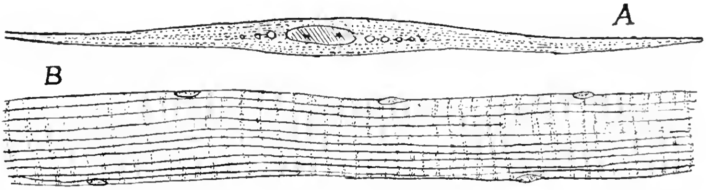


FIG. 87.—*A*, unstriated ("smooth") muscle cell with single nucleus; *B* shows a small portion of the length of a multinucleate striated fiber. (From Kingsley.)

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 or 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 complex system of transverse striations.

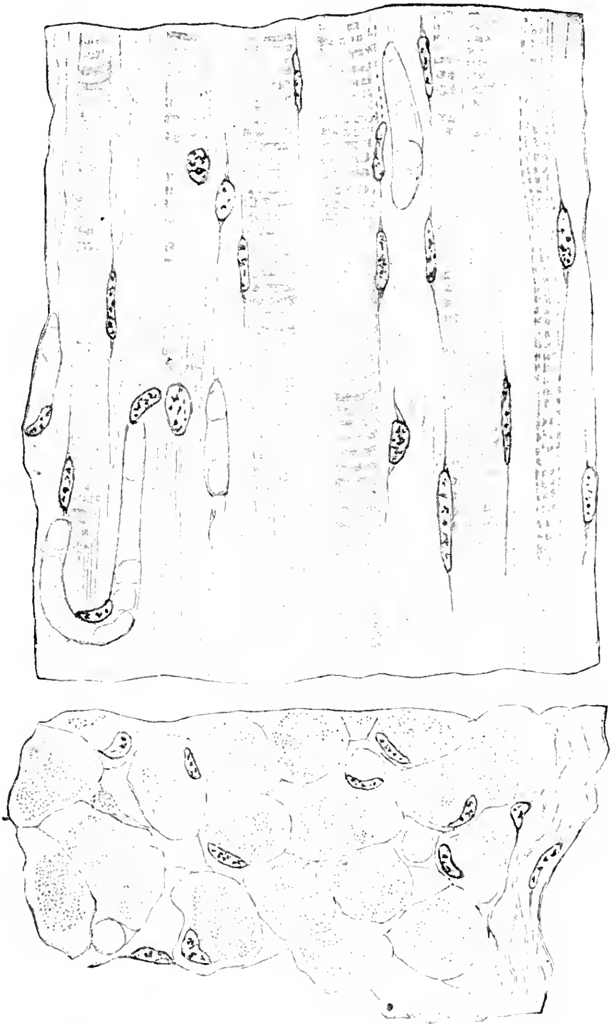


FIG. 88.—Striated muscle; human. Above, in longitudinal section, showing small portions of several fibers; below, section transverse to the length of the fibers. Nuclei lie at the surface of the fiber. (From Bremer, "Text-book of Histology.")

Vertebrates possess both striated and unstriated (or "smooth") muscle (Fig. 87). 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 connexion 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 and its muscle is accordingly striated. And in all vertebrates the muscle of the wall of the heart is striated.

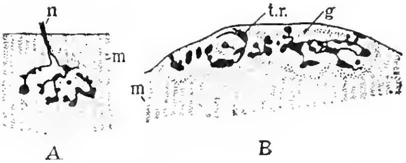


Fig. 89.—Motor plates. *A*, from guinea-pig; surface view of muscle fiber: *B*, from hedgehog; section perpendicular to surface of muscle fiber. *g*, granular substance of the motor plate; *m*, striated muscle; *n*, nerve fiber; *t.r.*, terminal ramification of the nerve fiber. (From Bremer, "Text-book of Histology"; after Böhm and Davidoff.)

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. 87*A*) lying in the tissue with their tapering ends overlapping.

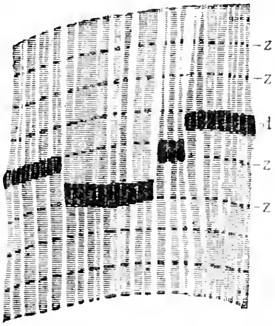


Fig. 90.—Human cardiac muscle; a very small portion seen under high magnification. *d*, intercalated disc; *Z*, Krause's membranes which lie transversely at regular intervals along each myofibril, bisecting each light band. The distinction between light and dark bands does not appear in the figure. (From Bremer, "Text-book of Histology"; after Heidenhain.)

The somatic striated fibers of vertebrates are enormously larger than unstriated fibers (Fig. 87*B*, 88). 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.

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**.

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 seen only under high magnification.

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 knot-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. 89) 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 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** (Fig. 90) which are quite distinct from the ordinary striations. Their significance is not known.

NERVOUS TISSUE

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.

Neurons are of various types depending on the form of the cell-body and the number of nerve processes (Figs. 91, 92). **Unipolar** cells, of comparatively rate 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 neuraxon may give off lateral branches (**collaterals**) and its distal extremity breaks up into fine branches forming the **terminal arborization.**

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 (Figs. 83*C*, 348*B*). In such cases, one neuron serves as both receptor and conductor. In other

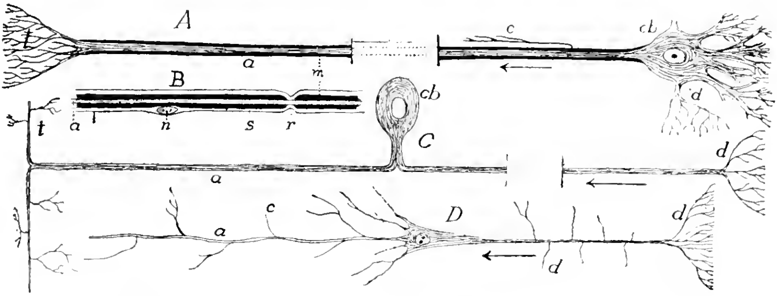


FIG. 91.—Types of nerve cells. *A*, multipolar cell; *B*, portion of nerve fiber with sheaths; *C*, unipolar cell (such a cell may arise by modification of a bipolar cell as shown in Fig. 93); *D*, pyramidal cell (from cerebral cortex). *a*, axon; *c*, collateral; *cb*. cell-body; *d*, dendrites; *m*, medullary sheath; *n*, nucleus of cell of Schwann's sheath; *r*, node of Ranvier; *s*, sheath of Schwann; *t*, telodendron. (From Kingsley.)

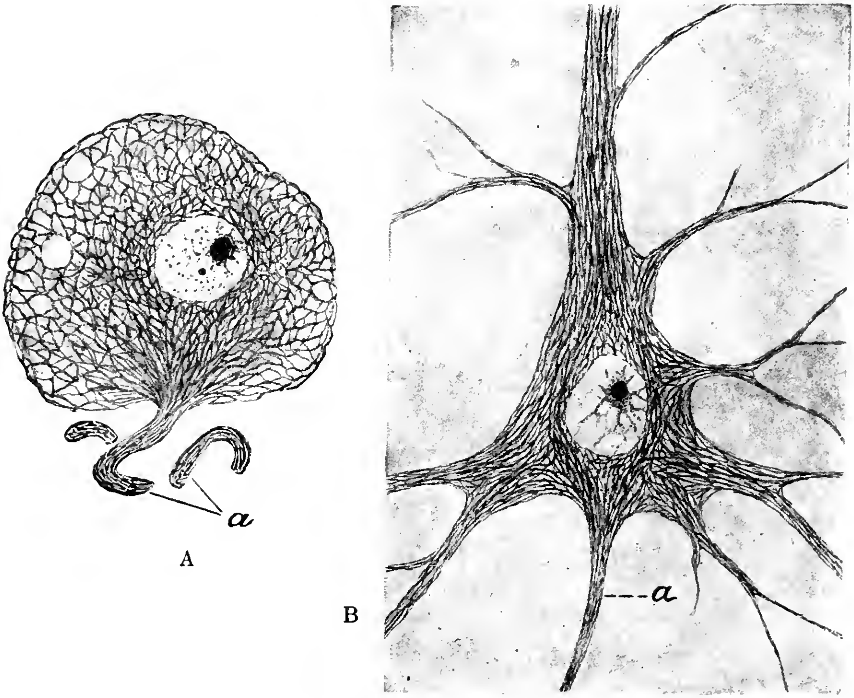


FIG. 92.—Cell-bodies of neurons showing arrangement of neurofibrils. *A*, from human spinal ganglion; two cut fragments of the neuraxon lie near the cell-body. *B*, "giant pyramidal cell" from human cerebral cortex. Highly magnified. *a*, neuraxon. (From Morris, "Human Anatomy.")

cases, as in the auditory organ and taste-buds (Figs. 84*B*, 348*D*), 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.

Nerve cells vary greatly in size, but in general are relatively large. They are often the largest cells in the body exclusive of eggs.

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. 94) 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. 92), 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.

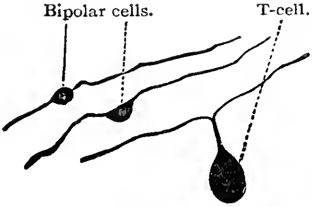


Fig. 93.—Diagram showing how an embryonic bipolar nerve cell is transformed into a unipolar cell ("T-cell") such as occurs in ganglia of the dorsal roots of spinal nerves. (From Bremer, "Text-book of Histology.")

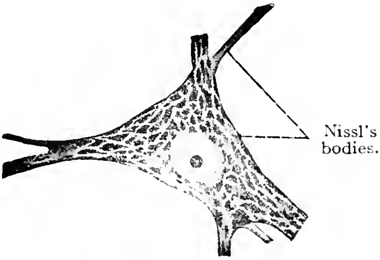


Fig. 94.—Nerve cell, with processes cut short; from human spinal cord. ×430. (From Bremer, "Text-book of Histology.")

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 two special ensheathing layers. The **medullary** or **myelin sheath** is a relatively thick layer of fat-like substance, myelin, fitting the neuraxon closely. The **neurilemma** or **sheath of Schwann** is an exceedingly thin cellular layer wrapped around the neuraxon. (Figs. 91, 304)

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 neurilemma there comes into close relation with the nerve fiber (Fig. 91*B*). The neuraxon therefore presents a segmented appearance due to these **nodes of Ranvier.**

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."

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

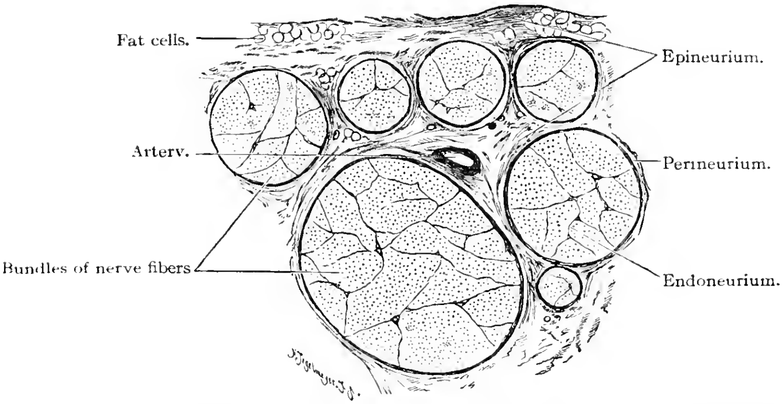


FIG. 95.—Structure of a nerve. The figure represents a small part of a transverse section of a large nerve constituted of many bundles of medullated fibers. ×20. (From Bremer, "Text-book of Histology.")

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. 95) 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.

TISSUES SERVING FOR MECHANICAL SUPPORT

Protoplasm is a substance of semi-fluid or gelatinous consistency. An elephant constituted of protoplasm only is a mechanical impossibility. Large animals, especially if they are land animals, require mechanical support. Protoplasm provides such support by appropriating various materials from the environment and building 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.

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 ectodermal neuroglia (page 99) of nervous organs.

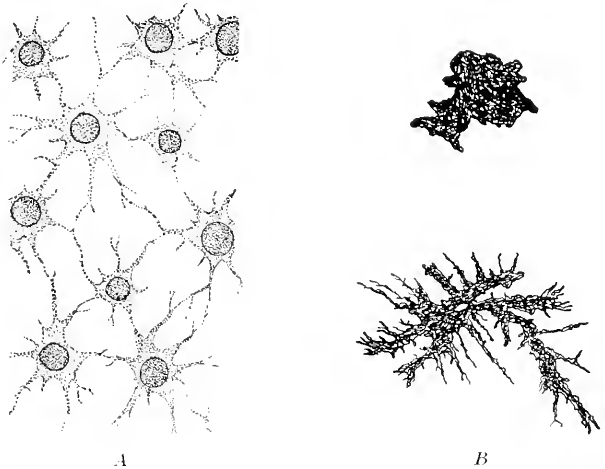


FIG. 96.—*A*, mesenchymal tissue from embryo of the amphibian, Ambystoma. *B*, pigment cells from Ambystoma; below, a cell with pigment dispersed in numerous branched processes of the cell; above, a "contracted" cell with pigment concentrated, the transparent processes not shown. (From Kingsley.)

The embryonic precursor of supporting tissues other than the exceptions mentioned is a more or less spongy mesenchyme (Fig. 96*A*) 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

The essential mechanical structures in connective tissue are relatively coarse white fibers 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 in the intercellular matrix.

Elastic fibers 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. 97). Elastic fibers commonly occur inter-mingled with collagenous fibers.

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.**

Tendons and **ligaments** are connective-tissue structures highly adapted to resisting tensile strain. They consist of coarse collagenous fibers arranged in compact bundles. Tendons are inelastic.

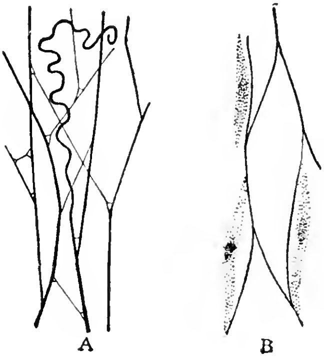


Fig. 97.—*A*, elastic fibers of the subcutaneous areolar tissue of a rabbit. *B*, cells related to elastic fibers, as seen after treatment with acetic acid; from subcutaneous tissue of a pig embryo. (From Bremer, Text-book of Histology: *A*, after Schäfer; *B*, after Mall.)

Chromatophores, pigment cells (Fig. 96*B*), 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. 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. 98). 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. 98, *ei*) composed of material secreted by an outer epithelioid layer of the notochord tissue, and a thick outer sheath of dense fibrous connective tissue. Mechanically, the notochord resembles a length of rubber tubing, closed at the ends, and filled with liquid under pressure.

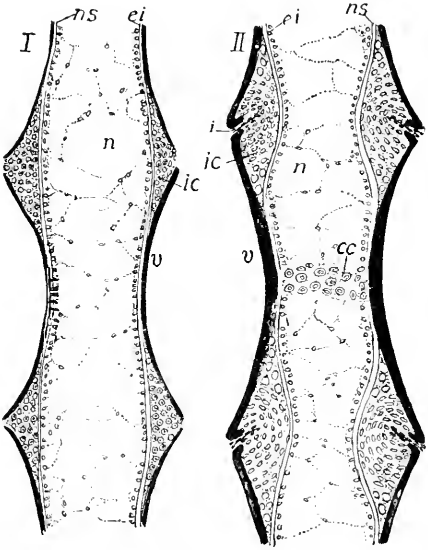


Fig. 98.—Developing vertebrae of the amphibian, Ambystoma; I, earlier; II, later. Longitudinal sections. Cartilage and bone are forming around the notochord. *cc*, cartilage in center of vertebra; *ei*, epithelioid internal elastic sheath of notochord; *i*, incisure cutting through *ic*, intercentral (intervertebral) cartilage; *n*, notochord; *ns*, outer notochordal sheath; *v*, developing bone (black) of centrum of a vertebra. (From Kingsley.)

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. 68, 99). The intercellular **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 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 connective-tissue membrane, the **perichondrium** (Fig. 99) which contains blood-vessels but they do not penetrate into the cartilage. Hence cartilage cannot occur in thick masses.

In growing cartilage, cells from the perichondrium become cartilage cells and add cartilage to the exterior of the mass already formed. At the same time deep cartilage cells divide. The resulting cells secrete matrix substance whereby they become separated, each to lie in a lacuna of its own.

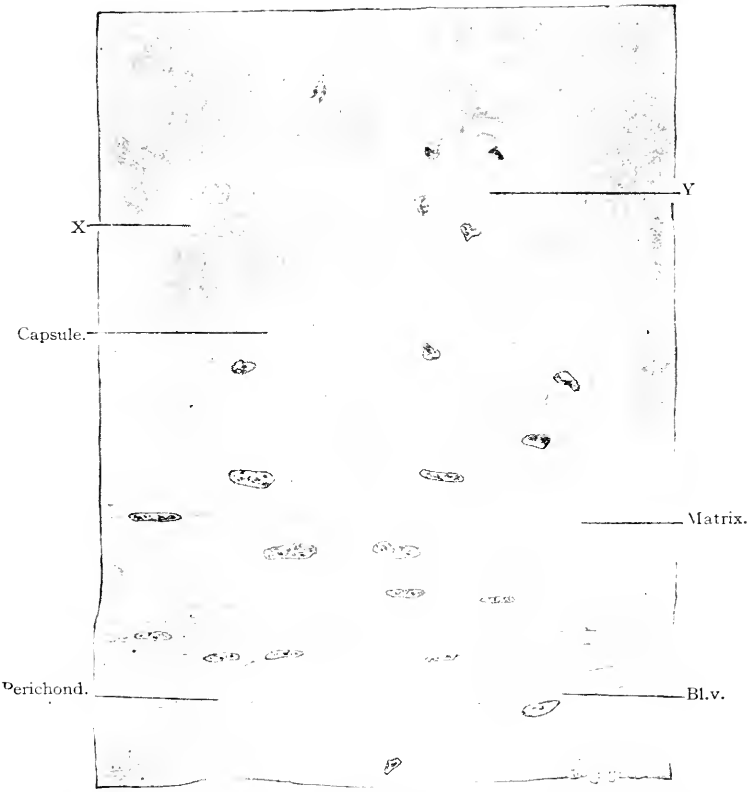


FIG. 99.—Hyaline cartilage, with perichondrium; from human trachea *Bl.v.*, blood-vessel; *x*, cartilage cell whose nucleus is not in section; *y*, new matrix forming between two cells resulting from a recent division of a cartilage cell. (From Bremer. "Text-book of Histology.")

Hyaline cartilage (Fig. 99), usually bluish and clear, is nearly devoid of fibrous material. In **fibrocartilage** the matrix contains fibers similar to those of ordinary connective tissue. **Elastic cartilage** contains numerous elastic fibers. **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 a non-living matrix within which are imbedded living cells. 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 (Fig. 100) is of a porous or spongy texture (**cancellous bone**) while the outer region is dense or solid (**compact bone**).

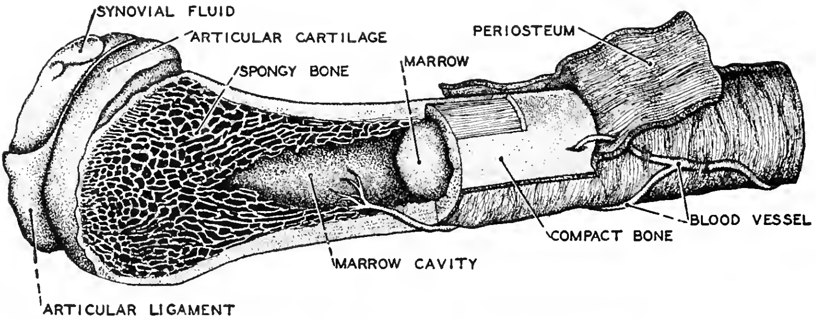


FIG. 100.—Diagram of the structure of a long bone. (Redrawn from Kahn's "Der Mensch," Albert Müller, Zürich.)

A section of fully developed compact bone, seen under high magnification, shows the matrix layers or **lamellae** arranged in parallel or concentric order (Fig. 101*B* and 102). Between adjacent lamellae are minute cavities, the **lacunae.** 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.

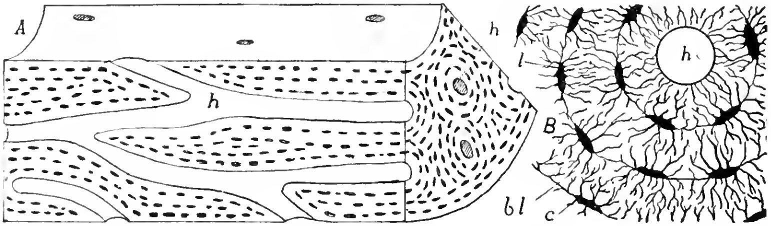


FIG. 101.—*A*, stereogram representing a sector of the shaft of a long bone. *B*, transverse section, much more enlarged, showing part of one Haversian system. *bl*, bone lamellae; *c*, canaliculi; *h*, Haversian canal; *l*, lacuna. (From Kingsley.)

All external surfaces of bone are covered by a membrane, the **periosteum** (Fig. 100), of dense fibrous connective tissue well supplied with blood-vessels which enter the bone and branch throughout it. Most bones, notably the long bones of the appendages, have internal cavities (Fig. 100) occupied by a more or less vascular soft tissue, the **marrow.** The "yellow marrow" of long bones contains much fat. "Red marrow" is highly vascular, contains little fat and may be a source of blood cells of various types.

In long bones the larger blood-vessels lie approximately parallel to the long axis of the bone. Around such vessels the bone lamellae are arranged in concentric order (Figs. 101 and 102) forming so-called **Haversian systems.** These concentric systems are much less prominently developed in flat bones.

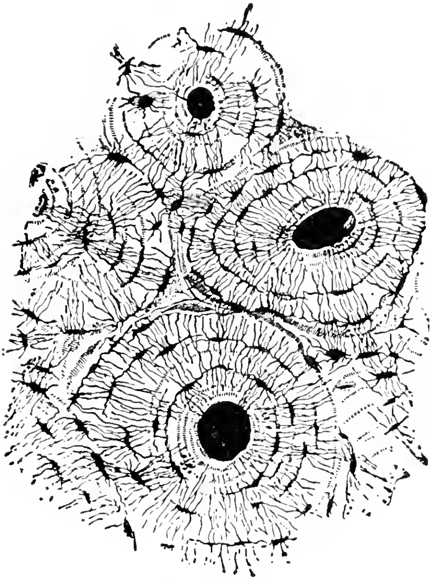


FIG. 102.—Section, highly magnified, of compact bone from the shaft of the human humerus. The section, cut transversely to the long axis of the bone, shows four Haversian systems with their central canals, concentric lamellae of bone, lacunae between adjacent lamellae, and canaliculi extending between lacunae. (From Bremer, "Text-book of Histology"; after Sharpey.)

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. Bone, because of the rigidity of its calcified matrix, is incapable of such interstitial growth as occurs in cartilage. 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.

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. 103). 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.

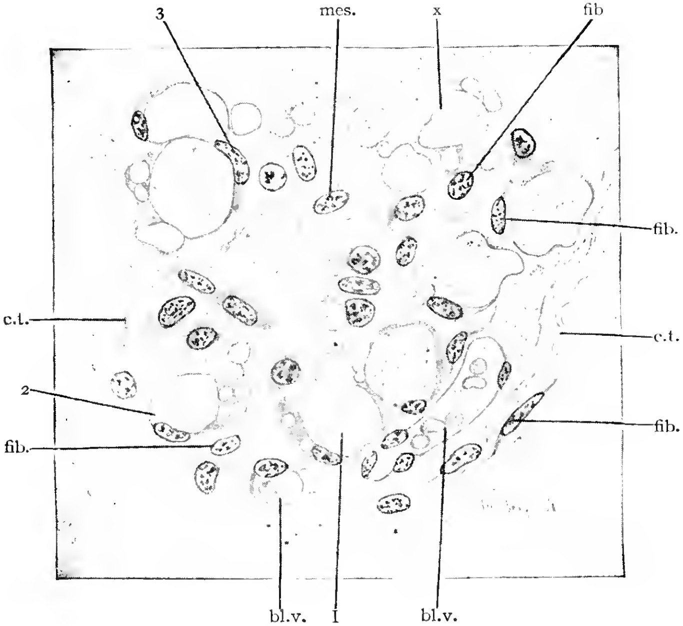


FIG. 103.—Fat cells in subcutaneous tissue of a human embryo of four months. *bl.v.*, blood-vessel; *c.t.*, white connective-tissue fibers; *fib.*, young fibrocyte; *mes.*, mesenchymal cell; *x*, young fat cell, nucleus not in section; 1, 2, 3, developing fat cells. (From Bremer, "Text-book of Histology.")

BLOOD

The circulatory function of blood 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 together with various hormones and the waste products of metabolism. In its inorganic chemical constitution, the plasma resembles sea water.

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. 104). The uncoagulated portion of the plasma is called **serum.** The "clot" is a mass of fibrin with blood cells caught in its meshes.

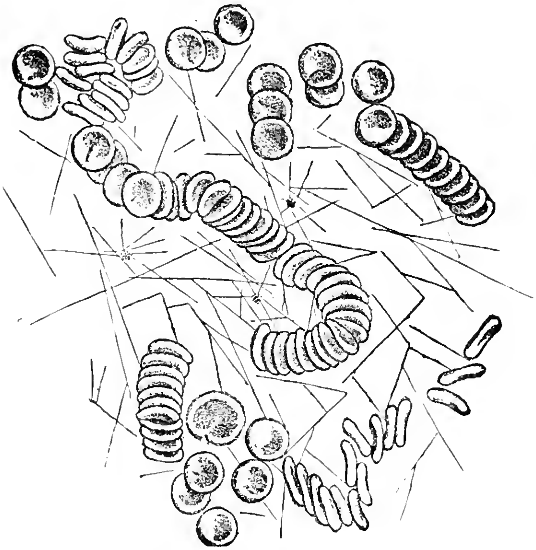


FIG. 104.—Coagulated blood. Biconcave red corpuscles arranged in "rouleaux"; filaments of fibrin radiating from minute blood plates. (From Bremer, "Textbook of Histology"; after Da Costa.)

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. 104 and 105) are relatively small and usually have the form of flat discs with elliptical outlines. These blood cells are the oxygen-carriers, being heavily loaded with **hemoglobin,** a complex protein substance containing iron and having a strong affinity for oxygen which the cells pick up at the respiratory surfaces of the animal. Their color is due to the hemoglobin. The mature erythrocytes of all vertebrates except mammals are nucleated. In adult mammals, the red cells in course of their differentiation lose their nuclei, thereby acquiring the form of biconcave discs. (Fig. 104)

Leucocytes are permanently nucleated and do not carry hemoglobin. Several types are recognized. (Fig. 105)

Lymphocyte: usually small, cytoplasm scanty and usually non-granular, nucleus spherical.

Large mononuclear leucocyte (monocyte): more abundant and non-granular cytoplasm, nucleus excentrically placed.

Polymorphonuclear leucocyte: large, with conspicuous granules in cytoplasm, nucleus indented, lobulated, irregular or separated into two or more parts. Several kinds 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. Many are phagocytic.

Blood plates (Fig. 105) are minute bodies which seem to be protoplasmic and yet are not nucleated. They probably result from fragmentation of cells in bone marrow or elsewhere. They seem to have some relation to the clotting of blood as indicated by the fact that the filaments of fibrin (Fig. 104) tend to radiate from blood plates.

Lymph resembles blood but lacks erythrocytes and is therefore colorless. The fluids occupying the 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. Unstriated muscle fibers appear much the same whether they are in the wall of a stomach or of a lung. Nevertheless tissues and cells usually 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. Epidermal tissue of a fish differs from that of a reptile.

It follows, therefore, that the individual tissue cell may, in its visible structure, exhibit characteristics reflecting as many as four grades of

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FIG. 105.—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 multi-lobed 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".)

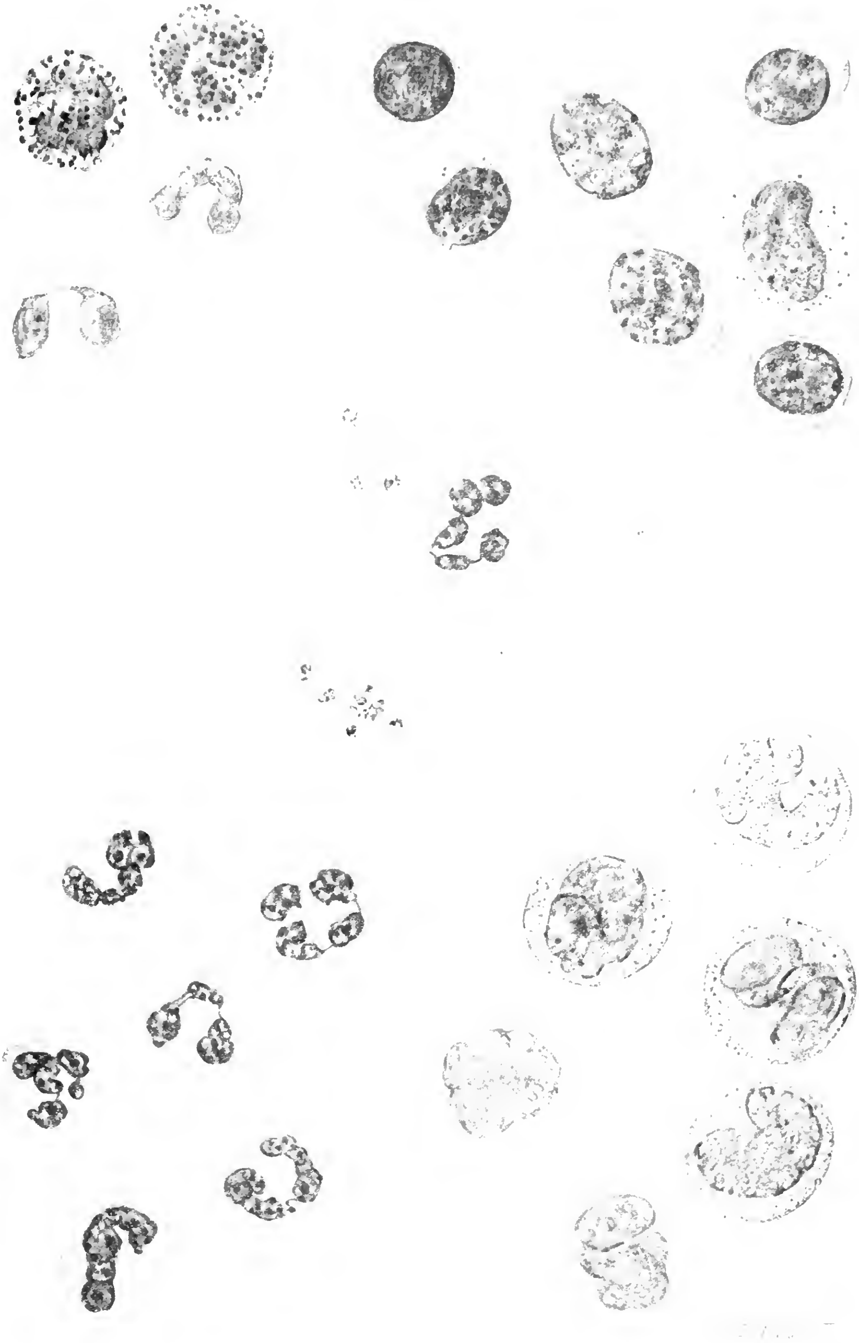


Fig. 105.—(See page 108 for description.)

organization. First there are those cell organs, such as nucleus and chromatin bodies, 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. Behind all of this visible differentiation and specificity of structure must be chemical specificity.

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 various 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. The layer secretes 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. 106.

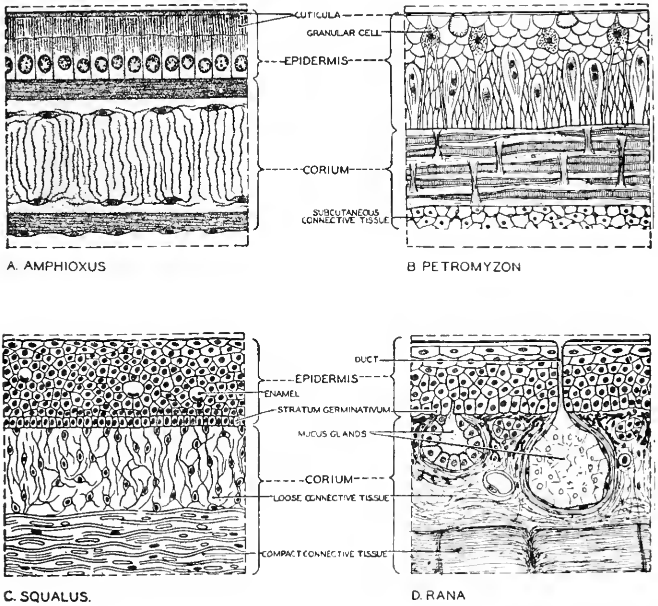


Fig. 106.—Cross sections of the skin of four chordates, Amphioxus, Petromyzon, Squalus, and Rana, showing the fundamental differentiation of the skin into corium and epidermis. The differentiation of the epidermis into a dead outer layer and an inner living layer began in aquatic animals. (Redrawn mainly after Plate and Schimkewitsch.)

The 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 amphibians 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.

STRUCTURE OF THE HUMAN SKIN

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

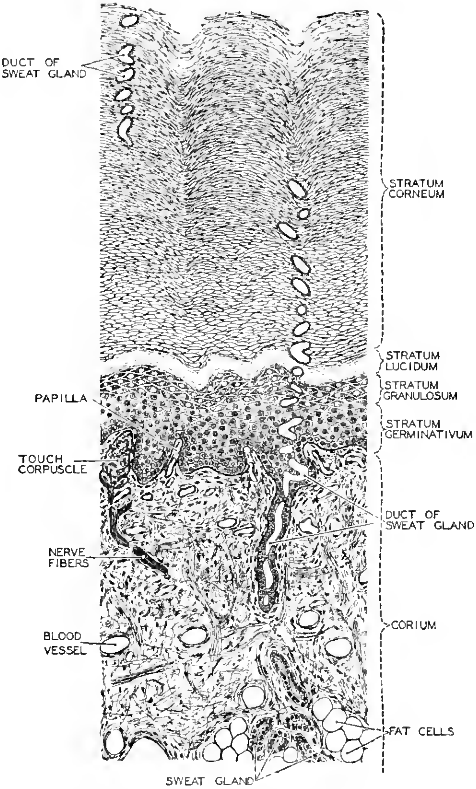


FIG. 107.—A cross section of the thickened skin of the sole. The stratum corneum is especially thickened on the sole and on the palm of the hand.

nearer the surface, replace their living protoplasm by 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. 107.

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. 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. See Fig. 108. 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?

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 finger-print 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.

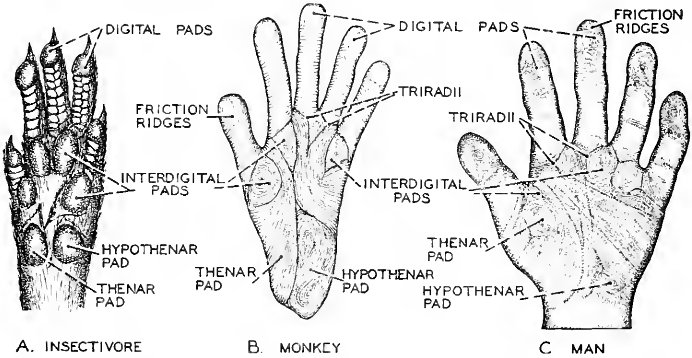


FIG. 108.—Friction-ridge patterns in three mammals—insectivore, monkey, and man. The presence of such useless and rudimentary concentrically arranged ridges in the human hand receives its only reasonable interpretation in the light of the evolution theory. (Redrawn after Wilder.)

APPENDAGES OF THE INTEGUMENT

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 defense, support of tissues, or attachment of muscles. The limy shells of molluscs and the chitinous exoskeletons of arthropods serve all three purposes.

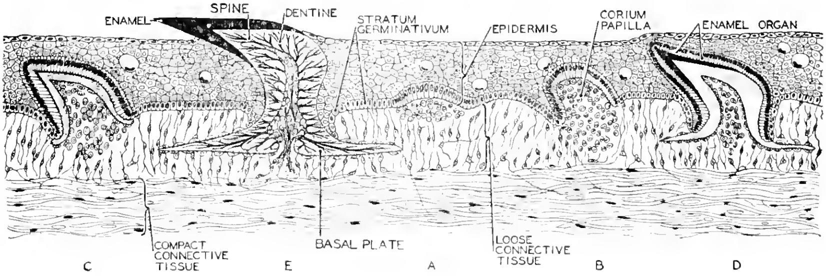


FIG. 109.—A vertical section of the skin of an elasmobranch, showing five stages in the development of a placoid scale. The development of a placoid scale is essentially like that of a tooth. This fact taken together with the similarity of their structure suggests that teeth may have evolved from placoid scales. (Redrawn after Schimkewitsch, modified.)

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, like a tooth, with hard enamel. 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.

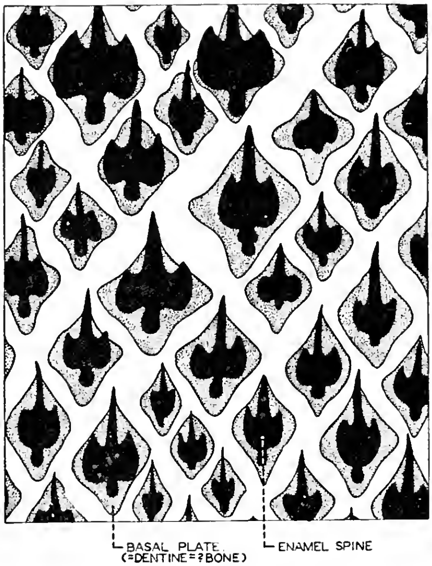


FIG. 110.—The imbricated pattern of placoid scale arrangement in elasmobranchs. The scales are arranged in rows and usually each scale is in line with the interval between scales of the lines in front and behind. (Redrawn after Klaatsch.)

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 horny 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.

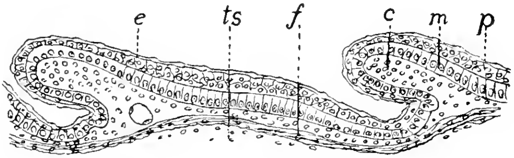


FIG. 111.—Section of developing scales of lizard, Sceloporus. *c*, papilla of corium; *e*, outer layer of epidermis which later becomes cornified; *f*, fibrous layer of skin; *m*, Malpighian (stratum germinativum) layer; *p*, periderm; *ts*, tela subjunctiva. (From Kingsley's "Comparative Anatomy of 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 rhinoceros. Those of the rhinoceros 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 extends 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 corneum** 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.

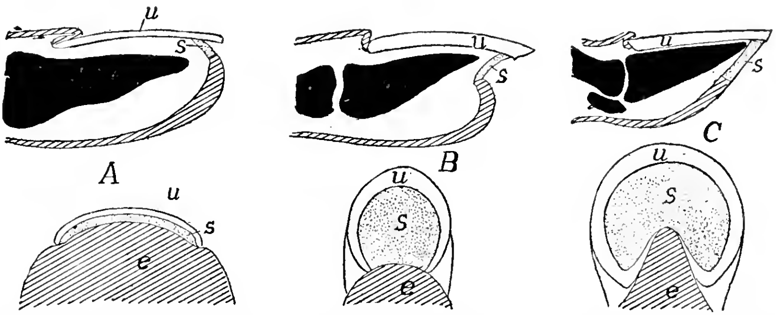


Fig. 112.—Diagrams of (*A*) nails, (*B*) claws, and (*C*) hoofs *e*, unmodified epidermis; *u*, unguis (outer plate); *s*, subunguis (ventral plate). (From Kingsley, after Boas.)

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 barbs and barbules of the developed feather (Fig. 113). 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 the development of hairs 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.

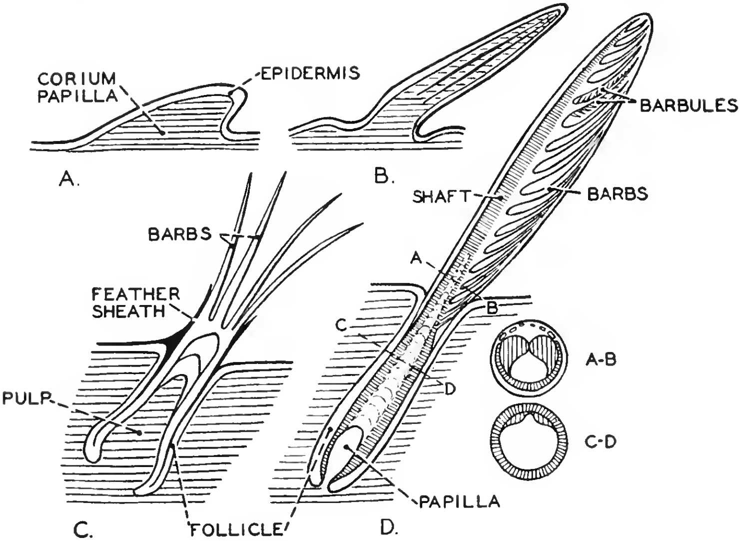


FIG. 113.—Four stages in the development of a feather. *A*, *B*, and *C* represent stages in the development of a down feather. *D* shows a contour feather in the feather-sheath. *A-B* and *C-D* are sections of a young contour feather at the levels indicated in *D*. In contrast with a hair the development of a feather is initiated by a corium papilla. (Redrawn from Ihle, after Butschli.)

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 hairs. It is made up of cuboidal cells usually in a double row.

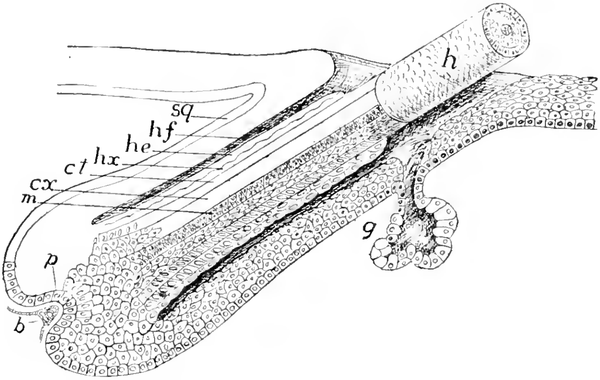


FIG. 114.—Diagram of structure of hair. *b*, blood-vessels; *ct*, cuticle of hair; *cx*, cortex; *g*, gland; *h*, hair; *he*, Henle's layer; *hf*, hair follicle; *hx*, Huxley's layer; *m*, medulla; *p*, papilla; *sg*, stratum germinativum of epidermis. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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.

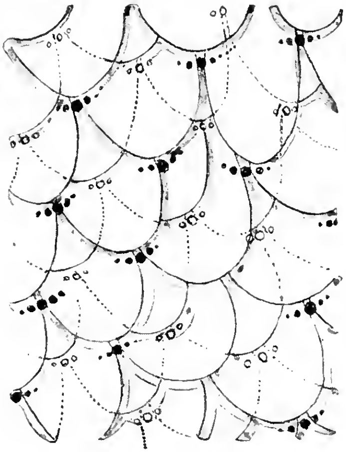


Fig. 115.—Arrangement of the hairs in groups of threes and fives in the human embryo, with the probable ancestral arrangement of the scales. (From Kingsley, after Stöhr.)

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. See Fig. 115.

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.** See Fig. 116. 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 hair-shaft 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 several 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.**

The human foetus before birth has 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.

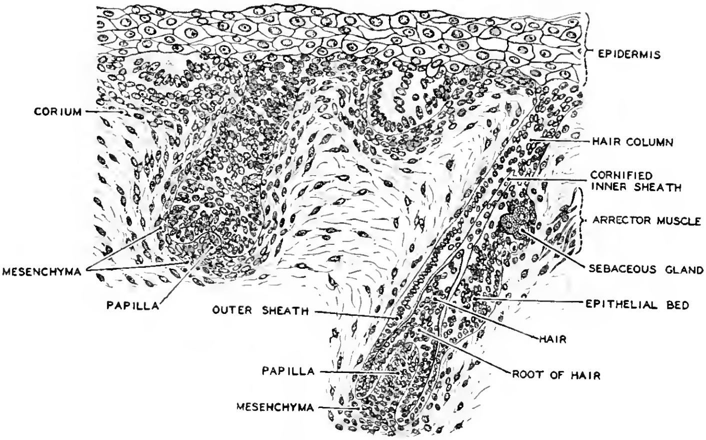


FIG. 116.—A vertical section of skin of a five month human embryo, showing four early stages in the development of a hair. The growth of a hair is initiated by the formation of an epidermal papilla projecting (down) into the underlying corium. (Redrawn from Bremer after Stöhr.)

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 sunlight. 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" (see page 101) 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.

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 unadmired carrot or orange. More brown carries the red over into auburn; still more gives bronze.

Hair that has lost its pigment 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 descendants 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.

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 groups of such epidermal cells 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 differentiates 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, in man, becomes watery under the influence of the nerves. See Fig. 117.

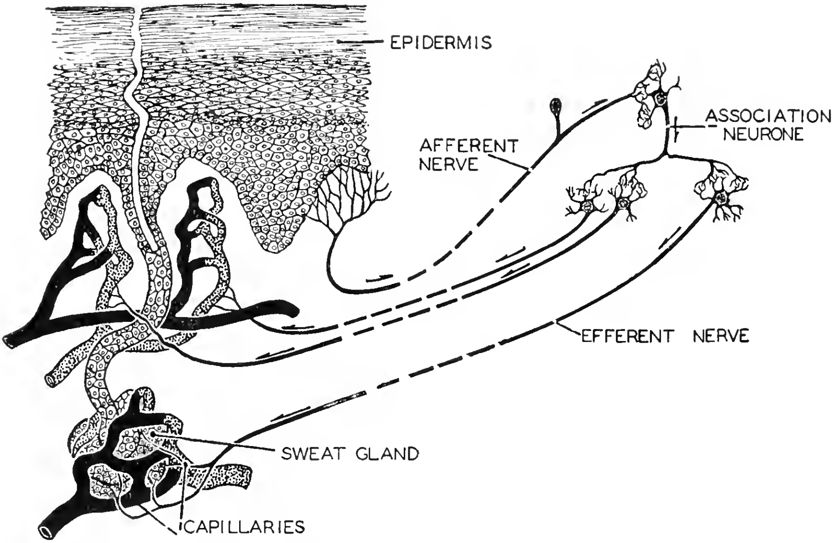


Fig. 117.—A diagram illustrating the nervous mechanism of temperature regulation in man. The quantity of secretion of tubular glands (and consequently the amount of sweat which may evaporate to cool the body) depends upon the quantity of blood in the capillaries associated with the glands and dermal papillae. Through a reflex arc the circulation is regulated by the temperature of the skin. (Redrawn after Hough and Sedgwick.)

Sebaceous Glands. Sebaceous glands in man 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 and anal glands, which occur in most mammals, and mammary glands in all 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.

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

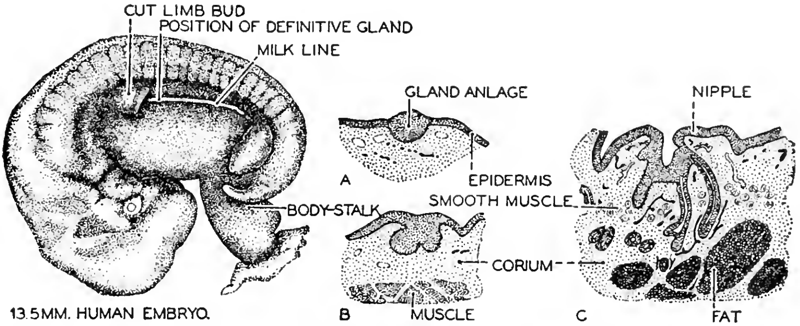


FIG. 118.—A figure illustrating the development of the mammary gland in man. A 13.5 mm. embryo shows the "milk line", a ridge which extends from the axillary region to the groin. The definitive gland develops only from the anterior portion of this line. Taken with the evidence of supernumerary teats 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.)

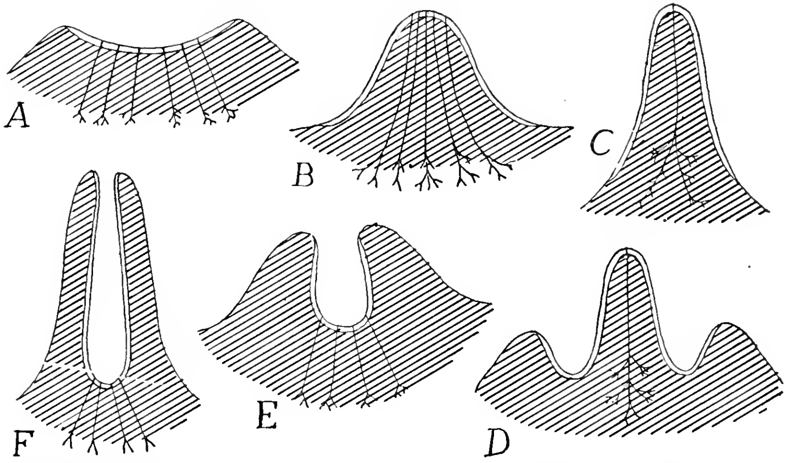


FIG. 119.—Scheme of different kinds of nipples. Single line, ordinary integument; double line, that of primary mammary pocket. *A*, primitive condition, found in Echidna; *B*, human nipple; *D*, Didelphys before lactation; *C*, same at lactation; *E*, embryonic, *F*, adult conditions in cow. *B* and *C* are true nipples, *F*, a pseudo-nipple (teat). (Based on figures by Weber from Kingsley.)

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.

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 mammals. 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. 120.

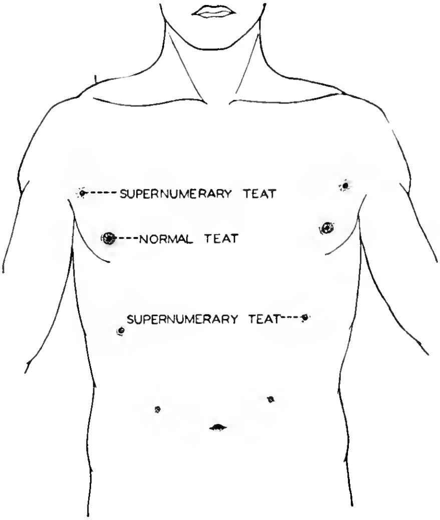


FIG. 120.—The presence of supernumerary teats (polymastism) in man supports the theory of the animal origin of the human body. Their repeated occurrence has received no other rational explanation. They are reversions or atavisms. (Redrawn after Wiedersheim.)

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

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. 122.

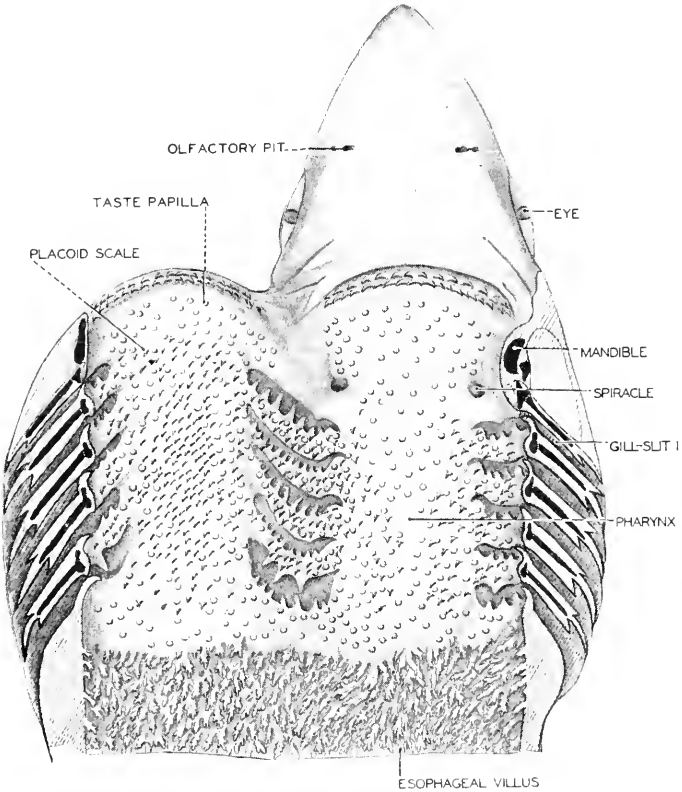


FIG. 121.—The pharynx of an elasmobranch (Squalus) laid open to show the double row of teeth in both upper and lower jaws. Such teeth differ only in size from the placoid scales of the pharynx and skin. Elasmobranch teeth, like scales, are fastened in the skin and are not attached to the jaw cartilages. (After Cook.)

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.

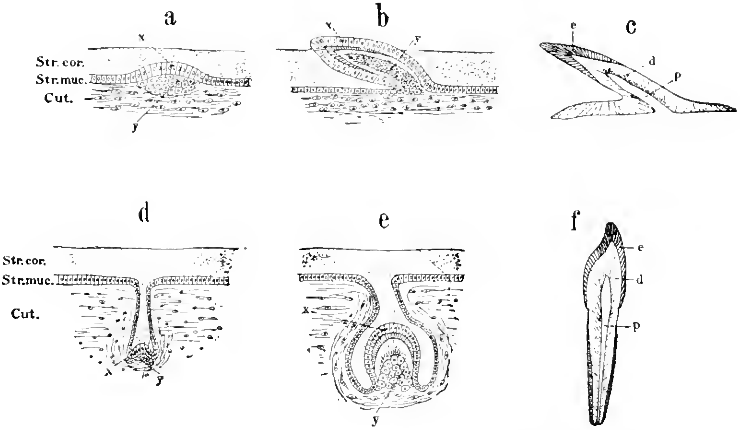


FIG. 122.—Comparison in development and structure between a placoid scale and a tooth. *a*, *b*, and *c* represent the scale; *d*, *e*, and *f* the tooth. In all the figures the epidermis is dotted, but its *stratum germinativum* is represented by a layer of large cells with nuclei; and the cutis is 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.)

Amphibia still farther reduce the number of teeth, but retain them on premaxilla, maxilla, mandible, vomer, and palatine bones, and more rarely on the parasphenoid. 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 amphibians, 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.

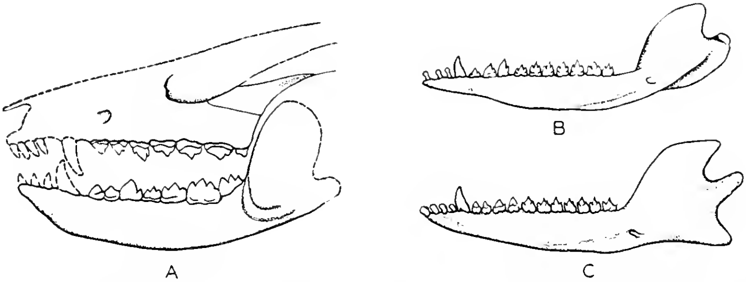


Fig. 123.—Jaws of some primitive Jurassic mammals. The resemblance of these jaws and teeth to those of the theriodont reptiles of the same period suggests a similar genetic origin. (Redrawn from Romer, after Simpson.)

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 pairs 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 acquired also a definite succession of sets of teeth, a set of "milk teeth" developed in early life being later replaced by a "permanent" set.

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 amphibians 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. 124.

The secondary tubercles of such teeth show a tendency to enlarge to the size of the protocone. 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. 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.

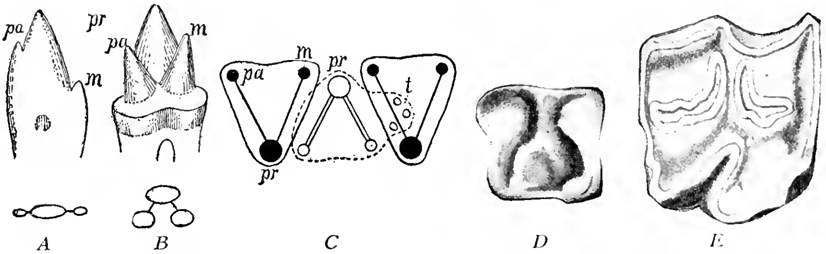


FIG. 124.—*A*, triconodont tooth of Dromatherium; *B*, tritubercular tooth of Spalacotherium; *C*, interlocking of upper (dark) and lower (light) tritubercular molar teeth (after Osborn); *D*, molar of Erinaceus; *E*, of horse (selenodont type); *c*, cingulum; *m*, metacone (metaconid); *pa*, paracone (paraconid); *pr*, protocone (protoconid); *t*, talon. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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 (conceptual), 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_3, c^1_1, p^4_4, m^4_4, the little hyrax or cony, allied to the ungulates, 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 incisor-form teeth from the upper jaw. Their dental formula is, therefore, in brief form: $\frac{0\text{-}0\text{-}3\text{-}3}{3\text{-}1\text{-}3\text{-}3}$.

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. They 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 remaining rudimentary, 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 $\frac{3\text{-}1\text{-}4\text{-}2}{3\text{-}1\text{-}4\text{-}3}$, the cat is reduced to $\frac{3\text{-}1\text{-}3\text{-}1}{3\text{-}1\text{-}2\text{-}1}$. 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 $\frac{3\text{-}1\text{-}2\text{-}1}{3\text{-}1\text{-}2\text{-}1}$. 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 $\frac{1\text{-}0\text{-}0\text{-}2}{1\text{-}0\text{-}0\text{-}2}$. 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.

Proboscidians. 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 a pair of 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.

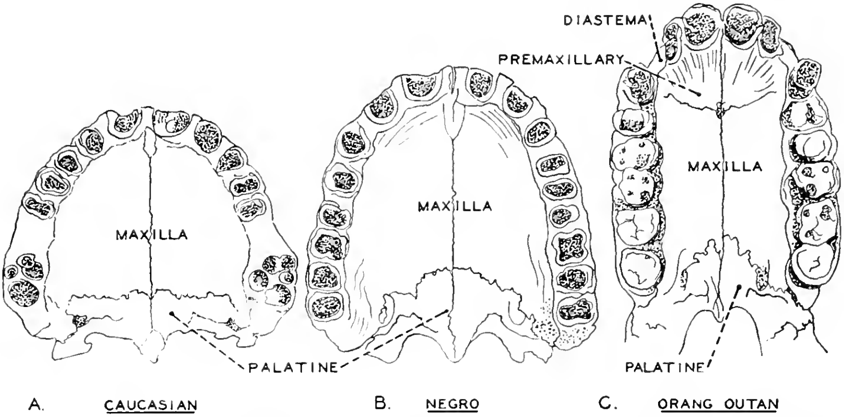


Fig. 125.—Dental arcades of ape, Negro and Caucasian. The form of the Negro arcade is transitional between that of the ape and white man. With the shortening of the human jaw the diastema between incisor and canine teeth seen in the ape jaw is lacking. The refinement of the face is one of the most striking results of primate evolution. (Redrawn after Wiedersheim.)

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. 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 beginning 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. Some fossil human molar teeth, however, are *taurodont*, having a relatively large pulp cavity as in Neanderthal man.

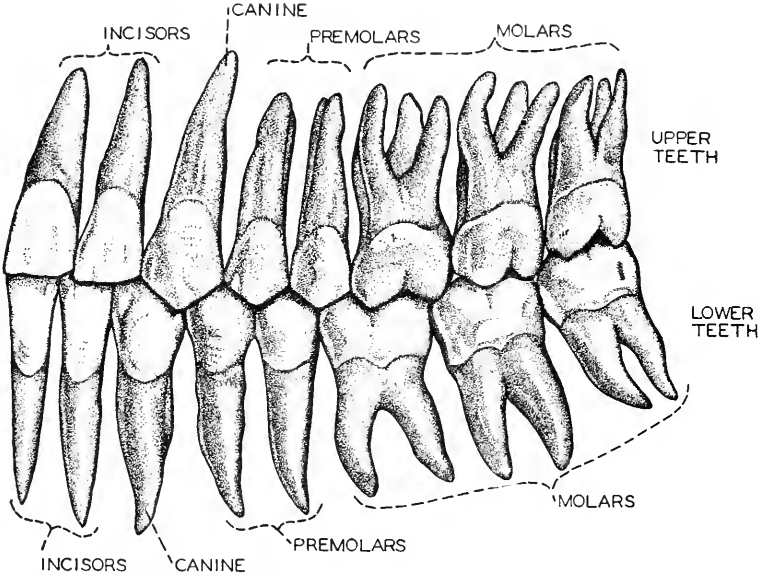


FIG. 126.—Human teeth viewed from the left side. The human dental formula is: i^2_2, c^1_1, pm^2_2, m^3_3. As a result of the shortening of the human jaws the third molars frequently do not erupt. The elongated root of the canine tooth suggests that as in lower primates the ancestors of man may have had fangs. (Redrawn after Braus.)

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 sometimes 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. 127. 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 fibrous 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.

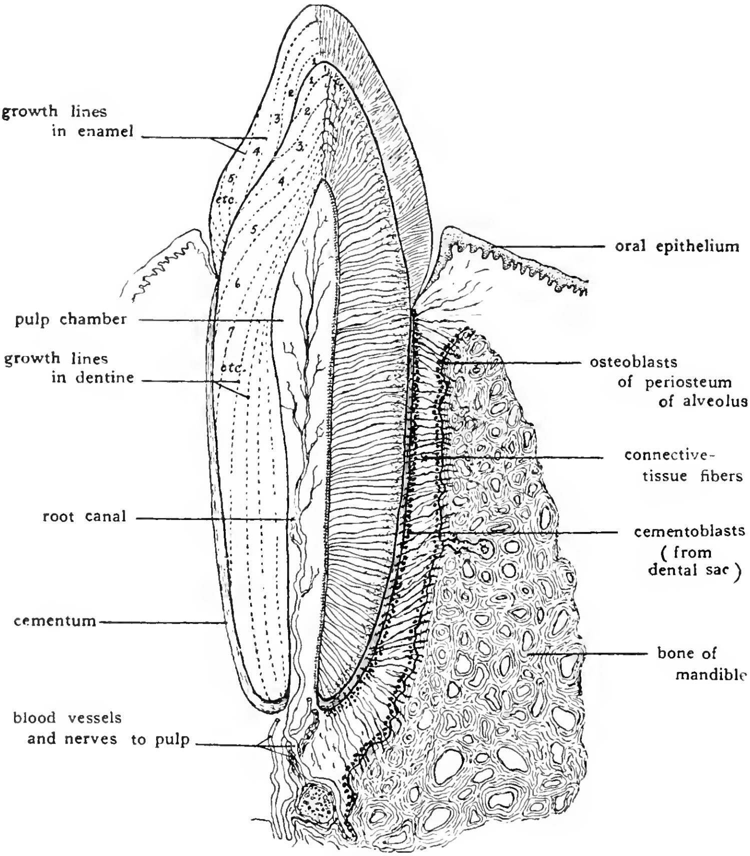


FIG. 127.—Schematic diagram showing the topography of a tooth and its relations to the bone of the jaw. The numbered zones indicate empirically the sequence of deposition of the dentine and enamel. The so-called growth lines in the dentine and enamel follow the general contours indicated by the dotted lines in the figure but are much more numerous. (From Patten's "Embryology of the Pig.")

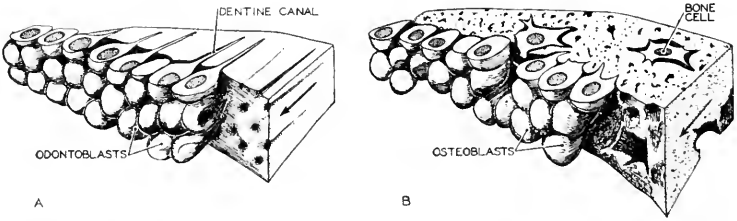


FIG. 128.—Diagrams illustrating the difference in the secretion of dentine, *A*; and of bone, *B*. The functional polarization of the odontoblasts and osteoblasts is, however, similar. (Redrawn after Braus.)

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.

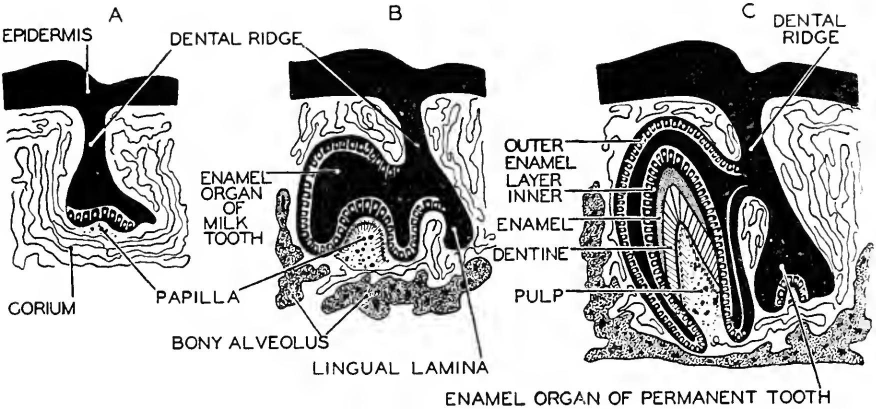


Fig. 129.—Diagrams of three stages in the development of a mammalian tooth as seen in sections of the jaw. The anlage of the permanent tooth lies on the lingual side of that of the milk-tooth. (Redrawn after O. Hertwig and Arey.)

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. 129). 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 $2\frac{1}{2}$ 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.

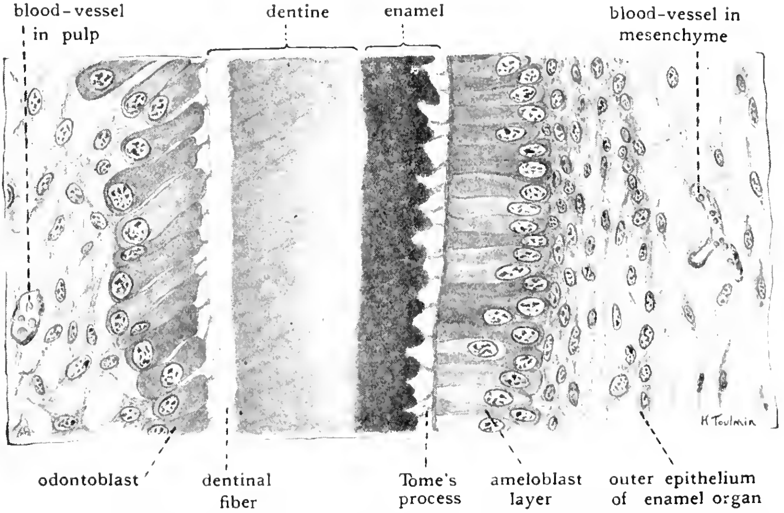


FIG. 130.—Projection drawing of small segment of developing incisor from 130 mm. pig embryo to show formation of enamel and dentine. ×350. (From Patten's "Embryology of the Pig.")

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 mesenchyme-like enamel pulp, and a layer of outer enamel cells. The ameloblast cells which line the enamel organs 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 are 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 thus forming 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, the dentine to the underlying 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.

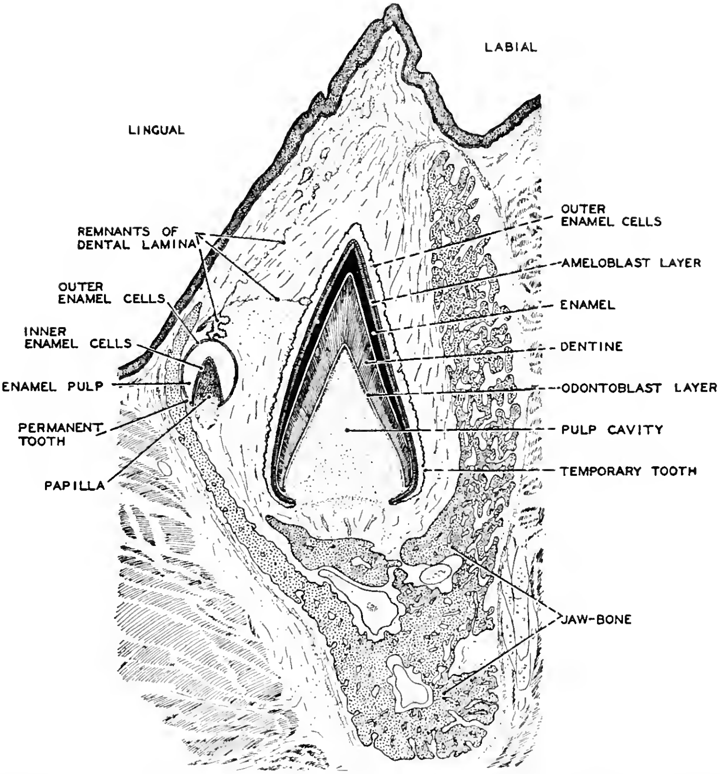


FIG. 131.—A section of the jaw of a nine-months human embryo, showing the anlage of a canine tooth. The enamel organ of the permanent incisor is seen on the lingual side of the milk-tooth. (Redrawn after Corning.)

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.

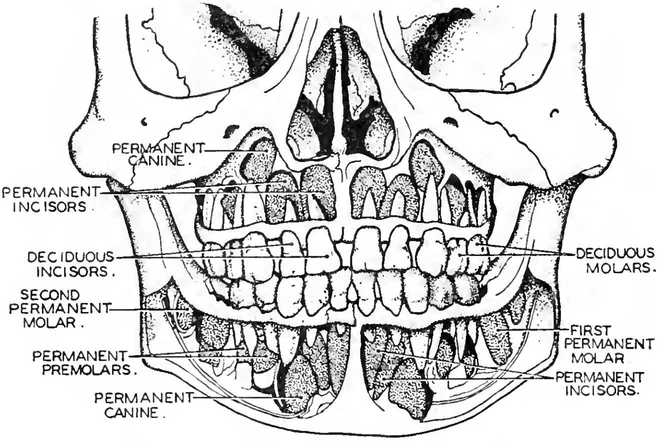


FIG. 132.—The teeth of a five-year-old child. Portions of the jaws have been removed so as to expose the roots of the milk teeth and the anlagen of the permanent teeth. The latter are stippled in the figure. (Redrawn after Sobotta.)

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 protozoans 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 attachment 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 euripterids 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 in the long bones.

The Two Parts of the Skeleton. Historically, the vertebrate skeleton consists of two parts, which began 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 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.

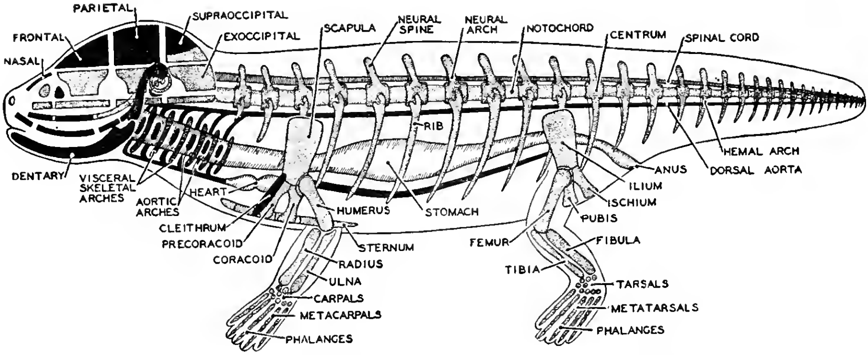


FIG. 133.—A diagram of the vertebrate skeleton, showing the division of the skeleton into axial, visceral, and appendicular. Membrane bones are shown in black, cartilage bones stippled.

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 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 (diplospondyly) 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

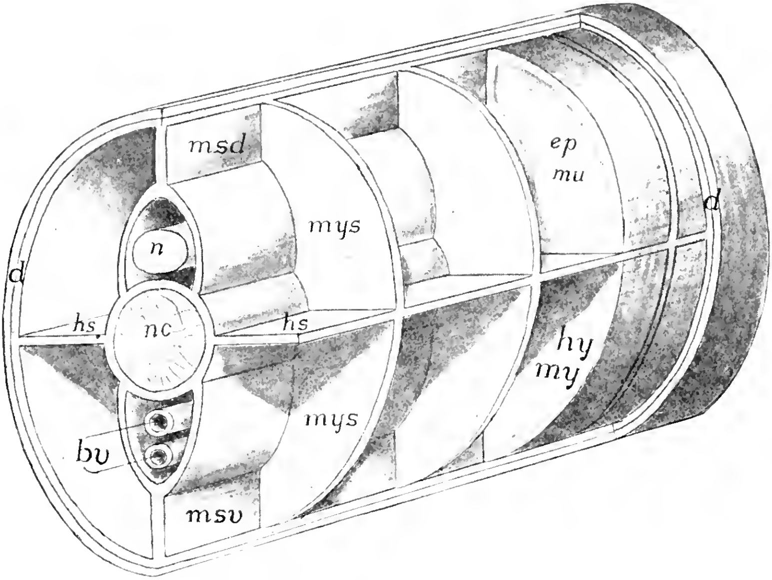


FIG. 134.—Diagram of the skeletogenous tissue in the caudal region of a vertebrate. *bv*, blood-vessels; *d*, corium; *epmu*, epaxial muscles; *hs*, horizontal septum; *hymy*, hypaxial muscles; *msd*, *msv*, dorsal and ventral median septa; *mys*, myosepta; *n*, spinal cord; *nc*, notochord. (From Kingsley's "Comparative Anatomy of Vertebrates.")

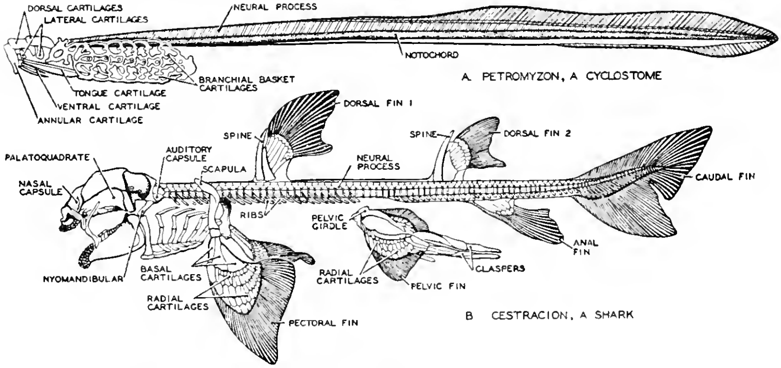


FIG. 135.—*A*, The skeleton of a cyclostome, Petromyzon; *B*, The skeleton of an elasmobranch, Cestracion. Elasmobranchs were the first animals to invent paired appendages and the skeletal elements to support them. Marked differences in the axial and branchial skeletons of cyclostomes and elasmobranchs also appear. (Redrawn after Dean.)

skeleton is still cartilaginous, but the cartilage is often hardened with lime.

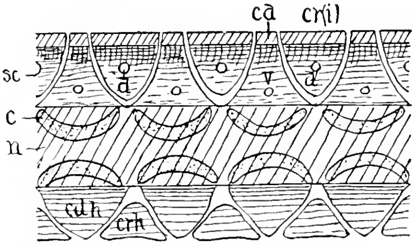


FIG. 136.—Sagittal section of Sqaulas vertebrae, cut surfaces obliquely lined. *c*, calcifications of centra; *cd*, caudineurals; *cdh*, caudihemals; *cr(i)*, cranineurals (intercalaria); *d*, exits of dorsal nerve roots; *crh*, cranihemals; *n*, notochord; *v*, exits of ventral nerve roots. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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 amphibians, 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.

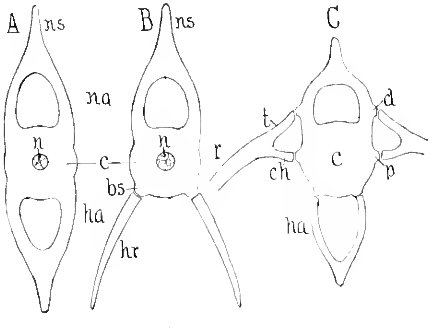


FIG. 137.

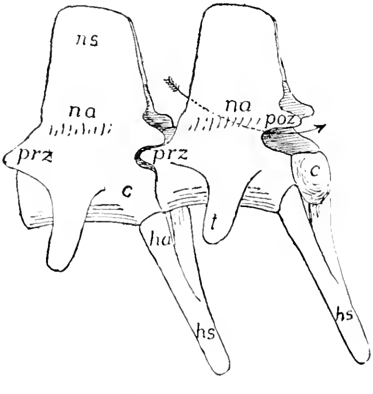


FIG. 138.

FIG. 137.—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. 138.—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.")

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—a diplospondylous 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 has two lesser curvatures, cervical and sacral, in the region of the neck and sacrum respectively.

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.

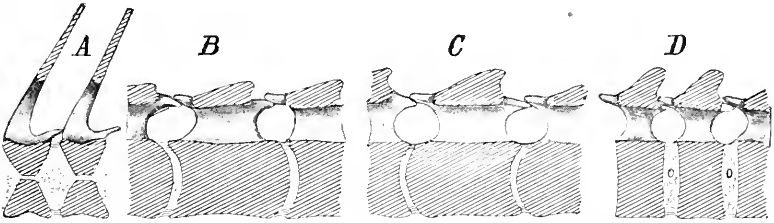


FIG. 139.—Diagrammatic sagittal sections of (*A*) amphicoelous; (*B*) procoelous; (*C*) opisthocoelous; and (*D*) amphiplatyan vertebrae. The head is supposed to be at the left. Cut surfaces obliquely lined. (After Kingsley modified.)

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.

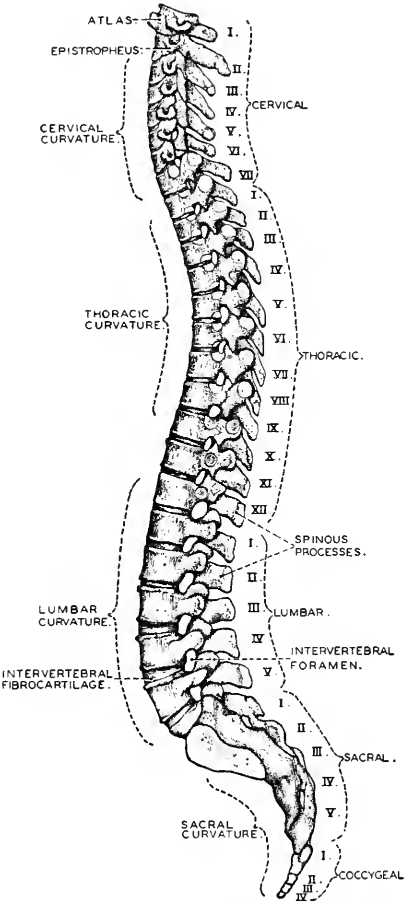


Fig. 140.—The human vertebral column viewed from the left side. (Redrawn after Sobotta.)

The Kinds of Vertebrae. 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 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.

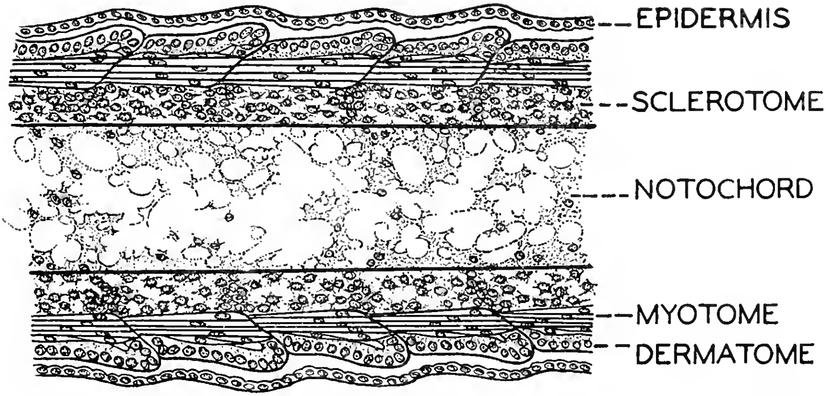


FIG. 141.—A horizontal section of an elasmobranch embryo, showing the differentiation of the mesoderm (epimere) into sclerotome, myotome and dermatome. The sclerotome surrounding the notochord gives rise to the centrum of the vertebra.

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.

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 **tuberculum,** 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.

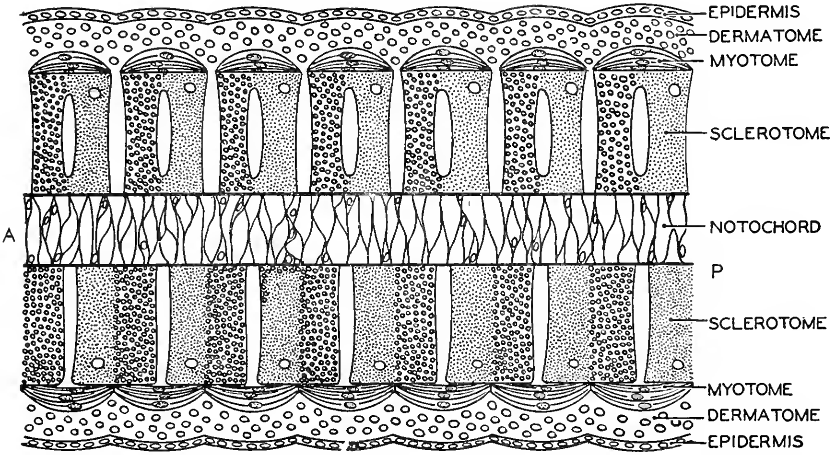


FIG. 142.—A diagram showing the relations of myotome and sclerotome as seen in a horizontal section of a vertebrate embryo. The upper half of the figure shows the relations in an earlier stage of development, while the lower half represents a later stage. The posterior half of each sclerotome unites 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.

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. Epiphyses at the capitulum and tuberculum make possible the elongation of thoracic ribs. The ventral extremities of the ribs do not ossify but remain throughout life as the **costal cartilages.**

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. 143.

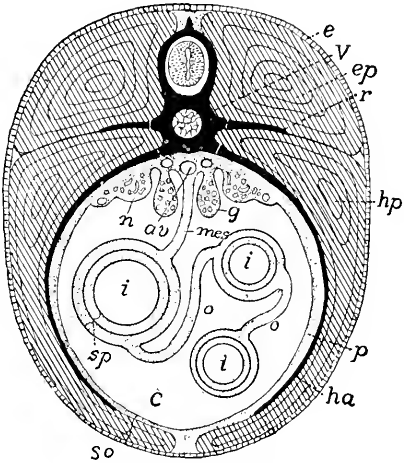


Fig. 143.—Diagrammatic section of a vertebrate to show the relation of ribs to the muscles of the body wall. *av*, aorta; *c*, coelom; *e*, ectoderm; *ep*, epaxial muscles; *g*, gonads; *ha*, hemal rib; *hp*, hypaxial muscles; *i*, intestine; *mes*, mesentery; *n*, nephridium; *o*, omentum; *r*, true rib; *p*, somatopleure; *sp*, splanchnopleure; *v*, vertebra. (From Kingsley's "Comparative Anatomy of Vertebrates.")

The 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

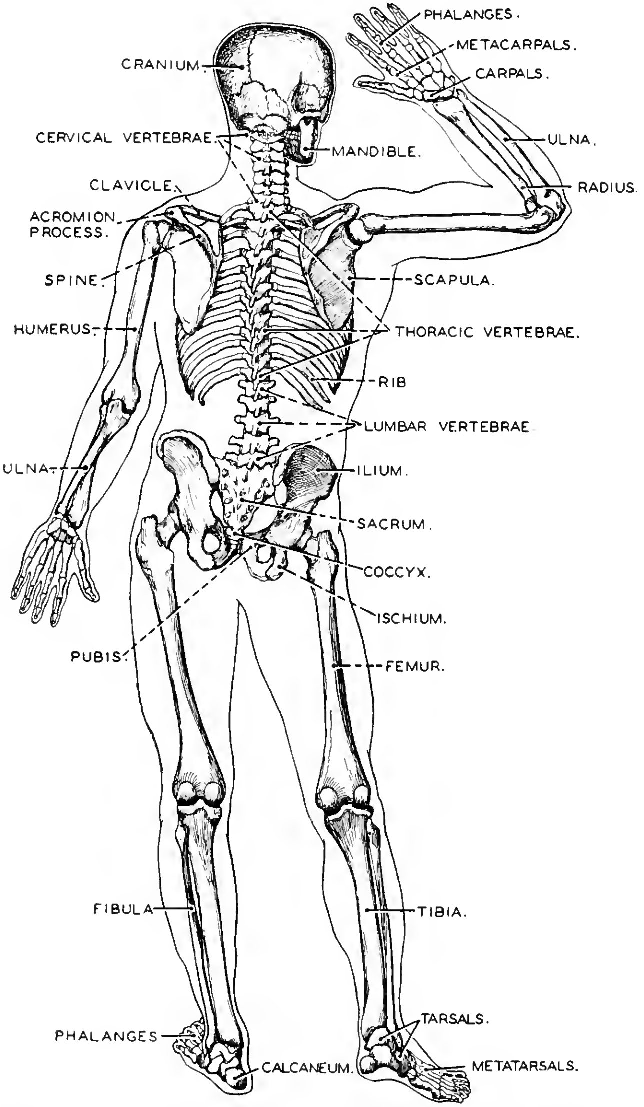


FIG. 144.—Human skeleton viewed from behind. (Reproduced in modified form from "The Human Body" by Dr. Logan Clendening, (Copyright 1927, 1930 by Alfred A. Knopf, Inc.) by permission of and special arrangement with Alfred A. Knopf, Inc., authorized publishers.)

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

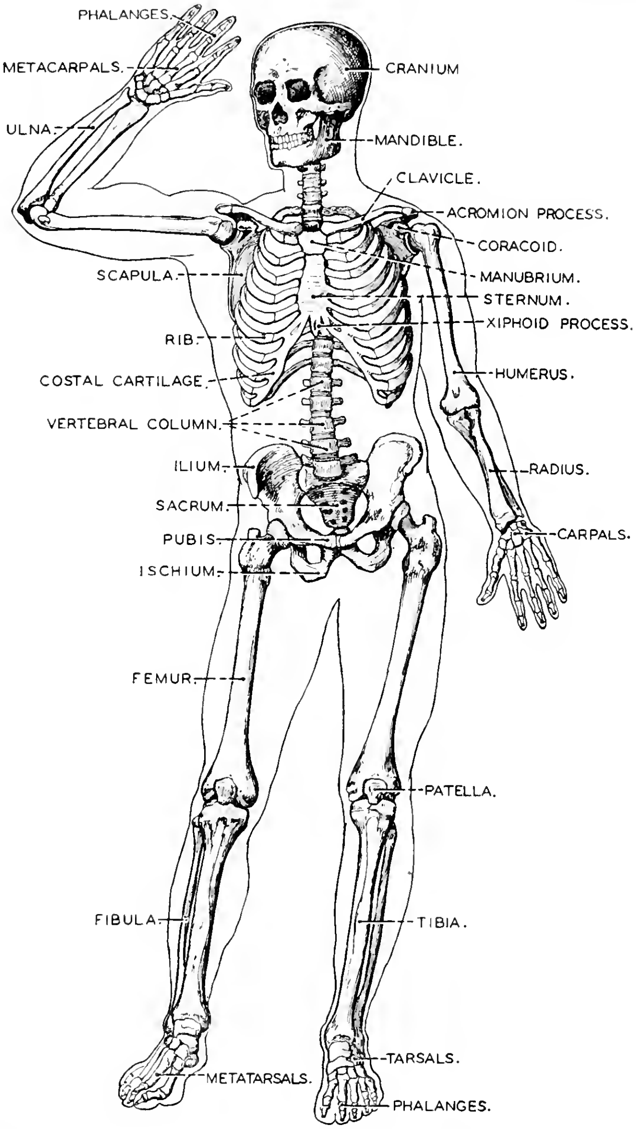


Fig. 145.—Human skeleton viewed from in front. (Reproduced in modified form from "The Human Body" by Dr. Logan Clendening, (Copyright 1927, 1930 by Alfred A. Knopf, Inc.) by permission of and special arrangement with Alfred A. Knopf, Inc., authorized publishers.)

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 metamerism 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, make it difficult to accept this hypothesis. See Fig. 147.

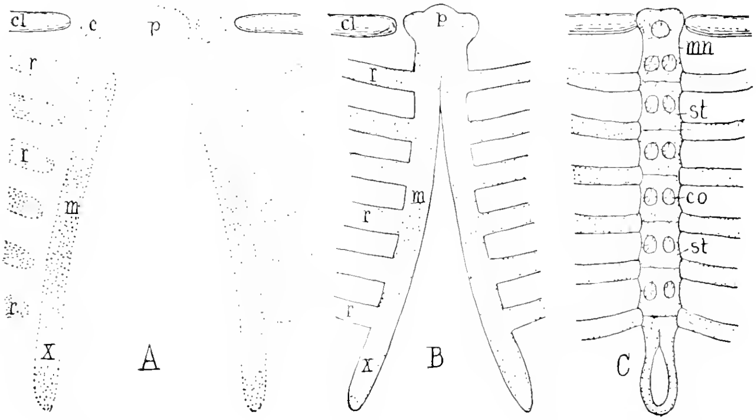


FIG. 146.—Scheme of development of mammalian sternum. *A*, early stage; *B*, cartilage, the halves uniting; *c*, coracoid(?) procartilage; *cl*, clavicle; *co*, centers of ossification; *m*, mesosternal parts; *mn*, manubrium; *p*, presternum; *st*, sternebrae; *x*, xiphisternum. (From Kingsley's "Comparative Anatomy of Vertebrates.")

A second and 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 amphibians in which the ribs were so extensive. The hypothesis that the sternum is a rib-sternum has at least so 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.

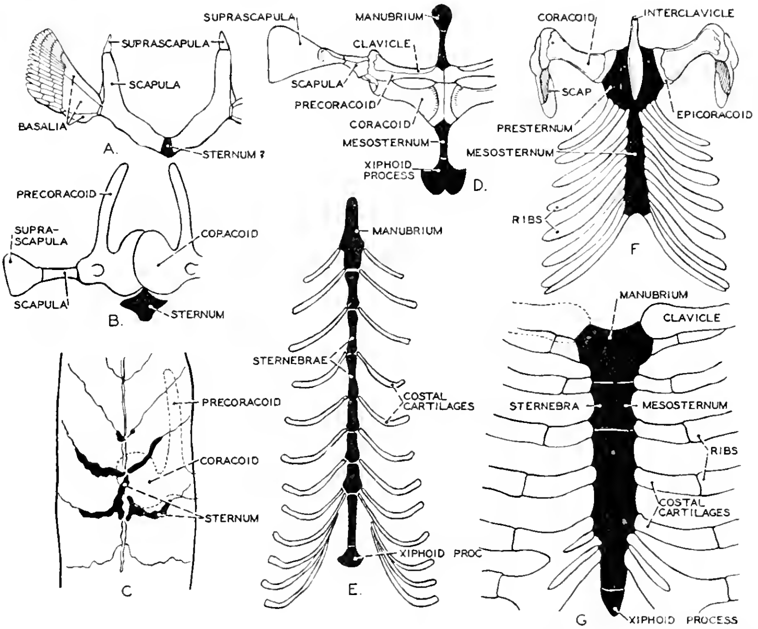
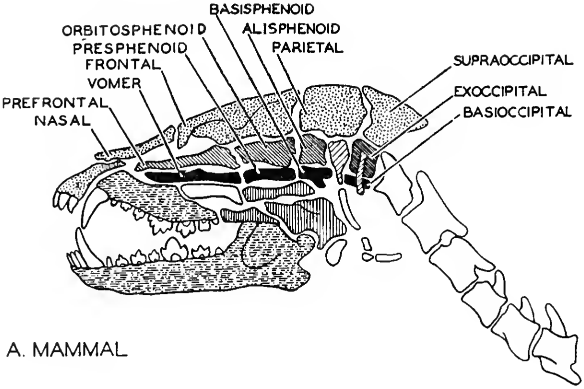


FIG. 147.—Types of vertebrate sterna. *A*, Squalus; *B*, Salamandra; *C*, Necturus; *D*, Rana; *E*, Felis; *F*, Crocodilus; *G*, Homo. The sternum is shown in black. While there is no doubt of the homology of the various amniote sterna, their homology with those of anamnia is in dispute.

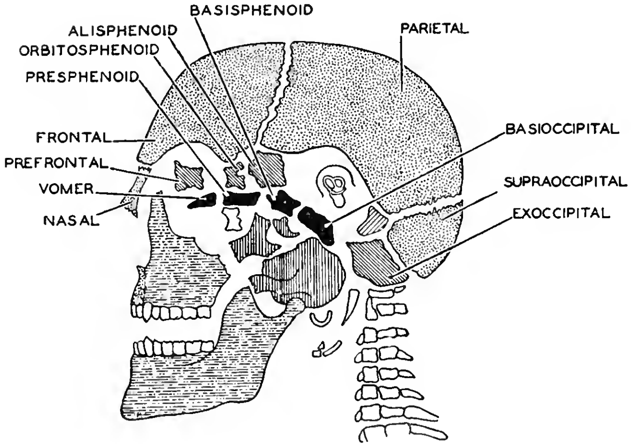
In the reptiles the sternum is converted into a metameric structure composed of a series of sternebrae and connected with the ribs as in mammals.

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.



A. MAMMAL



B. MAN

FIG. 148.—Owen's figures illustrating the Goethe-Oken vertebral theory of the skull. Owen believed that he could find in the mammalian skull four enlarged vertebrae, the components of which he identified with the elements of a trunk vertebra. Not knowing the embryology of the skull, he did not realize that vertebrae lack the membranous bones which are so conspicuous in the skull. (Redrawn from Wilder.)

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. See Fig. 148. 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.

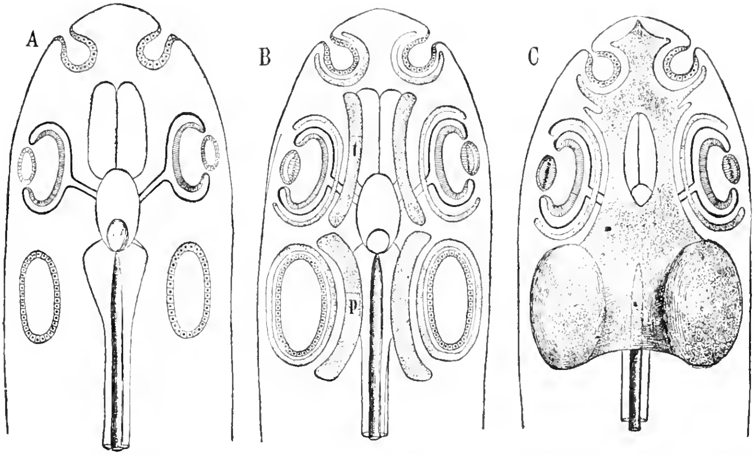


FIG. 149.—Diagrams showing the development of the primordial skull. Since this organ develops primarily beneath the brain as a support the figures represent the ventral aspect. (*A*) Early stage, before the appearance of cartilage. The notochord is seen lying along the nerve cord as far forward as the 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 notochord forms in chordates the primary skeleton of the head as well as of the trunk. Evidence from comparative anatomy and embryology 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. 149)

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.

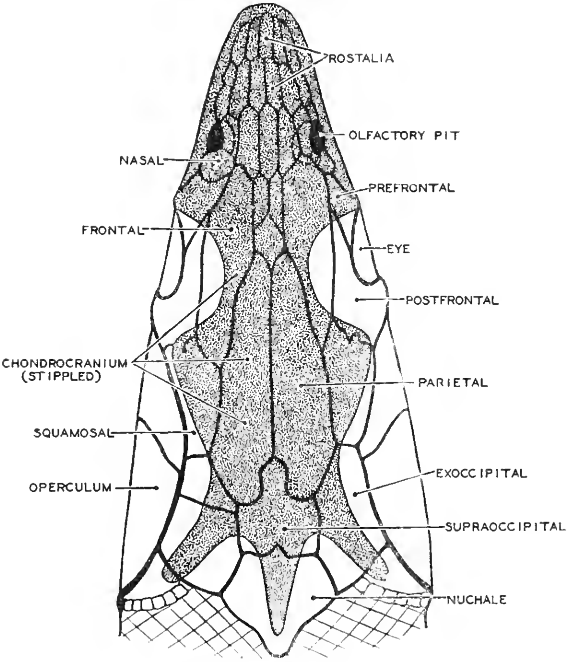


Fig. 150.—The head of a sturgeon, viewed from above as a translucent object. Membrane bones (scutes) are outlined and the inner cartilaginous cranium stippled. By means of comparative anatomy it is possible to identify certain scutes as homologues of bones in the mammalian skull. (Redrawn after Gegenbaur.)

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. See Fig. 150. The cartilaginous brain case within these dermal plates differs in no essentials

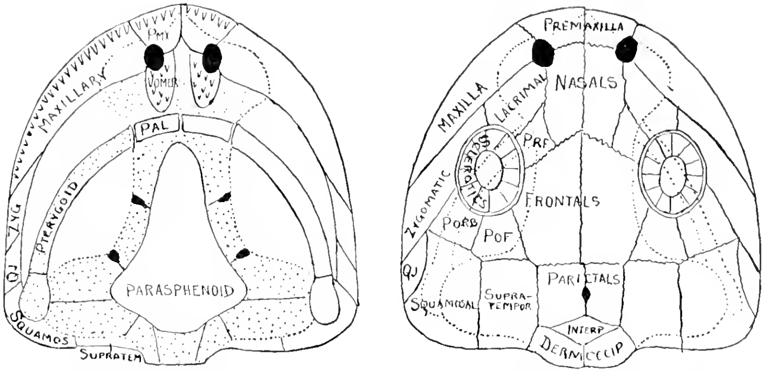


FIG. 151.—Membrane bones of typical tetrapod; chondrocranium in dotted outline. *interp*, interparietal; *pmx*, premaxilla; *pof*, postfrontal; *porb*, postorbital; *prf*, prefrontal; *qj*, quadratojugal, *zyg*, zygomatic. (From Kingsley's "Comparative Anatomy of Vertebrates.")

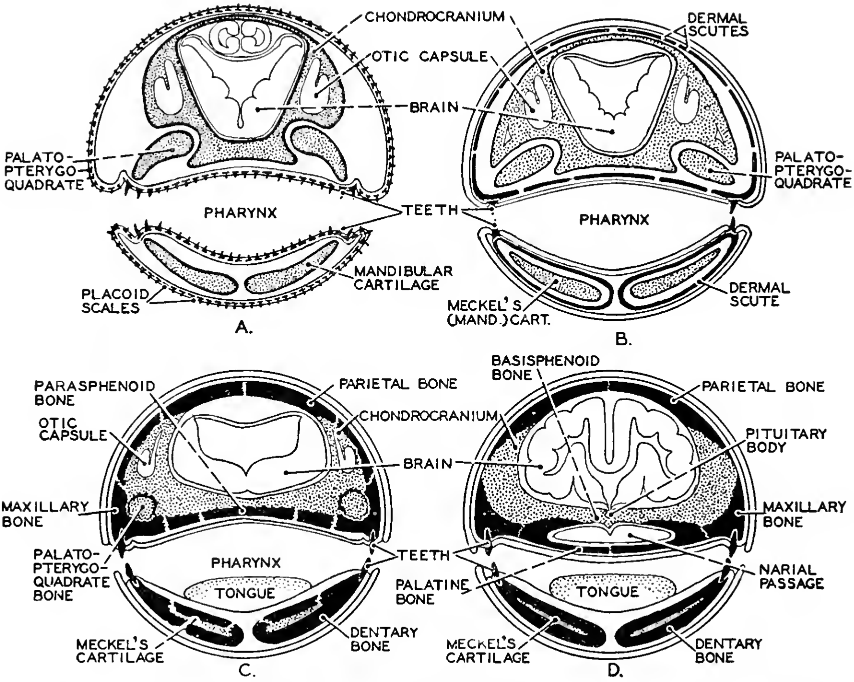


FIG. 152.—The diagrams *A*–*D* illustrate the growth and enlargement of the membrane bones of the skull and their encroachment upon the chondrocranium. Cartilage and pro-cartilage bones are stippled, membrane bones black. Membrane bone is represented in the basal plates of the placoid scales of elasmobranchs (*A*). In the ganoid (*B*) the scales have fused and enlarged to form bony scutes, 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.

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.

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.

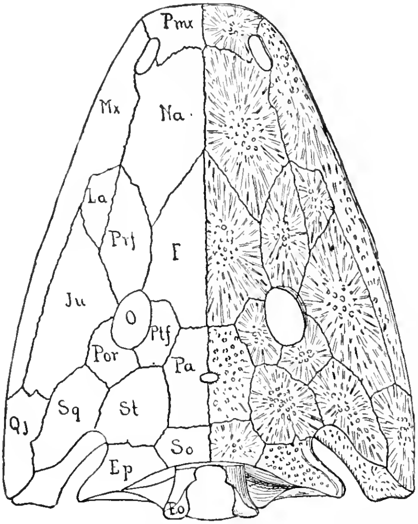


FIG. 153.—Skull of a stegocephalan (Capitosaurus). *eo*, exoccipital; *ep*, tabulare; *f*, frontal; *ju*, zygomatic (jugal); *la*, lacrimal; *mx*, maxilla; *na*, nasal; *o*, orbit; *pa*, parietal; *pmx*, premaxilla; *por*, postorbital; *prf*, prefrontal; *ptf*, postfrontal; *qj*, quadratojugal; *so*, dermoccipital; *sq*, squamosal; *st*, supratemporal. (From Kingsley's "Comparative Anatomy of Vertebrates," after Zittel.)

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 amphibians 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 DeVries 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.

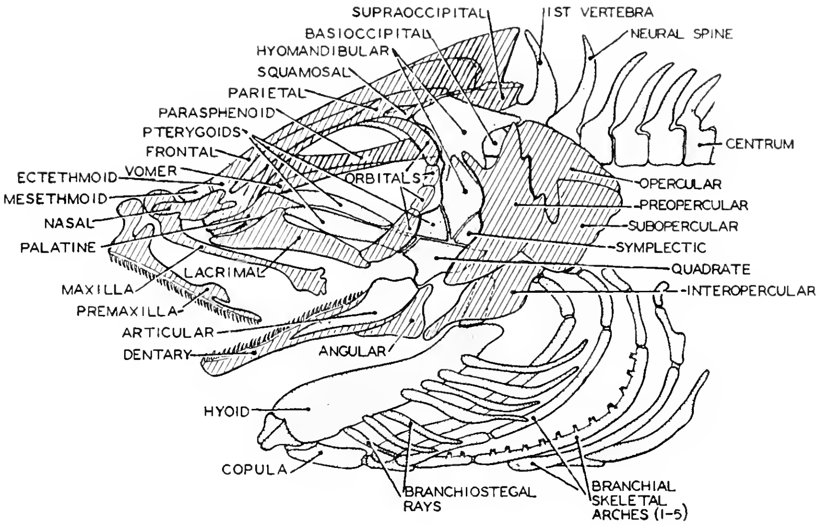


FIG. 154.—Skull of hake in left lateral aspect. Membrane bones are cross-hatched, pro-cartilage bones stippled. Compared with the skull of ganoids, that of teleosts shows an increasing dominance of membrane bones over those preformed in cartilage.

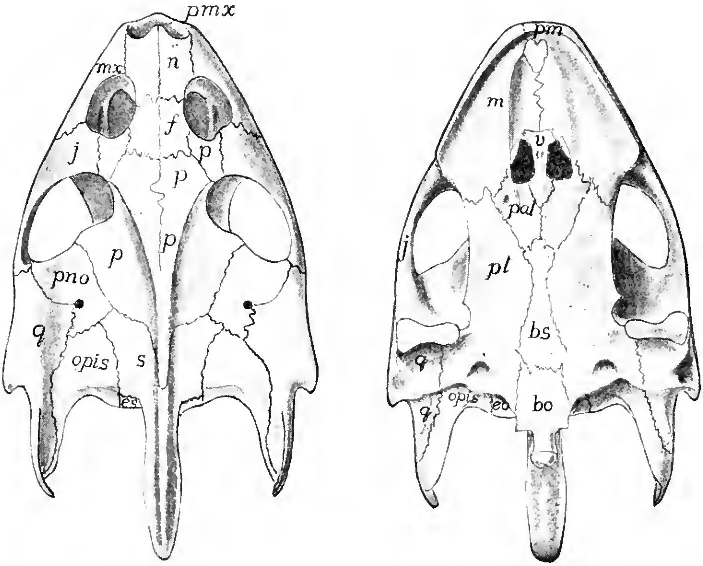


FIG. 155.—Dorsal and ventral views of the skull of turtle, Trionyx. Compared with the skull of the bony fish, that of reptiles shows increased compactness and integration of elements. *bo*, basioccipital; *bs*, basisphenoid; *eo*, *es*, exoccipital; *f*, frontal; *j*, zygomatic (jugal); *m*, *mx*, maxilla; *n*, prefrontal; *opis*, opisthotic; *p*, (behind orbit) postfrontal, (others) parietal; *pal*, palatine; *pmx*, premaxilla; *pno*, proötic; *pt*, pterygoid; *q*, quadrate; *s*, supraoccipital; *v*, vomer. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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 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 amphibians, 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.

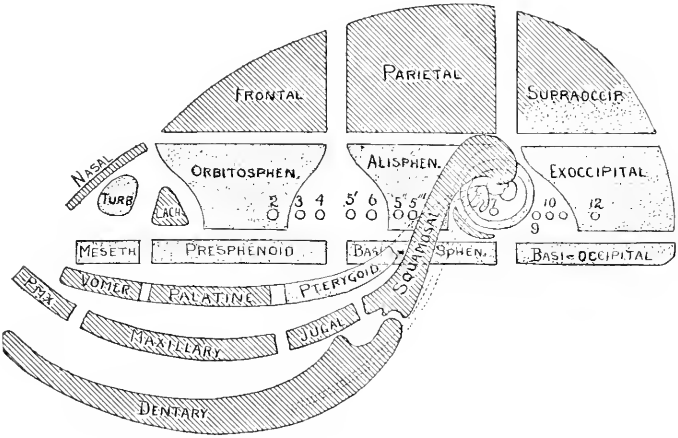


FIG. 156—Diagram of the bones of the mammalian skull. Cartilage bones dotted, membrane bones lined. With slight changes the skull of mammals may be derived directly from that of reptiles (Fig. 155). 2–12, nerve exits. (Altered from Flower, from Kingsley's "Comparative Anatomy of Vertebrates.")

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. 152.

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 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. 158.

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.

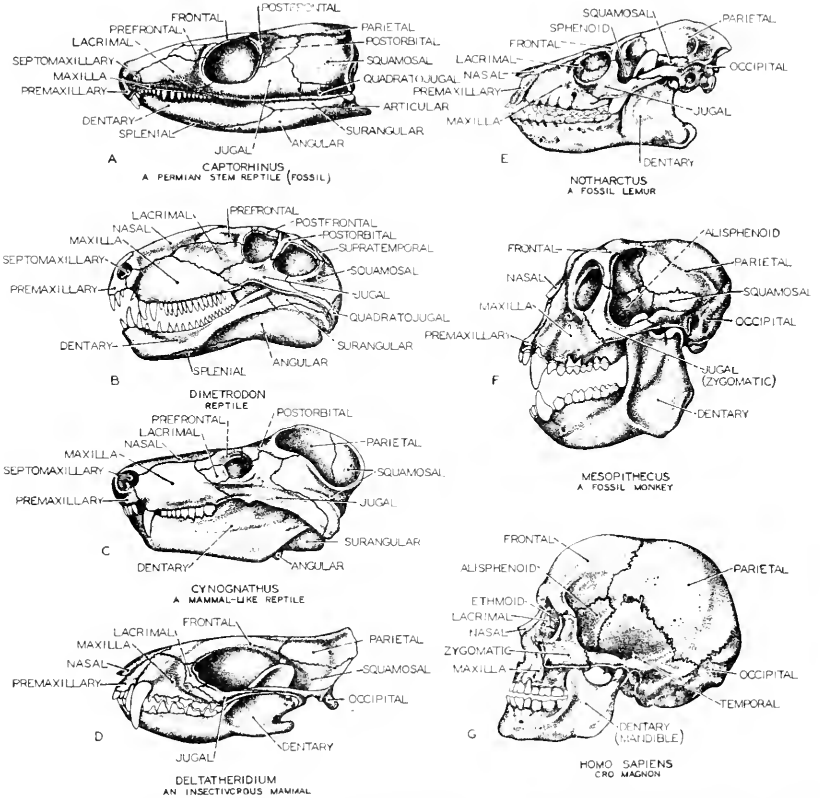


FIG. 157.—A series of fossil skulls (*A–G*) which are believed to represent fairly well the phylogenetic changes of the human skull. (Redrawn after Romer's "Man and the Vertebrates," University of Chicago Press.)

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

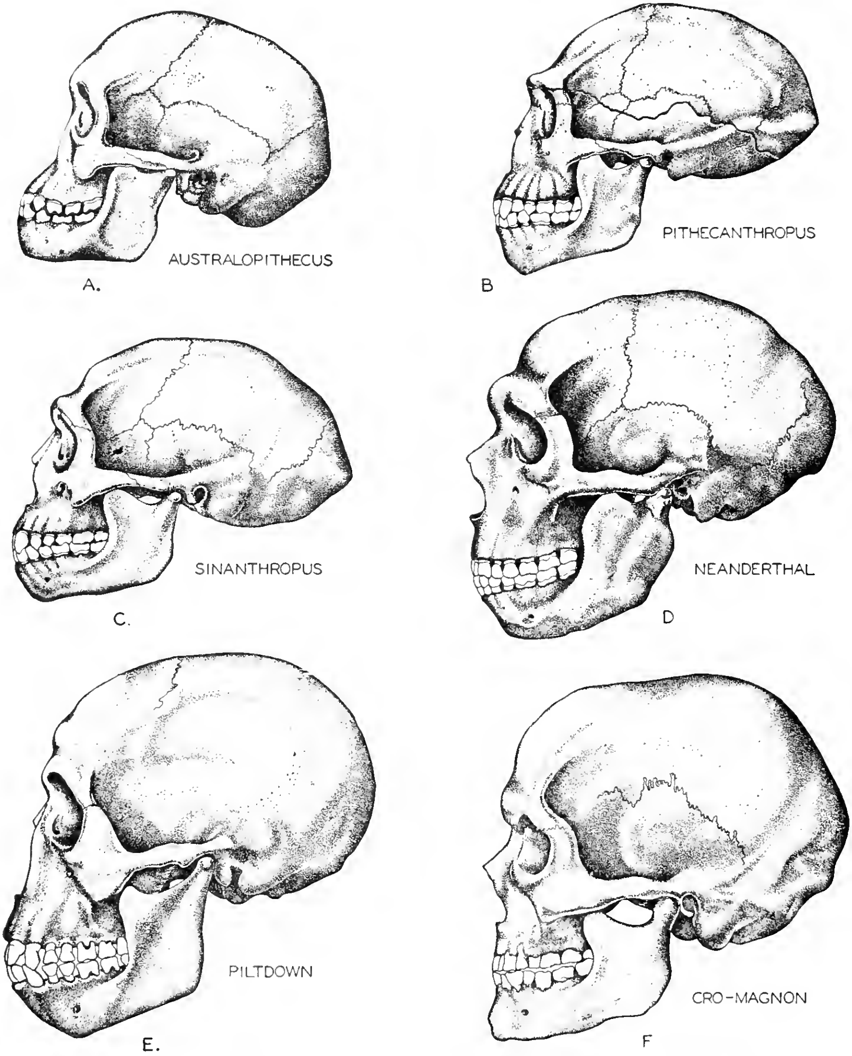


Fig. 158.—Skulls of fossil men restored, left lateral aspect. Australopithecus, however, as its name implies, is an ape rather than a man. Opinions differ as to whether Pithecanthropus is man or ape. Sinanthropus is indisputably human. While none of these fossil types is believed to be in the direct 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.)

CHIEF BONES OF SKULL OF RECENT VERTEBRATES

The cross (×) indicates that the bone is present in the group named at top of column. But it may not be present in every animal of that group.				FISH	AMPHIBIAN	REPTILE	BIRD	MAMMAL	MAN
CRANIAL BONES	OCCIPITAL ARCH		**Basioccipital** m, v	×	?	×	Later, extensive fusion obliterates sutures, so that, in adult, boundaries of bones cannot be recognized.	×	Fused to form single OCCIPITAL BONE
			Exoccipital l	×	×	×		×	
			Supraoccipital* m, d	×	?	×		×	
	PARIETAL ARCH		**Basisphenoid** m, v	×		×		×	Constituents of complex SPHENOID BONE
			Alisphenoid l	×				×‡	
			Parietal l	×	×	×		×	×
	FRONTAL ARCH		**Presphenoid** m, v			×		×	Constituents of complex SPHENOID BONE
			Orbitosphenoid l	×	×	×		×	
			Frontal l	×	×	×		×	×
	REGION of EAR		**Proötic**	×	×	×		Petrosal	Fused to form TEMPORAL BONE
			Opisthotic	×	×	×			
			Epiotic	×	×	×			
			Squamosal	×	×	×		×	
	REGION of ORBIT		*Postfrontal*	×	×	×			
			Postorbital	×		×			
			Supraorbital	×		×			
			Suborbital†	×					
			Prefrontal	×	×	×			
			Lacrimal	×	×	×		×	×
	NASAL REGION		**Ethmoid**† m and l	×	×	×		×	×
			Nasal	×	×	×		×	×
	ROOF of MOUTH		*Parasphenoid* m	×	×	×			
			Vomer	×	×	×		×‡	×
					Pterygoid, palatine, maxillary extend into roof of mouth				
VISCERAL SKELETAL ARCHES	MANDIBULAR ARCH	Upper Jaw	**Quadrate**	×	×	×	Nearly all bones of the reptilian skull occur in the young bird.	**Incus**	INCUS
			Pterygoid*†	×	×	×		×	Pterygoid processes on sphenoid
			Palatine	×	×	×		×	×
			Quadrato-jugal		×	×			
			Jugal	?		×		*Malar*	MALAR
			Maxillary	×	×	×		×	Fused to form MAXILLA
			Premaxillary	×	×	×		×	
		Lower Jaw	**Articular**	×	×	×		**Malleus**	MALLEUS
			Dentary	×	×	×		×	×
			Splenial	×	×	×		?	Adult lower jaw is a single dermal bone, the—MANDIBLE
			Coronoid	×	×	×		?	
			Supra-angular	×		×			
			Angular	×	×	×		*Tympanic*	Tympanic fused with temporal
	HYOID ARCH	Dorsal	**Hyomandibular**	×	**Columella**			**Stapes**	STAPES
			Symplectic	×	Columella and stapes ossify in dorsal part of embryonic hyoid arch.				Intermediate part of hyoid arch becomes STYLOID PROCESS of temporal bone, and STYLO-HYOID LIGAMENT
			Interhyal	×					
			Epihyal	×					
		Ventral	**Ceratohyal**	×	A variable number of ventral hyoid elements				
			Hypohyal	×					
			Basihyal m, v	×					HYOID BONE m, v.
	BRANCHIAL ARCHES		Maximum number in adult	7	4	2	1	1	1
					Additional and more posterior arches are represented in cartilages of larynx and perhaps of trachea.				
OPERCULUM OF FISHES			*Operculum*	×	Probably not represented in vertebrates above fishes				
			Preoperculum	×					
			Interoperculum	×					
			Suboperculum	×					

Cartilage bones are in **bold-face** type; *dermal bones* in *italics*.

d, dorsal; v, ventral; l, bones which are lateral and paired; m, a median bone. All bones not otherwise designated are lateral and paired.

* Cartilage bone more or less augmented by addition of dermal bone.

† A name which (with appropriate prefixes) applies to two or more bones which are closely related in origin and position: e.g., mesethmoid, ectethmoid; entopterygoid, metapterygoid, etc.

‡ Homology of alisphenoid and vomer of mammals with alisphenoid and vomer, respectively, of lower vertebrates is questionable.

(Modified from Rand, Comparative Anatomy of Vertebrates, Harvard University Press, 1929.)

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. See Fig. 158.

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 lie 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.

The Human Skull. The human skull consists of twenty bones of which eight form the cranium or brain-case and the remaining twelve make the facial skeleton. The eight bones of the cranium are the frontal, occipital, ethmoid, sphenoid and the paired parietals and temporals. The facial skeleton includes the mandible and vomer, and the paired maxillaries, zygomatics (malars), nasals, lacrimals, and palatines. Since the turbinal bones of the nose are extensions of the ethmoid they are not counted as separate bones. A comparison of the mammal skull with that of man reveals that the bones are homologous.

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, supports for the gills, and 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. 149.

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.

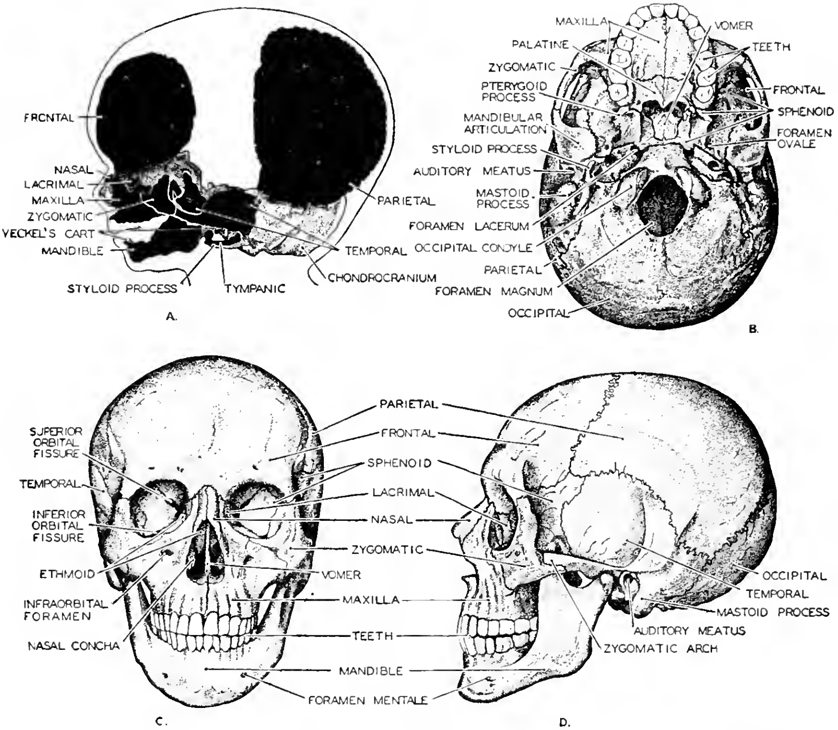


FIG. 159.—The human skull, embryonic (*A*) and adult (*B–D*). In the fetal skull (14 weeks) membrane bones are black, and the cartilage cranium (chondrocranium) stippled. Figure *B* shows the adult skull in basal aspect, figure *C* in frontal aspect, and figure *D* in left lateral aspect, approximately one quarter natural size. (Redrawn after Sobotta.)

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 ethmoid 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.

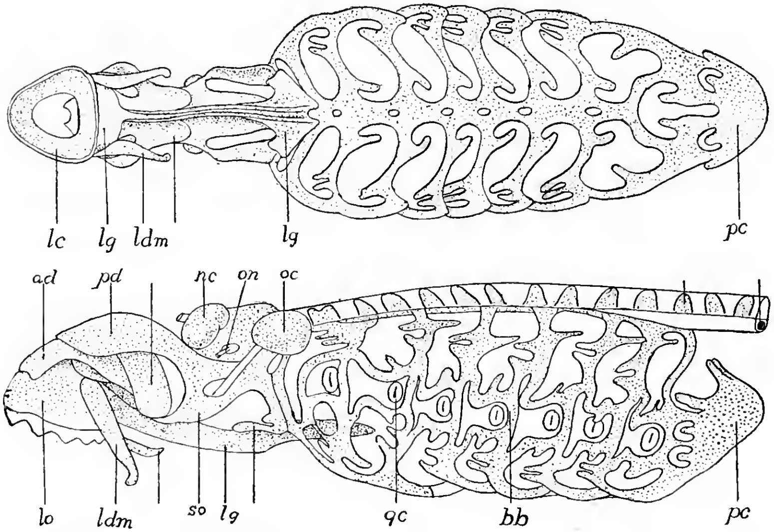


FIG. 160.—Ventral and lateral views of the skull of lamprey (Petromyzon marinus). *ad*, anterior dorsal cartilage; *bb*, branchial basket; *gc*, gill cleft; *lc*, labial cartilage; *ldm*, lateral distal mandibular; *lg*, lingual cartilage; *nc*, nasal capsule; *oc*, otic capsule; *on*, optic nerve; *pc*, pericardial cartilage; *pd*, posterior dorsal cartilage. (After Parker from Kingsley's "Comparative Anatomy of Vertebrates.")

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 **hyomandibular** 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-pterygo-quadrate cartilage, since palatal, pterygoid, and quadrate bones develop from it in amphibians 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.

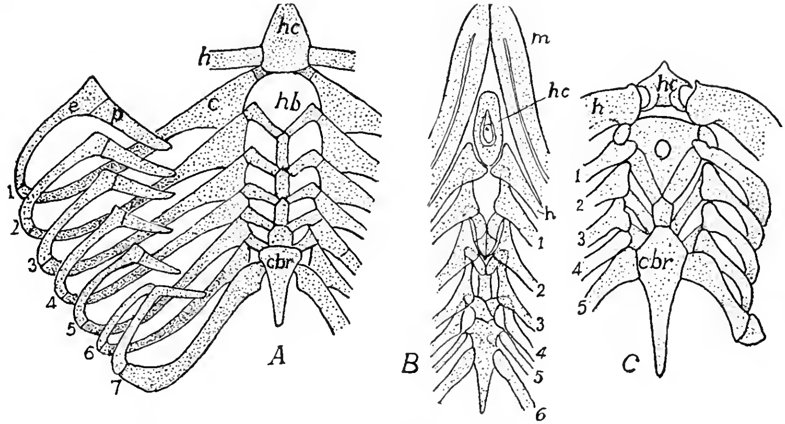


FIG. 161.—Branchial arches of (*A*) Heptanchus; (*B*) Chlamydoselachus; and (*C*) Cestracion. *c*, ceratobranchial; *e*, epibranchial; *h*, hyoid; *hb*, hyobranchial; *hc*, hyoid copula; *cbr*, cardiobranchial (posterior copula); *p*, pharyngobranchial; 1–7, branchial arches; *m*, Meckel's cartilage. (*A* and *C* after Gegenbaur, *B* after Garman; from Kingsley's "Comparative Anatomy of Vertebrates.")

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. Most teleosts have only four functional branchial arches, and in some the number is reduced to two. Perennibranch amphibians 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 **columella** 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 amphibians, 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 of the upper jaw and the dentary or mandibular of the lower. These membrane bones, however, do not extend as far as the articulation of the jaw which, as in amphibians, is between the quadrate of the upper jaw and the articular of the lower.

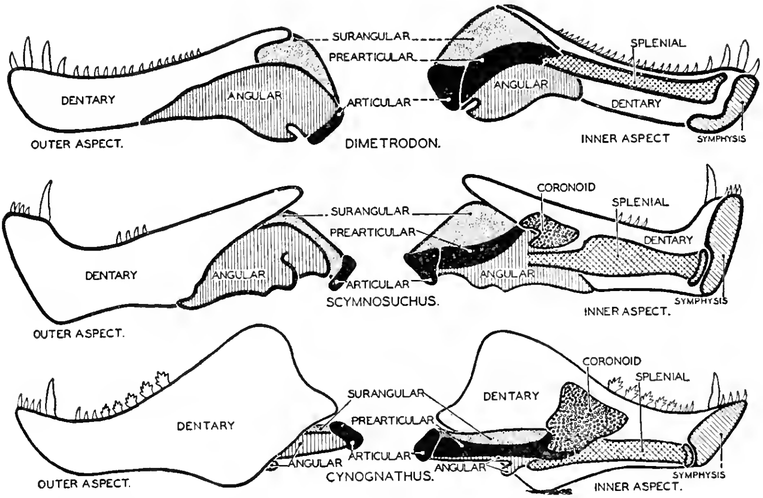


Fig. 162.—Jaws of Tertiary reptiles viewed from their inner and outer aspects. Dimetrodon belongs to the lower Tertiary, while Scymnosuchus and Cynognathus belong respectively to the middle and upper Tertiary. A notable increase in the size of the dentary and relative diminution in the size of the articular element is seen. 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. (Redrawn after D. M. S. Watson.)

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. 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. See Fig. 162.

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 articular element and a corresponding enlargement of the dentary. The relation of the two bones is such that the lower jaw at one time may have been hinged by both. The enlargement of the dentary and the diminution of the articular set free the latter to pass into the tympanic cavity and join the chain of ear bones 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. 164)

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 two pairs 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.

The **mandible** or lower jaw consists of a **body** and two **rami,** which extend upwards nearly at right angles with the body. 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. See Fig. 158. 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 sealring and consequently is called the **cricoid** cartilage . The cricoid expands

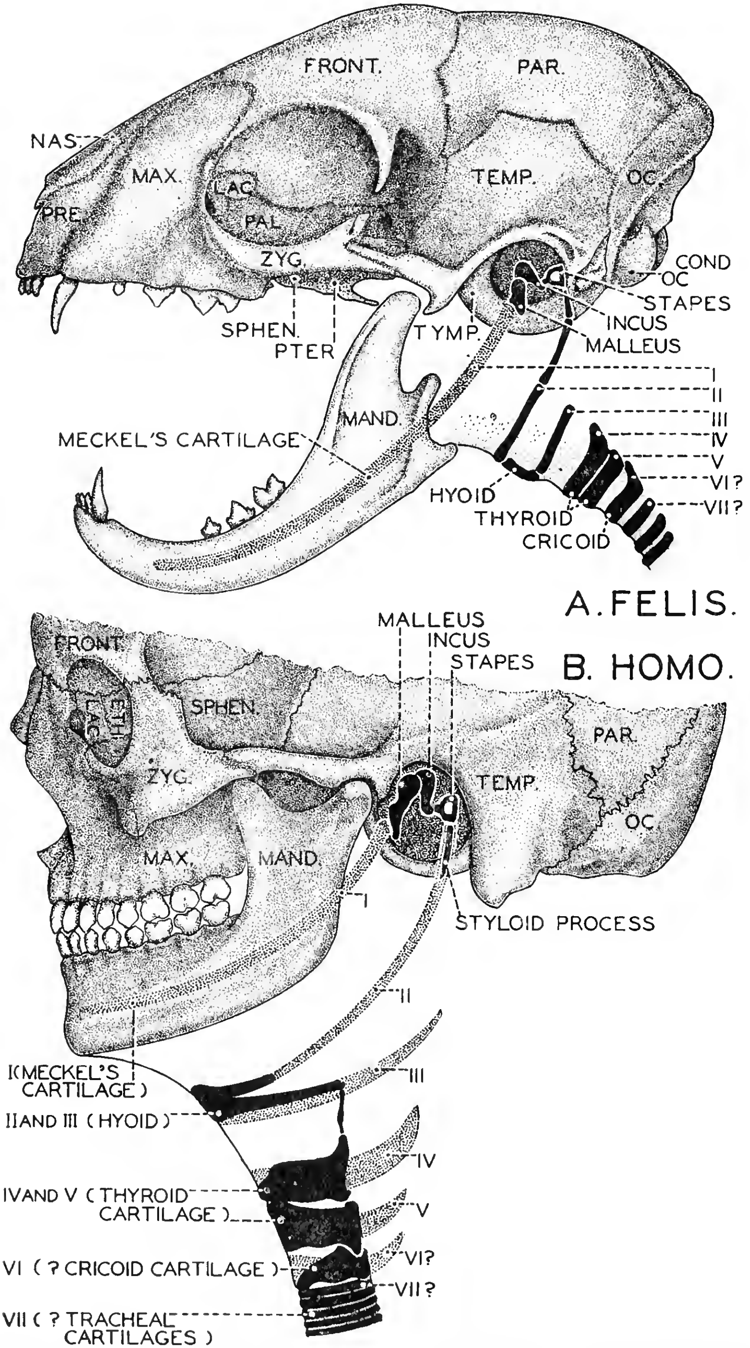
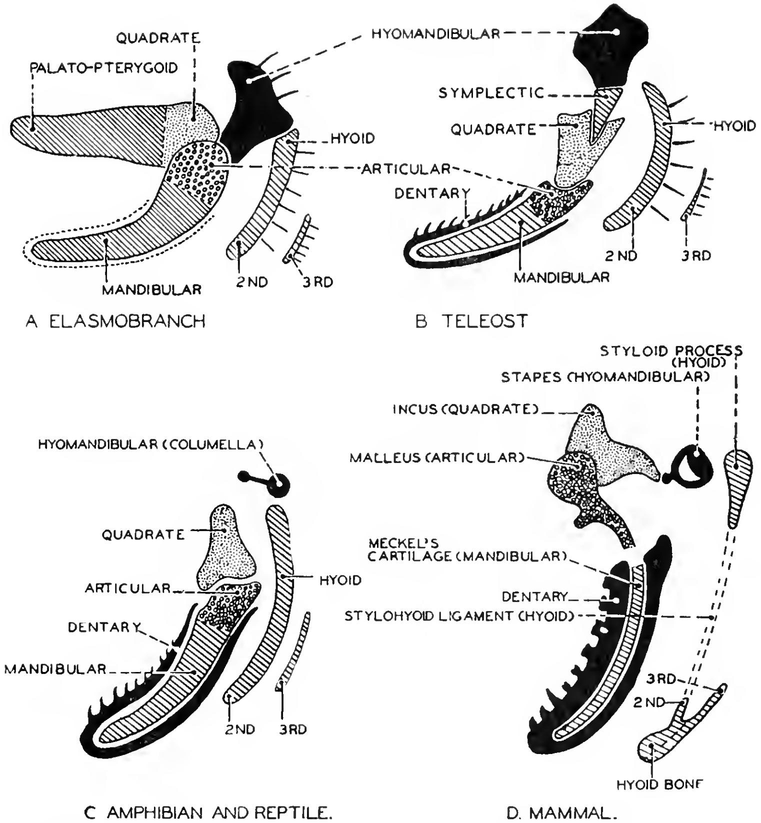


FIG. 163.—*A*. Diagram of the visceral skeleton of the cat. *B*. Visceral skeleton of man. The homologies of the 6th and 7th skeletal arches are uncertain.

into a broad lamina on its dorsal or posterior surface. Articulating with the cricoid on its dorsal cranial edge 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. 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.



A ELASMOBRANCH B TELEOST

C AMPHIBIAN AND REPTILE. D. MAMMAL.

Fig. 164.—Diagrams of the first and second visceral arches in *A*, Elasmobranch; *B*, Teleost; *C*, Amphibian and Reptile; and *D*, Mammal, illustrating the transformation of the hinge of the jaw of lower vertebrates into the malleus and incus of the mammal. The third earbone, the stapes, comes from the hyomandibular. (Redrawn after Gegenbaur and Stempell.)

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. See Fig. 369.

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 mandibular 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 middle 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 of the mandibular ossifies as the malleus.

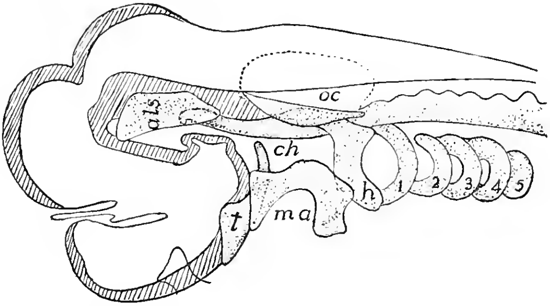


FIG. 165.—Early chondrocranium of Squalus. (The brain in outline.) *als*, alisphenoid cartilage; *ch*, anterior end of notochord; *h*, hyoid arch; *ma*, mandibular arch, not yet divided into pterygoquadrate and Meckelian; *oc*, otic capsule; *t*, trabecula; 1–5, branchial arches; cartilages dotted. (From Kingsley's "Comparative Anatomy of Vertebrates," after Sewertzoff.)

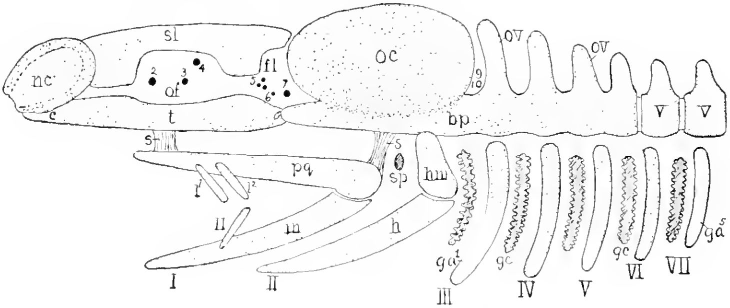


FIG. 166.—Diagram of early elasmobranch skull. *bp*, basal plate; *c*, trabecular cornu; *fl*, foramen lacerum; ga^{1-5}, gill arches; *gc*, gill cleft; *h*, hyale; *hm*, hyomandibular; l^1, l^2, upper labials; *ll*, lower labials; *m*, Meckel's cartilage; *nc*, nasal capsule; *oc*, otic capsule; *of*, orbital foramen; *ov*, occipital vertebrae; *pq*, pterygoquadrate; *s*, suspensor ligament; *sp*, spiracle; *sl*, sphenolateral; *t*, trabecula; *v*, vertebrae; I–VII, visceral arches; 1–10, cranial nerves. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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 form also 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 contributes to the formation of the cricoid. See Fig. 163.

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. See Fig. 167. 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 bases 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 second step in this evolution was the invasion of connective tissue and muscle into the fin-folds. A similar migration actually occurs in 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 intermyotomic 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.

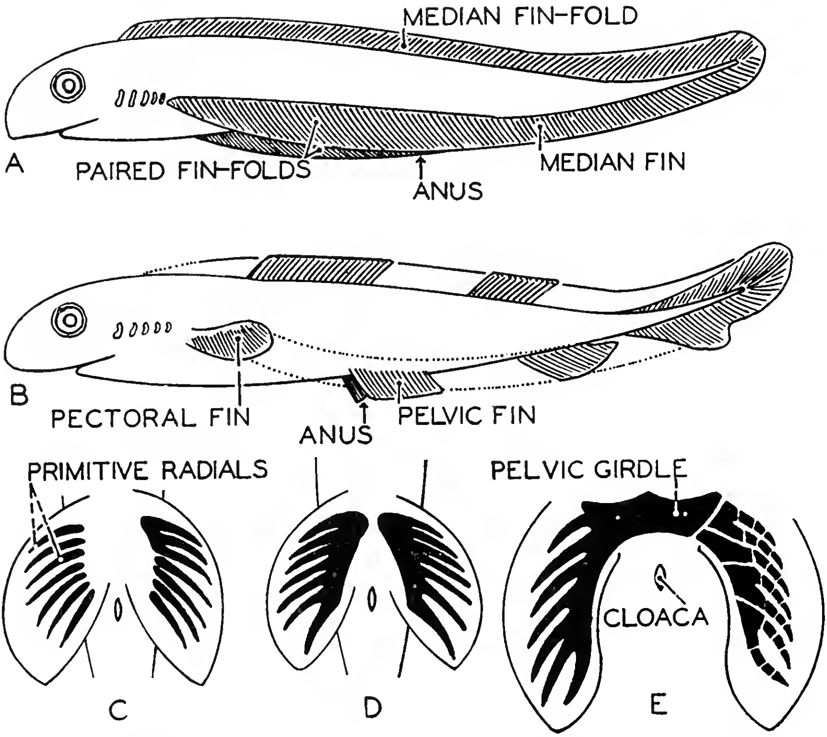


FIG. 167.—Diagram illustrating the hypothetical evolution of the paired fins and their skeletal supports. *A* represents the primitive stage of continuous fin-folds. The dorsal fin and the ventral fin posterior to the anus are median and unpaired. *B* is the definitive elasmobranch stage. The paired fin-folds persist only in the region of pectoral and pelvic fins. The median fins also become discontinuous. *C–E* illustrate hypothetical stages in the evolution of the skeleton of the pelvic fins of elasmobranchs. The right side of *C* and *E* represents a later stage in phylogenesis than the left. In *E* the skeletons of the girdle and extremity are differentiated. (After Wiedersheim.)

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 elasmobranchs. 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. 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 elasmobranchs 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 ganoids 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.

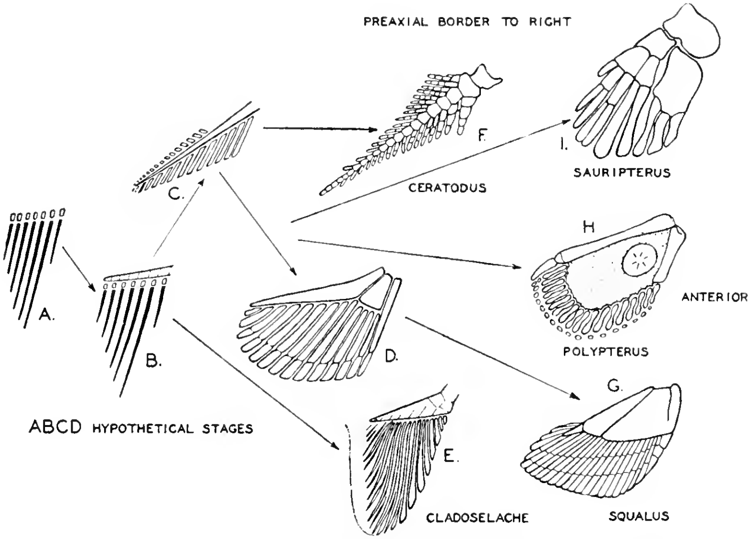


FIG. 168.—Diagrams illustrating the hypothetical evolution of the extremities of dipnoan (*I*), ganoid (*H*), and elasmobranch (*G*) from a fin-fold supported by a series of similar radial cartilages. By fusion basal elements are differentiated. The skeletal supports of fins eventually differ in the relations of the basal elements to the radialia. (Redrawn after A. Brazier Howell.)

A tripartite pectoral girdle makes its first appearance in amphibians. The ventral arm, which in fishes was single and undivided, becomes in amphibians 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 amphibians, the ventral portion of the pelvic girdle resembles that of ganoid fishes, and consists of a broad cartilaginous plate with which the femur articulates. See Fig. 169. Centers of ossification corresponding with the **ischium** and **pubis** of reptiles arise successively in this plate.

The girdles of reptiles are essentially like those of amphibians. 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 the descent of serpents from tetrapod ancestors.

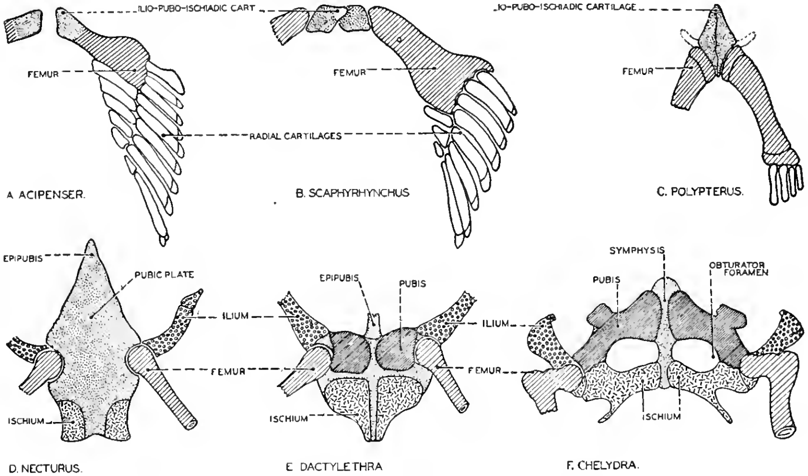


Fig. 169.—A series of six appendicular skeletons illustrating the gradual emergence of the elements of the pelvic girdle found in reptiles and mammals. They probably represent fairly well stages in the evolution of the human pelvis. First came the separation of girdle and extremity (*A* and *B*); then 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 ischium (*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.)

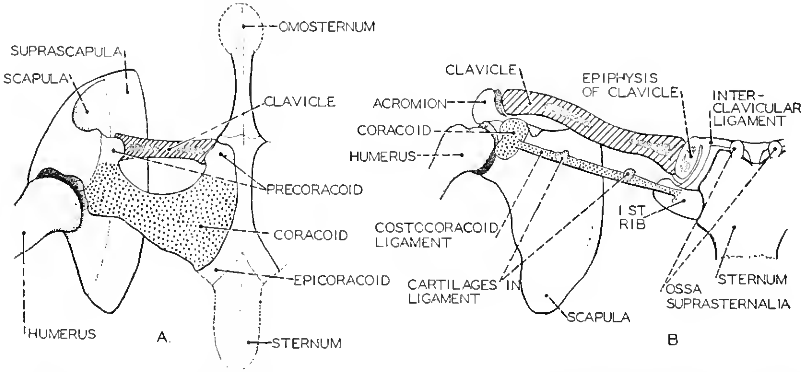


Fig. 170.—Diagrams illustrating the fundamental similarity of the human (*B*) and amphibian (*A*) pectoral girdle. In man the coracoid element has degenerated into a process (coracoid) and a connective-tissue ligament containing occasional cartilage nodules. (Redrawn after Huntington.)

In mammals, the coracoid is reduced to a process fused to 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 the precoracoid, remnants of which, however, usually occur within the clavicle. See Fig. 170.

The mammalian hip bone differs little from that of reptiles. The number of sacral vertebrae to which the coxal bone is attached increases in 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 amphibians 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 **ichthyopterygium** into the **cheiropterygium** has occurred. Interest has centered especially in the transformation of the skeleton.

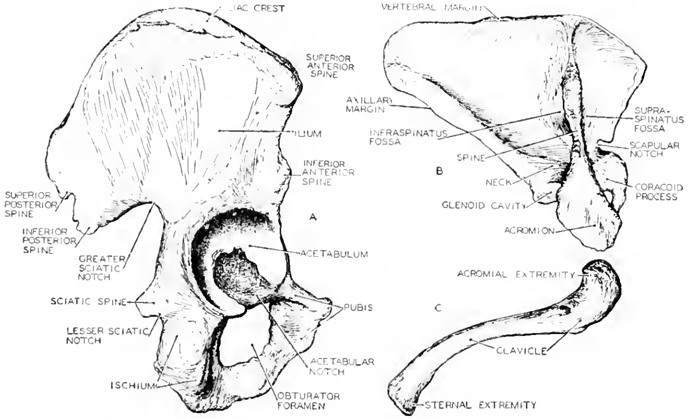
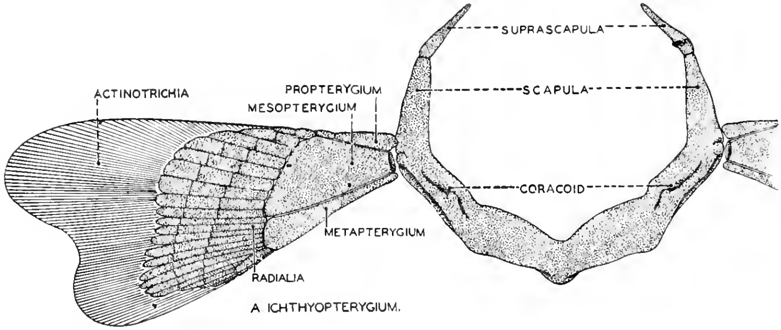


FIG. 171.—Human pelvic and pectoral girdles in lateral aspect. *A* is the pelvic girdle of the right side and *B–C* the pectoral girdle of the same side.

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 **metapterygium** (Fig. 172*A*), connect the fin with the girdle. Morphologists, however, 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.

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.



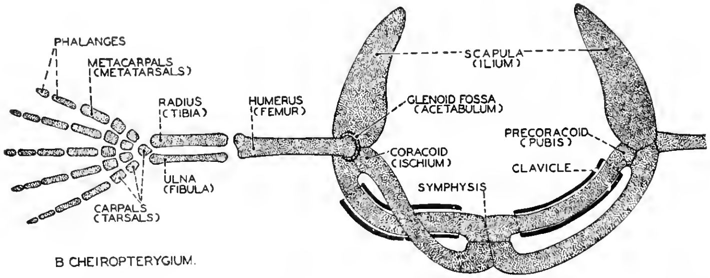


FIG. 172.—Diagrams of the pectoral appendages of lower and higher vertebrates. In *B*, names of corresponding parts of the pelvic appendage are shown in parentheses. A persistent problem of morphology is how the fish extremity or ichthyopterygium was transformed into the fingered extremity (cheiropterygium) of land vertebrates.

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 biting jaws, 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 (Fig. 173). 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 Eusthenopteron help to bridge over the structural gulf separating the ichthyopterygium and the cheiropterygium.

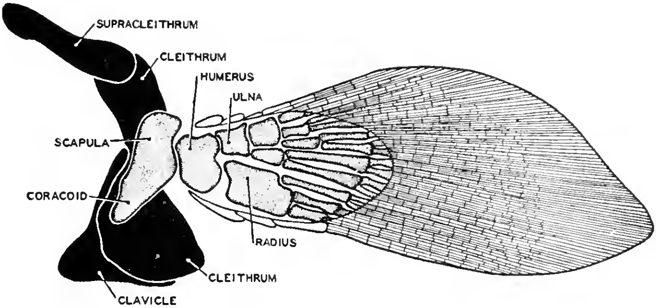


FIG. 173.—The pectoral girdle and fin of Sauripterus, an upper Devonian crossopterygian fish. Interest in this type of fish fin lies in the similarity of relations of the proximal elements of the extremity to those found in the pectoral extremity of tetrapods. (Redrawn after Broom.)

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 amphibians 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 amphibians.

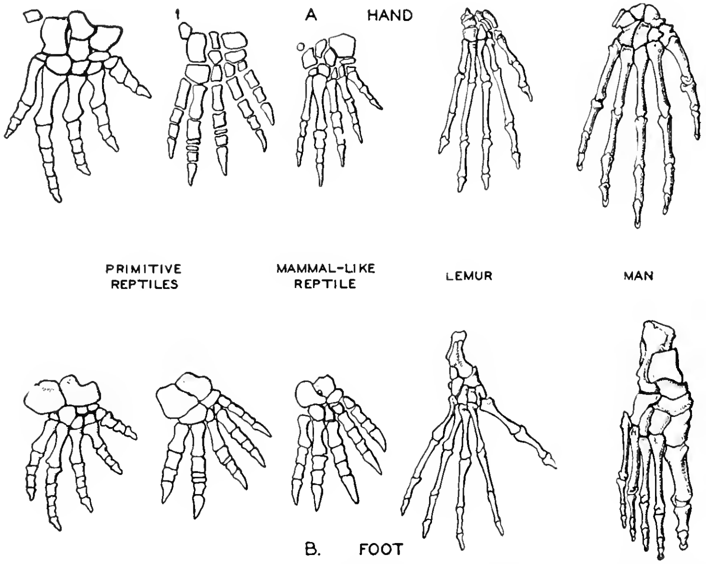


Fig. 174.—A series of skeletons of hands and feet of tetrapods showing the conjectured evolution of the human hand and foot. The human hand is evidently less specialized than is the foot. (Redrawn after Romer's "Man and the Vertebrates," University of Chicago Press.)

To assist their hind legs, amphibians connected the pelvic girdle with the sacrum; to assist their hearing, they converted the suspensorium of the jaw into an ear bone, the columella. Tripartite girdles made their appearance in amphibians. The sternum also is a novelty in this group. In the theromorph 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

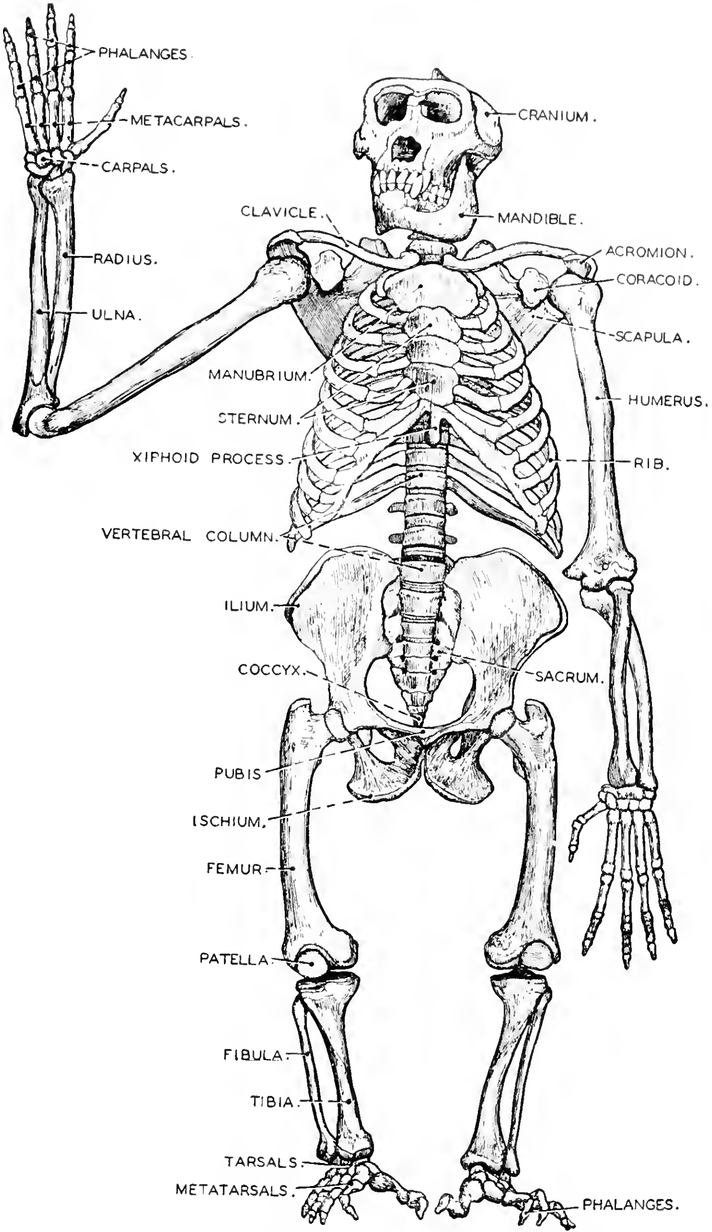


Fig. 175.—Skeleton of gorilla viewed from in front. The bones of the gorilla are identical with those of man. Differences of proportion, however, are seen. Among these differences, that of the relative length of arm and leg bones is most striking. The limb proportions of the human infant, however, tend to resemble those of the ape. (Redrawn after Brehm.)

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

In man, as in other mammals, each limb is divided into four regions. These are, in the upper limb, the pectoral girdle, upper arm, forearm and hand. In the lower limb they are hip, thigh, leg or shank, and foot. A comparison of the human skeleton (Figs. 144 and 145) with that of the gorilla (Fig. 175) shows that, bone for bone, the two correspond. The dif-

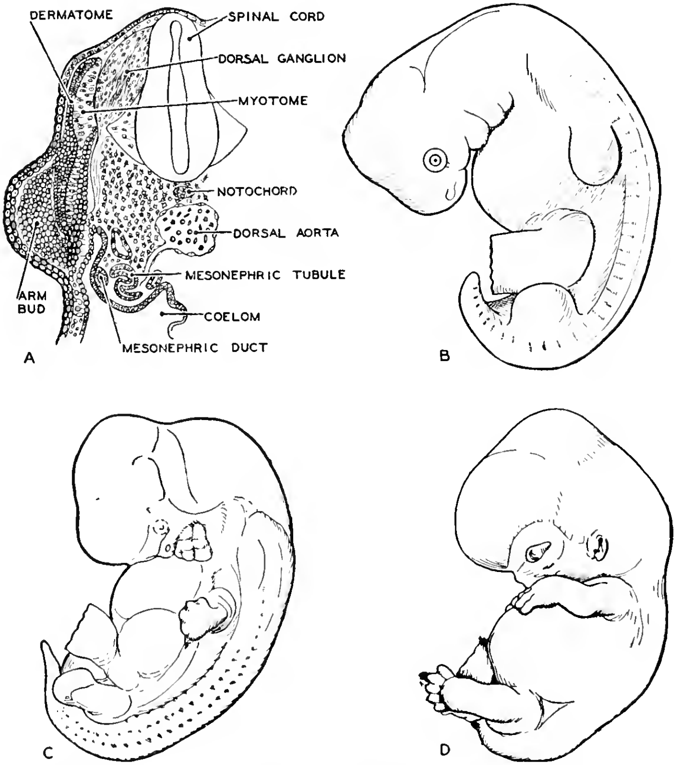


FIG. 176.—Stages in the development of the extremities in mammals. (Redrawn after Bardeen, Lewis and Corning.) *A* is a cross section of a monkey embryo showing an arm bud. (Redrawn from Arey after Kollman.) *B* is a seven-week human embryo in left lateral aspect. (Redrawn after Corning.) *C* is an eight-week human embryo in left lateral aspect. (Redrawn after Corning.) *D* is a nine-week human embryo in left lateral view.

ferences are those of proportion only. The facts are in harmony with the assumption that the two have evolved from a common ancestry.

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 evidence accords with expectation from the standpoint of the fin-fold theory of the origin of the extremities. See p. 177.

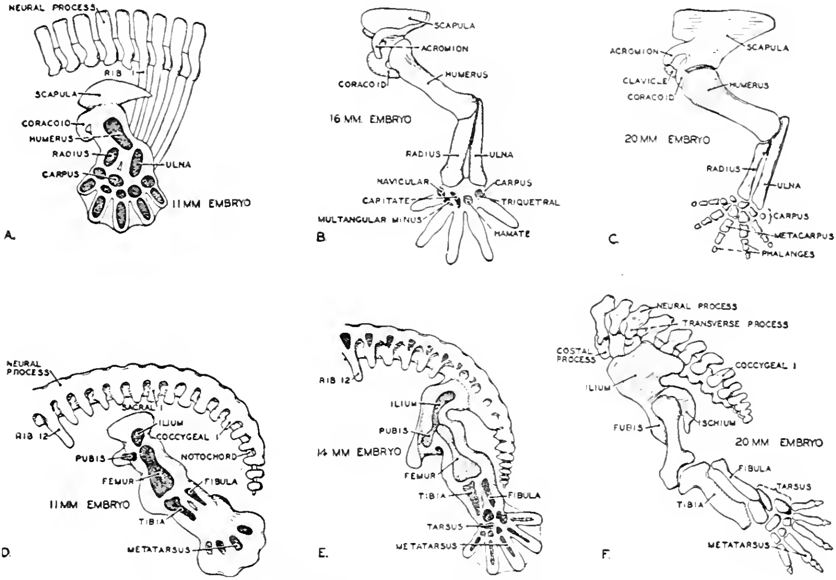


FIG. 177.—Stages in the development of the appendicular skeleton of man. *A*, left lateral aspect of arm in 11 mm. embryo; *B*, left lateral aspect of arm in 16 mm. embryo; *C*, left lateral aspect of arm in 20 mm. embryo; *D*, left lateral aspect of leg in 11 mm. embryo; *E*, left lateral aspect of leg in 14 mm. embryo; *F*, left lateral aspect of leg in 20 mm. embryo. (Redrawn after Bardeen and W. H. Lewis from Keibel and Mall.)

The Wolffian folds consist of an external covering of ectoderm and a core of mesenchyma, which in the human embryo is of uncertain origin. In their early development, both arms and legs take the form of shovel-shaped outgrowths (Fig. 176), which gradually elongate. The cartilaginous anlagen of the bones arise in the mesenchyma (Fig. 176*A*) and are slowly converted into bone through complex processes partly suggested in

Fig. 178. In the human embryo fingers and toes make their appearance at the ends of the extremities as early as the second month. (Fig. 176)

Four stages in the development of a long bone are shown in Fig. 179. The connective-tissue membrane or **perichondrium** which surrounds the cartilage anlage of the bone secretes a cylinder of bone around the shaft of the anlage. Thus the perichondrium is converted into a **periosteum** which persists throughout the life of the bone. Other perichondrial cells penetrate the cartilage and destroy it. Eventually a fatty marrow takes the place of the cartilage within the bony cylinder. The cylinder becomes the **diaphysis** of the adult bone. Since the diaphysis is formed

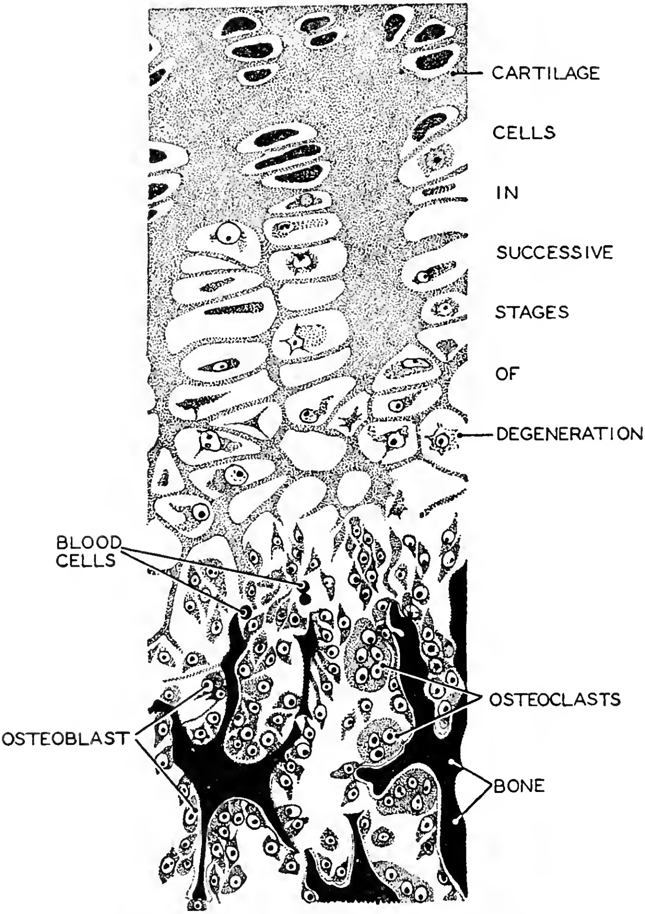


Fig. 178.—Endochondral bone formation at the end of a long bone. Destruction of cartilage is followed by the secretion of lime in the form of thin lamellae. Osteoblasts then lay down bone upon these lamellae. In this way cancellous bone replaces cartilage. (Redrawn after Dahlgren and Kepner.)

outside and around the original cartilage this mode of bone formation is known as **perichondral bone formation.** The diaphysis of the infant is converted into that of the adult by the continuous addition of new bone on the outside of the shaft. At the same time the marrow cavity of the shaft is enlarged through the destruction of bone on the inside of the shaft. In

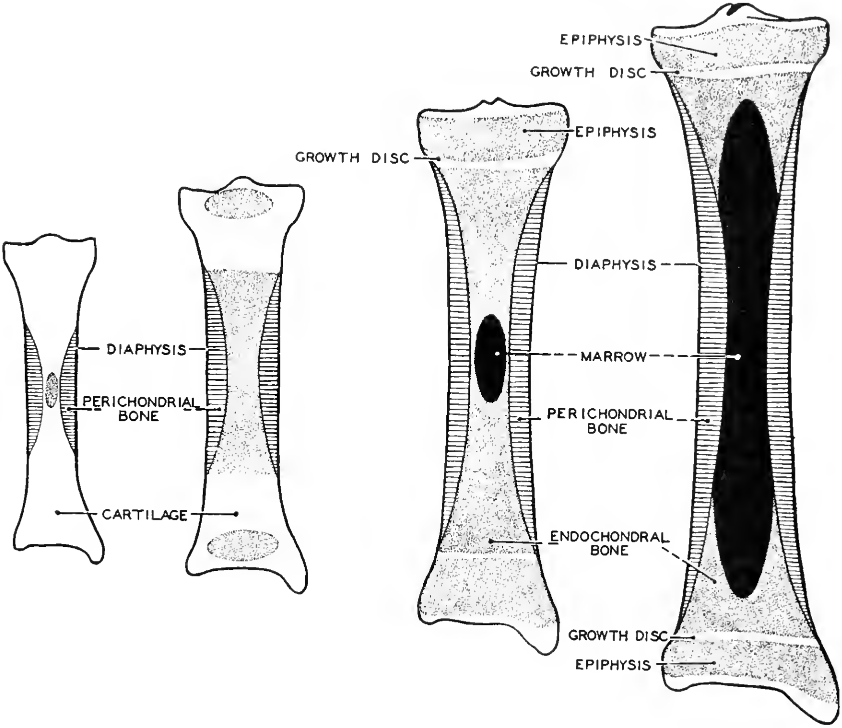


Fig. 179.—Diagrams illustrating four stages in the development of a long bone. Perichondral bone cross-hatched; endochondral bone stippled; marrow black; cartilage unshaded. (Redrawn from Corning's "Human Embryology," after Duval.)

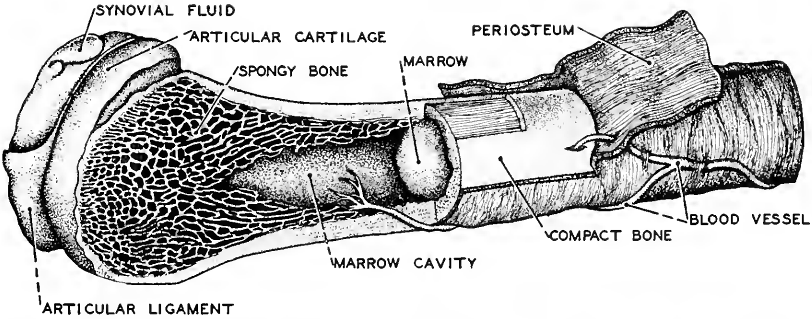


Fig. 180.—Diagram of the structure of a long bone. (Redrawn after Fritz Kahn, "Der Mensch," Albert Müller, Zürich.)

this way the marrow cavity of an adult bone becomes large enough to contain the entire bone of the infant.

The long bone grows in length at the two ends. Through **endochondral bone formation** centers of ossification are formed within the cartilage at the ends of the shaft. The bony centers are known as **epiphyses.** During growth new bone is added between epiphysis and diaphysis in a cartilaginous "growth-disc." When adult size is attained the growth-disc is converted into bone, the epiphyses fuse with the diaphysis, and growth ceases. The regulation of size is influenced through the action of endocrinal secretions of the pituitary and thyroid glands.

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 is 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.

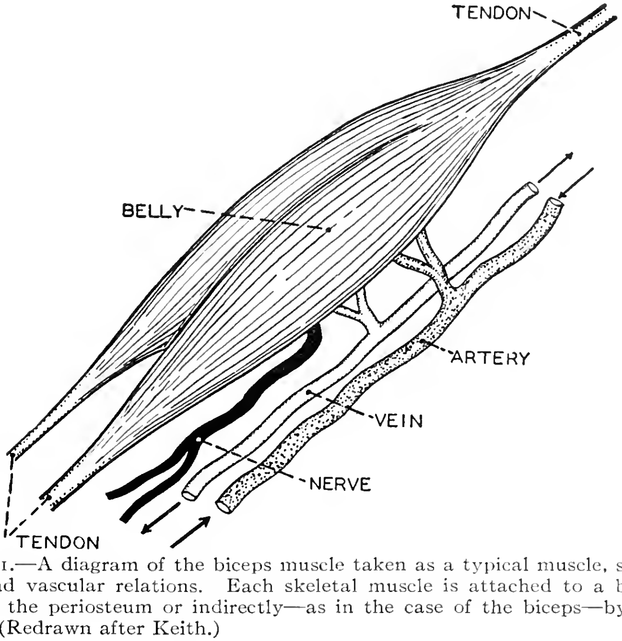


Fig. 181.—A diagram of the biceps muscle taken as a typical muscle, showing its nervous and vascular relations. Each skeletal muscle is attached to a bone either directly to the periosteum or indirectly—as in the case of the biceps—by means of tendons. (Redrawn after Keith.)

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.

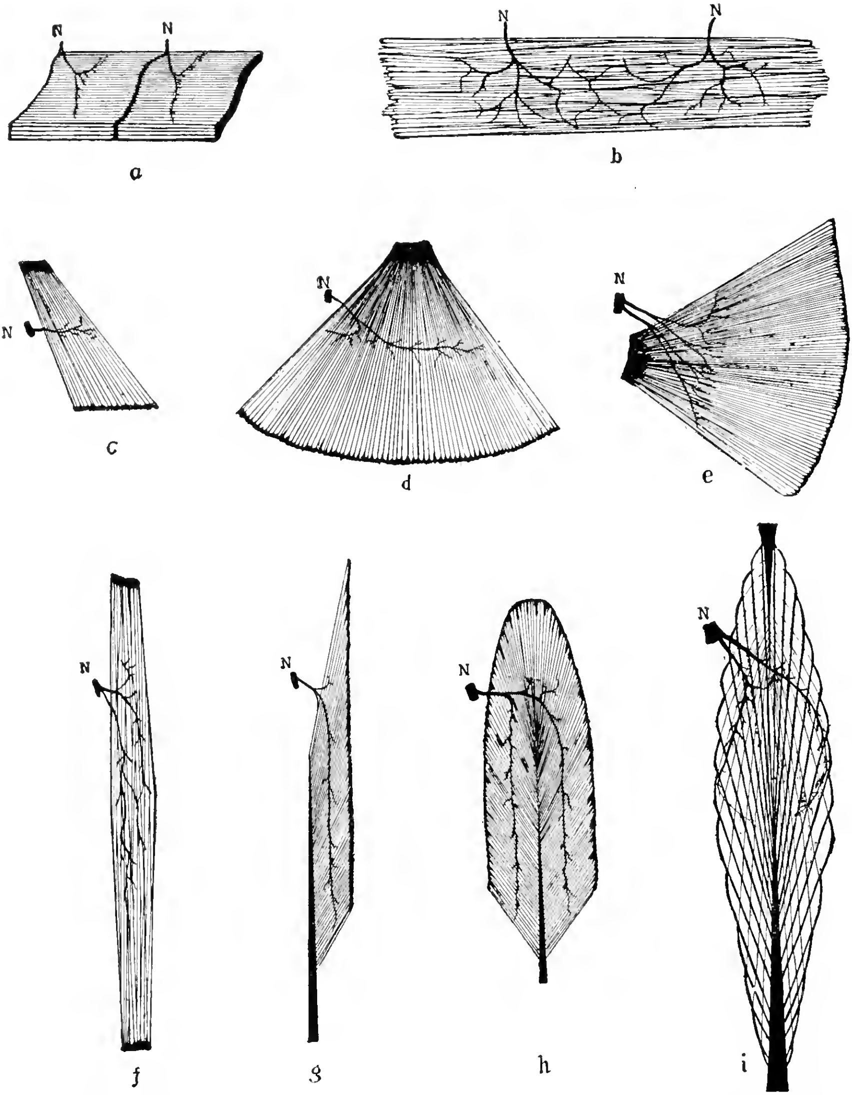


FIG. 182.—Diagrammatic outlines to illustrate various types of muscle architecture and the relations of the main nerve branches to the fiber-bundles of the muscle. *a*, Two segments of the rectus abdominis muscle of a small mammal. *b*, Portion of sheet-like muscle with two nerve-branches and intramuscular 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: **skeletal** (epimeric or myotomic), derived from the dorsal or epimeric portion of the mesoderm; and **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. Smooth visceral muscle fibers are found not only in the wall of the intestines, but also in the walls of blood-vessels, in the lungs, the bladder, the genital organs, and the skin.

Skeletal muscles are composed of striped fibers whose response to stimulation is a rapid contraction. Most visceral muscles, on the other hand, consist of slow-acting smooth or non-striped fibers. The former are voluntary (in man, "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 other 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.

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 tissues which extends around the side 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.

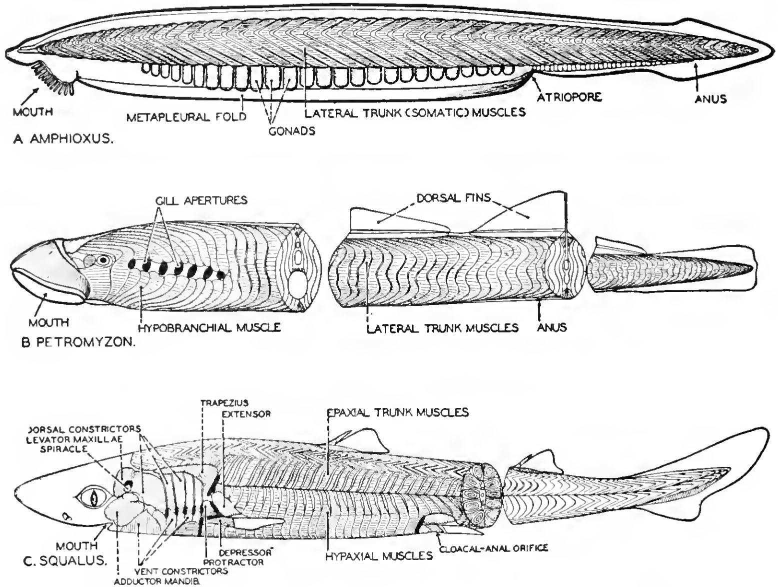


FIG. 183.—The lateral trunk muscles of a cephalochordate, a cyclostome, and an elasmobranch, showing their striking metamerism, and fundamental similarity. *A*, Amphioxus; *B*, Petromyzon; *C*, Squalus.

The visceral muscles in the wall of the intestine are non-metameric, and are differentiated into an inner circular and an outer longitudinal layer. 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.

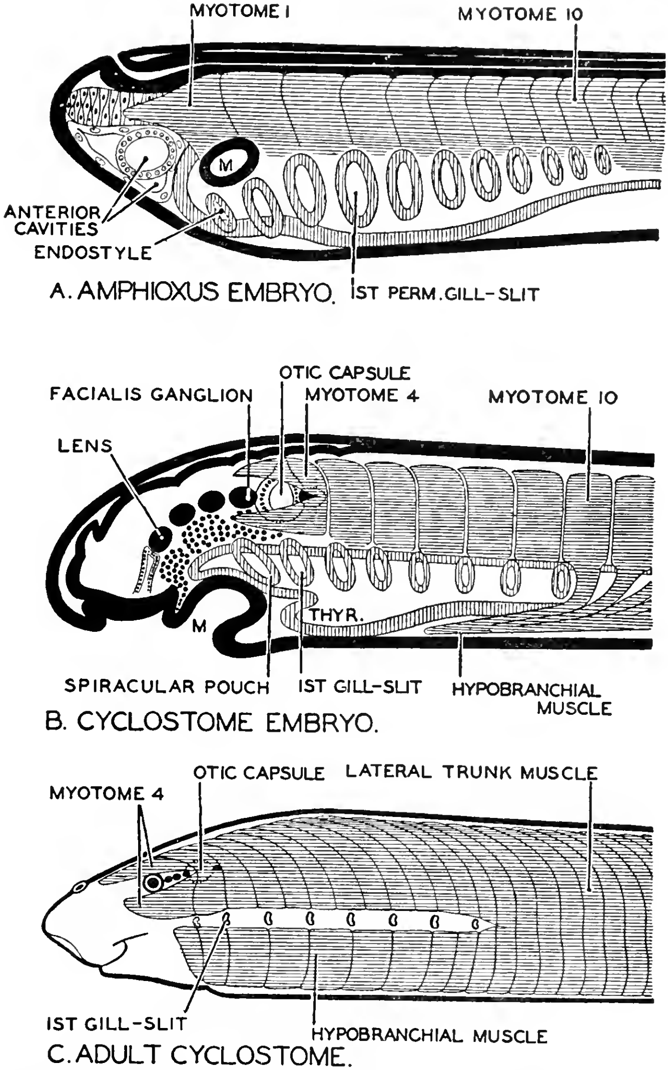


FIG. 184.—Diagrams illustrating the origin of the hypobranchial muscles of vertebrates. Lacking in cephalochordates (Amphioxus), hypobranchial muscles make their first appearance in cyclostomes in the form of muscle buds from post-branchial myotomes. They become the tongue muscles of tetrapods and are innervated by the hypoglossal (XII) nerve. In cyclostomes as in higher vertebrates myotomes 1, 2, and 3 form eye muscles.

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 six eye muscles like those found in all vertebrates up to man. All six are formed from the first three embryonic myotomes. 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. 184, 185, 186)

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. 184, *C*)

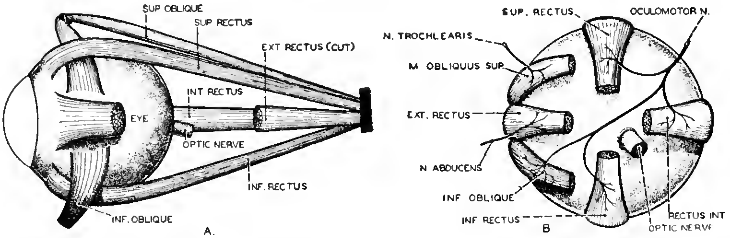


FIG. 185.—Diagrams of the eye muscles of man. *A* shows the left eye-ball and associated muscles viewed from the outer side. *B* is the left eye-ball with associated muscles and nerves viewed from the median side. (Redrawn after Warren and Carmichael. Courtesy of Houghton Mifflin & Co.)

The embryos of elasmobranchs 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 vesicle. Each of the two divisions of the first myotome splits again lengthwise, thus making the four eye muscles innervated by the oculomotor nerve. The dorsal of the two moieties of the second myotome forms the superior oblique muscle innervated by the trochlear nerve,

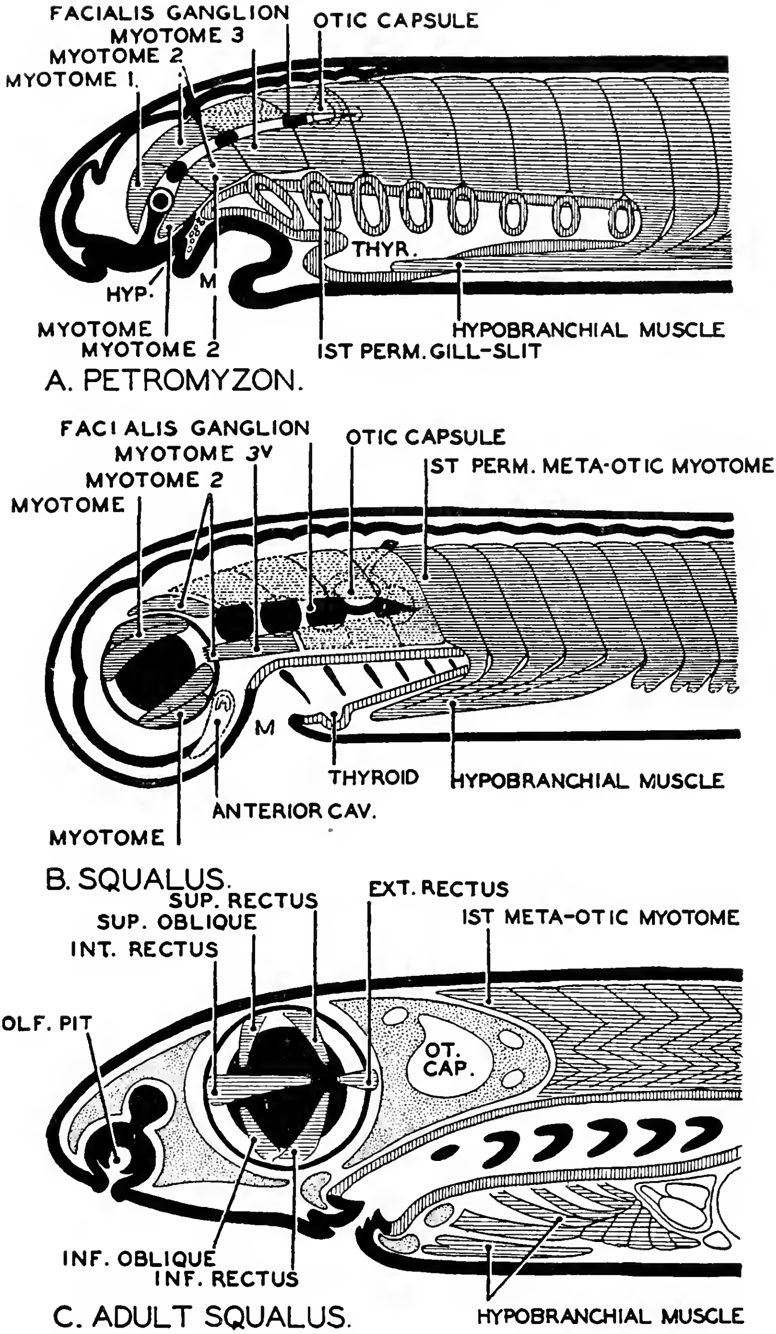


Fig. 186.—Diagrams based upon cyclostome and elasmobranch embryos illustrating the phylogenesis of the six eye muscles. The eye muscles develop from the first three embryonic myotomes. Myotomes are cross-hatched. Those which degenerate in ontogenesis are cross-hatched with broken lines. In *C* the eye muscles are shown as if viewed from the median side of the eye.

while the ventral portion unites with the third myotome to form the external rectus muscle innervated by the abducent nerve. The dorsal division of the third somite breaks up into loose mesenchyme to form connective tissue. The myotomes of the fourth, fifth, and sixth somites also break up into connective tissue, so that the first persistent trunk myotome is the seventh. In this way, a hiatus occurs 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. 186)

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. 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.

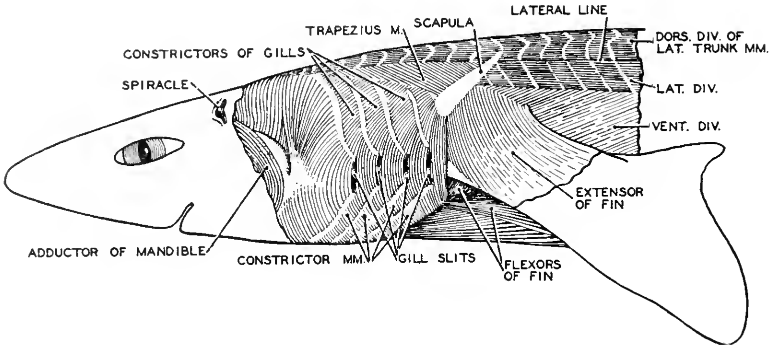


FIG. 187.—The superficial muscles in the shoulder region of Squalus. From such relatively simple beginnings have evolved the complex muscles of the arm and shoulder of man. The flexor protractor muscle which corresponds to the deltoid muscle in mammals is covered in the figure by the posterior gill constrictor. (Redrawn after A. Brazier Howell.)

In elasmobranchs the metamerism of the body muscles, which is such a characteristic feature of the musculature of cyclostomes, is retained with slight modification. 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

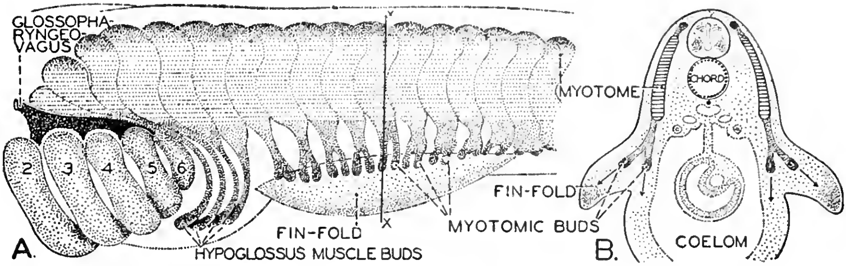
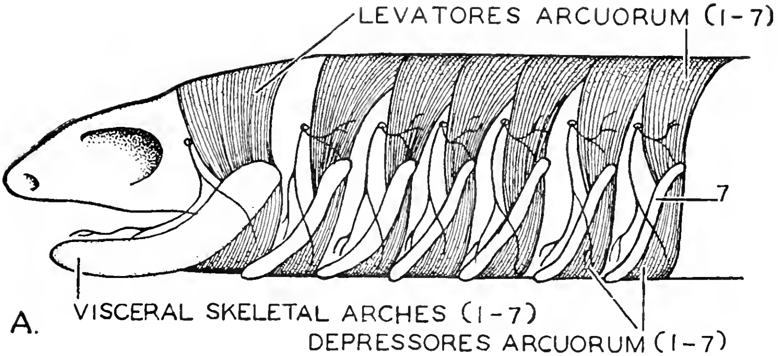


FIG. 188.—Diagram of budding of hypoglossal and pectoral fin muscles from trunk myotomes in an elasmobranch embryo. *A*. Lateral view after Braus. 2–6, visceral arches. *B*. Cross section in region of pectoral fin-fold.



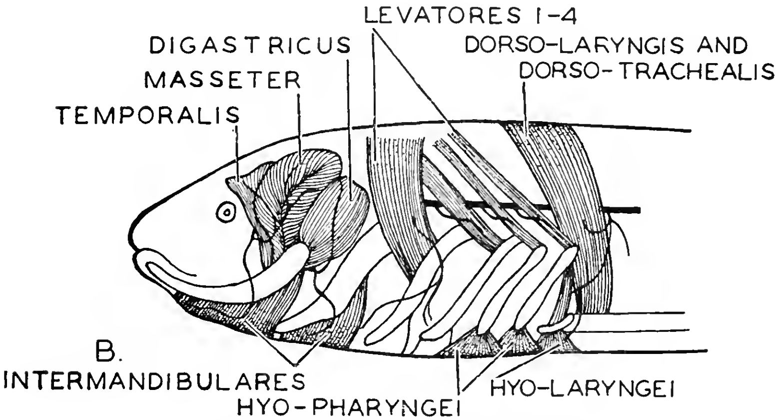


FIG. 189.—Diagrams illustrating the hypothetical evolution of the branchiomeric muscles. *A*. Hypothetical ancestral form. *B*. Branchiomeric muscles in urodele amphibian. (Redrawn after Wilder's "History of the Human Body," Henry Holt & Co.)

myotome so that the surface of attachment of the muscles is increased, it has not been proved that this increase is adaptive. See Fig. 186, *C*.

A novelty first appearing in this group is the division of the lateral trunk myotomes by a horizontal connective-tissue septum into epaxial

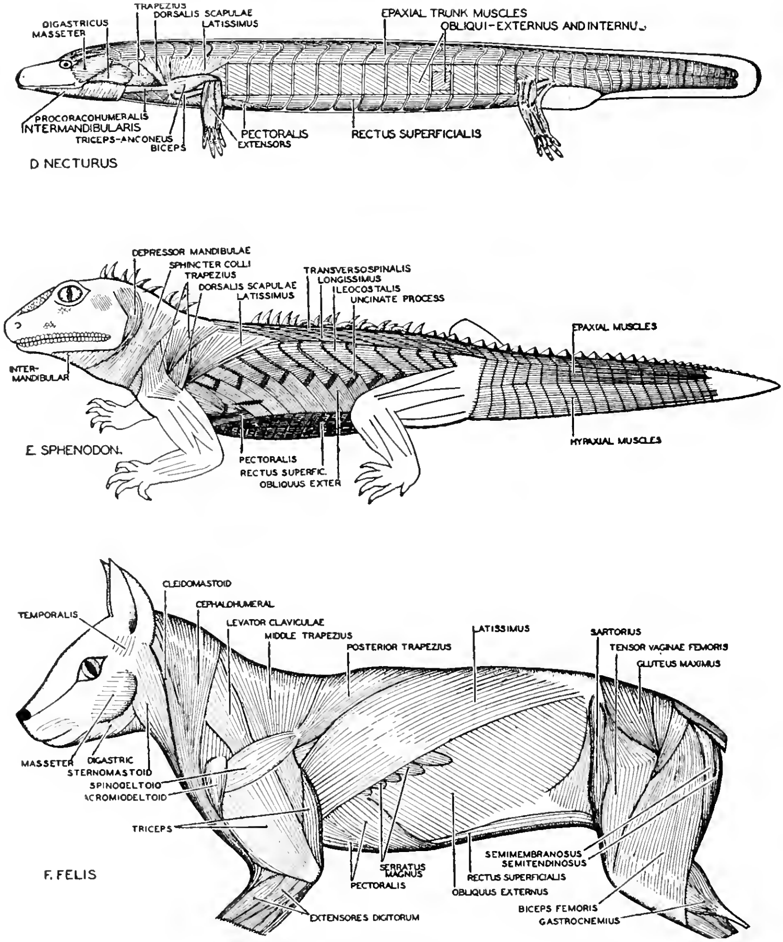


FIG. 190.—Superficial lateral trunk muscles in an amphibian, a reptile, and a mammal. D, Necturus. E, Sphenodon. F, Felis. The metamerism of the lateral trunk muscles which is such a striking feature of the lower vertebrates is retained in urodeles and reptiles, but disappears in mammals. The factors in this change are chiefly the increasing dominance of the appendicular muscles and the fusion of the primarily metameric embryonic trunk muscles. The primitive metamerism, however, appears in mammalian embryos

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. See Fig. 188. 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 the scapula anteriorly above the gills, makes its first appearance in this group.

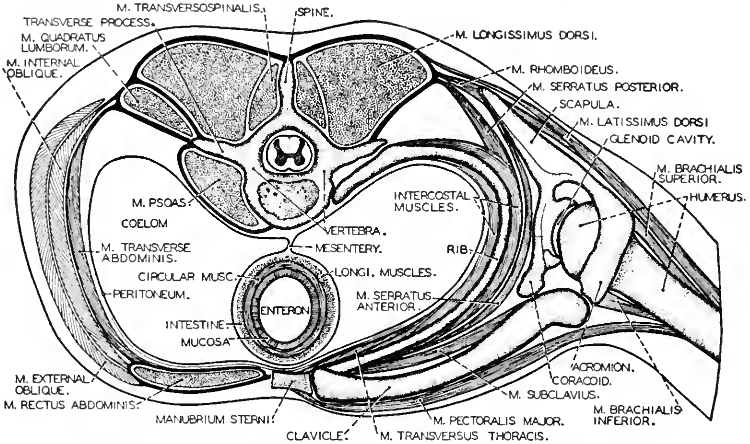


FIG. 191.—Thoracic and lumbar muscles of man as seen in cross section. Thoracic muscles on the right, lumbar on the left. The muscle arrangement is fundamentally like that of any mammal. (Redrawn after Braus.)

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, and pterygoids, while the depressors of these arches become the intermandibularis muscles. The muscles of the remaining visceral arches remain relatively unmodified. (Fig. 189)

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 amphibians having as many as four. The epaxial muscles of the trunk divide into longitudinal bundles connected with the head.

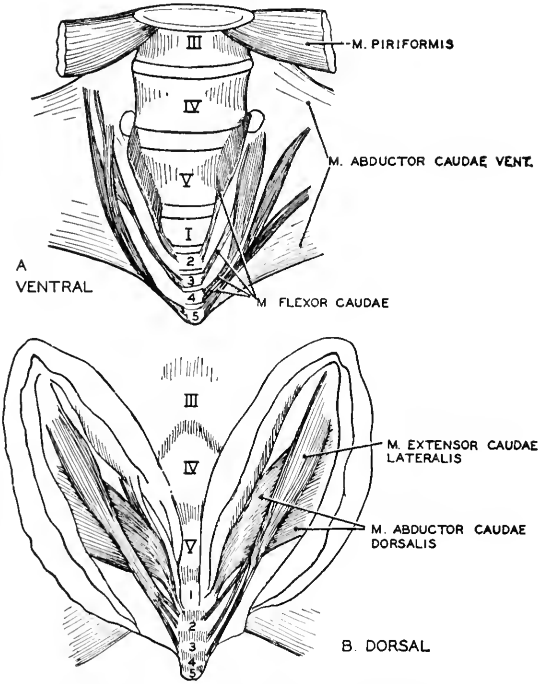


FIG. 192.—Human caudal muscles viewed from A. ventral and B. dorsal side. These rudimentary muscles are the last remnants of the powerful caudal muscles of the lower vertebrates. The presence of such useless rudiments receives its best interpretation in the evolution theory. (Redrawn from Wilder's "History of the Human Body," Henry Holt & Co.; after Lartschneider.)

A further novelty in amphibians 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 differentiated sternohyoid and geniohyoid muscles, which connect sternum and lower jaw respectively with the hyoid.

No very striking developments affect the muscles of **reptiles.** The three sets of epaxial muscles of the trunk,—transverso-spinalis, lumbocostalis, 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.

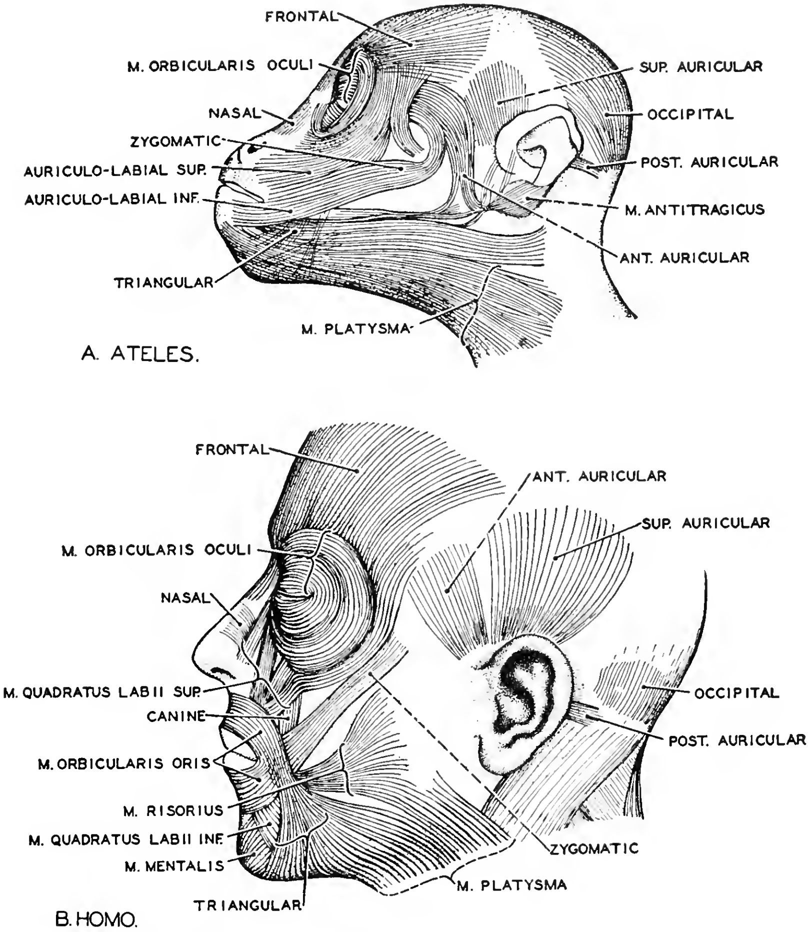


FIG. 193.—Mimetic muscles in monkey (Ateles) and man. A, Ateles (redrawn from Wilder after Ruge) and B, Homo. The similarity of these muscles both in function and relations attests their similar genetic derivation.

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 increase. 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.

Muscles in Man

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 suggests 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.

The human body has 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. Each part of the body—head, neck, back, abdomen, thorax, diaphragm, shoulder and chest, upper arm, forearm and hand, hip, thigh, lower leg and foot, pelvis—has its intrinsic set of muscles. Space does not permit the description of all these muscles.

There is no question that in fundamental pattern the muscles of vertebrates and of man are alike. (See Fig. 190.) Comparison of the superficial muscles of man (Figs. 194 and 195) with those of the cat (Fig. 190) reveals a surprising degree of resemblance. On account of their exact homology many of these muscles in the two forms are given identical names. The same is true of many of the deeper muscles. When the muscles of man are compared with those of another primate, the similarity is much greater. There is no reason to doubt that the similarity of the mimetic muscles in man and monkey (Fig. 193) has genetic significance. Few, if any, muscles in man are without homologues among primates.

The evolution theory in its application to the human body derives much support from the comparative anatomy of the muscles. The presence in man of useless muscle rudiments such as those of the coccyx and ear mentioned above (page 204) receives its only adequate interpretation in this theory. Pointing in the same direction is the existence in man of inconstant and variable muscles, the homologues of which are functional in lower animals. The **pyramidalis abdominis** muscle is an example. When present in man the pyramidalis arises from the pubic bone anterior (ventrad) to the rectus abdominis muscle. Its length varies greatly in individuals. It may occur on one or both sides or may be wanting. In non-placental mammals the pyramidalis is powerfully developed in connexion with the marsupial bones which it serves to support. Even in insectivores in which the marsupium has disappeared the pyramidalis muscle is well developed. The presence in man of such a useless rudiment suggests the animal origin of the human body.

Rudimentary integumentary muscles occasionally appear in individuals. Among these are the **sternalis** muscle of the chest and the **axillary** muscle connected with the pectoralis in the axillary region. They are normally present in apes, but occur in human individuals only exceptionally. They are interpreted as remnants of the **panniculus carnosus** of lower mammals.

Of similar significance is the fact that, although metamerism is evident in few adult mammalian muscles (intercostals, intervertebrals and the rectus abdominis), nevertheless all the skeletal muscles arise from the metameric somites of the embryo. Why are embryonic myotomes metameric when the muscles which develop from them are not metameric? The primary metamerism corresponds with the muscular metamerism of the skeletal muscles of the lower vertebrates. Does this fact not give the clue to the muscular metamerism of the human embryo?

Development of the Muscles. Classified on the basis of their ontogenetic development, muscles are of two kinds: (1) **Somatic Muscles,** derived from the mesodermal epimere, and (2) **Visceral Muscles,** which develop from the hypomere. With the exception of the smooth muscles of the eyeball, which are of ectodermal origin, all muscles are mesodermal.

We may then describe first the development of the **Somatic Muscles, derived from the Epimere or Somite.**

Very early in ontogenesis the mesoderm becomes divided into a metameric series of "somites." In all chordates above the cephalochordates (Amphioxus) the metamerism affects only the dorsal portion of the mesoderm, that is, the portion known as the epimere. In the trunk region—but not in the head—of vertebrate embryos the adjacent mesomere becomes segmented as the nephrotome. The epimere becomes later differentiated into (1) **myotome** which forms muscle, (2) **sclerotome** which forms skeletal material, and (3) **dermatome** which gives rise to loose connective tissue.

In the embryos of the lower vertebrates, as shown in Fig. 197, the somites extend in an unbroken series throughout head and trunk. In embryos of the higher vertebrates, however, the metamerism of the mesoderm in the head region disappears. Only in the embryos of Amphioxus and cyclostomes (Petromyzon) do all the somites produce myotomes. In the higher forms the series is broken in the ear region.

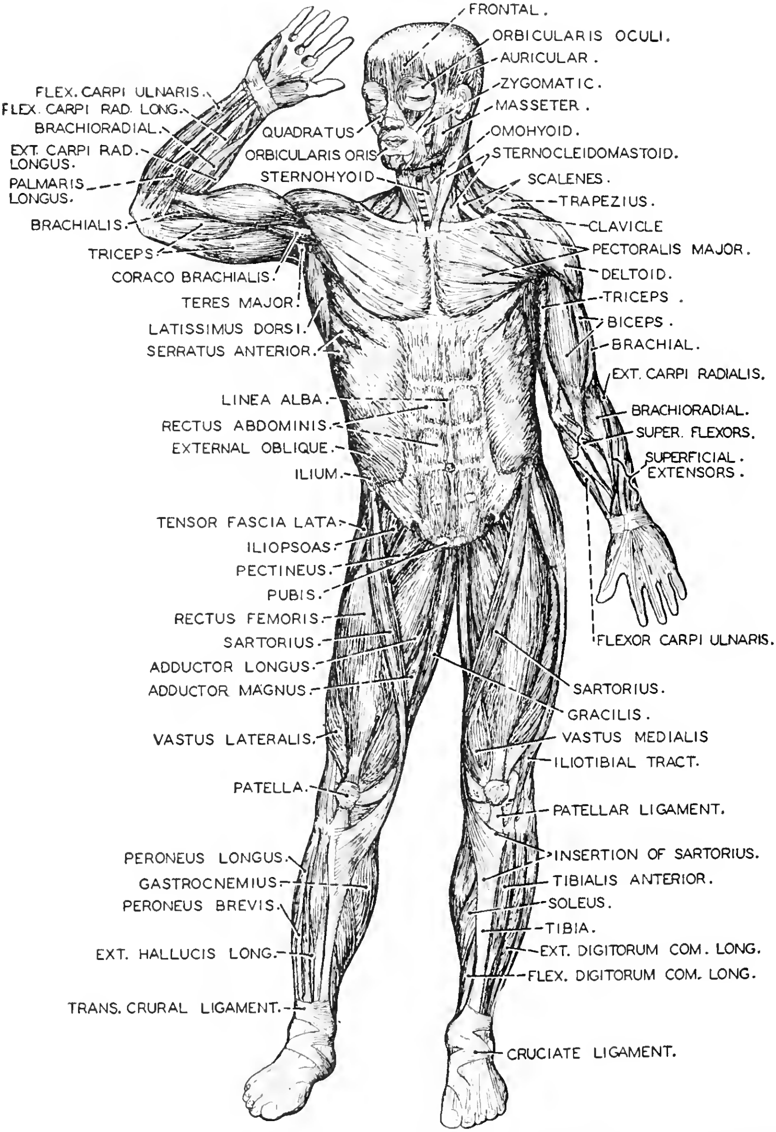


FIG. 194.—Superficial muscles of man; front view. (Reproduced in modified form from "The Human Body" by Dr. Logan Clendening (Copyright 1927, 1930 by Alfred A. Knopf, Inc.) by permission of and special arrangement with Alfred A. Knopf, Inc., authorized publishers.)

The serial homology of the head cavities or somites with trunk somites, which for many years was a controverted problem, has now been demonstrated 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 sclerotome, are innervated by somatic motor nerves, and are dorsal

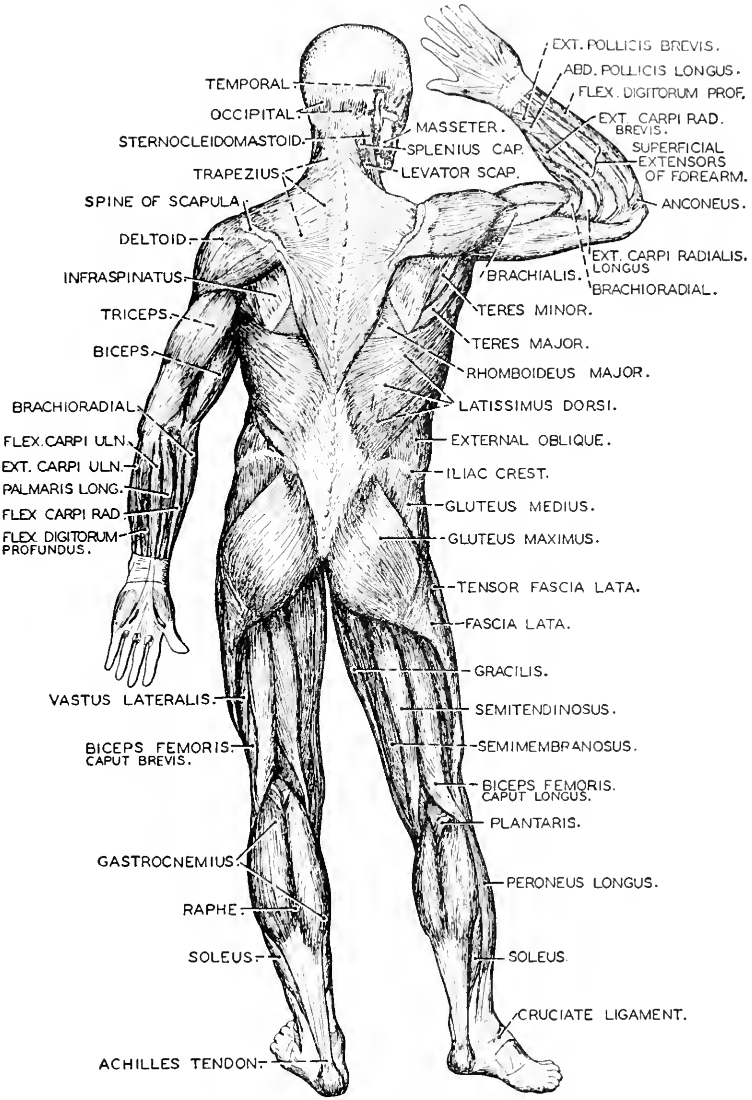


Fig. 195.—Superficial muscles of human body; back view. (Reproduced in modified form from "The Human Body" by Dr. Logan Clendening (Copyright 1927, 1930 by Alfred A. Knopf, Inc.) by permission of and special arrangement with Alfred A. Knopf, Inc., authorized publishers.)

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 resembles the fusion of trunk myotomes such as occurs in the formation of the tongue muscles.

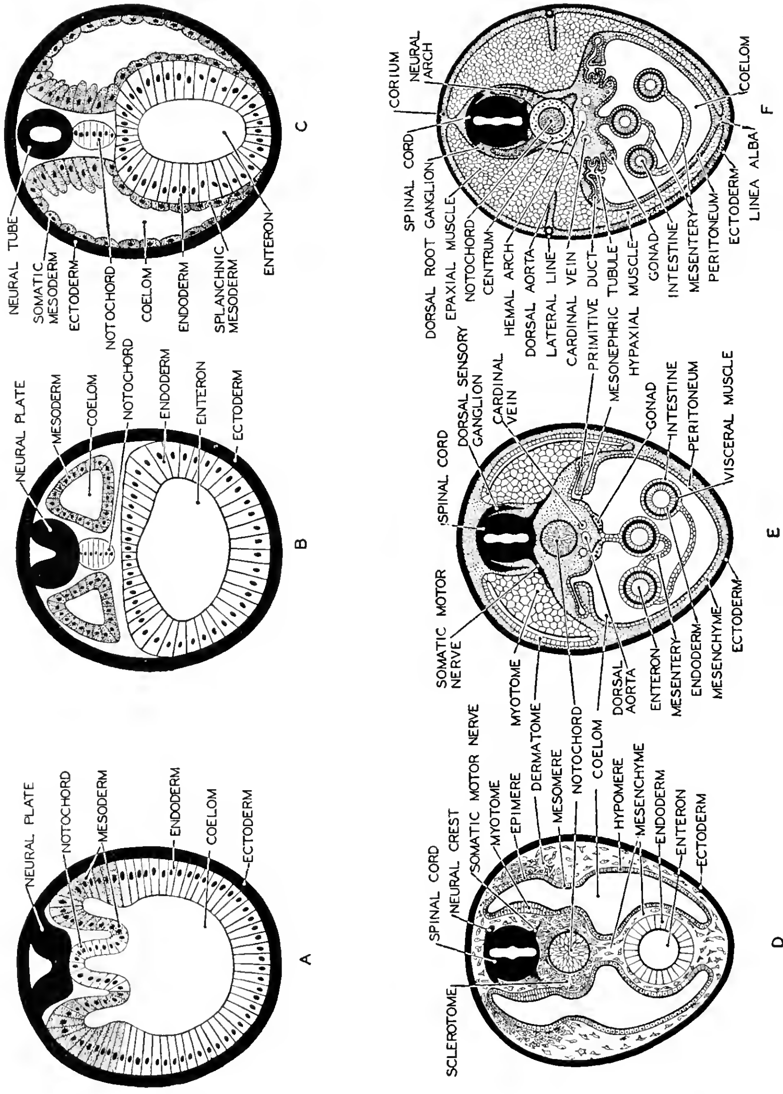
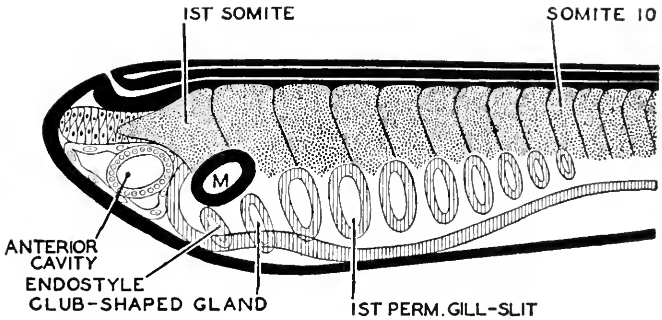
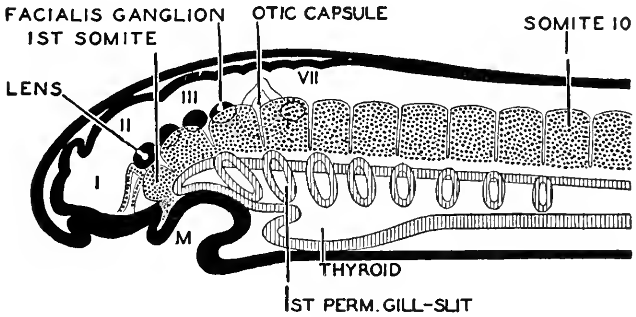


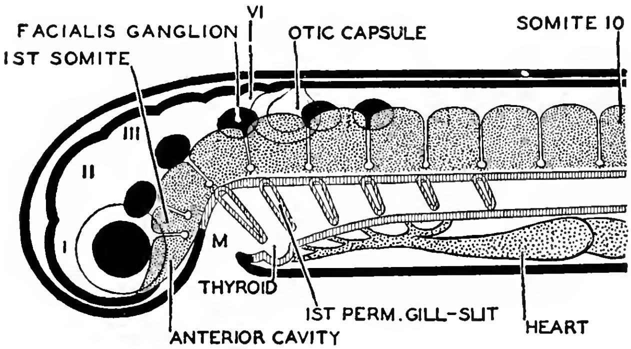
FIG. 196.—A series of diagrams *A–F* illustrating the ontogenesis of muscles in chordates. (Based upon figures by Hatschek and Kingsley modified.)



A. AMPHIOXUS EMBRYO



B. PETROMYZON



C. SQUALUS

FIG. 197.—Diagrams of the mesodermal (somatic) segmentation in the head region of embryos of lower chordates as viewed from the left side. In embryos of these lower vertebrates, just as in the adult Amphioxus, the somites (myotomes) extend in unbroken succession throughout head and trunk. Roman numerals number the brain "neuromeres."

Lateral Trunk Muscles. The lateral trunk muscles of man develop from myotomic segments which first appear in the fourth week of ontogenesis, 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

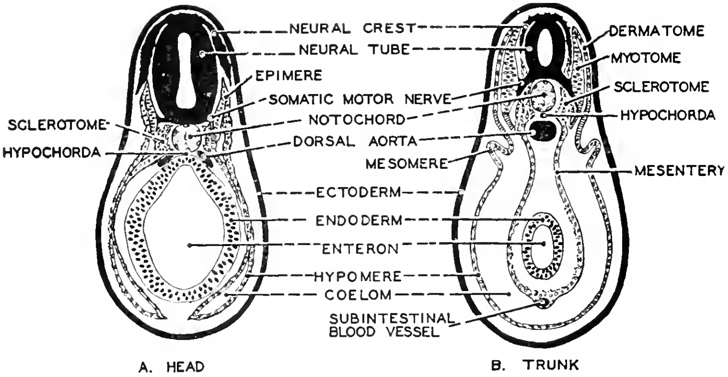


FIG. 198.—Diagrams of cross sections in *A*, head and *B*, trunk regions of an elasmobranch embryo showing the fundamental similarity of the two regions. The discovery that the coelom of elasmobranch embryos extends throughout head and trunk and that in this respect the two regions are alike was made by the English embryologist, Francis Balfour.

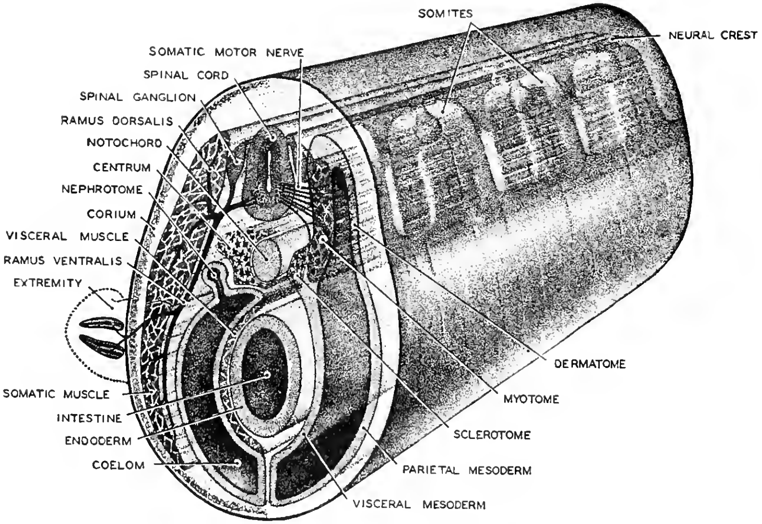
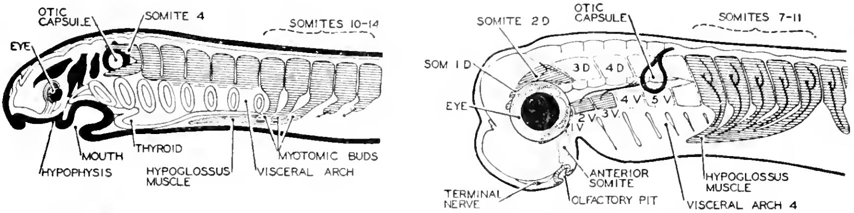


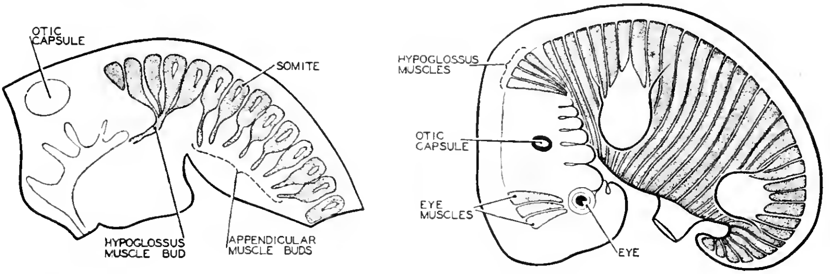
FIG. 199.—A stereogram of the trunk region of a vertebrate embryo, based upon elasmobranch embryos. The figure shows an earlier stage of development on the right side, a later stage on the left. The extension of the myotome to form the lateral trunk musculature is shown. The lateral trunk musculature of the ventral half of the body-wall thus arises as a secondary invasion. (Redrawn after Braus.)

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 **spinalis** and **iliocostalis.** Among the processes tending to obscure the original metamerism is the degeneration of myotomes into connective-tissue fasciae and aponeuroses, which may be very extensive. Migration of muscles may accompany their fusion. Among the other ontogenetic changes in trunk myotomes is tangential splitting of muscles into sheets. One of the most characteristic ontogenetic processes affecting the trunk muscles is the subdivision of a muscle mass into a number of bellies each of which acquires an independent origin or insertion, or both. The original segmentation of the trunk myotomes is, however, retained in such muscles as the **transversospinalis, intercostalis,** and **rectus abdominis.** By the growth of a horizontal connective-tissue septum which extends laterally from the transverse processes of the vertebrae, the lateral trunk muscles become divided into **epaxial** and **hypaxial** portions, of which the former are innervated by dorsal rami of the spinal nerves, the latter by ventral rami. 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.



A CYCLOSTOME

B ELASMOBRANCH



C. REPTILE

D MAMMAL

FIG. 200.—Diagrams illustrating the mode of origin of hypoglossal (hypobranchial) muscles in *A*. Cyclostome, *B*. Elasmobranch, *C*. Reptile, and *D*. Mammal. In *A*, *B*, and *C* cervical myotomes send myotomic buds into the hypobranchial region. In mammals such buds are not formed but a migration of mesenchyme cells from cervical myotomes provides material for these muscles. The number of myotomes which participate is usually four or five.

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 or 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 hypoglossal 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.

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 others, such as the trapezius, sterno-cleido-mastoid, 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 muscles 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 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.

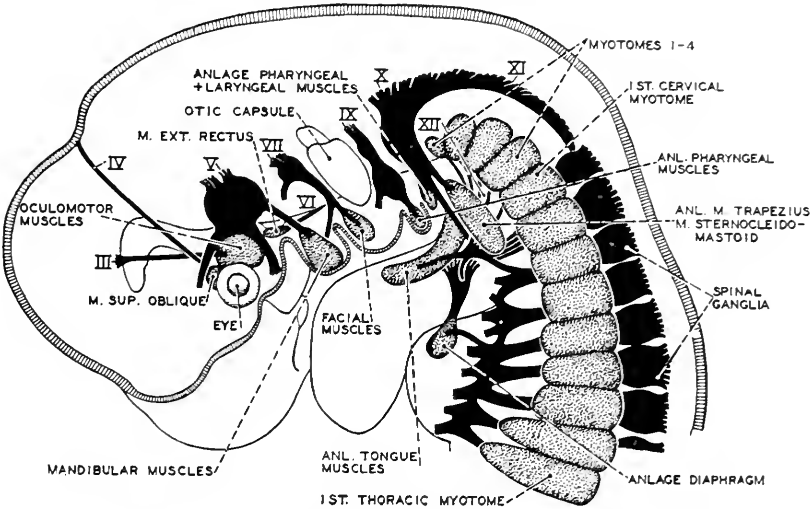


FIG. 201.—The anlagen of the cranial muscles with their nerve relations as seen in a 7 mm. human embryo. (Redrawn from Keibel and Mall, after W. H. Lewis.)

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 outpocketing of pharyngeal pouches, the hypomere becomes divided into a series of pouches each of which lies in a visceral arch. This hypomeric 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. (Fig. 201) From the same source come the tensor tympani of the ear and the anterior belly of the digastricus. The muscles innervated 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 glossopharyngeal 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 crustaceans, 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 catalyzers, 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 assimilates 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 the digestive tract. This has but one opening to the exterior, which serves both as mouth and anus. See Fig. 375.

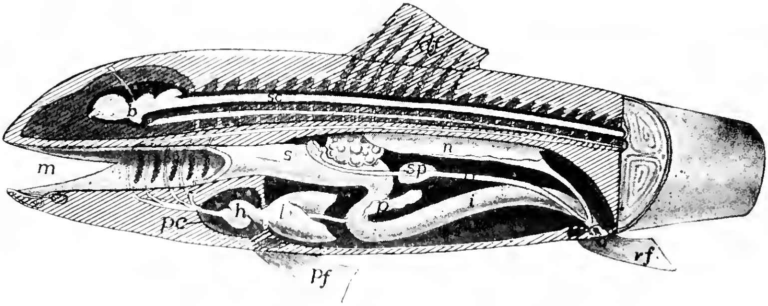


FIG. 202.—Diagram of a vertebrate. *a*, anus; *b*, brain; *df*, dorsal fin; *h*, heart; *i*, intestine; *l*, liver; *m*, mouth; *n*, nephridia; *p*, pancreas; *pc*, pericardium; *pf*, pectoral fin; *s*, stomach; *sc*, spinal cord; *sp*, spleen; *vf*, ventral fin. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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.

FIG. 203.—Spiral valve of Raia. Cartilaginous fishes increase the absorbing surface of their intestine not by elongation, as is done by higher animals, but by a spiral fold in the intestine. (From Kingsley's "Comparative Anatomy of Vertebrates," after Mayer.)

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 phylogenesis 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 cephalochordates. The cyclostomes contribute 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. To increase surface for absorbing digested food they develop a spiral fold or "valve" in the intestine. (Fig. 203) They develop also a new cavity, the cloaca, to receive the wastes and secretions of the urogenital and digestive systems.

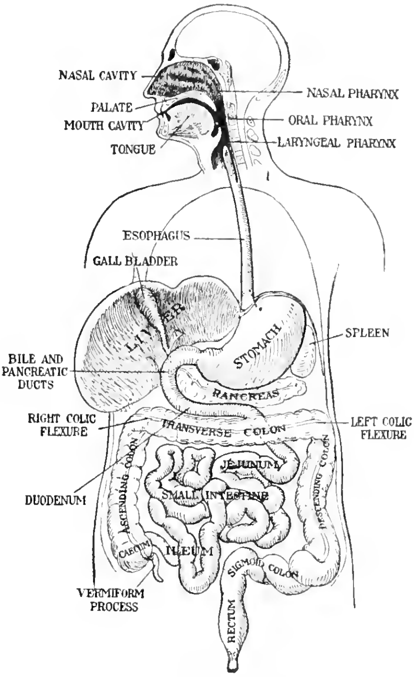


FIG. 204.—Diagram of the alimentary canal. (From Morris' "Human Anatomy.")

The amphibians 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 nasal passage above.

Development. At a relatively late state of ontogenesis, at the anterior end of the fore-gut where the mouth is to break through, the ectoderm invaginates to form the **stomodeum.** 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. The covering of the lips and gums is derived from the ectodermal stomodeum, while that of the rest of the mouth is endodermal.

Evolution. 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.

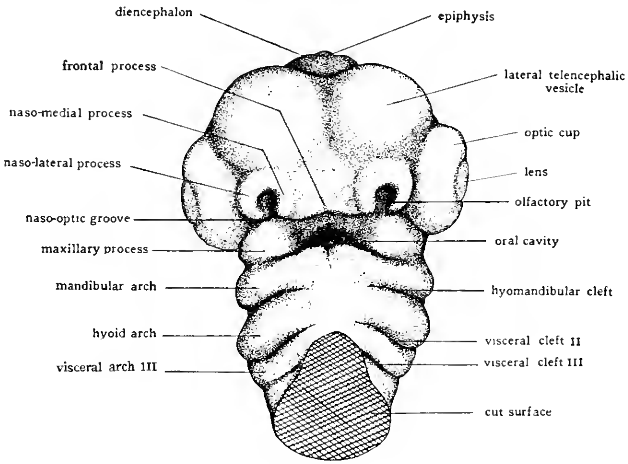


FIG. 205.—Drawing to show the external appearance of the structures in the oral region of a four-day chick. Ventral aspect. (From Patten's "Embryology of the Chick.")

Beard and Kupffer, however, 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. (See Fig. 206, *A*) According to Kupffer, the hypophysis of vertebrates represents a paleostoma which functioned as a mouth in prechordates, following their abandonment of the original 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. (Fig. 208)

Whatever view is held of the origin of vertebrates, we must believe that there have been at least two mouths in the course of vertebrate phylogenesis. The reason for this conclusion is that the original coelenterate mouth becomes the mouth in no vertebrate, while only in cyclostomes, dipnoans, and possibly some amphibians does it become the anus. 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.

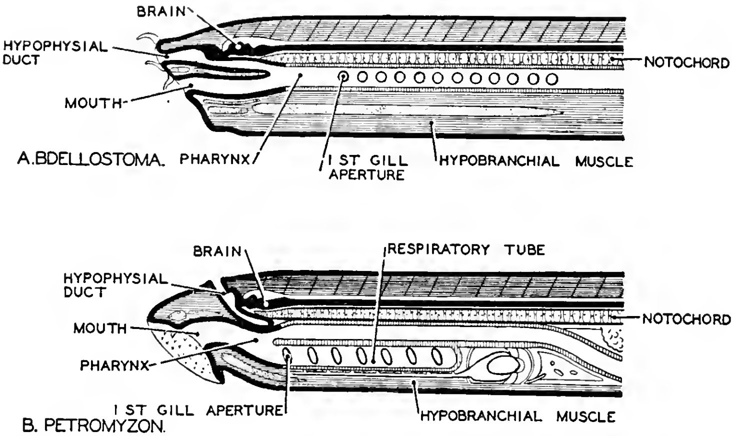


Fig. 206.—Diagrams of median longitudinal sections of the heads of Bdellostoma and Petromyzon, showing the relations of the hypophysial ducts in the two forms. In the former the hypophysial duct opens posteriorly into the pharynx, suggesting the possibility that it may once have served as a mouth (paleostoma). In Petromyzon the hypophysis fails to open into the pharynx and is converted into a pipette-like organ into which the olfactory pits open. On the basis of this difference cyclostomes are divided into two sub-classes, Hyperotreta and Hyperoartia.

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 annelidan mouth), and finally

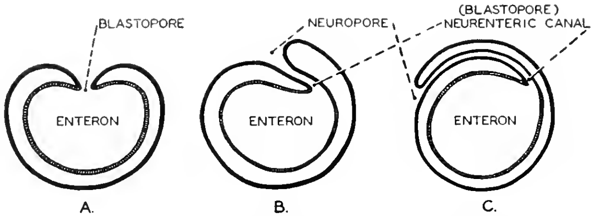


Fig. 207.—A diagram illustrating the way in which, according to Delsman, the blastoporic mouth of coelenterates is in chordates converted into the neurenteric canal. Delsman homologizes the chordate neural tube with the ectodermal foregut of annelids.

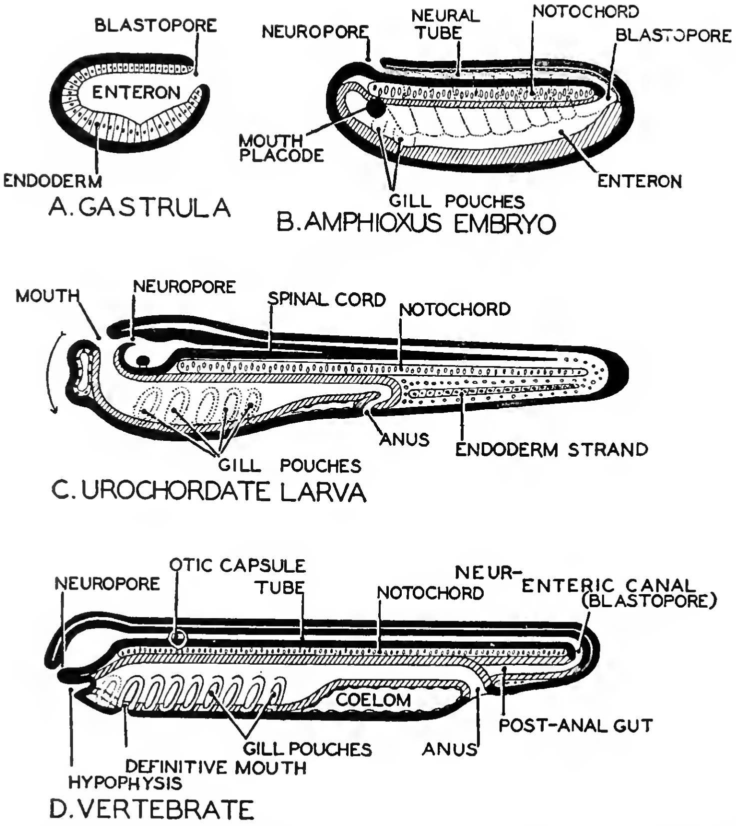


Fig. 208.—Diagrams illustrating the hypothetical phylogenesis of the vertebrate mouth. The primitive animal mouth, the blastopore, is converted in vertebrates either into an anus or a neurenteric canal. The definitive mouth of vertebrates therefore is a secondary mouth. But the relations of the neuropore are such that at one time in the ancestry of chordates this may have served as a mouth and the neural tube as a foregut. It is also possible that the mouth of urochordates is not homologous with the definitive mouth of vertebrates. The evidence of a paleostoma or hypophysial opening suggests that this may once have been a functional mouth. Thus the definitive mouth may have been the last in a series of four mouths.

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 change, which is no greater, however, than others which have occurred in phylogenesis.

If we add to the three mouths mentioned by Delsman the hypophysial "paleostoma" mentioned by Beard and Kupffer, then there have been four mouths in the phylogenesis of vertebrates, the present mouth being the fourth and last.

Diagrams showing the position of the four mouths mentioned are shown in Fig. 208. The objection to this idea that there have been a series of mouths in the course of animal phylogenesis, 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 into the alimentary canal, such as the gill-slits, have made their appearance in the course of phylogenesis.

The phylogenesis 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. But such assumptions are considered to have a relatively insecure foundation.

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-acinous gland, and empties by Stenon's duct into the vestibule of the mouth opposite the second upper molar tooth.

The **submaxillary** is a mixed (mucous and serous) tubulo-acinous gland located in the floor of the mouth near the angle of the lower jaw. Its secretions are carried by Wharton's duct which opens near the frenulum at the front margin of the tongue.

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. 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. The numerous glands of the tongue, however, are formed by the local proliferation of the stratum germinativum of the endodermal 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.

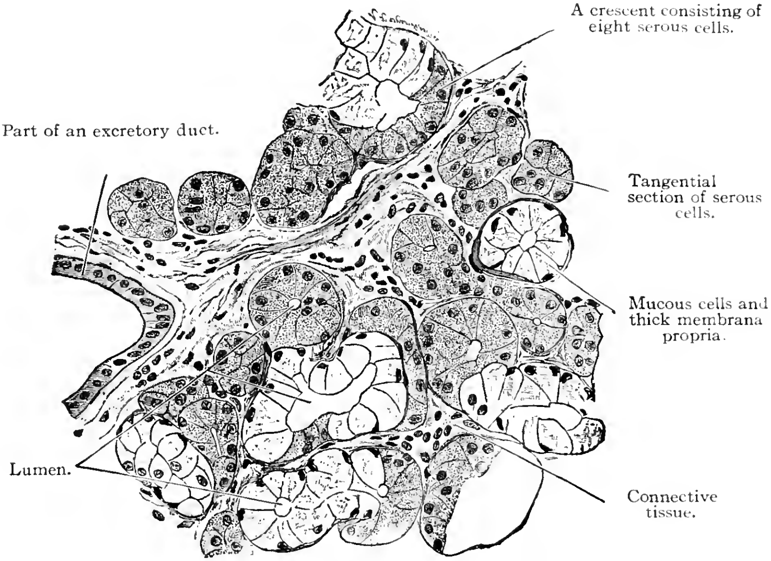


FIG. 209.—Section of a human sublingual gland, ×252. (From Bremer's "Text Book of Histology.")

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 amphibians have an intermaxillary gland, the duct of which opens between the intermaxillary bones. In some amphibians, e.g., Rana, mucus glands are located also in the posterior nasal passages. That enzymes are secreted by the mucus cells of fishes and amphibians 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 in mammals, 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.

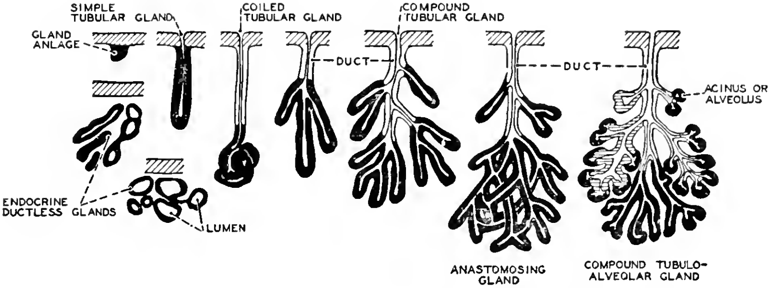


Fig. 210.—Various types of digestive and endocrinal glands which develop from the endodermal (mucous) lining of the alimentary canal. The endocrine glands are ductless. The digestive glands may be simple or compound, tubular or alveolar (acinous). (Redrawn after Braus.)

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** or 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.** See Fig. 211.

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. 211)

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 mandibular arch. (Fig. 212) 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.

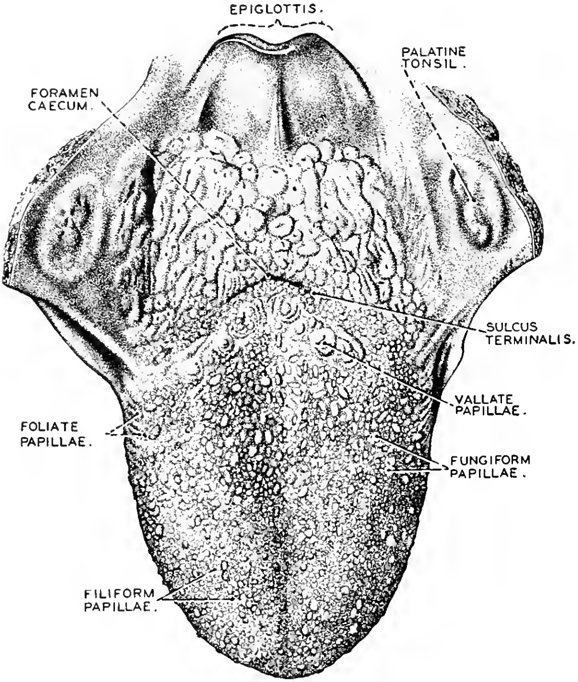


FIG. 211.—The dorsal surface of the tongue. The sulcus terminalis divides the body or apex of the tongue from the root. The two regions have a different embryonic origin. (Redrawn after Sobotta.)

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 connexion with the so-called tongue.

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 amphibians, 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.

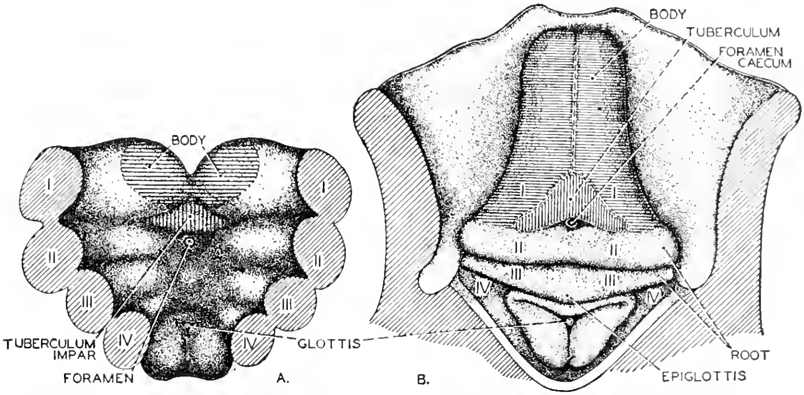


FIG. 212.—Two stages in the development of tongue and pharyngeal floor of man. The body of the tongue comes from paired and unpaired anlagen of the mandibular arch; the root from second and third visceral arches. That the fourth arch is involved is doubtful. (After Kallius.)

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 amphibians, 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. 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 hypertrophy of adenoid tissue, especially that of the soft palate in childhood, interferes with breathing and often requires surgical treatment. The **soft palate** is a muscular partition separating digestive and respiratory portions of the pharynx. From its posterior border hangs the **uvula.** (Fig. 213)

Seven cavities open into the pharynx—the mouth, the two nasal passages, the two Eustachian tubes, the larynx, and the esophagus.

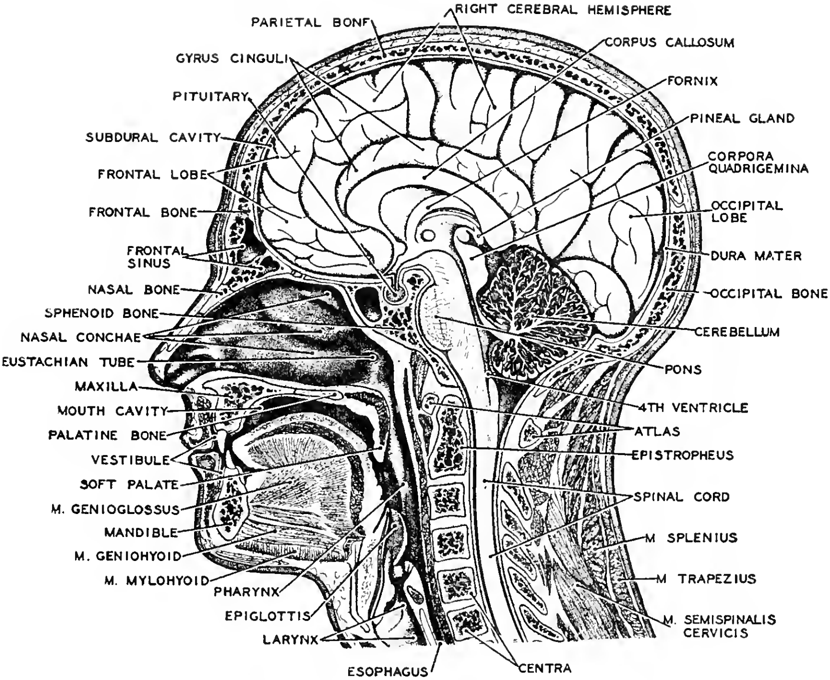


Fig. 213.—A median longitudinal section of the human head showing the relations between digestive and respiratory passages in the pharyngeal region. (Redrawn after Braus.)

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.

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 backbone 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. (Fig. 214)

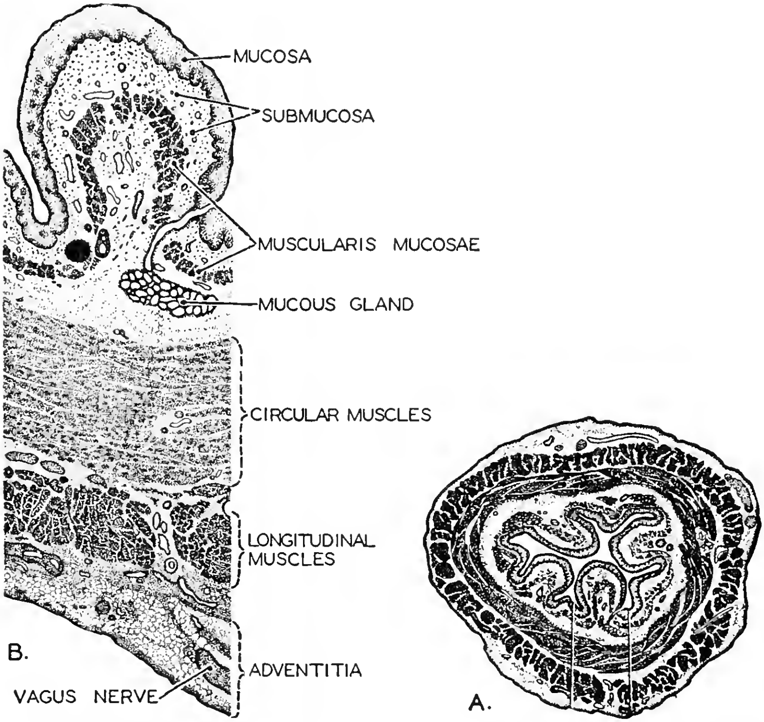


Fig. 214.—The esophagus as seen in cross section. *A* is a section of the entire esophagus. *B* is a small portion much enlarged. The layers of tissue characteristic of the entire alimentary canal are found in the esophagus. (Redrawn after Braus.)

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.

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 amphibians, 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 region is the **pyloric portion.** 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. The wall of the stomach contains the same four layers of tissue as are seen in the esophagus, plus an external serous layer.

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 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

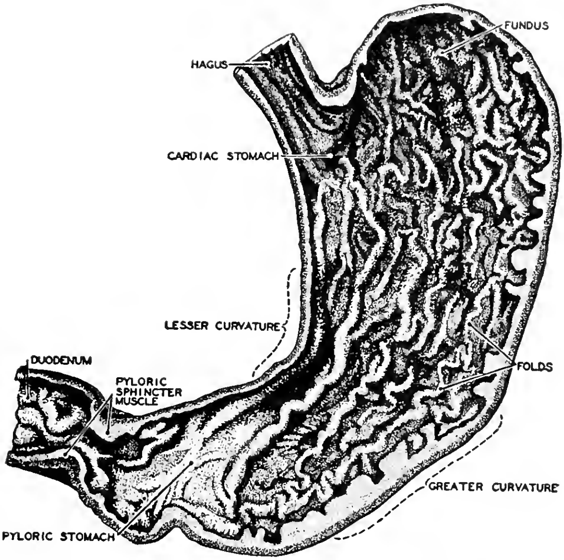


FIG. 215.—The right half of the human stomach, viewed from within. (Redrawn from Braus, after Elze.)

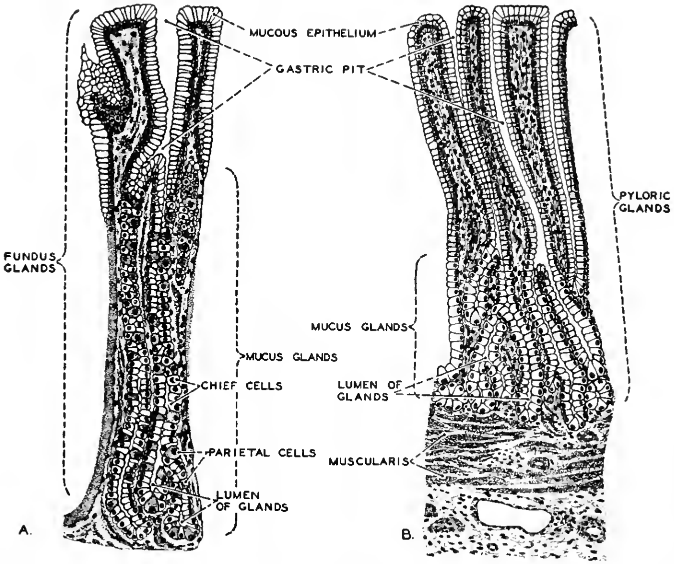


FIG. 216.—Cross sections of the wall of the human stomach, showing *A*, the structure of the gastric (fundus) glands, and *B*, that of the pyloric glands. While the secretions of gastric glands are chiefly digestive (gastric juice), the pyloric glands secrete mucus chiefly. (Redrawn after Braus.)

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. 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.

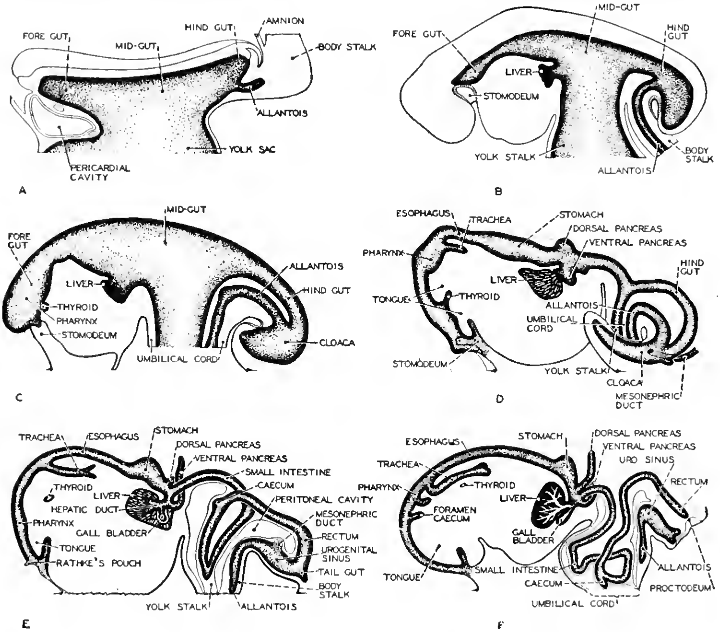


FIG. 217.—Stages *A–F* in the ontogenesis of the alimentary canal and associated structures in the human embryo. *A*, early embryo; *B*, three-weeks embryo; *C*, three to four weeks embryo; *D*, four weeks embryo; *E*, five weeks embryo; *F*, seven weeks embryo. Notable among the changes represented are the great elongation of the canal, the outgrowth of numerous appendages, and in the cloacal region the separation of the organs of excretion and digestion. (Redrawn after Thompson, Ingalls, F. T. Lewis and Arey.)

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 more rapid growth of the dorsal wall produces the **greater curvature** of the stomach. The **lesser curvature** develops from the ventral side. 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.

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 phylogenesis. detailed description is omitted.

THE INTESTINE

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.

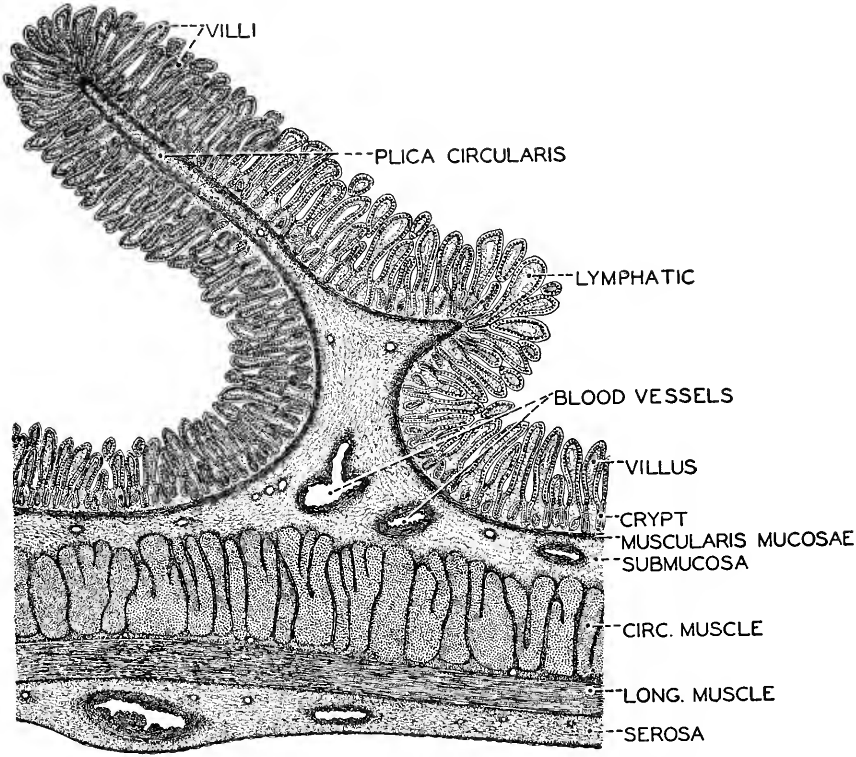


FIG. 218.—A longitudinal section of the human jejunum, showing in cross section one of the circular plicae (valvulae conniventes). ×15.

The **jejunum,** which forms two-fifths of the remainder of the small intestine, contains numerous transverse crescentic folds, the **plicae** or **valvulae conniventes,** covered with large villi. See Fig. 218. These plicae 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.

The four layers of tissue characteristic of the alimentary canal are present in the small intestine. 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 **Lieberkühn.** 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. (Figs. 218–219)

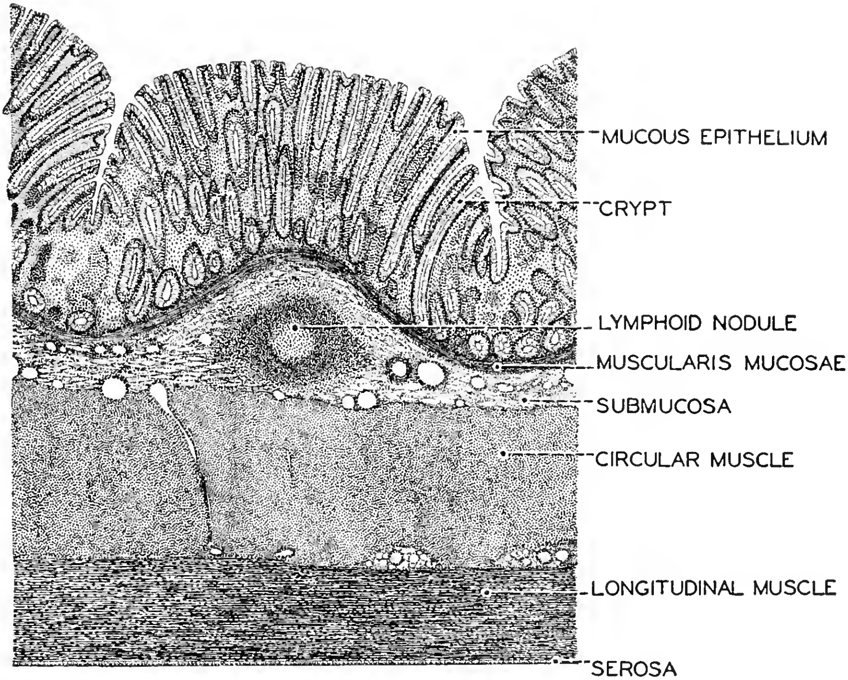


FIG. 219.—A longitudinal section of the human colon. ×15.

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.

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.**

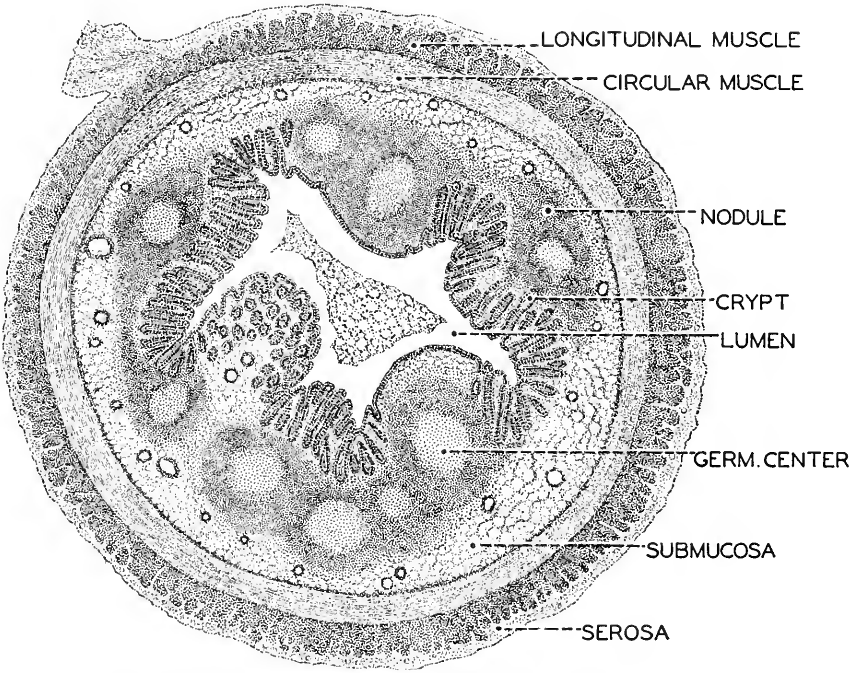


FIG. 220.—A cross section of the human vermiform appendix. ×15.

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 Lieberkühn'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 to form the transverse colon. Reaching the lower end of the spleen on the left side, it curves sharply downward, to become the descending colon. Passing down the left side to a point below the kidney, the descending colon bends toward 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. (Fig. 221) 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** (Fig. 72). 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** (Fig. 72*D*).

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. 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. (Fig. 217) The four layers of the intestinal wall develop as has been described for the stomach.

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. Vertebrate morphologists generally regard the anus of vertebrates as homologous throughout the group notwithstanding 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. 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 intestinal differentiation. The intestine of elasmobranchs contains a more elaborate spiral valve. Intestinal elongation has its inception in the sigmoid flexure of elasmobranchs. Increase of intestinal surface is effected in elasmobranchs and ganoids mainly by the development of a spiral valve. A finger-like rectal gland makes its appearance in elasmobranchs near the anus. 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 amphibians except Gymnophiona differentiate 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. (Fig. 221) The dorsal mesentery persists throughout life, but the greater part of the ventral mesentery disappears in ontogenesis. Only the anterior portion which connects stomach, liver and ventral body-wall

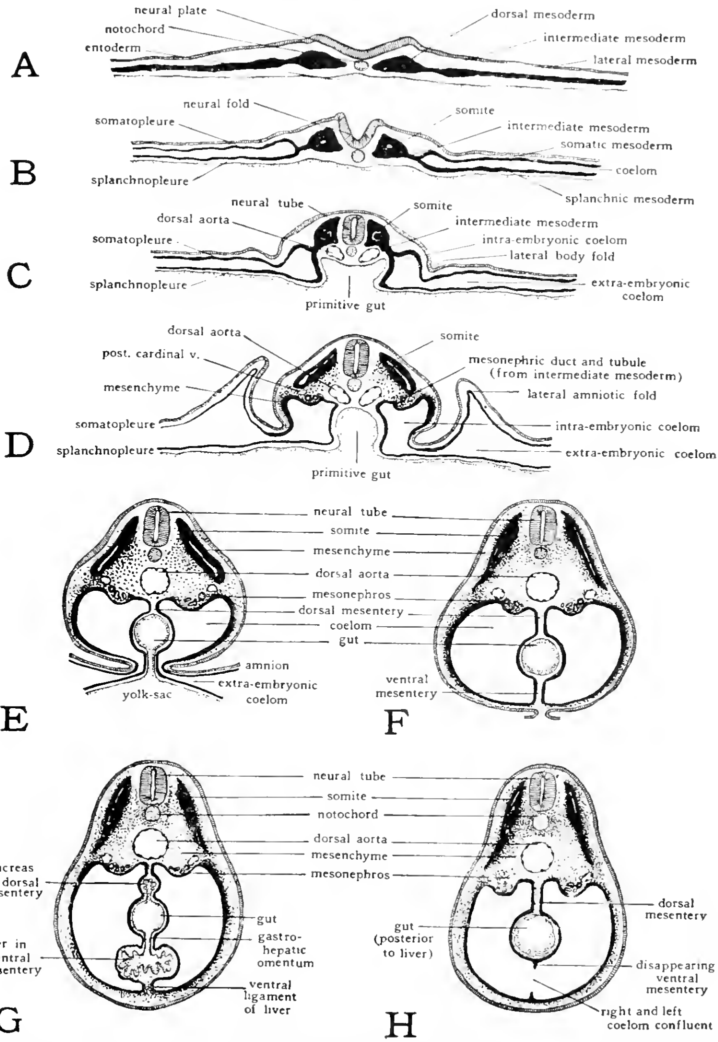


FIG. 221.—Schematic diagrams of cross sections at various stages to show the establishment of the coelom and mesenteries. (From Patten's "Embryology of the Chick.")

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.

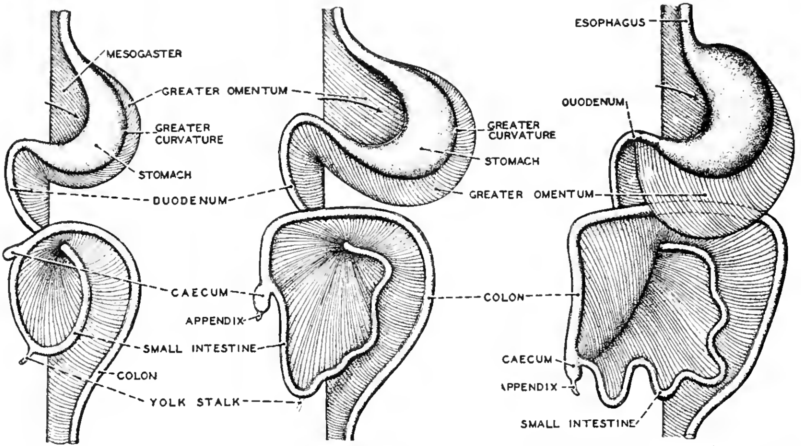


FIG. 222.—Diagrams illustrating the development of the mesenteries and omentum in the human embryo. An arrow marks the opening (foramen of Winslow) of the greater omentum. (Redrawn after Hertwig.)

As the sacculation 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.

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. The gall bladder lies below the right lobe near the duodenum. The postcaval vein passes through the right lobe.

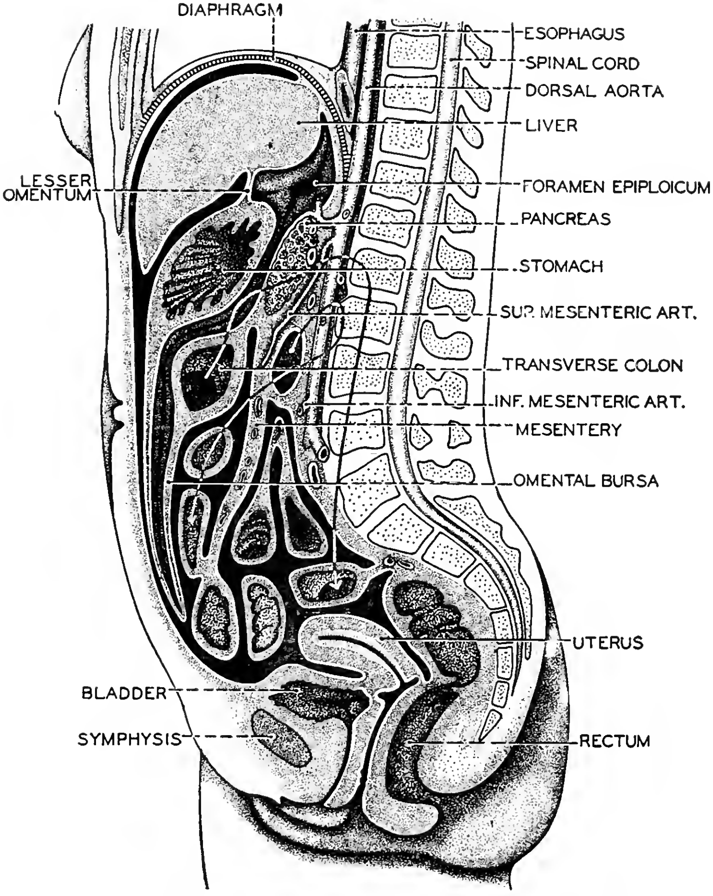


FIG. 223.—A median section of the abdominal cavity, showing the relations of the omental bursa. The diaphragm is cross-hatched. The course of the duodenum-jejunum and of the colon is shown by means of arrows. (Redrawn after Braus.)

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.** (Fig. 225) 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 examination of the diagram (Fig. 226). While branches of the vagus nerve reach the liver, most of its nerves belong to the sympathetic system.

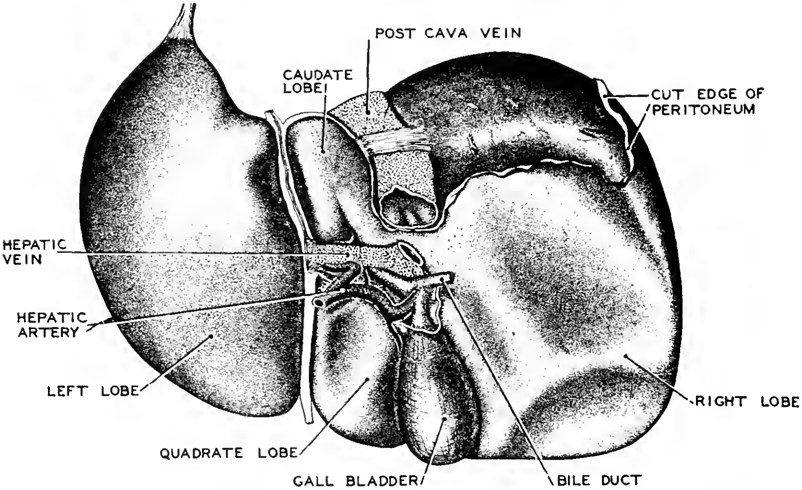


Fig. 224.—The human liver viewed from below. (Redrawn after Sobotta.)

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.

Development of the Liver. The anlage of the liver appears in a 2.5 mm. human embryo as a ventral outpocketing of the fore-gut near the anterior intestinal portal, between the two vitelline veins. See Fig. 217.

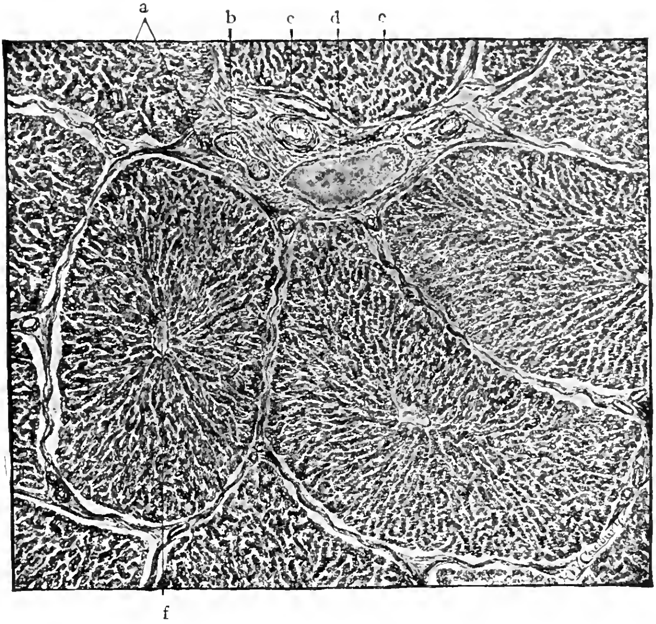


FIG. 225.—Liver of a pig. The lobules have artificially shrunken from the interlobular tissue, *a*; *b*, bile duct; *c*, hepatic artery; *d*, interlobular vein (a branch of the portal); *e*, trabeculae; *f*, central vein. Highly magnified. (From Bremer's "Text Book of Histology," after Radasch.)

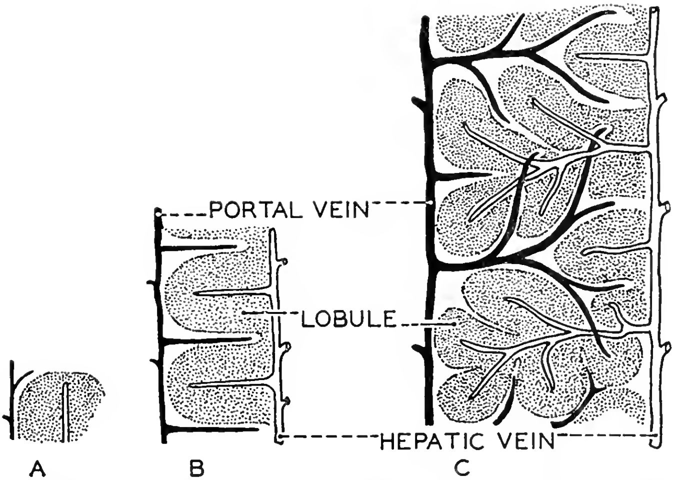


FIG. 226.—*A*, *B*, and *C*—diagrams of successive stages in the development of the lobules of the liver. The subdivision of the liver anlage into lobules is correlated with branching of the portal and hepatic veins. The branches of the hepatic vein are intralobular, and those of the hepatic portal vein—shown in black—are interlobular. (Redrawn after Mall.)

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 cords surrounded by branches of the vitelline veins, and a posterior hollow sac which later becomes the gall bladder. The multiplication of the cords, correlated with that of the blood capillaries associated with them, produces the lobules. Mesenchyme cells form the interlobular connective tissue. Bile capillaries appear within the cell cords, which thus become hepatic tubules, 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. 217, 221, 226)

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. Meanwhile it acquires its two chief lobes. The ventral mesentery into which it originally grew forms the falciform ligament. (Fig. 221)

History of the Liver. The vertebrate liver has no homolog among invertebrates, though many of these have organs which are called livers. 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. It 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.

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. 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 **amylopsin** 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 hormone **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.**

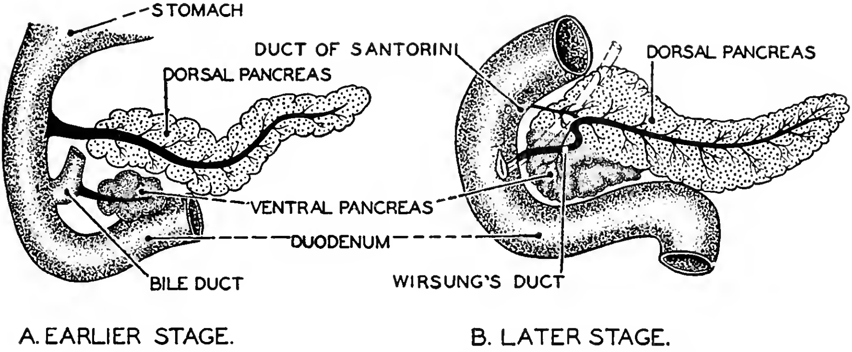


FIG. 227.—*A* and *B*, two stages in the development of the pancreas. The duct of the dorsal pancreas, Santorini's duct, may degenerate in ontogenesis. The two gland anlagen unite into a single organ in the adult. (Redrawn after Broman.)

Scattered irregularly among the acini of the pancreas are clusters of lightly-staining cells. The area of each cluster in section is considerably greater than that of a single acinus. These are the **islands of Langerhans,** endocrinal organs which secrete **insulin.** (Fig. 289)

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. They 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.

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. Other 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. The 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, intake of oxygen 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 amphibians. 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 amphibians, 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 higher vertebrates 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 the 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 amphibians 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.

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 the 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. 228)

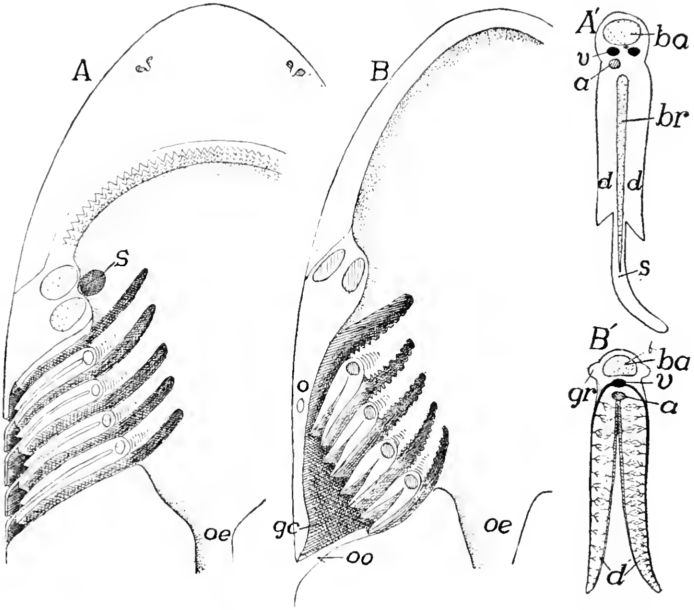


FIG. 228.—Diagram of gill clefts in (*A*) elasmobranchs and (*B*) teleosts. *A′* and *B′*, a single gill of each. *a*, artery; *ba*, branchial arch; *br*, branchial ray; *d*, demibranchs; *gc*, atrial chamber; *gr*, gill raker; *o*, operculum; *oe*, esophagus; *oo*, opercular opening; *s*, spiracle, in *A′*, septum; *v*, veins. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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.

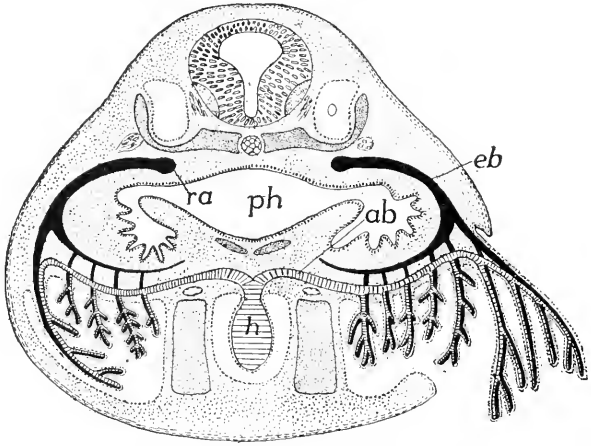


Fig. 229.—Diagram of the relations of external and internal gills in the anuran tadpole. *ab*, *eb*, afferent and efferent branchial arteries; *h*, heart; *o*, ear cavity; *ph*, pharynx; *ra*, radix aortae. (From Kingsley's "Comparative Anatomy of Vertebrates," after Maurer.)

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 gill system, developed in adaptation to special conditions. They have no genetic relation to any human structure.

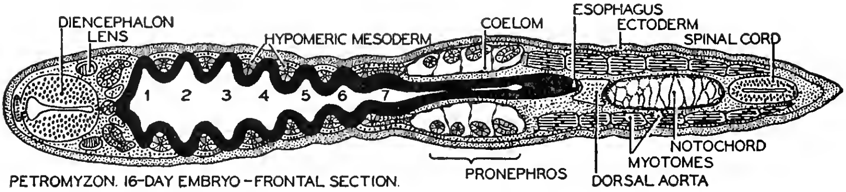


Fig. 230.—Frontal (horizontal) section of a 16-day Petromyzon embryo, showing seven pairs of gill pouches (1–7) formed as lateral diverticula of the pharynx. Slight invaginations of the ectoderm to meet the gill pouches are seen. By the rupture of the double (ectoderm-endoderm) membrane each gill pouch is converted into a gill cleft. 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.

Development of Gills. Gill-slits develop from a series of paired endodermic diverticula of the pharynx which meet corresponding invaginations of the ectoderm. (Fig. 230) 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 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.

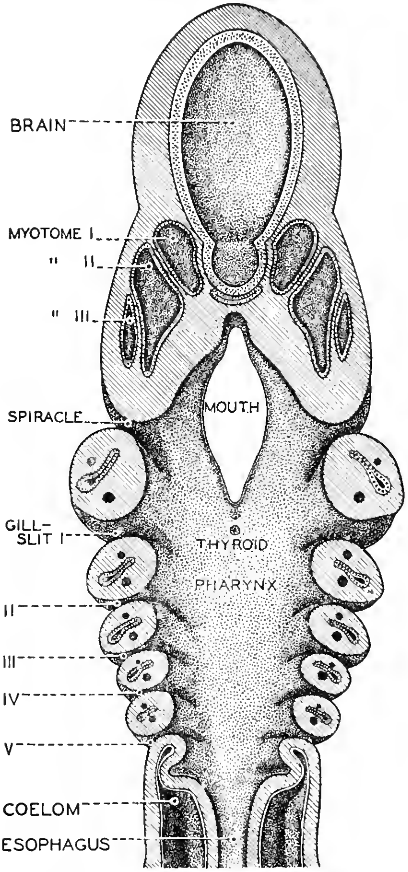


FIG. 231.—The pharyngeal region of a young Squalus embryo, showing the visceral arches and clefts.

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.

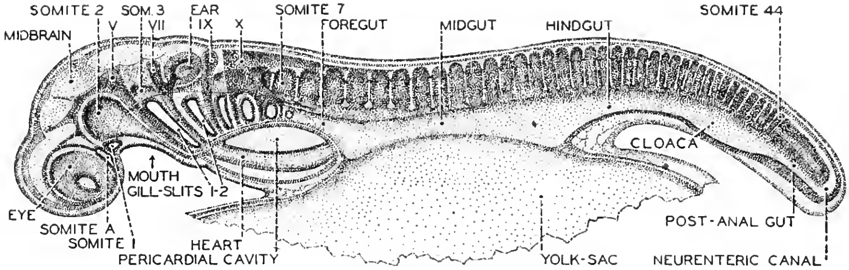
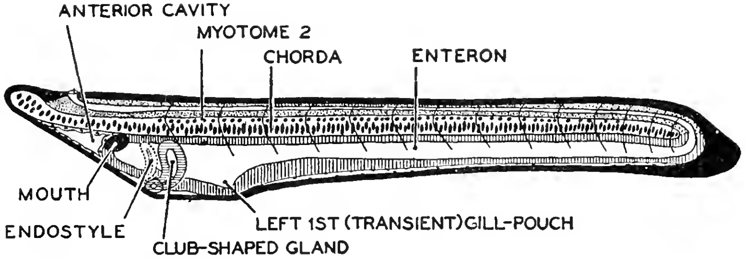
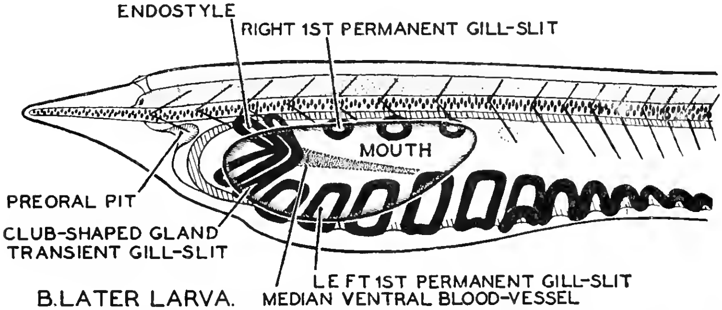


FIG. 232.—A 7 mm. Squalus embryo viewed as a cleared specimen from the left side. The yolk-sac has been mostly removed. Two gill-slits are open. Cranial nerve anlagen are indicated by Roman numerals.



A. EARLIER LARVA.



B. LATER LARVA.

FIG. 233.—*A*, young Amphioxus larva viewed from the left side as a translucent object. (Redrawn after Hatschek.) *B*, later larva. (Redrawn after van Wijhe.) The mouth of Amphioxus becomes enormously enlarged and, by its growth backward on the left side, interferes with the symmetry of development of the gill-slits. The gill-slits of the left side of the body develop before those of the right side. The median line of the ventral side of the pharynx is indicated by the median ventral blood-vessel. Modification of function and degeneration affect the anterior three pairs of gill-slits. The first pair become the endostyle. The second pair form the transient larval club-shaped gland. The left third slit has no mate and soon disappears. The fourth pair of slits form the first permanent pair.

Amphioxus, the typical genus of cephalochordates, has as many as one hundred and eighty paired openings or stigmata. As in hemichordates, the original number is doubled by formation 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 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. (Fig. 233) 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. 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.

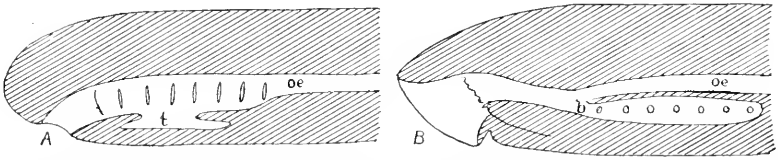


Fig. 234.—Diagram of relations of esophagus and respiratory tracts in (*A*) Myxine and Ammocoetes, and (*B*) Petromyzon; *b*, branchial duct ("bronchus"); *oe*, esophagus; *t*, thyroid gland. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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.

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.

Among elasmobranchs, Heptanchus has seven pairs of gill-slits in addition to the spiracles, which are evidently modified gill-slits since they bear rudimentary hemibranchs. Hexanchus and Pliotrema 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 amphibians, but are present in some aquatic urodeles. The number however is reduced. Some adult urodeles have three pairs of gill-slits, some two, and some only one. In the newts they disappear entirely. Cutaneous respiration is common 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 pharyngeal 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 in the human embryo receives its most 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 endocrinal glands, **thyroid, parathyroid, thymus,** and the **ultimobranchial bodies.** In addition to these which occur in man, some vertebrates have also **epithelial bodies** and **suprapericardial 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 endocrinal organs.

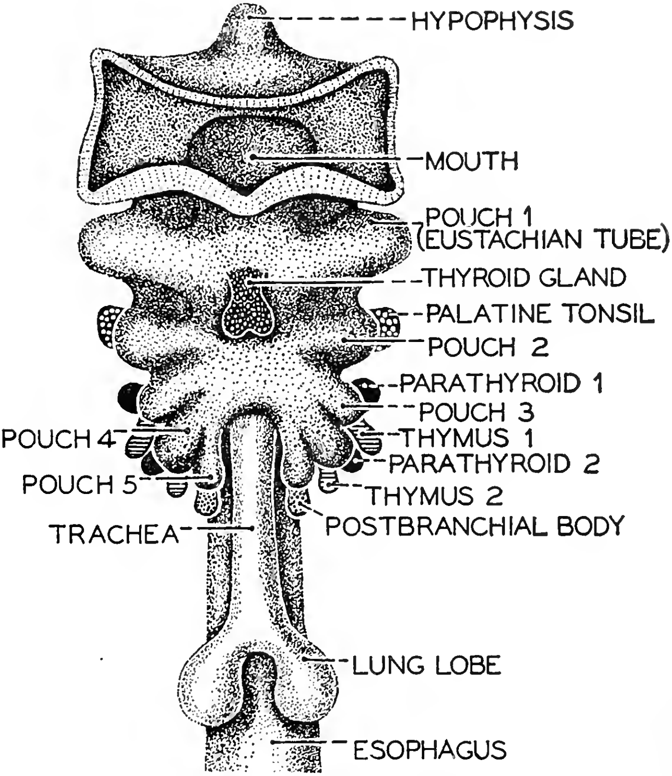


FIG. 235.—Ventral view of pharyngeal region of a human embryo showing the pharyngeal pouches and their glandular derivatives; semidiagrammatic.

B. The Pulmonary System. The respiratory system of man and mammals includes lungs, larynx, trachea, bronchial tubes, nasal 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 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 may become slaty grey in the adult as the result of the accumulation of soot.

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.

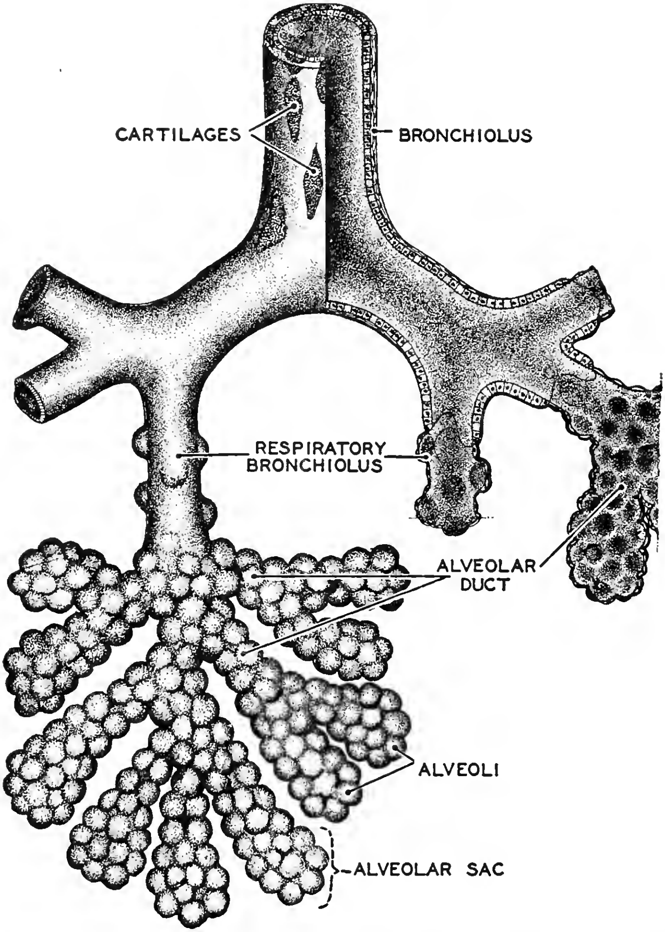


FIG. 236.—Diagram of a lung lobule showing the subdivision of a bronchiolus into alveolar ducts, sacs and alveoli. Respiratory epithelium may extend into the bronchioli. (Redrawn after Bremer.)

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 (Fig. 236). 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.

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 walls of the lobules of the lung, and 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 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 human trachea or wind-pipe 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

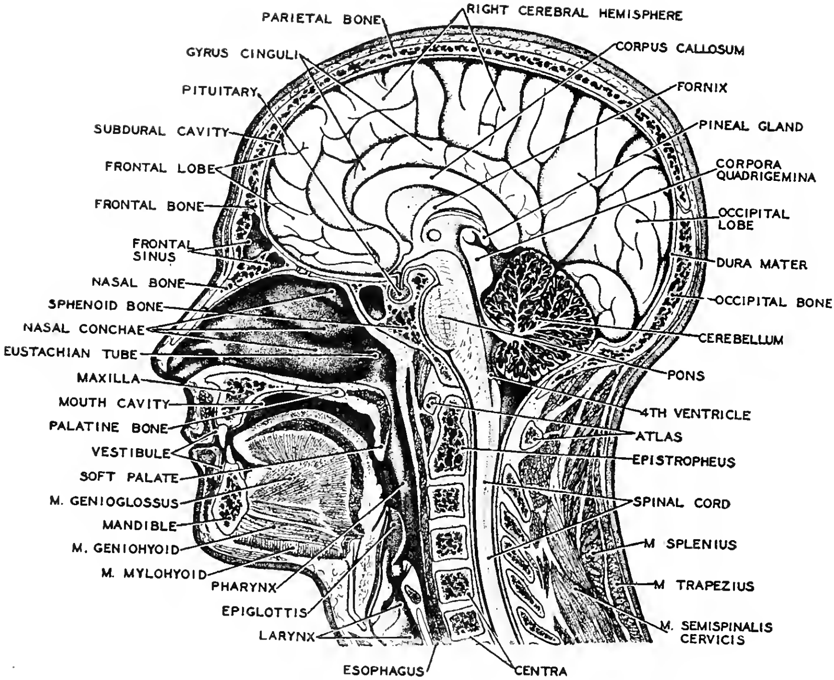


FIG. 237.—A median longitudinal section of the human head showing the relations between digestive and respiratory passages in the pharyngeal region. (Redrawn after Braus.)

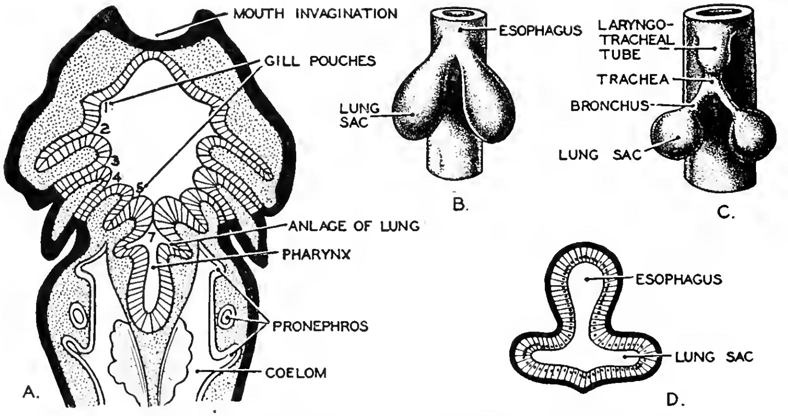


FIG. 238.—Stages in the development of lungs in vertebrates. *A* is a horizontal section of a salamander embryo showing the series of paired pouches which form the gill-slits; after Goette. The last pair of pharyngeal pouches are the anlagen of the lungs. Such evidence suggests that lungs may have arisen 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.)

ciliated stratified columnar epithelium. Below this is a submucous connective tissue containing many mucous glands derived from the 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.

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 pleuroperitoneal 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 amphibians 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 the human embryo 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 diverticulum swells to form the lung anlage while the less expanded anterior portion becomes the larynx and trachea (Fig. 235). The lung anlage later divides into two lateral buds which, by successive subdivision, gradually assume the adult structure. (Fig. 239)

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 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. 352).

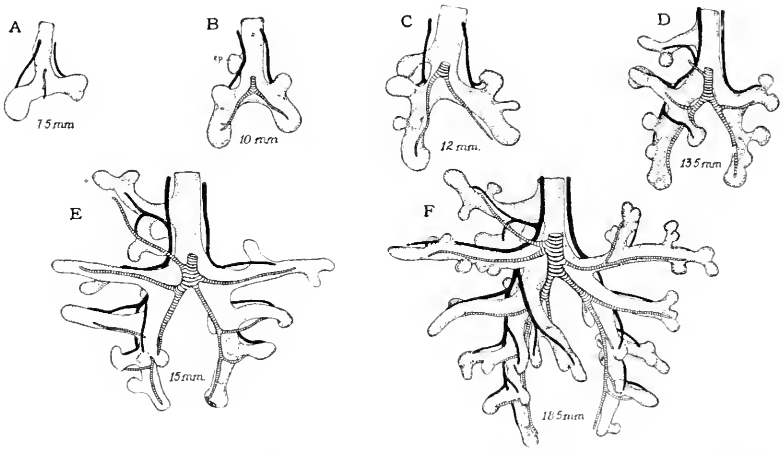


Fig. 239.—Stages in the development of the trachea, bronchi and lungs in the pig. The pulmonary arteries are shown in black; the veins are cross hatched. *Ep*, bud of eparterial bronchus. (From Patten's "Embryology of the Pig," after Flint.)

The development of the nasal passage in the human embryo is slightly different. In the month-old embryo a similar nasobuccal groove makes its appearance. The nasal 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. 353).

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. (Fig. 238) 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. Furthermore, 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.

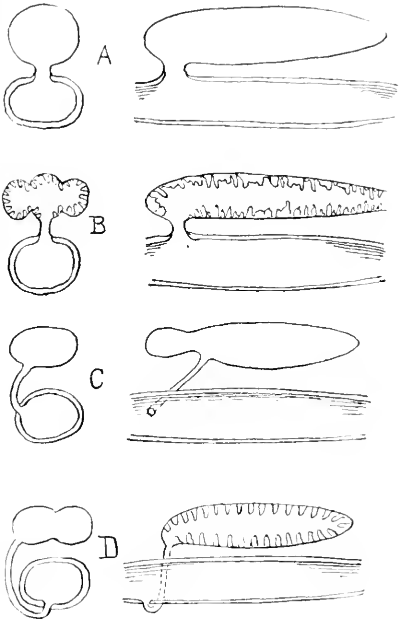


Fig. 240.—Diagrams of air bladder in fishes. *A*, Physostomous fishes; *B*, Lepidosteus and Amia; *C*, Erythrinus; *D*, Ceratodus. The air bladder of the crossopterygian fish, Polypterus, is, like the lungs of amphibians, bilobed and connected with the floor of the pharynx. (From Kingsley's "Comparative Anatomy of Vertebrates," after Dean.)

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.

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.

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. (Fig. 240) 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. 241.

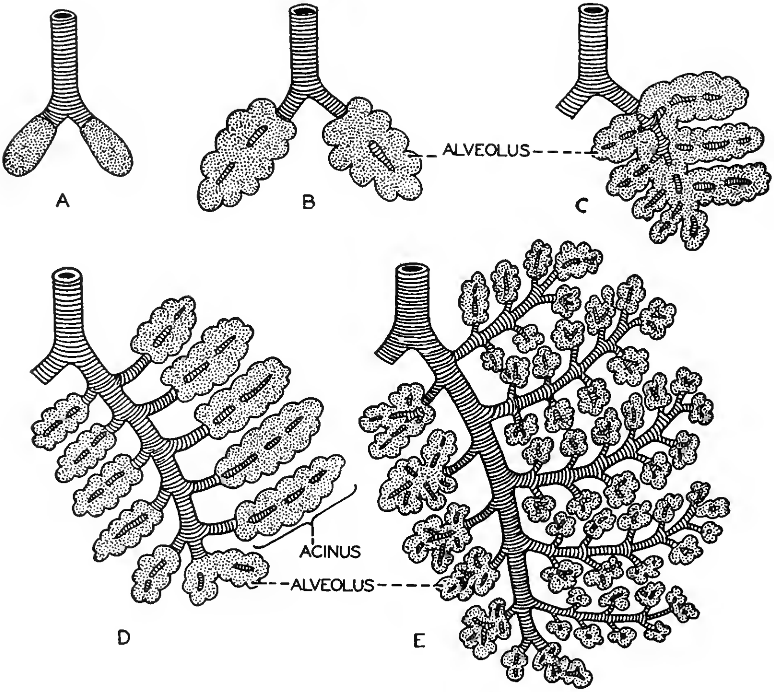


FIG. 241.—Diagrams of stages in the phylogenesis of the lungs. The respiratory surfaces are stippled, and conductory passages cross-hatched. Embryological stages corresponding with the comparative anatomical series shown in *A–E* occur in the ontogenesis of lungs in mammals. See Fig. 239. (Redrawn after Huntington.)

In birds a special modification of the lungs occurs. (Fig. 242) Air sacs grow from the bronchi into the abdominal cavity, the thorax, the neck, and even into some bones. Since they have very few blood-vessels in their walls, they function only slightly in gaseous exchange. They serve as a reservoir of non-vitiated air which is used when the vitiated air is forced

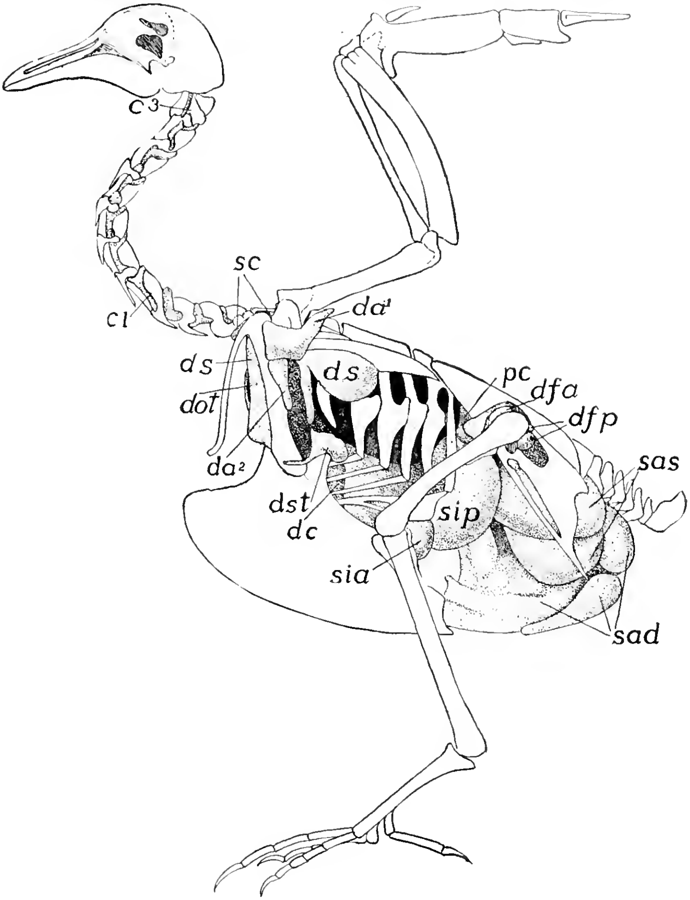


FIG. 242.—Air sacs and canals of pigeon. c^1–c^3, intertransverse canals; da^1–da^2, axillary sac and its ventral diverticulum; *dc*, canal for ribs; *dot*, infraclavicular canal; *ds*, subscapular sac; *dst*, sternal canal; *pc*, preacetabular canal; *sad*, *sas*, right and left abdominal sacs; *sc*, cervical sac; *sia*, *sip*, anterior and posterior intermediate sacs. (From Kingsley's "Comparative Anatomy of Vertebrates," after Bruno Muller.)

from the lungs. Thus there is a double tide of fresh air through the lungs. Wetmore suggests that they assist in the regulation of body temperature, which is higher in birds than in mammals.

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 to the heart, and microscopic **capillaries** connecting 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 to the veins by way of special vessels, the **lymphatics** which, like veins, permit flow in only one direction.

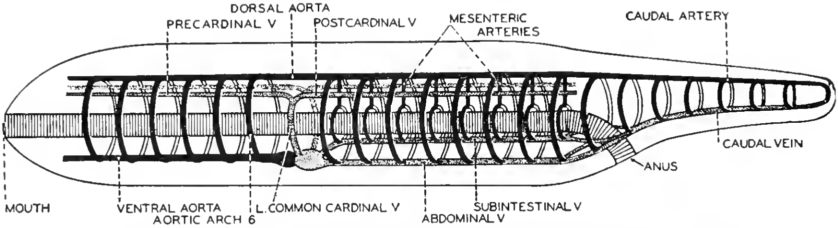


FIG. 243.—Diagram of the primitive chordate circulation. The arteries are shown in black, the veins are stippled. The similarity of this circulatory system to that of annelids has suggested to morphologists a common genetic origin. (After Kingsley, modified.)

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 may pass to the heart by a vein, while the liquid injected into a vein will not enter the heart from 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, therefore, may be regarded as a tissue composed of cells (corpuscles) and 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 hormones 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 contains also 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.

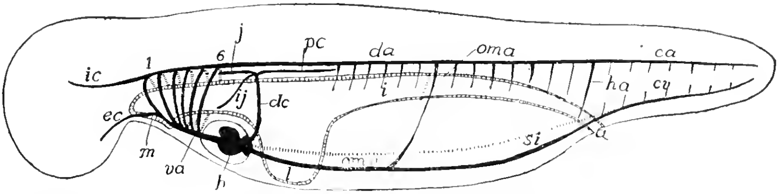


FIG. 244.—Diagram of the circulation in an early stage of a small-yolked vertebrate (amphibian). *a*, anus; *ca*, *cv*, caudal artery and vein; *da*, dorsal aorta; *dc*, Cuvierian duct; *ec*, external carotid; *h*, heart; *ha*, hypogastric artery; *i*, intestine; *ic*, internal carotid; *ij*, inferior jugular; *j*, superior jugular; *l*, liver; *m*, mouth; *oma*, *omv*, omphalomesenteric artery and vein; *pc*, postcardinal vein; *si*, subintestinal vein; 1–6, aortic arches. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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 metazoans, 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 in 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. Nemerteans 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 pseudocoelom provides an adequate mechanism of circulation in these 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. In spite of the necessity of inverting the worm, proponents of the annelid hypothesis of vertebrate ancestry have stressed the similarity of the vascular systems of the groups as 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. 243 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.

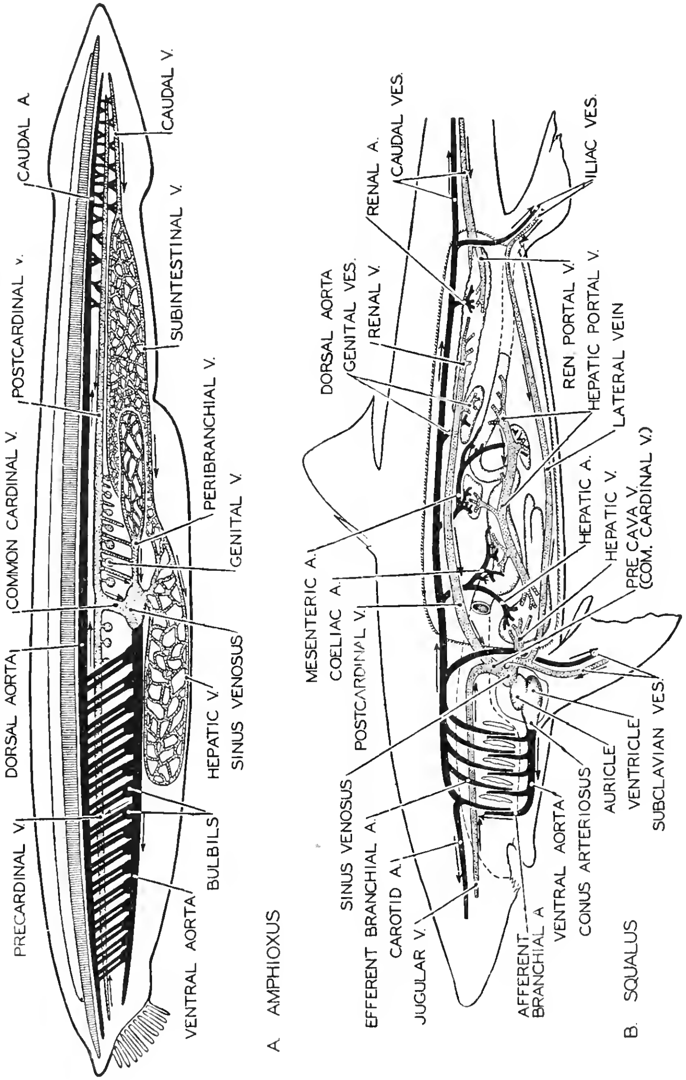


FIG. 245.—Diagrams of the circulatory system of Amphioxus, Squalus, Necturus, and Felis. Arteries black, veins stippled. The vessels are shown as if projected upon the median plane. Arrows indicate the direction of flow of blood. *A–D* are believed to represent an evolutionary series. In the mammal three aortic arches persist, viz., carotid (3), aorta (4), and pulmonary (6 in part). (Redrawn after Wierstratz, Woodruff, and Kingsley. Felis original.)

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

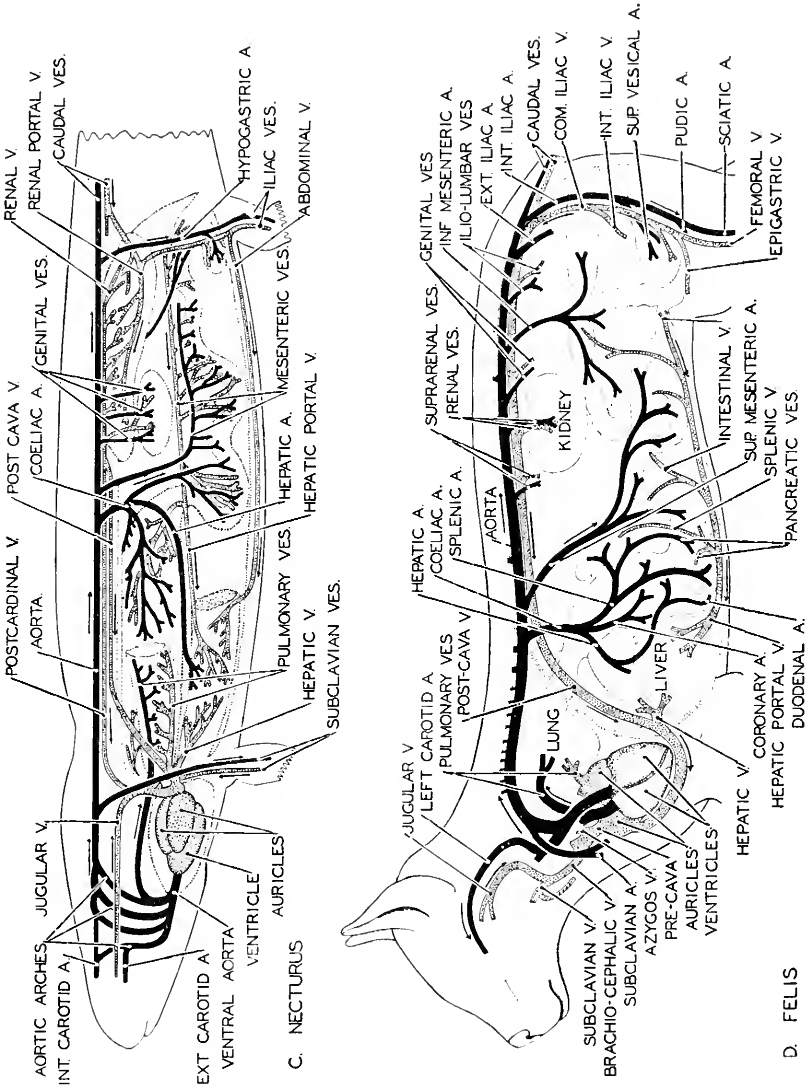


FIG. 245.—For descriptive legend see page 266.

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. These veins 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. 245, *A*)

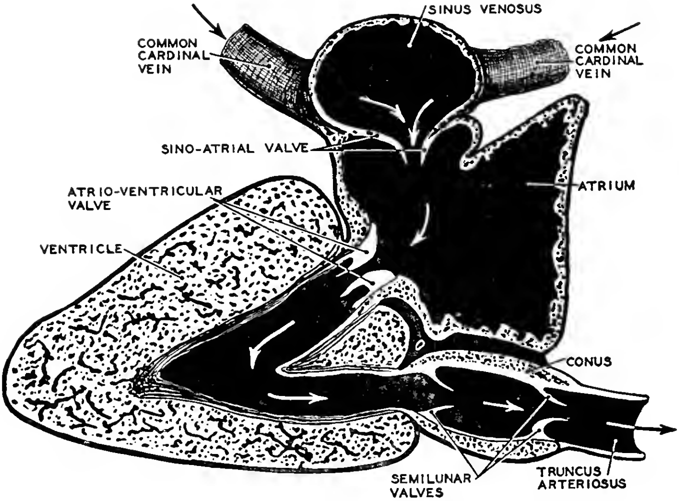


Fig. 246.—A diagram of the primitive (fish) heart, as seen in a median longitudinal section. Anterior is to the right. The course of blood in the heart—indicated by arrows—takes the form of a letter S. (Redrawn after Keith.)

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 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 each iliac vein drains into a lateral abdominal vein. The latter is believed to have been developed from the median ventral abdominal vein of the primitive chordates. Internal jugular veins paralleling 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 into 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. 245, *B*)

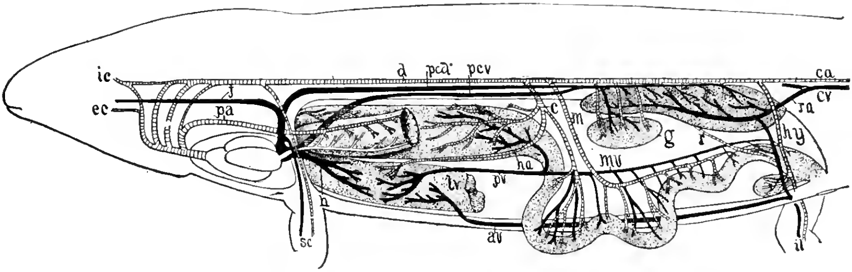


FIG. 247.—Diagram of vertebrate circulation based on a urodele. Arteries cross-lined; veins black except the pulmonary vein, white. *av*, abdominal vein; *c*, celiac artery; *ca*, *cv*, caudal artery and vein; *d*, dorsal aorta; *ec*, external carotid; *g*, gonad; *h*, hepatic vein; *ha*, hepatic artery; *hy*, hypogastric artery; *ic*, internal carotid; *il*, iliac artery and vein; *j*, jugular; *lv*, liver; *m*, *mv*, mesenteric artery and vein; *pa*, pulmonary artery; *pcd*, 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.")

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.

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, pulmonary arteries and veins, and 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 amphibians while in others only the third and fourth arches persist. One of the most important changes in circulation which occur within the group is the abandonment by the higher amphibians of the capillary branchial network characteristic of fishes. In the perennibranch amphibians 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 aortae 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 amphibians. Impure blood from the hindlegs may thus return to the heart either through the mesonephroi, or by the abdominal vein. The median ventral abdominal vein, which made its first appearance in Dipnoi, takes the place of the lateral abdominal veins of elasmobranchs. The increased flexure of the heart brings the atria anterior as well as dorsal to the ventricle. (Fig. 246)

Reptiles. The reptilian vascular system strikingly resembles that of amphibians. 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 in 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 the 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 Panizzae** 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 amphibians, may return to the heart either by the renal portal veins or by the abdominal vein.

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 **sinu-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

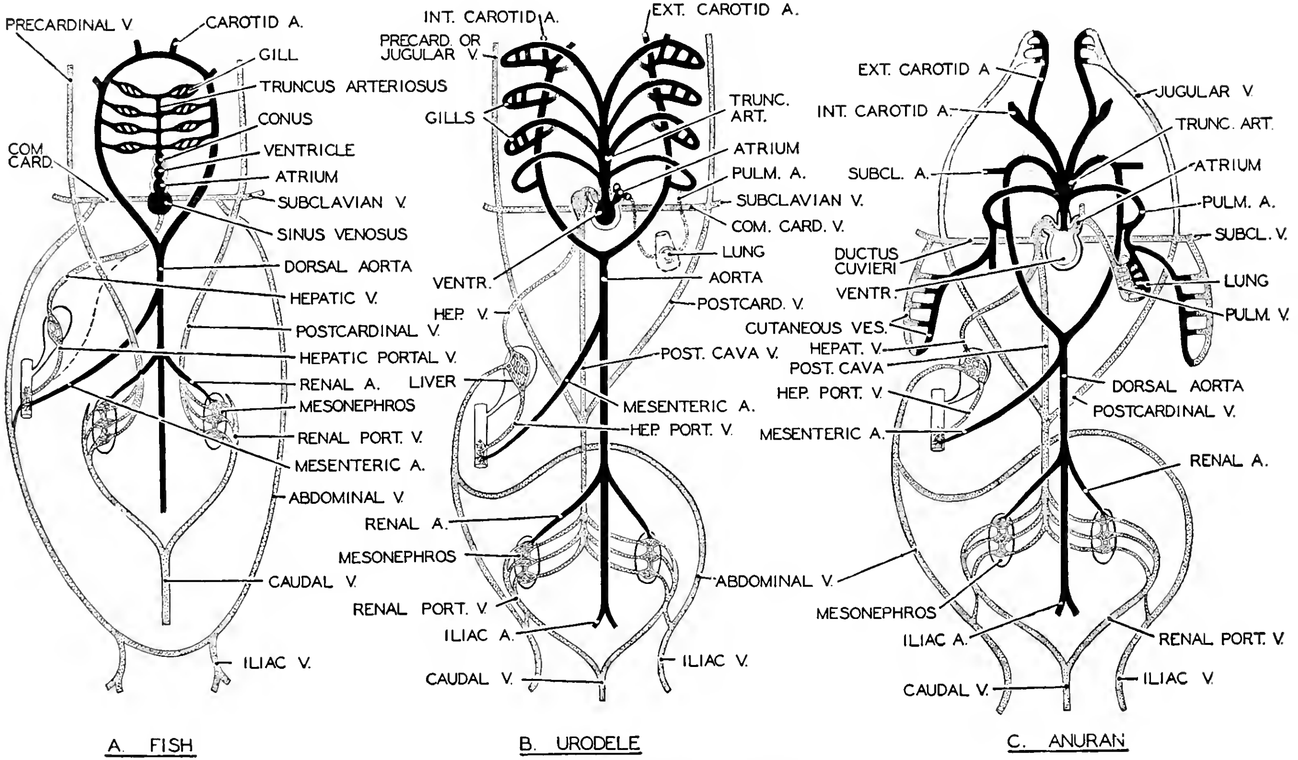


FIG. 248.—For descriptive legend see page 273.

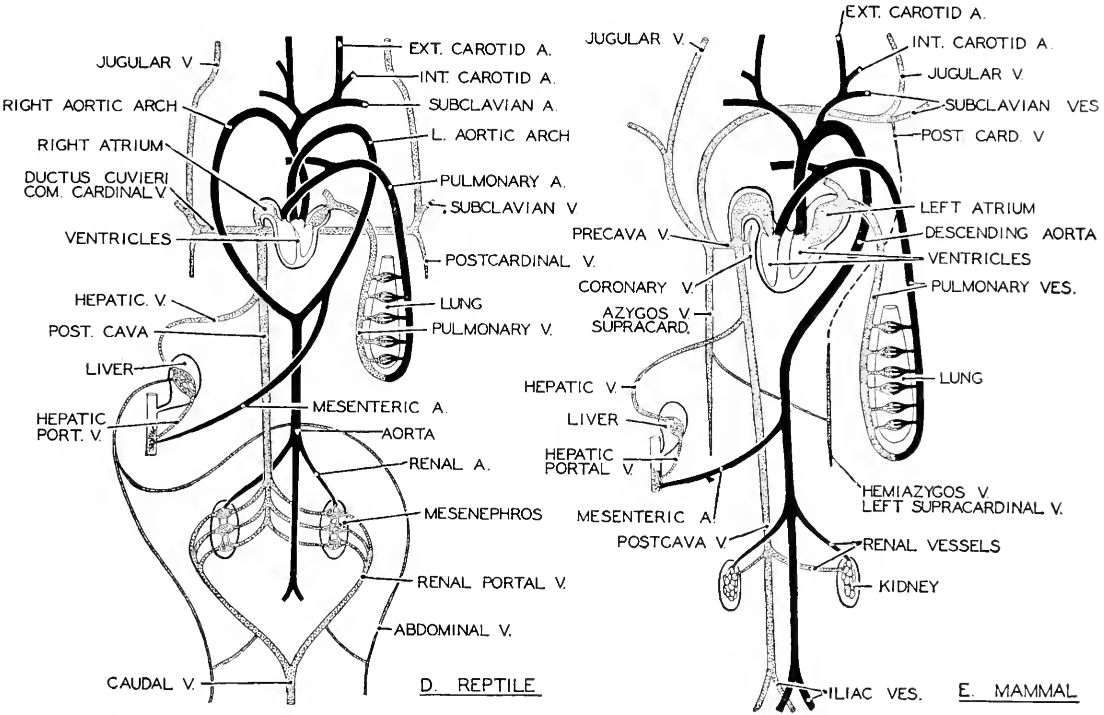


FIG. 248.—Diagrams of the circulatory system in fish, urodele, anuran, reptile, and mammal. Arteries black, veins stippled. In general features the series is believed to represent stages in the phylogenesis of the mammalian circulatory system. It will be noted that some blood-vessels persist throughout the entire series. (Redrawn after Stempell.)

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 their transverse anastomosis in the lumbar region.

The postcava of mammals appears to be only in part homologous with that of lower vertebrates. 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 amphibians to man. According to McClure subcardinal veins are present in all vertebrates.

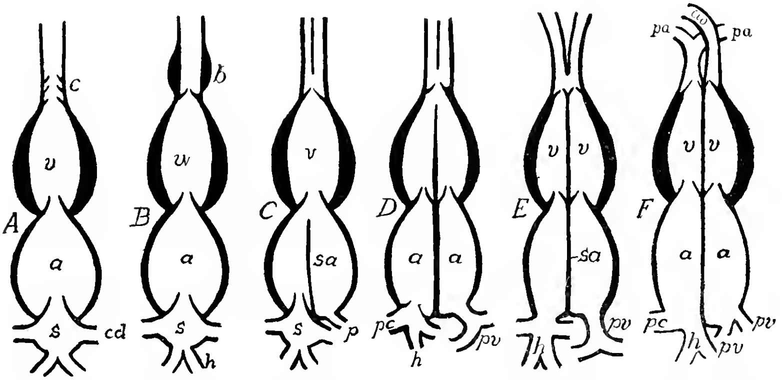


FIG. 249.—Different stages in the differentiation of the parts of the heart, ventral view. *A*, elasmobranch; *B*, teleosts; *C*, amphibia; *D*, lower reptiles; *E*, alligator; *F*, birds and mammals. *a*, atrium; *ao*, aorta; *b*, bulbus arteriosus; *c*, conus; *cd*, Cuvierian duct; *h*, hepatic veins; *pa*, pulmonary artery; *pc*, pre- and postcaval veins; *pv*, pulmonary vein; *s*, sinus venosus; *sa*, septum atriorum; *v*, ventricles. (From Kingsley's "Comparative Anatomy of Vertebrates.")

The origin of the azygos and hemiazygos veins is also in doubt. Most textbooks describe 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 inter-subcardinal 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, while the atrium became divided by an incomplete septum into right and left atria, 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, six pairs are usually the maximum 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 aortic arches are reduced. 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 three aortic arches persist in the adult, the 3rd, 4th, and 6th as in reptiles. The systemic arch of the

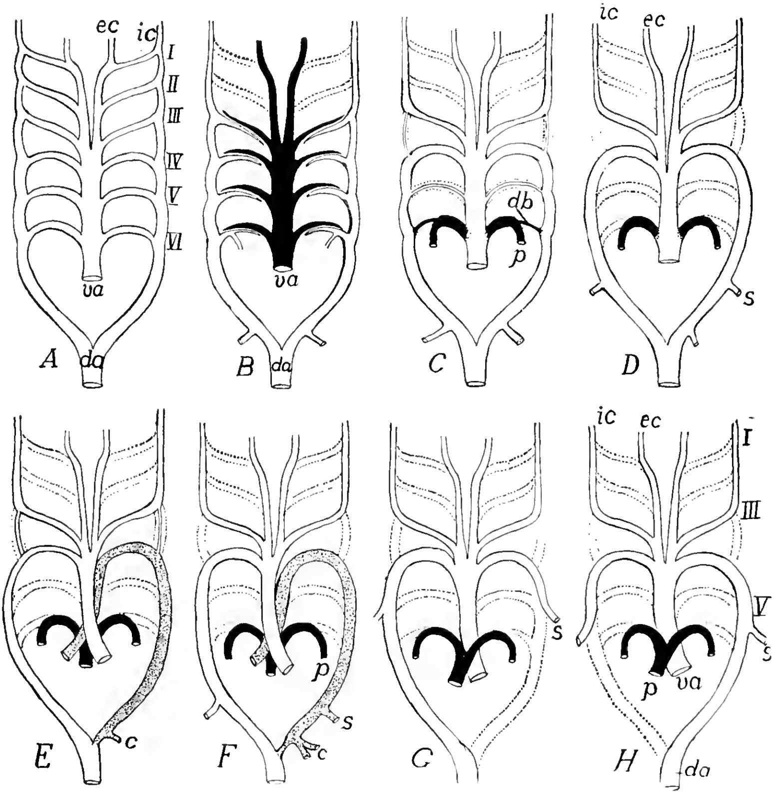


FIG. 250.—Modifications of the aortic arches in different vertebrates. *A*, primitive scheme; *B*, dipnoan; *C*, urodele; *D*, frog; *E*, snake; *F*, lizard; *G*, bird; *H*, mammal. *c*, celiac artery; *da*, dorsal aorta; *db*, ductus Botalli; *ec*, *ic*, external and internal carotids; *p*, pulmonary artery; *s*, subclavian; *va*, ventral aorta. Vessels carrying venous blood, black; those with mixed blood, shaded; those which disappear, dotted outlines. (From Kingsley's "Comparative Anatomy of Vertebrates," after Boas.)

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. 250)

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 (Fig. 248). The appearance of the subclavians and iliacs is correlated with that of the paired fins, but once invented these vessels persist in man to supply 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 sixth aortic arch with lungs persists throughout the vertebrate series. With the substitution of a metanephros for the mesonephros 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.

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 differentiated 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 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.

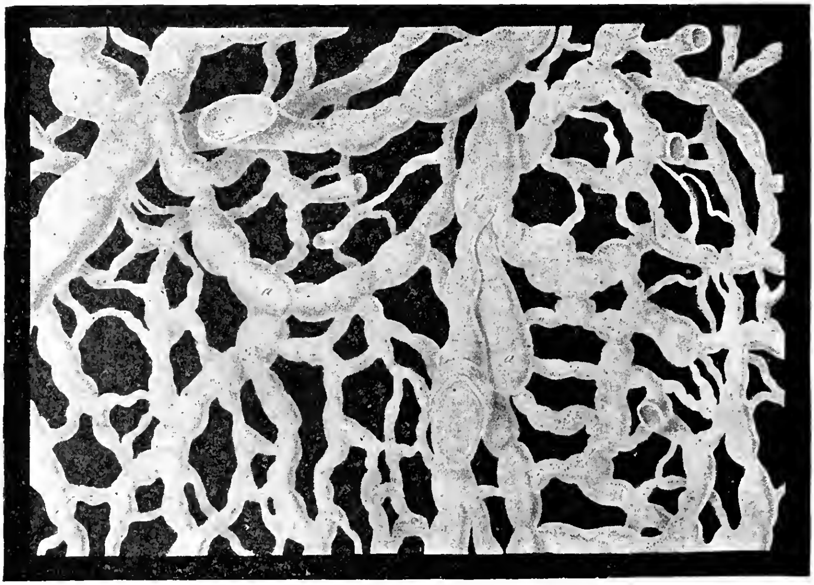


Fig. 251.—The lymphatics of the scrotum. Showing the transition of the capillaries to the vessels with valves (*a*, *a*, *a*). (From Morris, after Teichmann.)

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 are comparable to 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 also are 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 the right duct is rudimentary, having a length of only a few centimeters. One lymphatic sinus, the **cisterna** or **receptaculum 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.

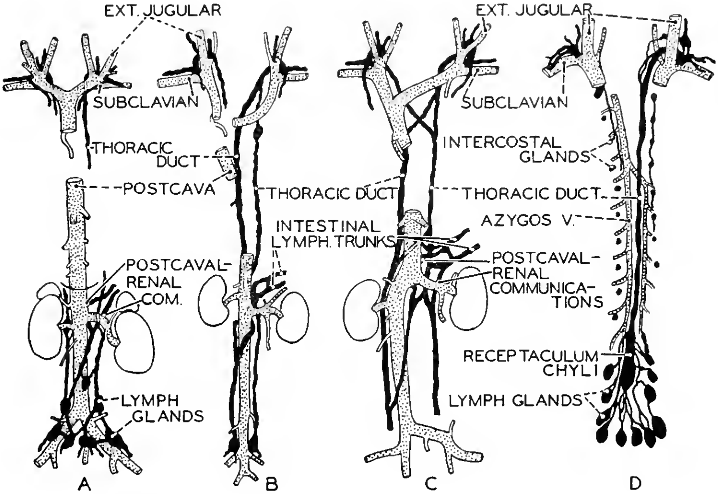


Fig. 252.—Diagrams illustrating the chief lymphatic trunks and their relations to the veins in mammals and man. *A*, South American monkeys; *B*, mammals (Lepus) in which postcaval-renal communications are wanting; *C*, mammals in general; *D*, man. In all mammals lymph enters the veins at the point 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.

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 Fig. 253.

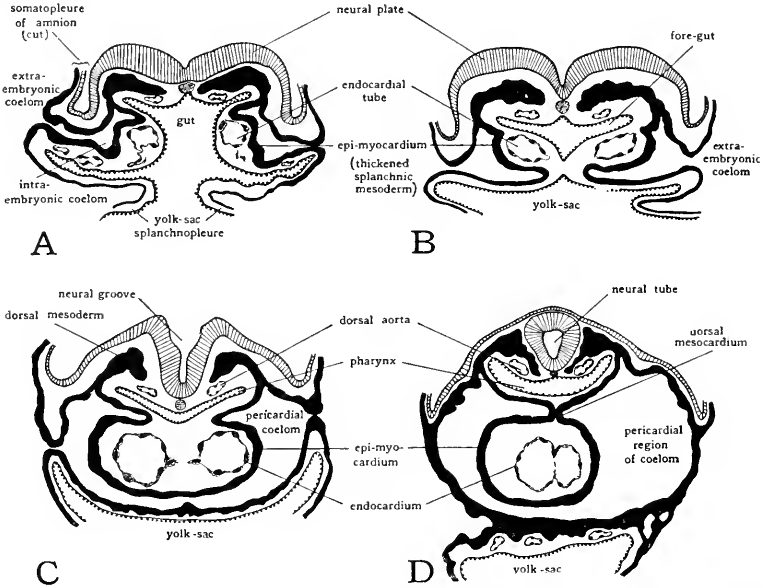


FIG. 253.—Sections cut transversely through the cardiac region of pig embryos of various ages to show the origin of the heart from paired primordia. *A*, 5-somite embryo; *B*, 7-somite embryo; *C*, 10-somite embryo; *D*, 13 somite embryo. (Projection diagrams ×50, from series in the Carnegie Collection.) (From Patten's "Embryology of the Pig.")

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 endothelial 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. When the human 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.

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 human embryo is two months old, the heart, although its size is minute, has reached its adult form and structure. (Fig. 254)

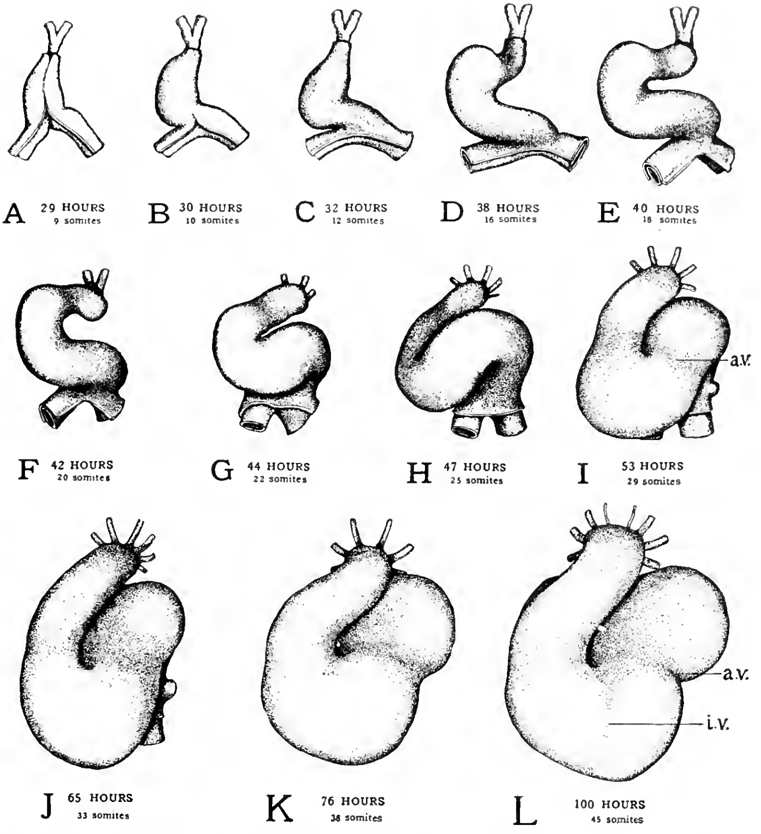


FIG. 254.—Ventral views of the heart of chick embryos at successive stages to show its changes of shape and its regional differentiation. Abbreviations: a.v., constriction between atrium and ventricle; i.v., interventricular groove. (From Patten's "Embryology of the Chick.")

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 more rapidly. 4. The separation of atria and ventricles by growth of atrio-ventricular valves. 5. The inclusion (in amniotes) 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. (Figs. 249, 254)

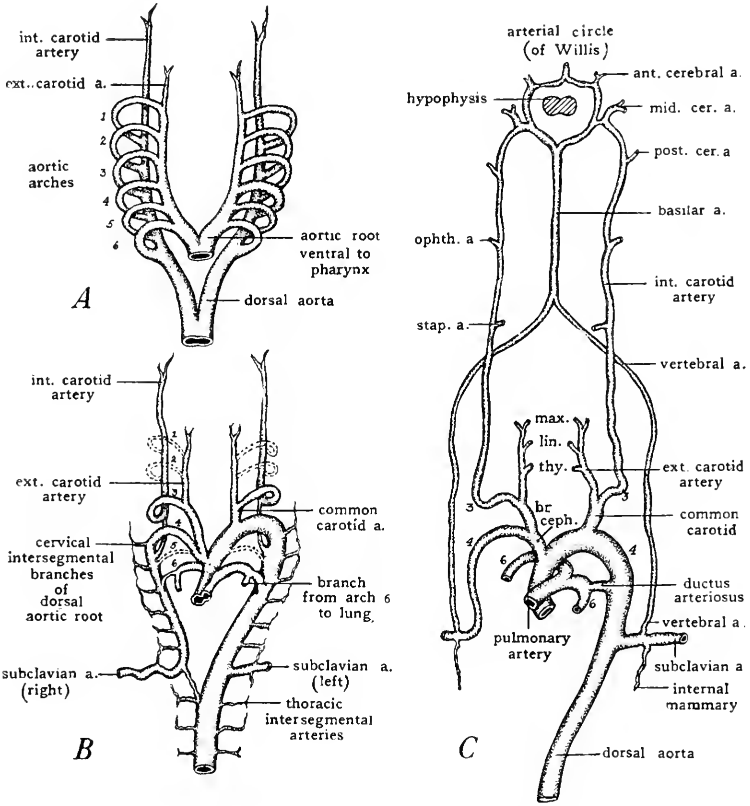


FIG. 255.—Diagrams illustrating the changes which occur in the aortic arches of mammalian embryos. *A*, ground plan of complete set of aortic arches; *B*, early stage in modification of arches; *C*, derivatives of aortic arches. Abbreviations: br. ceph., brachiocephalic artery; cer. a., cerebral artery; lin., lingual artery; max., maxillary artery; ophth. a., ophthalmic artery; stap. a., stapedial artery; thy., thyroid artery. (From Patten's "Embryology of the Pig," adapted from several sources.)

Development of the Aortic Arches. In early stages of human 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 part of 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.

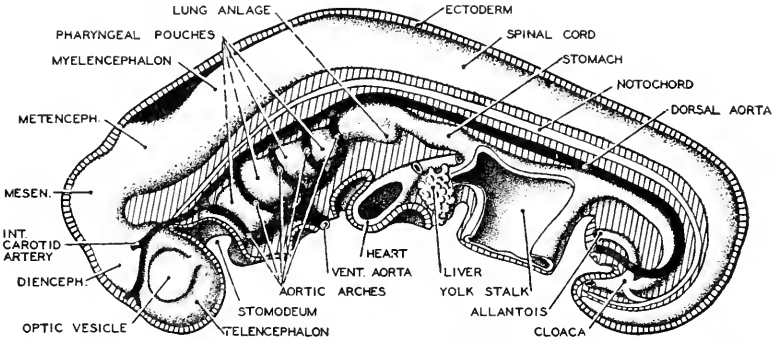


Fig. 256.—A diagram of a 4.2 mm. human embryo showing five aortic arches. (Redrawn after W. His.) Why does the human embryo have six aortic arches of which only three persist in the adult, unless man's ancestors had six functional arches?

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 **atrio-**

ventricular 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.

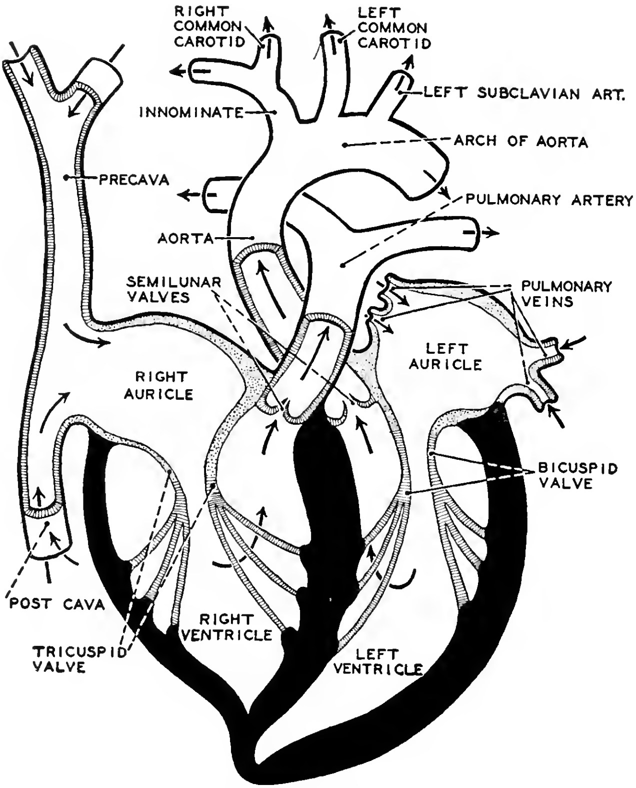


Fig. 257.—A diagram of the chambers of the mammalian heart and their associated vessels and valves. The walls of the ventricles are shown in black, those of the auricles are stippled. The direction of flow of blood is indicated by arrows. (Redrawn after Jammes.)

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 space 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 **atrio-ventricular** 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.** (Fig. 257)

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 contraction 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.

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.

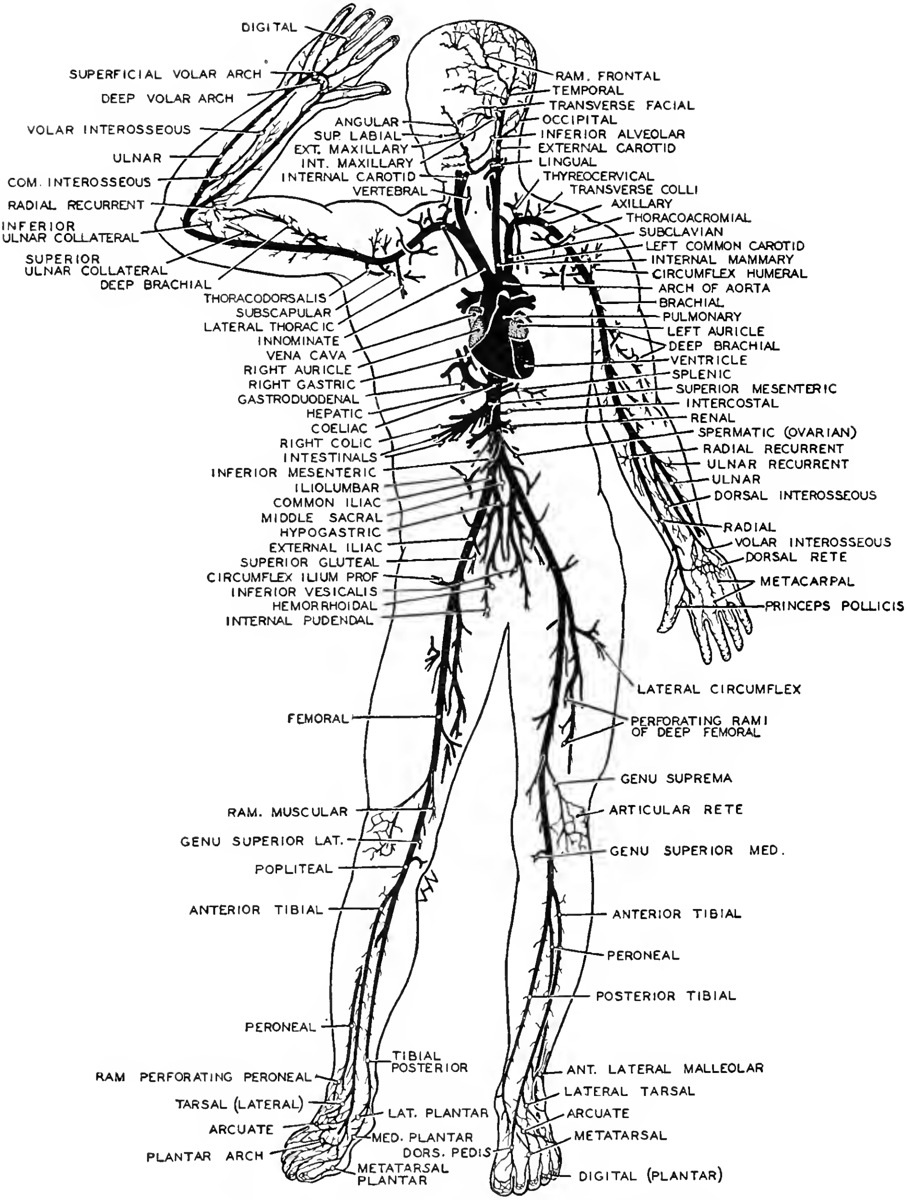


FIG. 258.—The chief arteries of the human body viewed from in front.

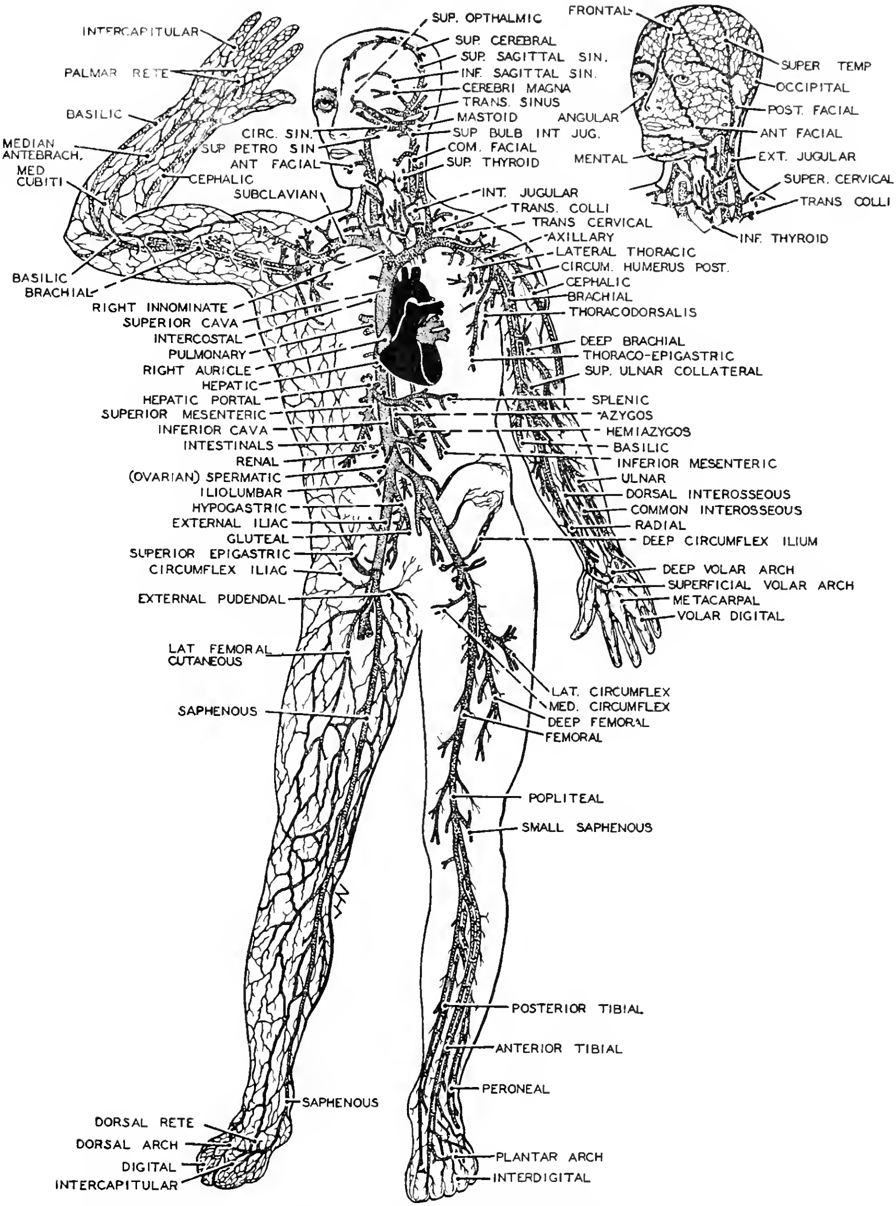


FIG. 259.—The chief veins of the human body viewed from in front. Superficial veins are shown on the right side, deeper vessels on the left side of the body.

Because of the strength and elasticity of their walls, arteries usually do not collapse after death.

Arteries have their own circulatory and nervous supply. The capillaries 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.

Pulmonary Circulation in Man. 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.

Systemic Circulation in Man. The systemic circulation in man differs in no essentials from that in other mammals. In a brief text such as this, space does not permit a detailed description of the arteries and veins in the human body. But a comparison of the human arteries and veins shown in Figures 258 and 259 with those of the cat will convince the student of their fundamental similarity. For this purpose the figures are probably more useful than detailed description would be.

The Lymphatic System in Man. The process of nutrition of the tissues involves constant loss of fluid or "leakage" from the capillaries. 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. 251)

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 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.

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. 252)

CHAPTER 11

THE UROGENITAL SYSTEM

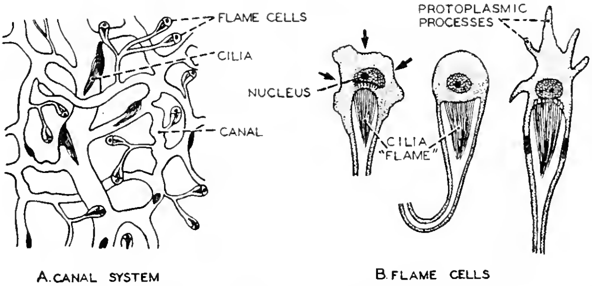
EVOLUTION OF THE UROGENITAL SYSTEM

The evolution of urinary and reproductive systems may be conveniently discussed as if the two were independent.

A. PHYLOGENESIS OF 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, necessary that all animals have mechanisms for removing the ashes of life, intra-cellular mechanisms in the Protozoa, Porifera, and Coelenterata, 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 protozoans 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.



A. CANAL SYSTEM

B. FLAME CELLS

FIG. 260.—Excretory organs in flatworms. *A* shows the branching excretory canals terminating in flame-cells. *B* shows three flame cells enlarged. By the action of the cluster of cilia (flame) a current carries wastes away from the excretory cell into the canals. (Redrawn after Benham.)

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. (Fig. 260) 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.

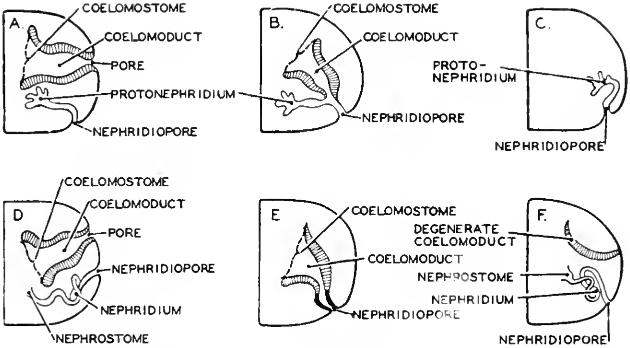


FIG. 261.—Diagrams illustrating the varying relations of coelomoducts and nephridia in different annelids. Nephridia like those seen in annelids occur also in cephalochordates. The coelomoducts are homologized with the renal tubules of vertebrates, although the latter are mostly excretory and not—as in annelids—reproductive in function. (Redrawn after Goodrich.)

Annelids. Two sorts of excretory organs occur in annelids, **protonephridia** and **metanephridia,** the former, as their name suggests, considered the more primitive. (Fig. 261)

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. 263)

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. Probably they are genetically related to the protonephridia.

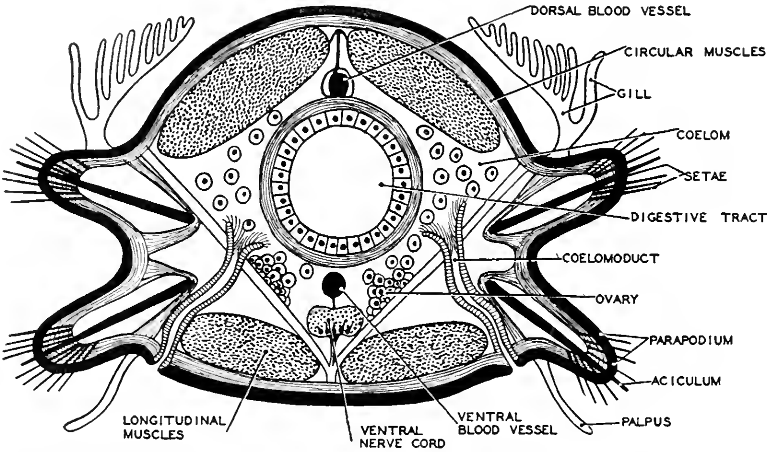


FIG. 262.—A diagrammatic cross section of an annelid, showing the coelomoducts. With a ciliated opening into the coelom and an external aperture, each coelomoduct serves as an outlet of the reproductive cells—eggs or spermatozoa. They are homologized with the renal tubules of chordates. (Redrawn after Lang.)

Coelomoducts. In addition to the two kinds of nephridia just described, many invertebrates have a third type of tubules, **coelomoducts.** 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 Amphioxus, 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.

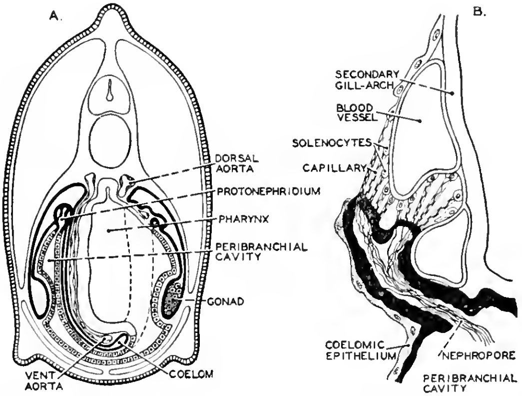


FIG. 263.—Diagrams of the protonephridia of Amphioxus. *A* is a section in the pharyngeal region—through a gill septum on the left and through a gill slit on the right. *B* is an enlarged section of a protonephridium showing the attached solenocytes. Such a protonephridium is practically identical in structure with a protonephridium of annelids. (Redrawn after Boveri and Goodrich.)

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. 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. (Fig. 261)

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 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 dipnoans. The mesonephros becomes the functional kidney of adult Anamnia, the metanephros of adult Amniota.

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.

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 possible 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.

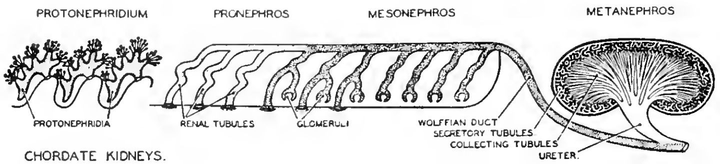
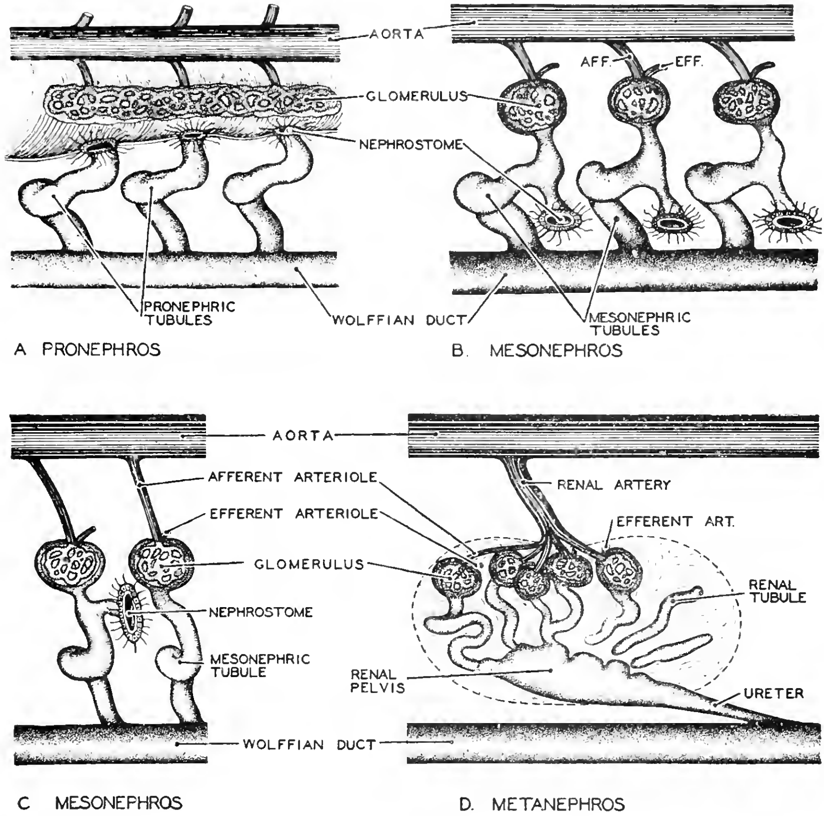


FIG. 264.—A diagram illustrating the four types of kidneys which occur in chordates. The excretory tubules of amphioxus are ectodermal in origin like the protonephridia of annelids, while they are mesodermal in vertebrates. In the course of phylogenesis the excretory organs of chordates have migrated farther and farther back in the body, as is shown in the diagram.

The pronephros functions in few adult vertebrates, but it appears to function in the early ontogenesis of those craniotes which have little yolk 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.

Mesonephros. 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.



A PRONEPHROS B. MESONEPHROS

C MESONEPHROS D. METANEPHROS

FIG. 265.—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 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. 266)

Metanephros. The third kidney or metanephros appears not to be an amniote novelty, since transitional conditions between mesonephros and metanephros occur in some amphibians in the form of a combined mesonephros-metanephros, the **opisthonephros.** The present ureter has been regarded also as an elongated renal tubule which secondarily acquires functional connexions with the numerous tubules of the metanephros.

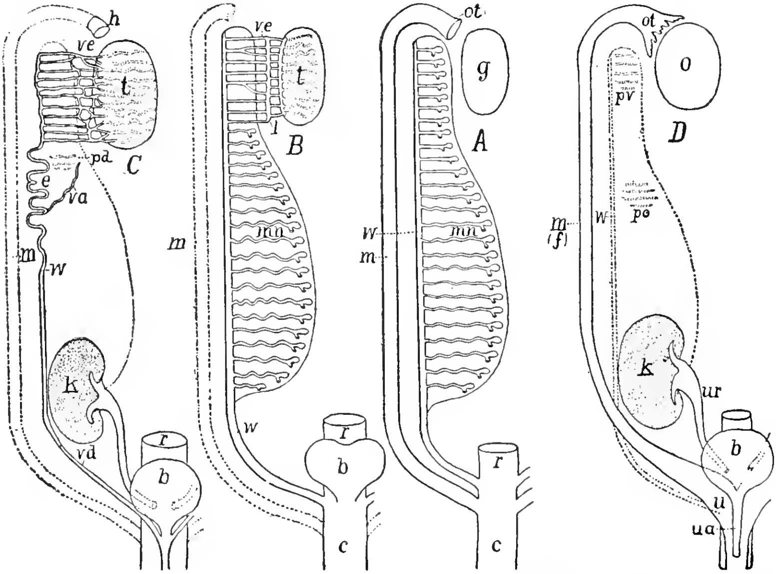


FIG. 266.—Diagrams of urogenital structures in (*A*) indifferent and female elasmobranchs and amphibians; (*B*) male elasmobranchs and amphibians; (*C*) male amniote (mammal); (*D*) female amniote (mammal). *b*, urinary bladder; *c*, cloaca; *e*, epididymis; *f*, Fallopian tube; *g*, gonad; *h*, "stalked hydatid"; *k*, kidney (metanephros); *l*, longitudinal tubule; *m*, Müllerian duct (oviduct), rudimetary in *B* and *C*; *mn*, mesonephros; *o*, ovary; *ot*, ostium tubae abdominale; *pd*, paradidymis; *po*, paroöphoron; *pv*, parovarium; *r*, rectum; *ti*, testis; *u*, uterus; *ua*, urethra; *ur*, ureter; *va*, vas aberrans; *vd*, vas (ductus) deferens; *ve*, 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.")

In the female amniote, the mesonephros disappears except in the form of functionless rudiments, the **epoöphoron,** the **paroöphoron,** and the **duct of Gärtner.** 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.** See Fig. 266.

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 amphibians 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.

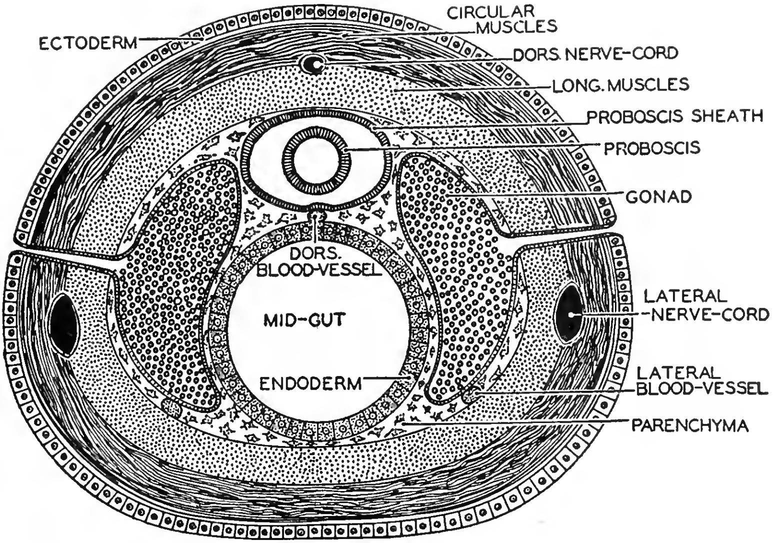


FIG. 267.—A cross section of a nemertean. While the nemertean lacks a coelom, the gonadic sacs have been compared with the coelomic sacs of coelomate animals. (Redrawn after Lang.)

B. PHYLOGENESIS OF 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. Many 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 spermatozoon 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.

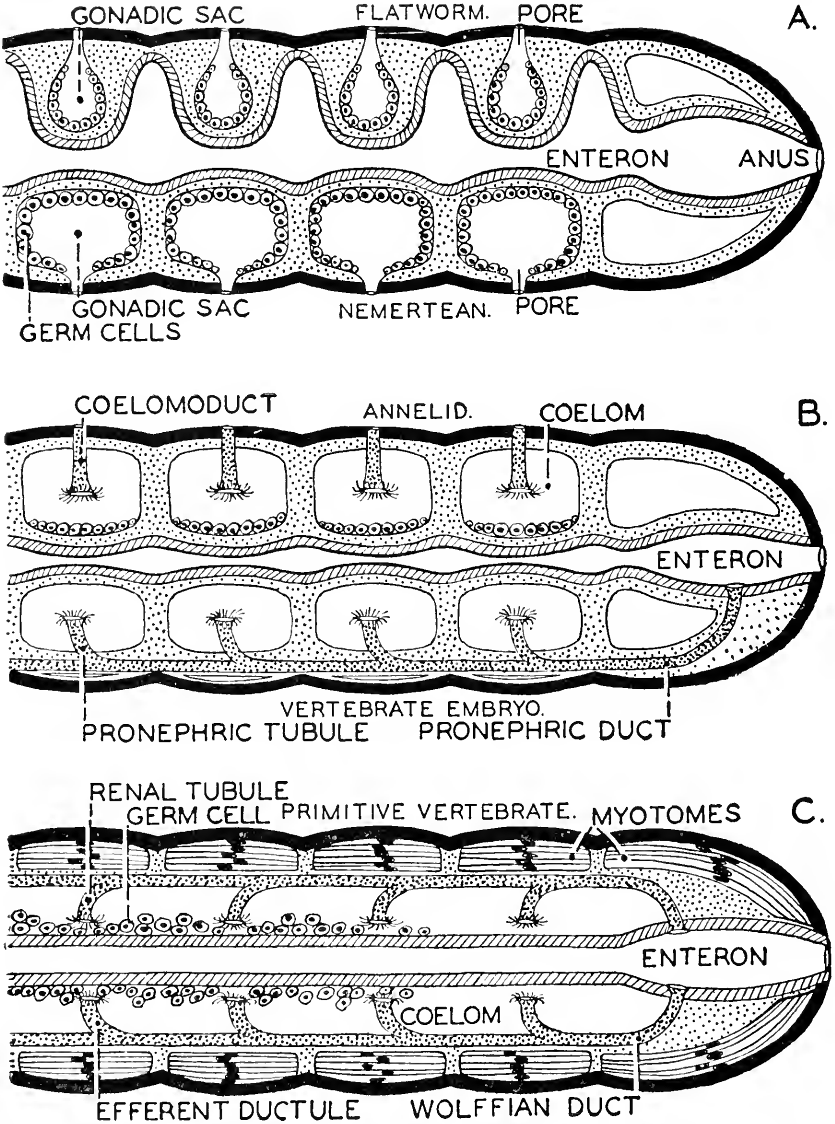


FIG. 268.—Diagrams illustrating the hypothetical evolution of the urogenital system of vertebrates, beginning with the gonadic sacs of flatworms. The diagrams assume that the gonadic sacs of flatworms have become the coelomic pouches of chordate embryos. The latter in turn unite to form the extended coelom of vertebrates. Coelomoducts appear first in annelids and become in vertebrates the renal tubules. Vertebrates "invent" a longitudinal (primitive) excretory duct. During phylogenesis the region of proliferation of germ-cells becomes greatly restricted.

Coelenterates. Among coelenterates the individual may be hermaphroditic as in the case of Hydra, or sexually differentiated as in the case of 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. For 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 metamerism characteristic of vertebrates had its origin in such a series of paired gonadic sacs. (Fig. 268)

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.

Protochordates. The gonads of Balanoglossus have a striking resemblance to those of flatworms. (Fig. 268.) 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 atriopore to the exterior.

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 seems 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 **abdom-**

inal 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. 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 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 Wolffian and Müllerian ducts. In the female the Wolffian ducts are purely excretory, while the Müllerian ducts form the oviducts. In the male, the Wolffian ducts combine both urinary and reproductive functions, while Müller'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.

Amphibia. The gonads of amphibians 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 Wolffian duct serves as a urogenital outlet in the male. The Müllerian 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.

Reptiles. The differences between the reproductive systems of amphibians 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 this affects 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 chelonians 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 to convey the semen through the intromittent organ 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 oöcytes 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 Gärtner'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.

In female mammals a tendency of the Müllerian 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 Müllerian 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 Müllerian ducts. The duplex character of the vagina appears in the marsupials (didelphians) which have two vaginae. 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 Müllerian ducts is retained in the paired uterine tubes. (Fig. 269)

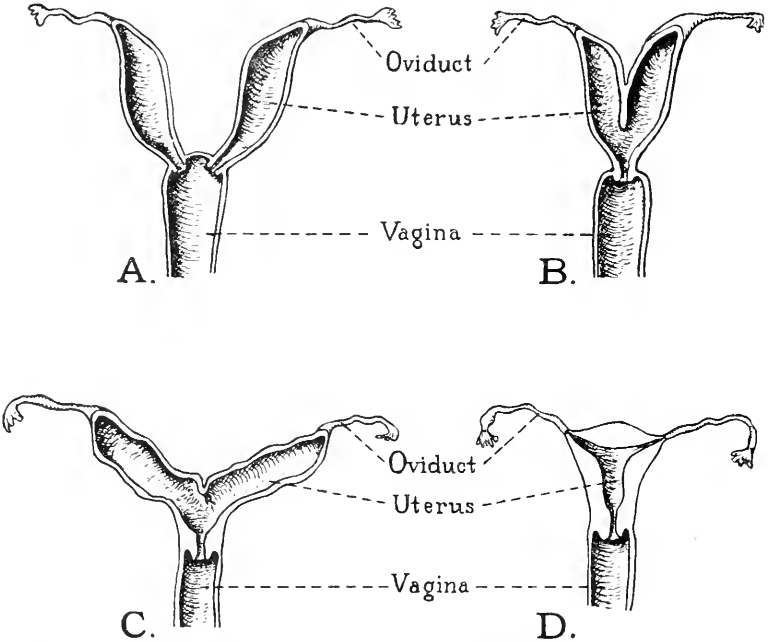


Fig. 269.—Four types of uteri occurring in different groups of mammals. *A*, duplex, the type found in rodents; *B*, bipartite, the type found in certain carnivores; *C*, bicornate, the type found in most insectivores and prosimians; *D*, simplex, the type characteristic of the primates. (From Patten's "Embryology of the Pig," after Wiedersheim.)

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 (seminal ridges) in the floor of the cloaca of Chelonia and Crocodilia 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 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. 270)

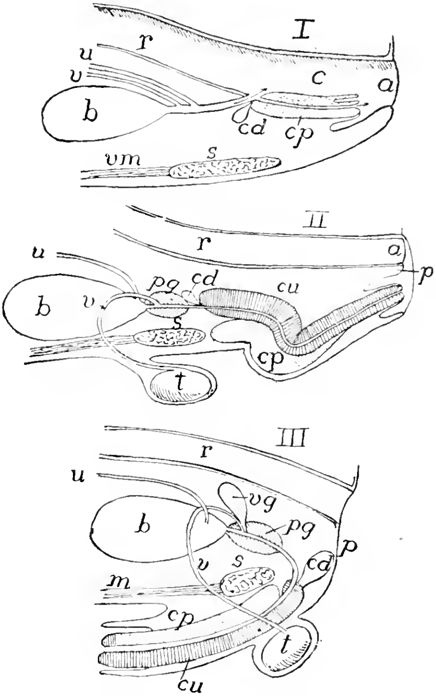


FIG. 270.—Diagrams of male urogenitalia in I, monotreme; II, marsupials; and III. monodelphs. *a*, anus; *b*, bladder; *c*, cloaca; *cu*, corpus cavernosum urethrae; *cp*, corp. cav. penis; *cd*, Cowper's gland; *p*, perineum; *pg*, prostate gland; *r*, rectum; *s*, symphysis pubis; *t*, testis; *u*, ureter; *v*, vas deferens; *vg*, vesicular gland; *vm*, ventral muscles. (From Kingsley's "Comparative Anatomy of Vertebrates," after Weber.)

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.

A. 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. The lateral border of each kidney is convex; the medial border is concave, with a slit-like aperture, the **hilum.**

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. 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.**

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.** (Fig. 271) The swollen termination of a tubule is a **Bowman's capsule** (Fig. 64). The portion of the tubule adjacent to the corpuscle is convoluted and thickened

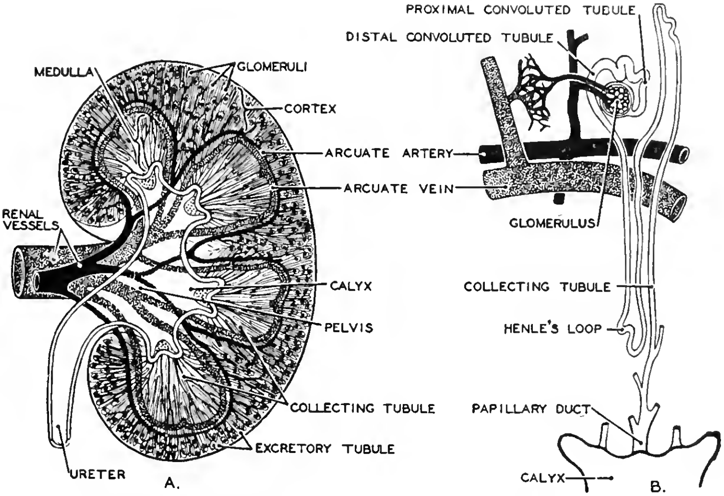


FIG. 271.—A diagram of the finer structure of a kidney. *A* is a section of the entire kidney showing the contrast between cortical and medullary regions. The relations of the chief arteries and veins are indicated. *B* is a reconstruction of a single tubule, showing its relations to the blood and the 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.)

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 believe 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. 271)

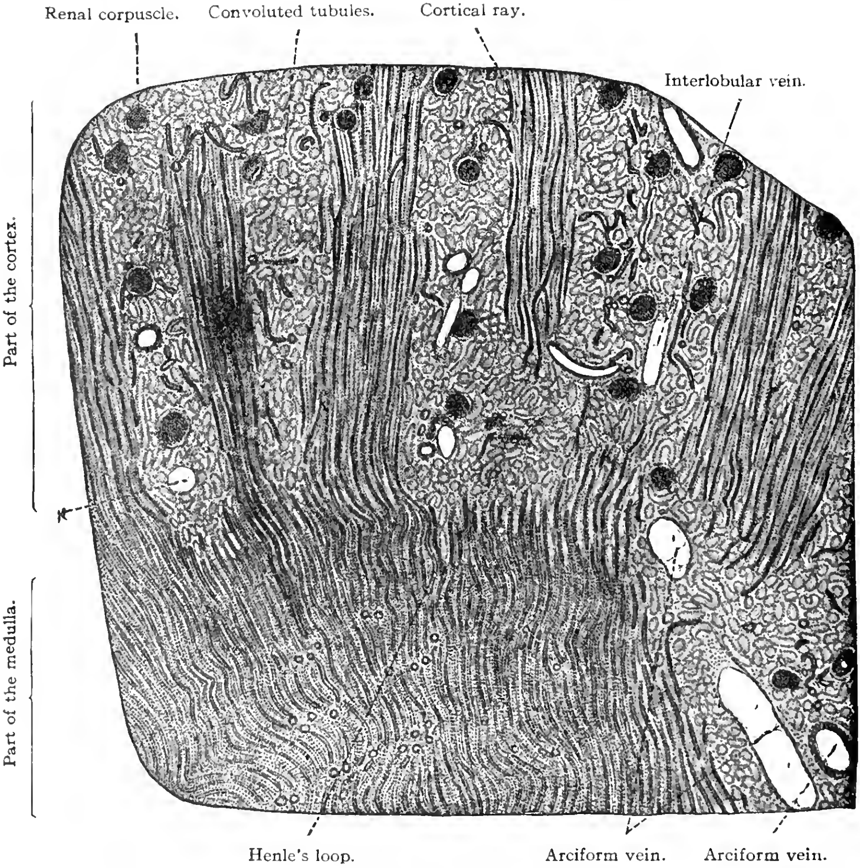
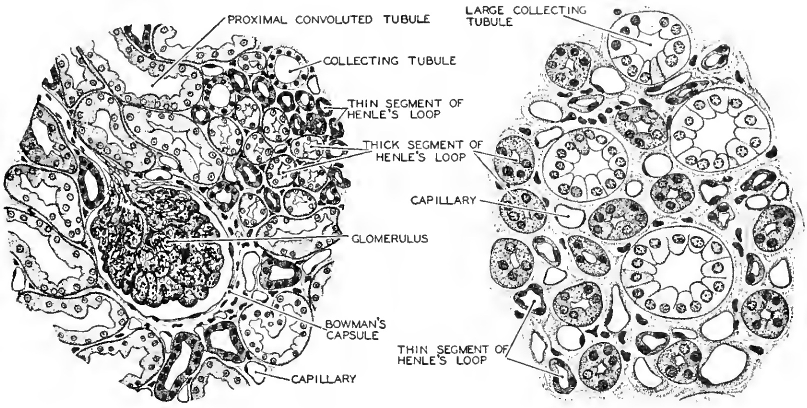


FIG. 272.—Part of a radial section of a human kidney. At *x* a renal corpuscle has dropped out. ×5. (From Bremer's "Text Book of Histology.")

Blood Supply. Arteries enter and veins leave the kidney by way of the hilum on the median side of each kidney. (Fig. 271) 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 excretions 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 into 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.



A CORTEX

B MEDULLA

FIG. 273.—Sections of the human kidney. Section *A* is taken from the region of the cortex, *B* from the medulla. Glomeruli which are abundant in the cortex are lacking in the medulla. (Redrawn from Bremer after Schaper.)

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 lining of the bladder is a layer of transitional epithelium capable of great 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.

B, 1. 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.

The ovary is covered by a layer of columnar epithelium, which is apparently 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 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. (Fig. 274) 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, the ovaries serve as endocrinal organs. In ontogenesis the ovaries of the embyro 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

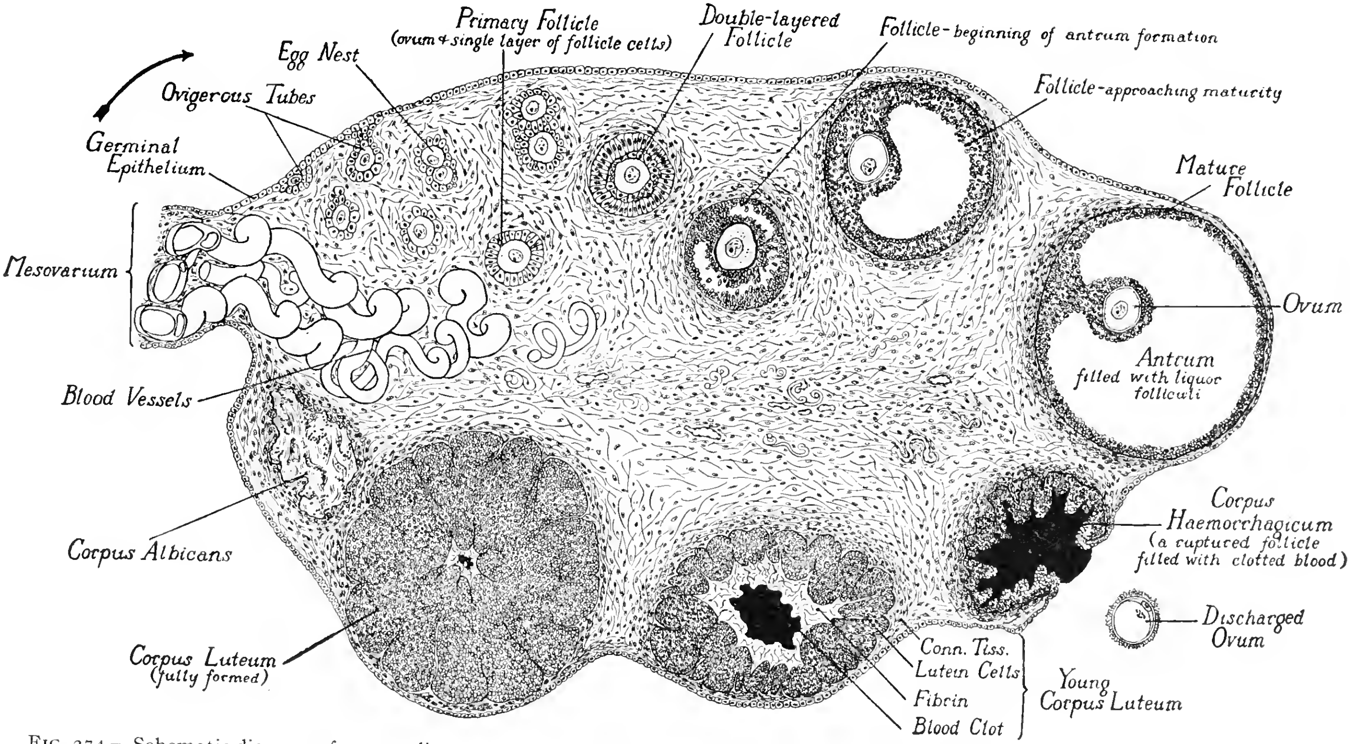


FIG. 274.—Schematic diagram of mammalian ovary showing the sequence of events in the origin, growth, and rupture of the ovarian (Graafian) follicle, and the formation and retrogression of the corpus luteum. Follow clockwise around the ovary starting at the arrow. (From Patten's "Embryology of the Pig.")

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. The number of cilia is greatly increased by the complex folding of the lining of the tubes. The blood supply of the tubes comes from ovarian and uterine vessels. The nerves are sympathetic. (Fig. 275)

The Uterus. The uterus is a median pear-shaped organ suspended in the **broad ligament. Round** and **ovarian 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.

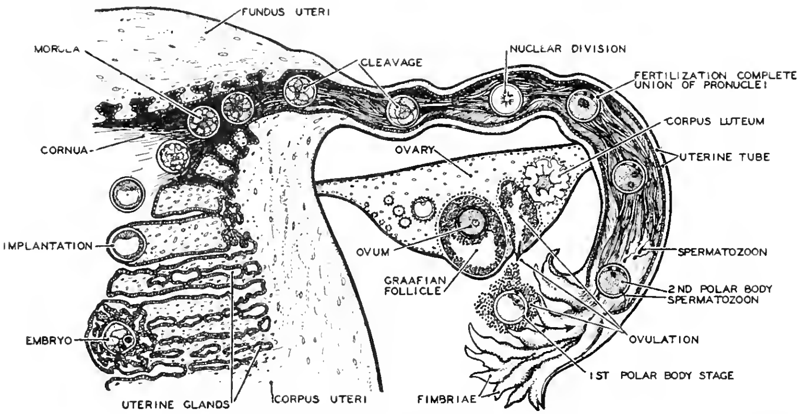


FIG. 275.—Diagram illustrating the passage of the fertilized egg from the ovary to the uterus. The ovum is a week in the tube and three days in the uterus before implantation takes place. (Redrawn after Dickinson's "Sex Anatomy," Williams & Wilkins Co.)

The 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. 276)

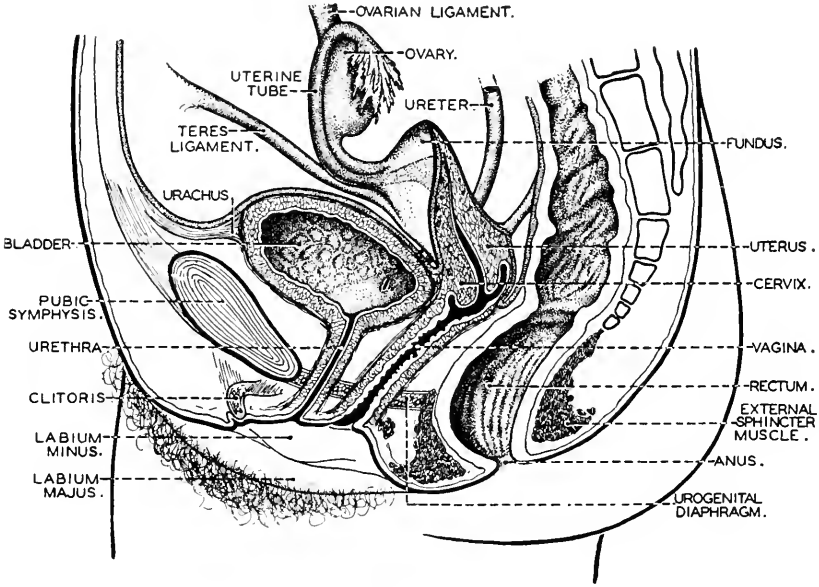


FIG. 276.—The urogenital system—female. (Sobotta.)

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.

B, 2. REPRODUCTIVE ORGANS: MALE

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.

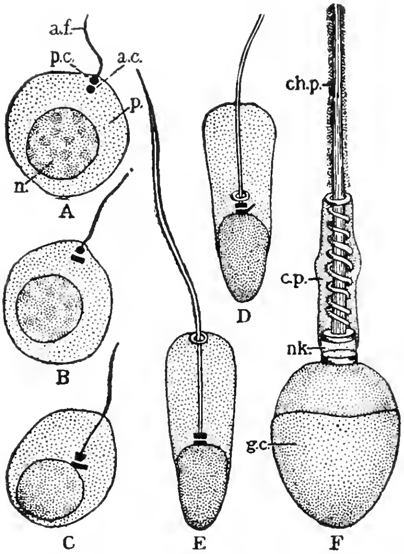


FIG. 277.—Diagrams of the development of spermatozoa. *a.c.*, anterior centrosome; *a.f.*, axial filament; *c.p.*, connecting piece; *ch.p.*, chief piece; *g.c.*, galea capitis; *n*, nucleus; *nk.*, neck; *p.*, protoplasm; *p.c.*, posterior centrosome. (From Bremer's "Text Book of Histology," after Meves.)

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 endocrinal 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. 278.

The seminiferous tubules are lined with an irregular many-layered epithelium from which the spermatozoa are proliferated, the multiplication 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 seminiferous tubules. Diminution in the activity of the tubules occurs 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.**

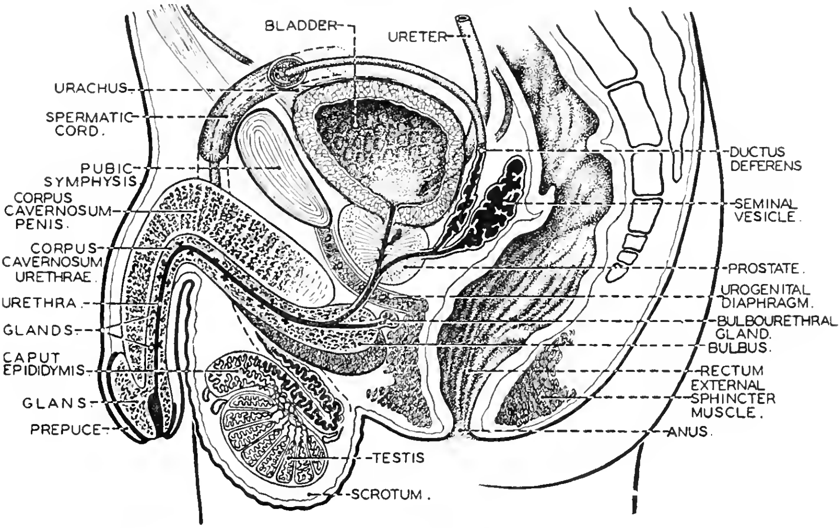


FIG. 278.—The male urogenital system. The glandular complications of the male urogenital system appear to be in part an adaptation to the double function of the urethra—excretory and reproductive. The alkaline secretions of the glands serve to neutralize the acidity of the urethra caused by the acid urine. (Sobotta.)

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. 278)

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 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 Müllerian 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.

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. 278)

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. 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 OF MAN

A. 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.

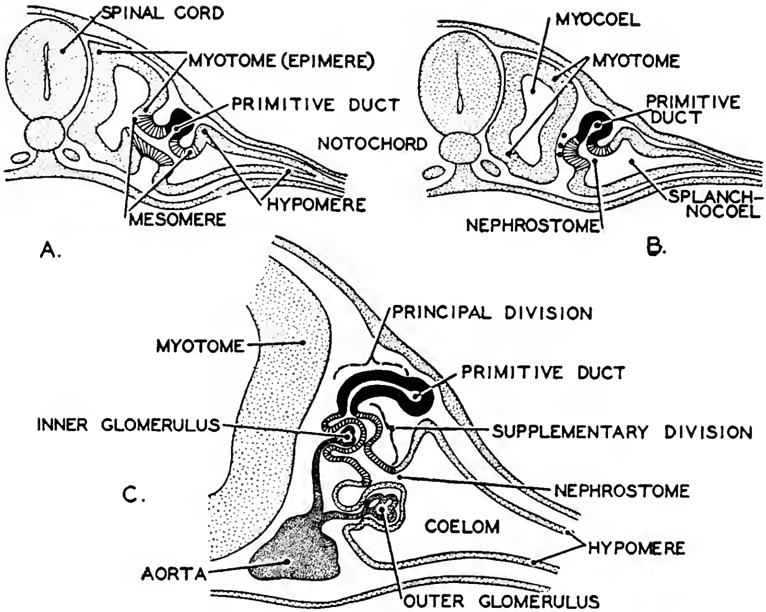


Fig. 279.—A diagram showing three stages, *A–C*, in the development of the primitive duct and a pronephric tubule. The duct and each tubule connected with it arise from the mesomere. Two types of glomeruli—outer and inner—become associated with the pronephric tubules. (Redrawn after Felix.)

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. The mesonephros probably functions during foetal life. The metanephros is the definitive kidney. The occurrence of three kidneys in the embryos of amniotes is best interpreted by the evolution theory.

Pronephros. The **pronephros** or "head kidney" is the most anterior 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 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, at least in part, persist in the adult as the **ostium tubae** (the anterior opening of the oviduct).

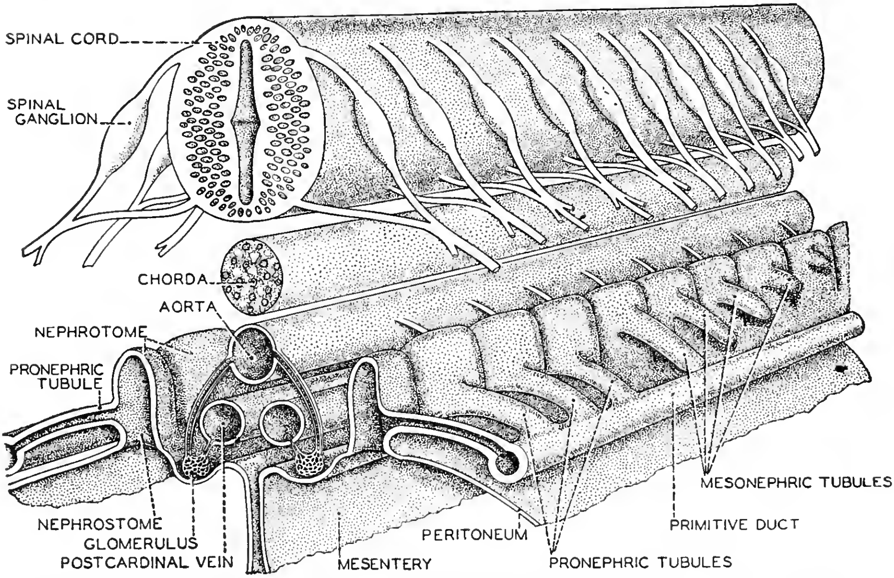


FIG. 280.—Stereogram of the developing pronephros and mesonephros. (After Kingsley, modified.)

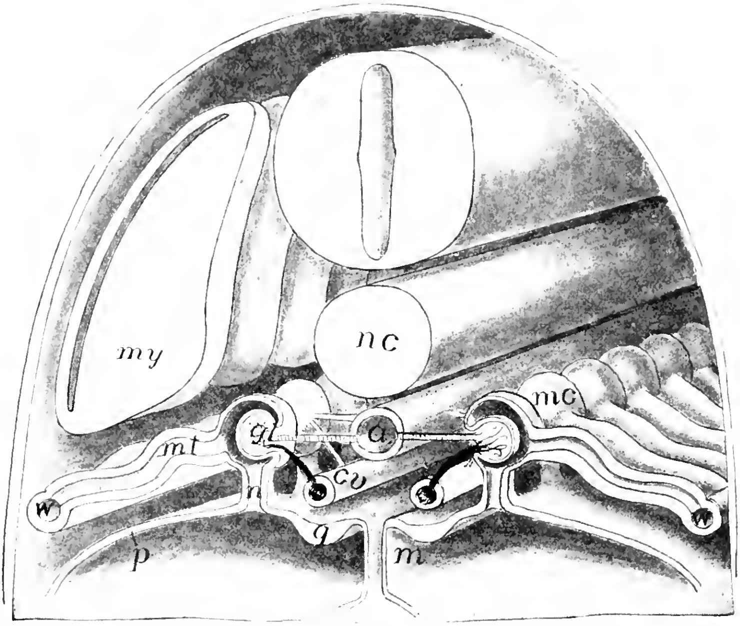


FIG. 281.—Stereogram of the developing mesonephros at a stage later than that of Fig. 280. (After Kingsley modified.)

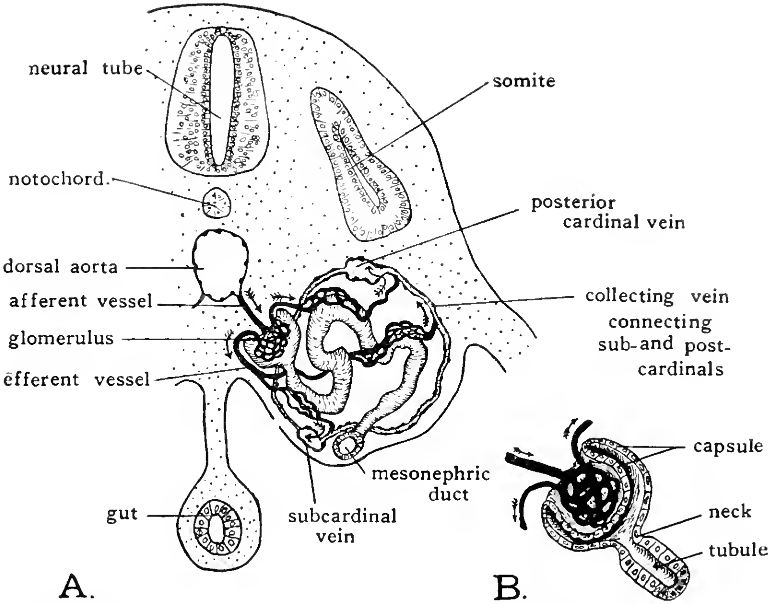


FIG. 282.—Diagrams showing the relations of the blood vessels to a mesonephric tubule. (From Patten's "Embryology of the Pig," based on figures by McCallum.)

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. While the anterior nephrotomes are segmented, the more 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. 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 or Wolffian ducts become the ductus deferentes.

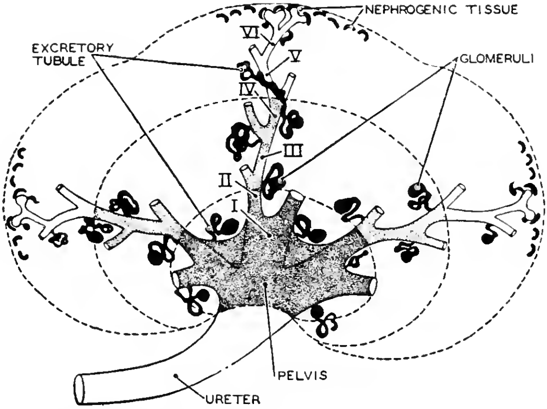


FIG. 283.—A diagram illustrating the repeated branching of the collecting tubules in a nine-weeks (30 mm.) human embryo. The diagram shows also the origin of secretory tubules from the nephrogenic tissue. (Redrawn from Braus, after Kampmeier.)

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.

The vesicular enlargement of the ureter becomes the **pelvis**. Two outgrowths from it, one anterior and one posterior, form two **major calyces**. (Fig. 271) 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 become the **papillary ducts** which convey urine from the collecting tubules and which open directly into each of the renal calyces. (Fig. 283)

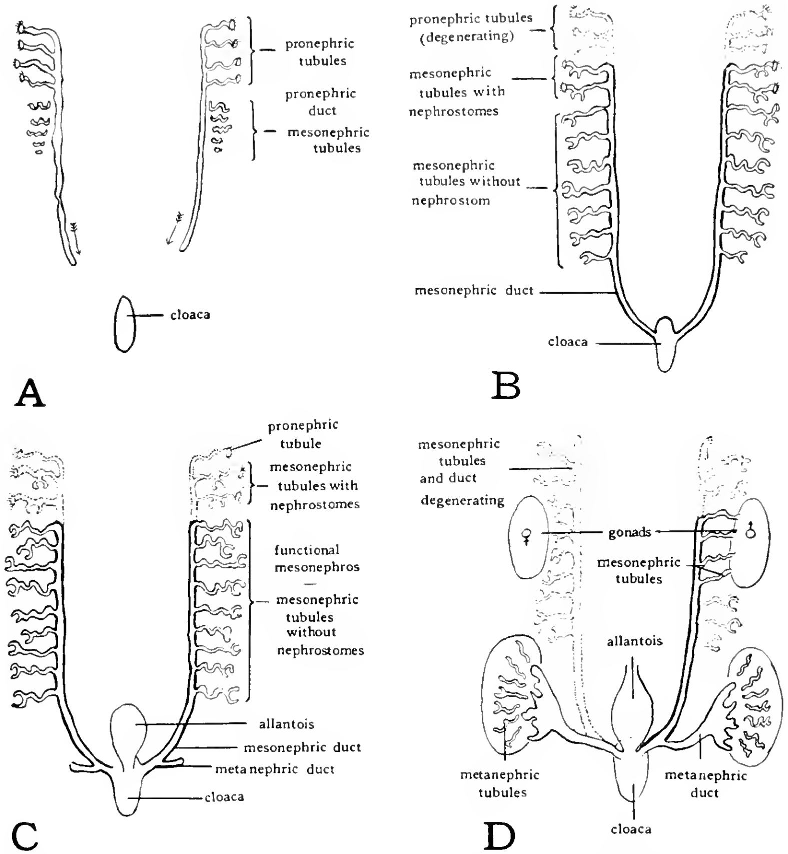


FIG. 284.—Schematic diagrams to show the relations of pronephros, mesonephros, and metanephros at various stages of development. In the adult male the mesonephric (Wolffian) duct is retained as the ductus deferens. (From Patten's "Embryology of the Chick.")

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. (Fig. 283) 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. (Fig. 282) These changes occur in the later months of intra-uterine life.

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 opening into the bladder and the mesonephric ducts into the urethra. The bladder, therefore, arises not from the allantois but from the cloaca. The bladder anlage, however, is continued ventrally as the allantoic stalk, which subsequently atrophies to form the middle umbilical ligament.

B. 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. (Figs. 66, 67, 281)

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.

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.

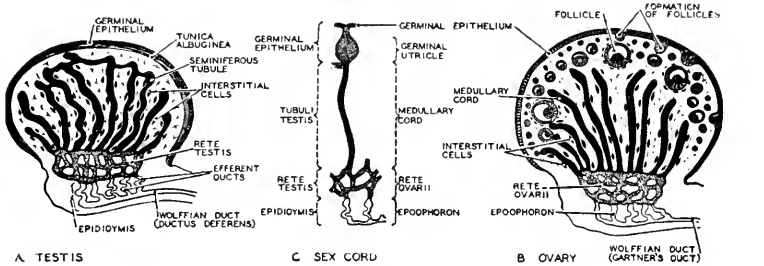


FIG. 285.—Diagrams of the testis (*A*) and ovary (*B*) showing the homologies of their components. (Redrawn after Mall, modified.)

The testis is originally an abdominal organ like the ovary, and its position in the scrotum is 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

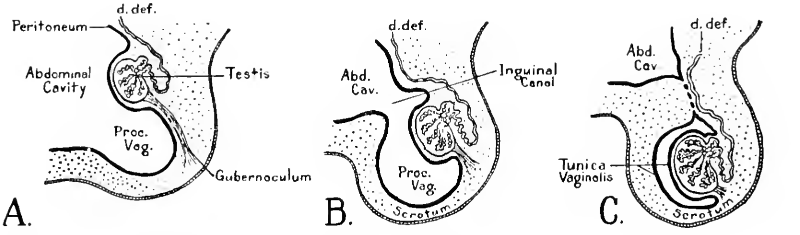


FIG. 286.—Schematic diagrams illustrating the descent of the testis as seen from the side. d. def., ductus deferens; Proc. Vag., processus vaginalis (the diverticulum of the peritoneum pushed into the scrotal sac). (From Patten's "Embryology of the Pig.")

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.

Reproductive Ducts. The mesonephric or Wolffian ducts are utilized by the male as reproductive ducts, the ductus deferentes. Müller's ducts are also developed in both sexes. Each Müller's duct arises from a longitudinal groove on the lateral side of the mesonephros. The peritoneal epithelium sinks into the underlying mesenchyma (Fig. 67). 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 external products 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, Müller'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 persist also in the female. Some anterior mesonephric tubules unite with the rete ovarii to form the **epoöphoron.** The posterior part of the mesonephros becomes the rudimentary **paroöphoron.** The functionless remnant of the Wolffian duct in the adult is known as Gärtner's duct.

Female Reproductive Ducts. Müller'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

Müllerian ducts unite to form **uterus** and **vagina.** The anterior portions form the uterine tubes.

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.**

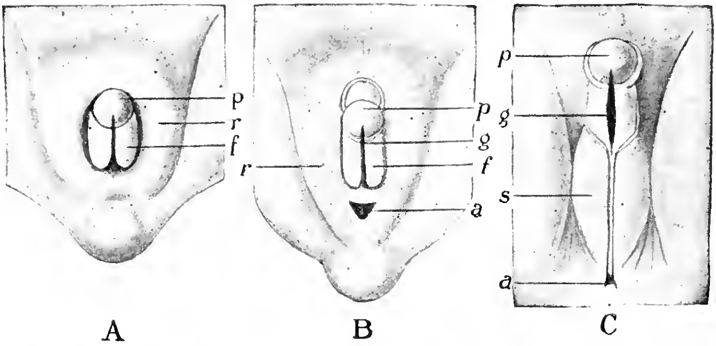


Fig. 287.—Development of the male external genitalia of man. *A*, indifferent stage from which either sex may develop; *B*, early, and *C*, later stages; *a*, anus; *f*, genital folds; *g*, urethral groove; *p*, genital tubercle; *r*, genital ridge (outer genital folds); *s*, scrotum. (From Kingsley's "Comparative Anatomy of Vertebrates," after O. Hertwig.)

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. 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 resembles the undeveloped male.

CHAPTER 12

THE ENDOCRINAL ORGANS

One necessity of a living organism is that its organs should work together. In fact, a 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.

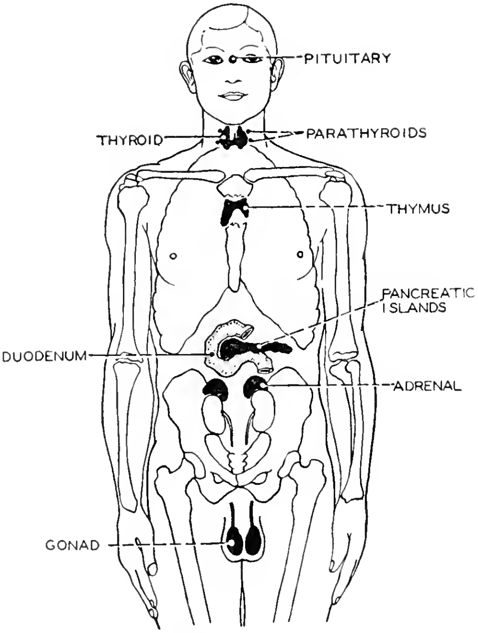


FIG. 288.—The endocrinal glands in man.

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, and 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. Hormones act chemically upon various parts of the body. Their effect generally is stimulatory. With the discovery that nerves produce neurohumors which act in the manner of hormones, the contrast between nervous and endocrinal action does not appear as great as was formerly thought.

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.

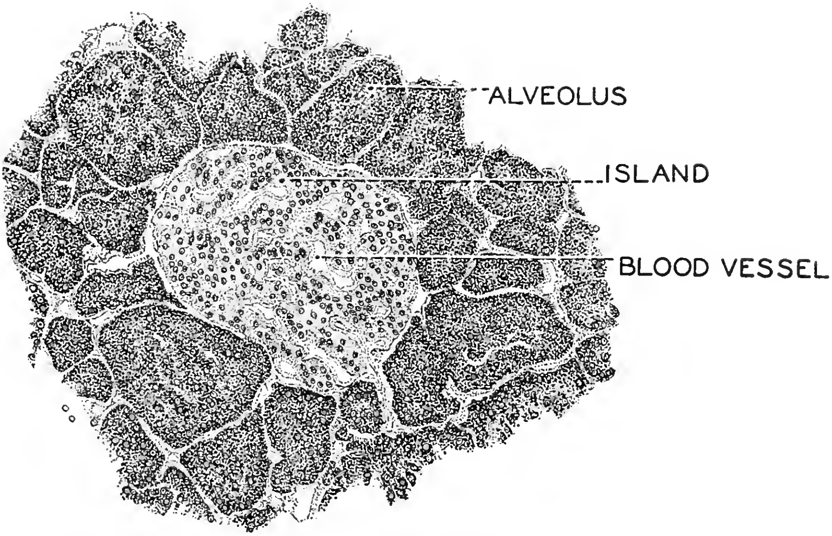


FIG. 289.—A section of the pancreas, showing an island among the alveoli of the gland. ×200.

The Pancreas. General interest in endocrine organs was increased by the important discovery that the pancreas has an endocrinal 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.** 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.

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 islands.

Male Sex Glands. 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. There is plenty of evidence that hormones influence the secondary sex traits, the first striking evidence appearing at puberty when the boy assumes some of his adult male 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.

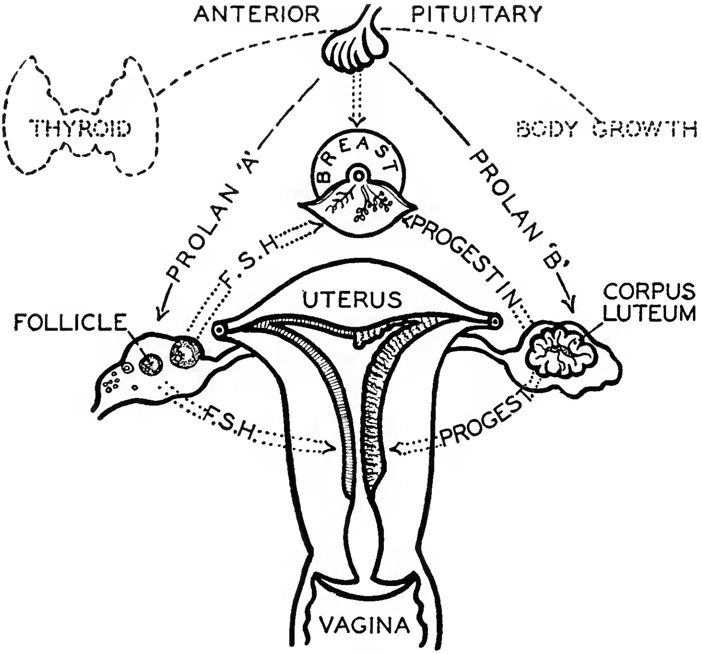


Fig. 290.—A diagram of the interactions of pituitary, follicular and luteal hormones. (Redrawn after Dickinson's "Sex Anatomy," Williams & Wilkins Co.)

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.

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.

The follicular hormone, **theelin,** has the chemical formula $C_{18}H_{24}O_3$ and is a fatty substance, soluble in alcohol and other lipoid solvents. It is used hypodermically to induce puberty and menstruation.

One of the names for the hormone of the corpus luteum 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.

Suprarenal Glands. 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.

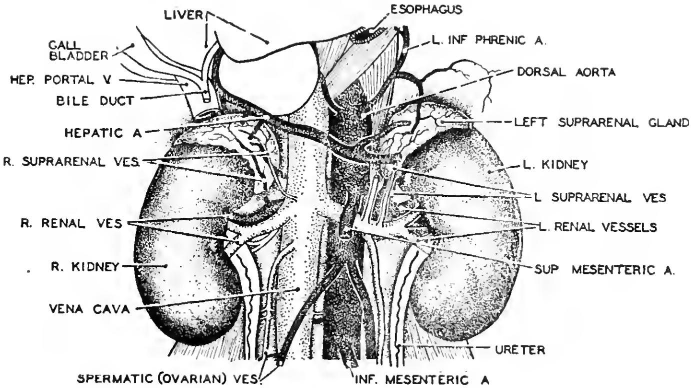


FIG. 291.—Shows the suprarenals in relation to the kidneys as seen when the fat which normally encloses them is removed. The relations of the blood vessels which supply them are also shown.

The adrenal gland has a rich blood supply. Arterial blood comes from three sources, phrenic, aortic, and renal vessels. 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.

An adrenal has two kinds of tissue, an outer yellowish **cortex** and an inner brownish **medulla.** 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. (Fig. 292)

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 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 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.

The endocrine secreted by the medullary tissue of the adrenal is **epinephrine** or **adrenin,** its empirical chemical formula being $C_9H_{13}O_3N$. Like the sympathetic nerves, adrenin has a stimulating effect upon smooth muscle. 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.

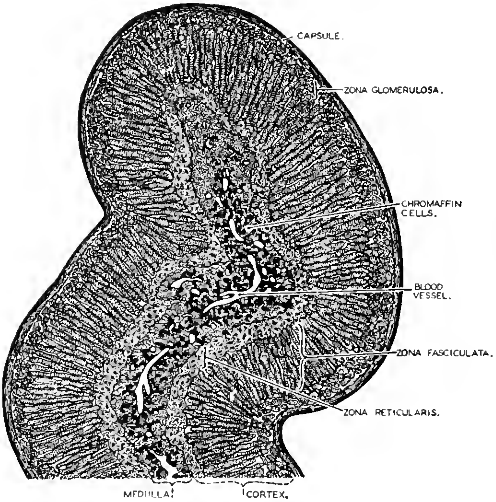


FIG. 292.—A portion of a section of the adrenal gland as seen under low-power microscope, showing the differentiation into cortical and medullary regions. Different endocrines are secreted by these two tissues, which have a different embryonic origin.

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 shown also 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.**

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 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.

Adrenal glands are limited to vertebrates. In cyclostomes, both the cortical material and the chromaffin are present, but are spatially separated. The cortical substance is represented by the **interrenal bodies,** which lie throughout the length of the body-cavity near the postcardinal 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 amphibians 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 amphibians 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 amphibians. 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.

Thyroid Gland. The thyroid gland of man is a bilobed brownish organ closely apposed to the trachea just below the larynx. Although the size of the thyroid varies greatly in different individuals, the average weight is thirty-four grams. 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 nerve supply is sympathetic.

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 most important, if not the exclusive, endocrinal secretion of the thyroid gland is an iodine compound, **thyroxine,** the empirical chemical formula for which is $C_{15}H_{11}O_4NI_4$. A substance with identical properties has been made synthetically, and it is generally the synthetic drug which is used in medical practice.

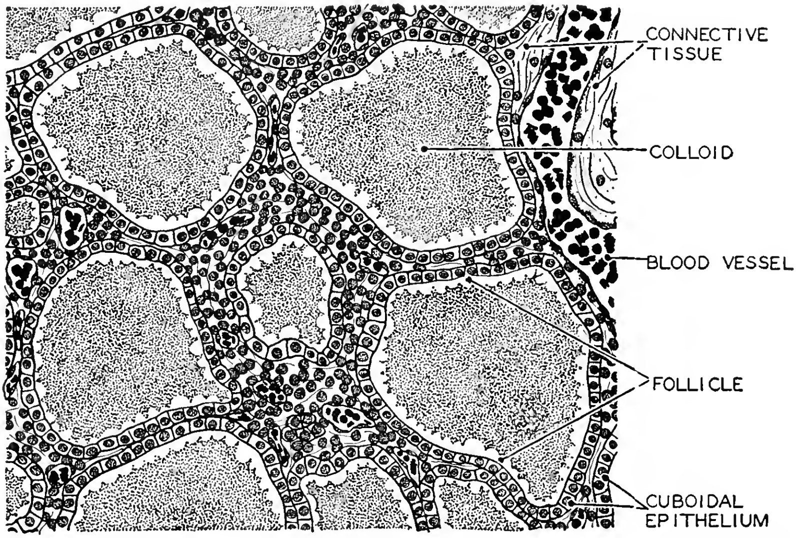


FIG. 293.—A portion of a section of the thyroid gland, enlarged, showing the secretory epithelium and the colloid-filled follicles.

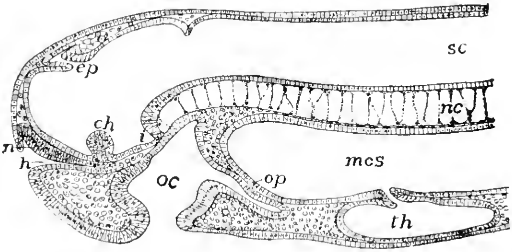


FIG. 294.—Longitudinal section of head of 19-day Petromyzon embryo showing the relation of the thyroid anlage to the floor of the pharynx. *ch*, optic chiasma; *ep*, epiphysial outgrowth; *h*, hypophysial ingrowth; mcs, mesenteron; *n*, nasal epithelium; *nc*, notochord; *oc*, oral cavity; *op*, oral plate; *sc*, canal of spinal cord; *th*, thyroid. (From Kingsley's "Comparative Anatomy of Vertebrates.")

One function of thyroxine is to control metabolism, especially of the carbohydrates, a thirtieth of a grain increasing oxidation by one percent. It regulates also growth before birth, through infancy, and at puberty, so that, in no small measure, we are what we are by 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 basal metabolism above normal, so that the patient loses weight. 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.

In man, as in other vertebrates, the thyroid gland arises as a median ventral outgrowth from the floor of the pharynx at the level of the first visceral pouch. Eventually connexion with the tongue is lost.

The thyroid gland is a peculiarity of chordates, and is found in all classes of this phylum. 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, mucus-glandular and ciliated. 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.

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 endocrinal. 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. 251) 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.

Parathyroid Glands. The parathyroid glands in appearance resemble lymph nodes, and there are usually four in man. 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.

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. 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. 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. The chemical nature of the parathyroid endocrine is not yet known.

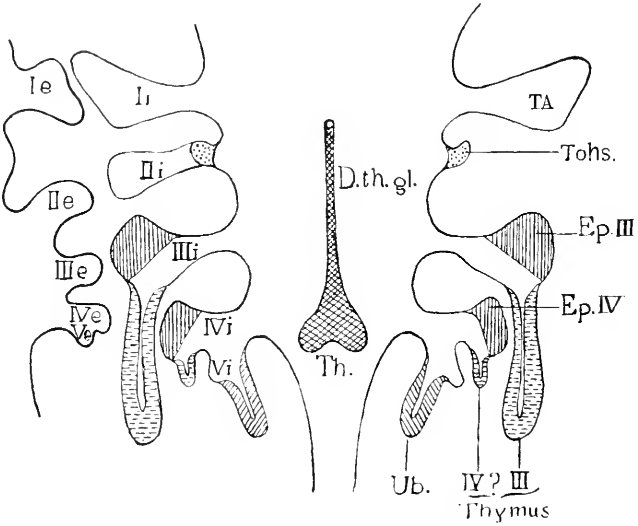


FIG. 295.—Diagram to show the derivatives of the pharyngeal pouches. *Ie, IIe, IIIe, IVe, Ve,* external pharyngeal grooves; *Ii, IIi, IIIi, IVi,* internal pharyngeal pouches; *TA,* auditory tube and tympanic cavity; *Tons.,* palatine tonsil; *EpIII, EpIV,* parathyroid glands; *Ub,* ultimobranchial body; *Th.,* thyroid gland. *D.th.gl.,* ductus thyroglossus. (From Morris, after Keibel and Mall.)

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.

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. The epithelial character of the cells of the parathyroid is retained during the histogenesis of the gland. (Fig. 295)

Parathyroid glands occur in all vertebrates except fishes, making their first appearance in Amphibia in which the gills have begun to degenerate. Comparison of lower with higher vertebrates reveals a progressive reduction in number but apparent increase in endocrinal importance.

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.

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.

Thymus Gland. The human thymus glands or "throat sweetbreads" are paired organs located where the throat joins the chest. They are pinkish in childhood, but in old age become yellow 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. 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.

Thymus glands first appear in a six-weeks human embryo as hollow tubular outpocketings of the third pair of pharyngeal pouches, dorsal to those of the parathyroid glands.

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. 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 amphibians the thymus 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 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.

Pituitary Gland. The human 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. (Fig. 296)

Like the suprarenals, the pituitary is formed of two elements of diverse origin and function. The chief parts are a larger anterior glandular lobe, and a smaller posterior nervous lobe 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. 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.

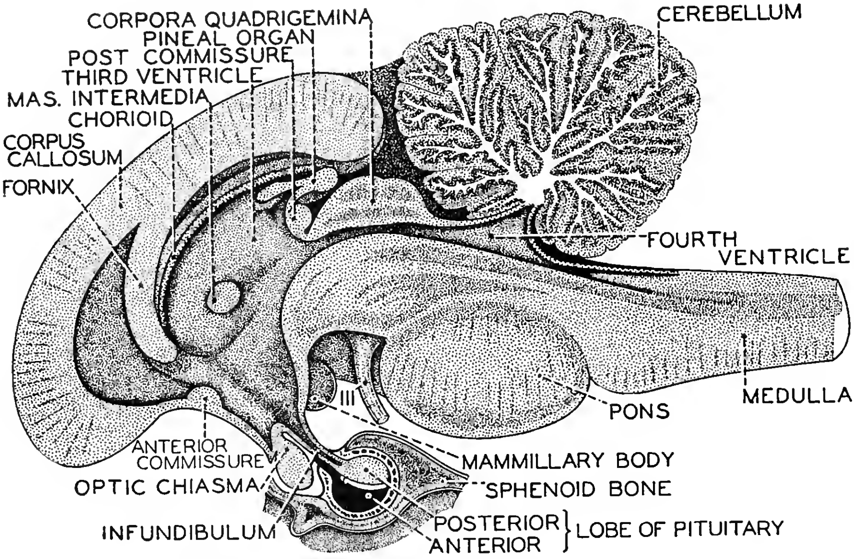


FIG. 296.—A median section of the human brain-stem, showing the relations of the pituitary gland. (After Sobotta.)

One of the important functions of the anterior lobe is the stimulation of growth. Enlarged pituitary in early life is accompanied by excessive growth of bone. Deficient secretion, on the other hand, produces a certain type of dwarf, the **ateliotic** dwarf or "midget."

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. Experiments demonstrate that deficiency of anterior lobe hormone in young animals results in failure of sexual development and atrophy of the sex glands.

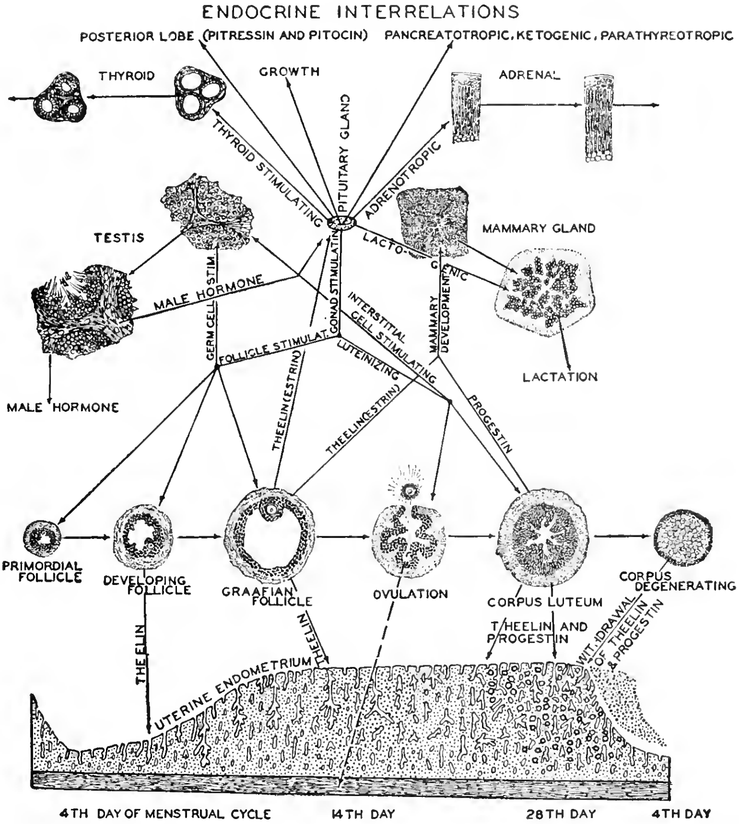


FIG. 297.—A diagram illustrating the complex interrelations of the endocrine organs. The multiplicity of pituitary influences is only partially indicated. For the sake of clearness the diagram over simplifies the relations. The pancreatropic, ketogenic, and parathyreotropic factors are not thoroughly understood. (Adapted from Therapeutic Notes through courtesy of Parke, Davis & Company.)

The pituitary gland has a double origin. The anterior lobe comes from an ectodermal sac, Rathke's pouch (hypophysis), in the roof of the mouth, while the posterior lobe is formed as an outgrowth of the base of the diencephalon. The posterior end of Rathke's pouch 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. The ventral end of the infundibulum becomes thickened as the anlage of the posterior lobe. The cells which later become differentiated as **pars intermedia** and **pars tuberalis** are derived from the anlage of the anterior lobe.

The pituitary gland occurs only in vertebrates. The elements of the pituitary make their first appearance in cyclostomes. In myxinoids (Myxine, Bdellostoma) the neural (posterior) lobe is represented 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. (Fig. 298, *A*) 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 hypophysial duct. 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. 298)

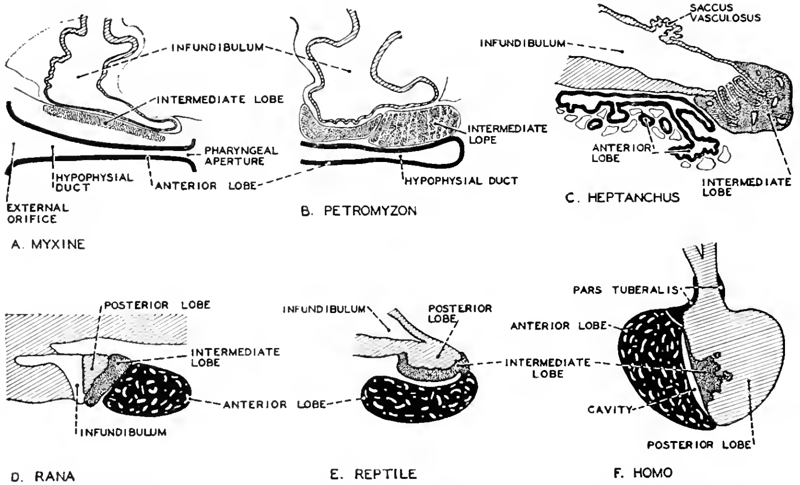


FIG. 298.—A series of diagrams showing conditions in six different vertebrates, which are believed to represent stages in the evolution of the pituitary gland. The complexity of origin of this gland is correlated with the complexity of its endocrinal functions. The posterior lobe is cross-hatched, intermediate lobe stippled, anterior (hypophysial) lobe piebald, and the pars tuberalis solid black. (Redrawn from Oppel, after Stendell.)

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 which 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 an anterior lobe, it is evident that the anterior lobe of the pituitary of Petromyzon is only partially homologous with that of higher vertebrates. The nervous lobe of the pituitary can hardly be said to exist in Petromyzon.

The evolution of these elements which have their inception in cyclostomes may be briefly summarized. In elasmobranchs the nervous portion of the gland is only slightly indicated. As one passes through the vertebrate 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 differentiation 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.

According to the view just expressed, the evolution of the hypophysis involves the metamorphosis of a tubular hypophysial duct into an endocrine 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.

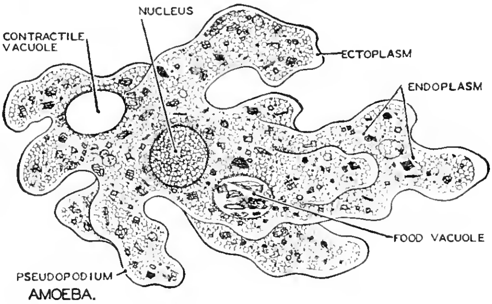


FIG. 299.—**Amoeba.** Amoeba shows primitive responsiveness to stimulation.

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 transmittor 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

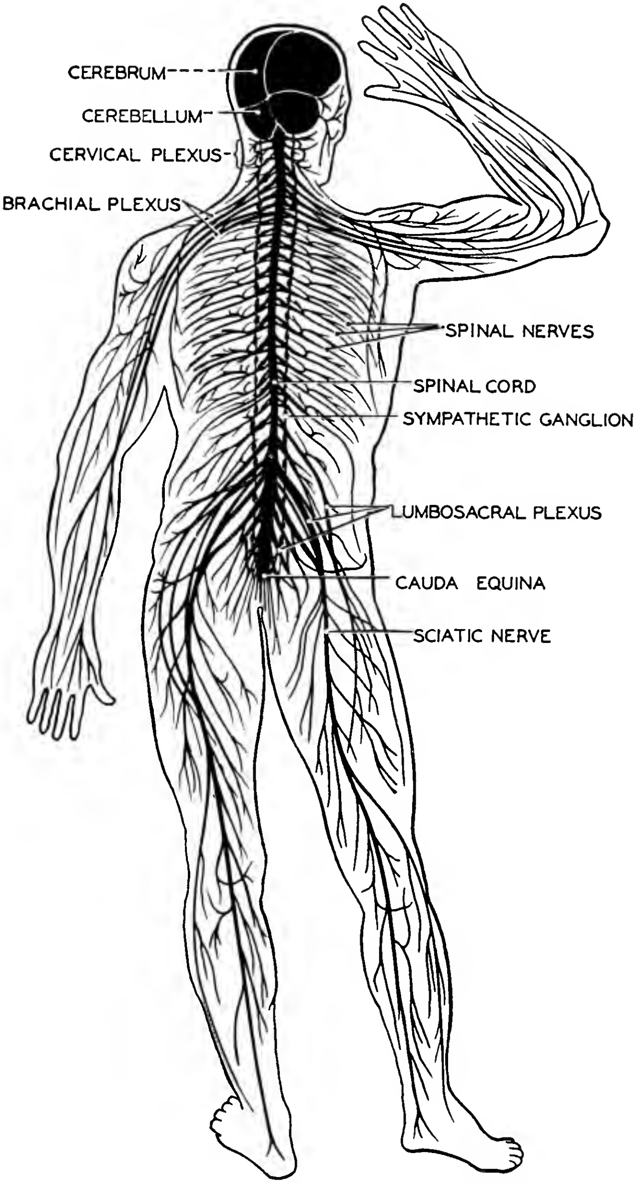


FIG. 300.—A general view of the nervous system of man as seen from behind.

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 grows away from the surface towards the underlying muscles. By branching into terminal **telodendria,** such a neurite may increase the number of its connexions.

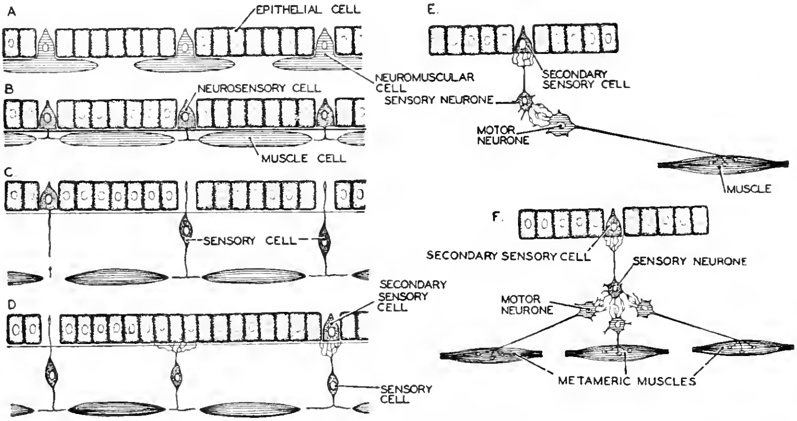


FIG. 301.—A diagram showing hypothetical stages in the evolution of the reflex arc of the higher animals. In *A* the series begins with the neuromuscular cell of coelenterates. In *B* the neurosensory cell becomes differentiated from the muscle fiber. In *C* the body of the neurosensory cell recedes from the surface. In *D* the neurosensory cell becomes a sensory neuron and a secondary sensory cell conveys external stimuli to the sensory neuron. In *E* a motor neuron is interpolated between the sensory neuron and the muscle fiber. Finally, in *F*, by means of several motor neurons, the connexion of a sensory neuron with several muscle fibers is effected. (Redrawn after Fritz Kahn, "Der Mensch," Albert Müller, Zürich.)

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. 303)

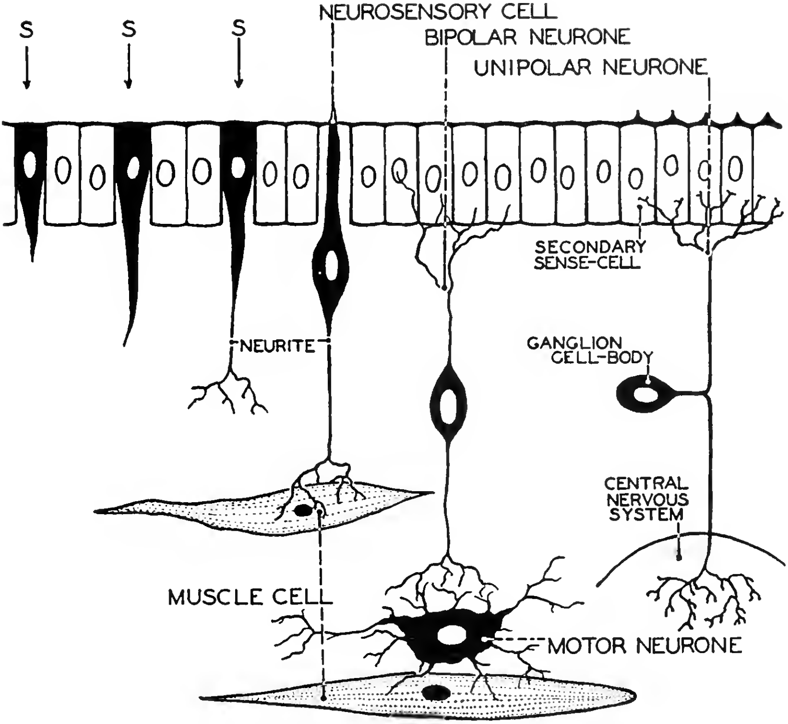


FIG. 302.—A diagram illustrating hypothetical stages in the phylogenesis of the characteristic sensory (afferent) neuron of vertebrates. Earlier stages at the left, final stage at the right. Arrows suggest that the direction of growth of the neurite is away from the source of stimulus. The diagram assumes 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.)

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, transmit nervous impulses in only one direction. In contrast with neurosensory cells, however, a neuron always 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.

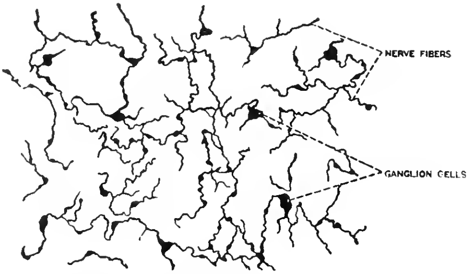


Fig. 303.—Plexus of ganglion cells and fibers in the tentacle of a coelenterate. From such a nerve-net as this it is believed that the nervous systems of higher animals have evolved. (Redrawn from Ariëns-Kappers, after Wolff.)

The differentiation of the neuron is accompanied by the appearance of two sheaths, **neurilemma** 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 neurilemma 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

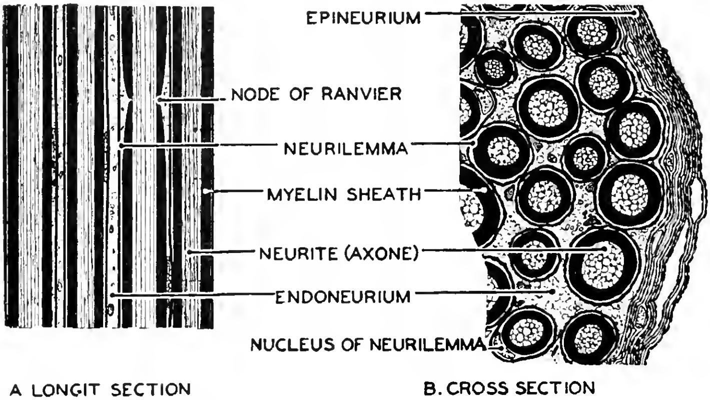


Fig. 304.—A portion of (*A*) longitudinal and (*B*) cross section of a nerve prepared by the vom Rath method. A nerve is a bundle of axons (neurites) covered by an epineurium. Each axon is surrounded by an inner myelin (fatty) sheath and an outer cellular neurilemma sheath.

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 neurilemma sheath, but are usually medullated. The presence of a neurilemma 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 neurilemma 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.

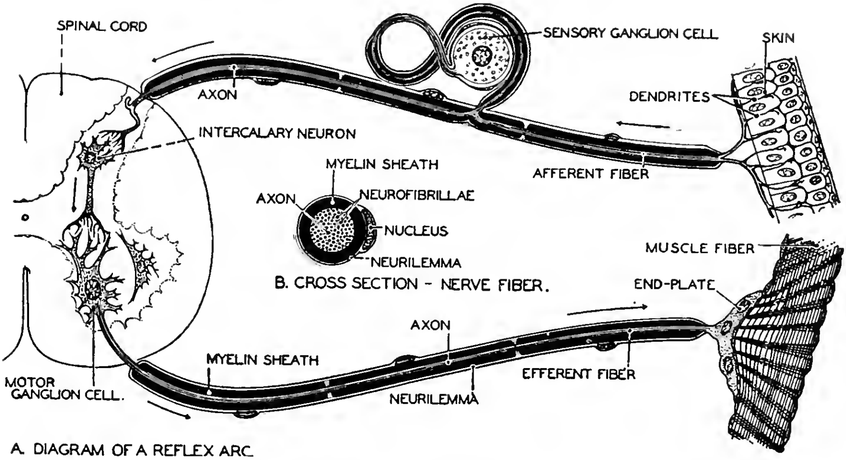


Fig. 305.—Diagram of a nervous arc. In *A* three neurons—afferent, intercalary, and efferent—are shown in their relations to one another and to the skin and muscle. The intercalary neuron is located in the gray matter of the spinal cord. *B* is an enlarged section of a nerve fiber.

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 functional relations. In ontogenesis, as in phylogenesis, all the processes of neurons are formed as processes of primarily 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, however, is 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. 305)

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 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.

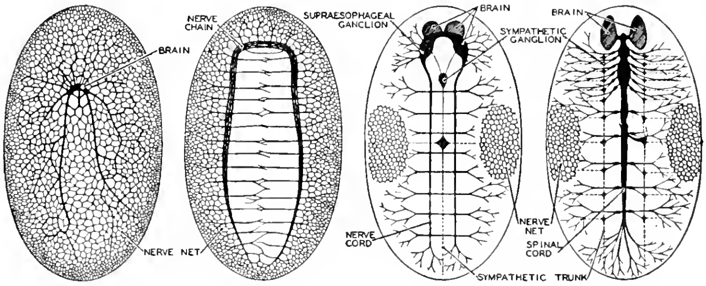
With the differentiation of a neuron having neurite and dendrites which normally convey nerve impulses in one direction only, and with tigroid bodies and neurofibrillae in its cytoplasm, the evolution of the nervous unit or **neuron** reaches its climax.

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 neurons 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.



A. LOWER FLATWORM B HIGHER FLATWORM C. ARTHROPOD D VERTEBRATE

FIG. 306.—Diagrams of the nervous system of *A*, lower flatworm, *B*, higher flatworm, *C*, arthropod, and *D*, vertebrates. The higher nerve centers are cross-hatched. The sympathetic cords are indicated by dotted lines. Many morphologists assume that the figures represent a phylogenetic series. (Redrawn after Stempell.)

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. 306)

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. (Fig. 307) 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.

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.

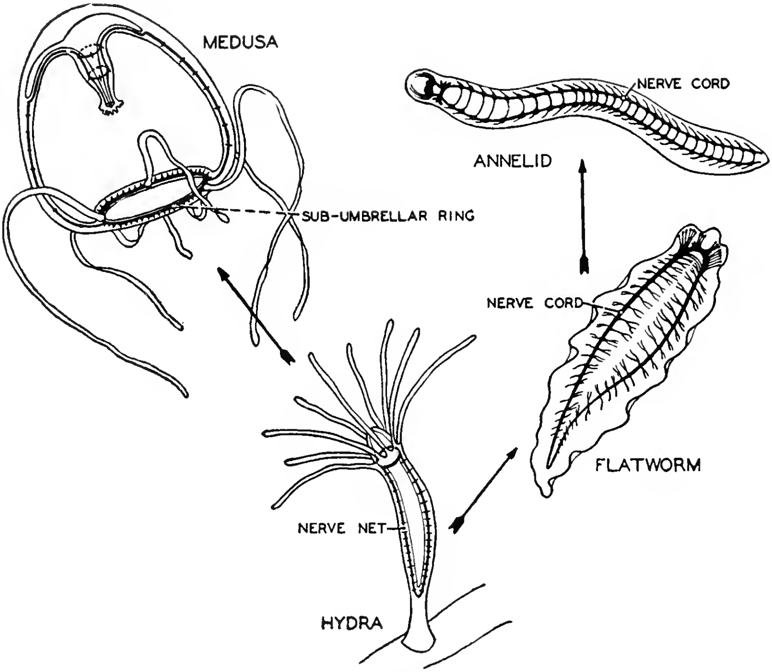


FIG. 307.—A diagram illustrating the hypothetical evolution of the nerve-net of a Hydra into the subumbrellar nerve-ring of a medusa on the one hand and into the paired nerve cords of flatworms and annelids on the other. The nerve cords are formed, it is assumed, by the concentration of the fibrillar and cellular elements of the nerve-net. (Redrawn after Fritz Kahn, "Der Mensch," Albert Müller, Zürich.)

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. 308)

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 upper 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.

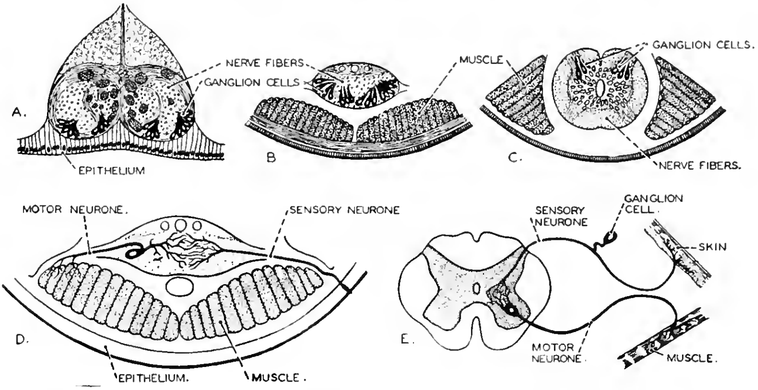


FIG. 308.—Invertebrate (annelid) and vertebrate nervous systems compared. In both sub-kingdoms the nervous system is derived from the ectoderm. The central nervous system of Sigalion (*A*) retains its original connexion with the skin. In Allolobophora (*B*), however, as in most annelids and in vertebrates (*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. (Fig. 4) 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 a 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.

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. 2, *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. 2, *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 hind-brain 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. 331)

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. 326, *A*)

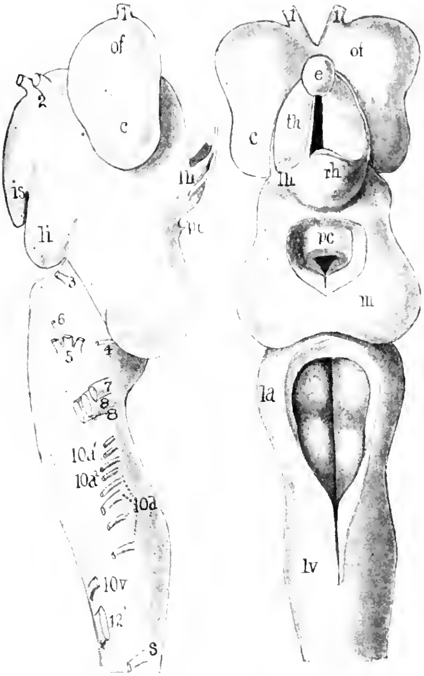


FIG. 309.—Dorsal and lateral views of the brain of Petromyzon planeri. The telae chorioideae removed, and the epiphysial structures not shown in the side view. *c*, olfactory lobes; *e*, epiphysial structures; *is*, saccular part of infundibulum; *la*, acoustic lobe; *lh*, left habenular ganglion; *li*, lobular part of infundibulum; *lv*, lobe of vagus; *m*, mid-brain; *of*, olfactory bulb; *pc*, posterior commissure; *rh*, right habenular ganglion; *s*, first spinal nerve; *th*, thalamus; 1–12, cranial nerves. (From Kingsley's "Comparative Anatomy of Vertebrates," after Ahlborn.)

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 fore-brain, which in the opinion of most morphologists corresponds to the prosencephalon of Amphioxus, becomes the telencephalon and diencephalon, the mid-brain continuing as the mesencephalon, and the original hind-brain 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. 309)

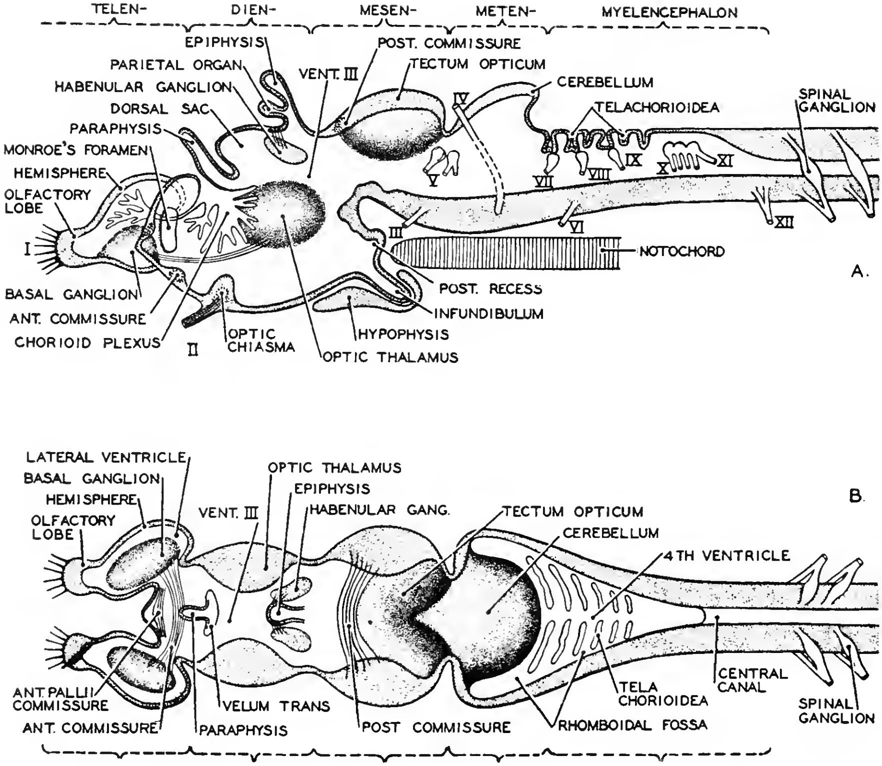


FIG. 310.—Diagrams of the vertebrate brain, based upon the brain of a cyclostome. *A* shows the brain in median longitudinal section, with nerves as if projected upon the median plane. *B* is the brain viewed from above. (Redrawn from Plate, after Bütschli.)

The **telencephalon** is paired, in correlation with the development of paired olfactory lobes. Although paired eyes develop from the fore-brain, 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. 310)

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 mid-brain is largely fibrous and is known as the **tegmentum.** The floor of the mid-brain contains the motor center of the oculomotor nerve, which innervates four of the eye muscles. The functions of the mid-brain 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 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.

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.

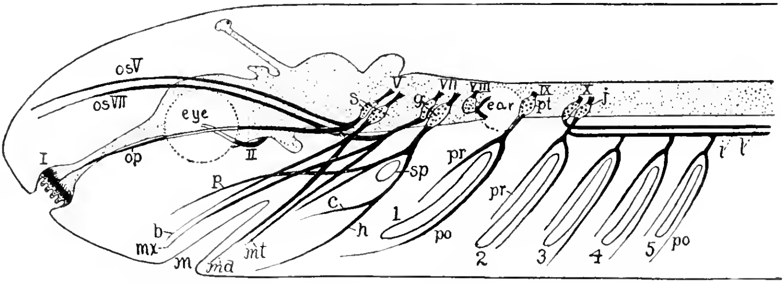


FIG. 311.—Diagram of cranial nerves of lower vertebrate. Eye-muscle nerves omitted; central nervous system dotted, fifth nerve represented as composed of two nerves; lateralis nerves separated from the ninth and tenth nerves. *I–X*, cranial nerves; 1–5, gill clefts; *b*, buccalis nerves; *c*, chorda 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; *osV*, *osVII*, 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.")

The anterior ten pairs of nerves in clycostomes 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 mid-brain, innervates four eye muscles, the 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 metencephalon 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 the nerve's root of origin from the medulla. With few exceptions, the sensory nerves of all vertebrates have similar ganglia near their roots of origin.

The **abducens** 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

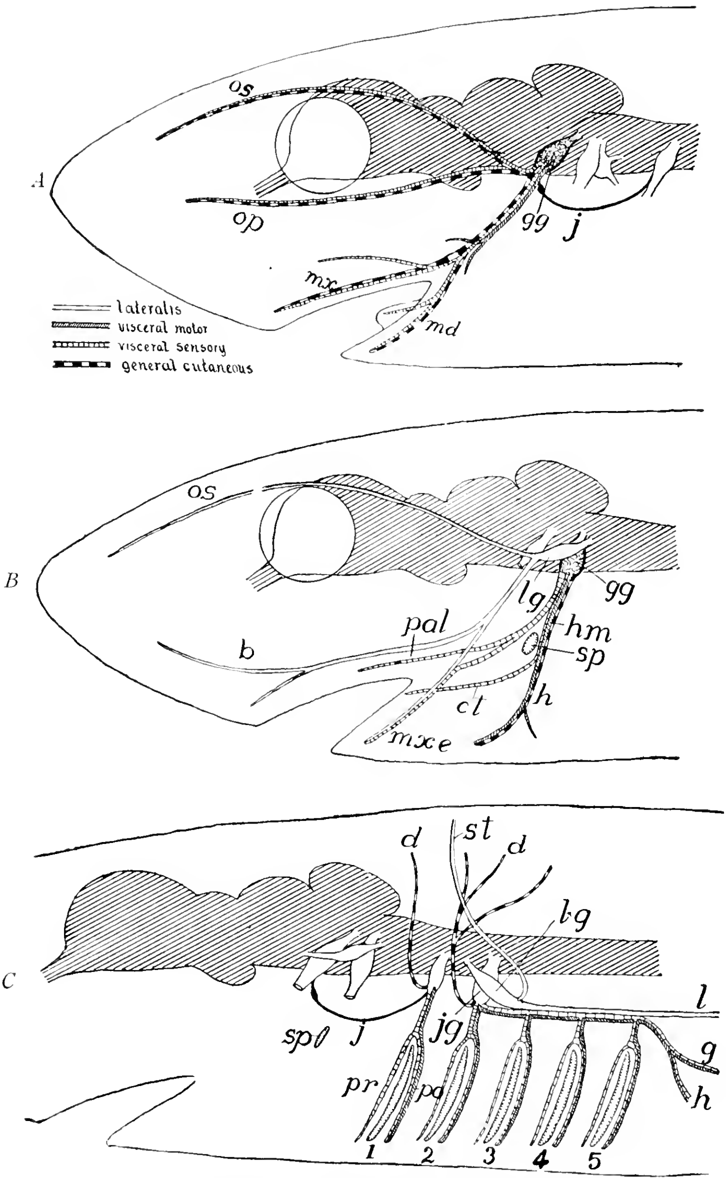


FIG. 312.—Diagrams of the branches and components of (*A*) the trigeminal, (*B*) facial, and (*C*) glossopharyngeal and vagus nerves of a lower vertebrate. *b*, buccalis nerve; *ct*, chorda tympani; *d*, dorsal rami of IX and X; *g*, gastric nerve; *gg*, in *A*, Gasserian ganglion, in *B*, geniculate 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.")

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 vesicle 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 vesicle is a modified lateral-line organ, the fibers of the auditory nerve belong to the group of **lateralis** or special somatic sensory components.

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 neurons 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.

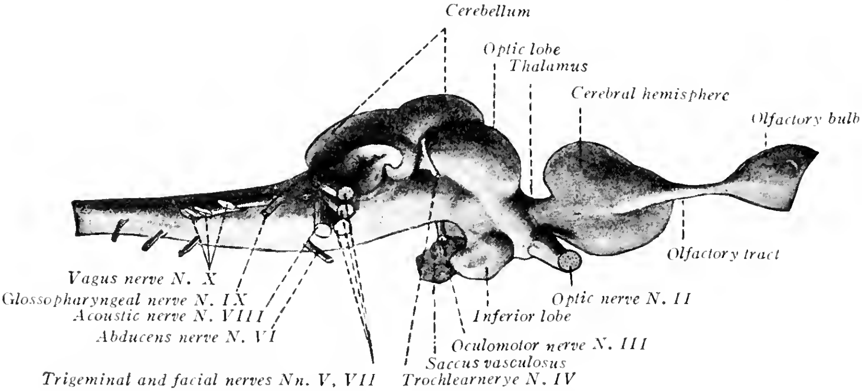


FIG. 313.—The brain of the dogfish, Squalus acanthias, lateral view. (From Ranson's "The Anatomy of the Nervous System," courtesy of W. B. Saunders Company.)

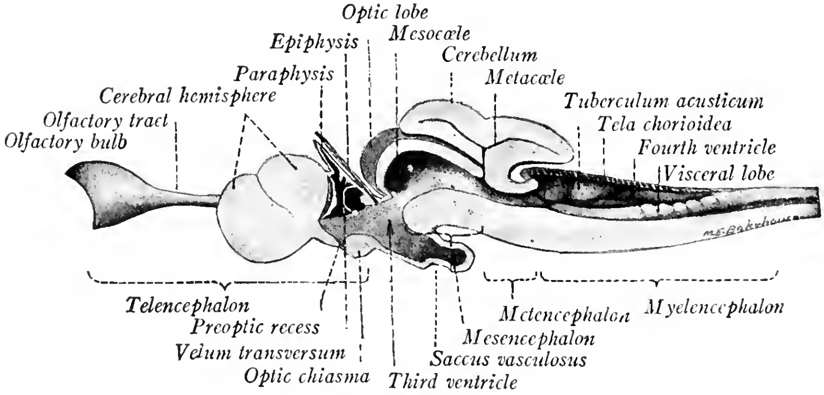


FIG. 314.—The brain of the dogfish, Squalus acanthias, medial sagittal section. (From Ranson's "The Anatomy of the Nervous System," courtesy of W. B. Saunders Company.)

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 mid-brain 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.

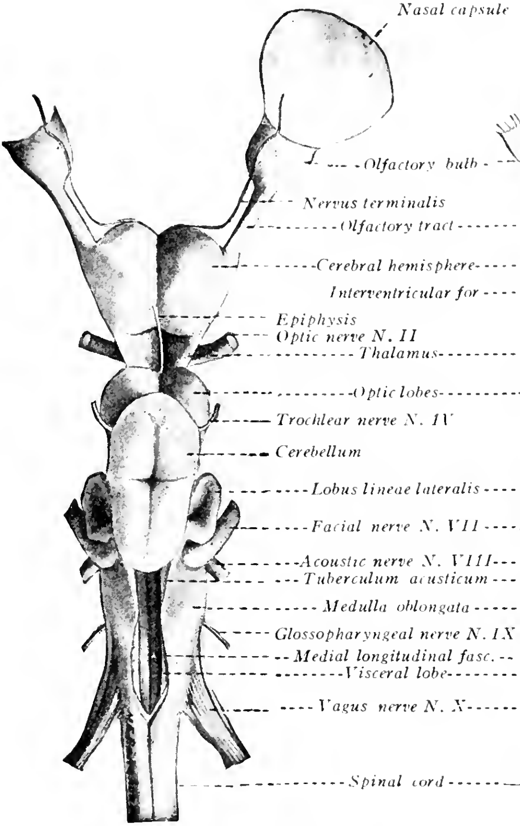


FIG. 315.—The brain of the dogfish, Squalus acanthias, dorsal view. (From Ranson's "The Anatomy of the Nervous System," courtesy of W. B. Saunders Company.)

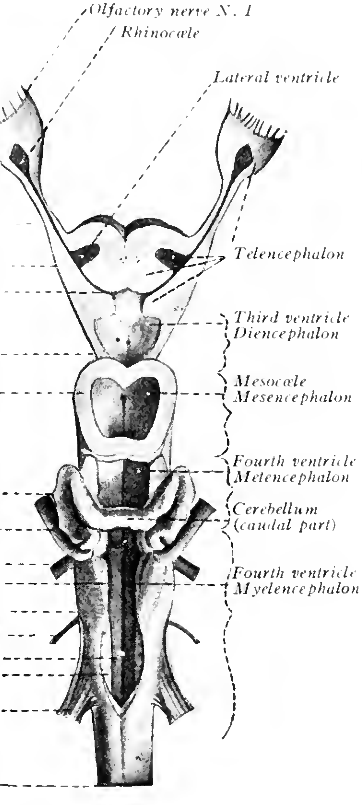


FIG. 316.—The brain of the dogfish, Squalus acanthias, with the ventricles opened, dorsal view. (From Ranson's "The Anatomy of the Nervous System," courtesy W. B. Saunders Company.)

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 neurilemma 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.

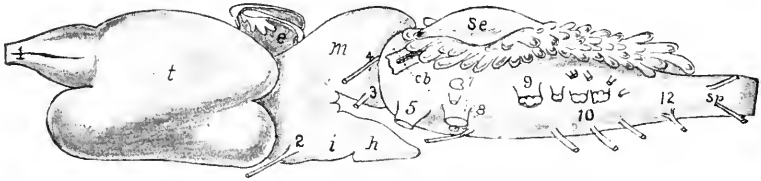


FIG. 317.—Brain of Protopterus, a dipnoan fish. *cb*, cerebellum; *e*, epiphysial structures; *h*, hypophysis; *i*, infundibulum; *m*, mid-brain; *se*, saccus endolymphaticus; *sp*, spinal nerves; *t*, cerebral hemisphere; 1–12, cranial nerves. (From Kingsley's "Comparative Anatomy of Vertebrates," after Burckhardt.)

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 dipnoans. 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,** ventral to it 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 (Fig. 324). 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 invaginates into the third ventricle. The saccus vasculosus of fishes has disappeared. The thickened walls of the mid-brain reduce the lumen to a narrow passage, the **aqueduct.** The cerebellum is rudimentary like that of cyclostomes.

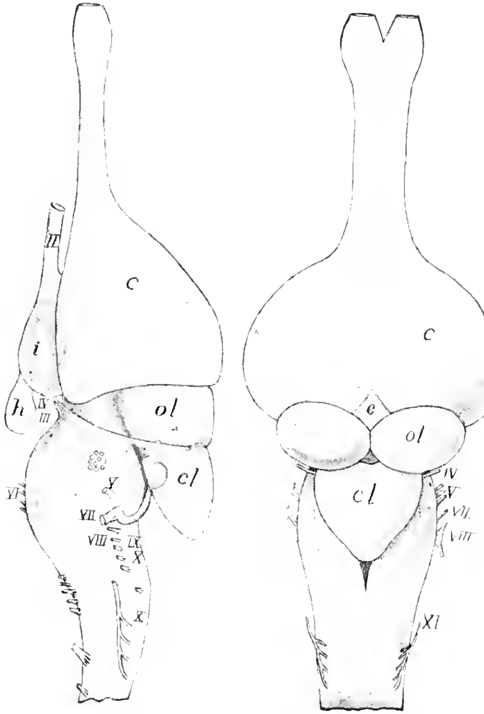


Fig. 318.—Side and dorsal views of brain of young alligator. *c*, cerebrum; *cl*, cerebellum; *e*, epiphysial structures; *h*, hypophysis; *i*, infundibulum; *ol*, optic lobes; II–XII, cranial nerves. (From Kingsley's "Comparative Anatomy of Vertebrates," after Herrick.)

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 psychic activities of man depend. (Figs. 318, 324)

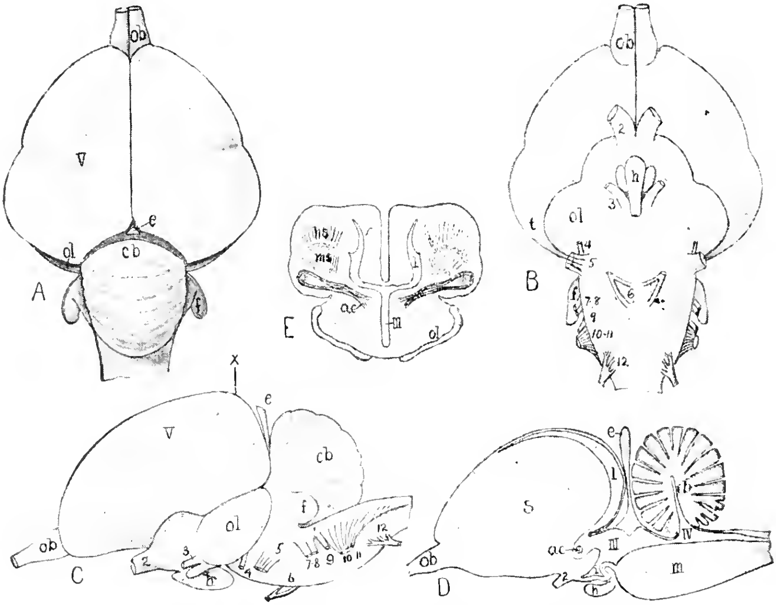


FIG. 319.—Brain of goose. *ac*, anterior commissure; *cb*, cerebellum; *e*, epiphysis; *f*, flocculus; *h*, hypophysis; *hs*, hyperstriatum; *i*, infundibulum; *l*, lateral ventricle; *m*, medulla oblongata; *ms*, mesostriatum; *ob*, olfactory bulb; *ol*, optic lobe; *s*, striatum; *t*, temporal lobe; III, third ventricle; *x*, plane of section *E*. (From Kingsley's "Comparative Anatomy of Vertebrates," after Butschli.)

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. 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 amphibians. 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, both being spinal in lower vetebrates, 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.

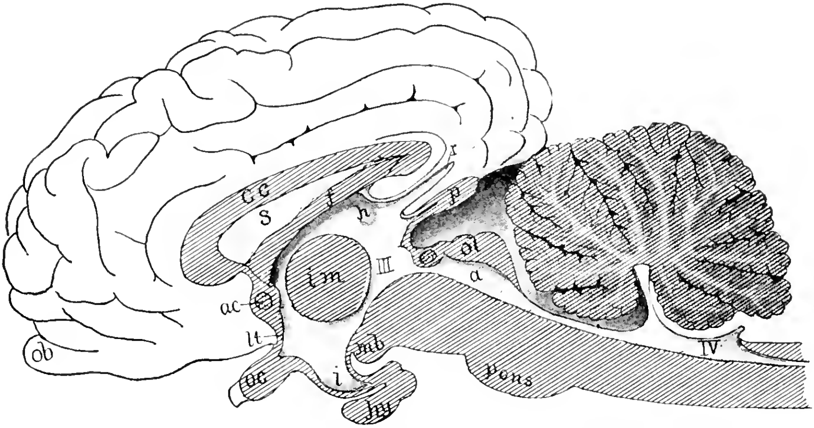


FIG. 320.—Median section of brain of calf. *a*, aqueduct; *ac*, anterior commissure; *cc*, corpus callosum; *f*, fornix; *h*, habenula; *hy*, hypophysis; *i*, infundibulum; *im*, intermediate mass ("soft commissure"); *mb*, mammillary body; *ob*, olfactory bulb; *oc*, optic chiasma; *ol*, optic lobes; *p*, pinealis; *pc*, posterior commissure; *r*, recessus suprapinealis; *s*, septum pellucidum; III, IV, third and fourth ventricles. (From Kingsley's "Comparative Anatomy of Vertebrates," based on a figure by Bütschli.)

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 mainly cellular, and consequently gray. The amount of cortical material increases many-fold, 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 layers of cells 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.

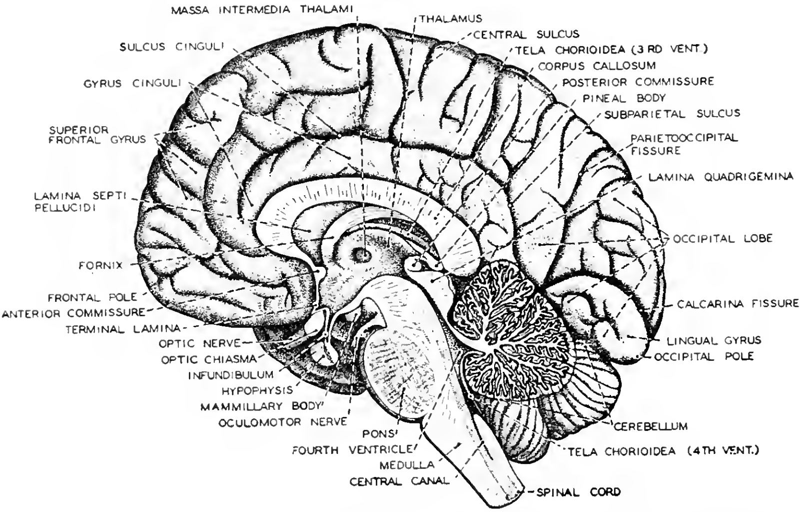


FIG. 321.—The human brain in median section and aspect. (Redrawn after Sobotta.) Besides the enormous enlargement of the cerebral hemispheres and cerebellum in the human brain, the great size of the corpus callosum and the pons Varolii is noteworthy.

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 region. 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 that of reptiles formidable. In 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 cerebral 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.

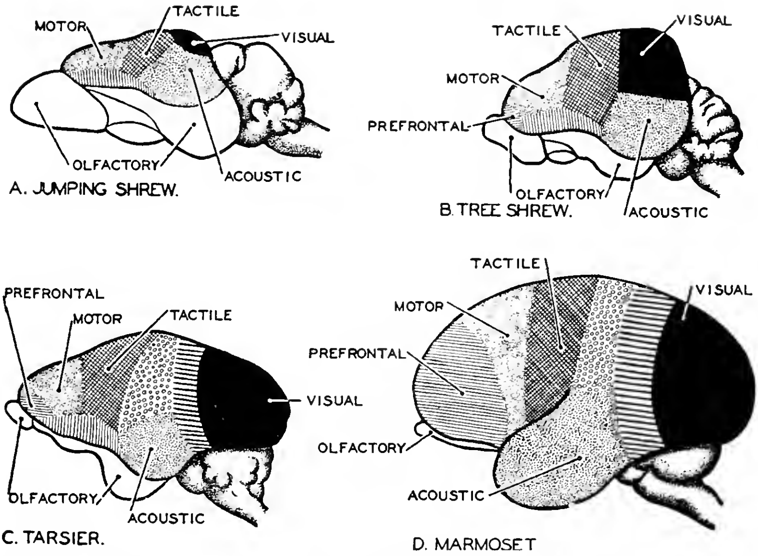


FIG. 322.—Diagrams of the brains of insectivores and of lower primates viewed from the left side. The figures show the increasing dominance of the centers of vision over those of smell. *A*, brain of jumping shrew. *B*, brain of tree shrew. *C*, brain of the primate Tarsius. *D*, brain of the marmoset. (Redrawn after G. Elliot Smith.)

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 disproportionately. Vision in primates is more important than smell, and changes in the brain express relative functional values.

Cortex. Two parts of the primitive vertebrate brain participate especially 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 dipnoans, which are more directly in the line of mammalian 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. 323)

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.** (Fig. 324)

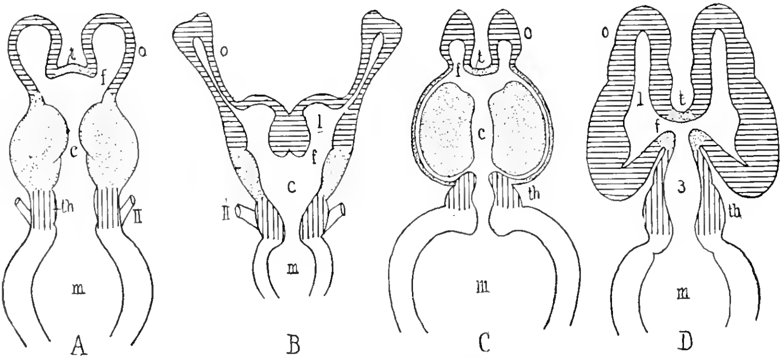


FIG. 323.—Horizontal diagrams of ichthyopsid brains. *A*, sturgeon; *B*, elasmobranch; *C*, teleost; *D*, amphibian. Primitive fore-brain wall stippled; telencephalic evaginations horizontally lined; thalamus vertical lines. *c*, common ventricle, *f*, interventricular foramen; *l*, lateral ventricle; *m*, mid-brain; *o*, olfactory bulb; *t*, terminal lamina; II, optic nerve; 3, third ventricle. (From Kingsley's "Comparative Anatomy of Vertebrates," after Herrick.)

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.

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.

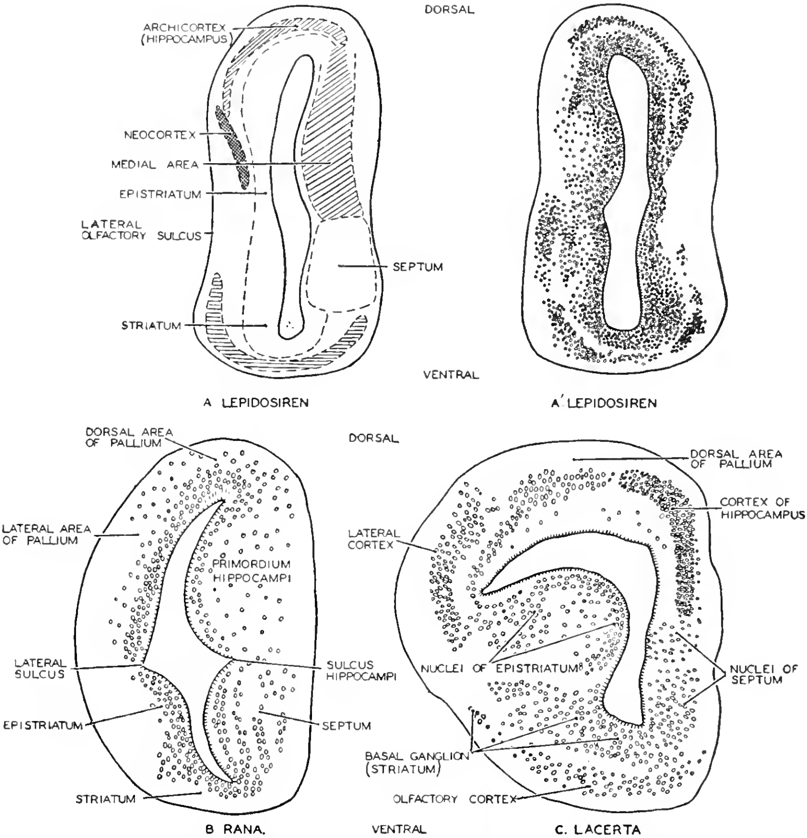


FIG. 324.—Cross sections of the left cerebral hemisphere of, *A–A'*, a fish (Lepidosiren), *B*, an amphibian (Rana), and *C*, a reptile (Lacerta), showing the increasing relative importance of the epistriatum. The epistriatum arises dorsal to the striatum as a local thickening of the ventro-lateral wall of the hemisphere. (Redrawn from Plate, after Kuhlenbeck.)

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.

Changes in the striate body (basal ganglion) are summarized in Fig. 324. In mammals each striate body extends posteriorly and rests upon the thalamus—like a sack of flour on a horse's back.

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. 325)

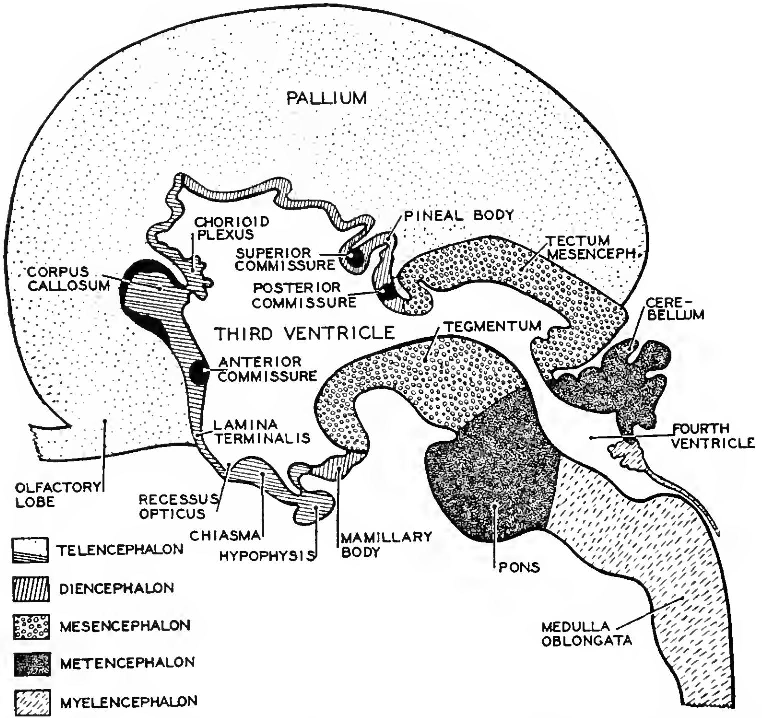


Fig. 325.—A diagram of the brain of a four-months fetus as seen in median longitudinal section. The figure shows the location of the more important brain commissures. (Redrawn from Corning's "Human Embryology," after Burckhardt.)

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 also from the hypothalamus 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 mid-brain connects the optic lobes.

In addition to the commissures, the fibers of two cranial nerves, the 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.

The dorsal commissure is lacking in fishes. In amphibians 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 neocortex. Its enlargement is correlated with that of the cerebral cortex.

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 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 the vertebrate series.

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 slit-like 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 caudad 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. 326)

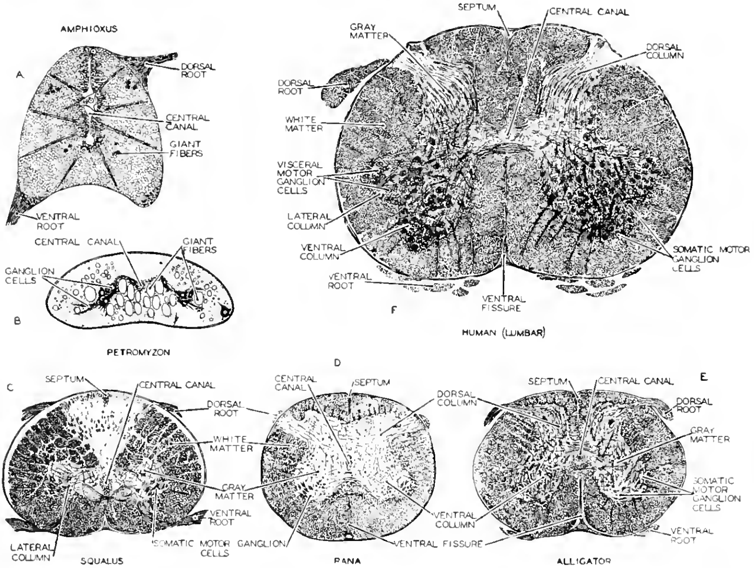


FIG. 326.—Cross sections of the spinal cord of various vertebrates:—*A*, Amphioxus; *B*, Petromyzon; *C*, Squalus; *D*, Rana; *E*, Alligator and *F*, Homo. The magnification is not to the same scale. The section of the cord of Amphioxus is enlarged four times as much as that of Petromyzon. In these two forms the axons are non-medullated. The striking differences between the cord of Amphioxus and that of man are bridged over by intermediate conditions in lower vertebrates.

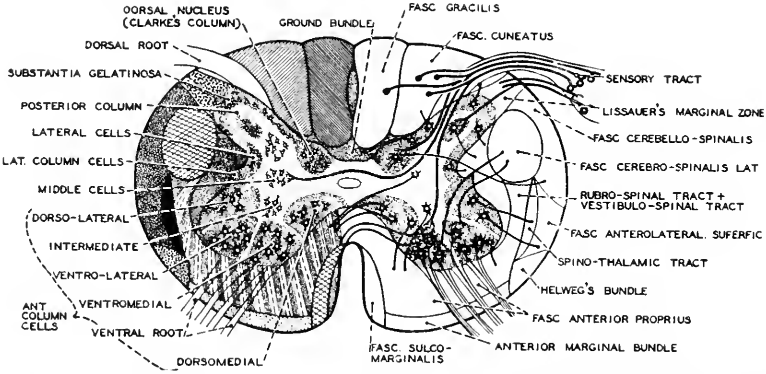


FIG. 327.—A diagram of a cross section of the spinal cord, showing the fiber tracts or fasciculi, and the arrangement of nuclei in the gray matter. (Redrawn after Sobotta.)

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 Müller'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. Relations of neuron 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. 326)

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, amphibians, 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. 326)

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 in connexion with 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. 326)

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 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 neurons located in the gray matter. The intermedio-lateral 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.

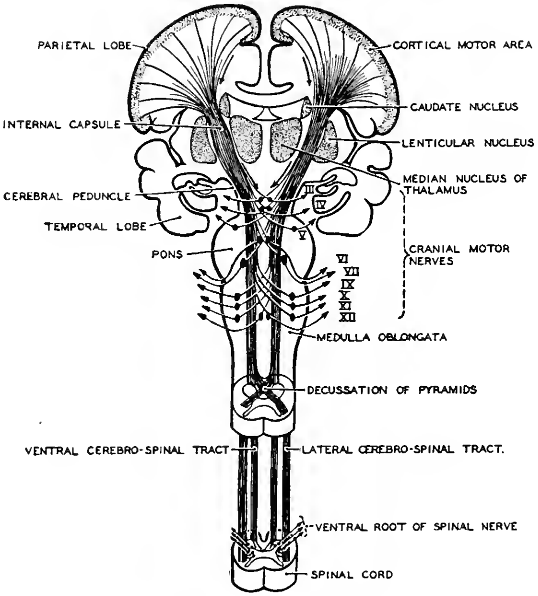


FIG. 328.—Diagram of the descending (pyramidal) conduction paths. (Redrawn after Morris.)

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

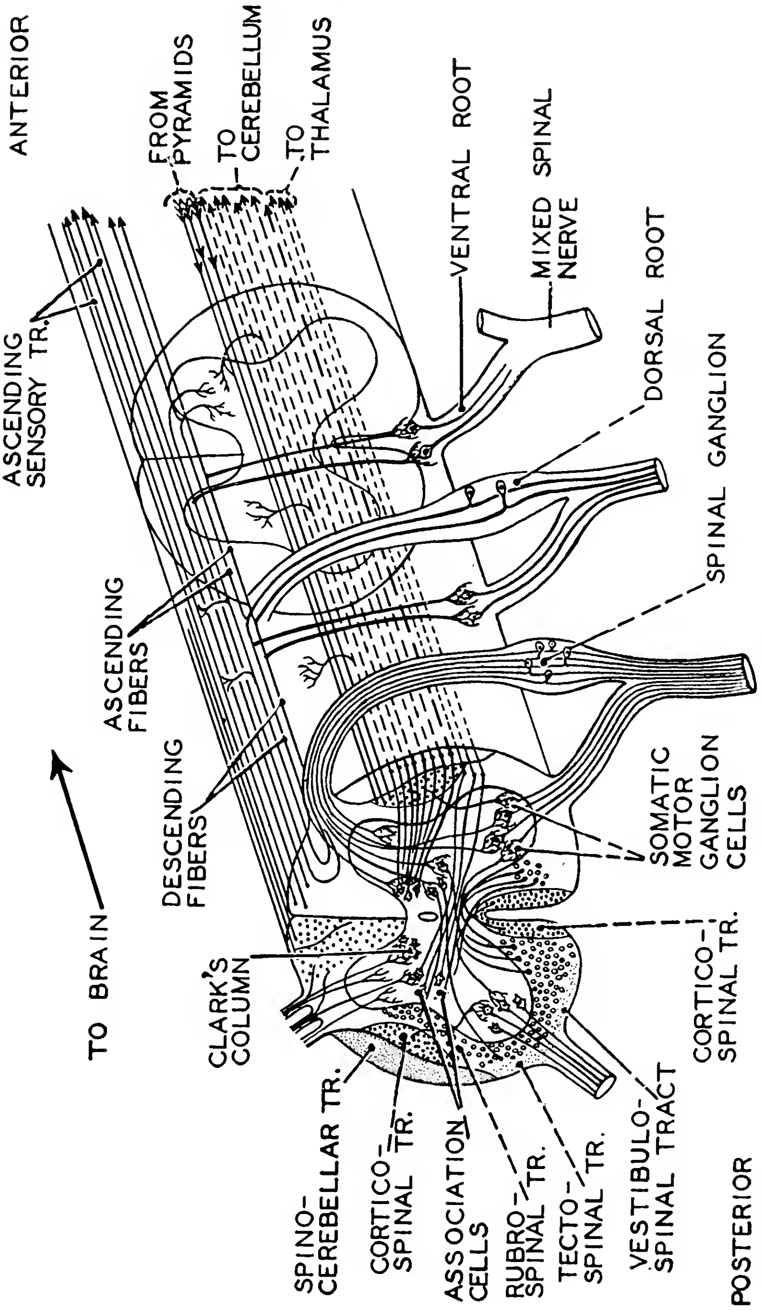


FIG. 329.—Diagram of fiber relations in spinal cord and nerves. (Redrawn after Plate.)

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. 329)

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 only two neurons 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 central 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, the nervous impulse being carried in the dorsal cerebellar tract; or they may pass to a commissural neuron, the impulse being 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 intermedio-lateral column. See Fig. 330.

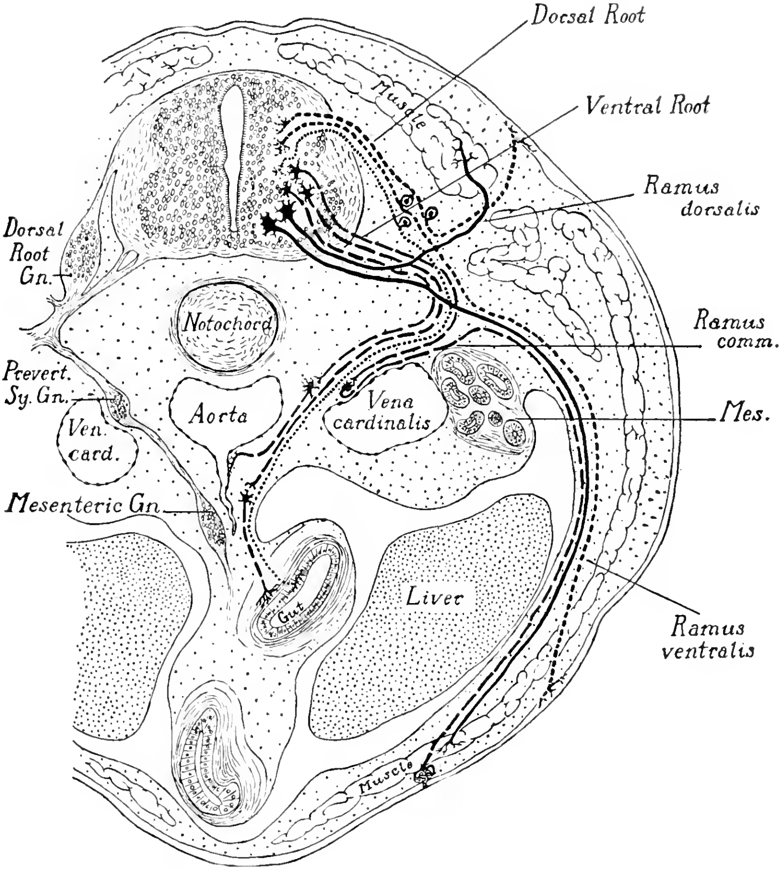


FIG. 330.—Diagram of the nerve components of a spinal nerve. Somatic motor fibers are indicated by continuous lines; visceral motor in long broken lines; somatic sensory in short broken lines; visceral sensory by fine dotted lines. (From B. Patten, after Froriep.)

EVOLUTION OF THE CRANIAL NERVES

The two anterior pairs of nerves of Amphioxus are purely sensory, while all posterior dorsal nerves are mixed. The second pair of sensory nerves of Amphioxus may be the homologues of the ophthalmic nerves of craniotes. 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.

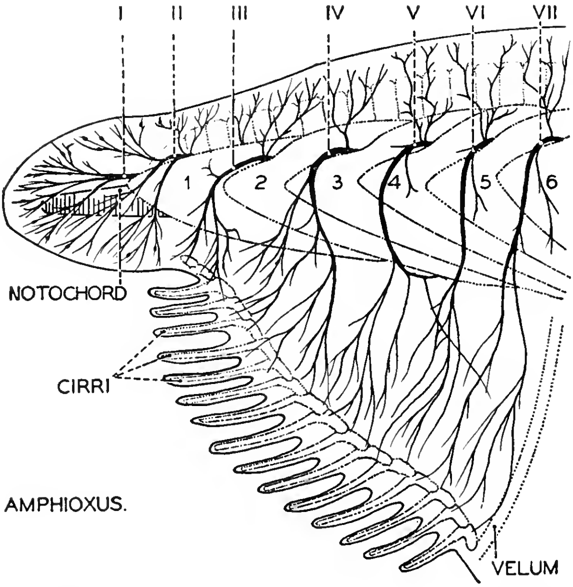


Fig. 331.—A diagram showing the distribution of the anterior nerves of Amphioxus. The two most anterior nerves of Amphioxus lie anterior to the myotomes and are purely sensory. The remaining nerves are either mixed like those shown in the figure or are purely motor. The former alternate, the diagram 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 amphibians have ten pairs; reptiles, birds, and mammals have twelve. These, beginning with the most anterior, are:

I. **Olfactory.** Special 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.

From the evolutionary standpoint it is a significant fact that man has the same ten cranial nerves as are found in fishes and amphibians. To these, two nerves are added in amniotes as a result of the addition of vertebrae to the occipital region of the skull, making twelve cranial nerves altogether in amniotes. Between fish and man in the course of phylogenesis few changes in individual cranial nerves have occurred. In all forms above cyclostomes the trochlearis has a dorsal chiasma which is lacking in cyclostomes. The factors in its formation are unknown. The ophthalmicus profundus, which is an independent nerve in cyclostomes, becomes united with the trigeminal in remaining vertebrates beginning with the elasmobranchs. With the disappearance of lateral-

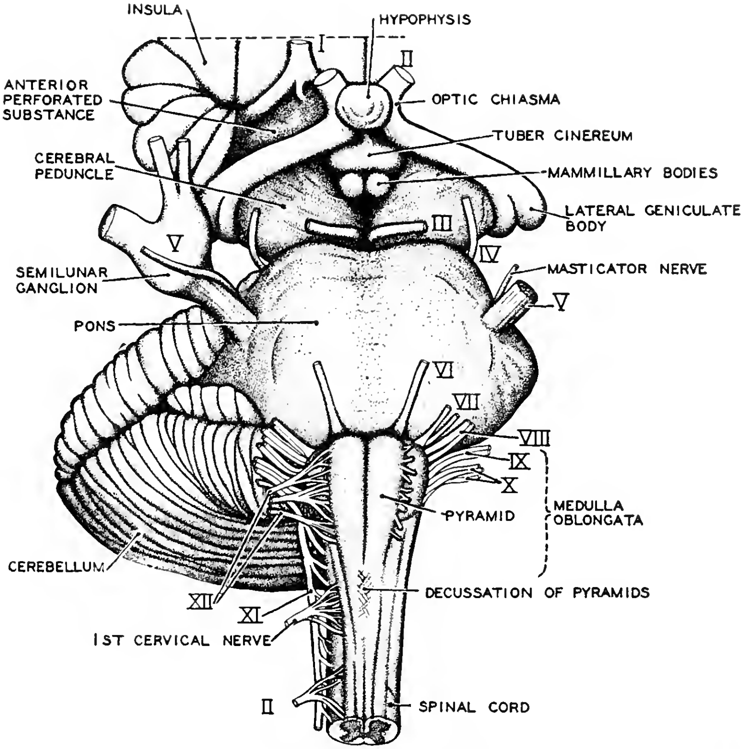


FIG. 332.—Human brain stem, showing nerve connexions. (Redrawn from Morris, after Allen Thomson.)

line organs in land animals the lateralis components of cranial nerves disappear. In mammals the facial nerve becomes largely motor. But these are all minor changes. Cranial nerves appear to be among the most conservative of vertebrate organs.

EVOLUTION OF SPINAL NERVES

Phylogenetic changes in the spinal nerves are not very great. Man has thirty-one pairs of nerves connected with the spinal cord. These are metamerically arranged just as are the nerves of Amphioxus. In Amphioxus nerves are of two sorts, dorsal (sensory and motor) and ventral (somatic motor). The two kinds alternate with one another and do not unite. Among vertebrates, however, the spinal nerves of Petromyzon alone show this primary independence. In all other vertebrates

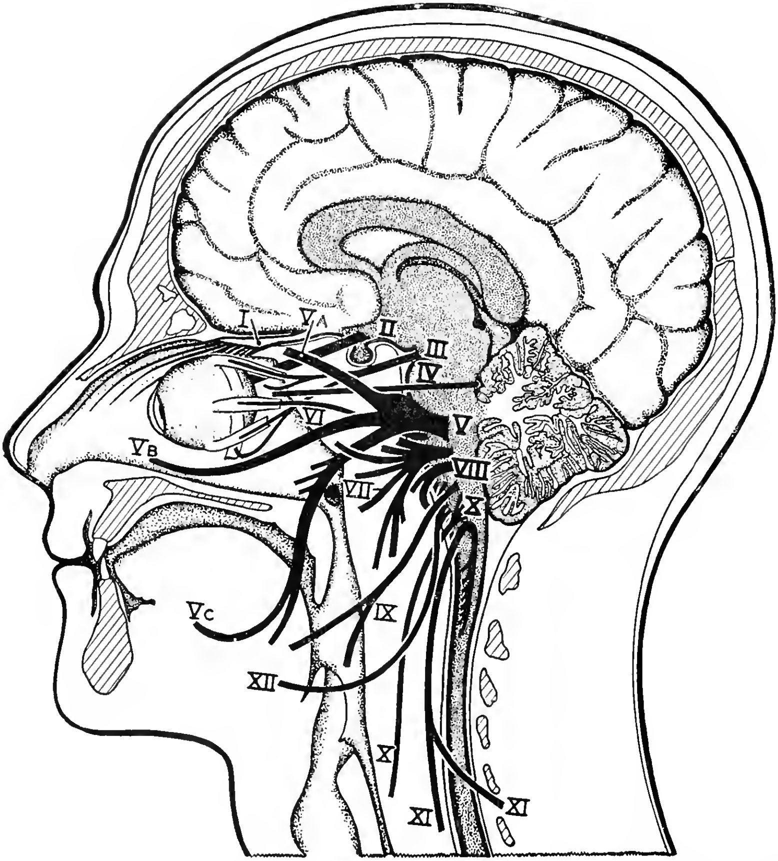


Fig. 333.—The twelve cranial nerves shown as if projected upon a median section of the head. I. Olfactory lobe. II. Optic. III. Oculomotor. IV. Trochlearis. V. Trigeminus. VI. Abducens. VII. Facialis. VIII. Acusticus. IX. Glossopharyngeus. X. Vagus. XI. Accessorius. XII. Hypoglossus.

the dorsal and the ventral nerve of each trunk segment unite to form a mixed nerve. In this way every spinal nerve possesses two "roots," a dorsal sensory and a ventral motor root.

Another phylogenetic change is the loss of motor fibers in the dorsal roots. This takes place in the vertebrate series. Anamnia retain in their dorsal spinal roots the visceral motor fibers characteristic of the dorsal nerves of Amphioxus. In amniotes, however, these visceral motor fibers have their exit from the spinal cord by way of the ventral roots. The meaning of this shift is not clear.

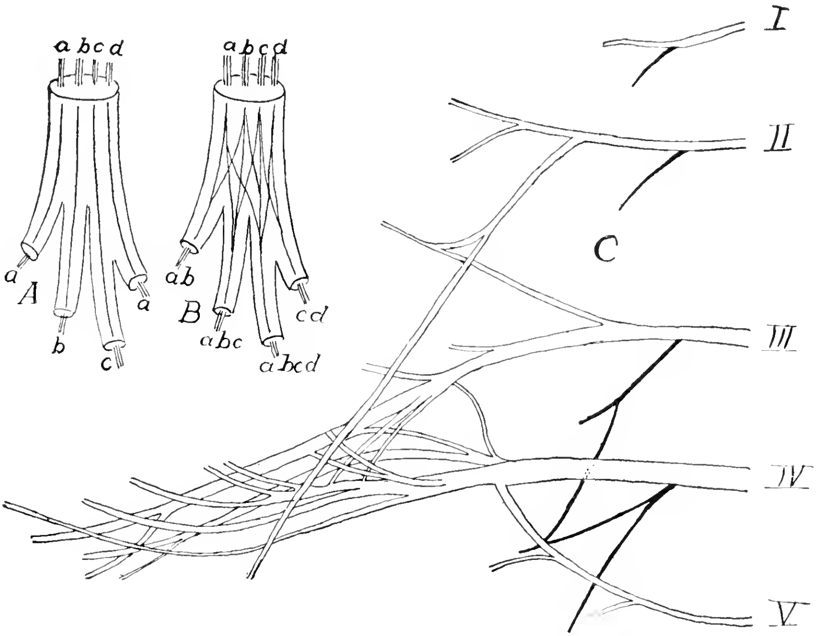


FIG. 334.—*A*, diagram of collector nerve; *B*, of a nerve plexus. (After Braus.) *C*, brachial plexus of Salamandra maculata. (From Kingsley's "Comparative Anatomy of Vertebrates," after Furbringer.)

Nerve plexuses are not found in Amphioxus. A cervical plexus appears in cyclostomes. In higher vertebrates four plexuses arise—cervical, brachial, lumbar and sacral. To form a plexus, the fibers of a number motor nerves unite in an interlaced network. In this way any muscle may be innervated by more than a single nerve and thus a summation of stimulation is effected.

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

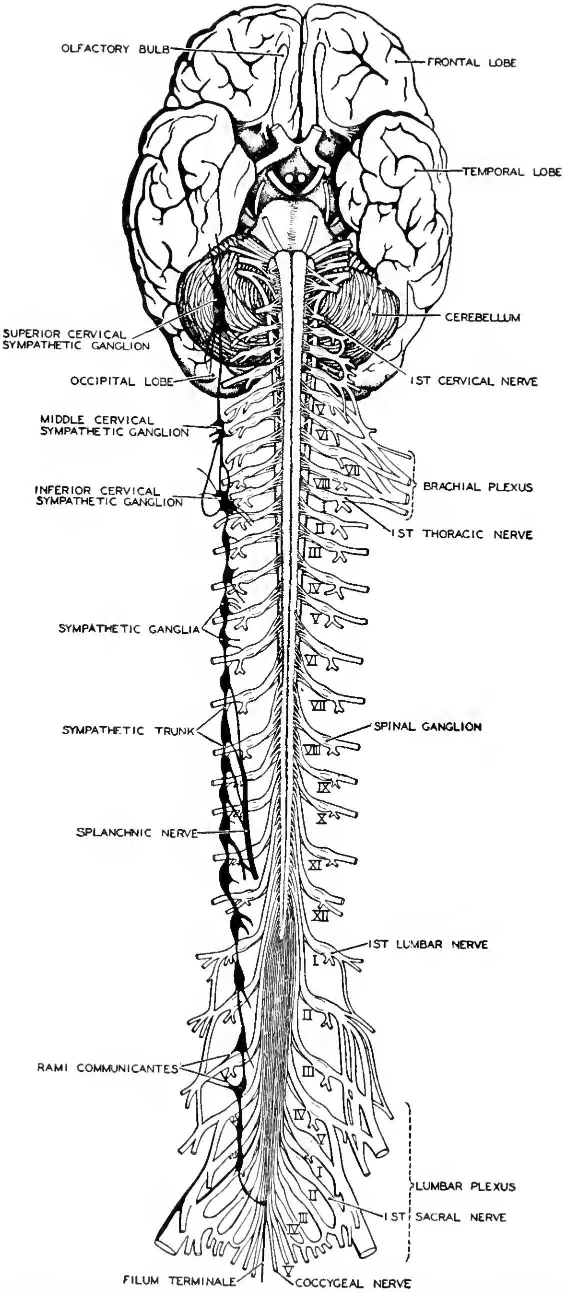


FIG. 335.—The brain and spinal cord of man, in ventral aspect, shown in relation to nerve roots and the chief autonomic ganglia. (Redrawn from Morris, after Allen Thomson.)

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 cerebro-spinal 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. 335, 336, 337)

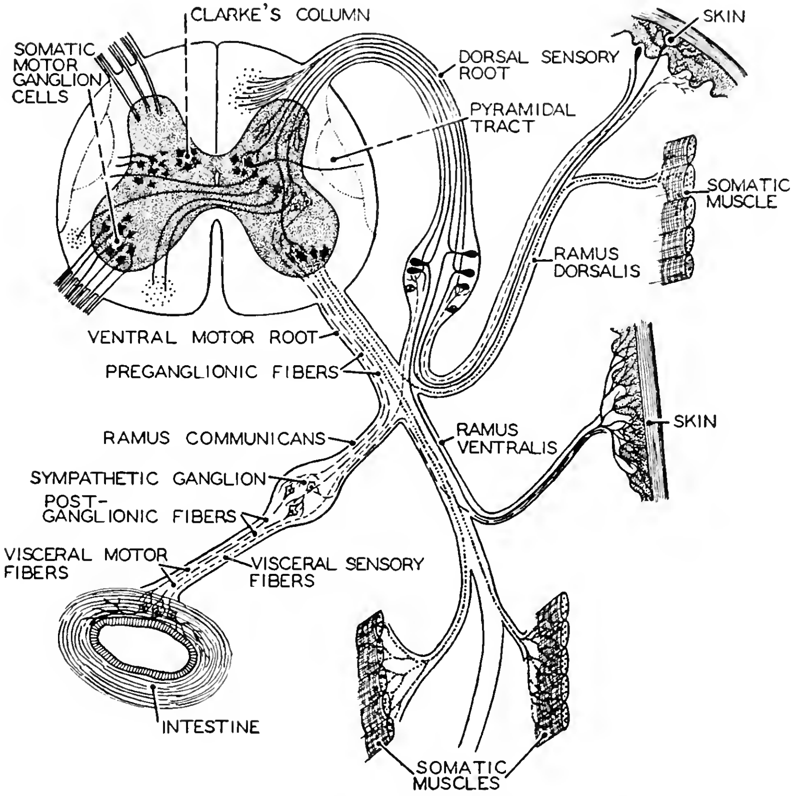


Fig. 336.—A diagram of neurons of the spinal cord and spinal nerves shown in their relations to one another and to their end-organs. Somatic sensory fibers are shown by continuous lines, somatic motor fibers by fine dots. Visceral sensory fibers are indicated by short broken lines, visceral motor by long broken lines. (Redrawn after Plate.)

Autonomic nerves are connected not only with the digestive and circulatory systems but also with respiratory and urogenital systems,

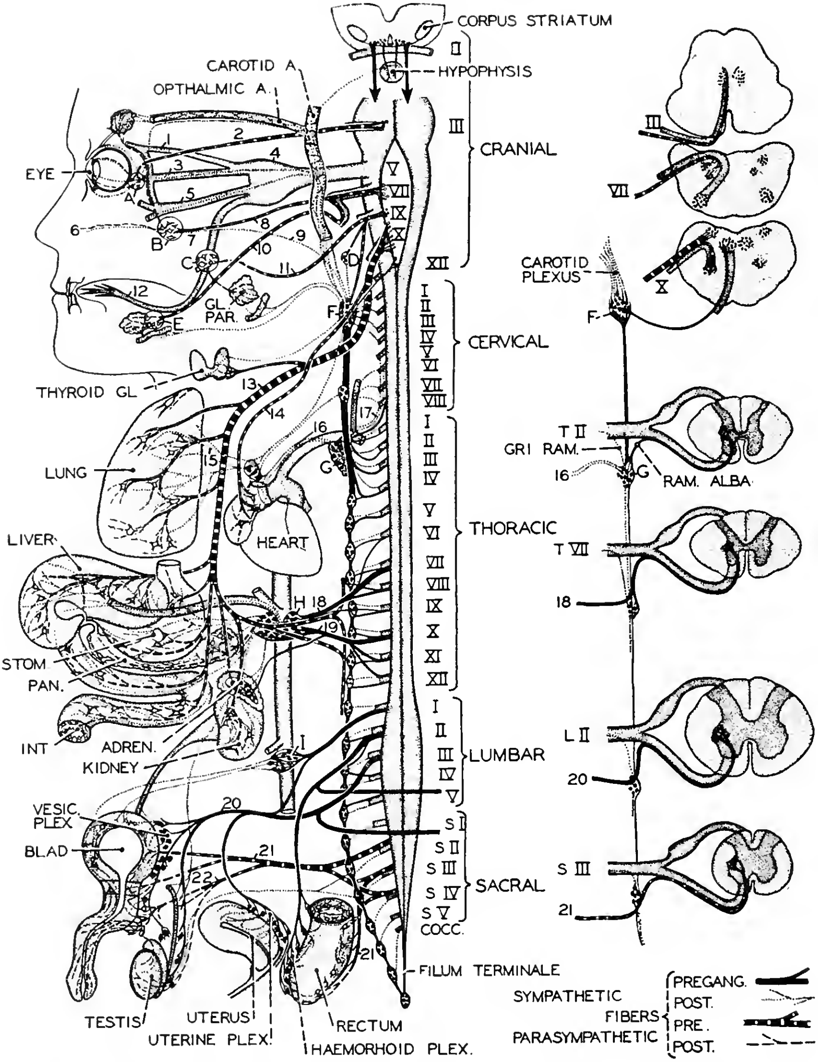


FIG. 337.—The autonomic nervous system in man. Autonomic ganglia are lettered, autonomic nerves given Arabic numerals, cranio-spinal nerves are indicated by Roman numerals. Relations to brain and spinal cord are shown to the right by a series of cross sections taken at various levels. 1, lacrimal nerve; 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, inhibitor 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*, spheno-palatine 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.)

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. 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 cranio-sacral division of the autonomic system. The thoracico-lumbar division constitutes the sympathetic portion of the autonomic system.

Autonomic nerves may be classified also, 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.

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. 117)

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. **Postganglionic** 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 postganglionic fibers are rarely medullated. They pass 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 parts 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 possible, therefore, 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 celiac 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 they 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.

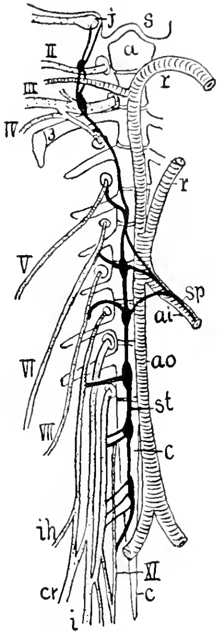


FIG. 338.—Sympathetic system of right side of a frog. Somatic nerves dotted, sympathetic black. *a*, atlas; *ai*, common intestinal artery; *ao*, aorta; *c*, coccyx; *cr*, crural nerve; *j*, jugal ganglion; *i*, sciatic nerve; *r*, radices aortae; *s*, base of skull; *sp*, splanchnic nerve; *st*, sympathetic trunk; *ih*, ilio-hypogastric nerve; II–XI, second to eleventh trunk nerves. (From Kingsley's "Comparative Anatomy of Vertebrates," after Gaupp.)

The autonomic system in tetrapods is essentially similar to that of man. A shift in the relations of the autonomic fibers occurs in phylogenesis. In Anamnia, 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 thoracicolumbar and sacral region of amniotes, on the other hand, enter the ventral or somatic motor roots. 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.

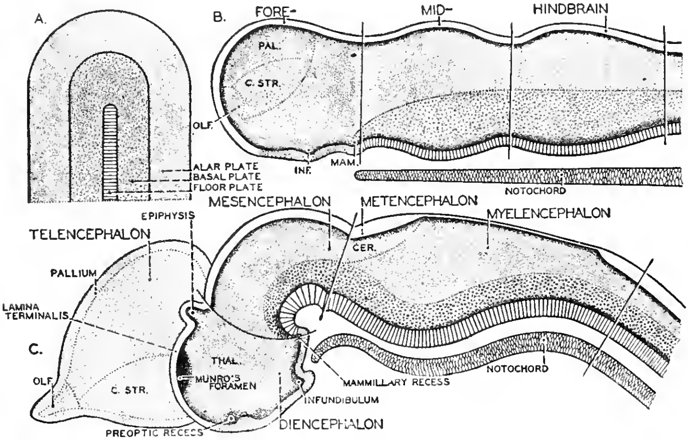


FIG. 339.—Diagrams of the development of the brain. *A*, early neural plate before closure, with zones marked; *B*, longitudinal section of early brain tube; *C*, later stage with parts differentiated. The dorsal zone (alar plate) is finely stippled; the ventral zone (basal plate) is coarsely stippled; the floor plate is cross-hatched. *Cer.*, cerebellum; *c.str.*, corpus striatum; *inf.*, infundibulum; *mam.*, mammillary recess; *olf.*, olfactory lobe; *pal.*, pallium; *thal.*, thalamus. (After Kingsbury, modified.)

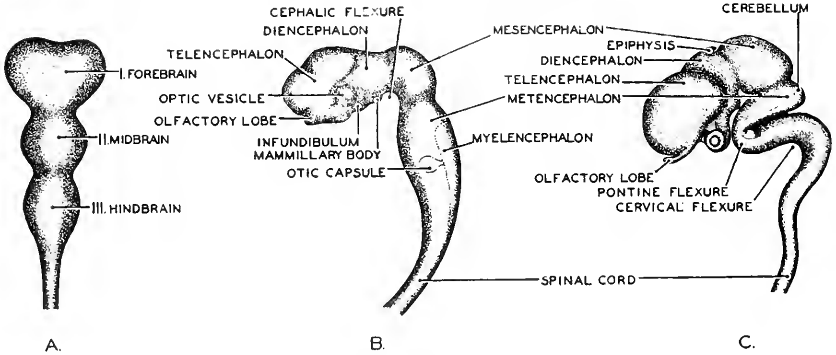


FIG. 340.—Three stages—*A*, *B*, and *C*—in the development of the human brain, showing the brain vesicles and flexures. *A* is an early stage, dorsal aspect, *B* the brain of a three-weeks embryo in lateral aspect, *C* that of an eight-weeks embryo in lateral aspect. (Redrawn after His and Hardesty.)

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 craniad and caudad. But even before the neural folds in the cephalic region unite, a series of three expansions appear, corresponding with fore-brain, mid-brain, and hind-brain, the fore-brain 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 mid-brain and hind-brain 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 mid-ventral line, and a **roof plate** in the mid-dorsal line. Since this sulcus does not develop in the fore-brain, and ends where the notochord ends, it appears that the fore-brain consists of alar and roof plates only. By the time a human embryo is a month old, the primitive fore-brain vesicle has begun to divide into the anterior **telencephalon** and posterior **diencephalon.** In a five-weeks embryo, the hind-brain has begun to divide into the anterior **metencephalon** and posterior **myelencephalon.** The undivided mid-brain is the **mesencephalon.** These five

BRAIN VESICLES AND THEIR DERIVATIVES
(After Keibel and Mall)

Primary vesicles	Secondary vesicles	Derivatives	Ventricles
Fore-brain	Telencephalon	Olfactory lobes Corpora striata Cerebral cortex Optic thalami	Lateral (1st & 2nd) ventricles Anterior part of 3rd ventricle
	Diencephalon	Epithalamus (pineal gland, etc.) Thalamus Hypothalamus Infundibulum Tuber cinereum Mammillary bodies Posterior lobe of pituitary	Posterior part of 3rd ventricle
Mid-brain	Mesencephalon	Corpora quadrigemina Tegmentum Crura cerebri (peduncles)	Aqueduct
Hind-brain	Metencephalon	Cerebellum Pons	Fourth ventricle
	Myelencephalon	Medulla	

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 mid-brain region, the other two in the region of the hind-brain. All three flexures are in a vertical plane, but the bend of the pontine is the reverse of the other two. The 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. 340)

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 mid-ventral portions remain as thin **roof** and **floor plates.**

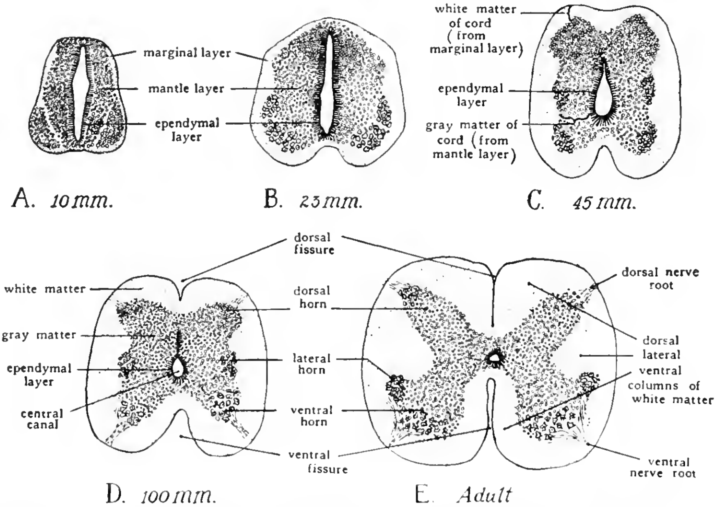


FIG. 341.—Transverse sections through spinal cord of the pig at various ages. Note especially the parts of the adult cord derived from the ependymal, mantle, and marginal layers of the embryonic neural tube. (From Patten's "Embryology of the Pig.")

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, however, 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 human 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.

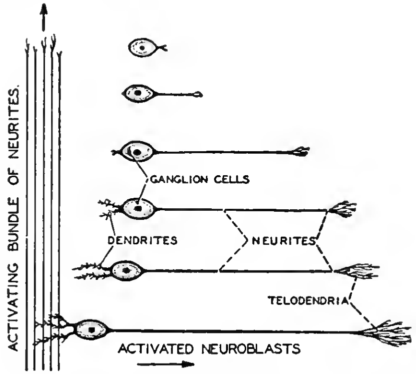


FIG. 342.—A diagram illustrating the theory of neurobiotaxis of Ariëns-Kappers. The diagram represents a series of motor neuroblast cells, lying in the wall of the spinal cord, as activated to form neurites by a longitudinal bundle of neurites. As the bundle of neurites passes a neuroblast, a stimulofugal process is formed. Later by a reverse or stimulopetal process the neuroblast is drawn towards the activating bundle and dendritic processes grow towards the bundle. Successive stages in the process are shown beginning at the top of the diagram. (Redrawn after Ariëns-Kappers.)

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 neurilemma 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 craniad and some caudad, 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. The time of myelination of fibers differs in the several tracts, depending upon the time when they begin to function. Some, such as the pyramidal, become medullated only after birth.

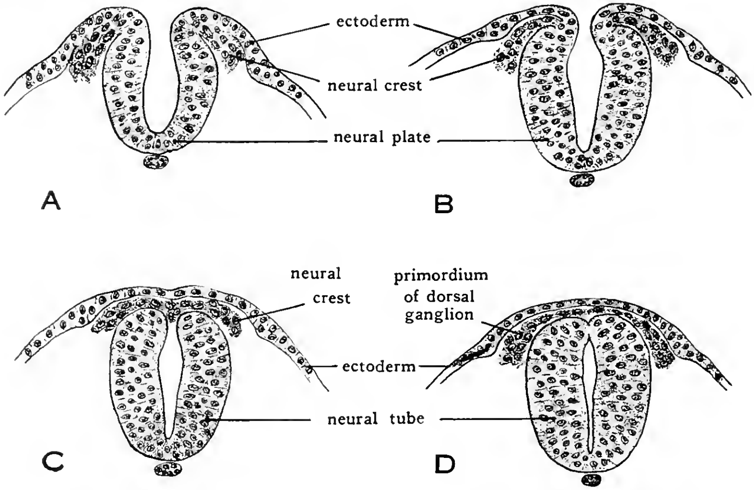


FIG. 343.—Drawing showing closure of the neural tube and formation of the neural crest. From pig embryos of:—*A*, 8 somites; *B*, 10 somites; *C*, 11 somites; *D*, 13 somites. ×135. (From Patten's "Embryology of the Pig.")

Development of Motor Nerves. How nerve and muscle become connected with one another has been a much discussed problem in biology. According to Hensen and Kerr the connexion is primary and not secondary. Nerve and muscle are assumed by them to be, like all the other cells of the body, in protoplasmic continuity which is never completely broken when cells divide. It has, however, been the general opinion of neurologists that the connexion of nerve and muscle is acquired secondarily. According to Francis Balfour chains of cells derived from the central nervous system form the motor nerves. Kupffer, however, claimed that a neurite grows out as a protoplasmic process from a motor ganglion cell and that neuro-muscular connexions are therefore secondary. Many years later Harrison demonstrated experimentally that Kupffer's assumption is correct. It is this process theory of neurogenesis which underlies Kappers' theory of neurobiotaxis.

Development of Sensory Nerves. While the neurites of cranio-spinal motor nerves are formed as outgrowths of neuroblastic cells located in the wall of the central nervous system, those of the sensory nerves are formed as processes of ganglion cells located in the sensory ganglia.

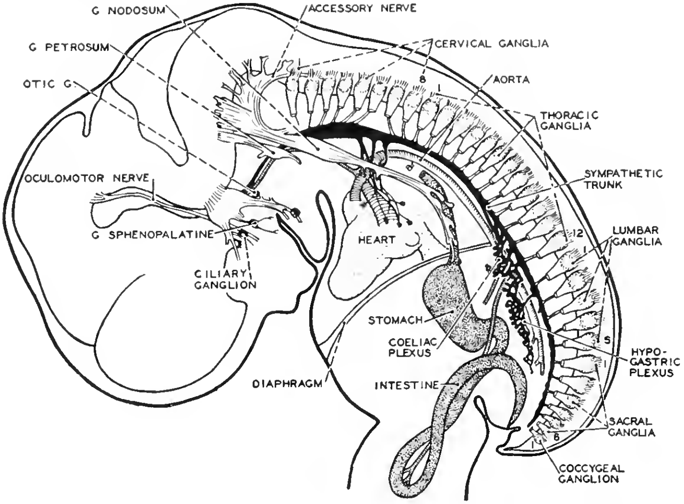


Fig. 344.—The autonomic system of a 16 mm. human embryo. The sympathetic trunk is shown in solid black. The intestine is stippled. (Redrawn from Bremer, after Streeter.)

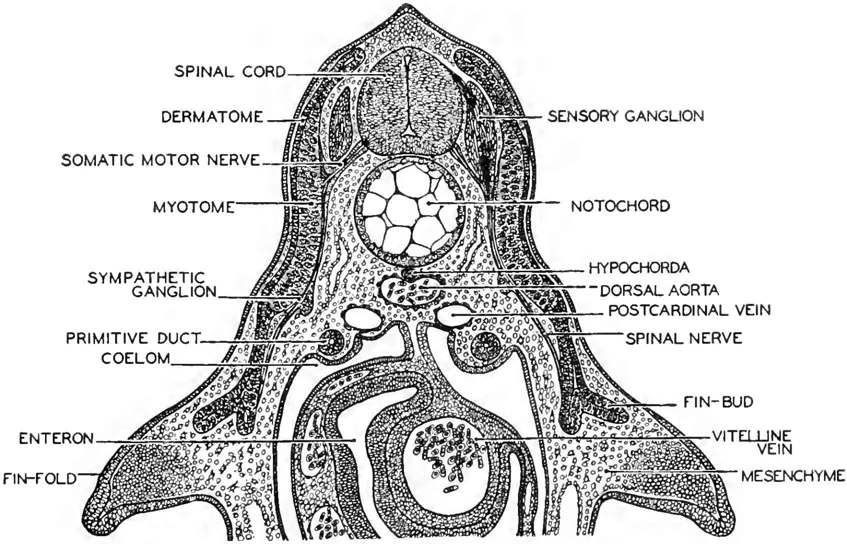


Fig. 345.—A cross section of a 17 mm. elasmobranch (Squalus) embryo, in the trunk region, showing an early stage in the formation of sympathetic ganglia. The yolk-sac to which the embryo is attached has been removed.

From each of these cells protoplasmic processes extend in two directions—one towards the central nervous system and one towards the periphery. The olfactory nerve is peculiar in its derivation from cells in the olfactory pit which extend their neurites towards the brain and hence are unipolar.

The **neural crest** is formed of cells left between the neural tube and the skin when the neural tube separates from the skin. The crest, which is primarily continuous, becomes secondarily broken up into the series of cranial and spinal ganglia.

Development of Sympathetic Ganglia. The sympathetic ganglia of vertebrates are derived, like the neurilemma cells, from the dorsal (sensory) ganglia by the migration of 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 appear as **rami communicantes.** The metameric ganglia become secondarily connected by a sympathetic cord which runs parallel with the dorsal aorta. The prevertebral plexuses, cardiac, celiac, and hypogastric, arise by the more extensive migration of cells from the ganglia of the vagus nerve.

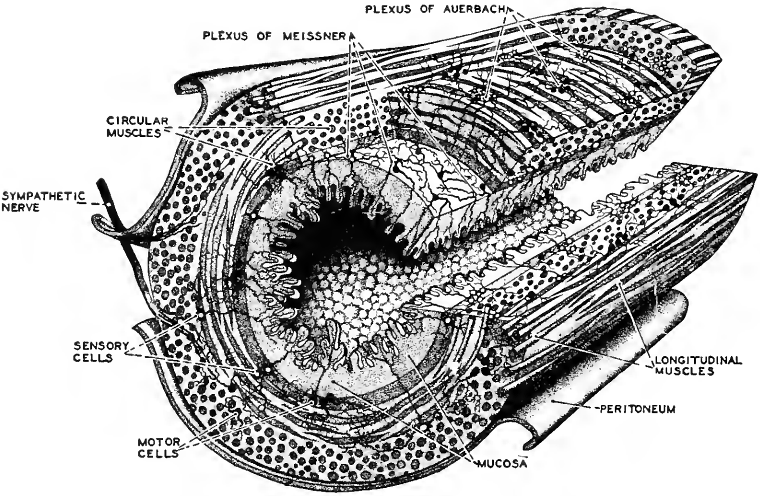


FIG. 346.—A stereogram of a portion of the small intestine, showing the arrangement of sympathetic neurons in the plexuses of Meissner and Auerbach. Motor cells are shown in black, sensory cells with white nuclei. (Redrawn after Kahn.)

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. 346)

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 vertebrae 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 organs. There it becomes the highly vascular **meninx primitiva**. Such connective-tissue membranes or **meninges**

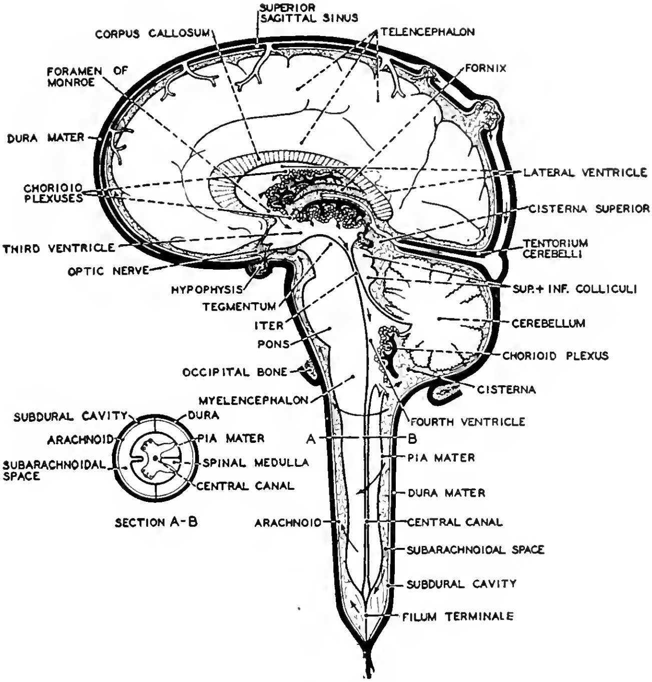


FIG. 347.—Diagram showing the relations of the meninges to the central nervous system, as shown in median longitudinal section and in cross section. (Redrawn after Rasmussen's "Principal Nervous Pathways," The Macmillan Co.)

surrounding the central nervous organs (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 carrying in blood-vessels, and supporting 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.

Vertebrates possess a considerable number of special senses. They 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 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 of an elongated process. Usually the outer termination of such a cell is beset with one or more hair-like sensory 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. Similar neurons may terminate within the underlying corium, where they may branch freely in the connective tissue, end between tactile cells, or become surrounded by a connective-tissue capsule.

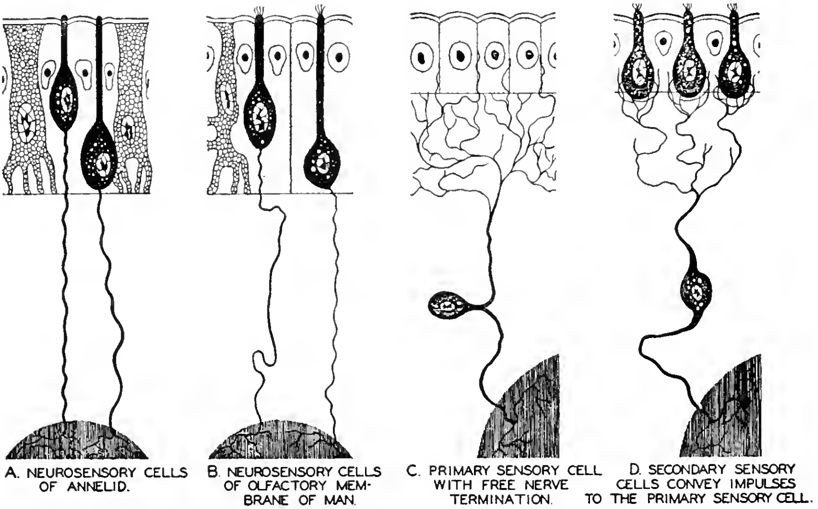


FIG. 348.—Stages in the hypothetical evolution of secondary sense cells. *A* and *B*, diagrams of neurosensory cells in invertebrate (*A*) and vertebrate (*B*). *C*, a sensory cell (neuron) with free nerve termination. *D*, secondary sense cells convey impulses to the primary sensory cell. The series assumes that the definitive receptor cells are secondary. The possibility that the neurosensory cells become the definitive sense cells and that the sensory nerve is secondary must be admitted. (Redrawn after Fritz Kahn, "Der Mensch," Albert Müller, Zürich.)

A definitive evolutionary stage is attained when a secondary sensory cell becomes the receptor element by means of 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 olfactory, the eye, and the ear.

CUTANEOUS SENSES

At least four human 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, there 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 epidermis, which by the outgrowth of neurites became 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. (Fig. 349, *A*, *C*)

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 being 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 the sensory mechanism of painful sensations arising in the skin. The sense of touch apparently depends chiefly upon the tactile cells or corpuscles in the corium, of which various forms occur.

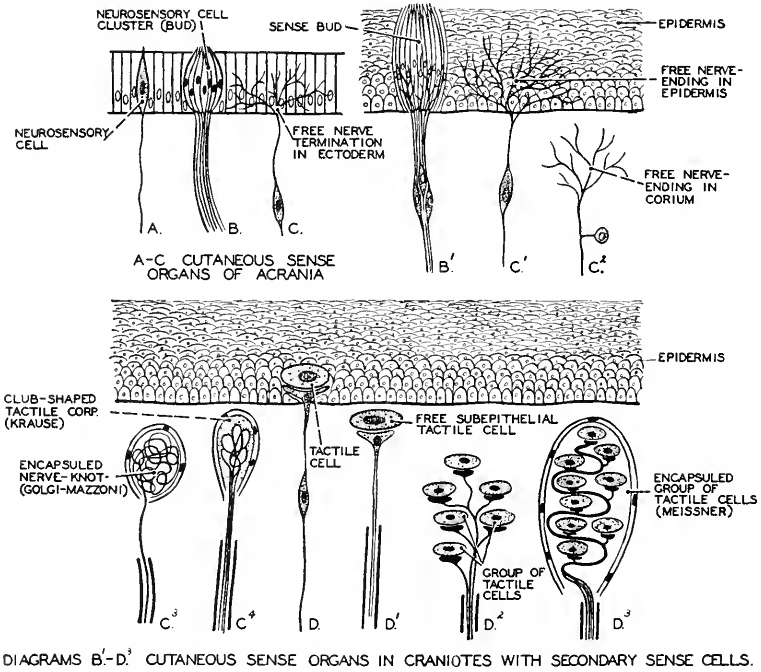


FIG. 349.—Varieties of cutaneous sense organs in chordates. *A*, *B*, *C* show sensory terminations in the skin of Acrania. *B'* to D^3 show varieties of terminations in craniotes. *C'* to C^4 and *D'* to D^4 respectively represent stages in the hypothetical evolution of encapsuled nerve terminations. (Redrawn after Plate.)

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 fiber 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.

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 amphibians. 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 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.

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 phylogenesis, however, sensory cells of the secondary type become the sensory elements of the neuromasts. How this change occurred is problematic.

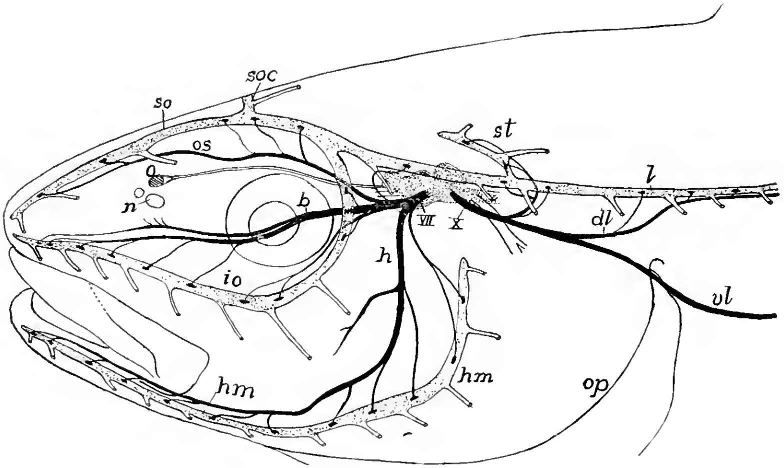


FIG. 350.—Head of pollack, showing lateral-line canals and nerves of the lateralis system. Lateralis nerves black, canals and brain dotted. *b*, buccalis ramus of VII nerve; *dl*, dorsal ramus of lateralis of X nerve; *h*, hyomandibularis nerve; *hm*, hyomandibular line of organs; *io*, infraorbital 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.)

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 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 amphibians each neuromast sinks into a separate pit. In the fishes lines of neuromasts sink below the surface. In Chimaera the grooves remain open through 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 ear appears to be derived from one or more lateral-line organs.

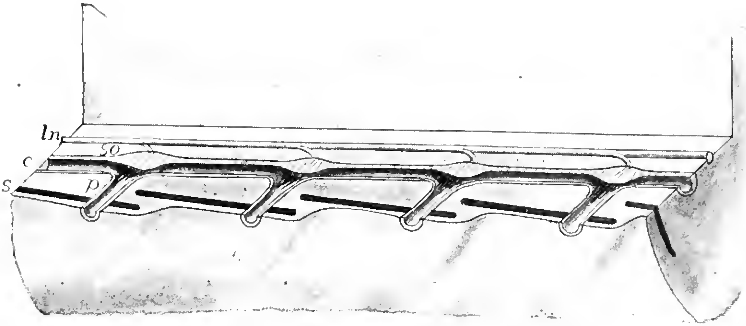


FIG. 351.—Stereogram of lateral-line organs of a fish. *c*, lateral-line canal; *ln*, lateralis nerve; *p*, pores connecting with the exterior; *s*, scales in skin; *so*, sense organs of lateral line. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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 on the tentacles, but not to food placed near the mouth. The chemical sense receptors are therefore probably neurosensory cells located in the tentacles.

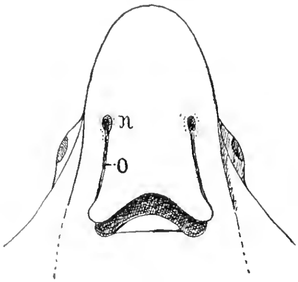


FIG. 352.—Head of a skate (Aetobatus), showing oronasal groove (*o*) leading from naris (*n*) to mouth. (From Kingsley's "Comparative Anatomy of Vertebrates," after Jordan-Evermann.)

Some flatworms search for bait placed at a distance and are therefore credited with an olfactory sense.

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.

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 into a neurite, which breaks up in numerous telodendria within the olfactory bulb.

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.

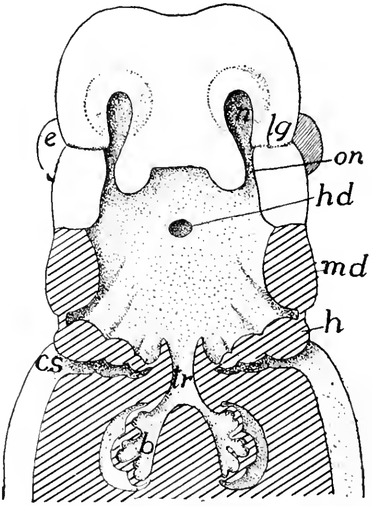


FIG. 353.—Head of human embryo with pharyngeal floor removed. Cut surfaces lined. Compare with Fig. 352; *b*, lung; *cs*, cervical sinus; *e*, eye; *h*, hyoid arch; *hd*, hypophysial duct (Rathke's pocket); *lg*, lacrimal groove, *md*, mandible; *n*. naris; *on*, oronasal groove; *tr*, trachea. (From Kingsley's "Comparative Anatomy of Vertebrates," after Hertwig.)

Amphioxus also lacks a specialized olfactory organ and does not hunt for its food, but lies buried in the sand. 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 are probably the chemoreceptors.

In cyclostomes, as in all the higher vertebrates, are paired olfactory pits and nerves. But, during development, the two pits join to form one median organ. 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 Pristiurus, 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 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 organ 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 found also in Amphibia; but the lamellated olfactory epithelium disappears as unsuited to life in the air. Nasal 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 nasal 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 nasal passage, and serves to moisten the olfactory epithelium.

Some reptiles, lizards for example, have added to the nasal 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 nasopharyngeal passage. By the formation of the palate, the nasopharyngeal cavity is both enlarged and elongated.

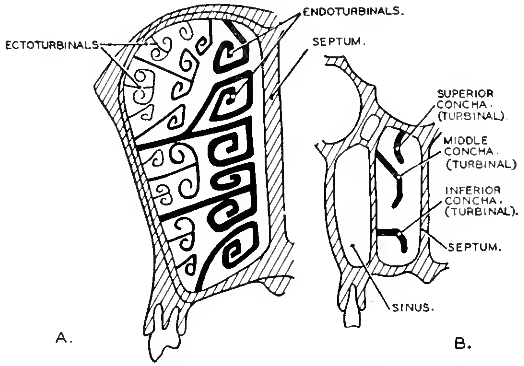


FIG. 354.—Diagrams of cross sections of the nasal passage in *A*, ruminant and *B*, man, showing the contrast in the number of turbinal bones. Since olfactory epithelium covers these bones, the keenness of the sense of smell is proportional to the number and size of turbinals. Compared with many mammals the sense of smell in man is degenerate.

In birds there are three pairs of conchae, and Jacobson's organ disappears.

In mammals there is an enormous enlargement of the nasal passages, and a corresponding multiplication of conchae, the single pair of reptilian conchae persisting as the maxillo-turbinals, while ethmo-turbinals, upper and lower, are 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. 354)

Ontogenesis. 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 telencephalic vesicle. In man a groove similar to the nasobuccal groove of elasmobranchs connects each olfactory pit with the corner of the mouth. The nasal 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 nasal passages into the mouth correspond with those of amphibians and reptiles. The secondary and definitive choanae arise 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.

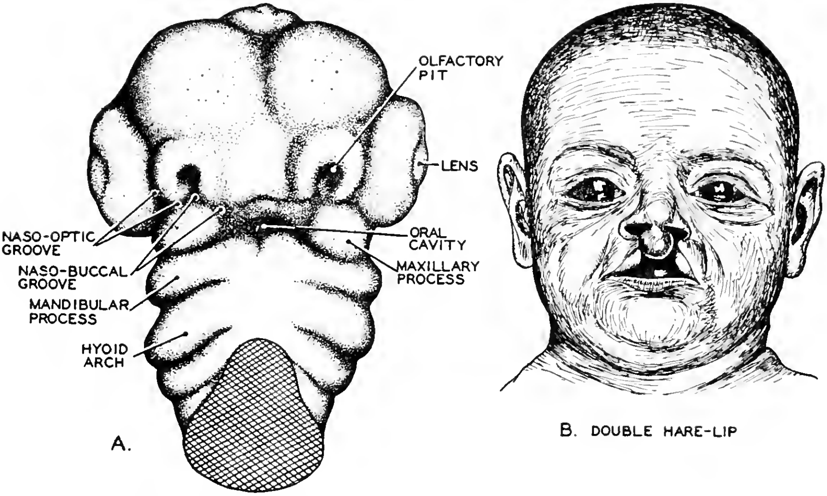


Fig. 355.—The development of the nasal passages in *A*, chick and *B*, man. In phylogenesis the nasal passages are believed to have arisen through the approximation and closure of the edges of the nasobuccal grooves. Such grooves appear in ontogenesis. Failure of such grooves to close over is the best explanation of hare-lip and perforate palate shown in *B*. In normal growth in the human embryo, however, the nasal 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.)

The inferior or maxillary conchae arise early in human ontogenesis. Five more pairs are formed by outgrowth from the ethmoid. Of these, three later disappear, leaving the maxillary and two ethmoid conchae 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 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. 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 in higher forms. (Fig. 356)

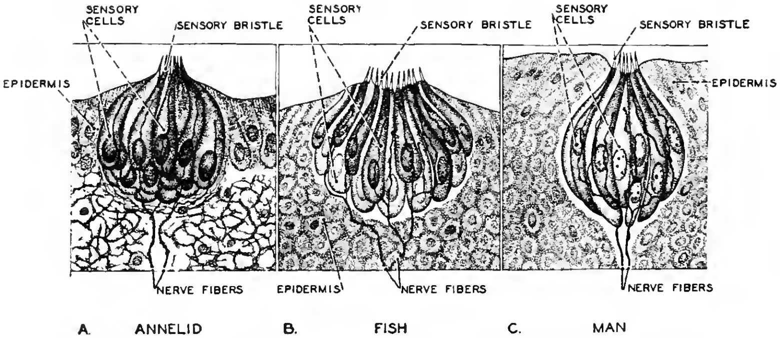


FIG. 356.—Diagrams of taste-buds in *A*, annelid, *B*, fish, and *C*, man, showing their fundamental similarity. (Redrawn after Fritz Kahn, "Der Mensch," Albert Müller, Zürich.)

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 phylogenesis 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 Ameiurus 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.

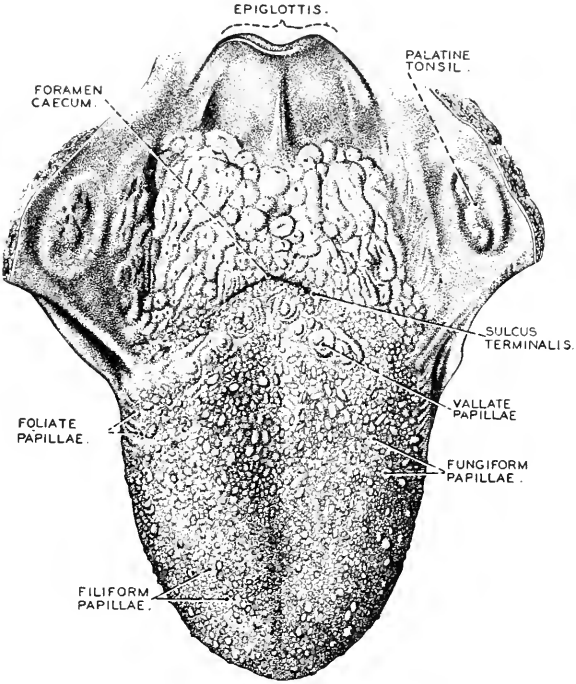


FIG. 357.—The dorsal surface of the tongue. The sulcus terminalis divides the body or apex of the tongue from the root. The two regions have a different embryonic origin. (Redrawn after Sobotta.)

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 peripheral layer are arranged like 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. 84)

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.

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, closely associated with the brain, paired pigment spots 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 among the various types of annelid eyes are so great that it is impossible to believe that the eyes are genetically related to one another.

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 of vertebrate 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 arise from 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 presumably 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 be useless.

On the other hand, we are still painfully ignorant as to the factors which started the growth of the eyes towards the skin and converted the skin into a lens. Possibly the invagination of the optic cup was primarily determined by the enlargement and ingrowth of the lens (Fig. 358). 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.

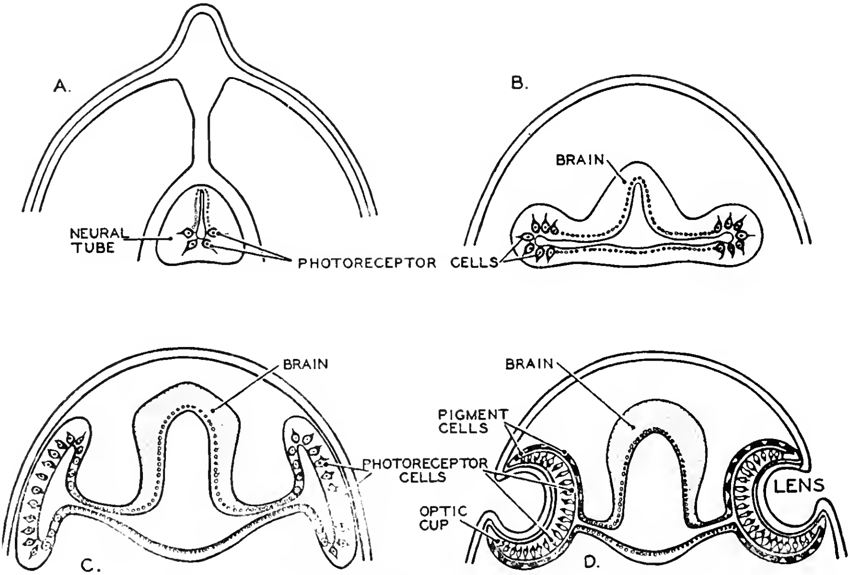


FIG. 358.—Diagrams illustrating Boveri's theory that the paired eyes of vertebrates have evolved from lateral outgrowths of the brain wall. The theory accords well with embryological evidence.

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 phylogenesis 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 of the neural plate, the eyes were carried into the fore-brain, 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, came 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. The "centers of vision," however, shift from the roof of the mid-brain to the occipital lobes of the cerebral hemispheres, where they are located in mammals. But the mid-brain of mammals persists as a reflex center. 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.

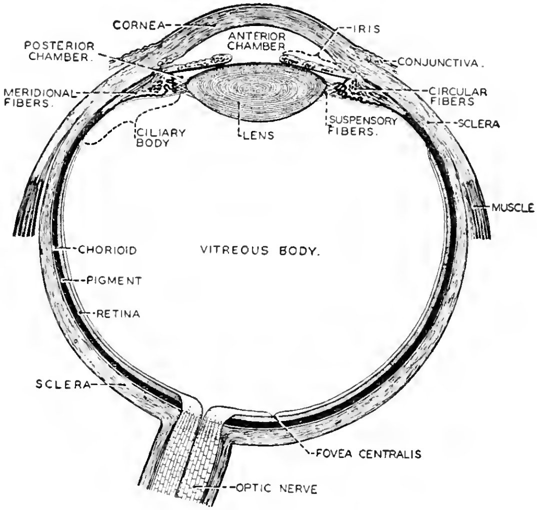


FIG. 359.—A diagram of a median section of the eye. (Redrawn after Sobotta.)

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** or **body.** 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.

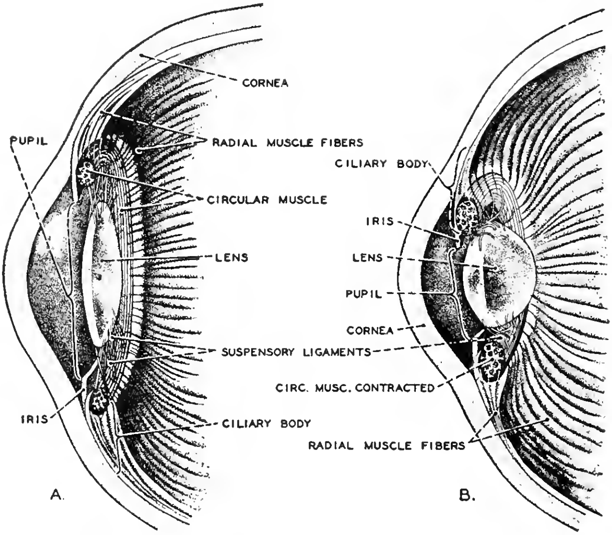


Fig. 360.—A diagram illustrating the mechanism of accommodation of the eye by means of the change of shape of the lens. The lens is flattened through the tension of the suspensory ligaments. When the circular muscle of the iris contracts, tension is relaxed and the lens assumes a more nearly spherical shape as a result of its natural elasticity. *A* shows the lens adapted for distant vision, *B* the accommodation of the lens for near vision. (Redrawn after Fritz Kahn, "Der Mensch," Albert Müller, Zürich.)

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.

The **retina** lines the cavity of the eye-ball, 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. 361)

By using special nerve stains, such as that of Golgi, the retina has been found to consist of three layers of neurons chained together and connected with the brain by the optic nerve. One set of neurons, 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 neurons 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.

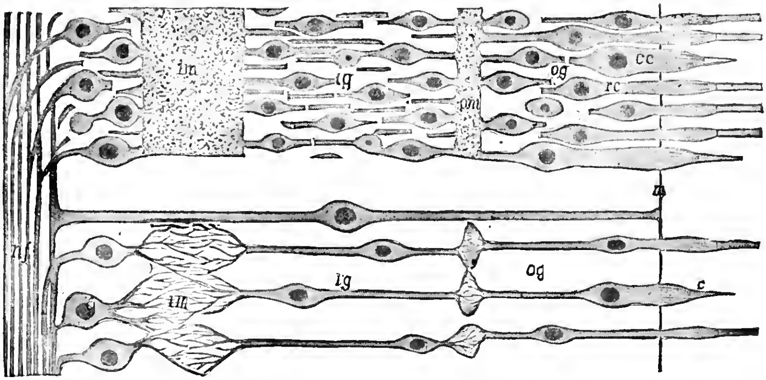


FIG. 361.—Mammalian retina; above, the general appearance, below the diagrammatic relations; the lens toward the left. *c*, cone; *cc*, cone cell; *g*, ganglion cells; *ig*, inner granular layer; *im*, inner molecular layer; *m*, basal membrane; *nf*, nerve fibres; *og*, outer granular layer; *om*, outer molecular layer; *r*, rod; *rc*, rod cell. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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 thalamus of the opposite side of the brain and half to that of the same side. The sensory centers of vision of mammals are located in the occipital lobes.

The outer layer of the eye-ball 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.

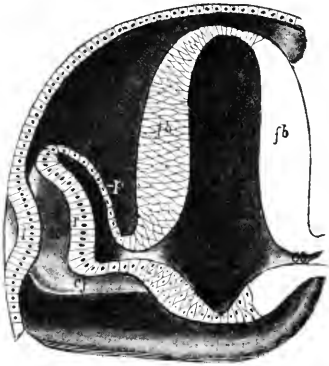


Fig. 362.—Stereogram of developing eye. *cf*, chorioid fissure; *fb*, cut wall of fore-brain; *l*, anlage of lens; *oc*, optic cup; *os*, optic stalk; *p*, layer for pigmented epithelium; *r*, retinal layer. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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 a **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 eye-ball to the lacrimal 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 chorioid, 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 fore-brain. In some animals, however, such as the elasmobranchs and amphibians, the anlagen of the optic vesicles appear primarily 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.

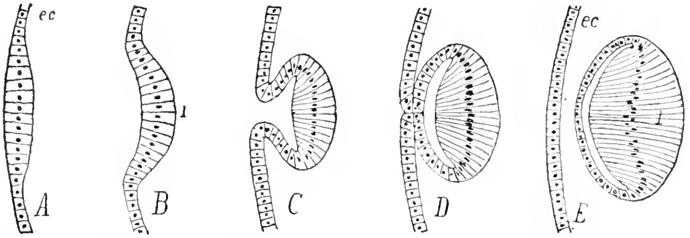


Fig. 363.—Sections of successive stages in the development of the lens of the eye from the first thickening of the ectoderm (*ec*) to the complete separation of the lens, *l*. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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.

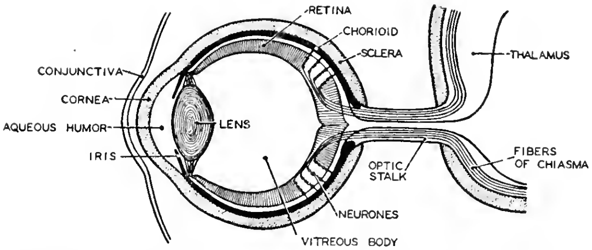


Fig. 364.—Diagram illustrating the growth of optic nerve fibers from the retina along the optic stalk into the brain. Some of the fibers cross below the brain to form the optic chiasma, while the remaining pass into the thalamus of the same side

While the lens is undergoing these changes, it becomes enclosed by the optic cup, formed by invagination of the optic vesicle. 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, the **chorioid fissure,** divides it along its lower side, and extends as a groove along the lower side of the optic stalk. (Fig. 362, *cf*)

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, forming the **chiasma** of the optic nerve. The cells of the optic stalk are converted into neuroglia cells.

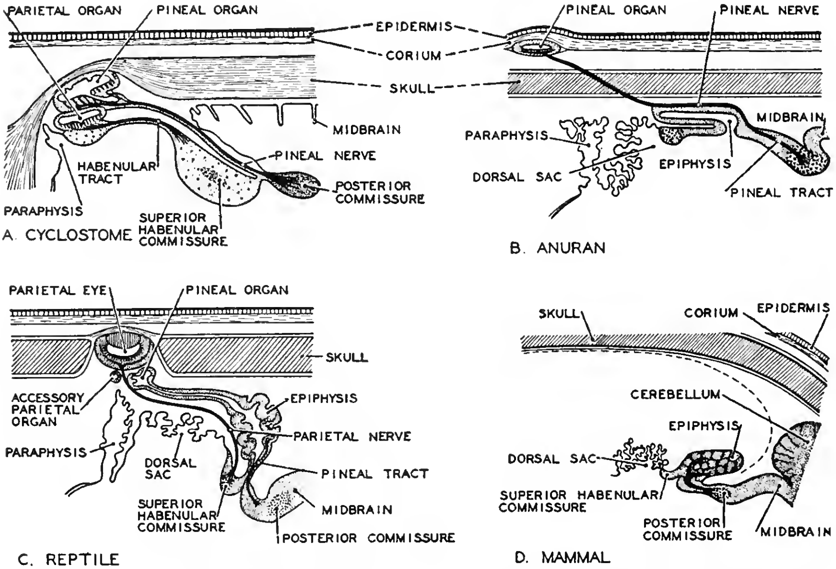


FIG. 365.—Parietal and pineal organs of vertebrates as seen in median longitudinal section. *A*, cyclostome; *B*, anuran; *C*, reptile; *D*, mammal. Both parietal and pineal organs have served as median eyes. In amphibians it is the pineal organ, in reptiles the parietal organ. In man and mammals the pineal organ becomes a gland of doubtful function. (Redrawn from Oppel, after Studnicka.)

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 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 hemispheres, which in mammals overlie the diencephalon.

STATIC AND AUDITORY ORGANS

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 in 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.

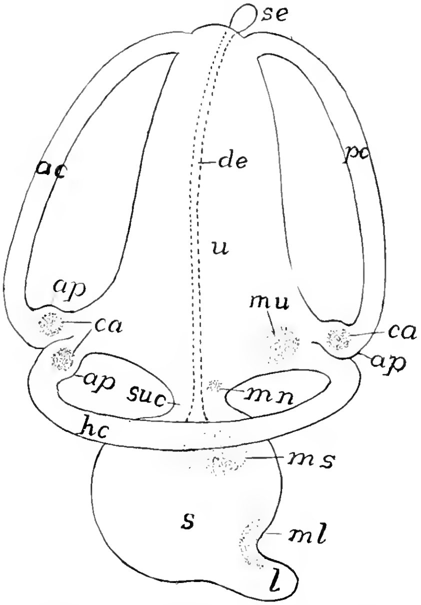


FIG. 366.—Diagram of the membranous labyrinth of a vertebrate, the sensory areas dotted. *ac*, anterior semicircular canal; *ap*, ampullae; *ca*, cristae acusticae in the ampullae; *de*, ductus endolymphaticus; *hc*, horizontal (external) canal; *l*, lagena; *ml*, *mn*, *ms*, *mu*, maculae (of lagena, neglecta, sacculi and utriculi); *pc*, posterior semicircular canal; *s*, sacculus; *se*, saccus endolymphaticus; *suc*, sacculo-utricular canal; *u*, utriculus. (From Kingsley's "Comparative Anatomy of Vertebrates.")

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.

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 consist of a hollow sac or **statocyst** containing 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 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 several groups. The fact that similar statocysts occur in such diverse forms as echinoderms, annelids, and molluscs points in the same direction.

Auditory organs have not been demonstrated in aquatic invertebrates. Indeed, it has not been demonstrated beyond question 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.

All vertebrates have a static organ, which is a novelty in this group and not a structure inherited from invertebrate ancestors. 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 amphibians, 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 endolymphatic 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 endolymphatic 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. 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 endolymphatic 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 cerebro-spinal fluid.

The cavity of the otic capsule in amphibians 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 amphibians now adds an auditory one. (Fig. 367)

The loss of gills in land amphibians 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.** Amphibians are, therefore, the first animals to add, to the inner membranous ear, structures corresponding to the middle ear of mammals. (Fig. 367)

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** which tightens the drum. (Fig. 164)

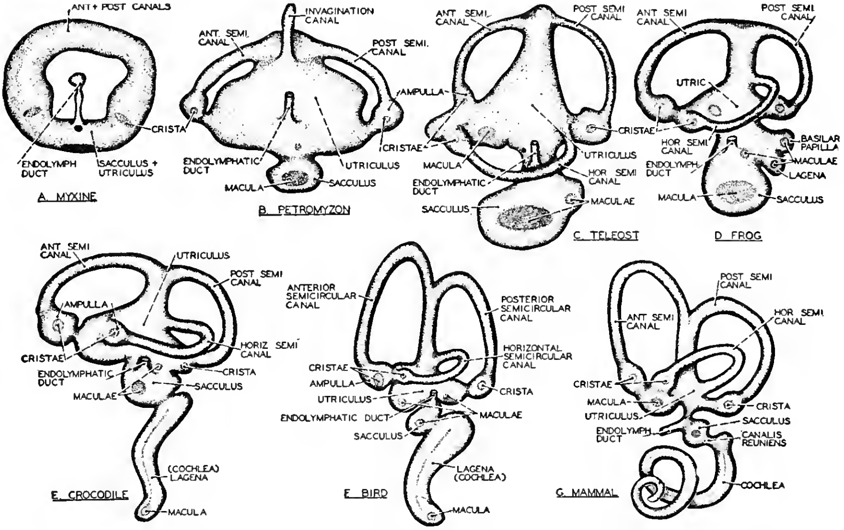


Fig. 367.—The left membranous labyrinth of vertebrates as seen in lateral view. *A*, Myxine; *B*, Petromyzon; *C*, teleost; *D*, frog; *E*, crocodile; *F*, bird; *G*, mammal. The series represents fairly closely an evolutionary series. (Redrawn after Hesse.)

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 aperture 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 occurs also 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.

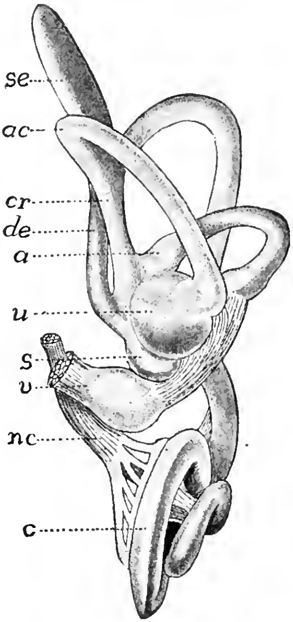


Fig. 368.—Labyrinth of human embryo, 30 mm. long. *a*, ampulla; *ac*, anterior canal; *c*, cochlea; *cr*, crus; *de*, endolymph duct; *nc*, cochlear nerve; *s*, sacculus; *se*, endolymph sac; *u*, utriculus; *v*, vestibular nerve and its ganglion. (From Kingsley's "Comparative Anatomy of Vertebrates," after Streeter.)

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. 368)

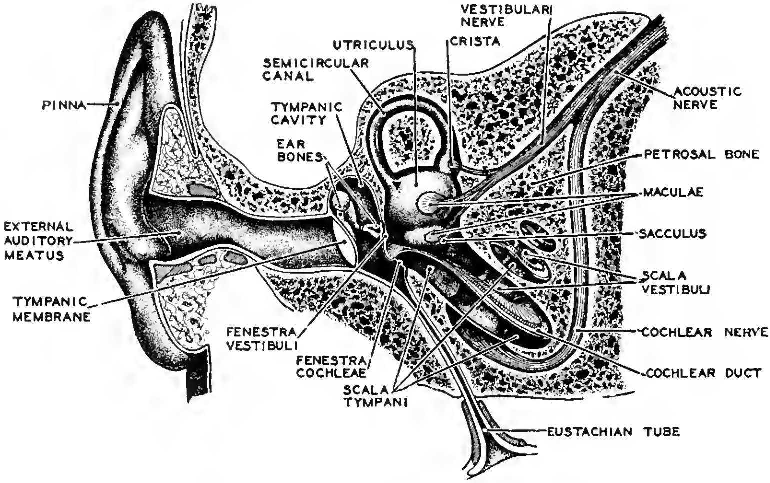


FIG. 369.—The human ear. "Sound waves" impinge upon the drum and are carried by the three ear bones to the fenestra vestibuli and thus to the scala vestibuli and the cochlear duct. (Redrawn from W. H. Howell after Czermak.) In life the apex of the cochlea lies toward the Eustachian tube. In the Figure, for diagrammatic purposes, it is rotated 180 degrees.

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 sacculus and, like the cristae, have a static function.

Proof of the static function of utriculus, sacculus, 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 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 sacculus by means of a narrow tubular **ductus reuniens.** The sacculus is also connected with a slender endolymphatic duct, which terminates in a swollen **saccus endolymphaticus** near the dura. The utriculus connects with the sacculus through the utriculo-saccular duct by means of the endolymphatic duct. (Fig. 367, *G*)

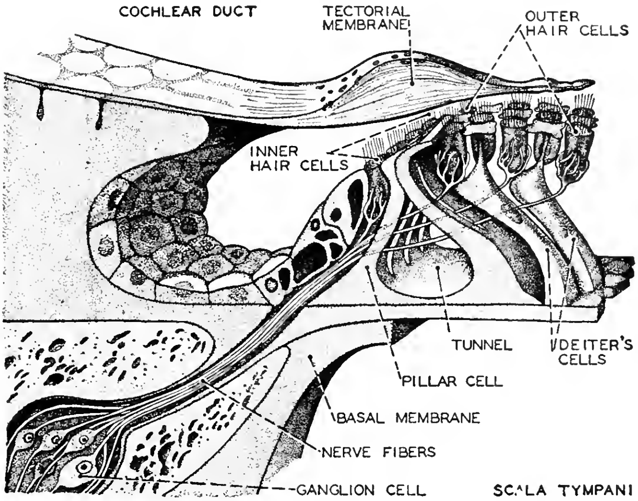


FIG. 370.—A stereogram of a portion of the organ of Corti (spiral organ) of man. The precise function of the tectorial membrane is uncertain. It may serve as a dampener or it may intensify the action of the "sound waves" upon the sensory hair cells. (Redrawn after Fritz Kahn, "Der Mensch," Albert Müller, Zurich.)

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 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. 371)

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. 370)

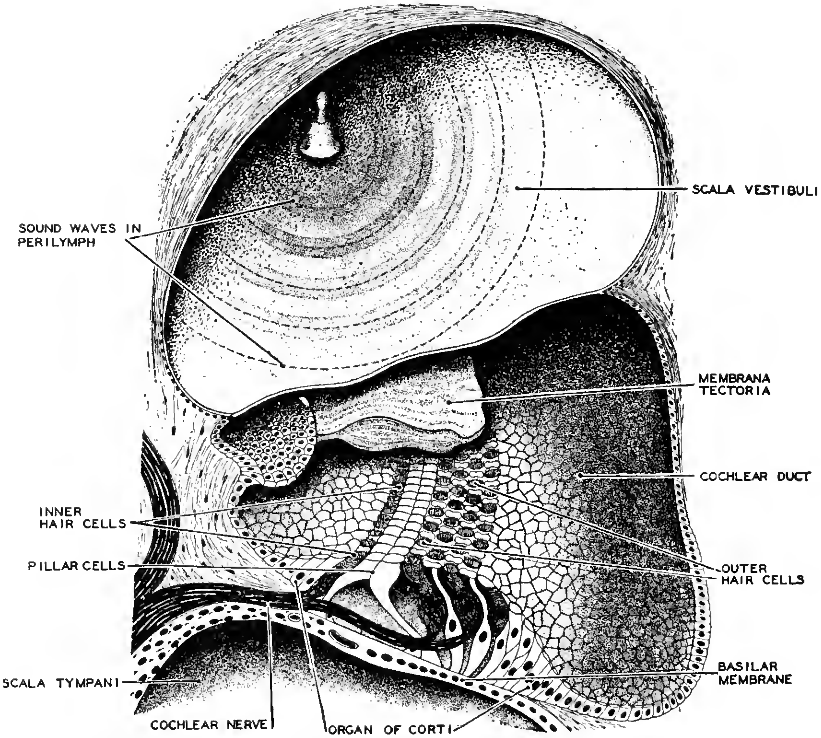


FIG. 371.—A stereogram of a portion of the cochlear duct of man. The figure suggests how "sound waves" are conveyed to the hair cells of the organ of Corti. (Redrawn after Fritz Kahn, "Der Mensch," Albert Müller, Zürich.)

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 about sixteen thousand. 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 hind-brain. 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 at 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 utriculo-saccular 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.

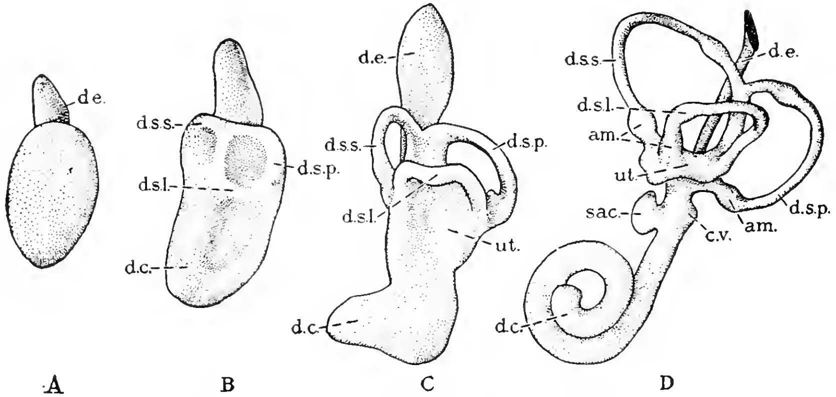


FIG. 372.—Lateral or external surfaces of models of the membranous portion of the left internal ear from human embryos. Different enlargements. *A*, from an embryo of 6.9 mm.; *B*, 10.2 mm.; *C*, 13.5; and *D*, 22 mm.; *am.*, ampulla; *c.v.*, cecum vestibulare of *d.c.*, cochlear duct; *d.e.*, endolymphatic duct; *d.s.l.*, *d.s.p.*, and *d.s.s.*, lateral, posterior, and superior semicircular ducts; *sac.*, sacculus; *ut.*, utriculus. (After His, Jr.) (From Bremer's "Text Book of Histology.")

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 several 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.

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 ear bones. 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.

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 neuro-muscular 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.

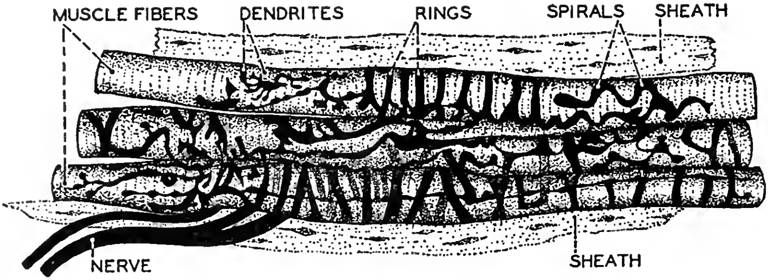


FIG. 373.—A portion of a muscle spindle from a gold-chloride preparation of a cat muscle. The sensory nerve terminations take the form of spirals, or rings, or branched dendrites. A connective-tissue sheath surrounds the spindle. (Redrawn from Jordan and Ferguson, after Ruffini.)

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.

Neuro-tendinous spindles resemble muscular, but are connected with tendons. These also serve to indicate the amount of muscular work and the resistance overcome.

CHAPTER 15

THE ANCESTRY OF VERTEBRATES

One of the many unsolved problems of biology is that of the ancestry of vertebrates. The problem has persisted even after morphologists ceased the vain attempt "to evolve the ancestor out of their inner consciousness." While great divergence of opinion still prevails, nevertheless as the result of recent advances in genetics the scope of the field of inquiry has been considerably narrowed.

Earlier morphologists made the erroneous assumption that phylogenetic changes have taken place through the transformation of adult organisms. In the light of genetic evidence, this notion can no longer be entertained. The belief that modifications of the body effect representative alterations in the germ cells is no longer tenable. Evolutionary change appears to be initiated within the germ cells and not within the body cells. It must be admitted that the cause of alteration in the genetic constitution of the germ cell remains unknown. But that is another problem. Somehow or other the potencies of germ cells have changed so as produce new phyla with fundamentally different types of organization.

To this generation of morphologists it no longer seems profitable to try to convert the body of a scorpion into that of a fish. The genetic potencies of highly specialized forms do not become so easily changed. The shift of morphological opinion has led to increased tolerance of the view that the larger subdivisions of the animal kingdom have made their appearance independently and much earlier in the history of organisms than morphologists formerly assumed. This has brought about an increased respect for the value of embryological evidence in its bearing upon the problem of phylogenesis.

If chordates have arisen as suggested in Fig. 374, none of the extant phyla of invertebrates—with the possible exception of Protozoa—can be said to be "ancestors" in a strict sense. If the diagram is correct, the evolution of the chordates has not involved the transformation of the types of invertebrates with which we are familiar, but a series of forms which have disappeared from the earth. The story of chordate phylogenesis has to be pieced together, as has been done in this text, from fragments of embryological and anatomical evidence. All pre-chordate ancestors are therefore highly conjectural.

To aid the speculative morphologist, however, there is evidence of parallelism in evolution. Some extant non-chordates possess structures which, there is reason to believe, resemble those of the predecessors of chordates. But this does not demonstrate that their possessors are ancestors of chordates. Consequently the phylogenesis of each organ system must be worked out more or less independently of other organs. To believe that the different phyla have acquired their systems of organs

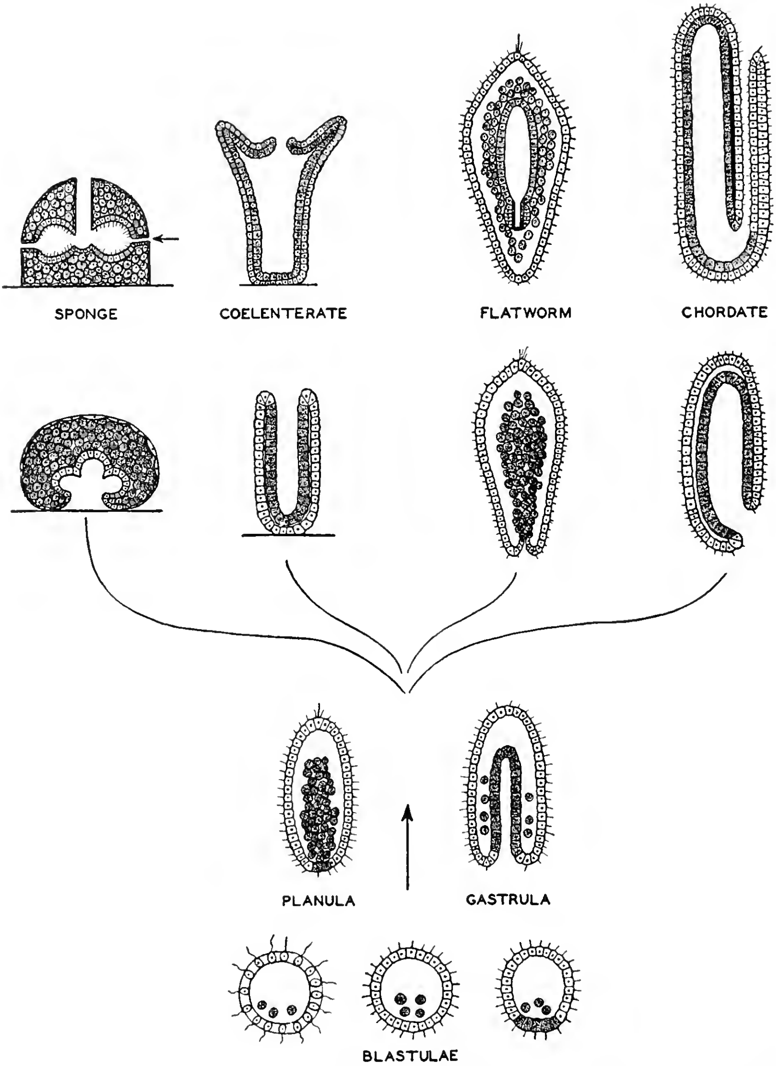


FIG. 374.—A diagram showing hypothetical stages in the ancestry of sponges, coelenterates, flatworms and chordates. Such a series is evidently based chiefly upon embryological evidence. If the diagram represents correctly the early phases of phylogenesis, chordates have split off from other phyla earlier than morphologists generally have assumed and not even coelenterates or flatworms can be said to be ancestral to chordates. (Redrawn after H. E. Ziegler.)

more or less independently should not stretch credulity beyond the breaking point. For there is abundant evidence that this is exactly what has occurred.

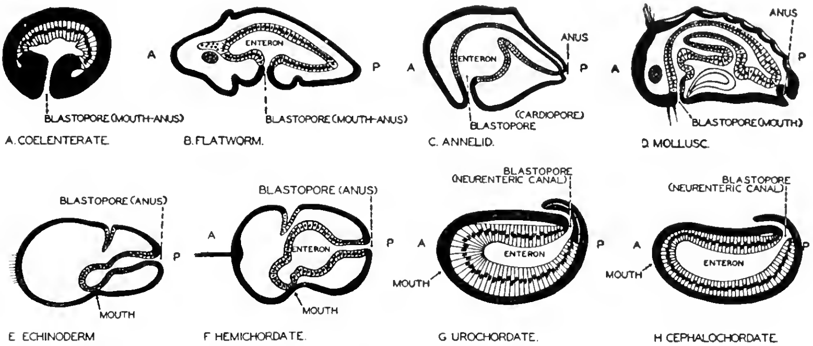


FIG. 375.—Diagrams of embryonic stages illustrating the contrast in the fate of the blastopore in various groups of animals. The forms in which the embryonic blastopore becomes the mouth were grouped together by Grobben as PROTEROSTOMIA. The DEUTEROSTOMIA include those animals in which the blastopore becomes the anus or lies in the anal region. The coelenterates, flatworms, annelids, and molluscs are Proterostomians, while echinoderms and chordates are Deuterostomians.

A somewhat similar view is that of Grobben who divides animals into two phylogenetic series based upon differences in the fate of the primitive mouth or blastopore. The forms in which the blastopore becomes the adult mouth (or cardiopore) reach their evolutionary climax in arthropods and molluscs. Those, on the other hand, in which the blastopore becomes the anus or lies near the anus lead to the chordates and vertebrates. (Fig. 375)

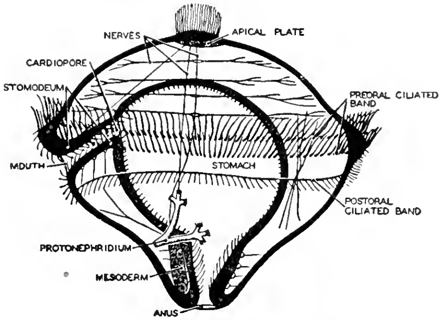


FIG. 376.—A diagram of a trochophore larva According to Delsman's theory of the origin of vertebrates, the cardiopore (blastopore) of the trochophore larva is homologous with the neurenteric canal of vertebrates. In other words, the relatively short stomodeum of the annelid is stretched to become the neural tube of vertebrates. (Redrawn after Hatschek.)

A third attempt to solve the phylogenetic problem on the basis of embryological evidence is that of Delsman, who derives chordates, annelids and molluscs from a form like that of the trochophore larva characteristic of free-swimming annelids. (Figs. 376, 377) According to Delsman, the fundamental differences between the adults of these three groups are due to alteration in the growth centers of the embryos of the three groups. The ectodermal foregut of the annelid is, he thinks, the homologue of the neural tube of the chordate.

If any one of these hypotheses is correct, it follows that none of the several extant types of invertebrates may be regarded as vertebrate "ancestors." Whatever resemblances to vertebrates they show do not prove that they are in the direct line of vertebrate ancestry, but simply illustrate the principle of parallelism or that of convergence. That such resemblances should occur in forms which started with similar potencies is not surprising.

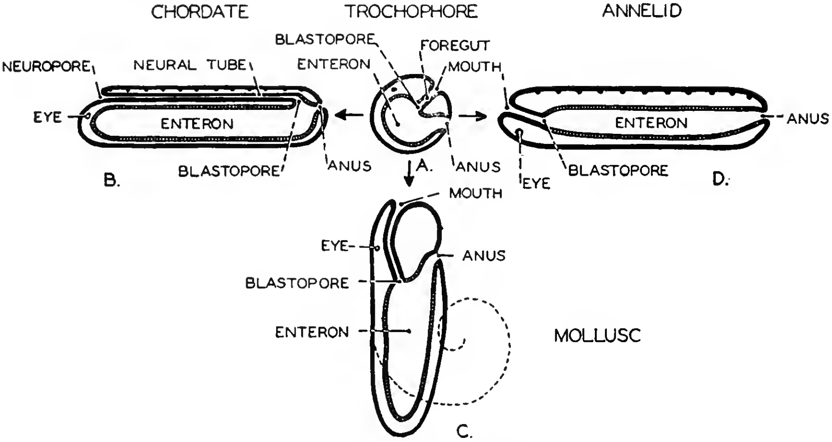
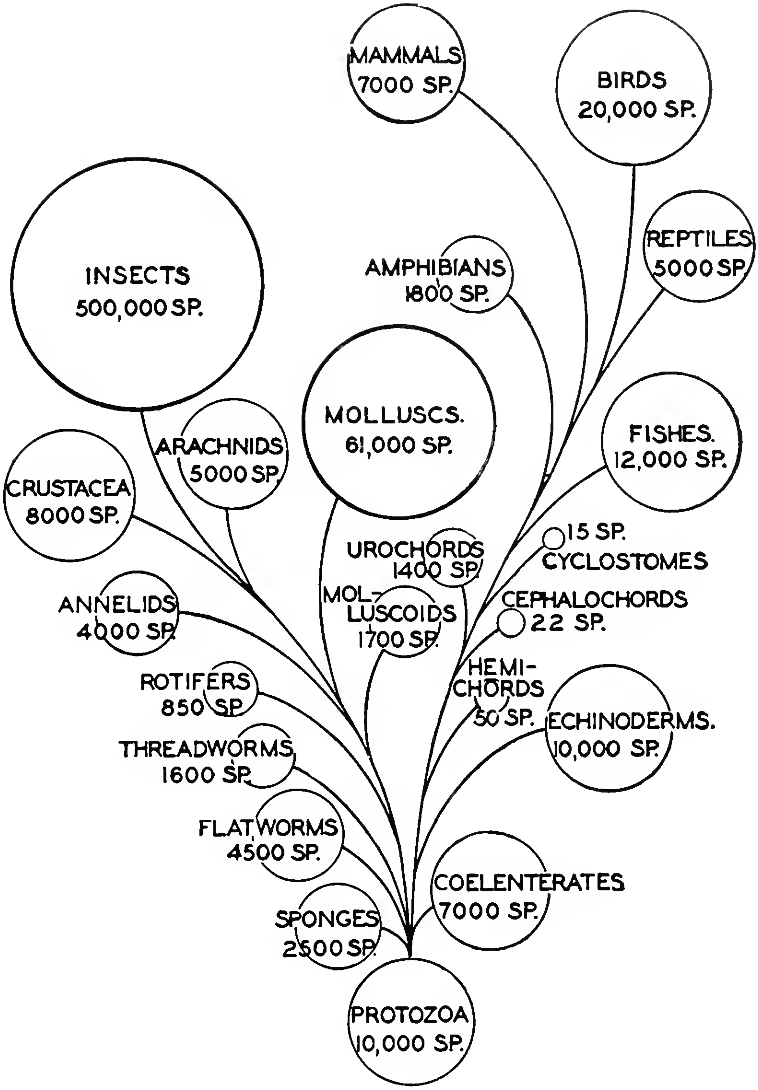


Fig. 377.—Diagram illustrating the theory of Delsman that, by change in the location of the growth center, a trochophore (*A*) may be converted into either a chordate (*B*), or a mollusc (*C*), or an annelid (*D*).

That the protochordates in many ways represent the ancestors of vertebrates seems highly probable. Cyclostomes, more especially their larval forms, 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 chordates and not inherited from metameric invertebrates.

A "family tree" which expresses these conclusions in regard to the phylogenesis of man is given in Fig. 378. The diagram assumes the dichotomy of Metazoa into Protero- and Deuterostomians. Chordates belong to the latter branch of the animal kingdom. There is general agreement among morphologists as to the phylogenetic series, from cyclostomes to man, shown in the Figure.



A PHYLOGENETIC TREE OF THE ANIMAL KINGDOM.

Fig. 378.—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."

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.

acoelomate. Without a body cavity (coelom).

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.

adenoid tissue. Lymphocyte-forming tissue.

adrenal (**suprarenal**) **gland.** An endocrine organ located near the kidney.

adrenin. The suprarenal medullary hormone.

afferent. Centripetal, conveying towards the center.

after-birth. 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.

alveolus. 1. A tooth-socket. 2. A terminal acinus of a gland. 3. A respiratory sac of the lung.

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.

antihelix. 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.

archenteron. The primitive digestive cavity.

archencephalon. The primitive forebrain of chordates.

archetype. An ideal original form.

archicortex (archipallium). The olfactory cerebral cortex including the hippocampus.

archinephros. The primitive kidney or mesonephros (Wolffian body).

archipterygium. The original appendicular skeleton of vertebrates.

areolar tissue. A fibrous tissue containing minute interspaces.

arrectores pilorum. Cutaneous muscles attached to hairs.

articulare. The bony articular element of the lower jaw of lower vertebrates.

arytenoid. A pitcher-like cartilage of the larynx or voice-box.

assimilation. Constructive metabolism.

astragalus. The ankle bone which articulates with the tibia.

ateliotic 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.

auditory bulla. A capsule-like portion of the tympanic bone.

auditory meatus. The external meatus extends from the drum to the outside.

auditory 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.

Australopithecus. A South African fossil anthropoid.

autonomic system. The sympathetic and parasympathetic nervous systems.

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 metamerism 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.
capitate. 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.

cenogenetic. 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.

cheiropterygium. 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 (choroid). 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.

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.

coracoid. 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.

cornified. Converted into horny tissue.

corona radiata. The projection fibers which radiate from the internal capsule to the cerebral cortex.

coronary. 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.

cribriform 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.

diaphragm. 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.

diplospondyly. 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.

endoderm. The innermost germ layer.

endolymph. The liquid contained in the membranous sac of the inner ear.

endometrium. The mucous lining of the uterus.

endoneurium. The connective tissue which subdivides a nerve into funiculi.

endoskeleton. The internal skeleton as distinguished from the dermal skeleton.

endostyle. A ciliated groove in the floor of the pharynx of lower chordates.

endothelium. The thin membrane which lines blood vessels and lymphatics.

end-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.

enteron. The cavity of the alimentary canal.

enterokinase. 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.

epaxial. 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.

epipharynx. 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.

epöophoron. A rudiment of the mesonephros near the ovary.

ereptose (erepsin). A peptone-splitting enzyme secreted by the intestinal mucosa.

erythrocytopoietic tissue. Tissue forming red blood corpuscles.

esophagus. The portion of the alimentary canal between pharynx and stomach.

ethmoturbinals. 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

excretion. The elimination of liquid wastes.

exoskeleton. That part of the skeleton which is derived from the skin.

exteroceptive. Receptive to external stimuli.

extirpation. 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.

flagellate. Having whip-like processes. A protozoon with flagellae.

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.

fornix. 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 Wolffian 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.

genetic. 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.

glans 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.

goiter. 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.
hemal. 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.
hemopoietic. Blood-forming.
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.
hernia. 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.

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 earbone.

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.

interoceptors. 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.

lacrimal. Pertaining to the tears.

lacteal. 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 (steapsin). 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.

maturation. 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.

medulla. 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 Wolffian body, the functional kidney of anamnia.

mesopterygium. The middle basal cartilage of the elasmobranch pectoral fin.

mesorchium. 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.

metabolism. The chemical cycle of matter in living organisms.

metacarpus. The group of five bones between the wrist and the fingers.

metacone. The postero-external cusp of the upper molar teeth of mammals.

metaconid. The postero-internal cusp of the lower molar teeth of mammals.

metamere. One of the serial divisions of the body of a segmented animal.

metamorphosis. A striking change of form during development, as seen in the transformation of the tadpole into a frog.

metanephros. The definitive kidney of the amniotes.

metaotic. Posterior to the ear vesicle.

metapleural folds. Paired folds on the ventral side of the body of Amphioxus.

metapterygium. The posterior basal cartilage of the pectoral fin of elasmobranchs and some ganoids.

metasternum. The posterior or xiphoid process of the breast bone.

metatarsus. The five bones between the ankle and the toes.

metazoa. Many-celled animals.

metencephalon. The fourth brain division which forms cerebellum and pons.

midbrain. The third or mesencephalon division of the brain.

mitral valve. The left atrioventricular valve of the heart.

moa. An extinct running bird of New Zealand.

molar teeth. The three grinding teeth of each half jaw.

monocytes. Large mononuclear leucocytes with kidney-shaped nuclei.
monoecious. 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 narial aperture.
monosaccharid. A sugar the molecules of which have only six carbon atoms.
mons pubis. The pubic eminence or mons veneris.
morphology. The science which treats of form and structure of organisms.
morula. The mulberry stage of segmentation of the egg.
motor (efferent) **neuron.** A nerve cell which conveys impulses away from a nervous center.
mucosa. The lining of the intestine.
Muellerian duct. The oviduct or uterine tube.
multitubercular. Having many cusps as the molar teeth do.
muscularis mucosae. The layer of smooth muscle fibers in the mucosa.
myelencephalon. The fifth or posterior division of the brain—the medulla oblongata.
myelin. The fat-like substance which forms the Schwann's sheath of nerve fibers.
myelocytes. Cells of red bone marrow usually with granular cytoplasm.
myenteric plexus. The network of sympathetic fibers on the muscles of intestine.
myocardium. The muscular layer of the heart.
myocoele. The coelom of the somite.
myocomma. The connective tissue between two myotomes.
myofibril. One of the fine fibrils within a muscle fiber.
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.
nares. The nostrils.
navicular. 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.
neurenteric 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.

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.

neurohumor. 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.

neurosensory 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-medullated. 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.

ovulation. The discharge of an egg from the ovary.

oxytocin. 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 endocrinal 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.

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.

pericardium. 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.

periosteum. The connective tissue membrane which surrounds a bone.

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.

phylogenesis. 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 elasmobranch 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.

plastron. 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.

pons. 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.

premandibular 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.

progestin. A luteal hormone which affects the endometrium of the uterus.

progynon. A proprietary name for the female sex hormone.

pronation. The act of turning the palm of the hand downwards.

pronephroi. The primitive vertebrate kidneys.

proprioceptors. The mechanisms for receiving stimuli from within the body.

propterygium. The anterior basal element of the fish extremity.

prosencephalon. 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.

sacculus. 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.

sarcolemma. The delicate elastic membrane which surrounds a muscle fiber.

sarcoplasm. The interfibrillar 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 is 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.

septula 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 earbone which is attached to the foramen vestibuli.
static organ. An organ of equilibration, a statocyst.
status thymicolymphaticus. 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.
syncytium. 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. With extended pulp-cavity as in some fossil human molar teeth—doubtfully primitive.
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.

theelin. 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).

trabeculae. 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.

trochlea. 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.

uncus. The backward-bent anterior portion of the hippocampal gyrus.

ungulate. 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.

INDEX

Bold numbers refer to figures.