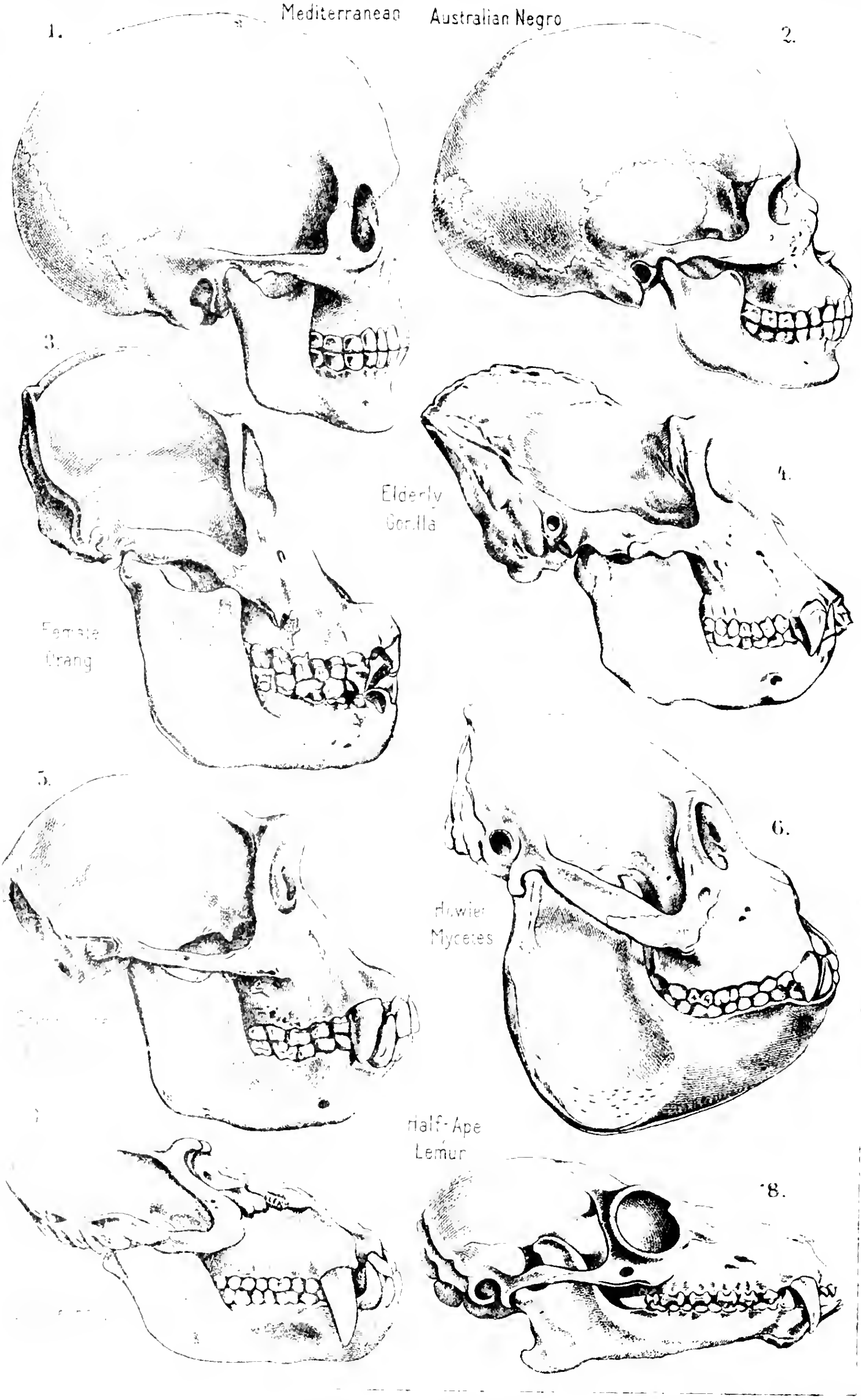
PRIMATE-SKULLS



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THE EVOLUTION OF MAN

A POPULAR SCIENTIFIC STUDY

BY

ERNST HAECKEL

Vol. II.

HUMAN STEM-HISTORY OR PHYLOGENY

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CHAPTER XVI.

STRUCTURE OF THE AMPHIOXUS AND THE ASCIDIA

Causal significance of the biogenetic law. Influence of curtailed and of disturbed heredity. Modification of palingenesis by cenogenesis. Methods of phylogeny modelled on those of geology. Ideal supplementation of the continuous evolutionary series by the arrangement of real fragments. Safety and justice of phylogenetic hypotheses. Significance of the amphioxus and the ascidia. Natural history and anatomy of the amphioxus. External appearance. Skin. Epidermis and corium. Axial rod or chorda. Medullary tube. Sense-organs. Gut with anterior respiratory section (branchial gut) and posterior digestive section (hepatic gut). Liver. Pulsating blood-vessels. Dorsal vessel over the gut (branchial vein and artery). Ventral vessel under the gut (visceral vein and branchial artery). Movement of the blood. Body-cavity and gill-cavity. Cœlom-pouches. Episomites (myotomes) and hyposomites (gonotomes). Mantle-cavity. Mantle-folds or gill-covers. Segmental pronephridia and gonades. Testicles and ovaries. Vertebrate character of the amphioxus. Comparison of the amphioxus with the young lampreys or petromyzonta. Comparison of the amphioxus with the ascidia. Organisation of the tunicates. Cellulose mantle. Branchial sac. Gut. Neural nodi. Sexual organs.

In turning now from the embryology to the phylogeny of man, we must bear in mind the direct causal connection that exists between these two main branches of the science of human evolution. This important causal nexus finds its simplest expression in "the fundamental law of organic development," the content and purport of which we have fully considered in the first Chapter. According to this biogenetic law, ontogeny is a brief and condensed recapitulation of phylogeny. If this compendious reproduction of phylogeny by embryology were complete in all cases, it would be very easy to construct the whole of phylogeny on an ontogenetic basis. When we wanted to know the ancestors of any higher organism, and, therefore, of man—to know from what forms the race as a whole has been evolved—we should merely have to follow the series of forms in the development of the individual from the ovum; we could then regard each of the successive forms as the representative of an extinct ancestral form. However, this direct application of ontogenetic facts to phylogenetic ideas is possible, without limitations, only in a very small section of the animal kingdom. There are, it is true, still a number of lower invertebrates (for instance, some of the zoophyta and vermalia) in which we are justified in recognising at once each embryonic form as the historical reproduction, or silhouette, as it were, of an extinct ancestor. But in the great majority of the animals, and in the case of man, this is impossible, because the embryonic forms themselves have been modified through the infinitely varied conditions of existence, and have lost their original character to some extent.

During the immeasurable course of organic history, the many millions of years during which life was developing on our planet, secondary changes of the embryonic forms have taken place in most animals. These were first clearly recognised by Fritz Müller-Desterro, in his able work, *For Darwin*, and expressed in the following principle: "The historical evidence preserved in the embryology (of the individual) is gradually obliterated, as the development is continually seeking a straighter path from the ovum to the mature animal, and it is frequently falsified by the struggle for existence which the detached larvæ have to sustain." The first phenomenon, the obliteration of the ontogenetic compendium, is accomplished by the law of simplified or curtailed heredity. The second phenomenon, the falsification (or, more correctly, disturbance) of the compendium, is determined by the law of modified, falsified, or disturbed heredity. In virtue of this second law, the young of animals (not only detached larvæ, but also the embryos enclosed in the womb) may be modified by the influence of the environment, just as well as the mature organisms are by adaptation to the conditions of life; even species are altered during the embryonic development. By the law of curtailed heredity, however, it is an advantage for all higher organisms (and the advantage is greater the more advanced they are) to curtail and simplify the original course of development, and thus to obliterate the reminiscence of their ancestors. The higher the individual organism is in the animal kingdom, the less completely does it reproduce in its ontogenesis the series of its ancestors, for reasons that are as yet only partly known to us. The fact is easily proved by comparing the different developments of higher and lower animals in any single stem.

In order to appreciate this important feature, we have distributed the embryological phenomena in two groups, *palingenetic* and *cenogenetic.* Under palingenesis we count those facts of embryology that we can directly regard as a faithful synopsis of the corresponding stem-history. By cenogenesis we understand those embryonic processes which we cannot directly correlate with corresponding phylogenetic processes, but must regard as modifications or falsifications of them. With this careful discrimination between palingenetic and cenogenetic phenomena, our biogenetic law assumes the following more precise shape:—The rapid and brief ontogeny is a condensed synopsis of the long and slow history of the stem (phylogeny): this synopsis is the more faithful and complete in proportion as palingenesis has been preserved by heredity, and cenogenesis has not been introduced by adaptation.

In order to distinguish correctly between palingenetic and cenogenetic phenomena in embryology, and deduce sound conclusions in connection with stem-history, we must especially make a comparative study of the former. It is only through the comparative ontogeny of related forms that we can detect traces of their phylogeny. In doing this it is best to employ the methods that have long been used by geologists for the purpose of establishing the succession of the sedimentary rocks in the crust of the earth. This solid crust, which encloses the glowing central mass like a thin shell, is composed of two different kinds of rocks: there are, firstly, the Plutonic or volcanic rocks which were formed directly by the cooling at the surface of the molten mass of the earth; secondly, there are the Neptunian (or sedimentary) rocks, that have been made out of the former by the action of water, and have been laid in successive strata at the bottom of the sea. Each of these sedimentary strata was at first a soft layer of mud ; but in the course of thousands of years it condensed into a solid hard mass of stone (sand-stone, lime-stone, marl, etc.), and at the same time permanently preserved the solid and imperishable bodies that had chanced to fall into the soft mud. Among these bodies, that were either fossilised or left characteristic impressions of their forms in the soft slime, we have especially the more solid parts of the animals and plants that lived and died during the deposit of the slimy strata.

Hence each of the sedimentary strata has its characteristic fossils, the remains of the animals and plants that lived during that particular period of the earth's history. When we make a comparative study of these strata, we can survey the whole series of such periods. All geologists are now agreed that we can demonstrate a definite historical succession in the strata, and that the lowest of them were deposited in very remote, and the uppermost in comparatively recent, times. However, there is no part of the earth where we find the series of strata in its entirety, or even approximately complete. The succession of strata and of corresponding historical periods generally given in geology is an ideal construction, formed by piecing together the various partial discoveries of the succession of strata that have been made at different points of the earth's surface (cf. Chapter XVIII.).

We must act in this way in constructing the phylogeny of man. We must try to piece together a fairly complete picture of the series of our ancestors from the various phylogenetic fragments that we find in the different groups of the animal kingdom. We shall see that we are really in a position to form an approximate picture of the paleontological evolution of man and the mammals by a proper comparison of the embryology of very different animals—a picture that we could never have framed from the ontogeny of the mammals alone. As a result of the above-mentioned cenogenetic processes—those of disturbed and curtailed heredity—whole series of lower stages have dropped out in the embryonic development of man and the other mammals, especially from the earliest periods, or been falsified by modification. But we find these lower stages in their original purity in the inferior vertebrates and their invertebrate ancestors. Especially in the lowest of all the vertebrates, the amphioxus, we have the oldest stem-forms completely preserved in the embryonic development. We also find important evidence in the fishes, which stand between the lower and higher vertebrates, and throw further light on the course of phylogenesis in certain periods. Next to the fishes come the amphibia, from the embryology of which we can also draw instructive conclusions. They represent the transition to the amniotes or higher vertebrates, in which the middle and older stages of ancestral development have been either distorted or curtailed, but in which we find the more recent stages of the phylogenetic process well preserved in ontogenesis. We are thus in a position to form a fairly complete idea of the paleontological development of man's ancestors within the vertebrate stem by putting together and comparing the embryological developments of the various groups of vertebrates. But when we go below the lowest vertebrates and compare their embryology with that of their invertebrate relatives, we can follow the genealogical tree of our animal ancestors much farther, down to the lowest vermalia and protozoa.

In entering the obscure paths of this phylogenetic labyrinth, clinging to the Ariadne-thread of the biogenetic law and guided by the light of comparative anatomy, we will first, in accordance with the methods we have adopted, discover and arrange those fragments from the manifold embryonic developments of very different animals from which the stem-history of man can be composed. I would call attention particularly to the fact that we can employ this method with the same confidence and right as the geologist. No geologist has ever had ocular proof that the vast rocks that compose our Carboniferous or Jurassic or Cretaceous strata were really deposited in water. Yet no one doubts the fact. Further, no geologist has ever learned by direct observation that these various sedimentary formations were deposited in a certain order; yet all are agreed as to this order. This is because the nature and origin of these rocks cannot be rationally conceived unless we hypothetically assume that they were so deposited. These hypotheses are universally received as safe and indispensable "geological theories," because they alone give a rational explanation of the strata.

Our phylogenetic hypotheses can claim the same value, for the same reasons. In formulating them we are acting on the same inductive and deductive methods, and with almost equal confidence, as the geologist. We hold them to be correct, and claim the status of "biological theories" for them, because we cannot understand the nature and origin of man and the other organisms without them, and because they alone satisfy our demand for a knowledge of causes. And just as the geological hypotheses that were ridiculed as dreams at the beginning of the nineteenth century are now universally admitted, so our phylogenetic hypotheses, which are still regarded as fantastic in certain quarters, will sooner or later be generally received. It is true that, as will soon appear, our task is not so simple as that of the geologist. It is just as much more difficult and complex as man's organisation is more elaborate than that of the rocks.

When we approach this task, we find an auxiliary of the utmost importance in the comparative anatomy and embryology of two lower animal-forms. One of these animals is the lancelet *(amphioxus)*, the other the ascidian. (Plates XVIII. and XIX.) Both of these animals are very instructive. Both are at the border between the two chief divisions of the animal kingdom—the vertebrates and invertebrates. The vertebrates comprise the already mentioned classes from the amphioxus to man (acrania, lampreys, fishes, dipneusts, amphibia, reptiles, birds, and mammals). Following the example of Lamarck, it is usual to put all the other animals together under the head of invertebrates. But, as I have often mentioned already, the group is composed of a number of very different stems. Of these we have no interest just now in the echinoderms, molluscs, and articulates, as they are independent branches of the animal-tree, and have nothing to do with the vertebrates. On the other hand, we are greatly concerned with a very interesting group that has only recently been carefully studied, and that has a most important relation to the ancestral tree of the vertebrates. This is the stem of the tunicates. One member of this group, the ascidian, very closely approaches the lowest vertebrate, the amphioxus, in its essential internal structure and embryonic development. Until 1866 no one had any idea of the close connection of these apparently very different animals; it was a very fortunate accident that the embryology of these related forms was discovered just at the time when the question of the descent of the vertebrates from the invertebrates came to the front. In order to understand it properly, we must first consider these remarkable animals in their fully-developed forms and compare their anatomy.

We begin with the lancelet—after man the most important and interesting of all animals. Man is at the highest summit, the lancelet at the lowest root of the vertebrate stem. (Cf. Fig. 245 and Plate XIX., Fig. 15.) The amphioxus was first described by the German scientist, Pallas, in 1774. He obtained this tiny animal from the English coast of the North Sea, thought it was a near relation of our common snail *(limax)*, and so called it *limax lanceolatus*. For more than half a century no further notice was taken of this supposed naked snail. It was not until 1834 that the almost invisible animal was discovered alive in the sand at Posilippo, near Naples, by the zoologist at this place, Costa. He declared that it was not a snail, but a fish, and called it *branchiostoma lubricum*. Almost simultaneously an English scientist, Yarrel, discovered an axial skeleton in it, and gave it the name of *amphioxus lanceolatus*. It was most carefully studied in 1839 by the famous Berlin zoologist, Johannes Müller, to whom we owe a thorough treatment of its anatomy. Of late years our anatomical knowledge of the lancelet has been substantially completed, and the finer details of its structure have been made clear, by the exhaustive studies of a number of distinguished observers, especially Hatschek and Boveri.[1]

The amphioxus lives on the flat, sandy parts of the Mediterranean coast, partly buried in the sand, and is apparently found in a number of seas. It has been found in the North Sea (on the British and Scandinavian coasts and in Heligoland) and at various places on the Mediterranean (for instance, at Nice, Naples, and Messina). It is also found on the coast of Brazil and the most distant parts of the Pacific Ocean (the coast of Peru, Borneo, China, Australia, etc.). Recently eight to ten species of the amphioxus have been determined, distributed in two to three genera. The two European species (*A. lanceolatus,* widely distributed, and *A. prototypus,* of Messina) belong to the genus *amphioxus* in the narrower sense (with two rows of gonades). The genus *paramphioxus* (also divided into *epigonichthys* and *asymmetron*, with a single row of gonades) contains several species that live in the southern hemisphere. The species of both genera resemble each other very much externally ; they differ chiefly in the number of metamera or segments, which varies between fifty and eighty.[2]

Johannes Müller classed the lancelet with the fishes, although he pointed out that the differences between this simple vertebrate and the lowest fishes are much greater than between the fishes and the amphibia. But this was far from expressing the real significance of the animal. We may confidently lay down the following principle : The amphioxus differs more from the fishes than the fishes do from man and the other vertebrates. As a matter of fact, it is so different

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[1] For bibliography see the extensive monograph of Arthur Willey, *Amphioxus and the Ancestry of the Vertebrates ;* Boston, 1894.

[2] I divided the species (eight to ten) of the genus amphioxus into two different genera in 1893—the older *amphioxus* with two rows of gonades (equally developed to right and left), and the younger *paramphioxus* with one row, right underneath the liver ; the latter genus may be divided into three sub-genera—*epigonichthys, heteropleuron,* and *asymmetron,* which differ in the formation of the fin border and the mouth-cirri. In the Australian *paramphioxus bassanus* the sexual glands are usually atrophied on the left side ; but I found rudiments of them in some specimens (1893). Cf. my *Systematische Phylogenie der Wirbelthiere* (1895, S. 214).

from all the other vertebrates in its whole organisation that the laws of logical classification compel us to distinguish two divisions of this stem: 1, the acrania (amphioxus and its extinct relatives); and 2, the craniota (man and the other vertebrates).

The first and lower division comprises the vertebrates without vertebræ or skull *(cranium).* Of these the only living representatives are the amphioxus and paramphioxus, though there must have been a number of different species at an early period of the earth's history. We may here formulate a general law that will be admitted by every evolutionist: Characteristic and isolated forms like the amphioxus, which seem to be cut off in the animal system, are always "the last of the Mohicans," the surviving remnants of an extinct group of which a number of different forms existed at an earlier epoch. As the amphioxus is quite soft, and has no solid and fossilisable organs, we must assume that all its extinct ancestors were similarly soft, and so could leave no impressions or fossils.

Opposed to the acrania is the second division of the vertebrates, which comprises all the other members of the stem, from the cyclostoma and fishes up to man. All these vertebrates have a head quite distinct from the trunk with a skull *(cranium)* and brain; all have a centralised heart, fully-formed kidneys, etc. Hence, they are called the *craniota.* These craniotes are, however, without a skull in their earlier period. As we already know from ontogeny, even man, like every other mammal, passes in the earlier course of his development through the important stage which we call the *chordula;* at this lower stage the animal has neither vertebræ nor skull nor limbs (Figs. 86-89). And even after the formation of the protovertebræ has begun, the segmented fœtus of the amniotes still has for a long time the simple form of a lyre-shaped disk or a sandal, without limbs or extremities. When we compare this embryonic condition, the sandal-fœtus (Plates IV. and V.), with the developed lancelet, we may say that the amphioxus is, in a certain sense, a permanent sandal-embryo, or a permanent embryonic form of the acrania; it never rises above a low grade of development which we have long since passed.

The fully-developed lancelet (Fig. 245) is about two inches long, is colourless or of a light red tint, and has the shape of a narrow lancet-formed leaf. The body is pointed at both ends, but much compressed at the sides. There is no trace of limbs. The outer skin is very thin and delicate, naked, transparent, and composed of two different layers, a simple external stratum of cells, the epidermis (Plate XVIII., Fig. 13 *h*), and a thin underlying cutis-layer (Fig. 13 *l*). Along the middle line of the back runs a narrow fin-border, which expands behind into an oval tail-fin, and is continued below in a short anus-fin. The fin-border is supported by a number of square elastic fin-plates (Plate XIX., Fig. 15 *f*). The fine parallel lines under the skin on each side, which form an acute angle (directed forwards) in the middle line (Fig. 15 *r* and *b*), are the terminal lines of the muscle-plates or myotomes; in the European *amphioxus lanceolatus* they number sixty to sixty-two, and sixty-three to sixty-five in the *amphioxus prototypus* (of Messina): this indicates the number of the metamera or primitive segments that make up the body and determine its internal articulation.

In the middle of the body we find a thin cartilaginous string, which goes the whole length of the body from front to back on the long axis, and is pointed at both ends (Fig. 245 *i*). This straight, cylindrical rod (somewhat compressed for a time) is the axial rod or the *chorda dorsalis;* in this case it alone represents the vertebral column. The chorda developes no further in the amphioxus, but retains its original simplicity throughout life. It is enclosed by a firm membrane, the chorda-sheath or *perichorda*. The real features of this and of its dependent formations are best seen in the transverse section of the amphioxus (Fig. 246; Plate XVIII., Fig. 13 *cs*). The perichorda forms a cylindrical tube immediately over the chorda, and the central nervous system, the medullary tube, is enclosed in it (Plate XIX., Fig. 15 *m*). This important psychic organ also remains in

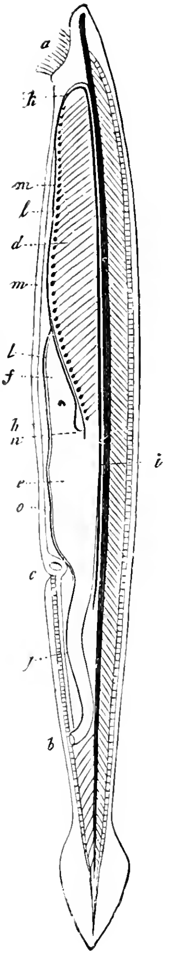


FIG. 245.

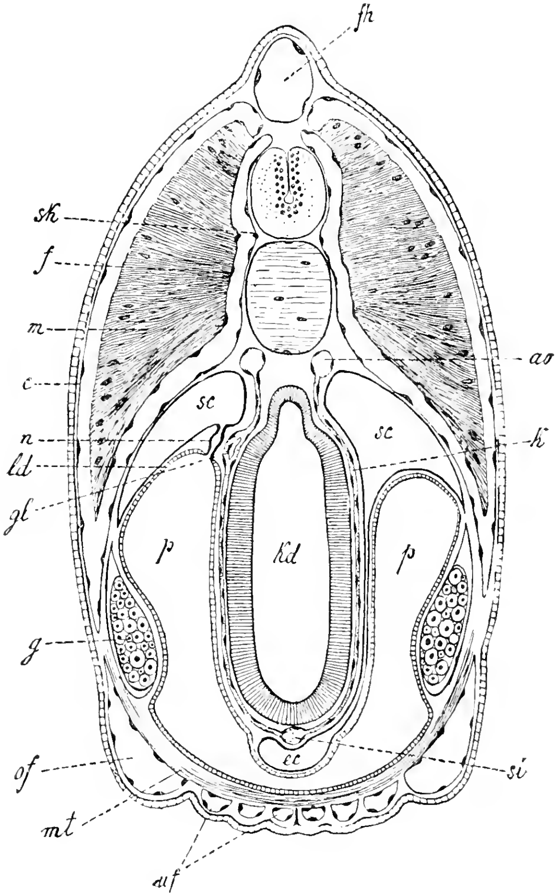


FIG. 246.

FIG. 245.—**The lancelet** *(amphioxus lanceolatus)* twice natural size, left view. The long axis is vertical; the mouth-end is above, the tail-end below, as in Plate XIX., Fig. 15. *a* mouth, surrounded by threads of beard, *b* anus, *c* gill-opening *(porus branchialis)*, *d* gill-crate, *e* stomach, *f* liver, *g* small intestine, *h* branchial cavity, *i* chorda (axial rod), underneath it the aorta, *k* aortic arches, *l* trunk of the branchial artery, *m* swellings on its branches, *n* vena cava, *o* visceral vein.

FIG. 246.—**Transverse section of the head of the amphioxus.** (From *Boveri.*) Above the branchial gut *(kd)* is the chorda, above this the neural tube (in which we can distinguish the inner grey and the outer white matter); above again is the dorsal fin *(fh)*. To the right and left above (in the episoma) are the thick muscular plates *(m)*; below (in the hyposoma) the gonades *(g)*. *ao* aorta (here double), *c* corium, *ec* endostyl, *f* fascie, *gl* glomerulus of the kidneys, *k* branchial vessel, *ld* partition between the cœloma *(sc)* and atrium *(p)*, *mt* transverse ventral muscle, *n* renal canals, *of* upper and *uf* lower canals in the mantle-folds, *p* peribranchial cavity (atrium), *sc* cœloma (subchordal body-cavity), *si* principal (or subintestinal) vein, *sk* perichorda (skeletal layer).

its simplest shape throughout life, as a cylindrical tube, terminating with almost equal plainness at either end, and enclosing a narrow canal in its thick wall. However, the fore end is a little rounder, and contains a small, almost imperceptible vesicular swelling of the canal (Fig. 15 *m*). This vesicle must be regarded as the trace of a real cerebral vesicle, or a rudimentary brain. At the foremost end of it there is a small black pigment-spot, a rudimentary eye; and a narrow canal leads to a superficial sense-organ. In the vicinity of this optic spot we find at the left side a small ciliated depression, the single olfactory organ. There is no organ of hearing. This defective development of the higher sense-organs is probably, in the main, not an original feature, but a result of degeneration.

Underneath the axial rod or chorda runs a very simple alimentary canal, a tube that opens on the ventral side of the animal by a mouth in front and anus behind. The oval mouth is surrounded by a ring of cartilage, on which there are twenty to thirty cartilaginous threads (organs of touch, Fig. 245 *a*). The alimentary canal divides into sections of about equal length by a constriction in the middle. The fore section, or head-gut, serves for respiration; the hind section, or trunk-gut, for digestion. The limit of the two alimentary regions is also the limit of the two parts of the body, the head and the trunk. The head-gut or branchial gut forms a broad gill-crate, the grilled wall of which is pierced by numbers of gill-clefts (Fig. 245 *d;* Plate XIX., Fig. 15 *k*). The fine bars of the gill-crate between the clefts are strengthened with firm parallel rods, and these are connected in pairs by cross-rods. The water that enters the mouth of the amphioxus passes through these clefts into the large surrounding branchial cavity or *atrium*, and then pours out behind through a hole in it, the respiratory pore *(porus branchialis*, Fig. 245 *c)*. Below, on the ventral side of the gill-crate, there is in the middle line a ciliated groove with a glandular wall (the hypobranchial groove), which is also found in the ascidia and the larvæ of the cyclostoma. It is interesting because the thyroid gland in the larynx of the higher vertebrates (underneath the "Adam's apple") has been developed from it (Fig. 15 *y*).

Behind the respiratory part of the gut we have the digestive section, the trunk or liver (hepatic) gut. The small particles that the amphioxus takes in with the water—infusoria, diatomes, particles of decomposed plants and animals, etc.—pass from the gill-crate into the digestive part of the canal, and are used up as food. From a somewhat enlarged portion, that corresponds to the stomach (Fig. 245 *e*), a long, pouch-like blind sac proceeds straight forward *(f)*; it lies underneath on the left side of the gill-crate, and ends blindly about the middle of it. This is the liver of the amphioxus, the simplest kind of liver that we meet in any vertebrate. In man also the liver developes, as we shall see, in the shape of a pouch-like blind sac, that forms out of the alimentary canal behind the stomach.

The formation of the vascular system in this animal is not less interesting. All the other vertebrates have a compressed, thick, pouch-shaped heart, which developes from the wall of the fore-gut at the throat, and from which the blood-vessels proceed; in the amphioxus there is no special centralised heart, driving the blood by its pulsations. This movement is effected, as in the annelids, by the thin tubular blood-vessels themselves, which discharge the function of the heart, contracting and pulsating in their whole length, and thus driving the colourless blood through the entire body. This circulation is so simple and yet so remarkable that we will examine it for a moment. We may begin in front on the under-side of the gill-crate. Here, in the middle line, there is the trunk of a large vessel that corresponds to the heart of the other vertebrates and the trunk of the branchial artery that proceeds from it; this drives the blood into the gills (Fig. 245 *l*). A number of small vascular arches arise on each side from this branchial artery, and form little heart-shaped swellings or *bulbilla (m)* at their points of departure; they advance along the branchial arches, between the gill-clefts and the fore-gut, and unite, as branchial veins, above the gill-crate in a large trunk blood-vessel that runs under the chorda dorsalis. This is the principal artery or primitive aorta (Plate XVIII., Fig. 13 *t;* Plate XIX., Fig. 15 *t*). The aorta runs between the gut and the chorda in the same way as in all the higher vertebrates (Fig. 249 *D*). The branches which it gives off to all parts of the body unite again in a larger venous vessel at the underside of the gut, called the subintestinal vein (Fig. 245 *o,* 247 *E;* Plate XVIII., Fig. 13 *v*; Plate XIX., Fig. 15 *v*). It continues over the liver-tube, forms a sort of portal vein there, investing the blind liver-sac with a fine vascular network, and then passes, as hepatic vein, into a stem that goes forward, the vena cava (Fig. 245 *n*). The latter returns straight to the ventral side of the gill-crate, and there passes directly into the branchial artery which was our starting-point. This single main vessel of the amphioxus goes like a closed circular water-conduit along the alimentary canal through the whole body, and pulsates in its whole length above and below. When the upper tube contracts the lower one is filled with blood, and *vice versâ.* In the upper tube the blood flows from front to rear, then back from rear to front in the lower vessel. The whole of the long tube that runs along the ventral side of the alimentary canal and contains venous blood may be called the "principal vein," and may be compared to the ventral vessel in the worms. On the other hand, the long straight vessel that runs along the dorsal line of the gut above, between it and the chorda, and contains arterial blood, is, on the one hand, clearly identical with the aorta or principal artery of the other vertebrates; and on the other side it may be compared to the dorsal vessel in the worms.

Johannes Müller recognised even in his time this instructive similarity in the structure of the vascular system in the lancelet and the worms. He pointed out the anology or physiological resemblance between the two, in the circumstance that in both the blood is driven by the pulsating contractions of the large vessels along their whole length, not by a centralised heart, as in the other vertebrates. However, we have here much more than a mere analogy. It is probably a real homology, and is based on a morphological identity of the organs compared. Thus we learn through the amphioxus that the aorta, the single principal artery of the vertebrates that runs between the gut and the chorda, was developed originally from the dorsal vessel of the older worms. On the other hand, the ventral vessel of the worms is only maintained in the single subintestinal vein of the amphioxus (and its forward continuation—portal vein, hepatic vein, vena cava, and branchial artery) that runs under the gut. In all the other vertebrates this subintestinal vein (originally the "principal vein") is far behind other veins in the developed body.

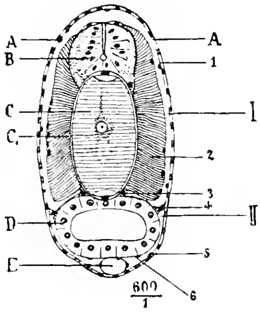


Fig. 247.

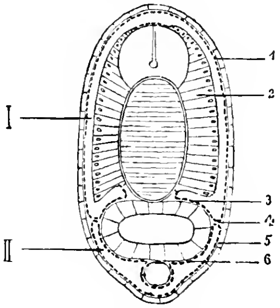


Fig. 248.

Fig. 247.—**Transverse section of an amphioxus-larva,** with five gill-clefts, through the middle of the body.

Fig. 248.—**Diagram of the preceding.** (From *Hatschek.*) *A* epidermis, *B* medullary tube, *C* chorda, C_1 inner chorda-sheath, *D* visceral epithelium, *E* subintestinal vein. *1* cutis, *2* muscle-plate (myotome), *3* skeletal plate (sclerotome), *4* cœloseptum (partition between dorsal and ventral cœloma), *5* skin-fibre layer, *6* gut-fibre layer, *I* myocœl (dorsal body-cavity), *II* splanchnocœl (ventral body-cavity).

The cœloma or body-cavity has some very important and distinctive features in the amphioxus. The embryology of it is most instructive in connection with the stem-history of the body-cavity in man and the other vertebrates. As we have already seen (Chapter X.), in these the two cœlom-pouches are divided at an early stage by transverse constrictions into a double row of somites or primitive segments (Fig. 162), and each of these subdivides, by a frontal or lateral constriction, into an upper (dorsal) and lower (ventral) pouch. From the inner or median wall of the episomites, or dorsal pouches, we get the muscle-plate (Fig. 247, 2); from the outer or lateral wall, the corium-plate (1): the two are divided by the muscular cavity or myocœl (I.). The hyposomites, or ventral pouches, combine to form a simple narrow body-cavity, the splanchnocœl (II.).

These important structures are seen very clearly in the trunk of the amphioxus (the latter third, Figs. 247–250), but it is otherwise in the head, the foremost third (Fig. 251). Here we find a number of complicated structures that cannot be understood until we have studied them on the embryological side in the next Chapter (cf. Fig. 265). The branchial gut lies free in a spacious cavity filled with water, which was wrongly thought formerly to be the body-cavity (Fig. 251 *A*). As a matter of fact, this *atrium* (commonly called the peribranchial cavity) is a secondary structure formed by the development of a couple of lateral mantle-folds or gill-covers (M_1, *U*). The real body-cavity (*Lh*) is very narrow and entirely closed, lined with cœlous epithelium. The peribranchial cavity (*A*) is full of water, and its walls

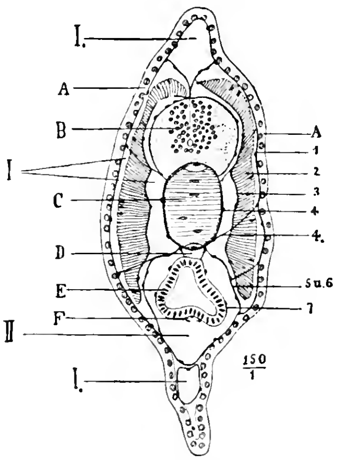


Fig. 249.

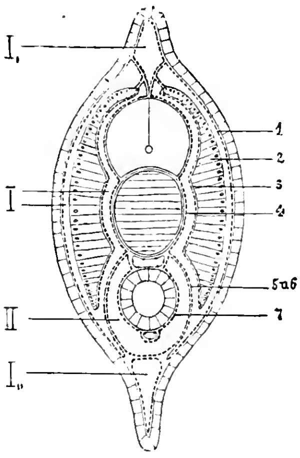


Fig. 250.

Fig. 249.—**Transverse section of a young amphioxus,** immediately after metamorphosis, through the hindermost third (between the atrium-hole and the anus).

Fig. 250.—**Diagram of preceding.** (From *Hatschek*.) *A* epidermis, *B* medullary tube, *C* chorda, *D* aorta, *E* visceral epithelium, *F* subintestinal vein, *1* corium-plate, *2* muscle-plate, *3* fascie-plate, *4* outer chorda-sheath, *5* myoseptum, *6* skin-fibre plate, *7* gut-fibre plate, *I* myocœl, *II* splanchnocœl, *I,* dorsal fin, *II,,* anus-fin.

are all lined with the skin-sense layer; it opens outwards in the rear through the respiratory pore (Fig. 245 *c*; Plate XIX., Fig. 15 *p*). The ectoderm covers the surface of the two large lateral gill-covers, the fold-shaped processes of the body-wall which grow out below from the original ventral side and unite in the middle line (in the ventral seam, Fig. 251 *R*).

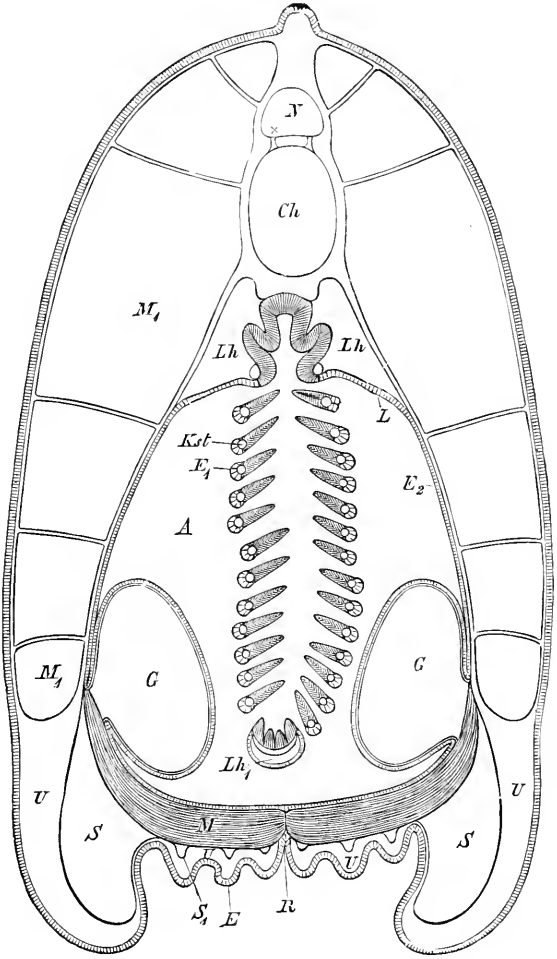


FIG. 251.—**Transverse section of the lancelet,** in the fore half. (From *Ralph.*) The outer covering is the simple cell-layer of the epidermis (*E*). Under this is the thin corium, the subcutaneous tissue of which is thickened; it sends connective-tissue partitions between the muscles (M_1) and to the chorda-sheath. *N* medullary tube, *Ch* chorda, *Lh* body-cavity, *A* atrium, *L* upper wall of same, E_1 inner wall, E_2 outer wall, Lh_1 ventral remnant of same, *Kst* gill-rods, *M* ventral muscles, *R* seam of the joining of the ventral folds (gill-covers), *G* sexual glands.

On the inner surface of these mantle-folds (M_1), in the ventral half of the wide mantle-cavity (atrium), we find the sex-organs of the amphioxus. At each side of the branchial gut there are between twenty and thirty ellipitical or roundish four-corned sacs, which can clearly be seen from without with the naked eye, as they shine through the thin transparent body-wall. These sacs are

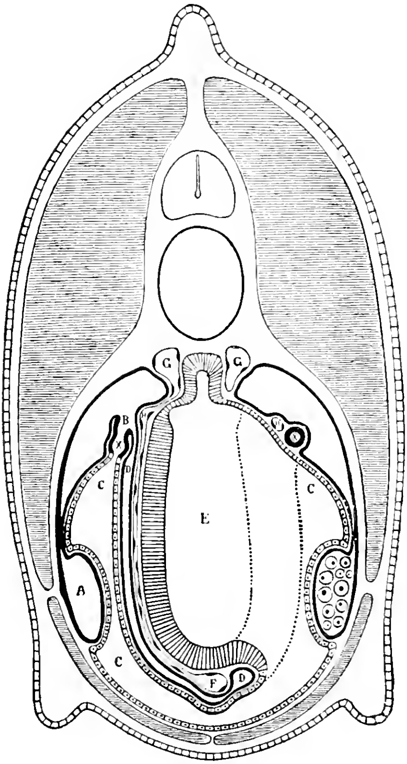


FIG. 252.

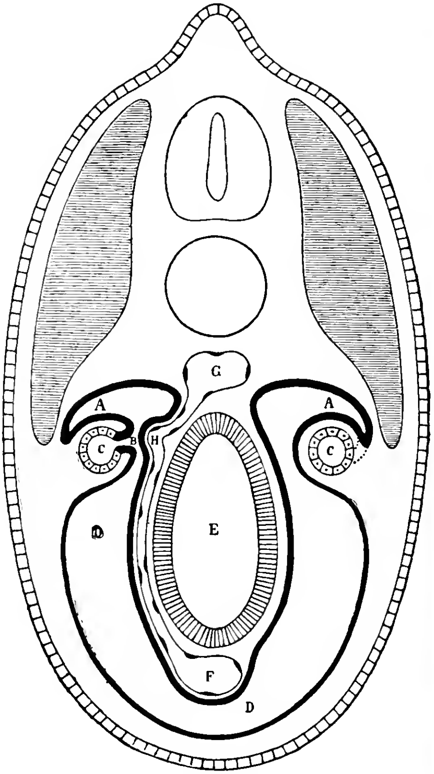


FIG. 253.

FIG. 252.—**Transverse section through the middle of the Amphioxus.** (From *Boveri.*) On the left a gill-rod has been struck, and on the right a gill-cleft; consequently on the left we see the whole of a prorenal canal *(x)*, on the right only the section of its fore-leg. *A* genital chamber (ventral section of the gonocœl), *x* pronephridium, *B* its cœlom-aperture, *C* atrium, *D* body-cavity, *E* visceral cavity, *F* subintestinal vein, *G* aorta (the left branch connected by a branchial vessel with the subintestinal vein), *H* renal vessel.

FIG. 253.—**Transverse section of a primitive fish embryo** (selachii-embryo, from *Boveri*), to the left pronephridia *(B)*, the right primitive kidneys *(A)*. The dotted lines on the right indicate the later opening of the primitive kidney canals *(A)* into the prorenal duct *(C)*. *D* body-cavity, *E* visceral cavity, *F* subintestinal vein, *G* aorta, *H* renal vessel.

the sexual glands *(gonades)*; they are the same size and shape in both sexes, only differing in contents. In the female they contain a quantity of simple ova (Fig. 254 *g*); in the male a number of much smaller cells that change into mobile ciliated cells (sperm-cells). Both sacs lie on the inner wall of the atrium, and have no special outlets. When the ova of the female and the sperm of the male are ripe, they fall into the atrium, pass through the gill-clefts into the fore-gut, and are ejected through the mouth. Closer study has discovered that these sex-pouches are segmental blind sacs of the body-cavity, or ventral cœlom-pouches; they originate from the lower part of the hyposomites, the upper parts of which coalesce and form the narrow metacœlom (Fig. 251 *Lh*). The latter remains in touch with the former by means of a mesodermic epithelial plate, that lies between the inner ectoderm of the mantle-folds *(E2)* and their muscular plate.

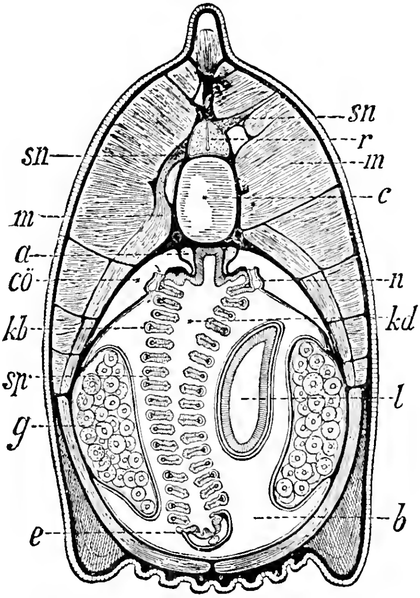


FIG. 254.—**Transverse section of the head of the amphioxus** (at the limit of the first and second third of the body). (From *Boveri*.) *a* aorta (here double), *b* atrium, *c* chorda, *cö* cœloma (body-cavity), *e* endostyle (hypobranchial groove), *g* gonades (ovaries), *kb* gill-arches, *kd* branchial gut, *l* liver-tube (on the right, one-sided), *m* muscles, *n* renal canals, *r* spinal cord, *sn* spinal nerves, *sp* gill-clefts.

The symmetrical development of the sexual glands varies considerably in the different species of the amphioxus, and these have led recently to the establishment of several genera. In two species which Professor Semon brought from Australia—*amphioxus bassanus* and *A. cultellus*—I found, in 1893, that the gonades were only developed on one side, the right (like the liver). Some specimens of *A.*

bassanus still had small rudiments on the left side; but, as a rule, they had completely disappeared on this side. There were also other features in which these Australian acrania were much less symmetrical than our European species, the common *A. lanceolatus* and the larger *A. prototypus* (of Messina). The cause of it is clearly to be sought in adaptation to the habit of lying on one side, as in the familiar asymmetrical flat-fishes, in which both eyes are on the same side of the head (*pleuronectides*, flounders, soles, etc.). However, if in the acrania the sexual glands and the liver are only developed on the right side, which lies flat on the floor of the sea, the respiratory movements gain proportionately in freedom on the opposite side.

As the less symmetrical species of the acrania, with their single row of gonades, differ in other respects also (such as the structure of the fins and the crown of tentacles) from the more symmetrical species, with two rows of gonades, I proposed to make a new genus of the former—*paramphioxus*. The same asymmetry of the sexual glands was simultaneously observed by Andrews in the American *A. lucayanus* (of the Bahamas), and the genus *asymmetron* was established. In any case this unequal development of the two halves of the body in the acrania is (as in the pleuronectides) a secondary phenomenon, due to change of habits of life; it was certainly not found in the extinct *prospondylus*, the hypothetical common ancestor of all the vertebrates. I have dealt more fully with the important phylogenetic relations of these ancient acrania and the modern leptocardia to the craniota in the third volume of the *Systematic Phylogeny* (pp. 206–15), and in an essay, *On the Phylogeny of the Australian Fauna* (introduction to the *Australian Voyages* of Richard Semon, 1893).

Above the sexual glands of the acrania, at the dorsal angle of the atrium, we find the kidneys. These important excretory organs could not be found in the amphioxus for a long time, on account of their remote position and their smallness; they were discovered in 1890 by Theodor Boveri (Fig. 252 *x*). They are short segmental canals, corresponding to the pronephridia of the other vertebrates

(Fig. 253 *B*). Their internal aperture (Fig. 252 *B*) opens into the mesodermic body-cavity; their outer aperture into the ectodermal atrium *C*. The prorenal canals lie in the middle of the line (or dorso-ventral axis) of the head, outwards from the uppermost section of the gill-arches, and have important relations to the branchial vessels *(H)*. For this reason, and in their whole arrangement, the segmental pronephridia of the amphioxus show clearly that they are equivalent or homologous to the prorenal canals of the craniotes (Fig. 253 *B*). The prorenal duct of the latter (Fig. 253 *C*) corresponds to the branchial cavity or atrium of the former (Fig. 252 *C*).

If we sum up the results of our anatomic study of the amphioxus, and compare them with the familiar organisation of man, we shall find an immense distance between the two. As a fact, the highest summit of the vertebrate organisation which man represents is in every respect so far above the lowest stage at which the lancelet remains that one would at first scarcely believe it possible to class both animals in the same division of the animal kingdom. Nevertheless, this classification is indisputably just. Man is only a more advanced stage of the vertebral type that we find unmistakeably in the amphioxus in its characteristic features. We need only recall the picture of the ideal primitive vertebrate given in a former Chapter, and compare it with the lower stages of human embryonic development, to convince ourselves of our close relationship to the lancelet. (Cf. Chapter XI., p. 253.)

It is true that the amphioxus is far below all other living vertebrates. It is true that it has no separate head, no developed brain or skull, the characteristic feature of the other vertebrates. It is (probably as a result of degeneration) without the auscultory organ and the centralised heart that all the others have; and it has no fully formed kidneys. Every single organ in it is simpler and less advanced than in any of the others. Yet the characteristic connection and arrangement of all the organs is just the same as in the other vertebrates. All these, moreover, pass, during their embryonic development, through a stage in which their whole organisation is no higher than that of the amphioxus, but is substantially identical with it. (Cf. Tables XVI.–XVIII.)

In order to see this quite clearly, it is particularly useful to compare the amphioxus with the youthful forms of those vertebrates that are classified next to it. This is the class of the cyclostoma. There are to-day only a few species of this once extensive class, and these may be distributed in two groups. One group comprises the hag-fishes or myxinoides, which are well known to us from Johannes Müller's classical work, *The Comparative Anatomy of the Myxinoides*. The other group are the petromyzontes, the familiar lampreys, which are a familiar delicacy in their marine form. All these cyclostoma are usually classified with the fishes. But they are far below the true fishes, and form a very interesting connecting-group between them and the lancelet. One can see how closely they approach the latter by comparing a young lamprey (Plate XIX., Fig. 16) with the amphioxus (Fig. 15). The chorda *(ch)* is of the same simple character in both; also the medullary tube *(m)* that lies above the chorda and the alimentary canal *(d)* below it. However, in the lamprey the spinal cord swells in front into a simple pear-shaped cerebral vesicle *(m_1)*, and at each side of it there are a very simple eye *(au)* and a rudimentary auditory vesicle *(g)*. The nose *(n)* is a single pit, as in the amphioxus. The two sections of the gut—the branchial *(k)* and the hepatic gut *(d)*—are also just the same and very rudimentary in the petromyzon. On the other hand, we see a great advance in the structure of the heart, which is found underneath the gills in the shape of a centralised muscular tube, and is divided into an auricle *(hv)* and ventricle *(hk)*. Later on the lamprey advances still further, and gets a skull, five cerebral vesicles, a series of independent gill-pouches, etc. This makes all the more interesting the striking resemblance of its immature larva to the developed and sexually mature amphioxus.

While the amphioxus is thus connected through the cyclostoma with the fishes, and so with the series of the higher vertebrates, it is, on the other hand, very closely related to a lowly invertebrate marine animal, from which it seems to be entirely remote at first glance. This remarkable animal is the sea-squirt or ascidian, which was formerly thought to be closely related to the mussel, and so classed in the molluscs. But since the remarkable embryology of these animals was discovered in 1866, there can be no question that they have nothing to do with the molluscs. To the great astonishment of zoologists, they were found, in their whole individual development, to be closely related to the vertebrates. When fully developed the ascidia are shapeless lumps that would not, at first sight, be taken for animals at all. The oval body, frequently studded with knobs or uneven and lumpy, in which we can discover no special external organs, is attached at one end to marine plants, rocks, or the floor of the sea. Many species look like potatoes, others like melon-cacti, others like prunes. Many of the ascidia form highly transparent crusts or deposits on stones and marine plants. Some of the larger species are eaten like oysters. Fishermen, who know them very well, think they are not animals, but plants. They are sold in the fish markets of many of the Italian coast-towns with other lower marine animals under the name of "sea-fruit" *(frutti di mare)*. There is nothing about them to show that they are animals. When they are taken out of the water with the net the most one can perceive is a slight contraction of the body that causes water to spout out in two places. The bulk of the ascidia are very small, at the most a few inches long. A few species are a foot or more in length. There are many species of them, and they are found in every sea. As in the case of the acrania, we have no fossilised remains of the class, because they have no hard and fossilisable parts. However, they must be of great antiquity, and must go back to the primordial epoch.

The name of tunicates is given to the whole class to which the ascidia belong, because the body is enclosed in a thick and stiff covering like a mantle *(tunica)*. This mantle—sometimes soft like jelly, sometimes as tough as leather, and sometimes as stiff as cartilage—has a number of peculiarities. The most remarkable of them is that it consists of a woody matter, cellulose—the same vegetal substance that forms the stiff envelopes of the plant-cells, the substance of the wood. The tunicates are the only class of animals that have a real cellulose or woody coat. Sometimes the cellulose mantle is brightly coloured, at other times colourless. Not infrequently it is set with needles or hairs, like a cactus. Often we find a mass of foreign bodies—stone, sand, fragments of mussel-shells, etc.—worked into the mantle. This has earned for the ascidian the name of "the microcosm." (See Plate 85 in *Art-Forms in Nature.)*

In order to understand properly the internal organisation of the ascidia, and compare it thoroughly with the amphioxus, we must examine it in the same position as the former (Plate XIX., Fig. 15, from the left; the mouth-end is upward, the back to the right, and the belly to the left). The hind end, which corresponds to the tail of the amphioxus, is usually attached, often by means of regular roots. The dorsal and ventral sides differ a good deal internally, but frequently cannot be distinguished externally. If we open the thick tunic or mantle in order to examine the internal organisation, we first find a spacious cavity filled with water—the mantle-cavity or respiratory cavity (Fig. 255 *cl;* Plate XIX., Fig. 14 *cl*). It is also called the branchial cavity and the cloaca, because it takes the excrements and sexual products as well as the respiratory water. The greater part of the respiratory cavity is occupied by the large grated branchial sac *(br).* This is so like the gill-crate of the amphioxus in its whole arrangement that the resemblance was pointed out by the English naturalist, Goodsir, years ago, before anything was known of the relationship of the two animals. As a fact, even in the ascidian the mouth *(o)* opens first into this wide branchial sac. The respiratory water passes through the lattice-work of the branchial sac into the branchial cavity, and is ejected from this by the respiratory pore *(a').* Along the ventral side of the branchial sac runs a ciliated groove—the hypobranchial groove which we have previously found at the same spot in the amphioxus (Plate XIX., Figs. 14 *y*, 15 *y*). The food of the ascidia also consists of tiny organisms, infusoria, diatomes, parts of decomposed marine plants and animals, etc. These pass with the water into the gill-crate and the digestive part of the gut at the end of it, at first into an enlargement of it that represents the stomach (Fig. 14 *mg*). The adjoining small intestine usually forms a loop, bends forward, and opens by an anus (Fig. 255 *a*), not directly outwards, but first into the mantle-cavity; from this the excrements are ejected by a common outlet *(a′)* together with the used-up water and the sexual products. The outlet is sometimes called the branchial pore and sometimes the cloaca or ejection-aperture (Plate XIX., Fig. 14 *q*). In many of the ascidia a glandular mass opens into the gut, and this represents the liver (Fig. 14 *lb*). In some there is another gland besides the liver, and this is taken to represent the kidneys (Fig. 14 *u*). The body-cavity proper, or cœloma, which is filled with blood and encloses the hepatic gut, is very narrow in the ascidia, as in the amphioxus, and is here also usually confounded with the wide atrium, or peribranchial cavity, full of water.

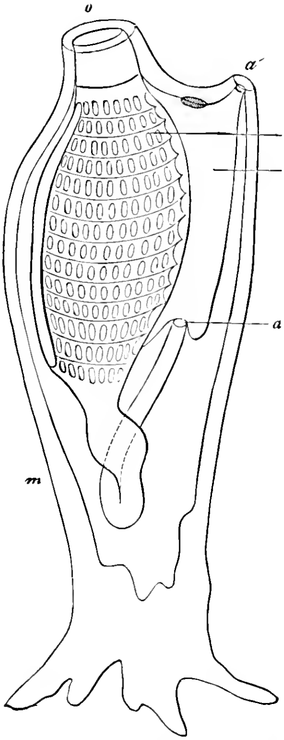


FIG. 255.—**Organisation of an ascidian** (left view, as in Plate XIX., Fig. 14); the dorsal side is turned to the right and the ventral side to the left, the mouth *(o)* above; the ascidian is attached at the tail end. The branchial gut *(br)*, which is pierced by a number of clefts, continues below in the visceral gut. The rectum opens through the anus *(a)* into the atrium *(cl)*, from which the excrements are ejected with the respiratory water through the mantle-hole or cloaca *(a)*. *m* mantle. (From *Gegenbaur.*)

There is no trace in the fully developed ascidian of a chorda dorsalis, or internal axial skeleton. It is the more interesting that the young animal that emerges from the ovum *has* a chorda (Plate XVIII., Fig. 5 *ch*), and that there is a rudimentary medullary tube above it (Fig. 5 *m*). The latter is wholly atrophied in the developed ascidian, and looks like a small nerve-ganglion in front above the gill-crate (Fig. 14 *m*). It corresponds to the upper "gullet-ganglion" or "primitive brain" in other vermalia. Special sense-organs are either wanting altogether or are only found in a very rudimentary form, as simple optic spots and touch-corpuscles or tentacles that surround the mouth (Fig. 14 *au*, eyes). The muscular system is very slightly and irregularly developed. Immediately under the thin corium, and closely connected with it, we find a thin cuticular muscle-tube, as in the worms. On the other hand, the ascidian has a centralised heart, and in this respect it seems to be more advanced than the amphioxus. On the ventral side of the gut, some distance behind the gill-crate, there is a spindle-shaped heart (Fig. 14 *hz*). It retains permanently the simple tubular form that we find temporarily as the first structure of the heart in the vertebrates (compare the heart of the human embryo, Fig. 229 *c*). This simple heart of the ascidian has, however, a remarkable peculiarity. It contracts in alternate directions. In all other animals the beat of the heart is always in the same direction (generally from rear to front); it changes in the ascidian to the reverse direction. The heart contracts first from the rear to the front, stands still for a minute, and then begins to beat the opposite way, now driving the blood from front to rear; the two large vessels that start from either end of the heart act alternately as arteries and veins. This feature is found in the tunicates alone.

Of the other chief organs we have still to mention the sexual glands, which lie right behind in the body-cavity. All the ascidia are hermaphrodites. Each individual has a male and a female gland, and so is able to fecundate itself. The ripe ova (Fig. 256 *o'*) fall directly from the ovary *(o)* into the mantle-cavity. The male sperm is conducted into this cavity from the testicle *(t)* by a special spermatic duct *(vd)*. Fertilisation is accomplished here, and in many of the ascidia developed embryos are found (Plate XIX., Fig. 14 z). These are then ejected with the breathing-water through the cloaca *(q)*, and so "born alive."

Many of the ascidia, especially of the smaller species, multiply by gemmation as well as by sexual generation. As many of these individuals born by budding remain closely connected through life, they form extensive stocks or cormi, like the familiar coral-stocks. Among these communistic ascidia special interest attaches to those genera in which the stock is formed of a number of star-shaped groups of individuals gracefully combined. Each stellate group consists of a smaller or larger number of individuals, each of which has its independent organisation and a special mouth. All the individuals have, however, a single common cloaca, which is found in the centre of the stellate group.

If we now glance at the entire structure of the simple ascidian (especially *phallusia*, *cynthia*, etc.) and compare it with that of the amphioxus, we shall find that the two have few points of contact. It is true that the fully developed ascidian resembles the amphioxus in several important features of its internal structure, and especially in the peculiar character of the gill-crate and gut. But in most other features of organisation it is so far removed from it, and is so unlike it in external appearance, that the really close relationship of the two was not discovered until their embryology was studied. We will now compare the embryonic development of the two animals, and find, to our great astonishment, that the same embryonic form developes from the ovum of the amphioxus as from that of the ascidian—a typical *chordula*.

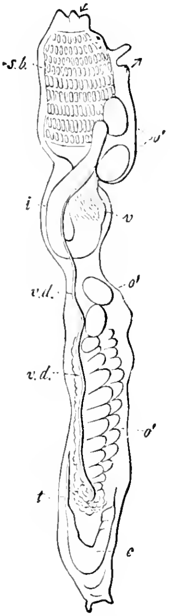


FIG. 256.—**Organisation of an ascidian** (as in Fig. 255 and Fig. 14, Plate XIX., seen from the left). *sb* branchial sac, *v* stomach, *i* small intestine, *c* heart, *t* testicle, *vd* sperm-duct, *o* ovary, *o'* ripe ova in the branchial cavity. The two small arrows indicate the entrance and exit of the water through the openings of the mantle. (From *Milne-Edwards.*)

SIXTEENTH TABLE

SYNOPSIS OF THE CHIEF HOMOLOGIES BETWEEN THE HUMAN EMBRYO, THE EMBRYO OF THE ASCIDIAN, AND THE DEVELOPED AMPHIOXUS ON THE ONE HAND AND THE FULLY-FORMED HUMAN BEING ON THE OTHER.

Ascidian Embryo.	**Developed Amphioxus.**	**Human Embryo.**	**Developed Man.**
Naked epidermis. (Simple stratum of cells.)	Naked epidermis. (Simple stratum of cells.)	Naked epidermis. (Simple stratum of cells.)	Hairy epidermis. (Several strata of cells.)
Simple medullary tube.	Simple medullary tube.	Simple medullary tube.	Separate spinal cord.
Brain one-chambered.	Brain one-chambered.	Brain one-chambered.	Brain five-chambered.
Pronephridia (?).	Prorenal canals.	Prorenal canals.	Pronephridia atrophied.
Mantle-cavity.	Mantle-cavity.	Prorenal duct.	Sexual ducts.
Simple thin corium.	Simple thin corium.	Simple thin corium.	Differentiated thick corium.
Simple cutaneous muscle-pouch.	Segmental muscle-plates.	Segmental muscle-plates.	Differentiated muscles of the trunk.
Chorda.	Chorda.	Chorda.	Vertebral column.
No skull.	No skull.	No skull.	Bony skull.
No limbs.	No limbs.	No limbs.	Two pairs of limbs.
Simple body-cavity (cœloma).	Segmental body-cavity (cœloma).	Segmental body-cavity (cœloma).	Separate thoracic and visceral cavities.
One-chambered ventral heart.	Simple ventral cardiac tube.	One-chambered ventral heart.	Many-chambered ventral heart.
Dorsal vessel.	Aorta.	Aorta.	Aorta.
Simple hepatic tube.	Simple hepatic tube.	Simple hepatic tubes.	Differentiated compact liver.
Simple fore-gut with gill-clefts.	Simple fore-gut with gill-clefts.	Simple fore-gut with gill-clefts.	Fore-gut without gill-clefts.

SEVENTEENTH TABLE

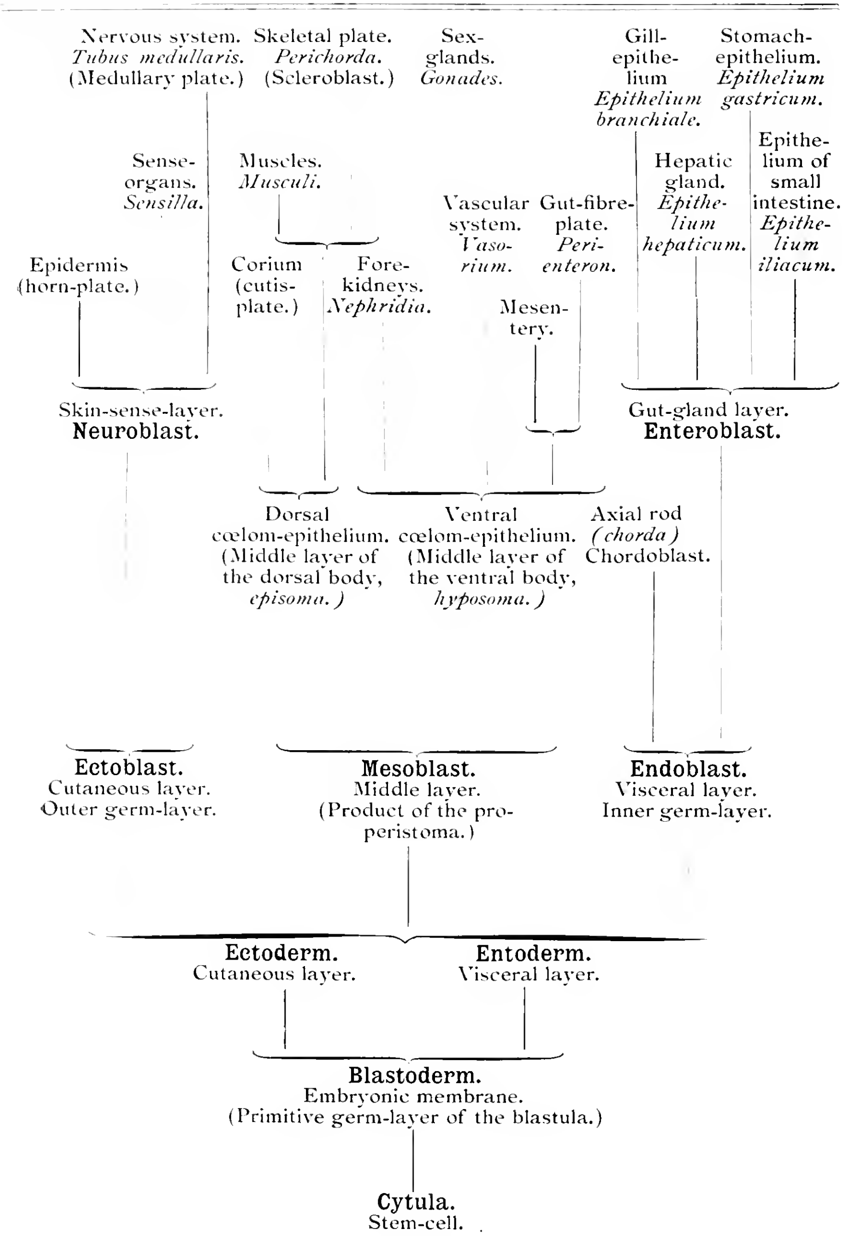
SYNOPSIS OF THE AFFINITY OF THE ASCIDIAN AND AMPHIOXUS ON THE ONE HAND, WITH THE FISH AND MAN ON THE OTHER, IN FULLY-DEVELOPED STATE.

Developed Ascidian.	Developed Amphioxus.	Developed Fish.	Developed Man.
Head and trunk articulated.	Head and trunk similarly articulated.	Head and trunk differently articulated.	Head and trunk differently articulated.
No limbs.	No limbs.	Two pairs of limbs.	Two pairs of limbs.
No skull.	No skull.	Developed skull.	Developed skull.
No tongue-bone.	No tongue-bone.	Tongue-bone.	Tongue-bone.
No jaws.	No jaws.	Upper and lower jaws.	Upper and lower jaws.
No vertebral column.	No vertebral column.	Segmental vertebral column.	Segmented vertebral column.
No ribs.	No ribs.	Ribs.	Ribs.
No separate brain.	No separate brain.	Separate brain with four chambers.	Separate brain with five chambers.
Rudimentary eyes.	Rudimentary eyes.	Developed eyes.	Developed eyes.
No auditory organ.	No auditory organ.	Auditory organ with three circular canals.	Auditory organ with three circular canals.
No sympathetic nerve.	No sympathetic nerve.	Sympathetic nerve.	Sympathetic nerve.
Gut-epithelium ciliated.	Gut-epithelium ciliated.	Gut-epithelium not ciliated.	Gut-epithelium not ciliated.
Simple (or no) liver.	Simple liver (blind gut).	Complex hepatic gland.	Complex hepatic gland.
No pancreas.	No pancreas.	Pancreas developed.	Pancreas developed.
No floating bladder.	No floating bladder.	Floating bladder (rudimentary lungs).	Lungs (floating bladder).
Simple fore-kidneys (protonephra ?).	Prorenal canals (pronephridia).	Primitive kidneys developed (mesonephra).	After-kidneys developed (metanephra).
Simple heart-tube.	Simple heart-tube (ventral vessel).	Heart with valves and chambers.	Heart with valves and chambers.
Blood colourless.	Blood colourless.	Blood red.	Blood red.
No spleen.	No spleen.	Spleen.	Spleen.
Ciliated groove at the gill-crate.	Ciliated groove at the gill-crate.	Thyroid gland (thyroidea).	Thyroid gland (thyroidea).

EIGHTEENTH TABLE

SYNOPSIS OF THE ORIGIN OF THE GERMINAL LAYERS OF THE AMPHIOXUS FROM THE STEM-CELL, AND OF THE CHIEF ORGANS FROM THE GERMINAL LAYERS

(ONTOGENETIC CELLULAR GENEALOGICAL TREE OF THE AMPHIOXUS)[1]



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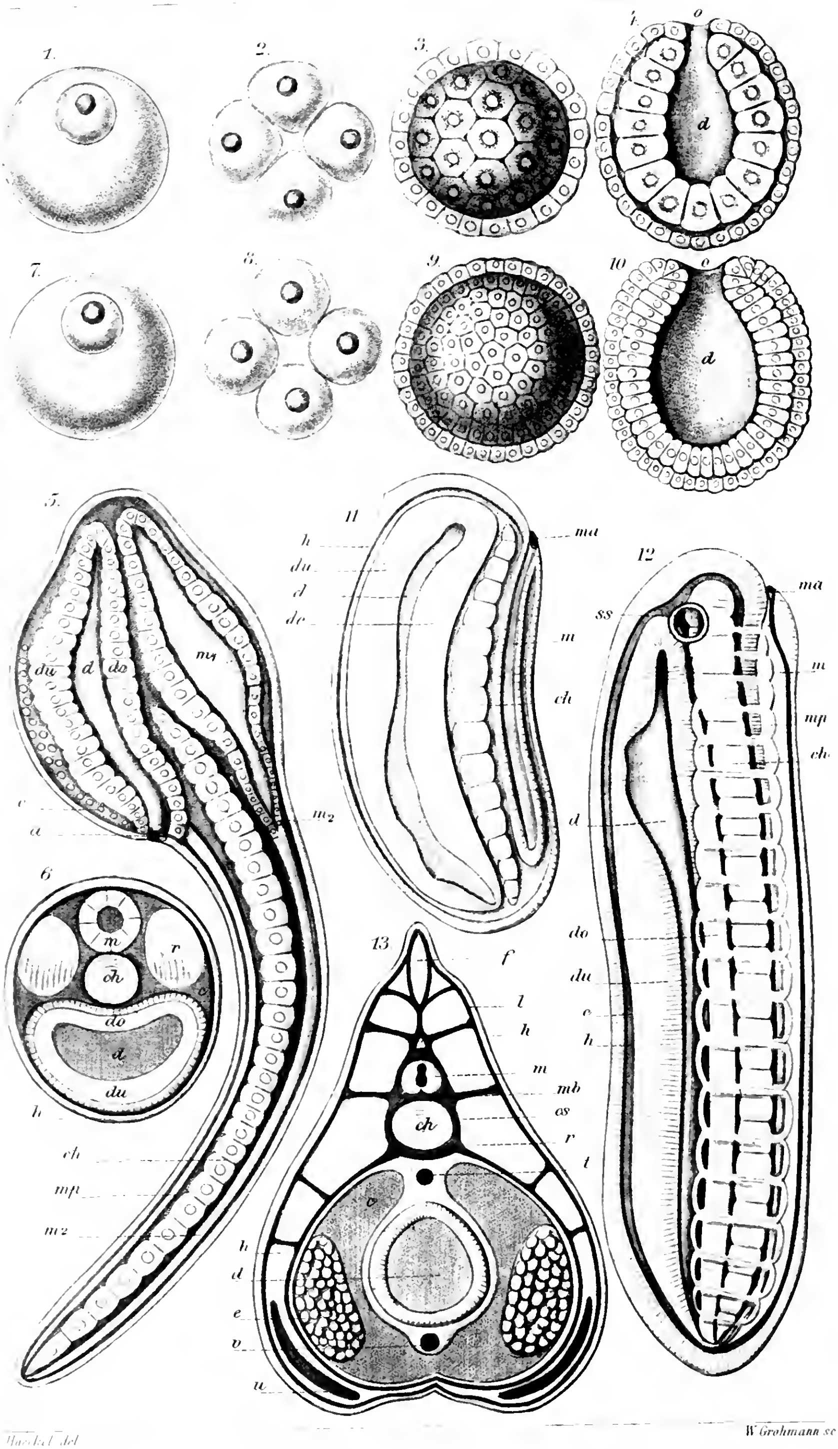
[1] This applies in all the chief features to all the vertebrates, including man; amphioxus has most faithfully reserved the palingenesis by a tenacious heredity.



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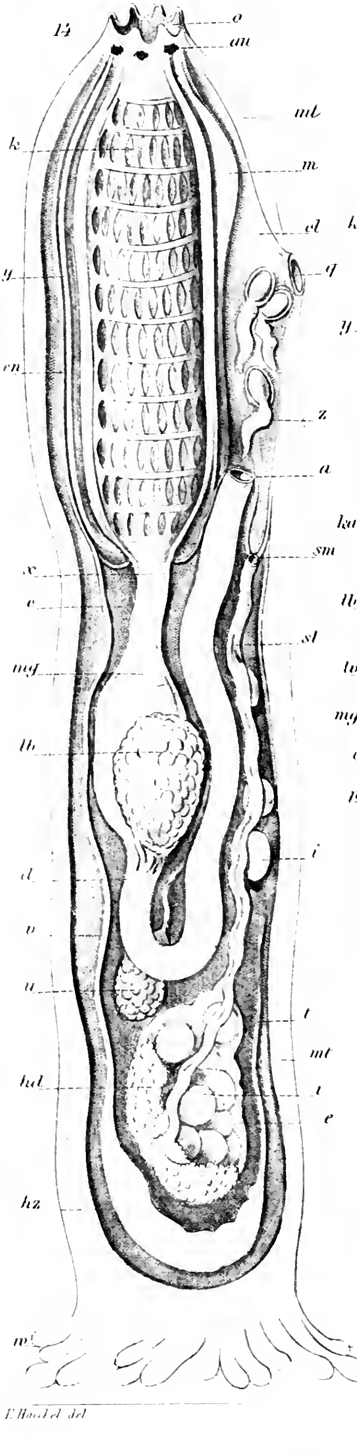

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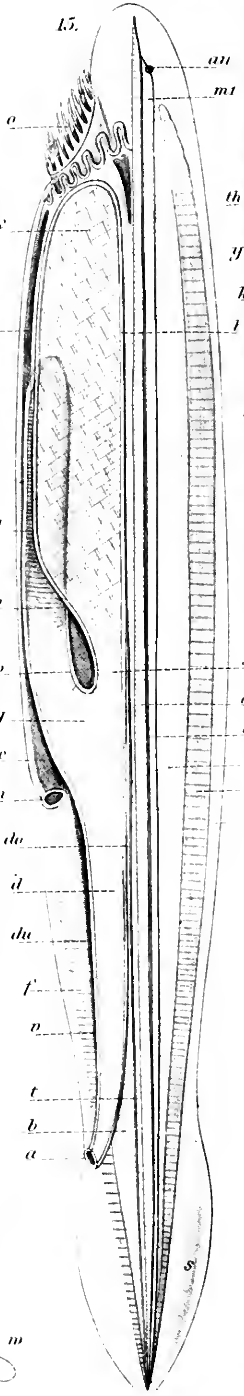

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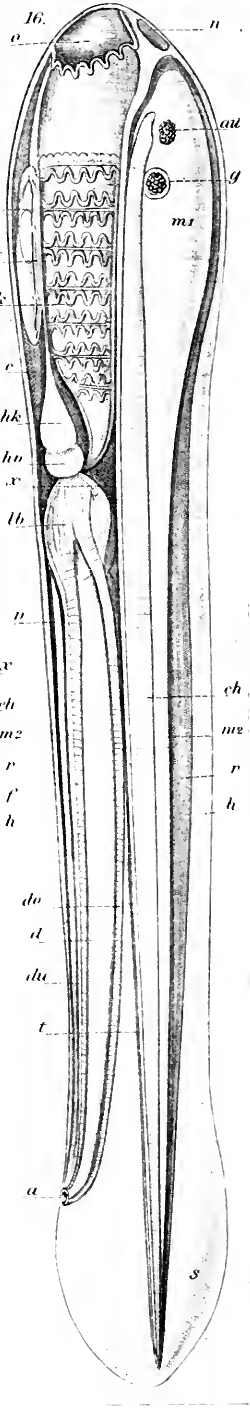

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EXPLANATION OF PLATES XVIII. AND XIX.

PLATE XVIII. EMBRYOLOGY OF THE ASCIDIAN AND AMPHIOXUS

(Mostly from *Kowalevsky*).

Figs. 1–6. Embryology of the Ascidian.

Fig. 1. **Stem-cell (cytula) of an ascidian.** In the clear protoplasm of the stem-cell there is a slight non-central globular nucleus, with a darker nuclear corpuscle.

Fig. 2. **An ascidian-ovum in segmentation.** The stem-cell has divided into four equal cells.

Fig. 3. **Blastula of the ascidian.** The cells formed from the cleavage of the ovum from a spherical vesicle, filled with fluid, the wall of which consists of a single stratum of cells, the blastoderm.

Fig. 4. **Gastrula of the ascidian,** formed from the blastula by invagination. The wall of the primitive gut *(d)* opens by the primitive mouth at *(o)*.

Fig. 5. **Free larva of the ascidian.** Between the medullary tube *(m)* and the alimentary canal *(d)* the chorda *(ch)* passes, and goes the whole length of the tail to the tip.

Fig. 6. **Transverse section of the larva of an ascidian** (Fig. 5), through the hinder part of the trunk, before the beginning of the tail. The section is just the same as that of the amphioxus larva (Figs. 11, 12). Between the medullary tube *(m)* and the gut *(d)* lies the chorda *(ch)*, and on each side the lateral muscles of the trunk *(r)*, products of the cœlom-pouches. (Cf. Figs. 82–87.)

Figs. 7–13. Embryology of the Amphioxus.

Fig. 7. **Stem-cell (cytula) of the amphioxus** (cf. Fig. 1).

Fig. 8. **An amphioxus-ovum in segmentation** (cf. Fig. 2).

Fig. 9. **Blastula of the amphioxus** (cf. Fig. 3).

Fig. 10. **Gastrula of the amphioxus** (cf. Fig. 4).

Fig. 11. **Young larva of the amphioxus.** Between the medullary tube *(m)* and the gut *(d)* is the chorda *(ch)*. The medullary tube has an opening (neuroporus, *ma*) at its anterior end.

Fig. 12. **Older larva of the amphioxus.** On each side of the medullary tube *(m)* and the chorda *(ch)* we see a long row of muscle-plates *(mp)*, formed by segmentation of the two cœlom-pouches: they are therefore called the primitive segments or metamera. In front a sense-organ has been developed *(ss)*. The wall of the alimentary canal *(d)* is much thicker on the ventral side *(du)* than on the dorsal side *(do)* above. The fore part of the gut expands to form the gill-crate.

Fig. 13. **Transverse section of the developed amphioxus** (Fig. 15), a little behind the centre of the body. Above the gut *(d)* we see the dorsal vessel or chief artery (aorta, *t*), under it the ventral vessel or subintestinal vein *(v)*. In the inner wall of the peribranchial or mantle-cavity *(v)* are the ovaries *(e)*, and near these the lateral canals of the mantle-folds or gill-covers *(u)*. The dorsal muscles *(r)* are divided into several pieces by intermuscular ligaments. *f* dorsal fin.

PLATE XIX. STRUCTURE OF THE ASCIDIAN, THE AMPHIOXUS, AND THE LARVA OF THE PETROMYZON.

For the purpose of comparison, all three have been arranged in the same way and reduced to the same size; seen from the left. The head is upward, the tail below; dorsal side to the right, ventral to the left. The skin has been removed from the left side of the body, in order to show the internal organs in their natural composition.

Fig. 14. **A simple ascidian** *(monascidia)*, magnified six times.

Fig. 15. **A developed amphioxus,** magnified four times.

In order to see it better, the amphioxus is drawn at double its natural width in Fig. 15. In reality, with the length here given, it would only be half as broad. (Cf. Fig. 245.)

Fig. 16. **A young lamprey-larva** *(petromyzon planeri)*, eleven days after creeping out of the egg, magnified forty-five times. (From *Max Schultze.*) The larva of the petromyzon, which afterwards undergoes a curious metamorphosis, was formerly distinguished as a special genus with the name *ammocœtes.*

The letters have the same meaning throughout.

ALPHABETICAL INDEX OF THE MEANING OF THE LETTERS IN PLATES XVIII. AND XIX.

a	Anus.
au	Eye.
b	Ventral muscles.
c	Mantle-cavity.
ch	Chorda.
cl	Cloaca.
cs	Chorda-sheath.
d	Alimentary canal (gut).
do	Dorsal wall of gut.
du	Ventral wall of gut.
e	Ovary.
en	Endostyle (wall of the gullet-groove).
f	Fin-border.
g	Auditory vesicle.
h	Horny plate.
hd	Testicles.
hk	Ventricle of heart.
hv	Auricle of heart.
hz	Heart.
i	Ova.
k	Gills.
ka	Branchial artery.
l	Corium (cutis).
lb	Liver.
lb'	Anterior end of liver.
lv	Hepatic vein.
m	Medullary tube.
m_1	Cerebral vesicle.
m_2	Spinal marrow.
ma	Anterior opening of spinal marrow.
mb	Muscular ligaments.
mg	Stomach.
mh	Mouth-cavity.
mp	Muscle-plate.
mt	Mantle.
n	Nose (olfactory pit).
o	Mouth-aperture.
p	Ventral pore (mantle-hole).
q	Ejection-opening (cloaca).
r	Dorsal muscles.
s	Tail-fin.
sl	Sperm-duct.
sm	Aperture of sperm-duct.
ss	Sense-organs.
t	Aorta (dorsal vessel).
th	Thyroid gland.
u	Lateral canal of the mantle-folds.
v	Subintestinal vein.
w	Fibrous roots of the ascidian.
x	Limit of the branchial gut and hepatic gut (also limit of head and trunk).
y	Gullet-groove (ciliated groove).
z	Ascidian embryos.

CHAPTER XVII.

EMBRYOLOGY OF THE AMPHIOXUS AND THE ASCIDIAN

Affinity of the vertebrates and invertebrates. Fecundation of the amphioxus. Total cleavage of the ovum gives rise to a spherical blastula. From this is formed by invagination the cup-larva (gastrula). This quickly developes into the chordula. In the middle of the back is formed the ectodermal nerve-tube, under this the entodermal chorda, and at each side of it the cœlom-pouches, proceeding from the two primitive mesodermic cells. The cœlom-pouches divide by a lateral fold into episomites and hyposomites. By transverse segmentation myotomes are formed from the first and gonotomes from the second. The gut divides into a fore or branchial, and a hind or hepatic, gut. From the lateral wall of the body a pair of cutaneous folds (mantle-folds or gill-covers) grow, and these form, by coalescence on the ventral side, the wide peribranchial (mantle) cavity. The ontogenesis is at first identical with that of the amphioxus. The same gastrula and chordula are formed. The tail and chorda are done away with. The ascidian becomes stationary, and covers itself with a cellulose mantle. Copelata or appendicularia, tunicates, which live permanently at the stage of the ascidian-larva, and retain the tail and chorda. General comparison and appreciation of the amphioxus and the ascidian.

THE structural features that distinguish the vertebrates from the invertebrates are so prominent that there was the greatest difficulty in the earlier stages of classification in determining the affinity of these two great groups. When, in harmony with the theory of descent, scientists began to speak of the affinity of the various animal groups in more than a figurative—in a genealogical—sense, this question came at once to the front, and seemed to constitute one of the chief obstacles to the carrying-out of the evolutionary theory. Even earlier, when they had studied the relations of the chief groups, the "types" of Baer and Cuvier, without any idea of real genealogical connection, they believed they had found here and there among the invertebrates points of contact with the vertebrates: some of the worms, especially, seemed to approach the vertebrates in structure, such as the marine arrow-worm *(sagitta)*. But on closer study the analogies proved untenable. When Darwin gave an impulse to the construction of a real stem-history of the animal kingdom by his reform of the theory of evolution, the solution of this problem was found to be particularly difficult. When I made the first attempt in my *Generelle Morphologie* (1866) to work out the theory and apply it to classification, I found no problem of phylogeny that gave me so much trouble as the linking of the vertebrates with the invertebrates.

But just at this time the true link was discovered, and at a point where it was least expected. Towards the end of 1866 two works of the Russian zoologist, Kowalevsky, who had lived for some time at Naples, and studied the embryology of the lower animals, were issued in the publications of the St. Petersburg Academy. A fortunate accident had directed the attention of this able observer almost simultaneously to the embryology of the lowest vertebrate, the amphioxus, and that of an invertebrate, the close affinity of which to the amphioxus had been least suspected, the ascidian. To the extreme astonishment of all zoologists who were interested in this important question, there turned out to be the utmost resemblance in structure from the commencement of development between these two very different animals—the lowest vertebrate and the mis-shaped sessile invertebrate. With this undeniable identity of ontogenesis, which can be demonstrated to an astounding extent, we had, in virtue of the biogenetic law, discovered the long-sought genealogical link, and definitely identified the invertebrate group that represents the nearest blood-relatives of the vertebrates. The discovery was confirmed by C. Kupffer, E. Van Beneden, and Julin, and afterwards by many other zoologists, and there can no longer be any doubt that of all the classes of invertebrates that of the tunicates is most closely related to the vertebrates, and of the tunicates the nearest are the ascidia. We cannot say that the vertebrates are descended from the ascidia—and still less the reverse—but we can say that of all the invertebrates it is the tunicates, and, within this group, the ascidia, that are the nearest blood-relatives of the ancient stem-form of the vertebrates. We must assume as the common ancestral group of both stems an extinct family of the extensive vermalia-stem, the *prochordonia* or *prochordata* ("primitive chorda-animals").

In order to appreciate fully this remarkable fact, and especially to secure the sound basis we seek for the genealogical tree of the vertebrates, it is necessary to study thoroughly the embryology of both these animals, and compare the individual development of the amphioxus step by step with that of the ascidian. (Cf. Plate XVIII. and p. 443.) We begin with the ontogeny of the amphioxus (cf. Figs. 247–265 and Plate XVIII., Figs. 7–12). We have now an accurate knowledge of this from very careful studies made by the Vienna zoologist, Hatschek, in the spring of 1879, which confirm and complete the statements of Kowalevsky. *Amphioxus prototypus* is found in myriads in the shore-sand of a small salt lake that lies in the neighbourhood of the fishing-village Faro, at the north entrance of the Straits of Messina, and is connected with the sea by a narrow channel. In the spring of 1893 I found thousands of them there in an hour. Professor Hatschek stayed ten weeks at this place (from April to June, 1879) in order to make a complete and uninterrupted study of the embryology of the lancelet. He succeeded so well that we may regard the *Studies of the Development of the Amphioxus,* which he published in 1881, as one of the chief foundations on which we can establish the immense importance of this lowest vertebrate in connection with anthropogeny.

From the concordant observations of Kowalevsky at Naples and Hatschek at Messina, it follows, firstly, that the total ovum-segmentation and regular gastrulation of the amphioxus are of the simplest character. They take place in the same way as we find them in many of the lower animals of different invertebrate stems, and which we have already described as original or primordial; the development of the ascidian is of the same type. Sexually-mature specimens of the amphioxus, which are found in great quantities at Messina from April or May onwards, begin as a rule to eject their sexual products in the evening; if you catch them about the middle of a warm night and put them in a glass vessel with sea-water, they immediately eject through the mouth their accumulated sexual products, in consequence of the disturbance. The males give out masses of sperm, and the females discharge ova in such quantity that many of them stick to the fibrils about their mouths. Both kinds of cells pass first into the mantle-cavity after the opening of the gonades, proceed through the gill-clefts into the branchial gut, and are discharged from this through the mouth.

The ova are simple round cells. They are only one-tenth of a millimetre in diameter, and thus are only half the size of the mammal ova, and have no distinctive features (Plate XVIII., Fig. 7). The clear protoplasm of the mature ovum is made so turbid by the numbers of dark granules of food-yelk or deutoplasm scattered in it that it is difficult to follow the process of fecundation and the behaviour of the two nuclei during it (p. 136). The mobile elements of the male sperm, the cone-shaped spermatozoa, are similar to those of most other animals (cf. Fig. 20). Fecundation takes place when these lively ciliated cells of the sperm approach the ovum, and seek to penetrate into the yelk-matter or the cellular substance of the ovum with their head-part—the thicker part of the cell that encloses the nucleus. Only one spermatozoon can bore its way into the yelk at one pole of the ovum-axis; its head or nucleus coalesces with the female nucleus, which remains after the extrusion of the directive bodies from the germinal vesicle. Thus is formed the "stem-nucleus," or the nucleus of the "stem-cell" (cytula, Fig. 29). This now undergoes total segmentation, dividing into two, four, eight, sixteen, thirty-two cells, and so on. In this way we get the spherical, mulberry-shaped body, which we call the *morula*.

The segmentation of the amphioxus is not entirely regular, as was supposed after the first observations of Kowalevsky (1866). It is not completely equal, but a little unequal. As Hatschek afterwards found (1879), the segmentation-cells only remain equal up to the morula-stage, the spherical body of which consists of thirty-two cells. Then, as always happens in unequal segmentation, the more sluggish vegetal cells—the mother-cells of the entoderm—are outstripped in the cleavage. At the lower or vegetal pole of the ovum a crown of eight large entodermic cells remains for a long time unchanged, while the other cells divide, owing to the formation of a series of horizontal circles, into an increasing number of crowns of sixteen cells each. Afterwards the segmentation-cells get more or less irregularly displaced, while the segmentation-cavity enlarges in the centre of the morula; in the end the former all lie on the surface of the latter, so that the fœtus attains the familiar blastula shape and forms a hollow sphere, the wall of which consists of a single stratum of cells (Fig. 257 *A–C*). This layer is the blastoderm, the simple epithelium from the cells of which all the tissues of the body

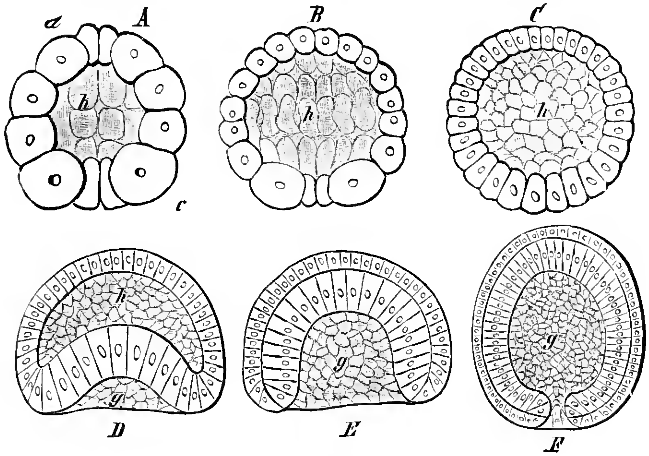

FIG. 257.

FIG. 257.—**Gastrulation of the amphioxus.** (From *Hatschek.*) (Vertical section through the axis of the ovum.) *A*, *B*, *C* three stages of blastula-formation; *D*, *E* invagination of the blastula; *F* complete gastrula. *h* segmentation-cavity, *g* primitive gut-cavity.

FIG. 258.—**Gastrula of the amphioxus,** in frontal longitudinal section (between the episoma and hyposoma). *d* primitive gut, *o* primitive mouth, *i* visceral layer or entoderm, *e* cutaneous layer or ectoderm.

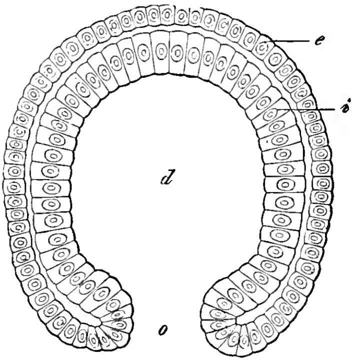

FIG. 258.

proceed. In the blastula the axis of the spherical body is made very clear by the larger cells of the vegetal pole and the smaller cells of the animal pole (Fig. 257 *A–C*); the former take up the lower third, the latter the upper two-thirds of the spherical blastula-wall.

These important early embryonic processes take place so quickly in the amphioxus that four or five hours after fecundation, or about midnight, the spherical blastula is completed. A pit-like depression is then formed at the vegetal pole of it, and in consequence of this the hollow sphere doubles on itself (Fig. 257 *D*). This pit becomes deeper and deeper (Fig. 257 *E*, *F*); at last the invagination is complete, and the inner or folded part of the blastula-wall lies on the inside of the outer wall. We thus get a hollow hemisphere, the thin wall of which is made up of two layers of cells (Fig. 257 *E*). From hemispherical the body soon becomes almost spherical once more, and then oval, the internal cavity enlarging considerably and its mouth growing narrower (Fig. 248 and Plate XVIII., Fig. 10). The form which the amphioxus-embryo has thus reached is a real "cup-larva or *gastrula*," of the original simple type that we have previously described as the "bell-gastrula or archigastrula" (Figs. 31–37).

As in all the other animals that form an archigastrula, the whole body is nothing but a simple gastric sac; its internal cavity is the primitive gut *(progaster archenteron*, Fig. 257 *g*, 258 *d)*, and its aperture the primitive mouth *(prostoma* or *blastoporus*, *o)*. The wall is at once gut-wall and body-wall. It is composed of two simple cell-layers, the familiar primary germinal layers. The inner layer, or the invaginated part of the blastoderm, which immediately encloses the gut-cavity, is the entoderm or endoblast, the inner or vegetal germ-layer, from which develop the wall of the alimentary canal and all its appendages, the cœlom-pouches, etc. (Fig. 258, 259 *i*.) The outer stratum of cells, or the non-invaginated part of the blastoderm, is the ectoderm or ectoblast, the outer or animal germ-layer, which provides the outer skin (epidermis) and the nervous system *(e)*. The cells of the entoderm are much larger, darker, and more fatty than those of the ectoderm, which are clearer and less rich in fatty particles. Hence before and during invagination there is an increasing differentiation of the inner, invaginated from the outer, non-invaginated layer. The animal cells of the outer layer soon develop vibratory hairs ; the vegetal cells of the inner layer do so much later. A thread-like process grows out of each cell, and effects continuous vibratory movements. By the vibrations of these slender hairs the gastrula of the amphioxus swims about in the sea, when it has pierced the thin ovolemma, like the gastrula of many other animals (Fig. 259). As in many other lower animals, the vibratory cells have only one whip-like hair each, and so are called *flagellate* (whip) cells (in contrast with the *ciliated* cells, which have a number of short lashes or cilia).

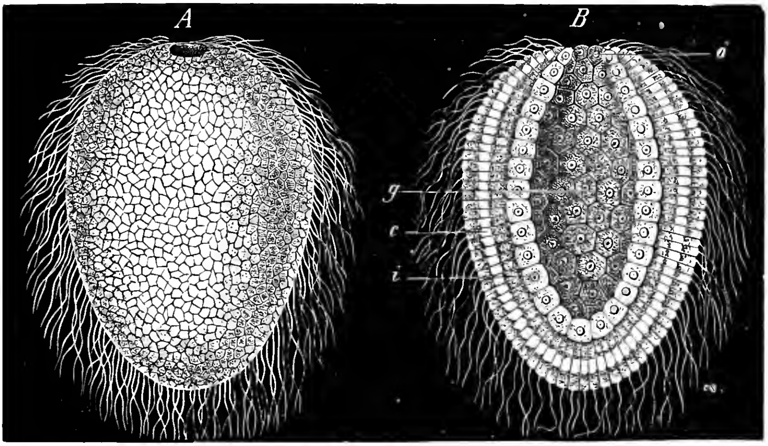

Fig. 259.—**Gastrula of a sponge** (olynthus). *A* external view, *B* longitudinal section through the axis. *g* primitive gut, *o* primitive mouth, *i* visceral layer or entoderm, *e* cutaneous layer or ectoderm.

The remarkable rapidity of the gastrulation of the amphioxus is subject to slight variations, according to Hatschek's observations, and these are greater in proportion to the increase of the temperature. On a warm spring evening the gastrula is usually formed in six hours. According to a careful observation of this distinguished scientist, the first cleavage of an ovum that has been ejected and fecundated at 8 o'clock in the evening takes place an hour afterwards ;

by 10 o'clock it has divided into four segmentation-cells, by 10.15 into eight, 10.30 into sixteen, and 11 o'clock into thirty-two cells. By about one in the morning the gastrula is complete; after three-quarters of an hour it begins to invaginate; and by about 3 o'clock the segmentation-cavity has disappeared. The gradual contraction of the gastrula-mouth then proceeds slowly until the morning. But on the morning of the first day, or after ten hours, it is still wide open; the closing is very slow, and usually occupies the greater part of the fore-noon.

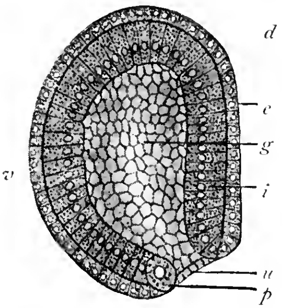

FIG. 260.—**Gastrula of the amphioxus, seen from the left side** (optic median section). (From *Hatschek.*) *g* primitive gut, *u* primitive mouth, *p* peristomal polar cells, *i* entoderm, *e* ectoderm, *d* dorsal side, *v* ventral side.

In the further course of development the roundish bell-gastrula becomes elongated, and begins to flatten on one side, parallel to the long axis. The flattened side is the subsequent dorsal side; the opposite or ventral side remains curved. The latter grows more quickly than the former, with the result that the primitive mouth is forced to the dorsal side (Fig. 260). In the middle of the dorsal surface a shallow longitudinal groove or furrow is formed (Fig. 263), and the edges of the body rise up on each side of this groove in the shape of two parallel swellings. This groove is, of course, the dorsal furrow, and the swellings are the dorsal or medullary swellings; they form the first structure of the central nervous system, the medullary tube. The medullary swellings now rise higher; the groove between them becomes deeper and deeper. The edges of the parallel swellings curve towards each other, and at last unite, and the medullary tube is formed (Figs. 261 *m*, 262 *m*; Plate XVIII., Fig. 11 *m*). Hence the formation of a medullary tube out of the outer skin takes place in the naked dorsal surface of the free-swimming larva of the amphioxus in just the same way as we have found in the embryo of man and the higher animals within the fœtal membranes. In both cases the neural tube at length separates completely from the horny plate. There is the special feature that the medullary tube remains open, and has a narrow external mouth, the *neuroporus*, at the part which afterwards becomes the fore or mouth-end of the amphioxus (Fig. 261 *np*). But at the other end the cavity of the neural tube passes directly into the primitive mouth. As the edges of the medullary groove grow over the primitive mouth, the remainder of it persists for a time as a narrow aperture, which forms a direct communication between the cavities of the primitive gut and the neural tube—the typical *neurentic canal* (Fig. 261 *ne;* cf. p. 297).

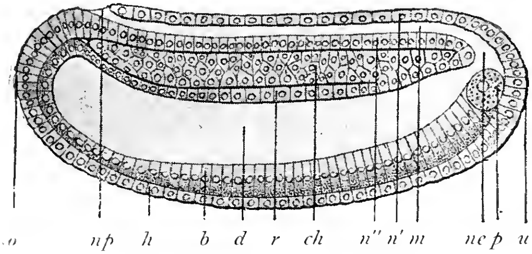

FIG. 261.

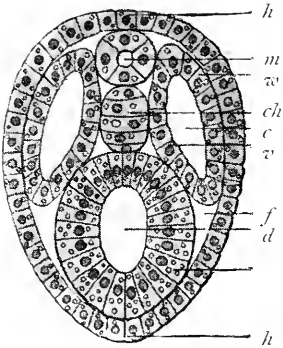

FIG. 262.

FIGS. 261 and 262.—**Chordula of the amphioxus.** Fig. 261. Median longitudinal section (from the left side). Fig. 262. Transverse section. (From *Hatschek.*) In Fig. 261 the cœlom-pouches have been omitted, in order to show the chorda plainly. Fig. 262 is rather diagrammatic. *h* horny plate, *m* medullary tube, *n* wall of same (*n'* dorsal, *n''* ventral wall), *ch* chorda, *np* neuroporus, *ne* neurenteric canal, *d* gut-cavity, *r* dorsal wall of the gut, *b* ventral wall of the gut, *u* primitive mouth, *o* position of the later mouth-pit, *p* promesoblasts (primitive or polar cells of the mesoderm), *w* parietal layer, *v* visceral layer of the mesoderm, *c* cœloma, *f* remainder of the segmentation-cavity.

Simultaneously with the construction of the medullary tube we have in the amphioxus-embryo the formation of the chorda, the cœlom-pouches, and the mesoderm proceeding from their wall. The processes also take place with characteristic simplicity and clearness, so that they are very instructive to compare with the lower bilaterals (vermalia) on the one hand and with the higher vertebrates (craniotes) on the other. While the medullary groove is sinking in the middle line of the flat dorsal side of the oval embryo, and its parallel edges unite to form the ectodermic neural tube, the single chorda is formed directly underneath them, and on each side of this a parallel longitudinal fold, from the entodermic dorsal wall of the primitive gut. These longitudinal folds of the entoderm proceed from the primitive mouth, or from its lower and hinder edge. Here we see at an early stage a couple of large entodermic cells, which are distinguished from all the others by their great size, round form, and fine-grained protoplasm; they are the two promesoblasts, or polar cells of the mesoderm (Fig. 261 *p*). They are of great importance, as Rabl, Hatschek, and others, have shown, since the formation of the middle germinal layers starts from them in the majority of the bilaterals or cœlomaria. In the amphioxus-embryo they lie just at the aboral pole of the long axis, at the posterior and lower edge of the gastrula-mouth, which is forced to the dorsal side of the hinder end. The two polar cells of the mesoderm indicate the original starting-point of the two cœlom-pouches, which grow from this spot between the inner and outer germinal layers, sever themselves from the primitive gut, and provide the cellular material for the middle layer (Figs. 263–272).

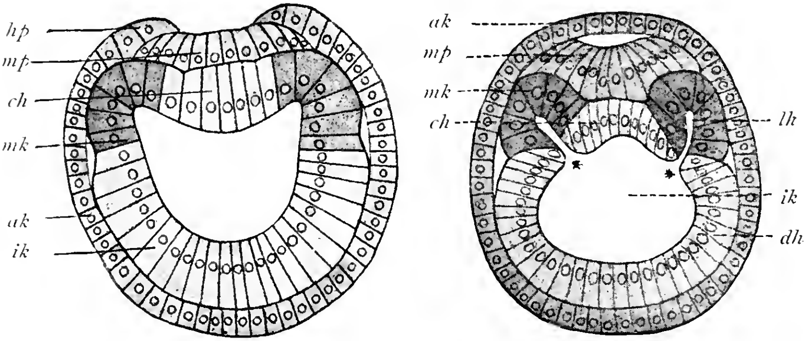

FIG. 263.

FIG. 264.

FIGS. 263 and 264.—**Transverse sections of amphioxus-larvæ.** (From *Hatschek.*) Fig. 263 at the commencement of cœlomation (still without primitive segments). Fig. 264 at the stage with four primitive segments. *ak, ik, mk* outer, inner, and middle germ-layers, *hp* horny plate, *mp* medullary plate, *ch* chorda, * and * position of the cœlom-pouches, *lh* body-cavity.

The brothers Hertwig have shown in their suggestive cœlom-theory the great importance of these cœlom-pouches. In the great majority of the bilateral metazoa they form the foundation of the body-cavity *(cœloma)*; the two cavities (right and left cœlom-sacs) usually blend into one, their attenuated walls breaking down either on the ventral side alone (vertebrates and echinoderms) or on the dorsal side also (articulates and most of the vermalia). The outer wall of the inflated cœlom-pouches, the parietal layer, attaches itself to the ectoderm, and becomes the skin-fibre layer ; their inner wall, the visceral layer, unites with the entoderm and becomes the gut-fibre layer (Figs. 263–272 ; cf. Chapter X.).

Hence in the amphioxus, as in all the other bilaterals, the middle layer is double, and originates from the entoderm —from the hindermost section of it which immediately passes into the ectoderm at the primitive mouth. Here we have at an early stage the two mesodermic cells, to the right and left of the primitive mouth. From this point proceeds the formation of the two lateral folds of the primitive gut, which separate from it in the form of the cœlom-pouches. The important question of the relations of the former to the latter is one of the most difficult problems of comparative embryology. The scientists who have made the most careful and extensive study of it, Hertwig and Rabl, take different views. The brothers Hertwig have endeavoured to show in their cœlom-theory that in all the bilaterals (except a few groups, the pseudocœlia) the body-cavity is formed by the invagination of a couple of cœlom-sacs out of the primitive

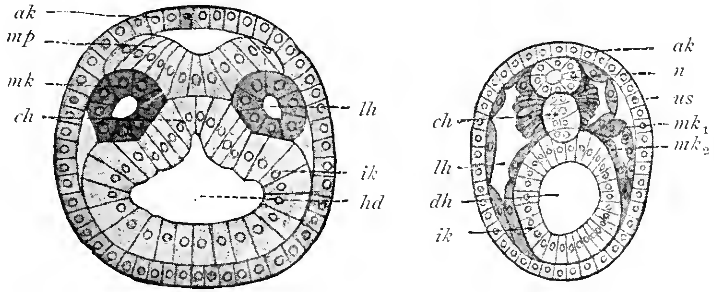

FIG. 265. FIG. 266.

FIGS. 265 and 266.—**Transverse section of amphioxus-embryos.** Fig. 265 at the stage with five somites. Fig. 266 at the stage with eleven somites. (From *Hatschek.*) *ak* outer germinal layer, *mp* medullary plate, *n* neural tube, *ik* inner germinal-layer, *dh* gut-cavity, *lh* body-cavity, *mk* middle germinal-layer (mk_1 parietal, mk_2 visceral), *us* primitive segment, *ch* chorda.

gut, and that the walls of these make the mesoderm. Rabl, however, believes that originally it is the formation of a couple of polar cells that leads to the construction of the two solid mesodermic parts. Perhaps the two opinions could be reconciled in the sense that the cœlom-pouches are further developments of the two strings of cells that were originally (in the earliest, tiny bilaterals with few cells) represented only by a couple of polar cells (primary sexual cells). From the phylogenetic point of view, whichever opinion is correct, the two mesodermic structures must in any case be regarded as a pair of gonades, the sexual glands of the lower bilaterals from which the vertebrates also are descended.

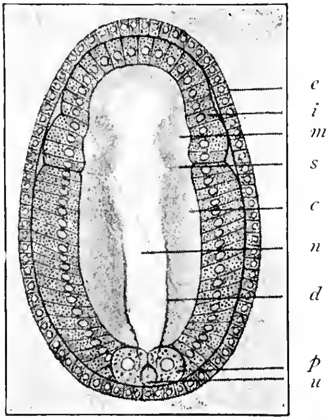

FIG. 267.—**Embryo of the amphioxus, sixteen hours old,** seen from the back. (From *Hatschek.*) *d* primitive gut, *u* primitive mouth, *p* polar cells of the mesoderm, *c* cœlom-pouches, *m* their first primitive segment, *n* medullary tube, *i* entoderm, *e* ectoderm, *s* first segment-fold.

Immediately after their formation the two mesodermic pouches of the amphioxus are divided into several parts by longitudinal and transverse folds. Each of the primary pouches is divided into an upper dorsal and a lower ventral section by a couple of lateral longitudinal folds (Fig. 266). But these are again divided by several parallel transverse folds into a number of successive sacs, the primitive segments or somites (formerly called by the unsuitable name of "primitive vertebræ"; Figs. 267–272). They have a different future above and below. The upper or dorsal segments, the *episomites*, round, thick-walled sacs, lose their cavity later on, and form with their cells the segmental muscular plates of the trunk. The lower or ventral segments, the *hyposomites*, corresponding to the lateral plates of the craniote-embryo, blend together in the upper part owing to the disappearance of their lateral walls, and thus form the perigastral body-cavity (metacœl); in the lower part they remain separate, and afterwards form the segmental gonades.

The severance of the vesicular primitive segments from the primitive gut always proceeds gradually from front to rear, so that the foremost pair of the cœlom-sacs (in the amphioxus at the limit of the first and second third of the embryo) are the first, oldest, and largest (Fig. 267 *m*). All the others are younger and smaller. They increase constantly in number, the hind third of the cœlom-folds, starting from the aboral polar cells, growing continuously, and fresh transverse folds taking place (Figs. 268 – 272). The longer the body becomes by the growth of its hinder section, the greater is the number of primitive segments.

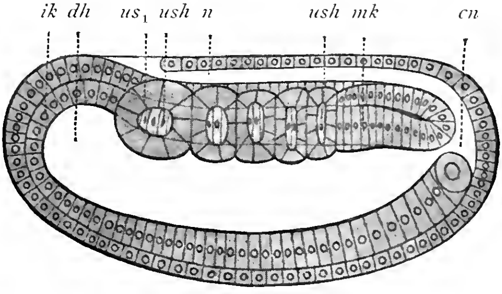

FIG. 268.

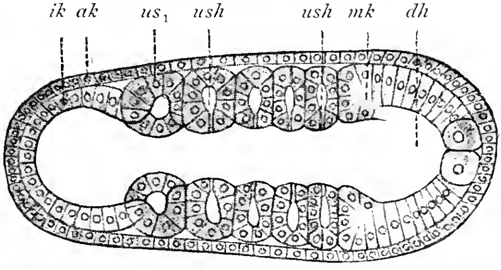

FIG. 269.

FIGS. 268 and 269.—**Amphioxus-embryo, twenty hours old, with five somites.** Fig. 268 from the left, Fig. 269 from the back. (From *Hatschek.*) *V* fore end, *H* hind end, *ak*, *mk*, *ik* outer, middle, and inner germinal-layers; *dh* visceral tube, *n* neural tube, *cn* neurenteric canal, *ush* cœlom-pouches (or primitive segment cavities), *us* first (foremost) primitive segment.

In the middle, between the two lateral cœlom-folds of the primitive gut, a single central organ detaches from this at an early stage in the middle line of its dorsal wall. This is the dorsal chorda (Figs. 261, 262 *ch*). This axial rod, which is the first foundation of the later vertebral column in all the vertebrates, and is the only representative of it in the amphioxus, originates from the entoderm. Careful observation has shown that this solid cylindrical axial rod does not first appear in this form, but as a sagittal fold of the entoderm, rising upwards. But the two parallel layers of this straight median fold immediately come so close together that the space between them disappears. Hence, the solid rod, seen from the back, seems to be composed of two parallel rows of entodermic cells.

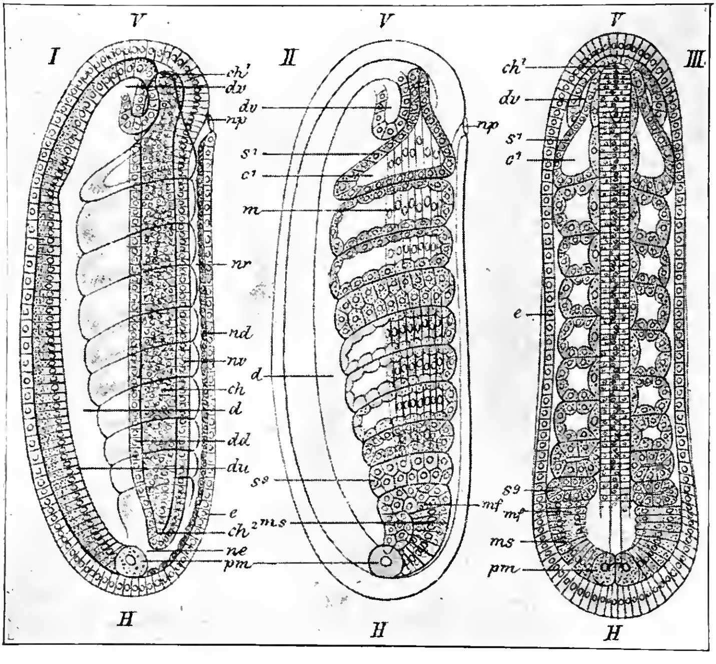

FIG. 270. FIG. 271. FIG. 272.

FIGS. 270-272.—**Amphioxus-embryo, twenty-four hours old, with eight somites.** (From *Hatschek.*) Figs. 270 and 271, side view (from the left). Fig. 272, back view. In Fig. 270 only the outlines of the eight primitive segments are indicated; in Fig. 271 their cavities and muscular walls. *V* fore end, *H* hind end, *d* gut, *du* lower and *dd* upper gut-wall, *ne* neurenteric canal, *nv* ventral, *nd* dorsal wall of the neural tube, *np* neuroporus, *dv* fore gut-pouch, *ch* chorda, *mf* mesodermic fold, *pm* polar cells of the mesoderm *(ms)*, *e* ectoderm.

In consequence of these important folding-processes in the primitive gut, the simple entodermic tube divides into four different sections :—I., underneath, at the ventral side, the permanent alimentary canal or permanent gut *(metagaster)*; II., above, at the dorsal side, the axial rod or chorda; and III., the two cœlom-sacs, which immediately sub-divide into two structures—IIIA., above, on the dorsal side, the *episomites*, the double row of primitive or muscular segments (myotomes); and IIIB., below, on each side of the gut, the *hyposomites*, the two lateral plates that give rise to the gonades, and the cavities of which partly unite to form the perigastral body-cavity. At the same time, the neural or medullary tube is formed above the chorda, on the dorsal surface, by the closing of the parallel medullary swellings. All these processes which outline the typical structure of the vertebrate take place with astonishing rapidity in the embryo of the amphioxus; in the afternoon of the first day, or twenty-four hours after fertilisation, the young vertebrate, the typical embryo, is formed; it then has, as a rule, six to eight somites.

The chief occurrence on the second day of development is the construction of the two permanent openings of the gut—the mouth and anus. In the stages given on Figs. 261–272 the alimentary tube is found to be entirely closed, after the closing of the primitive mouth; it only communicates behind by the neurenteric canal with the medullary tube. The permanent mouth is a secondary formation, at the opposite end (in the vicinity of *SS*, Fig. 12, Plate XVIII.). Here, at the end of the second day, we find a pit-like depression in the outer skin which penetrates inwards into the closed gut. The anus is formed behind in the same way a few hours later (in the vicinity of the additional gastrula-mouth). In man and the higher vertebrates also the mouth and anus are formed, as we have seen, as flat pits in the outer skin; they then penetrate inwards, gradually becoming connected with the blind ends of the closed gut-tube. During the second day the amphioxus-embryo undergoes few other changes. The number of primitive segments increases, and generally amounts to fourteen, some forty-eight to fifty hours after impregnation. The slow multiplication of them is effected by the same segmentation from front to rear (*i.e.*, transverse folding of the cœlom-pouches) by which the series of provertebral segments grows in the human embryo. Here, again, the foremost metamera are the oldest and the hindmost the youngest. To each metameron corresponds a certain section of the medullary tube and a pair of spinal nerves, which proceed from it to the muscles and skin. The muscular system is the one in which the articulation or metamerism of the body is first perceived.[1]

Almost simultaneously with the formation of the mouth the first gill-cleft breaks through in the fore section of the amphioxus-embryo (generally forty hours after the commencement of development). It now begins to nourish itself independently, as the food material stored up in the ovum is completely used up. The further development of the free larvæ takes place very slowly, and extends over several months. The body becomes much longer, and is compressed at the sides, the head-end being broadened in a sort of triangle. Two rudimentary sense-organs are developed in it. Inside we find the first blood-vessels, an upper or dorsal vessel, corresponding to the aorta, between the gut and the dorsal cord (Plate XVIII., Figs. 13 *t*, 15 *t*), and a lower or ventral vessel, corresponding to the subintestinal vein, at the lower border of the gut (Figs. 13 *v*, 15 *v*). Now, the gills or respiratory organs also are formed at the fore-end of the alimentary canal. The whole of the anterior or respiratory section of the gut is converted into a gill-crate, which is pierced trellis-wise by numbers of branchial holes, as in the ascidia. This is done by the foremost part of the gut-wall joining star-wise with the outer skin, and the formation of clefts at the point of connection, piercing the wall and leading into the gut from without. At first there are very few of these branchial clefts; but there are soon a number of them—first in one, then in two, rows. The foremost gill-cleft is the oldest. In the end we have a sort of lattice work of fine branchial clefts, supported on a number of stiff branchial rods; these are connected in pairs by transverse rods (Fig. 15 *k*).

I must draw special attention here to the fact that at first

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[1] The metamerism of the amphioxus, which does not take place in its muscular system until after the chordula-stage, shows indisputably that the simple chorda of the vertebrates existed before their metamerism, and was inherited from the unarticulated vermalia (prochordonia).

in the amphioxus-embryo, as in that of all other vertebrates, the lateral walls of the neck are pierced by a few clefts in such a way that we can get through them from the epidermis into the fore gut (Fig. 273 *K*). The respiratory water that is taken into the branchial gut through the mouth runs out again immediately by the branchial clefts. As the number of these gill-clefts increases rapidly, a longitudinal fold is made in the lateral wall of the body on each side over the uppermost row of the clefts (Fig. 274 *U*). The narrow body-cavity *(Lh)* is continued in the "mantle-folds." The two folds grow downwards, and hang down as loose gill-covers. They then bend together with their free borders, and unite in the middle line of the ventral side, in the ventral seam (Fig. 275 *R*). The branchial pore alone remains open (Fig. 245 *c*). In this way a wide mantle or peribranchial cavity *(atrium)* is formed round the branchial gut, and this receives the respiratory water from the gill-clefts and ejects it by the branchial pore behind. It may be compared with the branchial cavity of the fishes, covered with the gill-fold on the one side, or with the atrium of the ascidia on the other. This wide mantle-cavity, filled with water and communicating freely with the surrounding water, must be carefully distinguished from the narrow body-cavity filled with lymph, which has no opening outwards. This cœloma (Figs. 273–275 *Lh*) is very narrow in the adult amphioxus, and reduced to a very small space. After the peribranchial cavity of the amphioxus is formed, the respiratory water that enters at the mouth no longer passes directly out through the gill-clefts, but through the branchial pore (Plate XIX., Fig. 15 *p*). The part of the alimentary canal behind the gill-crate is converted into the stomach *(ma)*, and forms a single pouch-shaped fold that developes into the hepatic blind sac *(lb)*. This digestive part of the alimentary canal is enclosed by the narrow body-cavity.

At an early stage of embryonic development the structure of the amphioxus-larva is substantially the same as the ideal picture we have previously formed of the "primitive vertebrate" (Figs. 101–105). But the body afterwards undergoes various modifications, especially in the fore-part. These modifications do not concern us, as they depend on special adaptations, and do not affect the hereditary vertebrate type. When the free-swimming amphioxus-larva is three months old, it abandons its pelagic habits and changes into the young animal that lives in the sand. In spite of its smallness (about three millimetres), it has substantially the same structure as the adult. As regards the remaining organs of the amphioxus, we need only mention that the gonades or sexual glands are developed very late, immediately out of the inner cell-layer of the body-cavity, the cœlom-epithelium.

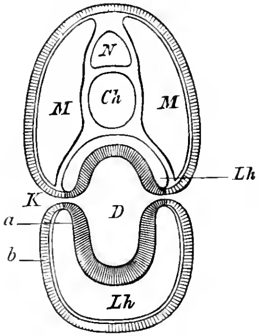


FIG. 273.

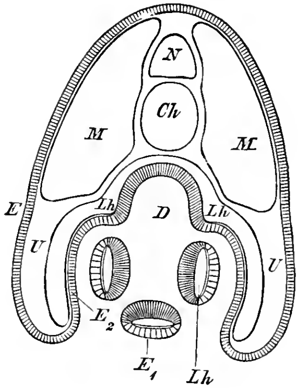


FIG. 274.

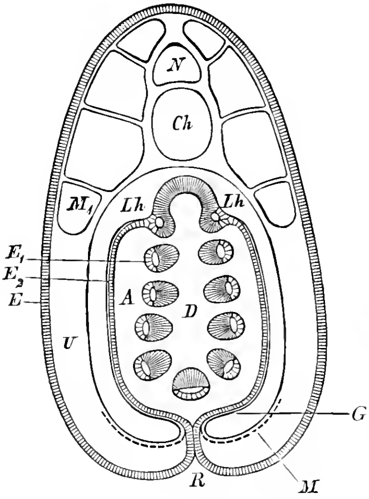


FIG. 275.

FIGS. 273–275.—**Transverse sections of young amphioxus-larvæ** (diagrammatic, from *Ralph*.) (Cf. also Fig. 251.) In Fig. 273 there is free communication from without with the gut-cavity *(D)* through the gill-clefts *(K)*. In Fig. 274 the lateral folds of the body-wall, or the gill covers, which grow downwards, are formed. In Fig. 275 these lateral folds have united underneath, and joined their edges in the middle line of the ventral side (*R* seam). The respiratory water now passes from the gut-cavity *(D)* into the mantle-cavity *(A)*. The letters have the same meaning throughout: *N* medullary tube, *Ch* chorda, *M* lateral muscles, *Lh* body-cavity, *G* part of the body-cavity in which the sexual organs are subsequently formed. *D* gut-cavity, clothed with the gut-gland layer *(a)*. *A* mantle-cavity, *K* gill-clefts, $b = E$ epidermis, E_1 the same as visceral epithelium of the mantle-cavity, E_2 as parietal epithelium of the mantle-cavity.

Although we can find afterwards no continuation of the body-cavity (Fig. 251 *U*) in the lateral walls of the mantle-cavity, in the gill-covers or mantle-folds (Fig. 275 *U*), there is one present in the beginning (Fig. 275 *Lh*). The sexual cells are formed below, at the bottom of this continuation, from a part of the cœlom-epithelium (Fig. 275 *S*). The segmental arrangement of the gonades shows that they originate from the hyposomites (cf. p. 433). For the rest, the subsequent development into the adult amphioxus of the larva we have followed is so simple that we need not go further into it here.

We may now turn to the embryology of the ascidian, an animal that seems to stand so much lower and to be so much more simply organised, remaining for the greater part of its life attached to the bottom of the sea like a shapeless lump. It was a fortunate accident that Kowalevsky first examined just those larger specimens of the ascidia that show most clearly the relationship of the vertebrates to the invertebrates, and the larvæ of which behave exactly like those of the amphioxus in the first stages of development. This resemblance is so close in the main features that we have only to repeat what we have already said of the ontogenesis of the amphioxus.

The ovum of the larger ascidia *(phallusia, cynthia, etc.)* is a simple round cell of one-tenth to one-fifth of a millimetre in diameter. In the thick fine-grained yelk we find a clear round germinal vesicle of about one-thirtieth of a millimetre in diameter, and this encloses a small embryonic spot or nucleolus (Fig. 1, Plate XVIII.). Inside the membrane that surrounds the ovum, the stem-cell of the ascidia, after fecundation, passes through just the same metamorphoses as the cytula of the amphioxus. It undergoes total segmentation; it divides into two, four, eight, sixteen, thirty-two cells, and so on. By continued total cleavage the morula, or mulberry-shaped cluster of cells, is formed. Fluid gathers inside it, and thus we get once more a globular vesicle (the blastula); the wall of this is a single stratum of cells, the blastoderm (Plate XVIII., Fig. 3). A real gastrula (a simple bell-gastrula) is formed from the blastula by invagination in the same way as in the amphioxus (Plate XVIII., Fig. 4).

Up to this there is no definite ground in the embryology of the ascidia for bringing them into close relationship with the vertebrates; the same gastrula is formed in the same way in many other animals of different stems. But we now find an embryonic process that is peculiar to the vertebrates, and that proves irrefragably the affinity of the ascidia to the vertebrates. From the epidermis of the gastrula a *medullary tube* is formed on the dorsal side, and, between this and the primitive gut, a *chorda;* these are organs that are otherwise only found in vertebrates. The formation of these very important organs takes place in the ascidian-gastrula in precisely the same way as in that of the amphioxus. In the ascidia (as in the other case) the oval uni-axial gastrula is first flattened on one side—the subsequent dorsal side. A groove or furrow (the medullary groove) is sunk in the middle line of the flat surface, and two parallel longitudinal swellings arise on either side from the cutaneous layer. These medullary swellings join together over the furrow, and form a tube; in this case, again, the neural or medullary tube is at first open in front, and connected with the primitive gut behind by the neurenteric canal. Further, in the ascidian-larva also the two permanent apertures of the alimentary canal only appear later, as independent and new formations. The permanent mouth does not develop from the primitive mouth of the gastrula; this primitive mouth closes up, and the later anus is formed near it by invagination from without, on the hinder end of the body, opposite to the aperture of the medullary tube (Plate XVIII., Fig. 5 *a*).

During these important processes, that take place in just the same way in the amphioxus, a tail-like projection grows out of the posterior end of the larva-body, and the larva folds itself up within the spherical ovolemma in such a way that the dorsal side is curved and the tail is forced on to the ventral side. In this tail is developed—starting from the primitive gut—a cylindrical string of cells, the fore end of which pushes into the body of the larva, between the alimentary canal and the neural canal, and is no other than the chorda dorsalis. This important organ had hitherto been found only in the vertebrates, not a single trace of it being discoverable in the invertebrates. At first the chorda only consists of a single row of large entodermic cells (Plate XVIII., Fig. 5 *ch*). It is afterwards composed of several rows of cells. In the ascidian-larva, also, the chorda developes from the dorsal middle part of the primitive gut, while the two cœlom-pouches detach themselves from it on both sides. The simple body-cavity is formed by the coalescence of the two.

If we make a transverse section through the middle of the body (where the tail passes into the trunk) at this stage, we find in the ascidian-larva the same characteristic arrangement of the chief organs as in the amphioxus-larva (Plate XVIII., Fig. 6). We find the chorda in the middle between the medullary tube and the alimentary canal, and the muscular plates of the back *(r)* on either side of it. The transverse section of the ascidian-larva is not now materially different from that of the vertebrate embryo (Fig. 262).

When the ascidian-larva has attained this stage of development it begins to move about in the ovolemma. This causes the membrane to burst. The larva emerges from it, and swims about in the sea by means of its rudder-like tail (Plate XVIII., Fig. 5). These free-swimming larvæ of the ascidia have been known for a long time. They were first observed by Darwin during his voyage round the world in 1833. They resemble tadpoles in outward appearance, and use their tails as rudders, as the tadpoles do. However, this lively and highly-developed condition does not last long. At first there is a progressive development; the foremost part of the medullary tube enlarges into a vesicular brain, and inside this two single sense-organs are developed, a dorsal auditory vesicle and a ventral eye. Then a heart is formed on the ventral side of the animal, or the lower wall of the gut, in the same simple form and at the same spot at which the heart is developed in man and all the other vertebrates. In the lower muscular wall of the gut we find a weal-like thickening, a solid, spindle-shaped string of cells, which becomes hollow in the centre; it begins to contract in different directions, now forward and now backward, as is the case with the adult ascidian. In this way the sanguineous fluid accumulated in the hollow muscular tube is driven in alternate directions into the blood-vessels, which develop at both ends of the cardiac tube. One principal vessel runs along the dorsal side of the gut, another along its ventral side. The former corresponds to the aorta and the dorsal vessel in the worms. The other corresponds to the subintestinal vein and the ventral vessel of the worms.

With the formation of these organs the progressive development of the ascidian comes to an end, and degeneration sets in. The free-swimming larva sinks to the floor of the sea, abandons its locomotive habits, and attaches itself to stones, marine plants, mussel-shells, corals, and other objects; this is done with the part of the body that was foremost in movement. The attachment is effected by a number of outgrowths, usually three, which can be seen even in the free-swimming larva. The tail is lost, as there is no further use for it. It undergoes a fatty degeneration, and disappears with the chorda dorsalis. The tailless body changes into an unshapely tube, and, by the atrophy of some parts and the new formation and modification of others, gradually assumes the appearance we have already described.

Among the living tunicates there is a very interesting group of small animals that remain throughout life at the stage of development of the tailed, free ascidian-larva, and swim about briskly in the sea by means of their broad rudder-tail. These are the remarkable copelata (*appendicaria* and *vexillaria*, Fig. 276). They are the only living vertebrates that have throughout life a chorda dorsalis and a neural string above it; the latter must be regarded as the dorsal prolongation of the cerebral ganglion and the equivalent of the medullary tube. Their branchial gut also opens directly outwards by a pair of branchial clefts. These instructive copelata, comparable to permanent ascidian-larvæ, come next to the extinct prochordonia, those ancient worms which we must regard as the common ancestors of the tunicates and vertebrates. The chorda of the appendicaria is a long, cylindrical string (Fig. 276 *c*), and serves as an attachment for the muscles that work the flat rudder-tail.

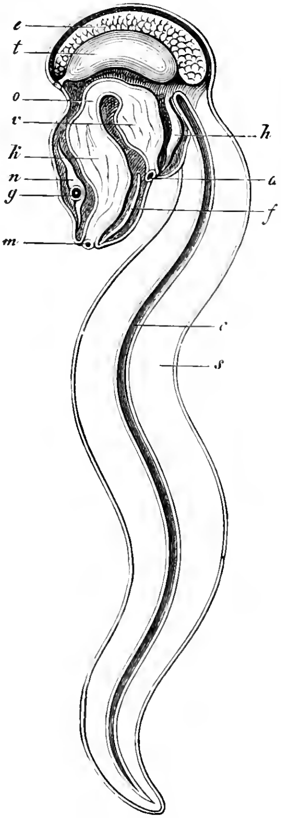


FIG. 276.—**An appendicaria (copelata),** seen from the left. *m* mouth, *k* branchial gut, *o* œsophagus, *v* stomach, *a* anus, *n* brain (ganglion above the gullet), *g* auditory vesicle, *f* ciliated groove under the gills, *h* heart, *t* testicles, *e* ovary, *c* chorda, *s* tail.

Among the various modifications which the ascidian-larva undergoes after its establishment at the sea-floor, the most interesting (after the loss of the axial rod) is the atrophy of one of its chief organs, the medullary tube. In the amphioxus the spinal marrow continues to develop, but in the ascidian the tube soon shrinks into a small and insignificant nervous ganglion that lies above the mouth and the gill-crate, and is in accord with the extremely slight mental power of the animal (Plate XIX., Fig. 14 *m*). This insignificant relic of the medullary tube seems to be quite beyond comparison with the nervous centre of the vertebrate, yet it started from the same structure as the spinal cord of the amphioxus. The sense-organs that had been developed in the fore part of the neural tube are also lost; no trace of them can be found in the adult ascidian. On the other hand, the alimentary canal becomes a most extensive organ. It divides presently into two sections—a wide fore or branchial gut that serves for respiration, and a narrower hind or hepatic gut that accomplishes digestion. The branchial or head-gut of the ascidian is small at first, and opens directly outwards only by a couple of lateral ducts or gill-clefts—a permanent arrangement in the copelata. The gill-clefts are developed in the same way as in the amphioxus. As their number greatly increases we get a large gill-crate, pierced like lattice work. In the middle line of its ventral side we find the hypobranchial groove. The mantle or cloaca-cavity (the atrium) that surrounds the gill-crate is also formed in the same way in the ascidian as in the amphioxus. The ejection-opening of this peribranchial cavity corresponds to the branchial pore of the amphioxus. In the adult ascidian the branchial gut and the heart on its ventral side are almost the only organs that recall the original affinity with the vertebrates.

Finally we will glance for a moment at the embryology of the remarkable external *mantle* or cellulose sac, which afterwards entirely encloses the ascidian and is characteristic of the tunicates [tunica = mantle]. Very different and curious opinions have been expressed as to the construction of this mantle. Some said that the animal does not form the mantle itself, but that special cells of the mother's body which surround the ovum become its parent-cells. On this view the mantle would be a permanent fœtal membrane. That would be against all analogy, and is most improbable. Others suppose that the mantle developes from cells that are formed before the fecundation of the ovum from the outer part of the yelk, and are quite separate from its inner part. This again is utterly obscure and improbable. It was first proved by the investigations of Hertwig, which I can confirm from my own, that the mantle developes in the form of a cuticula (skin). It is an exudation of the epidermic cells, which presently hardens, detaches itself from the body of the ascidian proper, and becomes a thick stiff envelope around it. From the chemical point of view the substance of it cannot be distinguished from vegetal cellulose. While the epidermic cells of the outer horny plate secrete this cellulose mass, some of them slip into it, live independently in the exuded mass, and promote the growth of the mantle. In this way is formed the large external envelope, which grows thicker and thicker, and amounts to more than two-thirds of the mass of the body in some of the ascidians.

The further development of the ascidian in detail has no particular interest for us, and we will not go into it. The chief result that we obtain from its embryology is the complete agreement with that of the amphioxus in the earliest and most important embryonic stages. They do not begin to diverge until after the medullary tube and alimentary canal, and the axial rod with the muscles between the two, have been formed. The amphioxus continues to advance, and resembles the embryonic forms of the higher vertebrates; the ascidian undergoes a retrogressive metamorphosis, and at last, in its adult condition, has the appearance of a very imperfect invertebrate.

If we now look back on all the remarkable features we have encountered in the structure and the embryonic development of the amphioxus and the ascidian, and compare them with the features of man's embryonic development which we have previously studied, it will be clear that I have not exaggerated the importance of these very interesting animals. It is evident that the amphioxus from the vertebrate side and the ascidian from the invertebrate form the bridge by which we can span the deep gulf that separates the two great divisions of the animal kingdom. The radical agreement of the lancelet and the sea-squirt in the first and most important stages of development shows something more than their close anatomic affinity and their proximity in classification ; it shows also their real blood-relationship and their common origin from one and the same stem-form. In this way it throws considerable light on the oldest roots of man's genealogical tree.

In some earlier essays, *On the Origin and Ancestral Tree of the Human Race* (1868), I pointed out the extreme importance of this relation, and said that "we must regard the amphioxus with particular respect as the venerable animal that alone, of all living things, can give us an approximate idea of the character of our earliest Silurian vertebrate-ancestors." This expression aroused a good deal of antagonism, not only on the part of ignorant theologians, but also from philosophers who still dally with the anthropocentric error, and fancy that man is the fore-ordained end of "creation" and the final goal of terrestrial life. The "dignity of man," said an ecclesiastical journal, "is trampled under foot, and his divine consciousness insulted," by such assertions.

I confess that I quite fail to understand this indignation at my genuine and great respect for the amphioxus. When we enter some ancient oak-forest, and express in glowing language our admiration of the venerable, thousand-year-old trees, everybody thinks this is natural enough. But how high the amphioxus is above the oak, and how much higher the organisation of even the ascidian is than that of the tree! Moreover, it teaches us the long historic process by which our ancestors have ascended from the lowly stage of the gastræa to the altitude of the vertebrates.

The enormous importance of the amphioxus and the ascidian in helping us to understand the evolution, and therefore the real character, of man is best seen in the comparative synopsis in which I have given the chief homologies of the highest and the lowest vertebrate (Tables XVI. and XVII., p. 440). They reveal the undeniable fact that the human embryo in the earlier stages of its development agrees in the main features of organisation with the amphioxus and the ascidian-embryo, but is totally different from the adult human frame. On the other hand, it is equally important to bear in mind the deep gulf that separates the amphioxus from all the other vertebrates. It is still given in most zoological manuals as a member of the fish-class. When I (in 1886) separated the lancelet entirely from the fishes, and divided the vertebrate stem into the two chief groups of acrania (amphioxus) and craniota (all the other vertebrates), it was pronounced a useless and unjustifiable innovation. The reader can judge for himself from the morphological comparative synopsis given in Table XVII. In all the essential features of organisation and development the true fishes are much nearer to man than to the amphioxus.

CHAPTER XVIII.

DURATION OF THE HISTORY OF OUR STEM

Comparison of ontogenetic and phylogenetic periods. Duration of embryonic development in man and various animals. Insignificant length of it in comparison with the immense duration of stem-history. Relation of the rapid ontogenetic metamorphosis to the slow phylogenetic changes. Duration of the organic history of the earth, based on the relative thickness of the sedimentary strata. Five chief divisions of it: I. Primordial or archeozoic age; II. Primary or paleozoic age; III. Secondary or mesozoic age; IV. Tertiary or cenozoic age; V. Quaternary or anthropozoic age. Relative length of the five periods. Results of comparative philology in connection with the phylogeny of species. The stems and branches of the Indo-Germanic race are related analogously to the classes and divisions of the vertebrate stem. The stem-forms are extinct in both cases. The chief stages of the human stem-forms. The origin of the monera by archigony. Necessity of archigony.

OUR comparative investigation of the anatomy and ontogeny of the amphioxus and ascidian has given us invaluable assistance for the study of anthropogeny. We have, in the first place, bridged the wide gulf that has existed up to the present in classification between the vertebrates and invertebrates; and, in the second place, we have discovered in the embryology of the amphioxus a number of ancient evolutionary stages that have long since disappeared from human embryology, and have been lost, in virtue of the law of curtailed heredity. The chief of these stages are the spherical *blastula* (in its simplest primary form) and the succeeding archigastrula, the pure, original form of the *gastrula* which the amphioxus has preserved to this day, and which we find in the same form in a number of invertebrates of various classes. Not less important are the later embryonic forms of the cœlomula, the chordula, etc.

Thus the embryology of the amphioxus and the ascidian has so much increased our knowledge of man's stem-history that, although our empirical information is still very incomplete, there is now no defect of any great consequence in it.

We may now, therefore, approach our proper task, and reconstruct the phylogeny of man in its chief lines with the aid of this evidence of comparative anatomy and ontogeny. In this you will soon see the immense importance of the direct application of the biogenetic law. But before we enter upon the work it will be useful to make a few general observations that are necessary to understand the processes aright.

We must first say a few words with regard to the period in which the human race was evolved from the animal kingdom. The first thought that occurs to one in this connection is the vast difference between the duration of man's ontogeny and phylogeny. The brief period that is occupied by man's embryonic development is not comparable in any respect to the immeasurable period that was needed for the phylogeny of the human stem. The individual man needs only nine months for his complete development, from the fecundation of the ovum to the moment when he leaves the maternal womb. The human embryo runs its whole course in the brief space of forty weeks (as a rule, 280 days). We should add that to a man's age as it is usually counted. The child that is said to be nine and a quarter, for instance, is really ten years old. The beginning of individual existence is certainly not birth, but the moment of conception (see p. 142).

In many other mammals the time of the embryonic development is much the same as in man—for instance, in the cow. In the horse and ass it takes a little longer, forty-three to forty-five weeks; in the camel, thirteen months. In the largest mammals the embryo needs a much longer period for its development in the womb—a year and a half in the rhinoceros, and ninety weeks in the elephant. In these cases pregnancy lasts twice as long as in the case of man, or one and three-quarter years. In the smaller mammals the embryonic period is much shorter. The smallest mammals, the dwarf-mice, develop in three weeks; hares in four weeks, rats and marmots in five weeks, the dog in nine, the pig in seventeen, the sheep in twenty-one, and the goat in thirty-six. Birds develop still more quickly. The chick only needs, in normal circumstances, three weeks for its full development. The duck needs twenty-five days, the turkey twenty-seven, the peacock thirty-one, the swan forty-two, and the cassowary sixty-five. The smallest bird, the humming-bird, leaves the egg after twelve days. Hence the duration of individual development within the fœtal membranes is, in the mammals and birds, clearly related to the absolute size of the body of the animal in question. But this is not the only determining feature. There are a number of other circumstances that have an influence on the period of embryonic development. In the amphioxus the earliest and most important embryonic processes take place so rapidly that the blastula is formed in four hours, the gastrula in six, and the typical vertebrate form in twenty-four.

In every case the duration of ontogenesis shrinks into insignificance when we compare it with the enormous period that has been necessary for phylogenesis, or the gradual development of the ancestral series. This period is not measured by years or centuries, but by thousands and millions of years. Many millions of years had to pass before the most advanced vertebrate, man, was evolved, step by step, from his ancient unicellular ancestors. The opponents of evolution, who declare that this gradual development of the human form from lower animal forms, and ultimately from a unicellular organism, is an incredible miracle, forget that the same miracle takes place within the space of nine months in the embryonic development of every human being. Each of us has, in the forty weeks—properly speaking, in the first four weeks—of his development in the womb, passed through the same series of transformations that our animal ancestors underwent in the course of millions of years.

All organic metamorphoses of plant and animal forms seem to us remarkable and wonderful in proportion to the rapidity with which they take place. Hence, if our opponents regard the historical evolution of the human race from lower animal forms as an incredible process, they must look upon the embryonic development of the individual from a simple cell as a still more astounding miracle. This ontogenetic metamorphosis, that takes place before our eyes, must seem just as much more wonderful than that of phylogeny as the duration of the latter exceeds that of embryonic growth. The human embryo has to accomplish the whole evolutionary process, from the simple ovum to the finished multicellular organism, in the short space of forty weeks. But we have millions of years to allow for the phylogenetic development of the ancestors of the human race from the simple unicellular stem-form.

It is impossible to determine even approximately, in hundreds or even thousands of years, the real and absolute duration of the phylogenetic period. But for some time now we have, through the research of geologists, been in a position to assign the relative length of the various sections of the organic history of the earth. The immediate data for determining this relative length of the geological periods are found in the thickness of the sedimentary strata—the strata that have been formed at the bottom of the sea or in fresh water from the mud or slime deposited there. These successive layers of limestone, sandstone, slate, marl, etc., which make up the greater part of the rocks, and are often several thousand feet thick, give us a standard for computing the relative length of the various periods.

To make the point quite clear, I must say a word about the evolution of the earth in general, and point out briefly the chief features of the story. In the first place, we encounter the principle that on our planet organic life began to exist at a definite period. That statement is no longer disputed by any competent geologist or biologist. We now know for certain that life had a beginning of existence on the earth, and has not been here from eternity, as has been affirmed. Irrefragable proof of this is afforded by physical-astronomic cosmogony on the one side and embryology on the other. Species and stems of organisms are no more eternal than individuals. They also had a definite beginning in time. Everything individual or personal in the world is a transitory phenomenon. The period that has elapsed since the first appearance of life on the earth, and with which alone we are concerned here, is called "the organic history of the earth," in contrast with the "inorganic history" that preceded the development of life. The latter was first explained by the natural philosophic studies of the great critical philosopher, Immanuel Kant, and was afterwards mathematically formulated by Laplace. A full treatment of the subject will be found in Kant's *General Natural History and Theory of the Heavens*, or in Carus Sterne's able *Werden und Vergehen*.

The organic history of the earth could not commence until it was possible for water to settle on the earth in fluid condition. Every organism, without exception, needs fluid water as a condition of existence, and contains a considerable quantity of it. Our own body, when fully formed, contains sixty to seventy per cent. of water in its tissues, and only thirty to forty per cent. of solid matter. There is even more water in the body of the child, and still more in the embryo. In the earlier stages of development the human fœtus contains more than ninety per cent. of water, and not ten per cent. of solids. In the lower marine animals, especially certain medusæ, the body consists to the extent of more than ninety-nine per cent. of sea-water, and has not one per cent. of solid matter. No organism can exist or discharge its functions without water. No water, no life!

But fluid water, on which the existence of life primarily depends, could not exist on our planet until the temperature of the surface of the incandescent sphere had sunk to a certain point. Up to that time it remained in the form of steam. But as soon as the first fluid water could be condensed from the envelope of steam, it began its geological action, and has continued down to the present day to modify the solid crust of the earth. The final outcome of this incessant action of the water—wearing down and dissolving the rocks in the form of rain, hail, snow, and ice, as running stream or boiling surge—is the formation of mud. As Huxley says in his admirable *Lectures on the Causes of Phenomena in Organic Nature*, the chief document as to the past history of our earth is mud; the question of the history of past ages resolves itself into a question about the formation of mud.

As I have said, it is possible to form an approximate idea of the relative age of the various strata by comparing them at different parts of the earth's surface. Geologists have long been agreed that there is a definite historical succession of the different strata. The various superimposed layers correspond to successive periods in the organic history of the earth, in which they were deposited in the form of mud at the bottom of the sea. The mud was gradually converted into stone. This was lifted out of the water owing to variations in the earth's surface, and formed the mountains. As a rule, four or five great divisions are distinguished in the organic history of the earth, corresponding to the larger and smaller groups of the sedimentary strata. The larger periods are then sub-divided into a number of smaller ones, which usually number from twelve to fifteen. The comparative thickness of the groups of strata enables us to make an approximate calculation of the relative length of these various periods of time. We cannot say, it is true, "In a century a stratum of a certain thickness (about two feet) is formed on the average; therefore, a layer 1,000 feet thick must be 600,000 years old." Different strata of the same thickness may need very different periods for their formation. But from the thickness or size of the stratum we can draw some conclusion as to the *relative* length of the period.

The first and oldest of the four or five chief divisions of the organic history of the earth, a knowledge of which is indispensable for the purposes of human phylogeny, is called the primordial, archaic, or archeozoic period. If we compute the total average thickness of the sedimentary strata at about 130,000 feet, this first period comprises 70,000 feet, or the greater part of the whole. For this and other reasons we may at once conclude that the corresponding primordial or archeolithic period must have been in itself much longer than the whole of the remaining periods together, from its close to the present day. It was probably much longer than the figures I have quoted (7 : 6) indicate—possibly 9 : 6. Of late years the thickness of the archaic rocks has been put at 90,000 feet.

NINETEENTH TABLE

SYNOPSIS OF THE PALEONTOLOGICAL PERIODS, OR THE CHIEF SECTIONS OF THE ORGANIC HISTORY OF THE EARTH

I. First Period: **Archeozoic Age.** Primordial Epoch.

(Age of Acrania and Tree-Algæ.)

1. Older archeolithic age	or	Laurentian period.
2. Middle archeolithic age	,,	Huronian period.
3. Later archeolithic age	,,	Cambrian period.

II. Second Period: **Paleozoic Age.** Primary Epoch.

(Age of Fishes and Tree-Ferns.)

4. Older paleolithic age	or	Silurian epoch.
5. Middle paleolithic age	,,	Devonian epoch.
6. Later paleolithic age	,,	Carboniferous epoch. Permian epoch.

III. Third Period: **Mesozoic Age.** Secondary Epoch.

(Age of Reptiles and Conifers.)

7. Older mesolithic age	or	Triassic epoch.
8. Middle mesolithic age	,,	Jurassic epoch.
9. Later mesolithic age	,,	Cretaceous epoch.

IV. Fourth Period: **Cenozoic Age.** Tertiary Epoch.

(Age of Mammals and Foliage Trees.)

10. Older cenolithic age	or	Eocene epoch. Oligocene epoch.
11. Middle cenolithic age	,,	Miocene epoch.
12. Later cenolithic age	,,	Pliocene epoch.

V. Fifth Period: **Anthropozoic Age.** Quaternary Epoch.

(Age of Man and Cultivated Trees.)

13. Older anthropolithic age	or	Glacial epoch.
14. Middle anthropolithic age	,,	Post-glacial epoch.
15. Later anthropolithic age	,,	Historical epoch.

TWENTIETH TABLE

SYNOPSIS OF THE PALEONTOLOGICAL FORMATIONS, OR THE FOSSILIFEROUS STRATA OF THE CRUST

Groups.	Systems.	Formations.	Synonyms of Formations.
V. Anthropolithic groups, or anthropozoic (quaternary) groups of strata.	XIV. Recent (alluvium).	38. Present.	Upper alluvial.
		37. Recent.	Lower alluvial.
	XIII. Pleistocene (diluvium).	36. Post-glacial.	Upper diluvial.
		35. Glacial.	Lower diluvial.
IV. Cenolithic groups, or cenozoic (tertiary) groups of strata.	XII. Pliocene (neo-tertiary).	34. Arverne.	Upper pliocene.
		33. Subapennine.	Lower pliocene.
	XI. Miocene (middle tertiary).	32. Falun.	Upper miocene.
		31. Limbourg.	Lower miocene.
	Xb. Oligocene (old tertiary).	30. Aquitaine.	Upper oligocene.
		29. Ligurium.	Lower oligocene.
	Xa. Eocene (primitive tertiary).	28. Gypsum.	Upper eocene.
		27. Coarse chalk.	Middle eocene.
		26. London clay.	Lower eocene.
III. Mesolithic groups, or mesozoic (secondary) groups of strata.	IX. Chalk (cretaceous).	25. White chalk.	Upper cretaceous.
		24. Green sand.	Middle cretaceous.
		23. Neoconian.	Lower cretaceous.
		22. Wealden.	Weald-formation.
	VIII. Jurassic.	21. Portland.	Upper oolithic.
		20. Oxford.	Middle oolithic.
		19. Bath.	Lower oolithic.
		18. Lias.	Liassic.
	VII. Triassic.	17. Keuper.	Upper triassic.
		16. Muschelkalk.	Middle triassic.
		15. Bunter.	Lower triassic.
II. Paleolithic groups, or paleozoic (primary) groups of strata.	VIb. Permian.	14. Zechstein.	Upper permian.
		13. Neurot sand.	Lower permian.
	VIa. Carboniferous (coal-measures).	12. Carboniferous sandstone.	Upper carboniferous.
		11. Carboniferous limestone.	Lower carboniferous.
	V. Devonian.	10. Pilton.	Upper devonian.
		9. Ilfracombe.	Middle devonian.
		8. Linton.	Lower devonian.
	IV. Silurian.	7. Ludlow.	Upper silurian.
		6. Wenlock.	Middle silurian.
		5. Llandeilo.	Lower silurian.
I. Archeolithic groups, or archeozoic (primordial) groups of strata.	III. Cambrian.	4. Potsdam.	Upper cambrian.
		3. Longmynd.	Lower cambrian.
	II. Huronian.	2. Labrador.	Upper laurentian.
	I. Laurentian.	1. Ottawa.	Lower laurentian.

The primordial period falls into three subordinate sections—the Laurentian, Huronian, and Cambrian, corresponding to the three chief groups of rocks that comprise the archaic formation. The immense period during which these rocks were forming in the primitive ocean probably comprises more than 50,000,000 years. At the commencement of it the oldest and simplest organisms were formed by spontaneous generation—the monera, with which the history of life on our planet opened. From these were first developed unicellular organisms of the simplest character, the protophyta and protozoa (paulotomea, amœbæ, rhizopods, infusoria, and other protists). During this archeolithic period the whole of the invertebrate ancestors of the human race were evolved from the unicellular organisms. We can deduce this from the fact that we already find remains of fossilised fishes (selachii and ganoids) towards the close of the following Silurian period. These are much more advanced and much younger than the lowest vertebrate, the amphioxus, and the numerous skull-less vertebrates, related to the amphioxus, that must have lived at that time. The whole of the invertebrate ancestors of the human race must have preceded these.

We may, therefore, describe this period as "the period of the invertebrate ancestors of the human race," or, if we wish to emphasise the earliest representatives of the vertebrate stem, as "the period of the acrania." During the whole of the archeolithic age, until the Silurian period, life probably consisted entirely of aquatic organisms; at all events, we have not yet found any remains of terrestrial animals or plants of this period. The oldest traces of terrestrial organisms are found in the Silurian period.

The primordial age is followed by a much shorter division, the *paleozoic* or primary age. It is divided into four long periods, the Silurian, Devonian, Carboniferous, and Permian. The Silurian strata are particularly interesting because they contain the first fossil traces of vertebrates—teeth and scales of selachii *(palæodus)* in the lower, and ganoids *(pteraspis)* in the upper Silurian. During the

Devonian period the "old red sandstone" was formed; during the Carboniferous period were deposited the vast coal-measures that yield us our chief combustive material; in the Permian (or the Dyas), in fine, the new red sandstone, the Zechstein (magnesian limestone), and the Kupferschiefer (marl-slate) were formed. The collective depth of these strata is put at 40,000 to 45,000 feet. In any case, the paleolithic age, taken as a whole, was much shorter than the preceding and much longer than the subsequent periods. The strata that were deposited during this primary epoch contain a large number of fossils; besides the invertebrate species there are a good many vertebrates, and the fishes preponderate. There were so many fishes, especially primitive fishes (of the shark type) and plated fishes, during the Devonian, and also during the Carboniferous and Permian periods, that we may describe the whole paleolithic period as "the age of fishes." Among the paleozoic plated fishes or ganoids the crossopterygii and the ctenodipterina (dipneusta) are of great importance.

During this period some of the fishes began to adapt themselves to living on land, and so gave rise to the class of the amphibia. We find in the Carboniferous period fossilised remains of five-toed amphibia, the oldest terrestrial, air-breathing vertebrates. These amphibia increase in variety in the Permian epoch. Towards the close of it we find the first amniotes, the ancestors of the three higher classes of vertebrates. These are lizard-like tocosauria; the first to be discovered was the *proterosaurus* from the marl at Eisenach. The rise of the earliest amniotes, among which must have been the common ancestor of the reptiles, birds, and mammals, is put back towards the close of the paleozoic age by the discovery of these reptile remains. The ancestors of our race during this period were at first represented by true fishes, then by dipneusts and amphibia, and finally by the earliest amniotes, or the protamniotes.

The third chief section of the organic history of the earth is the *mesozoic* or secondary period. This again is subdivided into three divisions: Triassic, Jurassic, and

Cretaceous. The thickness of the strata that were deposited in this period, from the beginning of the Triassic to the end of the Cretaceous period, is altogether about 15,000 feet, or not half as much as the paleozoic deposits. During this period there was a very brisk and manifold development in all branches of the animal kingdom. There were especially a number of new and interesting forms evolved in the vertebrate stem. Bony fishes *(teleostei)* make their first appearance. Reptiles are found in extraordinary variety and number; the extinct giant-serpents (dinosauria), the sea-serpents (halisauria), and the flying lizards (pterosauria) are the most remarkable and best known of these. On account of this predominance of the reptile-class, the period is called "the age of reptiles." But the bird-class was also evolved during this period; they certainly originated from some division of the lizard-like reptiles. This is proved by the embryological identity of the birds and reptiles and their comparative anatomy, and, among other features, from the circumstance that in this period there were birds with teeth in their jaws and with tails like lizards (archæopteryx, odontornis).

Finally, the most advanced and (for us) the most important class of the vertebrates, the mammals, made its appearance during the mesozoic period. The earliest fossil remains of them were found in the latest Triassic strata—lower jaws of small ungulates and marsupials. More numerous remains are found a little later in the Jurassic, and some in the Cretaceous. All the mammal remains that we have from this section belong to the lower promammals and marsupials; among these were most certainly the ancestors of the human race. On the other hand, we have not found a single indisputable fossil of any higher mammal (a placental) in the whole of this period. This division of the mammals, which includes man, was not developed until later, towards the close of this or in the following period.

The fourth section of the organic history of the earth, the tertiary or *cenozoic* age, was much shorter than the preceding.

The strata that were deposited during this period have a collective thickness of only about 3,000 feet. It is subdivided into four sections—the eocene, oligocene, miocene, and pliocene. During these periods there was a very varied development of higher plant and animal forms; the fauna and flora of our planet approached nearer and nearer to the character that they bear to-day. In particular, the most advanced class, the mammals, began to preponderate. Hence the tertiary period may be called "the age of mammals." The highest section of this class, the placentals, now made their appearance; to this group the human race belongs. The first appearance of man, or, to be more precise, the development of man from some closely-related group of apes, probably falls in either the miocene or the pliocene period, the middle or the last section of the tertiary period. Others believe that man properly so-called—man endowed with speech—was not evolved from the non-speaking ape-man *(pithecanthropus)* until the following, the anthropozoic, age.

In this fifth and last section of the organic history of the earth we have the full development and dispersion of the various races of men, and so it is called the *anthropozoic* as well as the *quaternary* period. In the imperfect condition of paleontological and ethnographical science we cannot as yet give a confident answer to the question whether the evolution of the human race from the apes took place at the beginning of this or towards the middle or the end of the tertiary period. However, this much is certain: the development of civilisation falls in the anthropozoic age, and this is merely an insignificant fraction of the vast period of the whole history of life. When we remember this, it seems ridiculous to restrict the word "history" to the civilised period. This period is, on the latest calculation, not a half per cent. of the time that has elapsed from the beginning of life to the present day. The historical period, in the ordinary sense, is itself only the latter half of the anthropozoic age, the first half being described as "prehistoric." Hence we may call the last section, from the end of the cenozoic period to the present day, "the age of humanity" only in the sense that during it took place the dispersion and differentiation of the various races of men, which had so powerful an influence on the other inhabitants of the earth.

Human vanity has been pleased to consider, ever since the dawn of human consciousness, that man is the end and goal of all terrestrial life, the centre of nature, to whose service and use the whole of the rest of the world has been directed from the beginning by a wise Providence. Nothing shows so clearly the folly of these anthropocentric notions as the comparison of the length of the anthropozoic period with its predecessors. Even if the quaternary period embraces hundreds of thousands of years, this is a mere fraction beside the millions of years that had elapsed from the beginning of life down to the appearance of man.

If we divide into a hundred equal parts the whole period of the history of life, from the spontaneous generation of the first monera to the present day, and if we then represent the relative duration of the five chief sections or ages, as calculated from the average thickness of the strata they contain, as percentages of this, we get something like the following relation :—

I.	Archeolithic or archeozoic (primordial) age	53	6
II.	Paleolithic or paleozoic (primary) age	32	1
III.	Mesolithic or mesozoic (secondary) age	11	5
IV.	Cenolithic or cenozoic (tertiary) age	2	3
V.	Anthropolithic or anthropozoic (quarternary) age	0	5
		100	0

In any case, the "historical period" is an insignificant quantity compared with the vast length of the preceding ages, in which there was no question of human existence on our planet. Even the important cenozoic or tertiary period, in which the first placentals or higher mammals appear, probably amounts to little over two per cent. of the whole organic age.

TWENTY-FIRST TABLE

SYNOPSIS OF THE FOSSILIFEROUS STRATA OF THE EARTH'S CRUST WITH REFERENCE TO THEIR AVERAGE THICKNESS (ABOUT 120,000–150,000 FEET).

IV. Cenozoic Systems. About 3,000 feet.	XIV. Pliocene. XIII. Miocene. XII. Oligocene. XI. Eocene.	**Mammals.** Placentals.
III. Mesozoic Systems. Secondary deposits. About 15,000 feet.	X. Cretaceous.	Proplacentals.
	IX. Jurassic.	Marsupials.
	VIII. Triassic.	Promammals.
II. Paleozoic or Paleolithic Systems. Primary deposits. About 40,000–50,000 feet.	VII. Permian.	**Reptiles** (Tocosauria).
	VI. Carboniferous.	**Amphibia** (Stegocephala).
	V. Devonian.	**Dipneusts** (Ctenodipterina).
	IV. Silurian.	**Fishes** (Selachii, ganoids). (Cyclostoma ?).
I. Archeozoic or Archæan Systems. Primordial deposits. About 70,000–90,000 feet.	III. Cambrian.	**Acrania** (Prospondylia ?).
	II. Huronian.	**Invertebrates** (Prochordonia ?).
	I. Laurentian.	**Vermalia ?** **Gastræada ?** **Protozoa ?**

Before we approach our proper phylogenetic task, and, with the aid of our ontogenetic acquirements and the biogenetic law, follow step by step the paleontological development of our animal ancestors, let us glance for a moment at another, and apparently quite remote, branch of science, a general consideration of which will help us in the solving of a difficult problem. I mean the science of comparative philology. Since Darwin gave new life to biology by his theory of selection, and raised the question of evolution on all sides, it has often been pointed out that there is a remarkable analogy between the development of languages and the evolution of species. The comparison is perfectly just and very instructive. We could hardly find a better analogy when we are dealing with some of the difficult and obscure features of the evolution of species. In both cases we find the action of the same natural laws.

All philologists of any competence in their science now agree that all human languages have been gradually evolved from very rudimentary beginnings. The idea that speech is a gift of the gods—an idea held by distinguished authorities only fifty years ago—is now generally abandoned, and only supported by theologians and others who admit no natural development whatever. In view of the brilliant results of comparative philology, a man must cover up his eyes with both hands not to see the natural evolution of language. For the scientist it is a matter of course. Speech is a physiological function of the human organism, and has been developed simultaneously with its organs, the larynx and tongue, and with the functions of the brain. Hence it will be quite natural to find in the evolution and classification of languages the same features as in the evolution and classification of organic species. The various groups of languages that are distinguished in philology as primitive, fundamental, parent, and daughter languages, dialects, etc., correspond entirely in their development to the different categories which we classify in zoology and botany as stems, classes, orders, families, genera, species, and varieties. The relation of these groups, partly co-ordinate and partly subordinate, in the general scheme is just the same in both cases; and the evolution follows the same lines in both. This instructive comparison was first made by one of the ablest German philologists, August Schleicher, who was at the same time a competent botanist. In his larger works we find the "comparative anatomy and evolution of languages" dealt with by the same phylogenetic methods that we use in the comparative anatomy and evolution of animal forms. He has done this especially for the Indo-Germanic languages, and has in a small work on *The Darwinian Theory and Philology* illustrated it by an interesting genealogical tree of that group.

When with the assistance of this tree we follow the formation of the various languages that have been developed from the common root of the ancient Indo-Germanic tongue, we get a very clear idea of their phylogeny. We shall see at the same time how analogous this is to the development of the various groups of vertebrates that have arisen from the common stem-form of the primitive vertebrate. The ancient Indo-Germanic root-language divided first into two principal stems—the Slavo-Germanic and the Aryo-Romanic. The Slavo-Germanic stem then branches into the ancient Germanic and the ancient Slavo-Lettic tongues; the Aryo-Romanic into the ancient Aryan and the ancient Greco-Roman. If we still follow the genealogical tree of these four Indo-Germanic tongues, we find that the ancient Germanic divides into three branches—the Scandinavian, the Gothic, and the German. From the ancient German came the High German and Low German; to the latter belong the Frisian, Saxon, and modern Low-German dialects. The ancient Slavo-Lettic divided first into a Baltic and a Slav language. The Baltic gave rise to the Lett, Lithuanian, and old-Prussian varieties; the Slav to the Russian and South-Slav in the south-east and to the Polish and Czech in the west.

We find an equally prolific branching of its two chief stems when we turn to the other division of the Indo-Germanic languages. The Greco-Roman divided into the

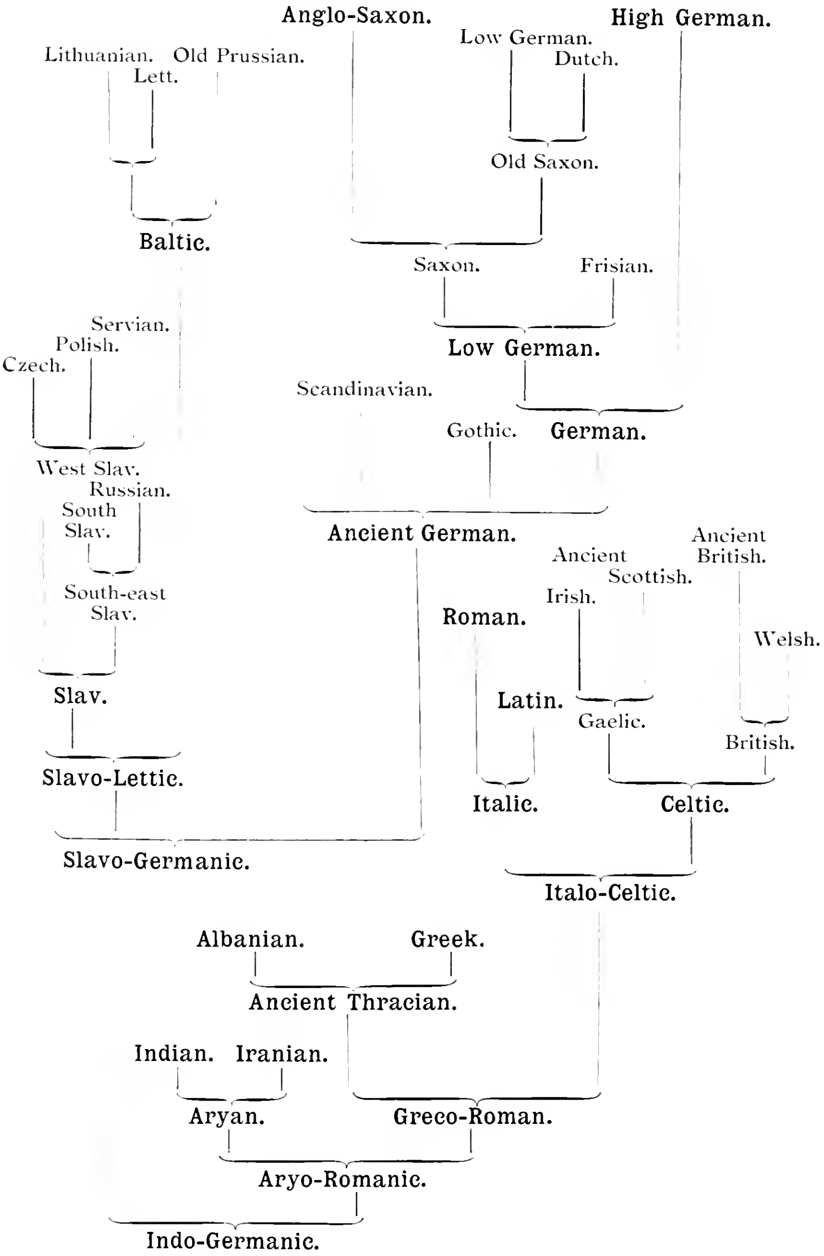
Thracian (Albano-Greek) and the Italo-Celtic. From the latter came the divergent branches of the Italic (Roman and Latin) in the south, and the Celtic in the north; from the latter have been developed all the British (ancient British, ancient Scotch, and Irish) and Gallic varieties. The ancient Aryan gave rise to the numerous Iranian and Indian languages.

It is extremely interesting in many ways to follow closely this genealogical tree of the Indo-Germanic languages. Comparative philology, to which we owe it, has thus proved itself a true science—a natural science. It has even anticipated in its own province the phylogenetic methods we now use with such success in zoology and botany. I cannot help observing how much better it would be to teach languages (certainly one of the most important elements of education) *comparatively* in our schools, and substitute a living and stimulating comparative philology for the dead and dry linguistic studies actually given. The one compares with the other much as the living evolution of organisms compares with the dead classification of species. How much more interest would be taken in languages in our public schools and colleges, and what living impressions would be gained, if the pupils were taught the elements of comparative philology, instead of being tortured with the composition of Latin themes in Circeronian style!

I have gone rather fully into the "comparative anatomy" and evolution of languages, because it admirably illustrates the phylogeny of species. It is clear that in structure and development the primitive languages, mother and daughter languages, and varieties, correspond exactly to the classes, orders, genera, and species of the animal world. In both cases the "natural" system is phylogenetic. As we have been convinced from comparative anatomy and ontogeny, and from paleontology, that all past and living vertebrates descend from a common ancestor, so the comparative study of dead and living Indo-Germanic tongues proves beyond question that they are all modifications of one primitive language. This monophyletic conception is now accepted

TWENTY-SECOND TABLE

GENEALOGICAL TREE OF THE INDO-GERMANIC LANGUAGES



by all the chief philologists who have worked in this branch and are unprejudiced.

But the point to which I desire particularly to draw your attention in this comparison of the Indo-Germanic languages with the branches of the vertebrate stem is, that you must never confuse direct descendants with collateral branches, nor extinct forms with living. This confusion is very common, and our opponents often make use of the erroneous ideas it gives rise to for the purpose of attacking evolution generally. When, for instance, we say that man descends from the ape, this from the half-ape (lemur), and the lemur from the marsupial, many people imagine we are speaking of the living species of these orders of mammals that they find stuffed in our museums. Our opponents then foist this idea on us, and say, with more astuteness than intelligence, that it is quite impossible; or they ask us, by way of physiological experiment, to turn a kangaroo into a lemur, a lemur into a gorilla, and a gorilla into a man! The demand is childish, and the idea it rests on erroneous. All these living forms have diverged more or less from the ancestral form; none of them could engender the same posterity that the stem-form really produced thousands of years ago.

It is certain that man has descended from some extinct mammal; and we should just as certainly class this in the order of apes if we had it before us. It is equally certain that this primitive ape descended in turn from an unknown lemur, and this from an extinct marsupial. But it is just as clear that all these extinct ancestral forms can only be claimed as belonging to the living order of mammals in virtue of their essential internal structure and their resemblance in the decisive anatomic characteristics of each *order*. In external appearance, in the characteristics of the *genus* or *species*, they would differ more or less, perhaps very considerably, from all living representatives of those orders. It is a universal and natural procedure in phylogenetic development that the stem-forms themselves, with their specific peculiarities, have been extinct for some time. The forms that approach nearest to them among the living species are more or less—

perhaps very substantially—different from them. Hence in our phylogenetic inquiry and in the comparative study of the living, divergent descendants, there can only be a question of determining the greater or less remoteness of the latter from the ancestral form. Not a single one of the older stem-forms has continued unchanged down to our time.

We find just the same thing in comparing the various dead and living languages that have developed from a common primitive tongue. If we examine our genealogical tree of the Indo-Germanic languages in this light, we see at once that all the older or parent-tongues, of which we regard the living varieties of the stem as divergent daughter or grand-daughter languages, have been extinct for some time. The Aryo-Romanic and the Slavo-Germanic tongues have completely disappeared; so also the Aryan, the Greco-Roman, the Slavo-Lettic, and the ancient Germanic. Even their daughters and grand-daughters have been lost; all the living Indo-Germanic languages are only related in the sense that they are divergent descendants of common stem-forms. Some forms have diverged more, and some less, from the original stem-form.

This easily demonstrable fact illustrates very well the analogous case of the origin of the vertebrate species. Phylogenetic comparative philology here yields a strong support to phylogenetic comparative zoology. But the one can adduce more direct evidence than the other, as the paleontological material of philology—the old monuments of the extinct tongue—have been preserved much better than the paleontological material of zoology, the fossilised bones and imprints of vertebrates.

We may, however, trace man's genealogical tree not only as far as the lower mammals, but much further—to the amphibia, to the shark-like primitive fishes, and, in fine, to the skull-less vertebrates that closely resembled the amphioxus. But this must not be understood in the sense that the existing amphioxus, or the sharks or amphibia of to-day, can give us any idea of the external appearance of these remote stem-forms. Still less must it be thought that the amphioxus or any actual shark, or any living species of amphibia, is a real ancestral form of the higher vertebrates and man. The statement can only rationally mean that the living forms I have referred to are *collateral lines* that are much more closely related to the extinct stem-forms, and have retained the resemblance much better than any other animals we know. They are still so like them in regard to their distinctive internal structure that we should put them in the same class with the extinct forms if we had these before us. But no direct descendants of these earlier forms have remained unchanged. Hence we must entirely abandon the idea of finding direct ancestors of the human race in their characteristic *external form* among the living species of animals. The essential and distinctive features that still connect living forms more or less closely with the extinct common stem-forms lie in the internal structure, not the external appearance. The latter has been much modified by adaptation. The former has been more or less preserved by heredity.

Comparative anatomy and ontogeny prove beyond question that man is a true vertebrate, and, therefore, man's special genealogical tree must be connected with that of the other vertebrates, which spring from a common root with him. But we have also many important grounds in comparative anatomy and ontogeny for assuming a common origin or a monophyletic descent for all the vertebrates. If the general theory of evolution is correct, all the vertebrates, including man, come from a single common ancestor, a long-extinct "primitive vertebrate." Hence the genealogical tree of the vertebrates is at the same time that of the human race.

Our task, therefore, of constructing man's genealogy becomes the larger aim of discovering the genealogy of the entire vertebrate stem. As we now know from the comparative anatomy and ontogeny of the amphioxus and the ascidian, this is in turn connected with the genealogical tree of the invertebrates (directly with that of the vermalia), but has no direct connection with the independent stems of the articulates, molluscs, and echinoderms. If we do thus follow our ancestral tree through various stages down to the lowest worms, we come inevitably to the *gastræa*, that most instructive form that gives the clearest possible picture of an animal with two germinal layers. The gastræa itself has originated from the simple multicellular vesicle, the *blastæa*, and this in turn must have been evolved from the lowest circle of unicellular animals, to which we give the name of protozoa. We have already considered the most important primitive type of these, the unicellular *amœba*, which is extremely instructive when compared with the human ovum. With this we reach the lowest of the solid data to which we are to apply our biogenetic law, and by which we may deduce the extinct ancestor from the embryonic form. The amœboid nature of the young ovum and the unicellular condition in which (as stem-cell or cytula) every human being begins its existence justify us in affirming that the earliest ancestors of the human race were simple amœboid cells.

But the further question now arises: "Whence came these first amœbæ with which the history of life began at the commencement of the Laurentian epoch?" There is only one answer to this. The earliest unicellular organisms can only have been evolved from the simplest organisms we know, the *monera*. These are the simplest living things that we can conceive. Their whole body is nothing but a particle of plasm, a granule of the living albuminous matter, discharging of itself all the essential vital functions that form the material basis of life. Thus we come to the last, or, if you prefer, the first, question in connection with evolution—the question of the origin of the monera. This is the real question of the origin of life, or of spontaneous generation (in the narrower sense, *archigony)*.

We have neither space nor occasion to go further in this Chapter into the question of spontaneous generation. For this I must refer the reader to the fifteenth chapter of the *History of Creation*, and especially to the second book of the *Generelle Morphologie*, or to the essay on "The Monera and Spontaneous Generation" in my *Studies of the Monera and* *other Protists.*[1] I have given there fully my own view of this important question. The famous botanist Nägeli afterwards (1884) developed the same ideas. I will only say a few words here about this obscure question of the origin of life, in so far as our main subject, organic evolution in general, is affected by it. Spontaneous generation in the definite and restricted sense in which I maintain it, and claim that it is a necessary hypothesis in explaining the origin of life, refers solely to the evolution of the monera from inorganic carbon-compounds. When living things made their first appearance on our planet, the very complex nitrogenous compound of carbon that we call *plasson*, and which is the earliest material embodiment of vital action, must have been formed in a purely chemical way from inorganic carbon-compounds. The first monera were formed in the sea by spontaneous generation, as crystals are formed in the mother-lye. Our demand for a knowledge of causes compels us to assume this. If we remember that the whole inorganic history of the earth has proceeded on mechanical principles without any intervention of a Creator, and believe that the history of life also has been determined by the same mechanical laws; if we see that there is no need to admit creative action to explain the origin of the various groups of organisms; it is utterly irrational to assume such creative action in dealing with the first appearance of organic life on the earth.

This much-disputed question of "spontaneous generation" seems so obscure, because people have associated with the term a mass of very different, and often very absurd, ideas, and have attempted to solve the difficulty by the crudest experiments. The real doctrine of the spontaneous generation of life cannot possibly be refuted by experiments. Every experiment that has a negative result only proves that no organism has been formed out of inorganic matter in the conditions—highly artificial conditions—we have established. On the other hand, it would be exceedingly difficult to prove the theory by way of experiment; and even if monera were still formed daily by spontaneous

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[1] The English reader will find a luminous and up-to-date chapter on the subject in Haeckel's recently-written and translated *Wonders of Life*.—TRANS.

generation (which is quite possible), it would be very difficult, if not impossible, to find a solid proof of it. Those who will not admit the spontaneous generation of the first living things in our sense must have recourse to a supernatural miracle; and this is, as a matter of fact, the desperate resource to which our "exact" scientists are driven, to the complete abdication of reason.

A famous English physicist, Lord Kelvin (then Sir W. Thomson), attempted to dispense with the hypothesis of spontaneous generation by assuming that the organic inhabitants of the earth were developed from germs that came from the inhabitants of other planets, and that chanced to fall on our planet on fragments of their original home, or meteorites. This hypothesis found many supporters, among others the distinguished German physicist, Helmholtz. However, it was refuted in 1872 by the able physicist, Friedrich Zöllner, of Leipzig, in his work *On the Nature of Comets*. He showed clearly how unscientific this hypothesis is; firstly in point of logic, and secondly in point of scientific content. At the same time he pointed out that our hypothesis of spontaneous generation is "a necessary condition for understanding nature according to the law of causality."

I repeat that we must call in the aid of the hypothesis only as regards the monera, the structureless "organisms without organs." Every complex organism must have been evolved from some lower organism by the differentiation of its parts. We must not assume the spontaneous generation of even the simplest cell, for this itself consists of at least two parts—the internal, firm nuclear substance, the caryoplasm or nucleus, and the external, softer cellular substance or the protoplasm of the cell-body *(cytosoma)*. These two parts must have been formed by differentiation from the indifferent plasson of a moneron, or a cytode. For this reason the natural history of the monera is of great interest; here alone can we find the means to overcome the chief difficulties of the problem of spontaneous generation. The actual living monera are specimens of such organless or structureless organisms, as they must have been formed by spontaneous generation at the commencement of the history of life.

CHAPTER XIX.

OUR PROTIST ANCESTORS

Relation of the general inductive law of evolution to the special deductions of the various evolutionary hypotheses. Incompleteness of the three great documents of creation, paleontology, ontogeny, and comparative anatomy. Unequal strength of the various special hypotheses. The series of man's ancestors in thirty stages—eleven invertebrate and nineteen vertebrate. Distribution of these thirty stem-forms in the five sections of the organic history of the earth. First stage, the monera. The structureless and homogeneous plasson of the monera. Differentiation of the plasson into nucleus and protoplasm in the cells. Cytodes and cells as two different forms of plastids. Vital phenomena of the monera. Organisms without organs. Chromacea. Metasitism. Amœbæ. Unicellular protozoa. The amœboid ova. The egg is older than the chick. Paulotomea, Synamœbium or moræa, ontogenetically reproduced in the morula. Blastæa, ontogenetically reproduced in the blastula. Gastræa, ontogenetically reproduced in the gastrula. Living gastræads, Gastremaria (pemmatodiscus, kunstleria). Cyemaria (diceyma, rhopalura). Olynthus and hydra.

UNDER the guidance of the biogenetic law, and on the basis of the evidence we have obtained, we now turn to the interesting task of determining the series of man's animal ancestors. In order to proceed with the utmost security, we must first of all understand the various operations of the mind that we employ in this natural-philosophical project. These are partly inductive and partly deductive: partly the massing of individual experiences in a general law, partly particular deductions from the general law.

Phylogeny as a whole is an inductive science. The theory of descent, an indispensable part of the general doctrine of evolution, is based on clear inductions. From the totality of the biological processes in the life of plants, animals, and man we have gathered a confident inductive idea that the whole organic population of our planet has been moulded on a harmonious law of evolution. This law has, in the hands of Lamarck and Darwin and their successors, taken the form of the theory of descent. All the interesting phenomena that we meet in ontogeny and paleontology, comparative anatomy and dysteleology, the chorology and œcology of organisms—all the important general laws that we abstract from the phenomena of these sciences, and combine in harmonious unity—are the broad bases of our great biological induction. It is just because the infinitely varied phenomena of these different branches can only be understood and explained in their intimate connection by the theory of descent, that we are forced to regard this as a comprehensive inductive law.

And when we come to the application of this law, and seek to determine with its aid the origin of the various species of organisms, we are compelled to frame phylogenetic hypotheses that have essentially a *deductive* character, and are inferences from the general law to particular cases. But these special deductions are just as much justified and necessitated by the rigorous laws of logic as the inductive conclusions on which the whole theory of evolution is built. The doctrine of the animal ancestry of the human race is a special deduction of this kind, and follows with logical necessity from the general inductive law of evolution.

As is generally admitted to-day, both by supporters and opponents of the theory of descent, we have now to choose, as regards the origin of the human race, between two radical alternatives; we must either subscribe to the belief that all the different species of animals and plants, including man, were created independently by a supernatural power that lies beyond scientific investigation, or we are forced to admit the theory of descent in its full extent, and to derive the various organic species and the human race from a primitive and very simple stem-form. There is no third alternative. Either blind faith in creation or a scientific theory of evolution. If we admit the latter, which is the only possible procedure in any scientific conception of the universe, we can, with the aid of comparative anatomy and ontogeny, determine to some extent the series of man's ancestors, just as we can, more or less, in the case of all other organisms.

It will be already clear, from our inquiry into the comparative anatomy and ontogeny of man and the other vertebrates, that we must seek the genealogy of the human race first within the vertebrate stem. There can be no doubt that (if evolution is generally correct) man has been evolved as a true vertebrate, or that he has originated from the same common stem-form as all the other vertebrates. This special deduction must be regarded as absolutely certain—assuming, of course, the correctness of the inductive theory of descent. No one who subscribes to the law can have any doubt about this deduction. Further, we can specify a series of different forms within the vertebrate stem that can confidently be regarded as the representatives of successive evolutionary stages, or as so many links in the chain of our ancestry. On the other hand, we can prove with the same confidence that the vertebrate stem as a whole has been evolved from a group of lower, invertebrate animals; and, again, we can recognise more or less clearly among these a series of links in the chain of our ancestry.

But I must point out at once that the certainty of these evolutionary hypotheses, which rest on clear special deductions, is not always equally strong. Some of these inferences are now beyond question; in the case of others it depends on the knowledge and the competence of the inquirer what degree of certainty he attributes to them. In any case, we must distinguish between the *absolute* certainty of the general (inductive) theory of descent and the *relative* certainty of special (deductive) evolutionary hypotheses. We can never determine the whole ancestral series of an organism with the same confidence with which we hold the general theory of evolution as the sole scientific explanation of organic modifications. The special indication of stem-forms in detail will always be more or less incomplete and hypothetical. This is quite natural. The evidence on which we build is imperfect, and always will be imperfect; just as in comparative philology.

The first of our documents, paleontology, is exceedingly incomplete. We know that all the fossils yet discovered are only an insignificant fraction of the plants and animals that have lived on our planet. For every single species that has been preserved for us in the rocks there are probably hundreds, perhaps thousands, of extinct species that have left no trace behind them. This extreme and very unfortunate incompleteness of the paleontological evidence, which cannot be pointed out too often, is easily explained. It is absolutely inevitable in the circumstances of the fossilisation of organisms. It is also due in part to the incompleteness of our knowledge in this branch. It must be borne in mind that the great majority of the stratified rocks that compose the crust of the earth have not yet been opened. We have only a few specimens of the innumerable fossils that are buried in the vast mountain ranges of Asia and Africa. Only a part of Europe and North America has been investigated carefully. The whole of the fossils known to us certainly do not amount to a hundredth part of the remains that are really buried in the crust of the earth. We may, therefore, look forward to a rich harvest in the future as regards this science. However, our paleontological evidence will (for reasons that I have fully explained in the sixteenth chapter of the *History of Creation*) always be defective.

The second chief source of evidence, ontogeny. is not less incomplete. It is the most important source of all for special phylogeny ; but it has great defects, and often fails us. We must, above all, clearly distinguish between palingenetic and cenogenetic phenomena, between the original "compendium of development" and the later "disturbance of development." We must never forget that the laws of curtailed and disturbed heredity often make the original course of development almost unrecognisable. The recapitulation of phylogeny by ontogeny is only fairly complete in a few cases, and is never wholly complete. As a rule, it is precisely the earliest and most important embryonic stages that suffer most from alteration and condensation. The earlier embryonic forms have had to adapt themselves to new circumstances, and so have been modified. The struggle for existence has had just as profound an influence on the freely moving and still immature young forms as on the adult forms. Hence in the embryology of the higher animals, especially, palingenesis is much restricted by cenogenesis; it is to-day, as a rule, only a faded and much altered picture of the original evolution of the animal's ancestors. We can only draw conclusions from the embryonic forms to the stem-history with the greatest caution and discrimination. Moreover, the embryonic development itself has only been fully studied in a few species.

Finally, the third and most valuable source of evidence, comparative anatomy, is also, unfortunately, very imperfect; for the simple reason that the whole of the living species of animals are a mere fraction of the vast population that has dwelt on our planet since the beginning of life. We may confidently put the total number of these at more than a million species. The number of animals whose organisation has been studied up to the present in comparative anatomy is proportionately very small. Here, again, future research will yield incalculable treasures.

In view of this patent incompleteness of our chief sources of evidence, we must naturally be careful not to lay too much stress in human phylogeny on the particular animals we have studied, or regard all the various stages of development with equal confidence as stem-forms. We shall often have to remind ourselves, in establishing our ancestral series, that the different hypothetical stem-forms have a very different evidential value. It is clear, from what I have said of corresponding phylogenetic forms in dealing with ontogeny, that some embryonic structures can be safely regarded as reproductions of corresponding stem-forms. The first and most important of these was the human ovum, the stem-cell that arises when it is fecundated. From the pregnant fact that the human germ is at first a simple cell like the germ of any other animal, we may with full confidence infer that there was a unicellular stem-form from which all the multicellular animals, including man, have descended. A second instructive embryonic form that clearly reproduces an ancient stem-form is the blastula, the simple hollow ball with its one-layered wall, the blastoderm. A third and most important embryonic structure that has a direct and certain phylogenetic bearing is the gastrula. This very interesting larva-form shows the animal body built up of two germinal layers, and already provided with the chief primitive organ, the gut. As the same two-layered structure with a primitive alimentary canal is found in all the different animal stems (with the exception of the unicellular protozoa), we may safely deduce from it the *existence* of a common ancestor that resembled the gastrula in structure, the gastræa. Not less useful for the purposes of human phylogeny are the important ontogenetic structures that we have called the cœlomula, chordula, etc., and that correspond to certain vermalia, acrania, fishes, and so on. On the other hand, there are great and unfortunate gaps between these certain and very valuable phylogenetic data, to which we will return later; these are sufficiently explained by the reasons I have already given, the incompleteness of the evidence of paleontology, comparative anatomy, and ontogeny.

In my first efforts to construct the series of man's ancestors (in the *Generelle Morphologie* and *History of Creation)* I drew up a list of, at first ten, afterwards twenty to thirty, forms that may be regarded more or less certainly as animal ancestors of the human race, or as stages that in a sense mark off the chief sections in the long story of evolution from the unicellular organism to man. Of these twenty to thirty stages, ten to twelve belong to the older group of the invertebrates and eighteen to twenty to the younger division of the vertebrates. I have shown in the twenty-sixth table how these ancestral forms may be hypothetically distributed among the five main sections of the organic history of the earth. Nearly half of them fall in the archeozoic age, or first period in the history of life.

In approaching, now, the difficult task of establishing the evolutionary succession of these thirty ancestors of humanity since the beginning of life, and in venturing to lift the veil that covers the earliest secrets of the earth's history, we must undoubtedly look for the first living things among the wonderful organisms that we call the monera; they are the simplest organisms known to us—in fact, the simplest we can conceive. Their whole body consists merely of a simple particle or vesicle of structureless plasm or plasson, of the very important group of nitrogenous carbon-compounds, which are now generally admitted to be the material substratum of all vital phenomena. The discoveries of the last four decades have led us to believe with increasing certainty that wherever a natural body exhibits the vital processes of nutrition, reproduction, voluntary movement, and sensation, we have the action of a nitrogenous carbon-compound of the chemical group of the albuminoids; this plasm (or protoplasm) is the material basis of all vital functions. Whether we regard the function, in the monistic sense, as the direct action of the material substratum, or whether we take matter and force to be distinct things in the dualistic sense, it is certain that we have not as yet found any living organism in which the exercise of the vital functions is not inseparably bound up with plasm. In the monera, the simplest organisms conceivable, the whole body consists of plasson, which corresponds to the "primitive slime" of the older natural philosophy.

The soft slimy plasson of the body of the moneron is generally called "protoplasm," and identified with the cellular matter of the ordinary plant and animal cells. But, as Eduard Van Beneden especially has pointed out in his admirable works on the gregarinæ, we must, to be accurate, distinguish between the plasson of the cytodes and the protoplasm of the cells. This distinction is of the utmost importance for the purposes of evolution. As I have often said, we must recognise two different stages of development in these "elementary organisms," or plastids ("builders"), that represent the ultimate units of organic individuality. The earlier and lower stage are the unnucleated cytodes, the body of which consists of only one kind of albuminous matter—the homogeneous plasson or "formative matter." The later and higher stage are the nucleated cells, in which we find a differentiation of the original plasson into two different formative substances—the caryoplasm of the nucleus and the cytoplasm of the body of the cell (cf. pp. 99 and 106).

The monera are permanent cytodes. Their whole body consists of soft, structureless plasson. However carefully we examine it with our finest chemical reagents and most powerful microscopes, we can find no definite parts or no morphological structure in it. Hence, the monera are literally organisms without organs; in fact, from the philosophic point of view, they are not organisms at all, since they have no organs. They can only be called organisms in the sense that they are capable of the vital functions of nutrition, reproduction, sensation, and movement. If we were to try to construct *à priori* the simplest organism imaginable, we should frame something like the moneron.

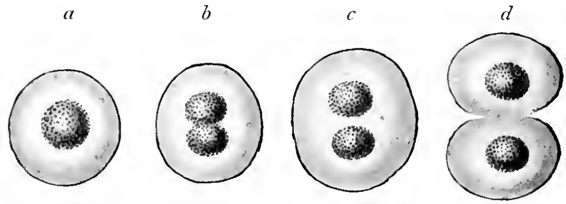

Fig. 277.—**Chroococcus minor** (*Nägeli*), magnified 1,500 times. A phytomoneron, the globular plastids of which secrete a gelatinous structureless membrane. The unnucleated globule of plasm (bluish-green in colour) increases by simple cleavage (*a–d*).

The monera that we find to-day in various forms fall into two groups according to the nature of their metabolism—the *phytomonera* with plasmodomous and the *zoomonera* with plasmophagous nutrition; from the physiological point of view, the former are the simplest specimens of the plant (*phyton*) kingdom, and the latter of the animal (*zoon*) world. The phytomonera, especially in their simplest form, the chromacea (*phycochromacea* or *cyanophycea*), are the most primitive and the oldest of living organisms. The typical genus *chroococcus* (Fig. 277) is represented by several fresh-water species, and often forms a very delicate bluish-green deposit on stones and wood in ponds and ditches. It consists of round, light green particles, 0.003–0.01 millimetres in diameter.

The whole life of these homogeneous globules of plasm consists of simple growth and reproduction by cleavage. When the tiny particle has reached a certain size by continuous plasmodomism (or carbon-assimilation) it divides into two equal halves, by a constriction in the middle. The two daughter-monera that are thus formed immediately begin a similar vital process. It is the same with the brown *procytella primordialis* (formerly called the *protococcus marinus);* it forms large masses of homogeneous plancton in the arctic seas. The tiny plasma-globules of this species are of a greenish-brown colour, and have a diameter of 0.002–0.004 millimetres. There is no membrane discoverable in the simplest *chroococcacea,* but we find one in other members of the same family ; in *aphanocapsa* (Fig. 278) the enveloping membranes of the social plastids combine ; in *glœocapsa* they are retained through several generations, so that the little plasma-globules are enfolded in many layers of membrane.

If we candidly compare these rudimentary protophyta of the present day with other organisms, they cannot be classed with real nucleated cells, but with the remarkable chromatella (or *chromatophora)* that we find in the body of real, nucleated plant-cells. These homogeneous, coloured plasma-particles also grow and multiply independently by cleavage in the same way. On the strength of this parallel, Fritz Müller pointed out, in 1893, that we have in each green vegetal cell a symbiosis between plasmodomous green and plasmophagous not-green associates.[1]

Next to the plasmodomous chromacea come the plasmophagous bacteria, which have been evolved from them by metasitism—*i.e.,* by the remarkable "reversal of metabolism," which gives us the simple explanation of the differentiation of plant and animal in the protist kingdom. Hence, if we logically divide the protist kingdom into plasma-forming protophyta and plasma-consuming protozoa, we must class the bacteria with the latter ; it is quite illogical to describe them—as is still often done—as *schizomycetes*, and

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[1] The interesting chromacea (commonly called *phycochromacea*, or *cyanophycea*, and classed with the "unicellular algæ") are the lowest protophyta, and entirely correspond to the theoretical requirements of the hypothesis of spontaneous generation. They are generally ignored by the dogmatic maintainers of the cellular theory in its prevailing form. But as real monera, or pre-cellular organisms, they are extremely interesting, and in a natural phylogenetic classification of plants should be placed at its very lowest stage as real archephyta or primitive monera.

class them with the true fungi (*i.e.*, multicellular, tissue-forming metaphyta). The bacteria have no nucleus like the chromacea, and are therefore *archezoa* or zoomonera. As is well known, they play an important part in modern biology as the causes of fermentation and putrefaction (zymogenetic), and of tuberculosis, typhus, cholera, and other infectious diseases (pathogenetic), and as parasites, symbionta, etc. But we cannot linger now to deal with these very interesting features; the bacteria have no relation to man's genealogical tree.

We may now turn to consider the remarkable protamœbæ, the unnucleated amœbæ that we distinguish as *lobomonera* from the similar *lobosa*, which are real nucleated amœbæ (Fig. 279). I have previously pointed out the great importance of the ordinary amœbæ in connection with several weighty questions of general biology (p. 117). The tiny protamœbæ, which are found both in fresh and salt water, have the same unshapely form and irregular movements of their simple naked body as the real amœbæ; but they differ from them very materially in having no nucleus in their homogeneous cell-body. The short, blunt, finger-like processes that are thrust out at the surface of the creeping protamœba serve for getting food as well as for locomotion. They multiply by simple cleavage (Fig. 279).

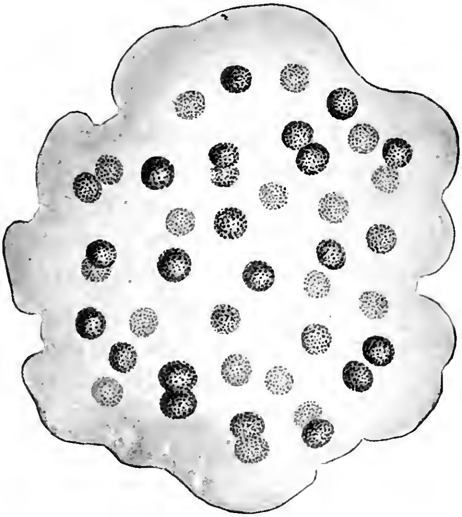

FIG. 278.—**Aphanocapsa primordialis** (*Nägeli*), magnified 1,000 times. A phytomoneron, the round plastids of which (bluish-green in colour) secrete a shapeless gelatinous mass; in this the unnucleated cytodes increase continually by simple cleavage.

The origin and significance of these living structureless plasson-bodies raise many questions, especially in connection with spontaneous generation. We have already seen that the hypothesis of spontaneous generation is absolutely necessary to explain the origin of the first plastids on our planet. We may return to the point with some interest now that we have recognised in the monera the simple organisms which we may in the present state of science, without serious difficulty, conceive to have been formed by spontaneous generation. The monera stand exactly at the limit between the organic and inorganic worlds.

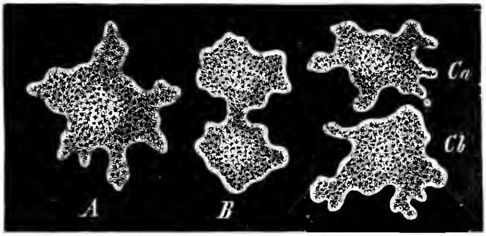

FIG. 279.—**A moneron (protamœba)** in the act of reproduction. *A* The whole moneron, moving like an ordinary amœba by thrusting out changeable processes. *B* It divides into two halves by a constriction in the middle. *C* The two halves separate, and each becomes an independent individual. (Highly magnified.)

The next stage to the simple cytode-forms of the monera in the genealogy of mankind (and all other animals) is the simple cell, or the most rudimentary form of the cell which we find living independently to-day as the amœba. The earliest process of organic differentiation in the homogeneous and structureless plasson-body of the monera led to its division into two different substances — the caryoplasm and the cytoplasm. The caryoplasm is the inner and firmer part of the cell, the substance of the nucleus. The cytoplasm is the outer and softer part, the substance of the body of the cell (or *cytosoma).* By this important differentiation of the plasson into nucleus and cytosoma, the organised cell was evolved from the structureless cytode, the nucleated from the unnucleated plastid. That the first cells to appear on the earth were formed from the monera by such a differentiation seems to us the only possible view in the present condition of histological science. We have a direct instance of this earliest process of histological differentiation to-day in the ontogeny of many of the lower protists (such as the gregarinæ).

The unicellular form that we have in the ovum, and in the stem-cell it is converted into by fecundation, has already been described as the reproduction of a corresponding unicellular stem-form, and to this we have ascribed the organisation of an amœba (cf. Chapter VI.). The irregular-shaped amœba, which we find living independently to-day in our fresh and salt water, is the least definite and the most primitive of all the unicellular protozoa (Fig. 280). As the unripe ova (the *protova* that we find in the ovaries of animals) cannot be distinguished from the common amœbæ, we must regard the amœba as the phylogenetic primitive form that is reproduced in the ontogenetic stage of the amœboid ovum to-day, in accordance with the biogenetic law. I have already pointed out, in proof of the striking resemblance of the two cells, that the ova of many of the sponges were formerly regarded as parasitic amœbæ (Fig. 281). Large unicellular organisms like the amœbæ were found creeping about inside the body of the sponge, and were thought to be parasites. It was afterwards discovered that they were really the ova of the sponge from which the embryos were developed. As a matter of fact, these sponge-ova are so much like many of the amœbæ in size, shape, the character of their nucleus, and movement of the ever-varying pseudopodia, that it is impossible to distinguish them without knowing their subsequent development.

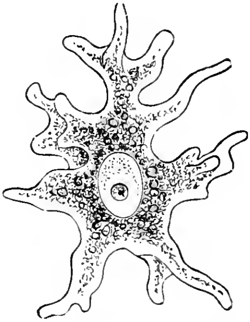

FIG. 280.—**A creeping amœba** (highly magnified). The whole organism is merely a simple naked cell, and moves about by means of the variable processes that it thrusts out from and withdraws into its protoplasmic body. There is a clear round nucleus in the middle of it.

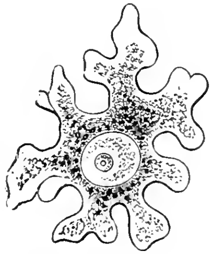

FIG. 281.—**Ovum of a calcareous sponge** (*calcolynthus*). The ovum creeps about in the body of the sponge by protruding variable processes, like the common amœba.

Our phylogenetic interpretation of the ovum, and the reduction of it to some ancient amœboid ancestral form, supply the answer to the old problem : " Which was first, the egg or the chick?" We can now give a very plain answer to this riddle, with which our opponents have often tried to drive us into a corner. The egg came a long time before the chick. We do not mean, of course, that the egg existed from the first as a bird's egg, but as an indifferent amœboid cell of the simplest character. The egg lived for thousands of years as an independent unicellular organism, the amœba. The egg, in the modern physiological sense of the word, did not make its appearance until the descendants of the unicellular protozoon had developed into multicellular animals, and these had undergone sexual differentiation. Even then the egg was first a gastræa-egg, then a platode-egg, then a vermalia-egg, and chordonia-egg; later still acrania-egg, then fish-egg, amphibia-egg, reptile-egg, and finally bird's egg. The bird's egg we have experience of daily is a highly complicated historical product, the result of countless hereditary processes that have taken place in the course of millions of years.

I have already pointed out the great importance of the circumstance that the original form of the ovum, as we find it in the animal's ovary, is always the same: it is an amœboid cell of the simplest character, and of indefinite and variable shape. In this first stage, immediately after the individual ovum has been formed by cleavage of the cells in the mother's ovary, it is impossible to detect any material differences in its character in animals of the most distant types (see Fig. 13, p. 111). This cannot be done until the primitive ova (or *protova)* have taken up various kinds of food-yelk, and have clothed themselves with different membranes, and been otherwise differentiated, and have thus been converted into *metova*. But these characteristics of the more advanced metova, or the ripe and fertilisable ova, are secondary acquisitions, due to adaptation to the environment of the ovum itself, and of the animal that forms it.

When we regard the amœbæ as the simplest and oldest of the unicellular protozoa (or of all *plasmophagous* protists) we can answer in two ways the important question of their origin. We may either hold that the first amœbæ were evolved from unnucleated protamœbæ by differentiation of nucleus and cell-body, or we may derive them by metasitism from the simplest unicellular protophyta (or the nucleated *plasmodomous* protists). Instances of these earliest protophyta are the paulotomea, the green palmellacea and the yellow xanthellacea. They live sometimes in isolation *(eremosphæra, pleurococcus)*, sometimes in common, the daughter-cells produced by cleavage remaining joined together in a common gelatinous secretion *(palmella, pleurococcus)*. The oldest forms of these nucleated, and therefore really unicellular, protophyta were certainly evolved from unnucleated phytomonera *(chromacea)* by differentiation of nucleus and cytosoma—to use a chemical expression, by separation of the central caryoplasm and the peripheral cytoplasm.

We cannot go any further here into the unicellular forms of life which we may hypothetically regard as the earliest (plasmodomous) protophyta on the one hand and the earliest (plasmophagous) protozoa on the other. This is not necessary, as for our purpose we have only to frame a general idea of the primitive character of the earliest embodiments of organic life on our planet. As the table on the next page shows, the gradual development of the lowest forms of life follows analogous lines in both divisions of the protist kingdom. First came unnucleated plastids of the simplest type—monera *(phytomonera* and *zoomonera)*. The unnucleated cytodes are then converted into real nucleated cells—*algaria* and *algetta* in the plant kingdom, and *rhizopoda* and *infusoria* in the animal kingdom. Finally, in both groups we get the social aggregations of the *cenobia*, or cell-communities: on the one hand the *volvocina* and *halosphæræ*, on the other the *catallacta* and *blastæada*. The former lead directly to the tissue-forming *metaphyta*, the latter to the *metazoa*.

The chemical-physiological process of *metasitism*, or *metatrophy*, the reversal of the mode of nutrition, has an important connection with many of the phylogenetic questions in this first section of the history of life. When and where took place the historical conversion of synthetic *phytoplasm* into analytic *zooplasm*? In other words, when

TWENTY-THIRD TABLE

SYNOPSIS OF THE PARALLEL PHYLOGENESES IN THE TWO DIVISIONS OF THE PROTIST-KINGDOM

Protophyta. Plasmodomous, or plasma-formers.	**Protozoa.** Plasmophagous, or plasma-eaters.
Reduction-organisms. With chemico-synthetic function, with vegetal metabolism.	**Oxydation-organisms.** With chemico-analytic function, with animal metabolism.
They convert the living force of sunlight into the chemical potential energy of organic compounds (especially carbo-hydrates and albuminoids).	They convert the potential energy of organic compounds into the living force of heat and motion (muscular and neural action).
Exchange of gases: Oxygen released, carbonic acid and ammonia taken in.	Exchange of gases: Oxygen taken in, carbonic acid and ammonia released.
I. First group. Unnucleated protophyta. **Phytomonera.** *Chromacea, probionta.*	I. First group. Unnucleated protozoa. **Zoomonera.** *Bacteria, protamœbæ.*
II. Second group. Nucleated (unicellular) protophyta.	II. Second group. Nucleated (unicellular) protozoa.
IIa. **Algaria.** Without vibratory movement (without lashes or cilia). *Paulotomea, diatomea.*	IIa. **Rhizopoda.** Without vibratory movement in maturity (without lashes or cilia). *Amœbinæ, radiolaria.*
IIb. **Algetta.** With vibratory movement (with lashes or cilia). *Mastigota, siphonea.*	IIb. **Infusoria** With vibratory movement (lashes or cilia). *Flagellata, ciliata.*
III. Third group. Vegetal cenobia. Plasmodomous cell-communities. *Volvocina, halosphæræ.*	III. Third group. Animal cenobia. Plasmophagous cell-communities. *Catallacta, blastæada.*

and where were the protozoa first evolved from the protophyta? The answer to this very important but very difficult question has been strangely neglected by botanists and zoologists hitherto. As I went into it carefully in the second chapter of my *Systematic Phylogeny of the Protists*, I must refer the reader thereto. I will only point out that metasitism is polyphyletic, or has occurred several times in the course of evolution. Zoomonera may have been repeatedly evolved from phytomonera, amœbinæ from paulotomea, cattallacta from volvocina, and so on, by this "reversal of the original order of metabolism."

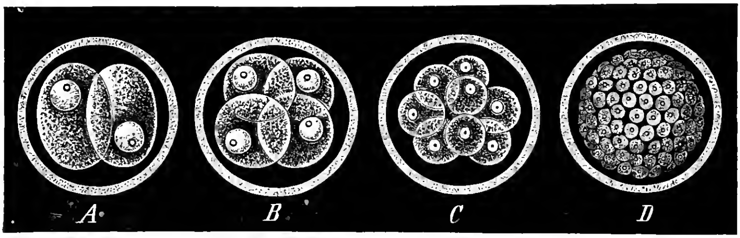

FIG. 282.—**Original or primordial ovum-cleavage.** The stem-cell or cytula, formed by fecundation of the ovum, divides by repeated regular cleavage first into two *(A)*, then four *(B)*, then eight *(C)*, and finally a large number of segmentation-cells *(D)*.

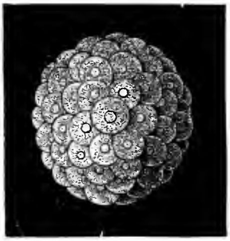

FIG. 283.—**Morula,** or **mulberry-shaped embryo.**

In any case, the earliest ancestors of our race were simple protophyta, and from these our protozoic ancestors were developed afterwards by metasitism. From the morphological point of view both the vegetal and the animal protists were simple organisms, individualities of the first order, or plastids. All our later ancestors are complex organisms, or individualities of a higher order—social aggregations of a plurality of cells. The earliest of these, the *moræada*, which represent the third stage in our genealogy, are very simple associations of homogeneous, indifferent cells—undifferentiated cenobia, colonies of social amœbæ or infusoria. To understand the nature and origin of these protozoa-colonies we need only follow step by step the first ontogenetic products of the stem-cell. In all the metazoa the first embryonic process is the repeated cleavage of the stem-cell, or first segmentation-cell (Fig. 282). We have already fully considered this process, and found that all the different forms of it may be reduced to one type, the original equal or primordial segmentation (cf. Chapter VIII., p. 152). In the genealogical tree of the vertebrates this palingenetic form of segmentation has been preserved in the amphioxus alone, all the other vertebrates having cenogenetically modified forms of cleavage (see the Third Table). In any case, the latter were developed from the former, and so the segmentation of the ovum in the amphioxus has a great interest for us (cf. Fig. 257). The outcome of this repeated cleavage is the formation of a round cluster of cells, composed of homogeneous, indifferent cells of the simplest character (Fig. 283). This is called the *morula* (= mulberry-embryo) on account of its resemblance to a mulberry or blackberry.

It is clear that this morula reproduces for us to-day the simple structure of the multicellular animal that succeeded the unicellular amœboid form in the early Laurentian period. In accordance with the biogenetic law, the morula recalls the ancestral form of the *moræa*, or simple colony of protozoa. The first cell-communities to be formed, which laid the early foundation of the higher multicellular body, must have consisted of homogeneous and simple amœboid cells. The oldest amœbæ lived isolated lives, and even the amœboid cells that were formed by the segmentation of these unicellular organisms must have continued to live independently for a long time. But gradually small communities of amœbæ arose by the side of these eremitical protozoa, the sister-cells produced by cleavage remaining joined together. The advantages in the struggle for life which these communities had over the isolated cells favoured their formation and their further development. We find plenty of these cell-colonies or communities, or *cenobia,* to-day in both fresh and salt water. They belong to various groups both of the protophyta and protozoa.

To have some idea of those ancestors of our race that succeeded phylogenetically to the moræada, we have only to follow the further ontogenetic development of the morula. We then see that the social cells of the round cenobium secrete a sort of jelly or a watery fluid inside their globular body, and they themselves rise to the surface of it (Fig. 284 *F*, *G*). In this way the solid mulberry-embryo becomes a hollow sphere, the wall of which is composed of a single layer of cells. We call this layer the *blastoderm*, and the sphere itself the *blastula* or embryonic vesicle (or *blastosphæra*).

This interesting blastula is very important. The conversion of the morula into a hollow sphere proceeds on the same lines originally in the most diverse stems—as, for instance, in many of the zoophytes and worms, the ascidia, many of the echinoderms and molluscs, and in the amphioxus. Moreover, in the animals in which we do not find a real palingenetic blastula the defect is clearly due to cenogenetic causes, such as the formation of food-yelk and other embryonic adaptations. We may, therefore, conclude that the ontogenetic blastula is the reproduction of a very early phylogenetic ancestral form, and that all the metazoa are descended from a common stem-form, which was in the main constructed like the blastula. In many of the lower animals the blastula is not developed within the fœtal membranes, but in the open water. In those cases each blastodermic cell begins at an early stage to thrust out one or more mobile hair-like protoplasmic processes; the body swims about by the vibratory movement of these lashes or whips (Fig. 284 *F*).

We still find, both in the sea and in fresh water, various genera of primitive multicellular organisms that substantially resemble the blastula in structure, and may be regarded in a sense as permanent blastula-forms—hollow vesicles or gelatinous balls, with a wall composed of a single layer of vibratory homogeneous cells. There are "blastæads" of this kind even among the protophyta—the familiar volvocina, formerly classed as "globular animals" with the infusoria. The common *volvox globator* is found in the ponds in the spring—

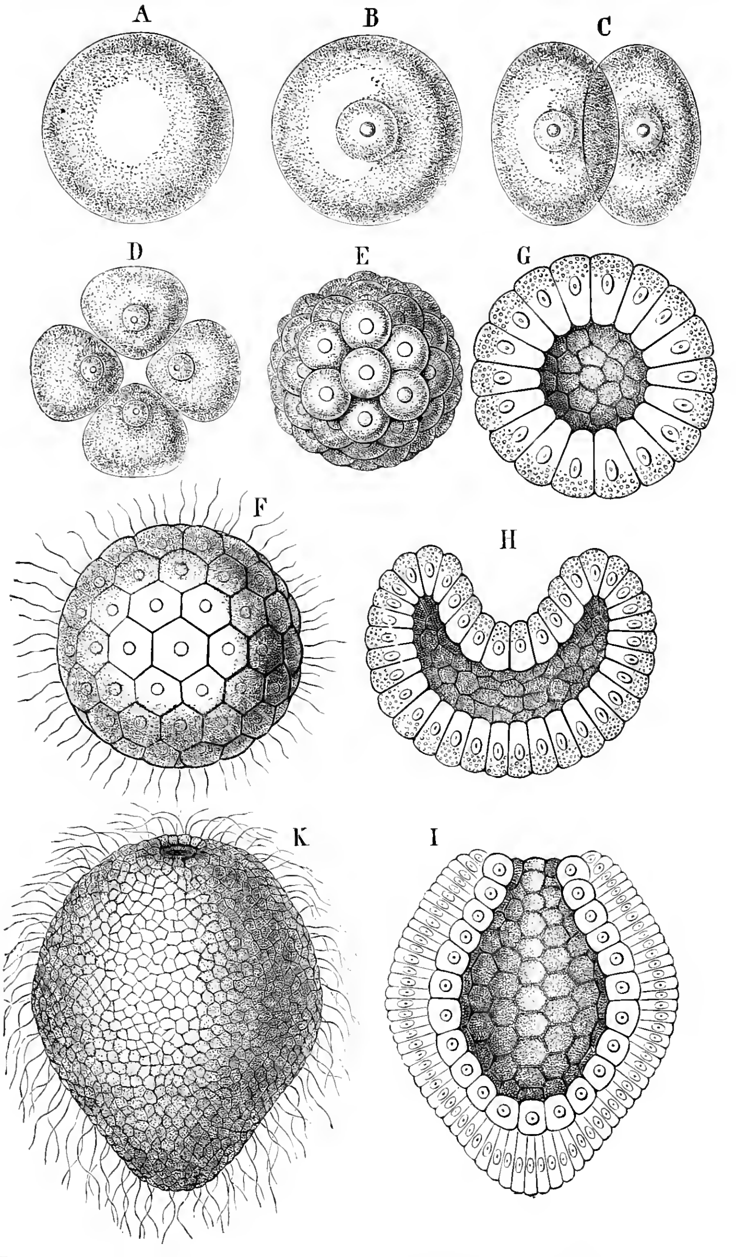

FIG. 284.—**Gastrulation of a coral** (*monoxenia Darwinii*). *A*, *B* stem-cell (cytula) or fertilised ovum. The fresh nucleus is seen in *B*, but not yet in *A*. *C* two segmentation-cells. *D* four segmentation-cells. *E* morula. *F* blastula. *G* blastula in section. *H* invaginated blastula (depula) in section. *I* gastrula in longitudinal section. *K* external view of gastrula, or cup-embryo.

a small, green gelatinous globule, swimming about by means of the stroke of its lashes, which rise in pairs from the cells on its surface. In the similar *halosphæra viridis* also, which we find in the marine plancton (floating matter), a number of green cells form a simple layer at the surface of the gelatinous ball ; but in this case there are no cilia.

Some of the infusoria of the flagellata-class *(signura, magosphæra,* etc.*)* are similar in structure to these vegetal cenobia, but differ in their animal metabolism ; they form the special group of the plasmophagous *catallacta.* In September, 1869, I studied the development of one of these graceful animals on the island of Gis-Oe, off the coast of Norway *(magosphæra planula,* Figs. 285 and 286*).* The fully-formed body is a gelatinous sphere, with its wall composed of thirty-two to sixty-four ciliated homogeneous cells ; it swims about freely in the sea. After reaching maturity the community is dissolved. Each cell then lives independently for some time, grows, and changes into a creeping amœba. This afterwards contracts and clothes itself with a structureless membrane. The cell then looks just like an ordinary animal ovum. When it has been in this condition for some time the cell divides into two, four, eight, sixteen, thirty-two, and sixty-four cells. These arrange themselves in a round vesicle, thrust out vibratory lashes, burst the capsule, and swim about in the same magosphæra-form with which we started. This completes the life-circle of the remarkable and instructive protozoon.

If we compare these permanent blastopheres with the free-swimming ciliated larvæ or blastula, with similar construction, of many of the lower animals, we can confidently deduce from them that there was a very early and long-extinct common stem-form of substantially the same structure as the blastula. We may call it the *blastæa.* Its body consisted, when fully formed, of a simple hollow ball, filled with fluid or structureless jelly, with a wall composed of a single stratum of homogeneous ciliated cells. There were probably many genera and species of these blastæads in the Laurentian period, forming a special class of marine protists.

As a remarkable illustration of the genius for natural philosophy with which Carl Ernst Baer penetrated the most profound mysteries of animal embryology, I may point out that in 1828 (ten years before the cell theory was established) he had a presentiment of the importance of the blastophere, and made prophetic reference to it in his classical *Animal Embryology* (vol. i., p. 223). The passage runs:—

> The further we go in embryology, the more resemblance we find between different animals. This suggests the question, whether all animals are not essentially alike at the beginning of development, and whether there is not a common primitive type of them all? As the embryo is the undeveloped animal, it may be said with some show of reason that the simple blastula is the common typical form from which all animals have been developed, not only in theory, but historically.

This sentence has a phylogenetic as well as an ontogenetic meaning, and is very remarkable when we remember that at that time the blastula of very different animals, and the composition of its wall from a single stratum of cells, were far from being known. Yet Baer ventured, in spite of the very meagre empirical grounds, to formulate the principle: "Probably all animals are alike—all hollow vesicles—in the beginning."

It is an interesting fact that in the plant kingdom also the simple hollow sphere is found to be an elementary form of the multicellular organism. At the surface and below the surface (down to a depth of 2,000 metres) of the sea there are green globules swimming about, with a wall composed of a single layer of chlorophyll-bearing cells. The botanist, Schmitz, gave them the name of *halosphæra viridis* in 1879, and showed that they propagate by means of spores produced by the division of the cells. I have described a second species *(halosphæra blastula)*, which attains a diameter of one millimetre, in my *Plancton-studies* (p. 34).

The next stage to the *blastæa*, and the sixth in our genealogical tree, is the *gastræa* that is developed from it. As we have already seen, this ancestral form is particularly important. That it once existed is proved with certainty by the *gastrula*, which we find temporarily in the ontogenesis of all the metazoa (Fig. 284 *J*, *K*). As we saw, the original, palingenetic form of the gastrula is a round or oval uni-axial body, the simple cavity of which (the primitive gut) has an aperture at one pole of its axis (the primitive mouth). The wall of the gut consists of two strata of cells, and these are the primary germinal layers, the animal skin-layer (ectoderm) and vegetal gut-layer (entoderm).

The actual ontogenetic development of the gastrula from the blastula furnishes sound evidence as to the phylogenetic origin of the *gastræa* from the *blastæa*. A pit-shaped depression appears at one side of the spherical blastula (Fig. 284 *H*). In the end this invagination goes so far that the outer or invaginated part of the blastoderm lies close on the inner or non-invaginated part (Fig. 284 *J*). In explaining the phylogenetic origin of the gastræa in the light of this ontogenetic process, we may assume that the one-layered cell-community of the blastæa began to take in food more largely at one particular part of its surface. Natural selection would gradually lead to the formation of a depression or pit at this alimentary spot on the surface of the ball. The depression would grow deeper and deeper. In time the vegetal function of taking in and digesting food would be confined to the cells that lined this hole; the other cells would see to

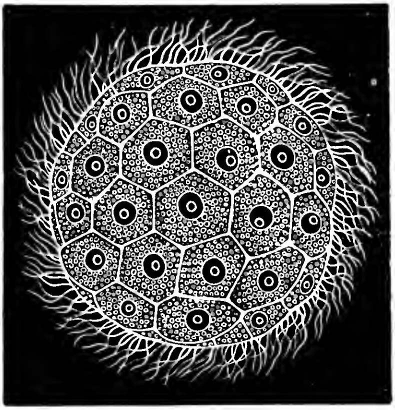

FIG. 285.

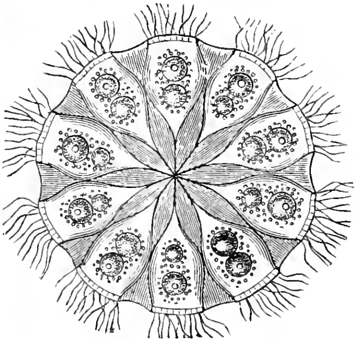

FIG. 286.

FIG. 285.—**The Norwegian magosphaera planula,** swimming about by means of the lashes or cilia at its surface.

FIG. 286.—**Section of same,** showing how the pear-shaped cells in the centre of the gelatinous ball are connected by a fibrous process. Each cell has a contractile vesicle as well as a nucleus.

the animal functions of locomotion, sensation, and protection. This was the first division of labour among the originally homogeneous cells of the blastæa.

The effect, then, of this earliest histological differentiation was to produce two different kinds of cells—nutritive cells in the depression and locomotive cells on the surface outside. But this involved the severance of the two primary germinal layers, a most important process. When we remember that even man's body, with all its various parts, and the body of all the other higher animals are built up originally out of these two simple layers, we cannot lay too much stress on the phylogenetic significance of this gastrulation. In the simple primitive gut or gastric cavity of the gastrula and its rudimentary mouth we have the first real organ of the animal frame in the morphological sense ; all the other organs were developed afterwards from these. In reality, the whole body of the gastrula is merely a "primitive gut." I have shown already (Chapters VIII. and IX.) that the two-layered embryos of all the metazoa can be reduced to this typical gastrula. This important fact justifies us in concluding, in accordance with the biogenetic law, that their ancestors also were phylogenetically developed from a similar stem-form. This ancient stem-form is the gastræa.

The gastræa probably lived in the sea during the Laurentian period, swimming about in the water by means of its ciliary coat much as free ciliated gastrulæ do to-day. Probably it differed from the existing gastrula only in one essential point, though extinct millions of years ago. We have reason, from comparative anatomy and ontogeny, to believe that it multiplied by sexual generation, not merely asexually (by cleavage, gemmation, and spores), as was probably the case with the earlier ancestors. Some of the cells of the primary germ-layers probably became ova and others fertilising sperm. We base these hypotheses on the fact that we do to-day find the simplest form of sexual reproduction in some of the living gastræads and other lower animals, especially the sponges.

The fact that there are still in existence various kinds of gastræads, or lower metazoa with an organisation little higher than that of the hypothetical gastræa, is a strong point in favour of our theory. There are not very many species of these living gastræads; but their morphological and phylogenetic interest is so great, and their intermediate position between the protozoa and metazoa so instructive, that I proposed long ago (1876) to make a special class of them. I distinguished three orders in this class—the gastremaria, physemaria, and cyemaria (or dicyemida). But we might also regard these three orders as so many independent classes in a primitive gastræad stem, as I showed in the second volume of the *Systematic Phylogeny* (pp. 43–48) and the tenth edition of the *History of Creation*.

The gastremaria and cyemaria (mesozoa or "cup-shaped animals"), the chief of these living gastræads, are small metazoa that live parasitically inside other metazoa, and are, as a rule, one-half to one millimetre long, often much less (Fig. 287, 1–15). Their soft body, devoid of skeleton, is generally oval or cylindrical, and round in transverse section (hence uni-axial). It consists of two simple strata of cells, the primary germinal layers; the outer of these is thickly clothed with long hair-like lashes, by which the parasites swim about in the various cavities of their host. The inner germinal layer furnishes the sexual products. The pure type of the original gastrula (or *archigastrula*, Fig. 284 *I*) is seen in the *pemmatodiscus gastrulaceus*, which Monticelli discovered in the umbrella of a large medusa *(pilema pulmo)* in 1895; the convex surface of this gelatinous umbrella was covered with numbers of clear vesicles, of one to three millimetres in diameter, in the fluid contents of which the little parasites were swimming. The cup-shaped body of the *pemmatodiscus* (Fig. 287, 1) is sometimes rather flat, and shaped like a hat or cone, at other times almost curved into a semi-circle. The simple hollow of the cup, the primitive gut *(g)*, has a narrow opening *(o)*. The cutaneous layer *(e)* consists of long slender cylindrical cells, which bear long vibratory hairs; it is separated by a thin structureless, gelatinous plate *(f)* from the visceral layer *(i)*, the prismatic

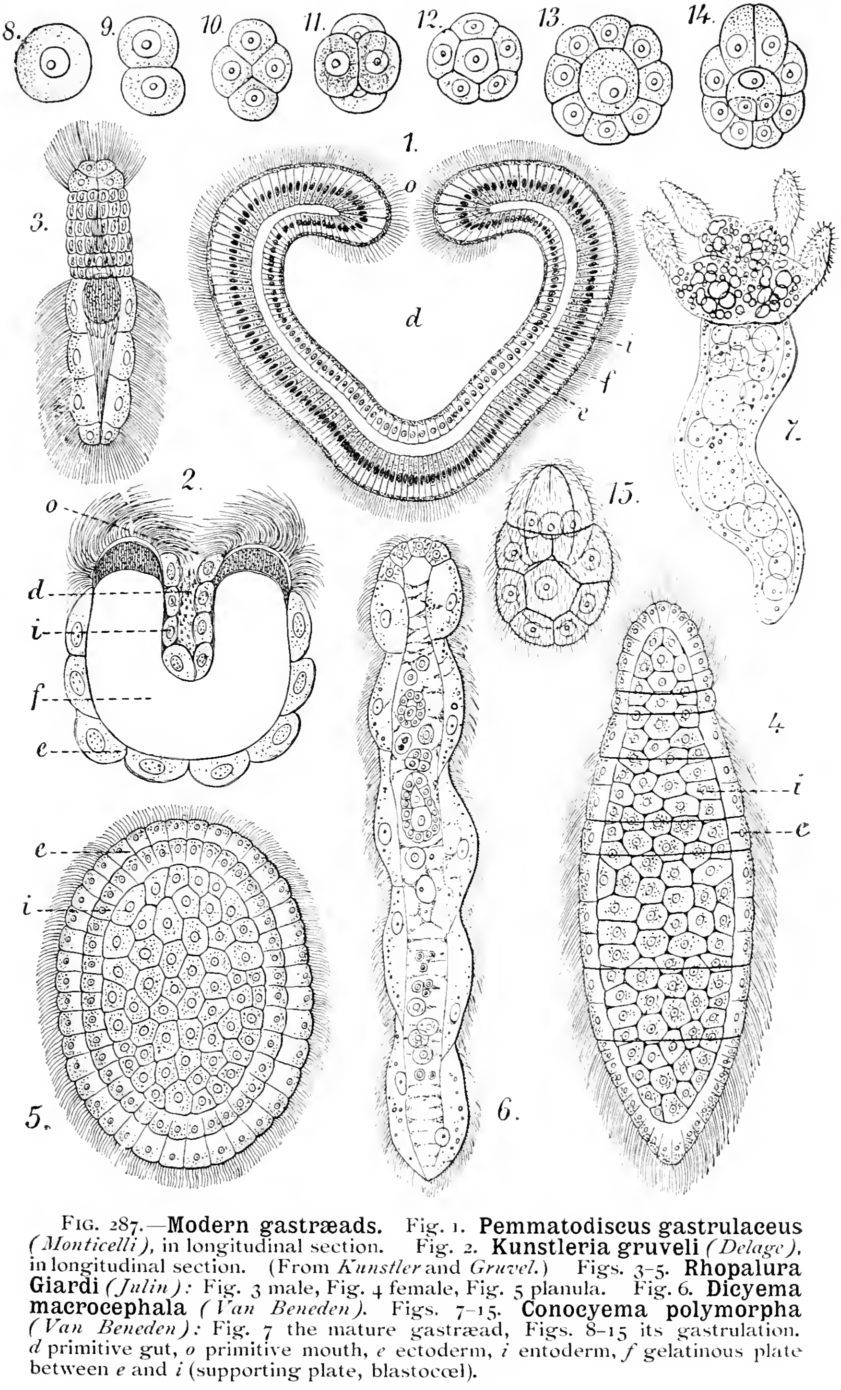

FIG. 287.—**Modern gastræads.** Fig. 1. **Pemmatodiscus gastrulaceus** *(Monticelli)*, in longitudinal section. Fig. 2. **Kunstleria gruveli** *(Delage)*, in longitudinal section. (From *Kunstler* and *Gruvel.*) Figs. 3–5. **Rhopalura Giardi** *(Julin)*: Fig. 3 male, Fig. 4 female, Fig. 5 planula. Fig. 6. **Dicyema macrocephala** *(Van Beneden)*. Figs. 7–15. **Conocyema polymorpha** *(Van Beneden)*: Fig. 7 the mature gastræad, Figs. 8–15 its gastrulation. *d* primitive gut, *o* primitive mouth, *e* ectoderm, *i* entoderm, *f* gelatinous plate between *e* and *i* (supporting plate, blastocœl).

cells of which are much smaller and have no cilia. *Pemmatodiscus* propagates asexually, by simple longitudinal cleavage; on this account it has recently been regarded as the representative of a special order of gastræads *(mesogastria)*.

Probably a near relative of the *pemmatodiscus* is the *Kunstleria Gruveli* (Fig. 287, 2). It lives in the body-cavity of vermalia (sipunculida), and differs from the former in having no lashes either on the large ectodermic cells *(e)* or the small entodermic *(i)*; the germinal layers are separated by a thick, cup-shaped, gelatinous mass, which has been called the "clear vesicle" *(f)*. The primitive mouth is surrounded by a dark ring that bears very strong and long vibratory lashes and effects the swimming movements (with the aboral pole). This ciliated ring seems to consist of a single large circular cell (with a nucleus); but it is probably composed of a number of ciliated cells, directed radially towards the centre of the primitive mouth. The entodermic cells are converted into sexual cells.

Pemmatodiscus and *Kunstleria* may be included in the family of the gastremaria. To these gastræads with open gut are closely related the orthonectida *(rhopalura*, Fig. 287, 3–5). They live parasitically in the body-cavity of echinoderms (ophiura) and vermalia; they are distinguished by the fact that their primitive gut-cavity is not empty, but filled with entodermic cells, from which the sexual cells are developed. These gastræads are of both sexes, the male (Fig. 3) being smaller and of a somewhat different shape from the oval female (Fig. 4). From the impregnated ovum a small gastrula is evolved by unequal segmentation, and the ectodermic cells of this afterwards grow into fine muscular fibres; these run the length of the body, and effect its contractions.

The somewhat similar *dicyemida* (Figs. 4–10) are distinguished from the preceding by the fact that their primitive gut-cavity is occupied by a single large entodermic cell instead of a crowded group of sexual cells. This cell does not yield sexual products, but afterwards divides into a number of cells (spores), each of which, without being impregnated, grows into a small embryo. The dicyemida live parasitically in the body-cavity, especially the renal cavities, of the cuttle-fishes. They fall in several genera, some of which are characterised by the possession of special polar cells; the body is sometimes roundish, oval, or club-shaped, at other times long and cylindrical. The genus *conocyema* (Figs. 5–17) differs from the ordinary *dicyema* in having four polar pimples in the form of a cross, which may be incipient tentacles.

The classification of the cyemaria is much disputed; sometimes they are held to be parasitic infusoria (like the *opalina*), sometimes platodes or vermalia, related to the suctorial worms or rotifers, but having degenerated through parasitism. There is only one fact in support of this idea. The resemblance to the ciliated larvæ of the trematodes to which I referred merely proves that the latter also pass through the gastrula-stage. I adhere to the phylogenetically important theory that I advanced in 1876, that we have here real gastræads, primitive survivors of the common stem-group of all the metazoa. In the struggle for life they have found shelter in the body-cavity of other animals. The gastremaria are the older and quite primitive gastræads (*pemmatodiscus* and *kunstleria*); from these the younger cyemaria (*rhopalura* and *dicyema*) were formed by the atrophy of the gut-cavity; they are related to the former like the gut-less tape-worms (*cestodes*) to the suctorial worms (*trematodes*). It is probable that the discoid trichoplacida (*trichoplax* and *treptoplax*) are directly descended from the gastremaria, possibly by forming the habit of opening their primitive mouth so wide that the primitive gut-cavity disappeared: the lower, ciliated epithelial layer of their thin round disk is the entoderm; the upper, non-ciliated is the ectoderm. These flat gastræads have the same relation to *pemmatodiscus* as a flat *discogastrula* to the cup-shaped *archigastrula*.

The small cœlenteria attached to the floor of the sea that I have called the physemaria (*haliphysema* and *gastrophysema*) probably form a third order (or class) of the living gastræads. The genus *haliphysema* (Figs. 288, 289) is externally very similar to a large rhizopod (described by the same name in 1862) of the family of the *rhabdamminida*, which was at first taken for a sponge. In order to avoid confusion with these, I afterwards gave them the name of *prophysema*. The whole mature body of the *prophysema* is a simple cylindrical or oval tube, with a two-layered wall. The hollow of the tube is the gastric cavity, and the upper opening of it the mouth (Fig. 289 *m*). The two strata of cells that form the wall of the tube are the primary germinal layers. These rudimentary zoophytes differ from the swimming gastræads chiefly in being attached at one end (the end opposite to the mouth) to the floor of the sea. Further, the cells of the cutaneous layer have coalesced, and

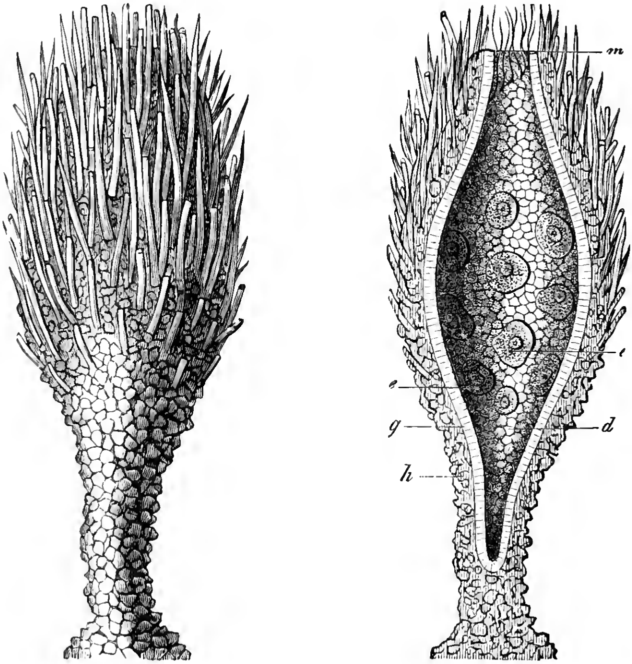

FIG. 288. FIG. 289.

FIGS. 288 and 289.—**Prophysema primordiale, a living gastræad.** Fig. 288. The whole of the spindle-shaped animal (attached below to the floor of the sea). Fig. 289. The same in longitudinal section. The primitive gut (*d*) opens above at the primitive mouth (*m*). Between the ciliated cells (*g*) are the amœboid ova (*e*). The skin-layer (*h*) is encrusted with grains of sand below and sponge-needles above.

it has taken on a quantity of foreign bodies—sponge-needles, grains of sand, etc.—to give additional strength to the body wall (Fig. 288). On the other hand, the visceral layer consists of one stratum of ciliated cells (Fig. 289 *d*). When these physemaria are sexually mature, some of their entodermic cells become ova and others sperm-cells; the former are fertilised by the latter inside the gastric cavity.

In prophysema the primitive gut is a simple oval cavity, but in the closely related *gastrophysema* it is divided into two chambers by a transverse constriction; the hind and smaller chamber above furnishes the sexual products, the anterior one being for digestion. A real palingenetic gastrula is developed from the impregnated ovum (just as in the *monoxenia*, Fig. 284). This swims about in the sea for some time, then attaches itself, and henceforth resembles the simple earlier form that we find in the evolutionary cycle of other zoophytes, the *ascula* (Figs. 290, 291). When its ectoderm covers itself with foreign bodies we get *prophysema*.[1]

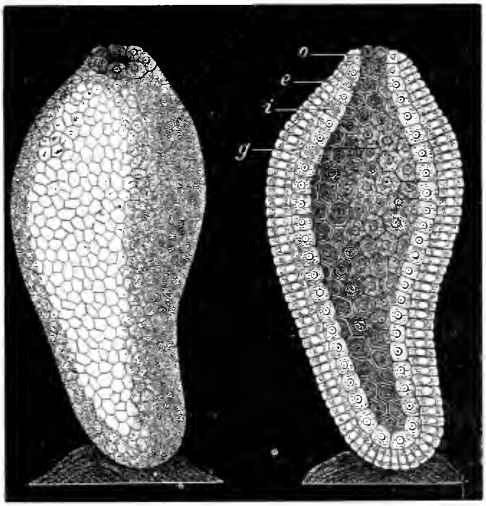

FIG. 290. FIG. 291.

FIGS. 290–291.—**Ascula of gastrophysema**, attached to the floor of the sea. Fig. 290 external view, 291 longitudinal section. *g* primitive gut, *o* primitive mouth, *i* visceral layer, *e* cutaneous layer. (Diagram.)

The simplest sponges (olynthus, Fig. 292) have the same organisation as the physemaria. The only material difference between them is that in the sponge the thin two-layered body-wall is pierced by numbers of pores. When these are closed they resemble the physemaria. Possibly the gastræads that

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[1] See my *Report on the deep-sea kerasota of H.M.S. Challenger*, pp. 26, 88; Plate VIII.

we call physemaria are only olynthi with the pores closed. The *ammoconida,* or the simple tubular sand-sponges of the deep-sea (*ammolynthus*, etc.), do not differ from the gastræads in any important point when the pores are closed. In my monograph on the sponges (with sixty plates) I endeavoured to prove analytically that all the species of this class can be traced phylogenetically to a common stem-form *(calcolynthus).*

The lowest form of the cnidaria is also not far removed from the gastræads. In the interesting common fresh-water polyp *(hydra)* the whole body is simply an oval tube with a double wall; only in this case the mouth has a crown of tentacles. Before these develop the hydra resembles an ascula (Figs. 290, 291). Afterwards there are slight histological differentiations in its ectoderm, though the entoderm remains a single stratum of cells. We find the first differentiation of epithelial and stinging cells, or of muscular and neural cells, in the thick ectoderm of the hydra.

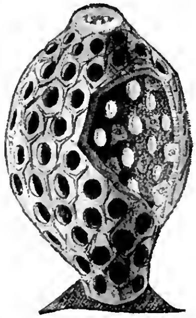


FIG. 292.—**Olynthus**, a very rudimentary sponge. A piece cut away in front.

Finally, we must draw special attention to the fact that the structure of the lowest platodes is also very little higher than that of the modern gastræads. The simplest and oldest forms of the platodes are the platodaria, or *acœlous* (more correctly, *cryptocœlous)*, coiled worms ; we have learned a good deal about these lately from the excellent monograph of Ludwig von Graff. These cryptocœla *(convoluta*, *aphanostomum*, etc.) have, it is true, the bilateral form of the real *turbellaria*, but morphologically they are nearer to the gastræads.

In all these rudimentary living cœlenteria the sexual cells of both kinds—ova and sperm-cells—are formed by the same individual ; it is possible that the oldest gastræads were hermaphroditic. It is clear from comparative anatomy that hermaphrodism—the combination of both kinds of sexual cells in one individual—is the earliest form of sexual differentiation ; the separation of the sexes (gonochorism) was a much later phenomenon. The gonidia or sexual cells originally proceeded from the edge of the primitive mouth of the gastræad.

CHAPTER XX.

OUR WORM-LIKE ANCESTORS

Development of the chordæa from the gastræa. Polyphyletic origin of the articulates from the non-articulates. Complete difference of the vertebration of the vertebrates and the articulation of the articulates. Untenability of the annelid-hypothesis (descent of the vertebrates from the articulates). Establishment of the chordonia-hypothesis (descent of the vertebrates and tunicates from prochordonia, like the chordula). Earlier ancestors of the chordonia of the group of the cœlenteria and vermalia. Uni-axial and tri-axial gastræads. Bilateral type of the latter. Platode-ancestors: Primitive worms (platodaria), coiled worms (turbellaria). Ventral displacement of their mouth. Primitive gut. Gonades. Primitive kidneys. Vermalia-ancestors (unsegmented worms). Gastrotricha (ichthydina) with anus. Constricted worms with blood and blood-vessels. Enteropneusta (balanoglossus) with branchial gut, gill-clefts, and gullet groove. Their distant relationship to the chordonia. Chordæa theory. Great palingenetic value of the chordula. Human progonotaxis (thirty ancestral stages).

THE gastræa theory has now convinced us that all the metazoa or multicellular animals can be traced to a common stem-form, the gastræa. In accordance with the biogenetic law, we find solid proof of this in the fact that the two-layered embryos of all the metazoa can be reduced to a primitive common type, the gastrula. Just as the countless species of the metazoa do actually develop cenogenetically from the simple embryonic form of the gastrula, so they have all descended phylogenetically from the common stem-form of the gastræa. In this fact, and the fact we have already established that the gastræa has been evolved from the hollow vesicle of the one-layered blastæa, and this again from the original unicellular stem-form, we have obtained a solid basis for our phylogenetic study. The clear path from the stem-cell to the gastrula—the history of gastrulation—represents the first section of our human stem-history (Chapters VIII., IX., and XIX.).

The second section, that leads from the gastræa to the prochordonia, is much more difficult and obscure. By the prochordonia we mean the ancient and long-extinct metazoa which the important embryonic form of the chordula proves to have once existed (cf. Figs. 86–89). This chordula, or primitive embryo of the chordonia, has a bilateral or bilateral-symmetrical body of a very simple unarticulated character; in the long axis of the body there is, as axial skeleton, a simple chorda between the dorsal nerve-tube and the ventral gut-tube; at each side of this single central organ are the two cœlom-pouches, originally sexual glands, that develop from the primitive mouth. The nearest of living animals to this embryonic structure are the lowest tunicates, the copelata *(appendicaria)* and the larvæ of the ascidia. As both the unarticulated tunicates and the articulated vertebrates develop ontogenetically from the same chordula, we may infer that there was a corresponding common ancestor of both stems. We may call this the *chordæa*, and the corresponding stem-group the *prochordonia* or *prochordata*.

From this important stem-group of the unarticulated prochordonia (or "primitive chorda-animals") the stems of the tunicates and vertebrates have been divergently evolved. We shall see presently how this conclusion is justified in the present condition of morphological science.

We have first to answer the difficult and much-discussed question of the development of the chordæa from the gastræa; in other words, "How and by what transformations were the characteristic animals, resembling the embryonic chordula, which we regard as the common stem-forms of all the chordonia, both tunicates and vertebrates, evolved from the simplest two-layered metazoa?" Before we attempt to answer this important question—one of the most obscure in the whole of anthropogeny—it will be useful to lay down a few guiding principles.

I. *All articulated animals have been evolved originally from unarticulated.* In other words: All animals whose body consists of a series of somites or metamera (vertebrates, articulates, cestodes) have descended from lower and simpler metazoa, whose whole body is only equal morphologically to a single one of these somites or metamera. This thesis will not be questioned now by any zoologist; it applies equally to ontogeny and phylogeny.

II. *The metamerism of the metazoa is a polyphyletic process;* the segmental articulation, or the repetition of homogeneous parts (somites) in the long axis of the animal, has taken place several times, independently of each other, in the course of organic history. Instances of this independent articulation in various stems are: (1) The vertebration of the vertebrates; (2) the articulation of the articulates; (3) the annulation of the echinoderms; (4) the strobilation of the tape-worms; (5) the strobilation of the scyphostoma or cup-shaped polypus (nurses of the acraspedous medusæ); (6) the stalk-articulation of the phanerogams. All these processes of articulation have the same form and the same result—namely, the multiplication of parts of the body (somites or metamera) and the arrangement of them along the long axis of the organism; but both the morphological processes and their physiological causes are, at bottom, very different; and the "general homology" of these somites, their *homodynamism*, has different values.

III. *The articulation of the vertebrates is first seen in the chordula*, the important embryonic structure that has a dorsal nerve-tube, a ventral gut-tube, and an axial chorda between the two—three unarticulated fundamental organs of the greatest morphological significance (Figs. 86–89, p. 229). As the same unarticulated chordula is found also in the embryonic development of tunicates, and as the body of these remains permanently unarticulated, we must ascribe a very great palingenetic importance to it. We are justified in concluding that there was a similar unarticulated stem-form *(chordæa)*, the common ancestor of both the chordonia-stems, the vertebrates and tunicates. This is gathered especially from the fact that the endoblastic chorda and the overlying ectoblastic neural tube appear at a very early stage in the embryonic development of all the vertebrates and tunicates, always originate in the same way from the primary germinal layers, and nowhere show any trace of articulation. The latter starts from the cœlom-pouches, the episomites (myotomes) of which develop into muscular plates, and the hyposomites (gonotomes) into sexual glands.

IV. *The articulation of the articulates is, therefore, a totally different thing from the vertebration of the vertebrates*, in spite of a certain superficial resemblance. The one affects, in the first place, the skin and the ventral nerve-tube of an animal that never at any time shows a trace of a chorda—apart from the fact that there are also great differences between the structure of the articulates and vertebrates. I pointed this out in the fourteenth Chapter. Hence we can neither suppose that the vertebrates have descended from the articulates, nor *vice versa*. The two stems have been evolved independently from different stem-forms, just as to-day they have totally different embryonic structures. The presence of the *chordula* in all the vertebrates is just as characteristic of them as its absence is of all the articulates.

The descent of the vertebrates from the articulates has been maintained by a number of zoologists during the last thirty years with more zeal than discernment; and, as a vast amount has been written on the subject, we must deal with it to some extent. All three classes of articulates in succession have been awarded the honour of being considered the "real ancestors" of the vertebrates: first, the ringed-worms or annelids (rain-worms, leeches, and the like), then the crustacea (crabs, etc.), and, finally, the tracheata (spiders, insects, etc.). The most popular of these hypotheses was the annelid theory, which derived the vertebrates from the worms. It was almost simultaneously (1875) formulated by Carl Semper, of Würtzburg, and Anton Dohrn, of Naples. The latter advanced this theory originally in favour of the failing degeneration theory, with which I dealt in my work, *Aims and Methods of Modern Embryology*.

This interesting degeneration theory—much discussed at that time, but almost forgotten now—was formed in 1875 with the aim of harmonising the results of evolution and ever-advancing Darwinism with religious belief and anthropocentric views. The spirited struggle that Darwin had occasioned by the reformation of the theory of descent in 1859, and that lasted for a decade with varying fortunes in every branch of biology, was drawing to a close in 1870–1872, and soon ended in the complete victory of transformism. To most of the disputants the chief point was not the general question of evolution, but the particular one of "man's place in nature"—"the question of questions," as Huxley rightly called it. It was soon evident to every clear-headed thinker that this question could only be answered in the sense of our anthropogeny, by admitting that man had descended from a long series of vertebrates by gradual modification and improvement.

In this way the real affinity of man and the vertebrates came to be admitted on all hands. Comparative anatomy and ontogeny spoke too clearly for their testimony to be ignored any longer. But in order still to save man's anthropocentric position, and especially the dogma of personal immortality, a number of natural philosophers and theologians discovered an admirable way of escape in the "theory of degeneration." Granting the affinity, they turned the whole evolutionary theory upside down, and boldly contended that "man is not the most highly developed animal, but the animals are degenerate men." It is true that man is closely related to the ape, and belongs to the vertebrate stem; but the chain of his ancestry goes upward instead of downward. In the beginning "God created man in his own image," as the prototype of the perfect vertebrate; but, in consequence of original sin, the human race sank so low that the apes branched off from it, and afterwards the lower vertebrates. When this theory of degeneration was consistently developed, its supporters were bound to hold that the entire animal kingdom was descended from the debased children of men.

This theory was most strenuously defended by the Catholic priest and natural philosopher, Michelis, in his *Hæckelogony: An Academic Protest Against Hæckel's Anthropogeny* (1875). In still more "academic" and somewhat mystic form the theory was advanced by a natural philosopher of the older Jena school—the mathematician and physicist, Carl Snell. But it received its chief support on the zoological side from Anton Dohrn, who maintained the anthropocentric ideas of Snell with particular ability. The amphioxus, which modern morphology now almost unanimously regards as the real primitive vertebrate, the ancient model of the original vertebrate structure, is, according to Dohrn, a late, degenerate descendant of the stem, the "prodigal son" of the vertebrate family. It has descended from the cyclostoma by a profound degeneration, and these in turn from the fishes; even the ascidia and the whole of the tunicates are merely degenerate fishes! Following out this curious theory, Dohrn came to contest the general belief that the cœlenterata and worms are "lower animals"; he even declared that the unicellular protozoa were degenerate cœlenterata. In his opinion "degeneration is the great *principium movens* that explains the existence of all the lower forms."

If this Michelis-Dohrn theory were true, and all animals were really degenerate descendants of an originally perfect humanity, man would assuredly be the true centre and goal of all terrestrial life; his anthropocentric position and his immortality would be saved. Unfortunately this trustful theory is in such flagrant contradiction to all the known facts of paleontology and ontogeny that it is no longer worth serious scientific consideration.

But the case is no better for the much-discussed descent of the vertebrates from the annelids, which Dohrn afterwards maintained with great zeal. Carl Semper also endeavoured to support this theory, and made a singular display of dogmatism and logical weakness. At the bottom it is merely a re-hash and phylogenetic setting of the notion of the older natural philosophers, that insects are vertebrates running on their backs, and that the spinal marrow of the latter corresponds to the ventral marrow of the former. The first modern comparative anatomist immediately showed how absurd and unscientific this comparison was. In the masterly essay on "The Position and Importance of Morphology," with which Carl Gegenbaur opened the first volume of his *Morphological Annual* in 1876, he describes this hypothesis as a "singular example of unscientific comparison," and very rightly says of it: "It ignores the chief points, and holds merely general considerations, that have no essential bearing on the particular case, to be conclusive. An unscientific parallel of this kind wanders about in a labyrinth, following one wrong path after another."

Of late years this annelid-hypothesis, which raised so much dust and controversy in morphology, has been entirely abandoned by most competent zoologists, even those who once supported it. The invaluable information that Hatschek, Boveri, and others, have given us of the morphology of the amphioxus, and the discovery of its close relations to the selachii-embryos (Rückert), have cut the ground from under it. Even its chief supporter, Dohrn, admitted in 1890 that it is "dead and buried," and made a blushing retractation at the end of his *Studies of the Early History of the Vertebrate.*

Now that the annelid-hypothesis is "dead and buried," and other attempts to derive the vertebrates from medusæ, echinoderms, or molluscs, have been equally unsuccessful, there is only one hypothesis left to answer the question of the origin of the vertebrates—the hypothesis that I advanced thirty-six years ago and called the "chordonia-hypothesis." In view of its sound morphological establishment and its profound significance it may very well claim to be a natural phylogenetic *theory*, and so should be described as the chordonia or chordæa theory.

I first advanced this theory in a series of university lectures in 1867, from which the *History of Creation* was composed. In the first edition of this work (1868) I endeavoured to prove, on the strength of Kowalevsky's epoch-making discoveries, that "of all the animals known to us the tunicates are undoubtedly the nearest blood-relatives of the vertebrates; they are the most closely related to the worms, from which the vertebrates have been evolved. Naturally, I do not mean that the vertebrates have descended from the tunicates, but that the two groups have sprung from a common root. It is clear that the real vertebrates (primarily the acrania) were evolved in the primordial epoch from a group of worms, from which the degenerate tunicates also descended in another and retrogressive direction." This common extinct stem-group are the prochordonia; we still have an ontogenetic silhouette of them in the chordula-embryo of the vertebrates and tunicates; and they still exist independently, in very modified form, in the class of the copelata (appendicaria, Fig. 276).

The chordæa theory received the most valuable and competent support from Carl Gegenbaur. This able comparative morphologist defended it in 1870, in the second edition of his *Elements of Comparative Anatomy;* at the same time he drew attention to the important morphological relations of the tunicates to a curious worm, *balanoglossus;* he rightly regards this as the representative of a special class of worms, which he called "gut-breathers" *(enteropneusta).* Gegenbaur referred on many other occasions to the close blood-relationship of the tunicates and vertebrates, and luminously explained the reasons that justify us in framing the phylogenetic hypothesis of the descent of the two stems from a common ancestor, an unarticulated worm-like animal with an axial chorda between the dorsal nerve-tube and the ventral gut-tube.

The theory afterwards received a good deal of support from the ontogenetic and morphological research of a number of distinguished zoologists and anatomists, especially C. Kupffer, B. Hatschek, F. Balfour, E. Van Beneden, and Julin. Since Hatschek's *Studies of the Development of the Amphioxus* gave us full information as to the embryology of this lowest vertebrate, it has become so important for the purposes of our anthropogeny that we must consider it a phylogenetic document of the first rank for answering the question we are dealing with.

The ontogenetic facts that we gather from this sole survivor of the acrania are the more valuable for phylogenetic purposes, as paleontology, unfortunately, throws no light whatever on the origin of the vertebrates. Their invertebrate ancestors were soft organisms without skeleton, and thus incapable of fossilisation, as is still the case with the lowest vertebrates—the acrania and cyclostoma. The same applies to the greater part of the worms or worm-like animals, the vast group of the vermalia or helmintha, the various classes and orders of which differ so much in structure. The isolated groups of this rich stem are living branches of a huge tree, the greater part of which has long been dead, and we have no fossil evidence as to its earlier form. Nevertheless, some of the surviving groups are very instructive phylogenetically, and give us clear indications of the way in which the chordonia were developed from the vermalia, and these from the cœlenteria.

When we seek the most important of these palingenetic forms among the groups of cœlenteria and vermalia, it is understood that not a single one of them must be regarded as an unchanged, or even little changed, copy of the extinct stem-form. One group has retained one feature, another a different feature, of the original organisation, and other organs have been further developed and characteristically modified. Hence here, more than in any other part of our genealogical tree, we have to keep before our mind the *full picture* of development, and separate the unessential secondary phenomena from the essential and primary. It will be useful first to point out the chief advances in organisation by which the simple gastræa gradually became the more developed chordæa.

We find our first solid datum in the bilateral gastrula of the amphioxus (Fig. 260). Its bilateral and tri-axial type indicates that the gastræads—the common ancestors of all the metazoa—divided at an early stage into two divergent groups. The uni-axial gastræa (the original oval type with round transverse section) became sessile, and gave rise to two stems, the sponges and the cnidaria (the latter all reducible to simple polyps like the hydra). But the tri-axial gastræa (the derivative bilateral type, with oval transverse section) assumed a certain pose or direction of the body on account of its swimming or creeping movement, and in order to sustain this it was a great advantage to share the burden equally between the two halves of the body (right and left). Thus arose the typical bilateral form, which is determined by three axes: (1) The chief or long axis (with oral and aboral pole); (2) the sagittal or dorso-ventral axis (with dorsal and ventral poles); (3) the transverse or frontal axis (with right and left pole). The two former are unequipolar, the third equipolar. The same bilateral type is found in all our artificial means of locomotion—carts, ships, etc.; it is by far the best for the movement of the body in a certain direction and steady position. Hence natural selection early developed this bilateral type in a section of the gastræads, and thus produced the stem-forms of all the bilateral animals.

The *gastræa bilateralis*, of which we may conceive the bilateral gastrula of the amphioxus to be a palingenetic reproduction, represented the two-sided organism of the earliest metazoa in its simplest form. The vegetal entoderm that lined their simple gut-cavity served for nutrition; the ciliated ectoderm that formed the external skin attended to locomotion and sensation; finally, the two primitive mesodermic cells, that lay to the right and left at the ventral border of the primitive mouth, were gonidia or sexual cells and effected reproduction. In order to understand the further development of the gastræa we must pay particular attention to: (1) the careful study of the embryonic stages of the amphioxus that lie between the gastrula and the chordula; (2) the morphological study of the simplest platodes *(platodaria* and *turbellaria)* and several groups of unarticulated vermalia *(gastrotricha*, *nemertina*, *enteropneusta)*.

We have to consider the platodes first because they are on the border between the two principal groups of the metazoa, the cœlenteria and the cœlomaria (cf. the genealogical tree on p. 538). With the former they share the lack of body-cavity, anus, and vascular system; with the latter they have in common the bilateral type, the possession of a pair of nephridia or renal canals, and the formation of a vertical brain or cerebral ganglion. It is now usual to distinguish four classes of platodes: the two free-living classes of the primitive worms *(platodaria)* and the coiled-worms *(turbellaria)*, and the two parasitic classes of the suctorial worms *(trematoda)* and the tape-worms *(cestoda)*. We have only to consider the first two of these classes; the other two are parasites, and have descended from the former by adaptation to parasitic habits and consequent degeneration.

The primitive worms *(platodaria)* are very small platodes of simple construction, but of great morphological and phylogenetic interest. They were hitherto, as a rule, regarded as a special order of the coiled-worms, and associated with the *rhabdocœla;* but they differ considerably from these and all the other platodes in the absence of renal canals *(nephridia)* and a special central nervous system; the structure of their tissue is also simpler than in the other platodes. Most of the platodes of this group *(aphanostomum, amphichœrus, convoluta, schizoprora*, etc.) are very soft and delicate animals, swimming about in the sea by means of a ciliary coat, and very small (a few millimetres long). Their oval body, without appendages, is sometimes spindle-shaped or cylindrical, sometimes flat and leaf-shaped. Their skin is merely a layer of ciliated ectodermic cells. Under this is a soft medullary substance, called the "digestive parenchyma," which consists of entodermic cells with vacuoles. The food passes through the anterior or median mouth directly into this digestive medullary substance, in which we do not generally see any permanent gut-cavity (it may have entirely collapsed); hence these primitive platodes have been called *acœla* (without gut-cavity or cœlom), or, more correctly, *crytocœla*, or *pseudocœla*. The sexual organs of these hermaphroditic platodaria are very simple—two pairs of strings of cells, the inner of which (the ovaries, Fig. 293 *o*) produce ova, and the outer (the spermaria, *s*) sperm-cells. These gonades are not yet independent sexual glands, but sexually differentiated cell-groups in the medullary substance, or, in other words, parts of the parenchymatose gut-wall. Their products, the sex-cells, are conveyed out behind by two pairs of short canals; the male opening *(m)* lies just behind the female *(f)*. Most of the platodaria have not the muscular pharynx, which is very advanced in the *turbellaria* and *trematoda*. On the other hand, they have, as a rule, before or behind the mouth, a vesicular sense-organ (auditory vesicle or organ of equilibrium, *g*), and many of them have also a couple of simple optic spots. The cell-pit of the ectoderm that lies underneath is rather thick, and (as epidermic "vertical plate") represents the first rudiment of a neural ganglion (vertical brain or acroganglion).

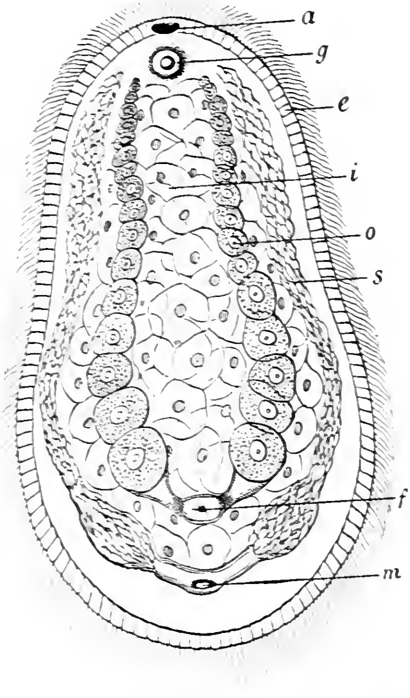


Fig. 293.—**Aphanostomum Langii** *(Haeckel)*, a primitive worm of the platodaria class, of the order of *cryptocoela* or *acoela*. This new species of the genus *aphanostomum*, named after Professor Arnold Lang of Zürich, was found in September, 1899, at Ajaccio in Corsica (creeping between fucoidea). It is two mm. long, one mm. broad, and violet in colour. *a* mouth, *g* auditory vesicle (statocyst), *e* ectoderm, *i* entoderm ("digestive parenchyma"), *o* ovaries, *s* spermaries, *f* female aperture, *m* male aperture.

The coil-worms *(turbellaria)*, with which the similar *platodaria* were formerly classed, differ materially from them in the more advanced structure of their organs, and especially in having a central nervous system (vertical brain) and excretory renal canals (nephridia); both originate from the ectoderm. But between the two germinal layers a parenchymatose mesoderm is developed, a soft mass of connective tissue, in which the organs are embedded. The *turbellaria* are still represented by a number of different forms, in both fresh and sea-water. The oldest of these are the very rudimentary and tiny forms that are known as "rod-gut animals" *(rhabdocœla)* on account of the simple construction of their gut; they are, as a rule, only a few millimetres long, and of a simple oval or lancet shape (Fig. 294). The surface is covered with ciliated epithelium, a stratum of ectodermic cells. The digestive gut is still the simple primitive gut of the gastræa *(d)*, with a single aperture that is both mouth and anus *(m)*. There is, however, an invagination of the ectoderm at the mouth, which has given rise to a muscular pharynx *(sd)*. It is noteworthy that the mouth of the turbellaria (like the primitive mouth of the gastræa) may, in this class, change its position considerably in the middle line of the ventral surface: sometimes it lies behind *(opisthostomum)*, sometimes in the middle *(mesostomum)*, sometimes in front *(prosostomum)*. This ventral displacement of the mouth from front to rear is very interesting, because it corresponds to a phylogenetic displacement of the mouth. This probably occurred in the platode ancestors of most (or all?) of the cœlomaria: in these the permanent mouth *(metastoma)* lies at the fore end (oral pole), whereas the primitive mouth *(prostoma)* lay at the hind end of the bilateral body.

In most of the turbellaria there is a narrow cavity, containing a number of secondary organs, between the two primary germinal layers, the outer or animal layer of which forms the epidermis and the inner vegetal layer the visceral epithelium. This is the remainder of the embryonic cavity (*blastocœl*, p. 152), or the "primary body-cavity": it must not be confused with the real or "secondary body-cavity" (*enterocœl*), which we find in most of the cœlomaria, but not in the platodes.

The earliest of these organs are the sexual organs: they are very variously constructed in the platode-class: in the simplest case there are merely two pairs of gonades or sexual glands—a pair of testicles (Fig. 295 *h*) and a pair of ovaries *(e)*. They open externally, sometimes by a common median aperture (*monogonopora*), sometimes by separate ones, the female behind the male (*digonopora*, Fig. 295). The sexual glands develop originally from the two promesoblasts or primitive mesodermic cells (Fig. 261 *p*). As these earliest mesodermic structures extended, and became spacious sexual pouches in the later descendants of the platodes, probably the two cœlom-pouches were formed from them, the first trace of the real body-cavity of the higher metazoa (*enterocœla*).

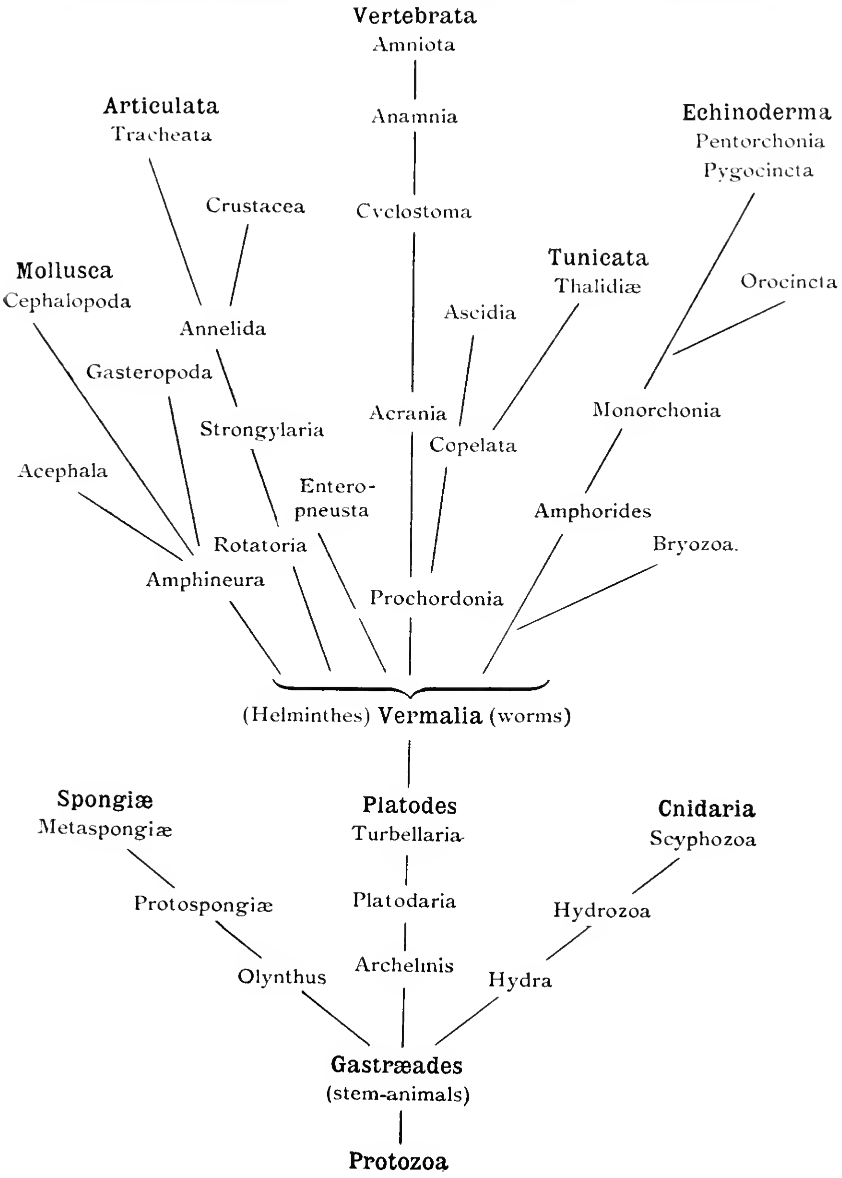
TWENTY-FOURTH TABLE

PHYLOGENETIC CLASSIFICATION OF THE ANIMAL KINGDOM, BASED ON THE GASTRÆA THEORY

Sub-kingdoms.	Princip Groups.	Stems.	Chief Classes.
I. **Protozoa** ("first animals"). Without primitive gut, germinal layers or tissues.	I. **Protozoa.** Unicellular animals (sometimes multicellular cenobia).	1. **Rhizopoda** ("root-animals").	1. Monera. 2. Amœbina. 3. Thalamophora. 4. Radiolaria.
		2. **Infusoria** (ciliated animals).	1. Flagellata. 2. Ciliata.
II. **Metazoa** (tissue-animals). With primitive gut, germinal layers and tissues. —— Multicellular animals with segmentation and *gastrulation*. Primary embryonic forms: *blastula* (one-layered) and *gastrula* (two-layered). —— The blastæads, on the frontier of the protozoa and metazoa (hollow vesicles with blastodermic membrane), have no primitive gut.	IIa. **Cœlenteria.** Zoophytes or **Cœlenterata.** —— Without body-cavity, blood, or anus.	3. **Gastræads.**	1. Gastremaria. 2. Cyemaria.
		4. **Sponges.**	1. Protospongiæ. 2. Metaspongiæ.
		5. **Cnidaria** ("stinging-animals").	1. Hydrozoa. 2. Scyphozoa.
		6. **Platodes** ("flat-animals").	1. Platodaria. 2. Turbellaria. 3. Trematoda. 4. Cestoda.
	IIb. **Cœlomaria** or **Bilaterata.** —— With body-cavity, generally with blood and anus.	7. **Vermalia** ("worm-animals").	1. Rotatoria. 2. Strongylaria. 3. Prosopygia. 4. Frontonia.
		8. **Mollusca** ("soft-animals").	1. Cochlides. 2. Conchades. 3. Tenthodes.
		9. **Articulata.**	1. Annelida. 2. Crustacea. 3. Tracheata.
		10. **Echinoderma.**	1. Monorchonia. 2. Pentorchonia.
		11. **Tunicata** ("mantle-animals").	1. Copelata. 2. Ascidia. 3. Thalidia.
		12. **Vertebrata.**	1. Acrania. 2. Craniota.

TWENTY-FIFTH TABLE

MONOPHYLETIC GENEALOGICAL TREE OF THE ANIMAL KINGDOM, BASED ON THE GASTRÆA THEORY



The gonades are among the phylogenetically oldest organs, but the few other organs that we find in the platodes between the gut-wall and body-wall are later evolutionary products. One of the oldest and most important of these are the kidneys or *nephridia*, which remove unusable matter from the body (Fig. 294 *nc*). These urinary or excretory organs (also often called "water-vessels") were originally enlarged cutaneous glands — a couple of canals that run the length of the body, and have a separate or common external aperture (*nm*). They often have a number of branches. These special excretory organs are not found in the other cœlenteria (gastræads, sponges, cnidaria) or the cryptocœla. They are first met in the *turbellaria*, and have been transmitted direct from these to the *vermalia*, and from these to the higher stems. We may give the name of *protonephridia* (in contrast to the permanent *metanephridia* of the higher metazoa) to the early form of the kidneys that we find in the lowest and oldest bilaterals (platodes, rotatoria, nematodes, etc.). In the higher animals the *protonephridia* are present in the

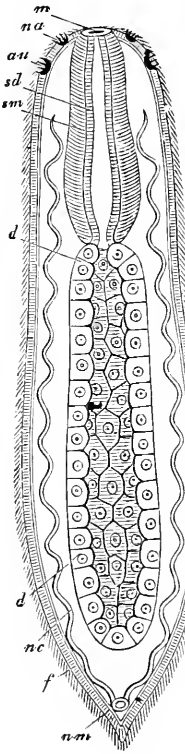


FIG. 294.

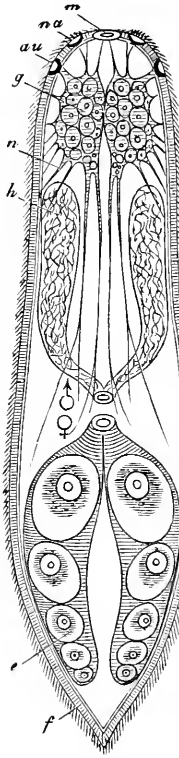


FIG. 295.

FIG. 294.—**A simple coiled-worm** (*rhabdocœlum*). *m* mouth, *sd* gullet epithelium, *sm* gullet muscles, *d* gastric gut, *nc* renal canals, *nm* renal aperture, *au* eye, *na* olfactory pit. (Diagram.)

FIG. 295.—**The same,** showing the other organs. *g* brain, *au* eye, *na* olfactory pit, *n* nerves, *h* testicles, ♂ male aperture, ♀ female aperture, *e* ovary, *f* ciliated epiderm. (Diagram.)

embryo, but are afterwards replaced by the *metanephridia* (Hatschek).

Finally, there is a very important new organ in the turbellaria, which we do not find in the *cryptocœla* (Fig. 293) and their gastræad ancestors—the rudimentary nervous system. It consists of a couple of simple cerebral ganglia (Fig. 295 *g*) and fine nervous fibres that radiate from them ; these are partly voluntary nerves (or motor fibres) that go to the thin muscular layer developing under the skin ; and partly sensory nerves that proceed to the sense-cells of the ciliated epiderm *(f)*. Many of the turbellaria have also special sense-organs ; a couple of ciliated olfactory pits *(na)*, rudimentary eyes *(au)*, and less frequently auditory vesicles. A pair of strong lateral nerves that develop in many of the platodes are interesting, because in some of their descendants these develop into the higher nervous central organs. The two cerebral ganglia *(g)* that lie forward under the dorsal skin and over the fore-gut are also very important ; this vertical brain *(acroganglion)*, originally developing as vertical plate *(acroplatea)* in the epidermis, is the ectodermic foundation of the "upper pharyngeal ganglia" that immediately develop from it and the brain of the higher animals.

On these principles I assume that the oldest and simplest turbellaria arose from platodaria, and these directly from bilateral gastræads. The chief advances were the formation of mesodermic gonades and nephridia, and of the ectodermic vertical brain. On this hypothesis, which I advanced in 1872 in the first sketch of the gastræa theory *(Monograph on the Sponges)*, there is no direct affinity between the platodes and the cnidaria ; the latter (hydrozoa and scyphozoa) were developed independently of the former from the uniaxial gastræads ; these gastræads secondarily adopted a stationary life, and assumed the radial type. In my opinion, there are no stationary or radial forms among the ancestors of the vertebrates.

Next to the ancient stem-group of the turbellaria come a number of more recent chordonia ancestors, which we class with the *vermalia* or *helminthes,* the unarticulated worms.

These true worms *(vermes*, lately also called *scolecida)* are the crux or the lumber-room of the zoological classifier, because the various classes have very complicated relations to the lower platodes on the one hand and the more advanced animals on the other. But if we exclude the platodes and the annelids from this stem, we find a fairly satisfactory unity of organisation in the remaining classes. I have in my *History of Creation* divided the vermalia stem (limited in this way) into four principal and subordinate classes. Two of these principal classes or *cladomes* do not concern us here, because, in my opinion, they contain no chordonia ancestors; they are the round-worms or *strongylaria* (nematodes, acanthocephala, chætognatha), and the arm-worms or *prosopygia* (bryozoa, brachiopoda, phoronea, sipunculea). But the other two cladomes are interesting for our purpose, the "wheel-worms" *(rotatoria)* and the "snout-worms" *(frontonia* or *rhyncocœla)*; to the former belong the ichthydina and rotifers, to the latter the nemertina and enteropneusta. Among these worms we find some important forms that show considerable advance in organisation from the platode to the chordonia stage.

Three of these phylogenetic phenomena are particularly instructive: (1) The formation of a true (secondary) body-cavity (cœloma); (2) the formation of a second aperture of the gut, the anus; and (3) the formation of a vascular system. The great majority of the vermalia have these three features, and they are all wanting in the platodes; in the rest of the worms at least one or two of them are developed.

Next and very close to the platodes we have the ichthydina *(gastrotricha)*, little marine and fresh-water worms, about 0·1–0·5 millimetres long. I associate these primitive vermalia with the rotifers proper in the chief class of the rotatoria. We may regard the gastrotricha as direct transitional forms from the turbellaria to the rotifers, as they lie mid-way between the two. Zoologists differ as to their position in classification. In my opinion, they approach very close to the rhabdocœla (Figs. 294, 295), and differ from them chiefly in the possession of an anus at the posterior end

(Fig. 296 *a*). Further, the cilia that cover the whole surface of the turbellaria are confined in the gastrotricha to two ciliated bands *(f)* on the ventral surface of the oval body, the dorsal surface having bristles. Otherwise the organisation of the two classes is the same. In both the gut consists of a muscular gullet *(s)* and a glandular primitive gut *(d)*.

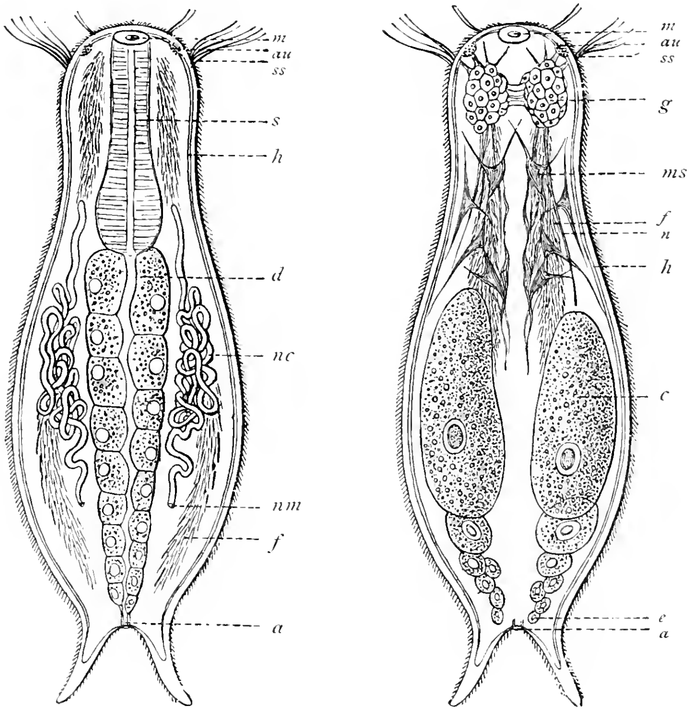


FIG. 296. FIG. 297.

FIGS. 296 and 297.—**Chætonotus, a rudimentary vermalian,** of the group of gastrotricha. *m* mouth, *s* gullet, *d* gut, *a* anus, *g* brain, *n* nerves, *ss* sensory hairs, *au* eye, *ms* muscular cells, *h* skin, *f* ciliated bands of the ventral surface, *nc* nephridia, *nm* their aperture, *e* ovaries.

Over the gullet is a double brain (acroganglion, *g*). At the side of the gut are two serpentine prorenal canals (water-vessels or pronephridia, *nc*), which open on the ventral side *(nm)*. Behind are a pair of simple sexual glands or gonades (Fig. 297 *e*). The narrow body-cavity that encloses the gut is usually regarded as a primary body-cavity (or blastocœl); but it is possible that it is formed by the extension of the two sexual pouches that grow out from the anus (or primitive mouth); in that case they would be a secondary body-cavity *(enterocœl)*.

While the ichthydina are thus closely related to the platodes, we have to go farther away for the two classes of vermalia which we unite in the cladome of the "snout-worms" *(frontonia)*. These are the *nemertina* and the *enteropneusta*. Both classes have a complete ciliary coat on the epidermis, a heritage from the turbellaria and the gastræads; also, both have two openings of the gut, the mouth and anus, like the gastrotricha. But we find also an important organ that is wanting in the preceding forms—the vascular system *(vasorium)*. In their more advanced mesoderm or middle germinal-layers we find a few contractile longitudinal canals which force the blood through the body by their contractions; these are the first blood-vessels.

The nemertina were formerly classed with the much less advanced turbellaria. But they differ essentially from them in having an anus and blood-vessels, and several other marks of higher organisation. They have generally long and narrow bodies, like a more or less flattened cord; there are, besides several small species, giant-forms with a width of five to ten millimetres and a length of several metres (even ten to fifteen). Most of them live in the sea, but some in fresh water and moist earth. In their internal structure they approach the turbellaria on the one hand and the higher vermalia (especially the enteropneusta) on the other. They have often been regarded of late as earlier stages of the higher metazoa, and directly connected with the ancestors of either the articulates or vertebrates. They were considered by Hubrecht especially to be ancestors of the vertebrates; he compares their peculiar snout to the vertebrate hypophysis, and the snout-sheath to the chorda; he also regards a couple of ciliated head-clefts as the rudiments of the gill-clefts, and a pair of strong lateral nerves as the first beginning of the medullary tube. I think these analogies of Hubrecht's are very unsafe. Nor can I attach much importance to the incipient articulation of the body, which consists in the formation of a couple of lateral gut-pouches and of sexual pouches that alternate with these, and of rudimentary transverse partitions. This imperfect metamerism seems to foreshadow the articulation of the articulates rather than the vertebration of the vertebrates. However, they have some relation to the latter in the sense that they agree in these and other respects with the following class, the enteropneusta. In any case the nemertina have a good deal of phylogenetic interest as the lowest and oldest of all animals with blood. In them we find blood-vessels for the first time, distributing real blood through the body, the important, nutritious sap that plays so great a part in the nutrition, respiration, and metabolism of all the higher animals. In the nemertina the blood is red, and the red colouring-matter is hæmoglobin, connected with elliptic discoid blood-cells, as in the vertebrates. Most of them have two or three parallel blood-canals, which run the whole length of the body, and are connected in front and behind by loops, and often by a number of ring-shaped anastomoses. The chief of these primitive blood-vessels is the one that lies above the gut in the middle line of the back (Fig. 298 *r*); it may be compared to either the dorsal vessel of the articulates or the aorta of the vertebrates. To the right and left are the two serpentine lateral vessels (Fig. 298 *l*).

After the nemertina, I take (as distant relatives) the *enteropneusta;* they may be classed together with them as *frontonia* or *rhyncocœla* (snout-worms). There is now only one genus of this class, with several species *(balanoglossus);* but it is very remarkable, and may be regarded as the last survivor of an ancient and long-extinct class of vermalia. They are related, on the one hand, to the nemertina and their immediate ancestors, the platodes, and to the lowest and oldest forms of the chordonia on the other.

The enteropneusta (Fig. 299) live in the sea sand, and are long worms of very simple shape, like the nemertina. From the latter they have inherited: (1) The bilateral type, with incomplete metamerism; (2) the ciliary coat of the soft epidermis; (3) the double rows of gastric pouches, alternating with a single or double row of gonades; (4) gonochorism, or separation of the sexes

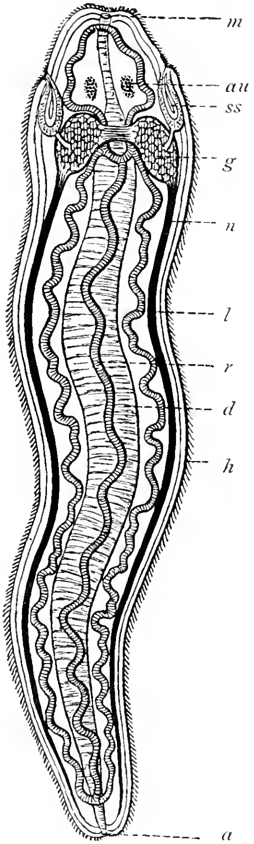


FIG. 298.

FIG. 298.—**A simple nemertine.** *m* mouth, *d* gut, *a* anus, *g* brain, *n* nerves, *h* ciliary coat, *ss* sensory pits (head-clefts), *au* eyes, *r* dorsal vessel, *l* lateral vessels. (Diagram.)

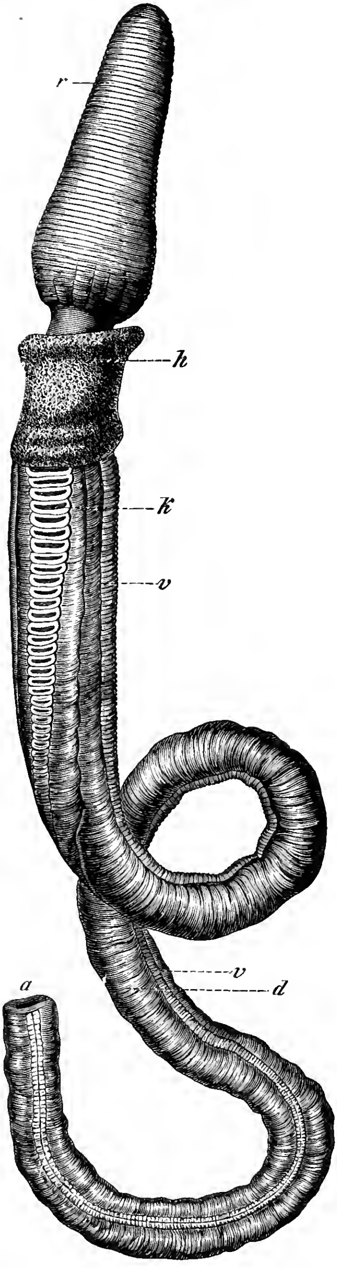


FIG. 299.

FIG. 299. — **A young enteropneust** (*balanoglossus*). (From *Alexander Agassiz.*) *r* acorn-shaped snout, *h* neck, *k* gill-clefts and gill-arches of the fore-gut, in long rows on each side, *d* digestive hind-gut, filling the greater part of the body-cavity, *v* intestinal vein or ventral vessel, lying between the parallel folds of the skin, *a* anus.

(the platode ancestors were hermaphroditic) ; (5) the ventral mouth, underneath a protruding snout ; (6) the terminal anus of the simple gut-tube ; and (7) several parallel blood-canals, running the length of the body, a dorsal and a ventral principal stem.

On the other hand, the enteropneusta differ from their nemertine ancestors in several features, some of which are important, that we may attribute to adaptation. The chief of these is the branchial gut (Fig. 299 *k*). The anterior section of the gut is converted into a respiratory organ, and pierced by two rows of gill-clefts ; between these there is a branchial skeleton, formed of rods and plates of chitine. The water that enters at the mouth makes its exit by these clefts. They lie in the dorsal half of the fore-gut, and this is completely separated from the ventral half by two longitudinal folds (Fig. 300 *A**). This ventral half, the glandular walls of which are clothed with ciliary epithelium and secrete mucus, corresponds to the pharyngeal or hypobranchial groove of the chordonia *(Bn)*, the important organ from which the later thyroid gland is developed in the craniota (cf. p. 424). The morphological agreement in the characteristic structure of the branchial gut of the enteropneusts, tunicates, and vertebrates was first recognised by Gegenbaur (1878) ; it is the more significant as at first we find only a couple of gill-clefts in the young animals of all three groups ; the number gradually increases. We can infer from this the common descent of the three groups with all the more confidence when we find the *balanoglossus* approaching the chordonia in other respects. Thus, for instance, the chief part of the central nervous

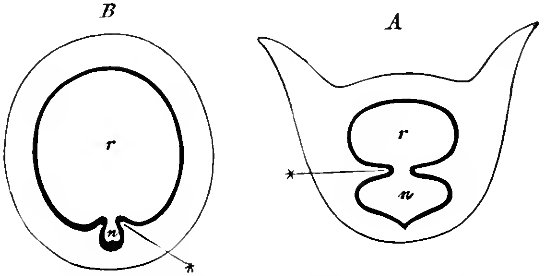


FIG. 300.—**Transverse section of the branchial gut.** *A* of *balanoglossus*, *B* of *ascidia*. *r* branchial gut, *n* pharyngeal groove, * ventral folds between the two. Diagrammatic illustration from *Gegenbaur*, to show the relation of the dorsal branchial-gut cavity *(r)* to the pharyngeal or hypobranchial groove *(n)*.

system is a long dorsal neural string that runs above the gut and corresponds to the medullary tube of the chordonia. Bateson believes he detected a rudimentary chorda between the two. We may regard the whole of the fore half of the enteropneusts (to the end of the branchial gut) as *head* (as in the amphioxus and copelata) and the hind half (with simple hepatic gut) as *trunk*.

Of all extant invertebrate animals the enteropneusts come nearest to the chordonia in virtue of these peculiar characters; hence we may regard them as the survivors of the ancient gut-breathing vermalia from which the chordonia also have descended. Again, of all the chorda-animals the copelata (Fig. 276) and the tailed larvæ of the ascidia (Fig. 5, Plate XVIII.) approach nearest to the young *balanoglossus*. Both are, on the other hand, very closely related to the *amphioxus*, the primitive vertebrate of which we have considered the phylogenetic importance (Chapters XVI. and XVII.). As we saw there, the unarticulated tunicates and the articulated vertebrates must be regarded as two independent stems, that have developed in divergent directions. But the common root of the two stems, the extinct group of the prochordonia, must be sought in the vermalia stem ; and of all the living vermalia those we have considered give us the safest clue to their origin. It is true that the actual representatives of the important groups of the copelata, balanoglossi, nemertina, icthydina, etc., have more or less departed from the primitive model owing to adaptation to special environment. But we may just as confidently affirm that the main features of their organisation have been preserved by heredity.

We must grant, however, that in the whole stem-history of the vertebrates the long stretch from the gastræads and platodes up to the oldest chordonia remains by far the most obscure section. We might frame another hypothesis to raise the difficulty—namely, that there was a long series of very different and totally extinct forms between the gastræa and the chordæa. Even in this modified chordæa theory the six fundamental organs of the chordula would retain their great palingenetic value. The medullary tube would be originally a chemical sensory organ, a dorsal olfactory tube, taking in respiratory-water and food by the neuroporus in front and conveying them by the neurenteric canal into the primitive gut. This olfactory tube would afterwards become the nervous centre, while the expanding gonades (lying to right and left of the primitive mouth) would form the cœloma. The chorda may have been originally a digestive glandular groove in the dorsal middle line of the primitive gut. The two secondary gut-openings, mouth and anus, may have arisen in various ways by change of functions. In any case, we should ascribe the same high value to the chordula as we did before to the gastrula.

In order to explain more fully the chief stages in the advance of our race, I add the hypothetical progonotaxis of man that I published in my *Last Link* [a translation by Dr. Gadow of the paper read at the International Zoological Congress at Cambridge in 1898]. In the earlier half of the progonotaxis (to the left) palæontological evidence is wanting, whereas it is conspicuous in the later (right) half. I have indicated in the three narrow columns (to the right) the relative value of the three kinds of phylogenetic evidence (in the present condition of our knowledge). The marks have the following meaning:—

Palæontological Evidence (first column).

0 complete absence of fossil remains.
— few and unimportant fossils.
= fairly abundant and important.
≡ very numerous and helpful.

Ontogenetic Evidence (second column).

? phylogenetic value doubtful.
! slight or ambiguous.
!! important.
!!! very important and instructive.

Morphological Evidence (third column).

I comparative anatomy tells little as to history.
II throws much light on phylogeny.
III throws very much light.

TWENTY-SIXTH TABLE

A. Human Progonotaxis, First Half:

EARLIER SERIES OF ANCESTORS, WITHOUT FOSSIL EVIDENCE, PRE-SILURIAN

Chief Stages.	Ancestral Stem-groups.	Living Relatives of Ancestors.	Paleontology.	Ontogeny.	Morphology.
Stages 1–5: **Protist ancestors.** Unicellular organisms. 1–2: Plasmodomous protophytes. 3–5: Plasmophagous protozoa.	1. **Monera.** (Plasmodoma.) Without nucleus.	1. **Chromacea.** *(Chroococcus.)* *Phycochromacea.*	0	!?	I
	2. **Algaria.** Unicellular algæ.	2. **Paulotomea.** *Palmellacea eremosphæra.*	0	!?	II
	3. **Lobosa.** Unicellular (amœbina) rhizopods.	3. **Amœbina.** *Amœba leucocyta.*	0	!!	II
	4. **Infusoria.** Unicellular.	4. **Flagellata.** *Euflagellata zoomonades.*	0	?	II
	5. **Blastæades.** Multicellular hollow vesicles (cenobia).	5. **Catallacta.** *Magosphæra, volvocina, blastula.*	0	!!!	III
Stages 6–11: **Invertebrate metazoa ancestors.** 6–8: Cœlenteria, without anus and body-cavity. 9–11: Vermalia, with anus and body-cavity.	6. **Gastræades.** With two germ-layers.	6. **Gastrula.** *Hydra, olynthus, gastremaria.*	0	!!!	III
	7. **Platodes I.** *Platodaria* (without nephridia).	7. **Cryptocœla.** *Convoluta proporus.*	0	?	I
	8. **Platodes II.** *Platodinia* (with nephridia).	8. **Rhabdocœla.** *Vortex monotus.*	0	?	I
	9. **Provermalia.** (Primitive worms.) *Rotatoria.*	9. **Gastrotricha.** *Trochozoa trochophora.*	0	?	I
	10. **Frontonia.** *(Rhynchelminthes.)* Snout-worms.	10. **Enteropneusta.** *Balanoglossus cephalodiscus.*	0	!	I
	11. **Prochordonia.** Chorda-worms.	11. **Copelata.** *Appendicaria.* Chordula-larvæ.	0	!	II
Stages 12–15: **Monorhina ancestors.** Oldest vertebrates without jaws or pairs of limbs, single nose.	12. **Acrania I.** (Prospondylia.)	12. **Amphioxus larvæ.**	0	!!!	III
	13. **Acrania II.** More recent.	13. **Leptocardia.** Amphioxus.	0	!	III
	14. **Cyclostoma I.** (Archicrania.)	14. **Petromyzoa larvæ.**	0	!!!	II
	15. **Cyclostoma II.** More recent.	15. **Marsipobranchia.** Petromyzoa.	0	!	III

TWENTY-SEVENTH TABLE

B. Human Progonotaxis, Second Half:

LATER ANCESTORS, WITH FOSSIL EVIDENCE, BEGINNING IN SILURIAN PERIOD

Geological Periods.	Ancestral Stem-groups.	Living Relatives of Ancestors.	Pale-onto-logy.	Onto-geny.	Mor-pho-logy.
Silurian.	16. **Selachii.** Primitive fishes. *Proselachii.*	16. **Natidanides.** Chlamdoselachus. Heptanchus.	I	! !	III
Silurian.	17. **Ganoides.** Plated-fishes. *Proganoides.*	17. **Accipenserides.** (Sturgeons.) Polypterus.	II	!	II
Devonian.	18. **Dipneusta.** *Paladipneusta.*	18. **Neodipneusta.** Ceratodus. Protopterus.	I	! !	II
Carbonife-rous.	19. **Amphibia.** *Stegocephala.*	19. **Phanero-branchia.** Salamandrina. (Proteus, triton.)	III	! ! !	III
Permian.	20. **Reptilia.** *Proreptilia.*	20. **Rhyncho-cephalia.** Primitive lizards. Hatteria.	III	! !	II
Triassic.	21. **Monotrema.** *Promammalia.*	21. **Ornitho-delphia.** *Echidna.* *Ornithorhyncus.*	I	! ! !	III
Jurassic.	22. **Marsupialia.** *Prodidelphia.*	22. **Didelphia.** *Didelphys.* *Perameles.*	I	! !	II
Cretaceous.	23. **Mallotheria.** *Prochoriata.*	23. **Insectivora.** Erinaceida. (Ictopsida +.)	II	!	I
Older Eocene.	24. **Lemuravida.** Older lemurs. Dentition 3. 1. 4. 3.	24. **Pachylemures.** *(Hyopsodus +.)* *(Adapis +.)*	III	! ?	II
Neo-Eocene.	25. **Lemurogona.** Later lemurs. Dent. 2. 1. 4. 3.	25. **Autolemures.** *Eulemur.* *Stenops.*	III	! ?	II
Oligocene.	26. **Dysmopitheca.** Western apes. Dent. 2. 1. 3. 3.	26. **Platyrrhinæ.** *(Anthropops +.)* *(Homunculus +.)*	I	!	II
Older Miocene.	27. **Cynopitheca.** Dog-faced apes (tailed).	27. **Papiomorpha.** *Cynocephalus.*	I	!	III
Neo-Miocene.	28. **Anthropoides.** Man-like apes (tail-less).	28. **Hylobatida.** Hylobates. Satyrus.	I	! !	III
Pliocene.	29. **Pithecanthropi.** Ape-men (alali, speechless).	29. **Anthropitheca.** Chimpanzee. Gorilla.	II	! ! !	III
Pleistocene.	30. **Homines.** Men, with speech.	30. **Weddahs.** Australian negroes.	I	! ! !	III

CHAPTER XXI.

OUR FISH-LIKE ANCESTORS

Genealogical evidence for the vertebrates. Phylogenetic classification of the vertebrates: eight classes. Acrania and craniota. Cyclostoma and gnathostoma. Intermediate position of the cyclostoma between the acrania and gnathostoma. Chief differences between the cyclostoma and the fishes. Archicrania. The characteristics of the gnathostoma or double-nosed animals: the branchial arch apparatus with the maxillary arches, the double nose, the floating bladder, the two pairs of legs. Affinity of the three groups of fishes: primitive fishes or selachii, scaly fishes or ganoids, bony fishes or teleostei. Proselachii, pleuracanthides. Crossopterygii. Commencement of terrestrial life. Conversion of the floating bladder into lungs. Intermediate position of the dipneusta between the primitive fishes and amphibia. Paleozoic dipneusta: ctenodipterina. Mesozoic dipneusta: ceratodina. The three surviving dipneusts (protopterus, lepidosiren, ceratodus).

OUR phylogenetic task of detecting the extinct ancestors of our race among the vast numbers of animals known to us encounters very different difficulties in the various sections of man's stem-history. These were very great in the series of our invertebrate vermalian ancestors; they are much slighter in the subsequent series of our vertebrate ancestors. Within the vertebrate stem there is, as we have already seen, so complete an agreement in structure and embryology that it is impossible to doubt their phylogenetic unity. In this case the evidence is much clearer and more abundant.

We are already aware of the great importance in this section of the comparative embryology of the vertebrates, and how, with the aid of the biogenetic law, we can draw very weighty conclusions from it with regard to the stem-history of the vertebrates. At the same time, the abounding supplementary evidence of palæontology and comparative anatomy is of incalculable value; it is our safest guide in constructing the vertebrate genealogical tree. Thanks to the classic studies of George Cuvier, Johannes Müller, Frederick Meckel, Richard Owen, Thomas Huxley, Carl Gegenbaur, Max Fürbringer, R. Wiedersheim, and others, we have such a quantity of morphological evidence in this principal section of our stem-history that we can establish with confidence at least the chief features of the evolutionary series of our vertebrate ancestors.

The characteristics that distinguish the vertebrates as a whole from the invertebrates have already been discussed in our description of the hypothetical primitive vertebrate (Chapter XI., Figs. 101–5). The chief of these are: (1) The evolution of the primitive brain into a dorsal medullary tube; (2) the formation of the chorda between the medullary tube and the gut; (3) the division of the gut into branchial and hepatic gut; and (4) the internal articulation or metamerism. The first three features are shared by the vertebrates with the ascidian-larvæ and the prochordonia; the fourth is peculiar to them. Thus the chief advance in organisation by which the earliest vertebrates took precedence of the related, unarticulated chordonia consisted in the development of internal articulation. This began with the division of the cœlom-pouches into a double row of somites or primitive segments. From the dorsal halves of these (the episomites) were formed the series of muscular pouches; from their ventral halves (hyposomites) the sexual pouches. Afterwards the internal articulation extended to the skeleton and the nervous and vascular systems as well.

We are greatly assisted in understanding the stem-history of the vertebrates by the natural classification of the stem that I proposed in my *Generelle Morphologie* (1866), and improved in my *History of Creation* (chap. xxiv.). On this we must distribute the living vertebrates first into the following eight classes:—

Classification of the Eight Vertebrate Classes.

A. Acrania (skull-less animals):			1. "Tube-hearts."	1. *Leptocardia.*
B. Craniota (skulled animals).	a "Round-mouthed," cyclostoma.		2. "Single-nosed."	2. *Monorhina.*
	b. "Jaw mouthed" (gnathostoma) or "double-nosed" (amphirina).	1. Anamnia.	3. Fishes.	3. *Pisces.*
			4. Dipneusts.	4. *Dipneusta.*
			5. Amphibia.	5. *Amphibia.*
		2. Amniota.	6. Reptiles.	6. *Reptilia.*
			7. Birds.	7. *Aves.*
			8. Mammals.	8. *Mammalia.*

The whole vertebrate stem divides first into the two chief sections of acrania and craniota. The amphioxus is the only surviving representative of the older and lower section, the acrania ("skull-less"). All the other vertebrates belong to the second division, the craniota ("skull-animals"). The craniota descend directly from the acrania, and these from the primitive chordonia. The exhaustive study that we made of the comparative anatomy and ontogeny of the ascidia and the amphioxus has proved these relations for us. (See Chapters XVI. and XVII., and Plates XVIII. and XIX. and Explanation.) I will merely point out again the most important fact, that the amphioxus developes from the ovum in just the same way as the ascidian. In both cases a spherical blastula is formed in the same way from the simple stem-cell, and this is converted by invagination into a cup-shaped gastrula. From this is developed the remarkable larva that we have called the chordula, and that forms a medullary tube on the dorsal side of the gut and a chorda between the two. The gut then divides (in both amphioxus and ascidian) into branchial gut and hepatic gut. In accordance with the biogenetic law, we can directly infer from these facts for our phylogenetic purpose the following thesis: The amphioxus, the lowest vertebrate, and the ascidian, the nearest related invertebrate, descend from a common extinct stem-form, the chordæa; and this must have had, substantially, the organisation of the chordula.

However, the amphioxus is not important merely because it fills the deep gulf between the invertebrates and vertebrates, but also because it shows us to-day the typical vertebrate in all its simplicity. We owe to it the most important data that we proceed on in reconstructing the gradual historical development of the whole stem. If we were not acquainted with the structure and the embryology of this invaluable organism, the earlier development of the vertebrate stem, and therefore of our own race, would be covered with a heavy veil. It is the careful anatomic and ontogenetic study of the amphioxus that has removed this veil. When we compare these ancient acrania with fully-developed man, or any other higher vertebrate, we find a number of conspicuous differences. The amphioxus, as we have seen, has no differentiated head or brain, no skull, jaws, or limbs; it is without a centralised heart, developed liver and kidneys, and articulated vertebral column; all its organs are more rudimentary than in the higher vertebrates and man (cf. Table XVII.). Nevertheless, in spite of these divergences in structure from the rest of the vertebrates, the amphioxus is undoubtedly a true vertebrate; and if, instead of a fully-developed man, we compare the human embryo at some earlier stage with it, we find a remarkable similarity between the two in all the main features (cf. Table XVI.). This instructive agreement justifies us in concluding that all the craniota descend from a common stem-form, and this was substantially identical in structure with the amphioxus. This stem-form, the primitive vertebrate (*prospondylus*, Figs. 101–105), had the characteristics of the vertebrate as such, but not the important features that distinguish the craniota from the acrania. Though the amphioxus has many peculiarities of structure and has much degenerated, and though it cannot be regarded as an unchanged descendant of the primitive vertebrate, it must have inherited from it the specific characters we enumerated above. We may not say that "amphioxus is the ancestor of the vertebrates"; but we can say: "Amphioxus is the nearest relation to the ancestor of all the animals we know." Both belong to the same small family, or lowest class of the vertebrates, that we call the acrania. In our genealogical tree this group forms the twelfth stage, or the first stage among the vertebrate ancestors (p. 550). From this group of acrania both the amphioxus and the craniota were evolved.

The vast division of the craniota embraces all the vertebrates known to us, with the exception of the amphioxus. All of them have a head clearly differentiated from the trunk, and a skull enclosing a brain. The head has also three pairs of higher sense-organs (nose, eyes, and ears). The brain is very rudimentary at first, a mere vesicular enlargement of the fore end of the medullary tube (Plate XIX., Fig. 16 m_1). But it is soon divided by a number of transverse constrictions into, first three, then five successive cerebral vesicles. In this formation of the head, skull, and brain, with further development of the higher sense-organs, we have the advance that the craniota made beyond their skull-less ancestors. Other organs also attained a higher development; they acquired a compact centralised heart with valves and a more advanced liver and kidneys, and made progress in other important respects.

We may divide the craniota generally into *cyclostoma* ("round-mouthed") and *gnathostoma* ("jaw-mouthed"). There are only a few groups of the former in existence now, but they are very interesting, because in their whole structure they stand mid-way between the acrania and the gnathostoma. They are much more advanced than the acrania, much less so than the fishes, and thus form a very welcome connecting-link between the two groups. We may therefore consider them a special intermediate group, the fourteenth and fifteenth stages in the series of our ancestors.

The few surviving species of the cyclostoma are divided into two orders—the myxinoides and the petromyzontes. The former have a long, cylindrical, worm-like body. They were classed by Linné with the worms, and by later zoologists with the fishes, or the amphibia, or the molluscs. They live in the sea, usually as parasites of fishes, into the skin of which they bore with their round suctorial mouths and their tongues, armed with horny teeth. They are sometimes found alive in the body-cavity of fishes (such as the torsk or sturgeon); in these cases they have passed through the skin into the interior. The second order, the petromyzontes, comprises the well-known lampreys; the small river lamprey *(petromyzon fluviatilis)* and the large marine lamprey *(petromyzon marinus*, Fig. 301). They also have a round suctorial mouth, with horny teeth inside it; by means of this they attach themselves by sucking to fishes, stones, and other objects (hence the name *petromyzon* = stone-sucker). It seems that this habit was very widespread among the earlier vertebrates; the larvæ of many of the ganoids and frogs have suctorial disks near the mouth.

The class that is formed of the myxinoides and petromyzontes is called the cyclostoma (round-mouthed), because their mouth has a circular or semi-circular aperture. The jaws (upper and lower) that we find in all the higher vertebrates are completely wanting in the cyclostoma, as in the amphioxus. Hence the other vertebrates are collectively opposed to them as gnathostoma (jaw-mouthed). The cyclostoma might also be called *monorhina* (single-nosed), because they have only a single nasal passage, while all the gnathostoma have two nostrils (*amphirhina* = two-nosed). But, apart from these peculiarities, the cyclostoma differ more widely from the fishes in other special features of their structure than the fishes do from man. Hence they are obviously the last survivors of a very ancient class of vertebrates, that was far from attaining the advanced organisation of the true fish. To mention only the chief points, the cyclostoma show no trace of pairs of limbs. Their mucous skin is quite naked and smooth and devoid of scales. There is no bony skeleton. The internal axial skeleton is a simple, unsegmented chorda, as in the amphioxus. There is only an incipient articulation in the petromyzontes, in the sense that there are upper arches in the medullary-sheath that proceeds from the perichorda. A very rudimentary skull is developed at the foremost end of the chorda. At this point a soft membranous (partly turning into cartilage), small skull-capsule is formed, and encloses the brain. The important apparatus of the

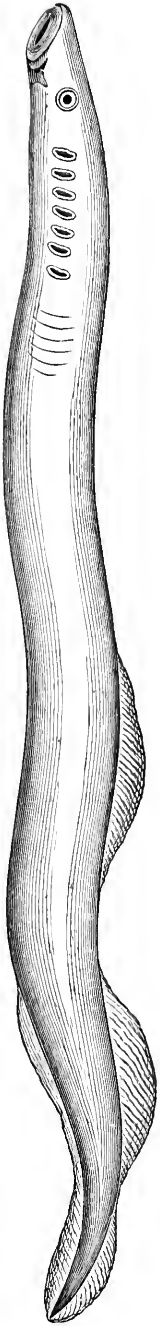


FIG 301.

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FIG. 301.—**The large marine lamprey** (*petromyzon marinus*), much reduced. Behind the eye there is a row of seven gill-clefts visible on the left, in front the round suctorial mouth.

gill-arches, hyoid bone, etc., that is transmitted from the fishes to man, is entirely wanting in the cyclostoma. They have, it is true, a cartilaginous superficial branchial skeleton, but it has quite a different morphological significance.

The brain of the cyclostoma is merely a very small and comparatively insignificant swelling of the spinal marrow, a simple vesicle at first (Plate XIX., Fig. 16 m_1). It afterwards divides into five successive cerebral vesicles, like the brain of the gnathostoma. These five primitive cerebral vesicles, that are found in the embryos of all the higher vertebrates from the fishes to man, and grow into very complex structures, remain at a very rudimentary stage in the cyclostoma. The histological structure of the nerves is also less advanced than in the rest of the vertebrates. In these the auscultory organ always contains three circular canals, but in the petromyzontes there are only two, and in the myxinoides only one. In most other respects the organisation of the cyclostoma is much simpler—for instance, in the structure of the heart, circulation, and kidneys. The fore section of the gut forms respiratory gills, as in the amphioxus; but they develop in a very characteristic way—namely, in the form of six to eight pairs of sacs at each side of the fore-gut, which open internally into the gullet and externally in the outer skin. This is a very peculiar formation of the respiratory organs, and is distinctive of this class. They have been called *marsipobranchia* ("pouch-gilled") on that account. We must especially note the absence of a very important organ that we find in the fishes—the floating bladder, from which the lungs of the higher vertebrates have been developed.

The cyclostoma have peculiarities in their embryonic development as well as in their whole structure. One of these is their unequal ovum-segmentation, which approaches that of the amphibia (Figs. 51, 52). It produces a tufted gastrula, as in the amphibia (Plate II., Fig. 11). From this is developed a very simply-organised larva, closely resembling that of the amphioxus, which we have already considered and compared with the latter (p. 434, and Plate XIX., Fig. 16). The gradual development of this larva throws a good deal of light on the gradual evolution of the craniota from the acrania. Later, a blind and toothless larva developes from this simple petromyzon-larva, and this differs so much from the full-grown lamprey that until 1856 it was generally described as a special genus of fish, with the name of *ammocœtes*. A further metamorphosis changes the blind and toothless ammocœtes into the lamprey with eyes and teeth.

When we consider all these peculiarities in the structure and embryology of the cyclostoma, we may formulate the following thesis: Two divergent lines proceeded from the earliest craniota, or the primitive craniota *(archicrania)*. One of these lines is preserved in a greatly modified condition: these are the cyclostoma or monorhina, a very backward and partly degenerate side-line. The other, the chief line of the vertebrate stem, advanced straight to the fishes, and by fresh adaptations acquired a number of important improvements.

In order to appreciate fully the phylogenetic interest of such surviving groups as the cyclostoma, it is necessary to examine their many characteristics with the philosophic measure of comparative anatomy. We must carefully distinguish between the *hereditary* characters that have been transmitted from earlier ancestors and preserved faithfully to the present time, and the features that have been acquired subsequently by *adaptation*. Of the latter we have, for instance, in the cyclostoma the peculiar formation of the single nostril and the round suctorial mouth, and certain peculiarities in the structure of the skin and the pouch-shaped gills. On the other hand, we must assign to the former class, which alone have any phylogenetic significance, the primitive formation of the chorda and the brain, the distinctive structure of the muscles and nerves, the absence of floating-bladder, jaws, and limbs, etc. These are typical features of the extinct archicrania, the ancient cyclostoma that we regard as the common stem-form of all the craniotes.

The cyclostoma are almost always classified by zoologists among the fishes; but the incorrectness of this may be judged from the fact that in all the chief and distinctive features of organisation the cyclostoma are further removed from the fishes than the fishes are from the mammals, and even man. With the fishes we enter upon the vast division of the jaw-mouthed or double-nosed vertebrates *(gnathostoma* or *amphirhina).* We have to consider the fishes carefully as the class which, on the evidence of palæontology, comparative anatomy, and ontogeny, may be regarded with absolute certainty as the stem-class of all the higher vertebrates or gnathostomes. Naturally, none of the actual fishes can be considered the direct ancestor of the higher vertebrates. But it is certain that all the vertebrates or gnathostomes, from the fishes to man, descend from a common, extinct, fish-like ancestor. If we had this ancient stem-form before us, we would undoubtedly class it as a true fish. Fortunately, the comparative anatomy and classification of the fishes are now so far advanced that we can get a very clear idea of these interesting and instructive features.

In order to understand properly the genealogical tree of our race within the vertebrate stem, it is important to bear in mind the characteristics that separate the whole of the gnathostomes from the cyclostomes and craniota. In these respects the fishes agree entirely with all the other gnathostomes up to man, and it is on this that we base our claim of relationship to the fishes (cf. Table XVII.). The following characteristics of the gnathostomes are anatomic features of this kind: (1) The internal gill-arch apparatus with the jaw-arches; (2) the pair of nostrils; (3) the floating bladder or lungs; and (4) the two pairs of limbs.

The peculiar formation of the framework of the branchial (gill) arches and the connected maxillary (jaw) apparatus is of importance in the whole group of the gnathostomes. It is inherited in a rudimentary form by all of them, from the earliest fishes to man. It is true that the primitive transformation (which we find even in the ascidia) of the fore gut into the branchial gut can be traced in all the vertebrates to the same simple type; in this respect the gill-clefts, which pierce the walls of the branchial gut in all the vertebrates and in the ascidia, are very characteristic. But the *external*, superficial branchial skeleton that supports the gill-crate in the cyclostoma is replaced in the gnathostomes by an *internal* branchial skeleton. It consists of a number of successive cartilaginous arches, which lie in the wall of the gullet between the gill-clefts, and run round the gullet from both sides. These branchial arches are at first segmental, or developed from hyposomites (branchiomerism). The foremost pair of gill-arches become the maxillary arches, from which we get our upper and lower jaws.

The olfactory organs are at first found in the same form in all the gnathostomes, as a pair of cutaneous depressions in the fore part of the head, above the mouth ; hence, they are also called the amphirhina ("double-nosed"). The cyclostoma are "one-nosed" *(monorhina)*; their nose is a single passage in the middle of the frontal surface. But as the olfactory nerve is double in both cases, it is possible that the peculiar form of the nose in the actual cyclostomes is a secondary acquisition (by adaptation to suctorial habits).

A third essential character of the gnathostomes, that distinguishes them very conspicuously from the lower vertebrates we have dealt with, is the formation of a blind sac by invagination from the fore part of the gut, which becomes in the fishes the air-filled floating bladder (Plate VII., Fig. 13 *lu*). This organ acts as a hydrostatic apparatus, increasing or reducing the specific gravity of the fish by compressing or altering the quantity of air in it. The fish can rise or sink in the water by means of it. This is the organ from which the lungs of the higher vertebrates are developed.

Finally, the fourth character of the gnathostomes in their simple embryonic form are the two pairs of extremities or limbs—a pair of fore legs (breast-fins in the fish, Fig. 304 *v*) and a pair of hind legs (ventral fins in the fish, Fig. 304 *h*). The comparative anatomy of these fins is very interesting, because they contain the rudiments of all the skeletal parts that form the framework of the fore and hind legs in all the higher vertebrates right up to man. There is no trace of these pairs of limbs in the acrania and cyclostomes.

Turning, now, to a closer inspection of the fish class, we may first divide it into three groups or sub-classes, the genealogy of which is well known to us. The first and oldest group is the sub-class of the selachii or primitive fishes, the best-known representatives of which to-day are the orders of the sharks and rays (Figs. 302–306). Next to this is the more advanced sub-class of the plated fishes or ganoids (Figs. 307–309). It has been long extinct for the most part, and has very few living representatives, such as the sturgeon and the bony pike ; but we can form some idea of the earlier extent of this interesting group from the large numbers of fossils. From these plated fishes the sub-class of the bony fishes or teleostei was developed, to which the great majority of living

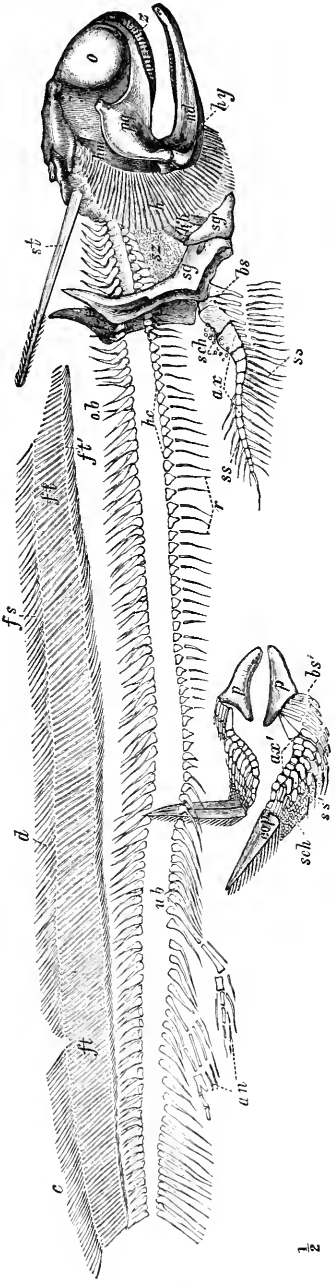


FIG. 302.

FIG. 302.—**Fossil Permian primitive fish** *(pleuracanthus Dechenii)*, from the red sandstone of Saarbrücken. (From *Döderlein.*) I. Skull and branchial skeleton : *o* eye-region, *pq* palatoquadratum, *nd* lower jaw, *hm* hyomandibular, *hy* tongue-bone, *k* gill-radii, *kb* gill-arches, *z* jaw-teeth, *sz* gullet-teeth, *st* neck-spine. II. Vertebral column : *ob* upper arches, *ub* lower arches, *hc* intercentra, *r* ribs. III. Single fins : *d* dorsal fin, *c* tail-fin (tail-end wanting), *an* anus-fin, *ft* supporter of fin-rays. IV. Breast-fin : *sg* shoulder-zone, *ax* fin-axis, *ss* double lines of fin-rays, *bs* additional rays, *sch* plates. V. Ventral fin : *p* pelvis, *ax* fin-axis, *ss* single row of fin-rays, *bs* additional rays, *sch* scales, *cop* penis (male organ).

fishes belong (especially nearly all our river fishes). Comparative anatomy and ontogeny show clearly that the ganoids descended from the selachii, and the teleostei from the ganoids. On the other hand, a collateral line, or rather the advancing chief line of the vertebrate stem, was developed from the earlier ganoids, and this leads us through the group of the dipneusta to the important division of the amphibia.

This instructive affinity of the three groups of fishes cannot be called into question after the investigations of Carl Gegenbaur. The luminous explanation of the position of the selachii that he gave in the introduction to his classic *Study of the Head-skeleton of the Selachii* (1872) definitively establishes the point. The scales (appendages of the skin) and teeth (appendages of the jaws) are of the same structure only in the primitive fishes or selachii; in the other two groups of fishes (plated and bony) they are differentiated and variously constructed. The cartilaginous skeleton also (vertebral column, skull, and limbs) is found in its simplest character in the primitive fishes, and the more advanced structure of the bony skeleton in the ganoids and teleostei has been developed from this. The branchial apparatus of the latter and the brain are more advanced than in the selachii. In one important respect—the formation of the heart and alimentary canal—the ganoids resemble the sélachii, and differ from the teleostei. A comparative study of all these anatomic features proves beyond question that the ganoids are a connecting-group between the selachii and teleostei on the one hand, and the selachii and the dipneusts on the other.

The earliest fossil remains of vertebrates that we know were found in the Upper Silurian (p. 484), and belong to two groups—the selachii and the ganoids. The most primitive of all known representatives of the earliest fishes are probably the remarkable *pleuracanthida*, the genera *pleuracanthus*, *xenacanthus*, *orthocanthus*, etc. (Fig. 302). These ancient cartilaginous fishes agree in most points of structure with the real sharks (Figs. 303, 304); but in other respects they seem

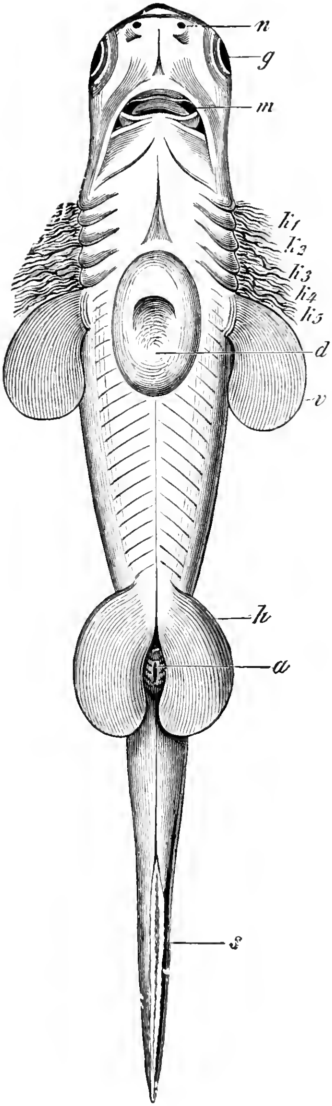


FIG. 303.

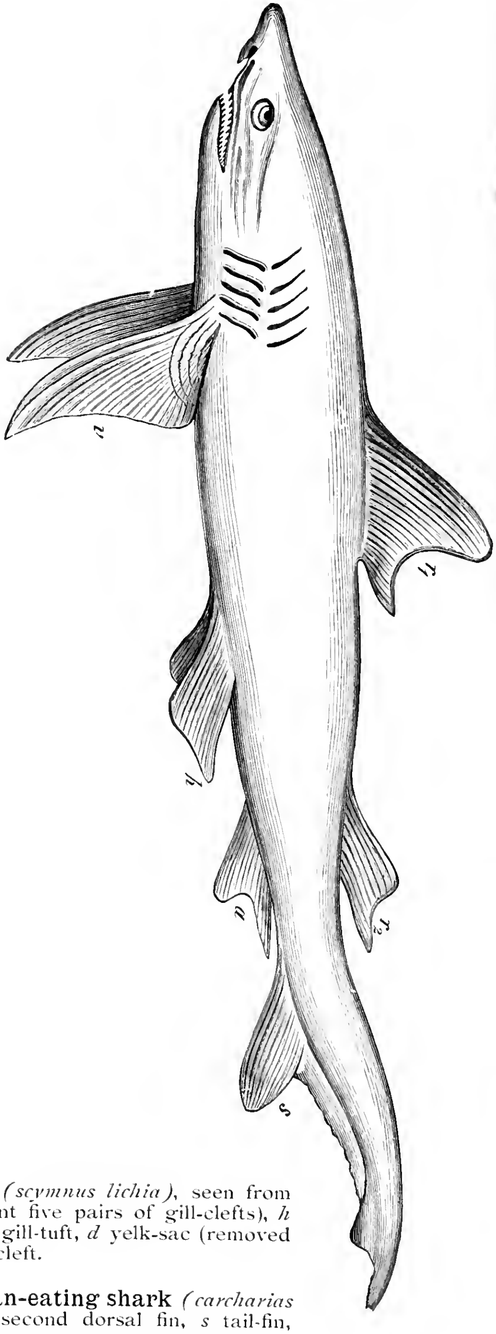


FIG. 304.

FIG. 303.—**Embryo of a shark** *(scymnus lichia)*, seen from the ventral side. *v* breast-fins (in front five pairs of gill-clefts), *h* belly-fins, *a* anus, *s* tail-fin, *k* external gill-tuft, *d* yelk-sac (removed for most part, *g* eye, *n* nose, *m* mouth-cleft.

FIG. 304. — **Fully-developed man-eating shark** *(carcharias melanopterus)*, left view. r_1 first, r_2 second dorsal fin, *s* tail-fin, *a* anus-fin, *v* breast-fins, *h* belly-fins.

to be so much simpler in organisation that many palæontologists (such as Doederlein) separate them altogether, and regard them as proselachii ; they are probably closely related to the extinct ancestors of the gnathostomes. We find well-preserved remains of them in the Permian period. Well-preserved impressions of other sharks are found in the Jurassic schist, such as of the angel-fish (*squatina*, Fig. 305). Among the extinct earlier sharks of the Tertiary period there were some twice as large as the biggest living fishes ; *carcharodon* was more than 100 feet long. The sole surviving species of this genus (*c. Rondeleti*) is ten metres long, and has teeth five to six cm. long ; but among the fossil species we find teeth fifteen cm. long (Fig. 306).

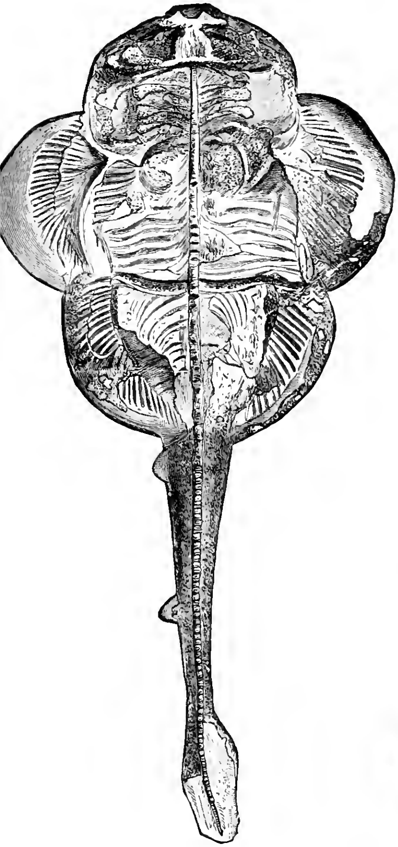


Fig. 305.

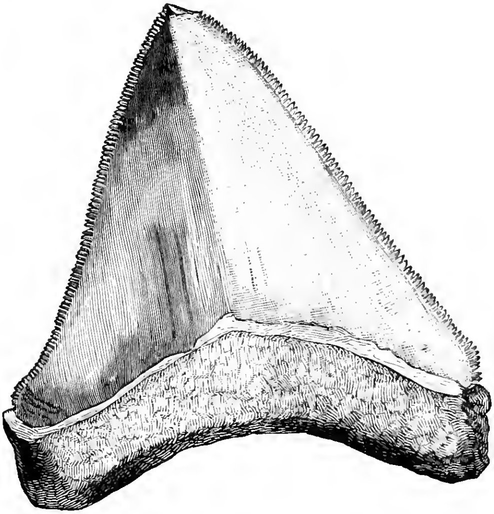


Fig. 306.

Fig. 305.—**Fossil angel-shark** (*squatina alifera*), from the upper Jurassic at Eichstätt. (From *Zittel.*) The cartilaginous skull is clearly seen in the broad head, and the gill-arches behind. The wide breast-fin and the narrower belly-fin have a number of radii ; between these and the vertebral column are a number of ribs.

Fig. 306.—**Tooth of a gigantic shark** (*carcharodon megalodon*), from the Pliocene at Malta. Half natural size. (From *Zittel.*)

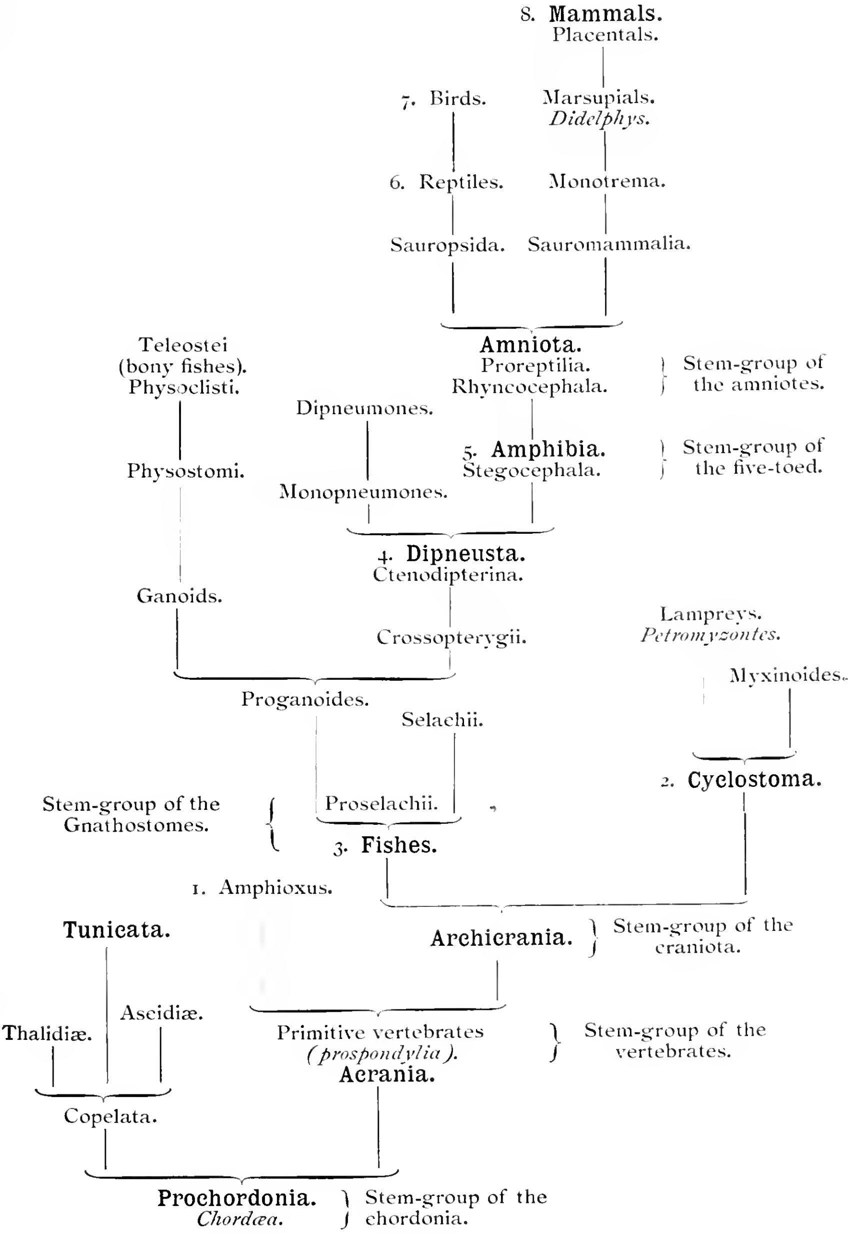
TWENTY-EIGHTH TABLE

SYNOPSIS OF THE PHYLOGENETIC CLASSIFICATION OF THE VERTEBRATES

Four Cladomes of the Vertebrates.	Eight Classes of the Vertebrates.	Sub-classes of the Vertebrates.	Classification Names of the Sub-classes.
I. **Acrania.**	I. A. **Provertebrata.**	1. Primitive vertebrates +.	1. *Prospondylia* +.
	I. B. **Leptocardia.**	2. Lancelets.	2. *Amphioxus.*
II. **Cyclostoma.**	II. A. **Archicrania.**	3. Primitive craniotes +.	3. *Procraniota* +.
	II. B. **Marsipobranchia.**	4. Single-nosed.	4. *Monorhinus.*
III. **Ichthyoda** or **Anamnia.**	III. **Pisces** (fishes).	5. Primitive fishes.	5. *Selachii.*
		6. Plated fishes.	6. *Ganoides.*
		7. Bony fishes.	7. *Teleostei.*
	IV. **Dipneusta.**	8. One-lunged.	8. *Monopneumones.*
		9. Two-lunged.	9. *Dipneumones.*
	V. **Amphibia.**	10. Mailed amphibia (phractamphibia).	10a. *Stegocephala.* 10b. *Peromela.*
		11. Naked amphibia (lissamphibia).	11a. *Urodela.* 11b. *Batrachia.*
IV. **Amniota.**	VI. **Reptilia.**	12. Primitive serpents and lizards.	12a. *Proreptilia.* 12b. *Lepidosauria.*
		13. Sauromammals.	13. *Theromora.*
		14. Tortoises.	14. *Chelonia.*
		15. Crocodiles and sea-serpents.	15a. *Crocodilia.* 15b. *Halisauria.*
		16. Flying serpents and dragons.	16a. *Pterosauria.* 16b. *Dinosauria.*
	VII. **Aves** (birds).	17. Primitive birds and toothed birds.	17a. *Saururæ.* 17b. *Odontornithes.*
		18. Crested birds and keel-birds.	18a. *Ratitæ.* 18b. *Carinatæ.*
	VIII. **Mammalia.**	19. Monotremes (*ornithodelphia*).	19. *Monotrema* (prototheria).
		20. Marsupials (*didelphia*).	20. *Marsupialia* (metatheria).
		21. Placentals (*monodelphia*).	21. *Placentalia* (epitheria).

TWENTY-NINTH TABLE

GENEALOGICAL TREE OF THE VERTEBRATES



From the primitive fishes or selachii, the earliest gnathostomes, was developed the legion of the ganoids (plated fishes). There are very few genera now of this interesting and varied group—the ancient sturgeons *(accipenser)*, the eggs of which are eaten as caviare, and the stratified pikes *(polypterus,* Fig. 309) in African rivers, and bony pikes *(lepidosteus)* in the rivers of North America. On the other hand, we have a great variety of specimens of this group in the fossil state, from the Upper Silurian onward. Some of these fossil ganoids approach closely to the selachii ; others are nearer to the dipneusts ; others again represent a transition to the teleostei. For our genealogical purposes the most interesting are the intermediate forms between the selachii and the dipneusts. Huxley, to whom we owe particularly important works on the fossil ganoids, classed them in the order of the *crossopterygii.* Many genera and species of this order are found in the Devonian and Carboniferous strata (Fig. 307) ; a single, greatly modified survivor of the group is still found in the large rivers of Africa *(polypterus,* Fig. 309, and the closely related *calamichthys).* In many impressions of the crossopterygii the floating bladder seems to be ossified, and therefore well preserved—for instance, in the *undina* (Fig. 308, immediately behind the head).

Part of these crossopterygii approach very closely in the chief anatomic features to the dipneusts, and thus represent phylogenetically the transition from the Devonian ganoids to the earliest air-breathing vertebrates. This important advance was made in the Devonian period. The numerous fossils that we have from the first two geological sections, the Laurentian and Cambrian periods, belong exclusively to aquatic plants and animals. From this palæontological fact, in conjunction with important geological and biological indications, we may infer with some confidence that there were no terrestrial animals at that time. During the whole of the vast archeozoic period—many millions of years—the living population of our planet consisted almost exclusively of aquatic organisms ; this is a very remarkable fact when we remember that this period embraces the larger half of the whole history of life. The lower animal-stems are wholly (or with very few exceptions) aquatic. But the higher

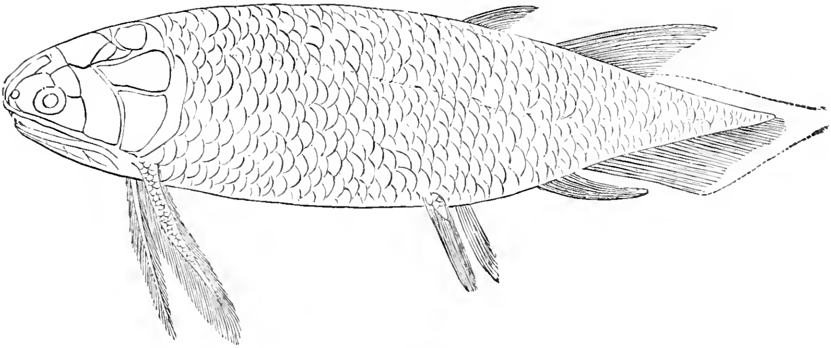


FIG. 307.

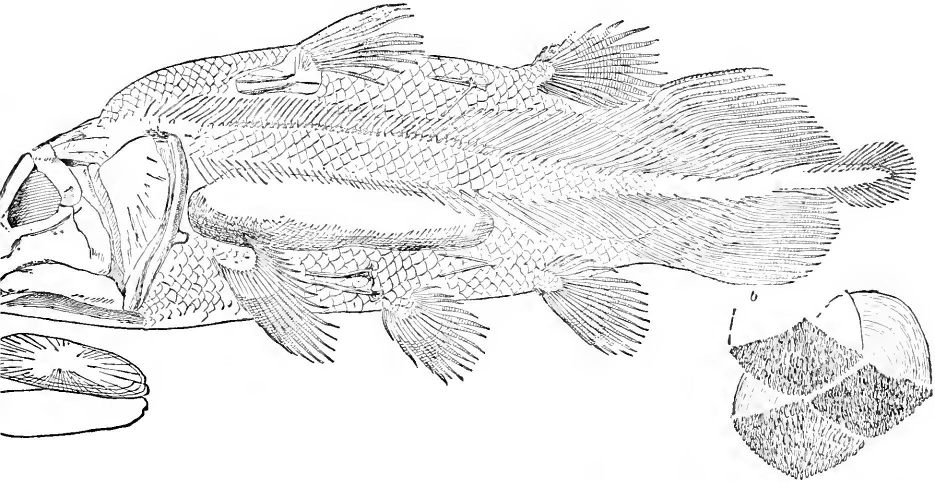


FIG. 308.

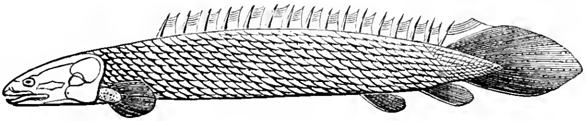


FIG. 309.

FIG. 307.—**A Devonian crossopterygius** *(holoptychius nobilissimus)*, from the Scotch old red sandstone. (From *Huxley*.)

FIG. 308.—**A Jurassic crossopterygius** *(undina penicillata)*, from the upper Jurassic at Eichstätt. (From *Zittel*.) *j* jugular plates, *b* three ribbed scales.

FIG. 309.—**A living crossopterygius,** from the upper Nile *(polypterus bichir)*.

stems also remained in the water during the primordial epoch. It was only towards its close that some of them came to live on land. We find isolated fossil remains of terrestrial animals first in the Upper Silurian, and in larger numbers in the Devonian strata, which were deposited at the beginning of the second chief section of geology (of the paleozoic age). The number increases considerably in the Carboniferous and Permian deposits. We find many species that lived on land and breathed the atmosphere both of the articulate and the vertebrate stem; their aquatic ancestors of the Silurian period only breathed water. This physiologically important change in respiration is the chief modification that the animal organism underwent in passing from the water to the solid land. The first consequence was the formation of lungs for breathing air; up to that time the gills alone had served for respiration. But there was at the same time a great change in the circulation and its organs; these are always very closely correlated to the respiratory organs. Moreover, the limbs and other organs were also more or less modified, either in consequence of remote correlation to the preceding or owing to new adaptations.

In the vertebrate stem it was unquestionably a branch of the fishes—in fact, of the ganoids—that made the first fortunate experiment during the Devonian period of adapting themselves to terrestrial life and breathing the atmosphere. This led to a modification of the heart and the nose. The true fishes have merely a pair of blind olfactory pits on the surface of the head; but a connection of these with the cavity of the mouth was now formed. A canal made its appearance on each side, and led directly from the nasal depression into the mouth-cavity, thus conveying atmospheric air to the lungs even when the mouth was closed. Further, in all true fishes the heart has only two sections—an atrium that receives the venous blood from the veins, and a ventricle that propels it through a conical artery to the gills; the atrium was now divided into two halves, or right and left auricles, by an incomplete partition. The right auricle alone now received the venous blood from the body, while the left auricle received the venous blood that flowed from the lungs and gills to the heart. Thus the double circulation of the higher vertebrates was evolved from the simple circulation of the true fishes, and, in accordance with the laws of correlation, this advance led to others in the structure of other organs.

The vertebrate class, that thus adapted itself to breathing the atmosphere, and was developed from a branch of the ganoids, takes the name of the *dipneusts* or *dipnoa* ("double-breathers"), because they retained the earlier gill-respiration along with the new pulmonary respiration, like the lowest amphibia. This class was represented during the paleozoic age (or the Devonian, Carboniferous, and Permian periods) by a number of different genera. The families of the phaneropleurida *(uronemus, phaneropleuron)* and the ctenodipterina *(dipterina*, Fig. 310, and *ctenodina)* are only found in fossil form in paleozoic strata. These are followed in the Triassic and Jurassic by the *ceratodina* (Fig. 311). There are only three genera of the class living to-day: *Protopterus annectens* in the rivers of tropical Africa (the White Nile, the Niger, Quelliman, etc.), *lepidosiren paradoxa* in tropical South America (in the tributaries of the Amazon), and *ceratodus Forsteri* in the rivers of East Australia. This wide distribution of the three isolated survivors proves that they represent a group that was formerly very large. In their whole structure they form a transition from the fishes to the amphibia. The transitional formation between the two classes is so pronounced in the whole organisation of these remarkable animals that zoologists had a lively controversy over the question whether they were really fishes or amphibia. Several distinguished zoologists classed them with the

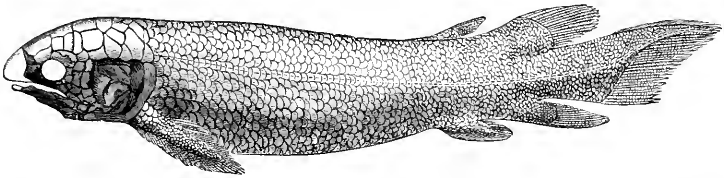


FIG. 310.—**Fossil dipneust** *(dipterus Valenciennesi)*, from the old red sandstone (Devon). (From *Pander*.)

amphibia, though most now associate them with the fishes. As a matter of fact, the characters of the two classes are so far united in the dipneusts that the answer to the question depends entirely on the definition we give of "fish" and "amphibium." In habits they are true amphibia. During the tropical winter, in the rainy season, they swim in the water like the fishes, and breathe water by gills. During the dry season they bury themselves in the dry mud, and breathe the atmosphere through lungs, like the amphibia and the higher vertebrates. In this double respiration they resemble the lower amphibia, and have the same characteristic formation of the heart; in this they are much superior to the fishes. But in most other features they approach nearer to the fishes, and are inferior to the amphibia. Externally they are entirely fish-like.

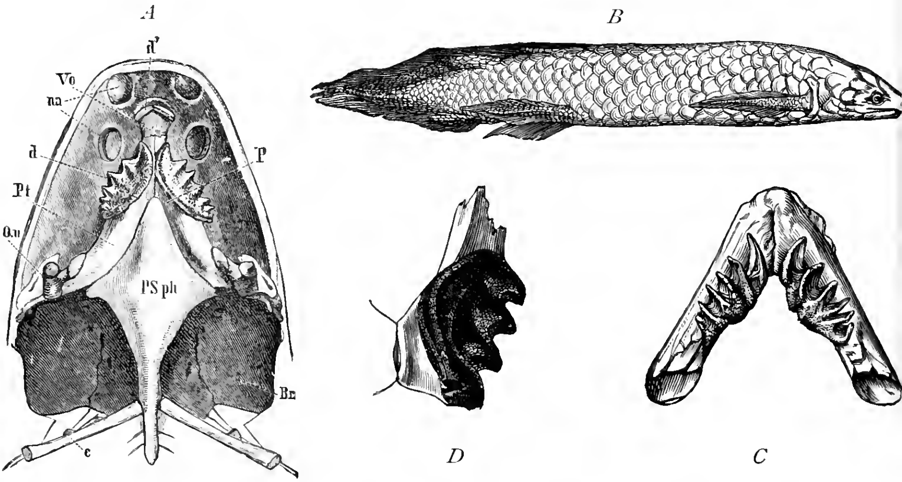


FIG. 311.—**The Australian dipneust** (*ceratodus Forsteri*). *A* view from the right, *B* lower side of the skull, *C* lower jaw. (From *Günther*.) *Qu* quadrate bone, *Psph* parasphenoid, *PtP* pterygopalatinum, *Vo* vomer, *d* teeth, *na* nostrils, *Br* branchial cavity, *C* first rib. *D* lower-jaw teeth of the fossil *ceratodus Kaupi* (from the Triassic).

In the dipneusts the head is not marked off from the trunk. The skin is covered with large scales. The skeleton is soft, cartilaginous, and at a low stage of development, as in the lower selachii and the earliest ganoids. The chorda is completely retained, and surrounded by an unsegmented sheath. The two pairs of limbs are very simple fins of a primitive type, like those of the lowest selachii. The formation of the brain, the gut, and the sexual organs is also the same as in the selachii. Thus the dipneusts have preserved by heredity many of the less advanced features of our primitive fish-like ancestors, and at the same time have made a great step forward in adaptation to air-breathing by means of lungs and the correlative improvement of the heart.

The great phylogenetic importance of the dipneusts has been fully explained in my *Systematic Phylogeny of the Vertebrates* (1896), and I have there divided the class into two orders—the *paladipneusta* and the *neodipneusta*. To the former belongs the extinct stem-group of the class, the family of the *phaneropleurida* (besides the *uronemida*, found in fossil state in the Devonian and Carboniferous); also the later family of the *ceratodina*, the characteristic comb-like teeth of which are found in the Triassic and Jurassic. To this group belongs the comb-tooth Australian fish *(ceratodus Forsteri)*, the sole living representative of the paladipneusta (Figs. 311–13). It was described in 1870 by Gerard Krefft, of Sydney, is more than eighty inches long, and is now only found in a few rivers on the east coast of Australia, Burnett River and Mary River. Professor Richard Semon has given us full details of its habits and remarkable internal structure, and he has also investigated the very important, but hitherto unknown, embryonic development of the ceratodus. Full information will be found in his extensive work, *Zoological Journeys in Australia* (1893–1903). He has given briefer

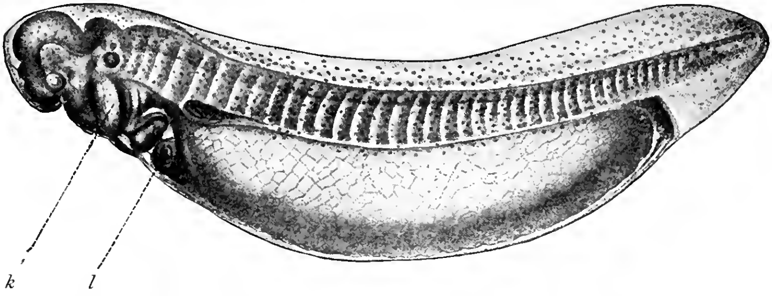


FIG. 312.—**Young ceratodus,** shortly after issuing from the egg, magnified ten times. *k* gill-cover, *l* liver. (From *Richard Semon.*)

accounts in his admirable *In the Australian Bush and on the Shores of the Coral Sea* (1903).

Ceratodus is particularly interesting on account of the primitive build of its skeleton ; the cartilaginous skeleton of its two pairs of fins, for instance, has still the orginal form of a bi-serial or feathered leaf, and was on that account described by Gegenbaur as a "primitive fin-skeleton" *(archipterygium)*. On the other hand, the skeleton of the pairs of fins is greatly reduced in the African dipneust *(protopterus)* and the American *(lepidosiren)*. Further, the lungs are double in these *neodipneusta* as in all the other air-breathing vertebrates ; they have on that account been called "double-lunged" *(dipneumones)* in contrast to the ceratodus ; the latter has only a single lung *(monopneumones)*. At the same time the gills also are developed as water-breathing organs in all these lung-fishes. Protopterus has external as well as internal gills.

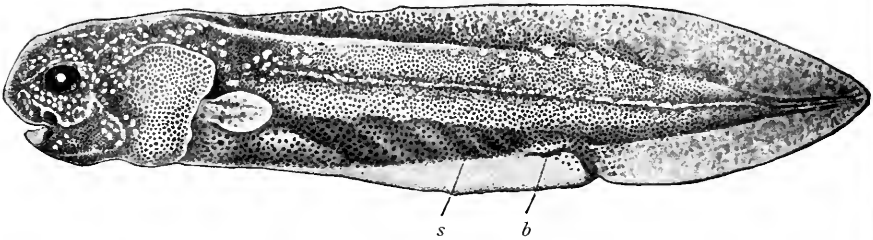


FIG. 313.—**Young ceratodus**, six weeks after issuing from the egg. *s* spiral fold of gut, *b* rudimentary belly-fin. (From *Richard Semon.*)

The paleozoic dipneusts that are in the direct line of our ancestry, and form the connecting-bridge between the ganoids and the amphibia, differ in many respects from their living descendants, but agree with them in the above essential features. This is confirmed by a number of interesting facts that have lately come to our knowledge in connection with the embryonic development of the ceratodus and lepidosiren ; they give us important information as to the stem-history of the lower vertebrates, and therefore of our early ancestors of the paleozoic age.

THIRTIETH TABLE

SYNOPSIS OF THE DIFFERENCES IN ORGANISATION BETWEEN THE FOUR OLDEST GROUPS OF VERTEBRATES

[Both in the class of the *acrania* (1, 2) and that of the *cyclostoma* (3, 4) the original characters of the hypothetical ancestors (1 and 3) are contrasted with the modified features of their modern representatives (2 and 4).]

I. Acrania (skull-less).		**II. Cyclostoma** (jaw-less).	
No cranium or jaws. Perichorda without cartilaginous arches. Epidermis a simple layer of cells. Gullet-groove permanently open. Liver a hollow blind-sac.		Cranium cartilaginous, without jaws. Perichorda forms metamerous cartilaginous arches. Epidermis with several layers of cells. Gullet-groove forms a thyroid gland. Liver a compact gland.	
1. Prospondylia.	**2. Leptocardia.**	**3. Archicrania.**	**4. Marsipobranchia.**
Primitive vertebrates. ⊙ Hypothetical ancestor of all the vertebrates (progressive stem).	Amphioxus. V Living representative of the prospondylia (regressive branch).	Primitive craniotes. ⊙ Hypothetical ancestor of all the craniotes (progressive stem).	Round-mouthed. V Living representative of the archicrania (regressive branch).
Brain a simple round vesicle (anterior swelling of the medullary tube).	Brain atrophied (in embryonic state vesicular, afterwards atrophied).	Brain club-shaped, at first single, afterwards dividing into three vesicles.	Brain with three primary vesicles, afterwards dividing into five secondary ones.
Nasal funnel opening behind in the medullary tube (permanent neuroporus).	Nasal funnel opening at first into the medullary tube, afterwards cut off.	Nasal passage closed against the medullary tube.	Nasal passage closed behind (petromyzontes) or secondarily opening into the gullet (myxinoides).
Eyes well developed.	Eyes atrophied (pigment rudiments).	Eyes well developed.	Eyes small or degenerate.
Auditory vesicles simple, round.	Auditory vesicles completely lost.	Auditory vesicles simple, round, without circular canals.	Auditory vesicles with one or two circular canals.
Gullet-groove (endostyl) permanent, broad.	Gullet-groove (endostyl) permanent, narrow.	Gullet-groove changing into the thyreoidea.	Gullet-groove changed into the thyreoidea.
Gills numerous (at least 8–12 pairs of gullet-clefts) with free openings outwards.	Gill-clefts very numerous, opening into a peribranchial cavity.	Gills 8–12 pairs of pouches (or more), with free openings outwards.	Gills 6–14 pairs of pouches with free (separate or combined) openings.
Heart spindle-shaped, one-chambered.	Heart atrophied, tube-shaped.	Heart with ventricle and auricle.	Heart with ventricle and auricle
Liver a median single blind sac.	Liver a single blind sac on right side.	Liver compact, forming two symmetrical folds.	Liver compact, forming two unequal folds.
Gonades numerous, in metamerous pairs.	Gonades numerous, in metamerous pairs.	Gonades numerous or combined in one pair?	Gonades combined in a single mass.

THIRTY-FIRST TABLE

SYNOPSIS OF THE HEART AND FOOT-FORMATION IN THE VERTEBRATES

Heart-structure in the Vertebrates.	Eight Classes.	Sub-classes of the Vertebrates.	Foot-structure in the Vertebrates.
I. Chief group : **Leptocardia** (tube-hearted). Cold-blooded vertebrates with simple, one-chambered cardiac tube. Heart filled with carbonised blood.	1. **Acrania.**	1. Primitive vertebrates (*prospondylia*). 2. Amphioxina (*cephalocorda*).	I. Chief group : **Vertebrata adactylia** (*impinnata*). Vertebrates without limbs.
II. Chief group : **Ichthyocardia** (fish-hearted). Cold-blooded vertebrates with two-chambered heart (auricle and ventricle). Blood in heart carbonised.	2. **Cyclostoma.**	1. Primitive craniotes (*archicrania*). 2. Pouch-gilled (*marsipobranchia*).	
	3. **Pisces** (fishes).	1. Primitive fishes (*selachii*). 2. Plated fishes (*ganoides*). 3. Bony fishes (*teleostei*).	II. Chief group : **Vertebrata polydactylia** (*pinnifera*). With at first two pairs of fins, each with four fingers or radii.
III. Chief group : **Amphicardia** (reptile-hearted). Cold-blooded vertebrates with three-chambered heart (two auricles and a ventricle). Blood in heart mixed.	4. **Dipneusta.**	1. One-lunged (*monopneumones*). 2. Two-lunged (*dipneumones*).	
	5. **Amphibia.**	1. Mailed amphibia (*phractamphibia*). 2. Naked amphibia (*lissamphibia*).	III. Chief group : **Vertebrata pentadactylia** (*pentanomia*). At first with two pairs of limbs each with three parts (upper bone, lower bone, and foot), and five fingers or toes on each foot.
	6. **Reptilia.**	1. Stem-reptiles (*tocosauria*). 2. Sea-reptiles (*hydrosauria*). 3. Tortoises (*chelonia*). 4. Flying reptiles (*pterosauria*).	
IV. Chief group ; **Thermocardia** (warm-hearted). Warm-blooded vertebrates with four-chambered double heart (two auricles and two ventricles). Left heart with oxydised and right with carbonised blood.	7. **Aves** (birds).	1. Lizard-tailed birds (*saururæ*). 2. Bird-tailed (*ornithuræ*).	
	8. **Mammalia.**	1. Monotrema. 2. Marsupialia. 3. Placentalia.	

CHAPTER XXII.

OUR FIVE-TOED ANCESTORS

Fossil amphibia of the Carboniferous period : mailed amphibia (stegocephala). Transition from aquatic to terrestrial life. Conversion of the many-toed fin into the five-toed foot. Causes and effects of this. Decimal system. Descent of all the higher vertebrates from a five-toed amphibium. Median position of the amphibia between the lower and higher vertebrates. Metamorphosis of the frog. Modification of the organs of circulation and respiration. Various stages in the metamorphosis of the reptiles. Branchial reptiles (proteus and axolotl). Tailed reptiles (salamander). Batrachia (frogs and toads). Chief groups of the amniotes (reptiles, birds, and mammals). Descent of all the amniotes from a lacertilian common ancestor (protamnion). Rhyncocephala, hatteria. First formation of the allantois and the amnion. Division of the amniotes into two lines : reptiles (and birds) and mammals. Transition from the reptiles to the mammals ; sauromammalia. Sub-classes of the mammals : monotremes, marsupials, and placentals.

WITH the phylogenetic study of the four higher classes of vertebrates, which must now engage our attention, we reach much firmer ground and more light in the construction of our genealogy than we have, perhaps, enjoyed up to the present. In the first place, we owe a number of very valuable data to the very interesting class of vertebrates that come next to the dipneusts and have been developed from them—the amphibia. To this group belong the salamander, the frog, and the toad. In earlier days all the reptiles were, on the example of Linné, classed with the amphibia (lizards, serpents, crocodiles, and tortoises). But the reptiles .are much more advanced than the amphibia, and are nearer to the birds in the chief points of their structure. The true amphibia are nearer to the dipneusta and the fishes ; they are also much older than the reptiles. There were plenty of highly-developed (and sometimes large) amphibia during the Carboniferous period ; but the earliest reptiles are only found in the Permian period. It is probable that the amphibia were evolved even earlier—during the Devonian period—from the dipneusta. The extinct amphibia of which we have fossil remains from that remote period (very numerous especially in the Triassic strata) were distinguished for a graceful scaly coat or a powerful bony armour on the skin

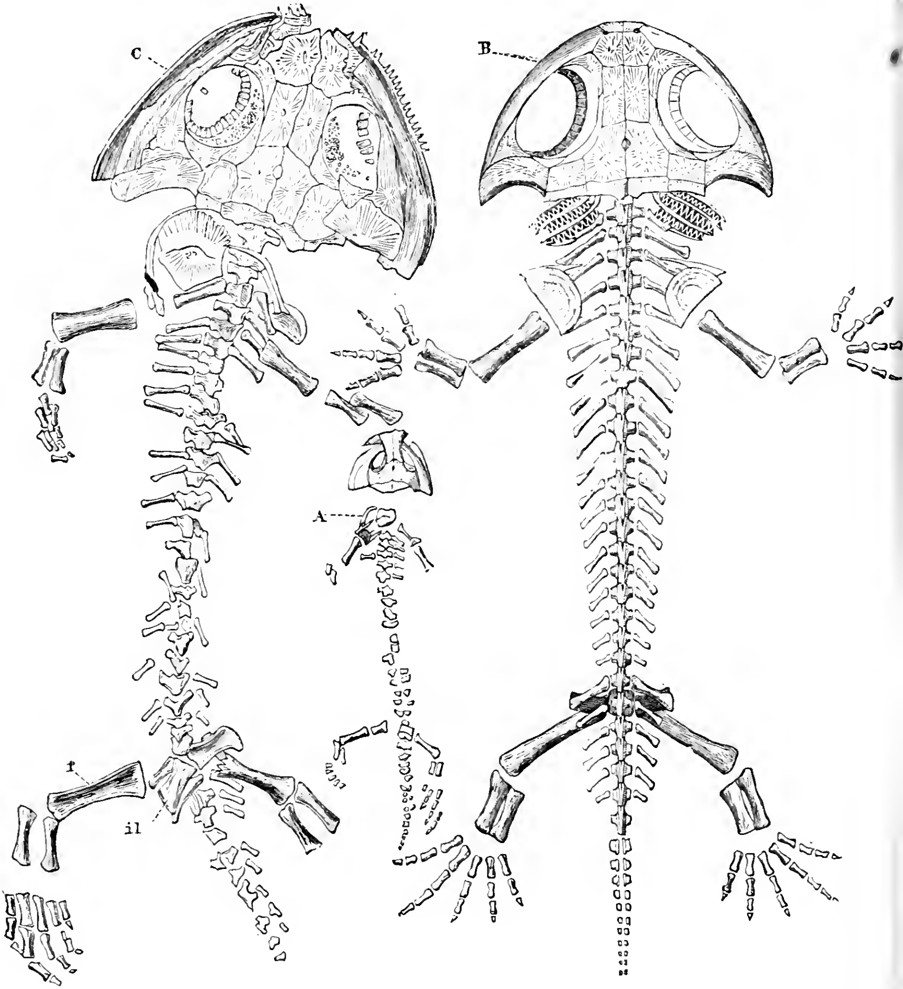


Fig. 314.—**Fossil phractamphibium from the Permian,** found in the Plauen terrain near Dresden *(branchiosaurus amblystomus).* (From *Credner.*) *A* skeleton of a young larva. *B* larva, restored, with gills. *C* the adult form, natural size.

(like the crocodile), whereas the living amphibia have usually a smooth and slippery skin.

The earliest of these armoured amphibia *(phractamphibia)* form the order of stegocephala ("roof-headed"), of which a number of well-preserved impressions and skeletons have been found in the Carboniferous, Permian, and Triassic. Credner discovered in 1866, near Dresden, more than a thousand specimens of the remarkable *branchiosaurus amblystomus* (Fig. 314), many of them well preserved, and was able to establish with some confidence the anatomy and ontogeny of this important ancestral form. The young larvæ of these salamander-like animals (Fig. 314 *A*) showed clearly four pairs of gill-arches (Fig. 314 *B*). Young animals of sixty to seventy mm. in length lost the gill-tufts and breathed by lungs; the trunk was longer, the legs stronger; the belly was covered with a scaly armour.

It is among these paleozoic stegocephala, not among the actual amphibia, that we must look for the forms that are directly related to the genealogy of our race, and are the ancestors of the three higher classes of vertebrates. But even the existing amphibia have such important relations to us in their anatomic structure, and especially their embryonic development, that we may say: Between the dipneusts and the amniotes there was a series of extinct intermediate forms which we should certainly class with the amphibia if we had them before us. In their whole organisation even the actual amphibia seem to be an instructive transitional group. In the important respects of respiration and circulation they approach very closely to the dipneusta, though in other respects they are far superior to them.

This is particularly true of the development of their limbs or extremities. In them we find these for the first time as five-toed feet. The thorough investigations of Gegenbaur have shown that the fish's fins, of which very erroneous opinions were formerly held, are many-toed feet. The various cartilaginous or bony radii that are found in large numbers in each fin correspond to the fingers or toes of the higher vertebrates. The several joints of each fin-radius correspond to the various parts of the toe. Even in the dipneusta the fin is of the same construction as in the fishes; it was afterwards gradually evolved into the five-toed form, which we first encounter in the amphibia. This reduction of the number of the toes to six, and then to five, probably took place in the second half of the Devonian period—at the latest, in the subsequent Carboniferous period—in those dipneusta which we regard as the ancestors of the amphibia. We have several fossil remains of five-toed amphibia from this period. There are numbers of fossil impressions of them in the Triassic of Thuringia *(chirotherium)*.

The fact that the toes number five is of great importance, because they have clearly been transmitted from the amphibia to all the higher vertebrates. Man entirely resembles his amphibian ancestors in this respect, and indeed in the whole structure of the bony skeleton of his five-toed extremities. A careful comparison of the skeleton of the frog with our own is enough to show this. It is well known that this hereditary number of the toes has assumed a very great practical importance from remote times; it is on this "pentadactylism" that our whole system of enumeration (the decimal system applied to measurement of time, mass, weight, etc.) is based. There is absolutely no reason why there should be five toes in the fore and hind feet in the lowest amphibia, the reptiles, and the higher vertebrates, unless we ascribe it to inheritance from a common stem-form. Heredity alone can explain it. It is true that we find less than five toes in many of the amphibia and of the higher vertebrates. But in all these cases we can prove that some of the toes atrophied, and were in time lost altogether. We may, therefore, bracket together the four higher classes of vertebrates, the amphibia and amniotes, under the head of *pentanoma* or *pentadactyla* ("five-toed").

The causes of this evolution of the five-toed foot from the many-toed fin in the amphibian ancestor must be sought in adaptation to the entire change of function that the limbs experienced in passing from an exclusively aquatic to a partly terrestrial life. The many-toed fin had been used almost solely for motion in the water; it had now also to support the body in creeping on the solid ground. This led to a modification both of the skeleton and the muscles of the limbs. The number of the fin-radii was gradually reduced, and sank finally to five. But these five remaining radii became much stronger. The soft cartilaginous radii became bony rods. The rest of the skeleton was similarly strengthened. Thus from the one-armed lever of the many-toed fish-fin arose the improved many-armed lever system of the five-toed amphibian limbs. The movements of the body gained in variety as well as in strength. The various parts of the skeletal system and correlated muscular system began to differentiate more and more. In view of the close correlation of the muscular and nervous systems, this also made great advance in structure and function. Hence we find, as a matter of fact, that the brain is much more developed in the higher amphibia than in the fishes, the dipneusta, and the lower amphibia.

The parts that were most modified by the amphibian life are, as we have seen in the case of the dipneusta, the organs of respiration and circulation. The first advance in organisation that was occasioned by the adoption of life on land was naturally the construction of an organ for breathing air—a lung. This was formed directly from the floating-bladder inherited from the fishes. At first its function was insignificant beside that of the gills, the older organ for water-respiration. Hence we find in the lowest amphibia, the gilled amphibia, that, like the dipneusta, they pass the greater part of their life in the water, and breathe water through gills. They only come to the surface at brief intervals, or creep on to the land, and then breathe air by their lungs. But some of the tailed amphibia—the salamanders—remain entirely in the water when they are young, and afterwards spend most of their time on land. In the adult state they only breathe air through lungs. The same applies to the most advanced of the amphibia, the batrachia (frogs and toads); some of them have entirely lost the gill-bearing larva form.[1] This is also the case with certain small, serpentine amphibia, the cæcilia (which live in the ground like rain-worms).

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[1] The tree-frog of Martinique *(hylodes martinicensis)* loses the gills on the seventh, and the tail and yelk-sac on the eighth, day of fœtal life. On the ninth or tenth day after fecundation the frog emerges from the egg.

The great interest of the natural history of the amphibia consists especially in their intermediate position between the lower and higher vertebrates. The lower amphibia approach very closely to the dipneusta in their whole organisation, live mainly in the water, and breathe by gills; but the higher amphibia are just as close to the amniotes, live mainly on land, and have pulmonary respiration. But in their younger state the latter resemble the former, and only reach the higher stage by a complete metamorphosis. The embryonic development of most of the higher amphibia still faithfully reproduces the stem-history of the whole class, and the various stages of the advance that was made by the lower vertebrates in passing from aquatic to terrestrial life during the Devonian or the Carboniferous period are repeated in the spring by every frog that developes from an egg in our ponds.

The common frog leaves the egg in the shape of a larva, like the tailed salamander (Fig. 315), and this is altogether different from the mature frog (Fig. 316). The short trunk ends in a long tail, with the form and structure of a fish's tail (*s*). There are no limbs at first. The respiration is exclusively branchial, first through external *(k)* and then internal gills. In harmony with this the heart has the same structure as in the fish, and consists of two sections—an atrium that receives the venous blood from the body, and a ventricle that forces it through the arteries into the gills *(ichthyocardia)*.

We find the larvæ of the frog (or tadpoles, *gyrini*) in great numbers in our ponds every spring in this fish-form, using their muscular tails in swimming just like the fishes and young ascidia. When they have reached a certain size, the remarkable metamorphosis from the fish-form to the frog begins. A blind sac grows out of the gullet, and expands into a couple of spacious sacs: these are the lungs. The simple chamber of the heart is divided into two sections by the development of a partition, and there are at the same time considerable changes in the structure of the chief arteries. Previously all the blood went from the auricle through the aortic arches into the gills, but now only part of it goes to the lungs, the other part passing to the lungs through the new-formed pulmonary artery. From this point arterial blood returns to the left auricle of the heart, while the venous blood gathers in the right auricle. As both auricles open into a single ventricle, this contains mixed blood. The dipneust-form has now succeeded to the fish-form. In the further course of the metamorphosis the gills and the branchial vessels entirely disappear, and the respiration becomes exclusively pulmonary. Later, the long swimming tail is lost, and the frog now hops to the land with the legs that have grown meantime *(amphicardia)*.[1]

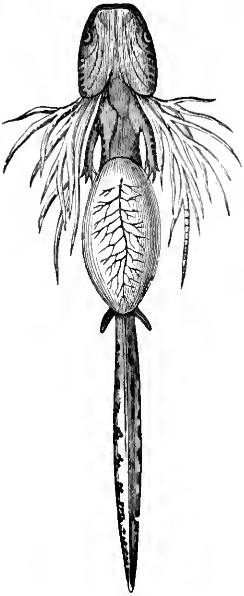

FIG. 315.

FIG. 316.

FIG. 315.—**Larva of the spotted salamander** *(salamandra maculata)*, seen from the ventral side. In the centre a yelk-sac still hangs from the gut. The external gills are gracefully ramified. The two pairs of legs are still very small.

FIG. 316.—**Larva of the common grass-frog** *(rana temporaria)*, or "tad-pole." *m* mouth, *n* a pair of suckers for fastening on to stones, *d* skin-fold from which the gill-cover developes; behind it the gill-clefts, from which the branching gills *(k)* protrude, *s* tail-muscles, *f* cutaneous fin-seam of the tail.

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[1] The metamorphosis of the amphibia lasts longer or shorter according to the species of frog or toad; on the whole, it forms a complete phylogenetic series of the original and full to the later and greatly abbreviated heredity.

This remarkable metamorphosis of the amphibia is very instructive in connection with our human genealogy, and is particularly interesting from the fact that the various groups of actual amphibia have remained at different stages of their stem-history, in harmony with the biogenetic law. We have first of all a very low order of amphibia—the *sozobranchia* ("gilled-amphibia"), which retain their gills throughout life like the fishes. Among others of this group there are the blind salamander of the Adelsberg Grotto *(proteus anguineus)*, the arm-salamander of South Carolina *(siren lacertina)*, and the axolotl of Mexico *(siredon pisciformis)*. All these gilled-salamanders are fish-like, long-tailed animals, and remain throughout life at the same stage as the dipneusts in regard to the organs of respiration and circulation. They have both gills and lungs, and can breathe either water or air as they need. In a second order of the salamanders the gills are lost in the metamorphosis, and when fully grown they have only pulmonary respiration. They are called the "tailed-amphibia" *(sozura)*, because they retain the long tail throughout life. To this order belong the common water-salamander *(triton)*, which is found in great quantities in the ponds during summer, and the black, yellow-spotted ground-salamander *(salamandra)* that lives in damp woods. The latter are among the most remarkable of our native animals, as they are proved by many anatomic peculiarities to be very primitive and little modified vertebrates. Some of the tailed amphibia still retain the gill-clefts in the side of the neck, though they have lost the gills themselves *(menopoma)*. If we force the larvæ of our salamanders (Fig. 315) and tritons to remain in the water, and prevent them from reaching the land, we can in favourable circumstances make them retain their gills. In this fish-like condition they reach sexual maturity, and remain throughout life at the lower stage of the gilled amphibia.

We have the reverse of this experiment in a Mexican gilled salamander, the fish-like axolotl *(siredon pisciformis)*. It was formerly regarded as a permanent gilled amphibium, persisting throughout life at the fish-stage. But some of the hundreds of these animals that are kept in the Botanical Garden at Paris got on to the land for some reason or other, lost their gills, and changed into a form closely resembling the salamander *(amblystoma)*. Other species of the genus became sexually mature for the first time in this condition.[1] This has been regarded as an astounding phenomenon, although every common frog and salamander repeats the metamorphosis in the spring. The whole change from the aquatic and gill-breathing animal to the terrestrial lung-breathing form may be followed step by step in this case. But what we see here in the development of the individual has happened to the whole class in the course of its stem-history.

The metamorphosis goes farther in a third order of amphibia, the *batrachia* or *anura*, than in the salamander. To this belong the various kinds of toads, ringed snakes, water-frogs, tree-frogs, etc. These lose, not only the gills, but also (sooner or later) the tail, during metamorphosis. The different species are not at all alike in this. In most of the batrachia the larvæ very soon abandon the tail, so that in these cases the tail-less frog-form is conspicuous. But others, such as the Brazilian "pseudo-frog" *(pseudes paradoxus)*, and also our native garlic-toad *(pelobates fuscus)*, persist in the fish-form for a long time, and retain a lengthy tail until they reach their full size; hence after metamorphosis they are smaller than before. We find the other extreme in certain frogs that have been discovered lately, which have lost their whole historical metamorphosis, and in which we get from the egg, not the tailed gill-bearing larvæ, but the developed tail-less and gill-less frog. These frogs live in isolated islands with a dry climate, and are often without fresh water for a long time. As fresh water is indispensable for the gill-breathing tadpoles, the frogs have adapted

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[1] There are very different opinions as to the phylogenetic significance of the change of the Mexican axolotl into an amblystoma. These contradictions are due to the fact that *amblystoma Mexicanum* normally retains its gills and becomes sexually mature in this form, while other closely-related species *(A. punctatum, ovatum, fasciatum)* do so only in the salamander form, after losing the gills.

themselves to the local defect, and abandoned their original metamorphosis (thus, for instance, the tree frog of Martinique, *hylodes martinicensis;* see note, p. 581).

The ontogenetic loss of the gills and the tail in the frog and toad can only be explained phylogenetically on the assumption that they are descended from long-tailed amphibia of the salamander type. This is also clear from the comparative anatomy of the two groups. This remarkable metamorphosis is, however, also interesting because it throws a certain light on the phylogeny of the tail-less apes and man. Their ancestors also had long tails and gills like the gilled amphibia, as the tail and the gill-arches of the human embryo clearly show.

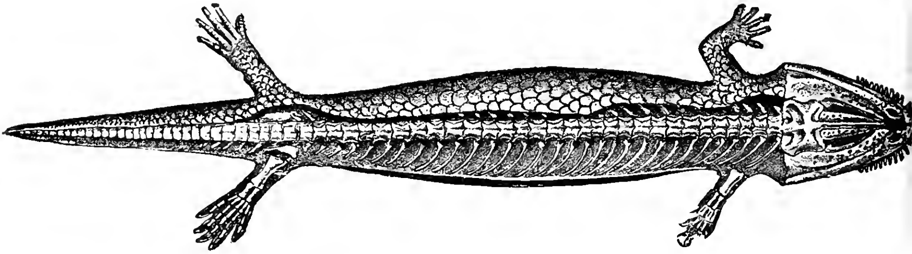

FIG. 317.—**Fossil mailed amphibium,** from the Bohemian Carboniferous *(Seeleya).* (From *Fritsch.*) The scaley coat is retained on the left.

The class of amphibia most certainly contained during the paleozoic age (and even during the Carboniferous period) a series of forms that must be regarded as direct ancestors of the mammals, and therefore of man. But, for comparative anatomical and ontogenetic reasons, we must not seek these amphibian ancestors of ours—as one would be inclined to do, perhaps—among the tail-less batrachia, but among the tailed lower amphibia. We can, with confidence, single out at least two extinct groups as direct ancestors of our race—the gill-breathing stegocephala (Fig. 317) and the lung-breathing mailed amphibia, which had lost their gills. Among the existing smooth amphibia *(lissamphibia)* the older gilled amphibia *(perennibranchia)* still retain the external gills throughout life, while the younger salamanders *(urodela)* only have them in the larva stage. The gill-less amphibian ancestors of the amniotes, which we have to regard as the phylogenetically latest members of the amphibia class, were covered with scales, but otherwise very much like the ordinary salamanders. Nevertheless, in 1725 the fossil skeleton of an extinct salamander (resembling the actual giant salamander of Japan) was described by the Swiss naturalist Scheuchzer as the skeleton of a fossilised man of the period of the deluge! *(Homo diluvii testis.)*

The vertebrate form that comes next to the amphibia in the series of our ancestors is a lizard-like animal, the earlier existence of which can be confidently deduced from the facts of comparative anatomy and ontogeny. The living *hatteria* of New Zealand (Fig. 318) and the extinct rhyncocephala of the Permian period (Fig. 319) are closely related to this important stem form; we may call them the *protamniotes*, or primitive amniotes. All the vertebrates above the amphibia—or the three classes of reptiles, birds, and mammals—differ so much in their whole organisation from all the lower vertebrates we have yet considered, and have so great a resemblance to each other, that we put them all together in a single group with the title of *amniotes*. In these three classes alone we find the remarkable embryonic membrane, already mentioned, which we called the *amnion;* a cenogenetic adaptation that we may regard as a result of the sinking of the growing embryo into the yelk-sac.[1] (Cf. p. 312.)

All the amniotes known to us—all reptiles, birds, and mammals (including man)—agree in so many important points of internal structure and development that their descent from a common ancestor can be affirmed with tolerable certainty. If the evidence of comparative anatomy and ontogeny is ever entirely beyond suspicion, it is certainly the case here. All the peculiarities that accompany and follow the formation of the amnion, and that we have

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[1] The formation of the amnion in the three higher classes of vertebrates has no connection with the similarly but independently acquired *(analogous*, but not *homologous)* amnion of the higher articulates. The resemblance is based on convergence. The valuable protection that the amnion affords to the delicate embryo, sinking in the yelk, has led to the formation of the same organ in the *amniote* vertebrates and the articulates.

learned in our consideration of human embryology; all the peculiarities in the development of the organs which we will presently follow in detail; finally, all the principal special features of the internal structure of the full-grown amniotes—prove so clearly the common origin of all the amniotes from a single extinct stem-form that it is difficult to entertain the idea of their polyphyletic evolution from several independent stems. This unknown common stem-form is our primitive amniote *(protamnion)*. In outward appearance it was probably something between the salamander and the lizard.

It is very probable that some part of the Permian period was the age of the origin of the protamniotes. This follows from the fact that the amphibia are not fully developed until the Carboniferous period, and that the first fossil reptiles *(palæhatteria, homœosaurus, proterosaurus)* are found towards the close of the Permian period. Among the important changes of the vertebrate organisation that determined the rise of the first amniotes from salamandrine amphibia during this period the following three are especially noteworthy: the entire disappearance of the water-breathing gills and the conversion of the gill-arches into other organs, the formation of the allantois or primitive urinary sac, and the development of the amnion.

One of the most salient characteristics of the amniotes is the complete loss of the respiratory gills. All amniotes, even if living in water (such as sea-serpents and whales), breathe air through lungs, never water through gills. All the amphibia (with very rare exceptions) retain their gills for some time when young, and have for a time (if not permanently) branchial respiration; but after these there is no question of branchial respiration. The protamnion itself must have entirely abandoned water-breathing. Nevertheless, the gill-arches are preserved by heredity, and develop into totally different (in part rudimentary) organs—various parts of the bone of the tongue, the frame of the jaws, the organ of hearing, etc. But we do not find in the embryos of the amniotes any trace of gill-leaves, or of real respiratory organs on the gill-arches.

With this complete abandonment of the gills is probably connected the formation of another organ, to which we have already referred in embryology—namely, the allantois or primitive urinary sac (cf. p. 375). It is very probable that the urinary bladder of the dipneusts is the first structure of the allantois. We find in these a urinary bladder that proceeds from the lower wall of the hind end of the gut, and serves as receptacle for the renal secretions. This organ has been transmitted to the amphibia, as we can see in the frog. But it is only in the three higher classes of vertebrates that the allantois becomes a special embryonic development, proceeds at an early stage far out of the body of the embryo, and forms a sac filled with fluid, on which are distributed a considerable number of large blood-vessels. This sac always undertakes a part of the function of nutrition. In the higher mammals and man the same urinary sac afterwards forms the placenta.

The formation of the amnion and the allantois and the complete disappearance of the gills and exclusively pulmonary respiration are the chief characteristics that distinguish the amniotes from the lower vertebrates we have hitherto considered. To these we may add several subordinate features that are transmitted to all the amniotes, and to none of the anamnia. One striking embryonic character of the amniotes is the great curve of the head and neck in the embryo. In the anamnia the embryo is either fairly straight from the first, or else the whole body is bent like a sickle, corresponding to the curve of the yelk-sac on which it lies on its ventral side; but there are no sharp angles in the course of the long axis. In the amniotes, however, there is a conspicuous curve of the body from an early stage (p. 364); the back of the embryo is greatly curved, the head sinks down towards the breast almost at a right angle, and the tail is turned up towards the belly. The tail-end is pushed up so far that it often almost touches the forehead (Plates VIII.-XIII.). This conspicuous triple curve of the embryo, which we have considered in the ontogenetic section, is a common characteristic of the embryos of reptiles, birds, and mammals (cf. Figs. 207 and 208).

But we also find an advance in the structure of several of the internal organs of the amniotes which raises them above the highest of the anamnia. In particular, a partition is formed in the simple ventricle of the heart, dividing into right and left chambers. In connection with the complete metamorphosis of the gill-arches we find a further development of the auscultory organs. Also, there is a great advance in the structure of the brain, skeleton, muscular system, and other parts. Finally, one of the most important changes is the re-construction of the kidneys. In all the earlier vertebrates we have found the primitive kidneys as excretory organs, and these appear at an early stage in the embryos of all the higher vertebrates up to man. But in the amniotes these primitive kidneys cease to act at an early stage of embryonic life, and their function is taken up by the permanent or secondary kidneys, which develop from the terminal section of the prorenal ducts.

Taking all these peculiarities of the amniotes together, it is impossible to doubt that all the animals of this group—all reptiles, birds, and mammals—have a common origin, and form a single blood-related stem. Our own race belongs to this stem. Man is, in every feature of his organisation and embryonic development, a true amniote, and has descended from the protamnion with all the other amniotes. Though they appeared at the end (possibly even in the middle) of the paleozoic age, the amniotes only reached their full development during the mesozoic age. The birds and mammals made their first appearance during this period. Even the reptiles show their greatest growth at this time, so that it is called "the reptile age." The extinct protamnion, the ancestor of the whole group, belongs in its whole organisation to the reptile class. The ancient Permian transitional group, to which these protamniotes belong, have been designated the *tocosauria* (stem-reptiles) in my *Systematic Phylogeny of the Vertebrates*, and have been divided into three orders: (1) Proreptilia (*protamnion*, *palæhatteria*, and *sauromammalia)*; (2) progonosauria *(proterosaurus* and *mesosaurus)*; (3) rhyncocephalia *(rhyncosaurus* and *hatteria)*.

The genealogical tree of the amniote group is clearly indicated in its chief lines by their paleontology, comparative anatomy, and ontogeny. The group succeeding the protamnion divided into two branches. The branch that will claim our whole interest is the class of the mammals. The other branch, which developed in a totally different direction, and only comes in contact with the mammals at its root, is the combined group of the reptiles and birds; these two classes may, with Huxley, be conveniently grouped together as the *sauropsida*. Their common stem-form is an extinct lizard-like reptile of the order of the rhyncocephalia. From this have been developed in various directions the serpents, crocodiles, tortoises, etc.—in a word, all the members of the reptile class. But the remarkable class of the birds has also been evolved directly from a branch of the reptile group, as is now established beyond question. The embryos of the reptiles and birds are identical until a very late stage, and have an astonishing resemblance even later. (Cf. Plates VIII., IX., and X.) Their whole structure agrees so much that no anatomist now questions the descent of the birds from the reptiles. On the other hand, the mammal line has descended from the group of the sauromammalia, a different branch of the proreptilia. It is connected at its deepest roots with the reptile line, but it then diverges completely from it and follows a distinctive development. Man is the highest outcome of this class, the "crown of creation."

The phylogenetic hypothesis, that the three higher vertebrate classes represent a single amniote-stem, and that the common root of this stem is to be found in the amphibian class, is now generally admitted. I advanced this hypothesis in my *Generelle Morphologie* in 1866, and gave the name of *protamniotes*, afterwards *proreptilia* or *tocosauria*, to the hypothetical common stem-group. But it was not until much later that the many paleozoic fossils were discovered which gave a solid paleontological foundation to the hypothesis I had raised on the facts of comparative anatomy and ontogeny. Only in the course of the last two decades (since 1881) did the able studies of Credner and Cope give us a closer acquaintance with the important orders of vertebrates that have so much interest in connection with this section of our genealogy—the Carboniferous *stegocephala*, with which the series of pentanomous (five-toed) vertebrates begins, and the Permian *tocosauria*, which descend from the preceding and are the root of the amniote stem.

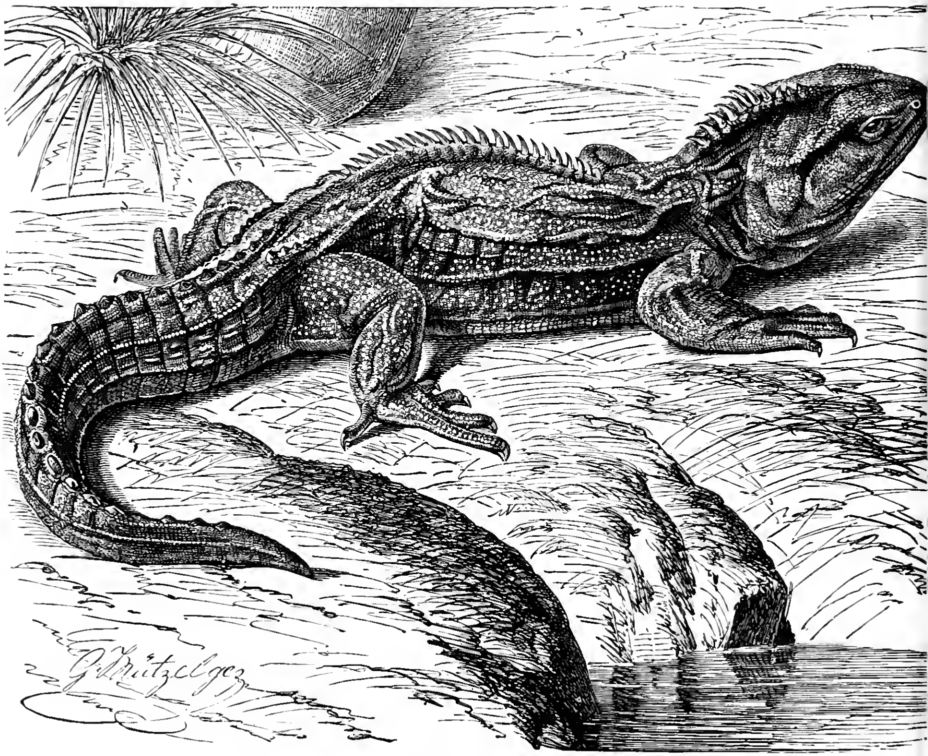


FIG. 318.—**The bridge-lizard** *(hatteria punctata = sphenodon punctatus)* of New Zealand. The sole surviving proreptile. (From *Brehm*.)

The instructive group of the Permian tocosauria, the common root from which the divergent stems of the sauropsids and mammals have issued, merits our particular attention as the stem-group of all the amniotes. Fortunately a living representative of this extinct ancestral group has been preserved to our day; this is the remarkable bridge-lizard of New Zealand, *hatteria punctata* (Fig. 318). Externally it differs little from the ordinary lizard; but in many important points of internal structure, especially in the primitive construction of the vertebral column, the skull, and the limbs, it occupies a much lower position, and approaches its amphibian ancestors, the stegocephala. Hence hatteria is the phylogenetically oldest of all living reptiles, an isolated survivor from the Permian period, closely resembling the common ancestor of the amniotes. It must differ so little from this extinct form, our hypothetical protamniote, that we put it next to the proreptilia. The remarkable Permian *palæhatteria*, that Credner discovered in the Plauen terrain at Dresden in 1888, belongs to the same group (Fig. 320).

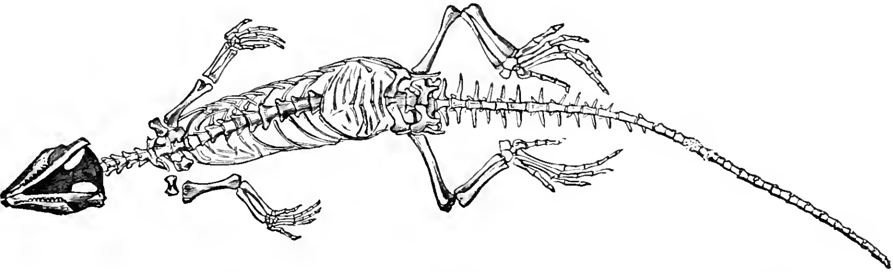


FIG. 319.—**Homœosaurus pulchellus,** a Jurassic proreptile from Kehlheim. (From *Zittel.*)

The Jurassic genus *homœosauras* (Fig. 319), of which well-preserved skeletons are found in the Solenhofen schists, is perhaps still more closely related to them. The Permian proterosauria or progonosauria diverge a little farther from the stem-forms; to these belongs the famous "primitive lizard" of the Eisenach cupriferous slate; it was described as a "crocodile" by the Berlin physician, Spener, in 1706, and afterwards called the *proterosauras Speneri* in his honour.

Unfortunately, the numerous fossil remains of Permian and Triassic tocosauria that we have found in the last two decades are, for the most part, most imperfectly preserved. Very often we can make only precarious inferences from these skeletal fragments as to the anatomic characters of the soft parts that went with the bony skeleton of the extinct

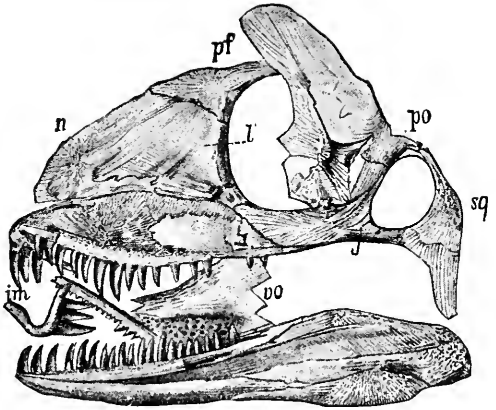


Fig. 320.—**Skull of a Permian bridge-lizard** *(palæhatteria longicaudata)*. (From *Credner*.) *n* nasal bone, *pf* frontal bone, *l* lachrymal bone, *po* postorbital bone, *sq* covering bone, *i* cheek-bone, *vo* plough-bone, *im* inter-maxillary.

tocosauria. Hence it has not yet been possible to arrange these important fossils with any confidence in the ancestral series that descend from the protamniotes to the sauropsids on the one side and the mammals on the other. Opinions are particularly divided as to the place in classification and the phylogenetic significance of the remarkable *theromorpha*. Cope gives this name to a very interesting and extensive group of extinct terrestrial reptiles, of which we have only fossil remains from the Permian and Triassic strata. Forty years ago some of these therosauria (fresh-water animals) were described by Owen as *anomodontia*. But during the last twenty years the distinguished American paleontologists, Cope and Osborn, have

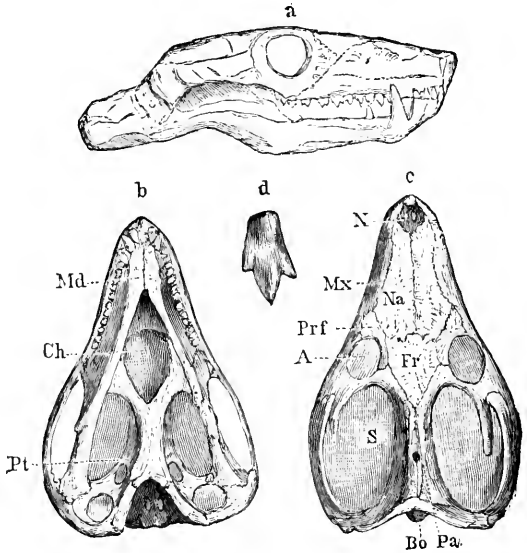


Fig. 321.—**Skull of a Triassic theromorphum** *(galesaurus planiceps)*, from the Karoo formation in South Africa. (From *Owen*.) *a* from the right, *b* from below, *c* from above, *d* tricuspid tooth. *N* nostrils, *NA* nasal bone, *Mx* upper jaw, *Prf* prefrontal, *Fr* frontal bone, *A* eye-pits, *S* temple-pits, *Pa* occipital eye, *Bo* joint at back of head, *Pt* wing-bone, *Md* lower jaw.

greatly increased our knowledge of them, and have claimed that the stem-forms of the mammals must be sought in this order. As a matter of fact, the theromorpha are nearer to the mammals in the chief points of structure than any other reptiles. This is especially true of the thereodontia, to which the *pureosauria* and *pelycosauria* belong (Fig. 321). The whole structure of their pelvis and hind-feet has attained the same form as in the monotremes, the lowest mammals. The formation of the scapula and the quadrate bone shows an approach to the mammals, such as we find in no other group of reptiles. The teeth also are already divided into incisors, canines, and molars. Nevertheless, it is very doubtful whether the theromorpha really are in the ancestral line of the sauromammals, or lead direct from the tocosauria to the earliest mammals. Other experts on this group believe that it is an independent legion of the reptiles, connected, perhaps, at its lowest root, with the sauromammals, but developed quite independently of the mammals—though parallel to them in many ways. I have gone fully into this difficult question in my *Systematic Phylogeny* (pp. 301–307); and I have advanced the hypothesis that one order of the theromorpha—namely, the anomodontia—is rather to be regarded as the stem-group of the chelonia.

One of the most important of the zoological facts that we rely on in our investigation of the genealogy of the human race is the position of man in the mammal class. However different the views of zoologists may have been as to this position in detail, and as to his relations to the apes, no scientist has ever doubted that man is a true mammal in his whole organisation and development. Linné drew attention to this fact in the first edition of his famous *Systema Naturæ* (1735). As will be seen in any museum of anatomy or any manual of comparative anatomy, the human frame has all the characteristics that are common to the mammals and distinguish them conspicuously from all other animals.

If we examine this undoubted fact from the point of view of phylogeny, in the light of the theory of descent, it follows at once that man is of a common stem with all the other mammals, and comes from the same root as they. But the various features in which the mammals agree and by which they are distinguished are of such a character as to make a polyphyletic hypothesis quite inadmissible. It is impossible to entertain the idea that all the living and extinct mammals come from a number of separate roots. If we accept the general theory of evolution, we are bound to admit the monophyletic hypothesis of the descent of all the mammals (including man) from a single mammalian stem-form. We may call this long extinct root-form and its earliest descendants (a few genera of one family) "primitive mammals" or "stem-mammals" *(promammalia).* As we have already seen, this root-form developed from the primitive proreptile stem in a totally different direction from the birds, and soon separated from the main stem of the reptiles. The differences between the mammals and the reptiles and birds are so important and characteristic that we can assume with complete confidence this division of the vertebrate stem at the commencement of the development of the amniotes. The reptiles and birds, which we group together as the *sauropsids*, generally agree in the characteristic structure of the skull and brain, and this is notably different from that of the mammals. In most of the reptiles and birds the skull is connected with the first cervical vertebra (the *atlas)* by a single, and in the mammals (and amphibia) by a double, condyle at the back of the head. In the former the lower jaw is composed of several pieces, and connected with the skull so that it can move by a special maxillary bone (the *quadratum);* in the mammals the lower jaw consists of one pair of bony pieces, which articulate directly with the temporal bone. Further, in the sauropsids the skin is clothed with scales or feathers; in the mammals with hair. The red blood-cells of the former have a nucleus; those of the latter have not. In fine, two quite characteristic features of the mammals, which distinguish them not only from the birds and reptiles, but from all other animals, are the possession of a complete diaphragm and of mammary glands that produce the milk for the nutrition of the young. It is only in the mammals that the diaphragm forms a transverse partition of the body-cavity, completely separating the pectoral from the abdominal cavity (cf. p. 329, Plate VII., Fig. 16 *z*). It is only in the mammal that the mother suckles its young, and this rightly gives the name to the whole class (*mamma* = breast).

From these pregnant facts of comparative anatomy and ontogeny it follows absolutely that the whole of the mammals belong to a single natural stem, which branched off at an early date from the reptile-root. It follows further with the same absolute certainty that the human race is also a branch of this stem. Man shares all the characteristics I have described with all the mammals, and differs in them from all other animals. Finally, from these facts we deduce with the same confidence those advances in the vertebrate organisation by which one branch of the sauromammals was converted into the stem-form of the mammals. Of these advances the chief were: (1) The characteristic modification of the skull and the brain; (2) the development of a hairy coat; (3) the complete formation of the diaphragm; and (4) the construction of the mammary glands and adaptation to suckling. Other important changes of structure proceeded step by step with these.

The epoch at which these important advances were made, and the foundation of the vertebrate class was laid, may be put with great probability in the first section of the mesozoic or secondary age—the Triassic period. The oldest fossil remains of mammals that we know were found in strata that belong to the earliest Triassic period—the upper Keuper. We find many remains of the oldest sauria in the same strata. It is certainly possible that the stem-forms of the mammals were developed earlier (perhaps towards the close of the paleozoic age, in the Permian period) from the tocosauria. But as yet we have no fossil remains of them from that period. Moreover, they are still very rare during the whole mesozoic age—the Triassic, Jurassic, and Cretaceous periods—and seem to indicate a very sparse development of the class at this time. The reptiles play the chief part in this age; the mammals are quite in the background. Unfortunately, our knowledge of the mesozoic mammals is almost restricted to lower jaws; we have only insignificant traces here and there of the rest of the skeleton. One of the earliest forms is the genus *dromatherium*, from the North American Triassic (Fig. 322). Their teeth still strikingly recall those of the pelycosauria. Hence we may assume that this small and probably insectivorous mammal belonged to the stem-group of the promammals. To the same group belongs also, according to Bardeleben, a remarkable mesozoic transitional form, the limbs of which were described by Seeley under the name of *theriodesmus phylarchus*. The majority of the earlier fossil mammal remains that we find in the mesozoic deposits (especially the Jurassic) belong to marsupials. We do not find any positive trace among them of the third and most advanced division of the mammals—the placentals. These (including man) are much younger, and we do not find indisputable fossil remains of them until the cenozoic age, or the Tertiary period. This paleontological fact is very important, because it fully harmonises with the evolutionary succession of the mammal orders that is deduced from their comparative anatomy and ontogeny.

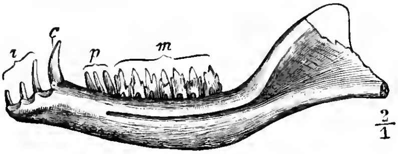


FIG. 322.—**Lower jaw of a primitive mammal or promammal** (*dromatherium silvestre*), from the North American Triassic. *i* incisors, *c* canine, *p* premolars, *m* molars. (From *Döederlein*.)

The latter science teaches us that the whole mammal class divides into three main groups or sub-classes, which correspond to three successive phylogenetic stages. These three stages, which also represent three important stages in our human genealogy, were first distinguished in 1816 by the eminent French zoologist, Blainville, and received the names of *ornithodelphia*, *didelphia*, and *monodelphia*, according to the construction of the female organs (*delphys* = uterus or womb). Huxley afterwards gave them the names of *prototheria*, *metatheria*, and *epitheria*.

But the three sub-classes differ so widely from each other, not only in the construction of the sexual organs, but in many other respects also, that we may confidently draw up the following important phylogenetic thesis: The monodelphia or placentals descend from the didelphia or marsupials; and the latter, in turn, are descended from the monotremes or ornithodelphia.

Thus we must regard as the twenty-first stage in our genealogical tree the earliest and lowest chief group of the mammals—the sub-class of the monotremes ("cloaca-animals," ornithodelphia, or prototheria, Figs. 323 and 324). They take their name from the cloaca which they share with all the lower vertebrates. This cloaca is the common outlet for the passage of the excrements, the urine, and the sexual products. The urinary ducts and sexual canals open into the hindmost part of the gut, while in all the other mammals they are separated from the rectum and anus. The latter have a special uro-genital outlet *(porus urogenitalis)*. The bladder also opens into the cloaca in the monotremes, and, indeed, apart from the two urinary ducts; in all the other mammals the latter open directly into the bladder. It was proved by Haacke and Caldwell in 1884 that the monotremes lay large eggs like the reptiles, while all the other mammals are viviparous. In 1894 Richard Semon further proved that these large eggs, rich in food-yelk, have a partial segmentation and discoid gastrulation, as I had hypothetically assumed in 1876; here again they resemble their reptilian ancestors. The construction of the mammary gland is also peculiar in the monotremes. In them the glands have no teats for the young animal to suck, but there is a special part of the breast pierced with holes like a sieve, from which the milk issues, and the young monotreme must lick it off. On this account they have also been called "teat-less" *(amasta)*. Further, the brain of the monotremes is very little advanced. It is feebler than that of any of the other mammals. The fore-brain or cerebrum, in particular, is so small that it does not cover the cerebellum. In the skeleton (Fig. 324) the formation of the scapula among other parts is curious; it is quite

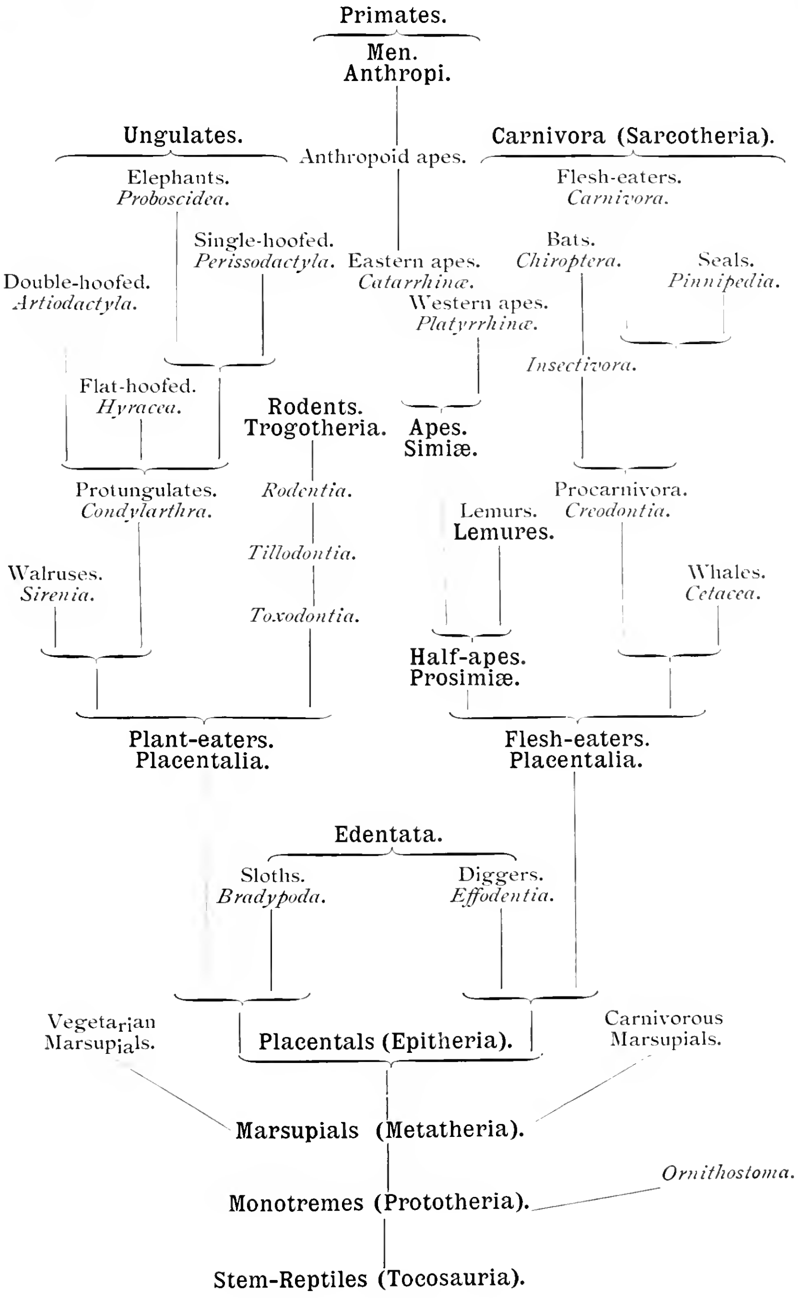
THIRTY-SECOND TABLE

SYNOPSIS OF THE PHYLOGENETIC SYSTEM OF THE MAMMALS

Sub-classes of the Mammals.	**Legions of the Mammals.**	**Orders of the Mammals.**	**Classification names of Orders.**
I. Sub-class : **Monotrema** (ornithodelphia).	I. **Prototheria.**	1. Promammals.	*Promammalia.*
		2. Pantotheria.	*Tricuspidata.*
		3. Allotheria.	*Multituberculata.*
		4. Duck-bills.	*Ornithostoma.*
II. Sub-class : **Marsupialia** (didelphia).	II. **Metatheria.** Marsupials.	5. Promarsupials.	*Prodidelphia.*
		6. Carnivorous marsupials.	*Polyprotodontia.*
		7. Vegetal marsupials.	*Diprotodontia.*
III. Sub-class : **Placentalia** (monodelphia) or **Epitheria.** —— (III.-V.: Lower Placentals, generally without decidua.) —— (VI.-IX.: Higher Placentals, generally with decidua.)	Proplacentals. III. **Mallotheria.**	8. Ictopsala.	*Banotheria.*
		9. Lemuravala.	*Idotheria.*
	IV. **Trogontia.** Rodents.	10. Prorodents.	*Tillodontia.*
		11. Stem-rodents.	*Typotheria.*
		12. Chief-rodents.	*Rodentia.*
	V. **Edentata** (few teeth).	13. Diggers.	*Effodienta.*
		14. Sloths.	*Bradypoda.*
	VI. **Ungulata.** Hoofed animals.	15. Protungulates.	*Condylarthra.*
		16. Single-hoofed.	*Perissodactyla.*
		17. Double-hoofed.	*Artiodactyla.*
		18. Heavy-hoofed.	*Amblypoda.*
		19. Muzzle-hoofed.	*Proboscidea.*
		20. Flat-hoofed.	*Hyracea.*
	VII. **Ceto-morpha.** Whales.	21. Whales.	*Cetacea.*
		22. Walruses.	*Sirenia.*
	VIII. **Sarco-theria.** Carnassia beasts of prey.	23. Insect-eaters.	*Insectivora.*
		24. Procarnivora.	*Creodontia.*
		25. Carnivora.	*Carnivora.*
		26. Seals.	*Pinnipedia.*
		27. Chiroptera.	*Chiroptera.*
	IX. **Primates.**	28. Lemurs.	*Prosimiæ.*
		29. Apes.	*Simiæ.*
		30. Man.	*Anthropi.*

THIRTY-THIRD TABLE

GENEALOGICAL TREE OF THE MAMMALS



different from that of the other mammals, and rather agrees with that of the reptiles and amphibia. Like these, the monotremes have a strongly developed *caracoideum*, a powerful bone that connects the scapula with the sternum. In all the other mammals (and man) this bone degenerates, combines with the shoulder-blade, and seems to be merely an unimportant process of this.

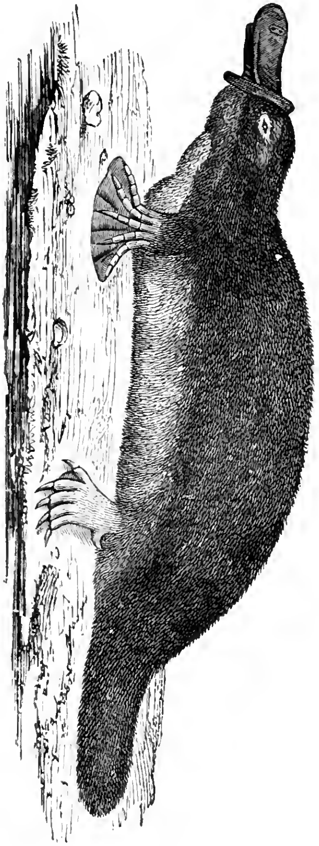


FIG. 323.

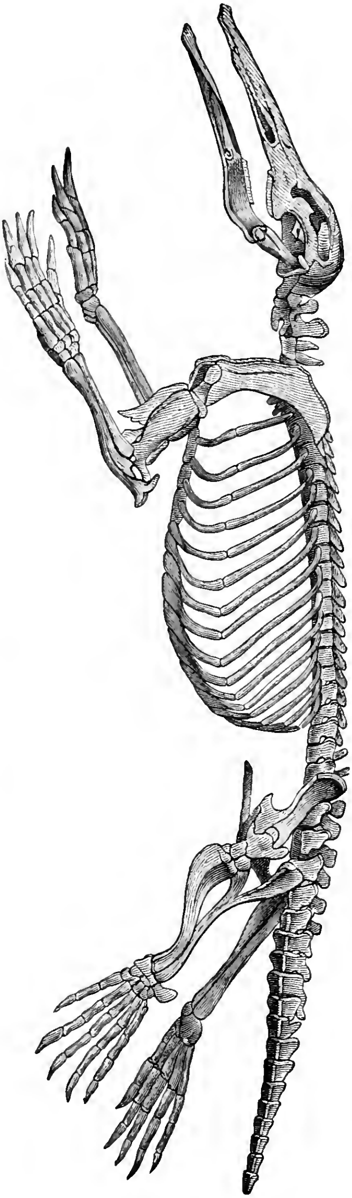


FIG. 324.

FIG. 323.—The water-ornithorhyncus *(ornithorhyncus paradoxus).*
FIG. 324—Skeleton of the preceding.

From these and other less prominent characteristics it follows absolutely that the monotremes occupy the lowest place among the mammals, and represent a transitional group between the tocosauria and the rest of the mammals. All these remarkable reptilian characters must have been possessed by the stem-form of the whole mammal class, the promammal of the Triassic period, and have been inherited from the proreptiles.

During the Triassic and Jurassic periods the sub-class of the monotremes was represented by a number of different stem-mammals. Numerous fossil remains of them have lately been discovered in the mesozoic strata of Europe, Africa, and America. To-day there are only two surviving specimens of the group, which we place together in the family of the duck-bills, *ornithostoma*. They are confined to New Holland and the neighbouring island of Van Diemen's Land (or Tasmania); they become scarcer every year, and will soon, like their blood-relatives, be counted among the extinct animals. One form lives in the rivers, and builds subterraneous dwellings on the banks; this is the *ornithorhyncus paradoxus*, with webbed feet, a thick soft fur, and broad flat jaws, which look very much like the bill of a duck (Figs. 323, 324). The other form, the land duck-bill, or billed hedge-hog *(echidna hystrix)*, is very much like the ant-eaters in its habits and the peculiar construction of its thin snout and very long tongue; it is covered with needles, and can roll itself up like a hedge-hog. A cognate form *(parechidna Bruyni)* has lately been found in New Guinea.

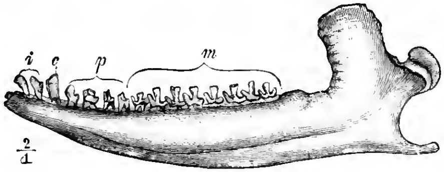


Fig. 325.—**Lower jaw of a promammal** *(dryolestes priscus)*, from the Jurassic of the Felsen strata. (From *Marsh*.)

These modern ornithostoma are the scattered survivors of the vast mesozoic group of monotremes; hence they have the same interest in connection with the stem history of the mammals as the living stem-reptiles *(hatteria)* for that of the reptiles, and the isolated acrania *(amphioxus)* for the phylogeny of the vertebrate stem. Hence, it was a very useful thing of Professor Richard Semon to spend two years (1891 and 1892) in the lonely bush of East Australia, in order to make a thorough study of the biology, and especially the embryology, of these "living fossils." The valuable results of his inquiry are given in his large work, *Zoological Journeys in Australia and the Malay Archipelago;* the chief of them are also given in his popular *In the Australian Bush.*

The Australian duck-bills are distinguished externally by a tooth-less bird-like beak or snout. This absence of real bony teeth is a late result of adaptation, as in the tooth-less placentals *(edentata,* armadillos and ant-eaters). The extinct monotremes, to which the promammalia belonged, must have had developed teeth, inherited from the reptiles. The ancient carnivorous pantotheria *(tricuspidata)* had a full set of carnivorous teeth, with simple incisors, conical canines, and tricuspid molars—the two families of the dromatheria and the triconodonta (Fig. 325). But the teeth of the vegetarian allotheria *(multituberculata)* were incomplete; the rodent-like incisors are separated by a wide gap from the molars, which have two or three rows of protuberances. Lately small rudiments of real molars have been discovered in the young of the ornithorhyncus, which has horny plates in the jaws instead of real teeth. They are of the same shape as those of many *multituberculata* that have been found in the uppermost strata of the Keuper in Würtemberg and in England *(microlestes antiquus).* Other and more specialised teeth of these allotheria are found fossilised in the Jurassic and Cretaceous *(bolodon, plagiaulax).*

The living ornithostoma and the stem-forms of the marsupials (or *didelphia)* must be regarded as two widely diverging lines from the promammals. This second sub-class of the mammals is very interesting as a perfect intermediate stage between the other two. While the marsupials retain a great part of the characteristics of the monotremes, they have also acquired some of the chief features of the placentals. Some features are also peculiar to the marsupials, such as the construction of the male and female sexual organs and the form of the lower jaw. The marsupials are distinguished by a peculiar hook-like bony process that bends from the corner of the lower jaw and points inwards. As most of the placentals have not this process, we can, with some probability, recognise the marsupial from this feature alone. Most of the mammal remains that we have from the Jurassic and Cretaceous deposits are merely lower jaws. We have the jaws of many mesozoic mammals of whose existence we should otherwise have been totally unaware, as the rest of the frame has perished. If we went by the ordinary logic which the "exact" critics of the theory of evolution apply in paleontology, we should be bound to conclude that these animals had no other bones but the lower jaw. However, the explanation is really very simple. As the lower jaw of the mammal is a massive and particularly solid bone, but loosely connected with the skull, it easily drops off the corpse in the river, falls to the bottom, and is preserved in the mud. The rest of the corpse is rolled on further, and is gradually destroyed. Now, most of the mammal lower jaws that have been found in the Jurassic deposits at Stonesfield and Purbeck have the peculiar hook-like process that characterises the lower jaw of the marsupial. On the strength of this paleontological fact, we may suppose that they belonged to marsupials. Placentals do not seem to have existed at the middle of the mesozoic age—not until towards its close (in the Cretaceous period). At all events, we have no fossil remains of indubitable placentals from that period.

The existing marsupials, of which the plant-eating kangaroo and the carnivorous opossum (Fig. 326) are the best known, differ a good deal in structure, shape, and size, and correspond in many respects to the various orders of placentals. Most of them live in Australia, New Holland, and a small part of the Australian and East Malayan islands. There is now not a single living marsupial on the mainland of Europe, Asia, or Africa. It was very different during the mesozoic and even during the cenozoic age. The sedimentary deposits of these periods contain a great number and variety of marsupial remains, sometimes of a colossal size, in various parts of the earth, and even in Europe. We may infer from this that the existing marsupials are the remnant of an extensive earlier group that was distributed all over the earth. It had to give way in the struggle for life to the more powerful placentals during the Tertiary period. The survivors of the group were able to keep alive in Australia and South America because the one was completely separated from the other parts of the earth during the whole of the Tertiary period, and the other during the greater part of it.

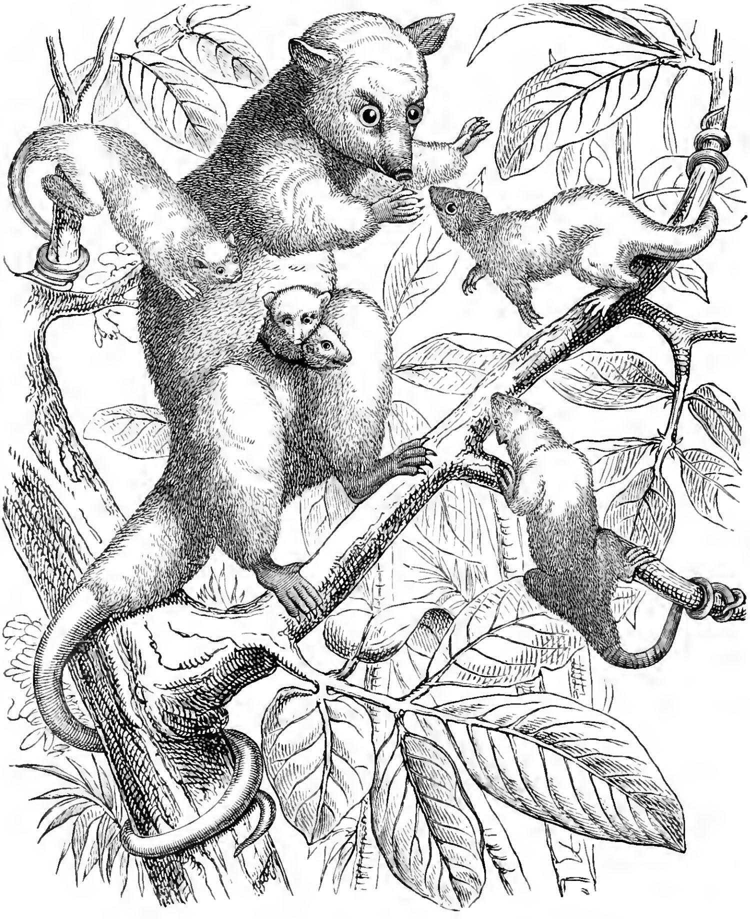


FIG. 326.—**The crab-eating opossum** *(philander cancrivorus).* The female has three young in the pouch. (From *Brehm.*)

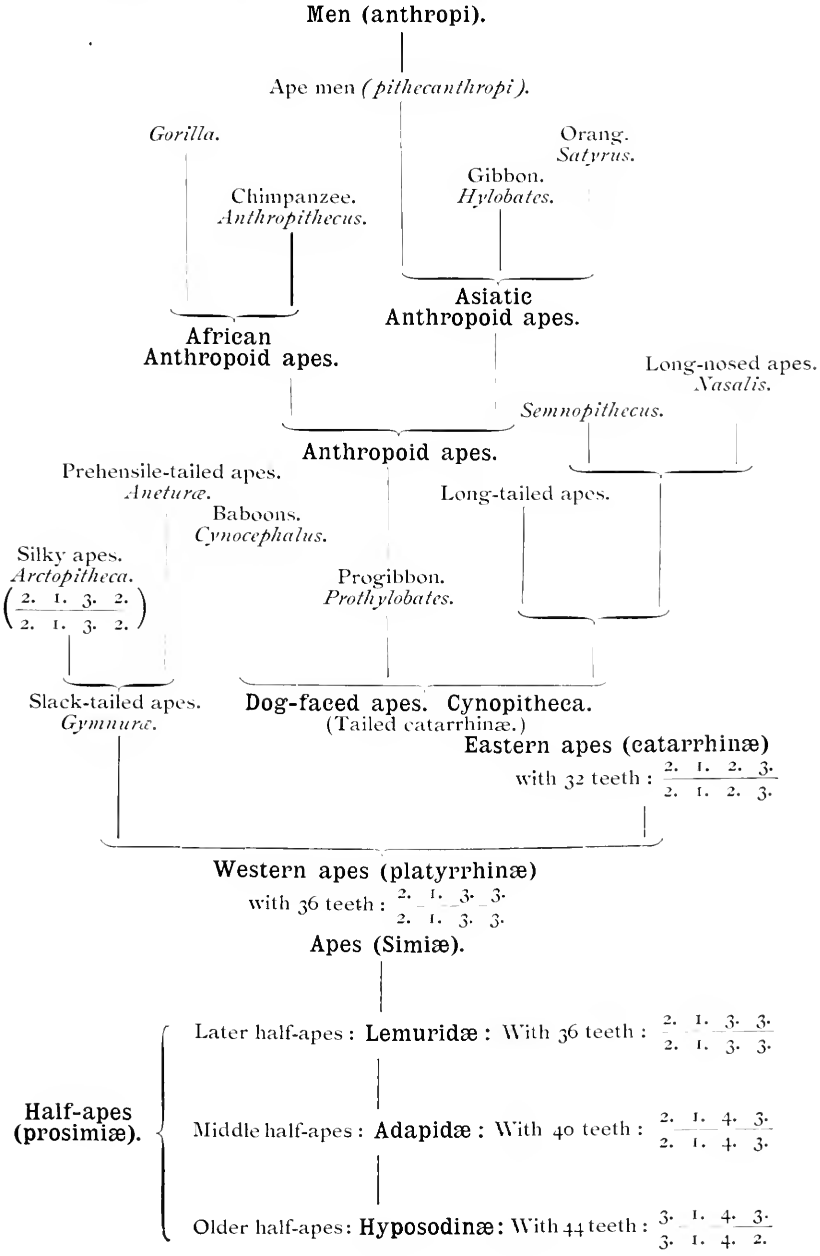
From the comparative anatomy and ontogeny of the existing marsupials we may draw very interesting conclusions as to their phylogenetic intermediate position between the earlier monotremes and the later placentals. The defective development of the brain (especially the cerebrum), the possession of marsupial bones, and the simple construction of the allantois (without any placenta as yet) were inherited by the marsupials, with many other features, from the monotremes, and preserved. On the other hand, they have lost the independent bone *(caracoideum)* at the shoulder blade. But we have a more important advance in the disappearance of the cloaca; the rectum and anus are separated by a partition from the uro-genital opening *(sinus urogenitalis)*. Moreover, all the marsupials have teats on the mammary glands, at which the new-born animal sucks. The teats pass into the cavity of a pouch or pocket on the ventral side of the mother, and this is supported by a couple of marsupial bones. The young are born in a very imperfect condition, and carried by the mother for some time longer in her pouch, until they are fully developed (Fig. 326). In the giant kangaroo, which is as tall as a man, the embryo only developes for a month in the uterus, is then born in a very imperfect state, and finishes its growth in the mother's pouch *(marsupium)*; it remains in this about nine months, and at first hangs continually on to the teat of the mammary gland.

From these and other characteristics (especially the peculiar construction of the internal and external sexual organs in male and female) it is clear that we must conceive the whole sub-class of the marsupials as one stem-group, which has been developed from the promammalia. From one branch of these marsupials (possibly from more than one) the stem-forms of the higher mammals, the placentals, were afterwards evolved. Of the existing forms of the marsupials, which have undergone various modifications through adaptation to different environments, the family of the opossums *(didelphida* or *pedimana)* seems to be the phylogenetically oldest and nearest to the common stem-form of the whole class. To this family belong the crab-eating opossum of Brazil (Fig. 326) and the opossum of Virginia, on the embryology of which Selenka has given us a valuable work (cf. Figs. 66–70 and 134–138). These didelphida climb trees like the apes, grasping the branches with their hand-shaped hind feet. We may conclude from this that the stem-forms of the primates, which we must regard as the earliest lemurs, were evolved directly from the opossum. We must not forget, however, that the conversion of the five-toed foot into a prehensile hand is polyphyletic. By the same adaptation to climbing trees the habit of grasping their branches with the feet has in many different cases brought about that opposition of the thumb or great toe to the other toes which makes the hand prehensile. We see this in the climbing lizards (chameleon), the birds, and the tree-dwelling mammals of various orders.

Some zoologists have lately advanced the opposite opinion, that the marsupials represent a completely independent sub-class of the mammals, with no direct relation to the placentals, and developing independently of them from the monotremes. But this opinion is untenable if we examine carefully the whole organisation of the three sub-classes, and do not lay the chief stress on incidental features and secondary adaptations (such as the formation of the marsupium). It is then clear that the marsupials—viviparous mammals without placenta—are a necessary transition from the oviparous monotremes to the higher placentals with chorion-villi. In this sense the marsupial class certainly contains some of man's ancestors.

THIRTY-FOURTH TABLE

GENEALOGICAL TREE OF THE PRIMATES



CHAPTER XXIII.

OUR APE ANCESTORS

Organisation and stem-unity of the placentals. Significance of the placenta. Its origin from the allantois. Uterine and fœtal placenta. Formation of the decidua. Different forms of the placenta and its importance in classification. Indecidua and deciduata. Malloplacenta, cotyloplacenta, zonoplacenta, discoplacenta. The human discoid placenta (with decidua capsularis and ventral pedicle) only shared by the anthropoid apes. The ancient stem-group of the half-apes or lemurs. Lemuravidæ (older lemurs) and lemurogonæ (recent lemurs). Descent of man from the apes. The Huxleian law: The differences in structure between man and the anthropoid apes are less than between the anthropoid and the rest of the apes. The peculiar formation of the placenta and its pedicle in man is only found in the anthropoid apes besides. Bimana and quadrumana. Western (platyrrhinæ) and eastern (catarrhinæ) apes. Teeth of the apes. Tailed and anthropoid apes. Primitive men without speech.

THE long series of animal forms which we must regard as the ancestors of our race has been confined within narrower and narrower circles as our phylogenetic inquiry has progressed. The great majority of known animals do not fall in the line of our ancestry, and even within the vertebrate stem only a small number are found to do so. In the most advanced class of the stem, the mammals, there are only a few families that belong directly to our genealogical tree. The most important of these are the apes and their predecessors, the half-apes, and the earliest placentals *(prochoriata)*.

The placentals (also called *choriata, monodelphia, eutheria*, or *epitheria)* are distinguished from the lower mammals we have just considered, the monotremes and marsupials, by a number of striking peculiarities. Man has all these distinctive features; that is a very significant fact. We may, on the ground of the most careful comparative-anatomical and ontogenetic research, formulate the thesis: "Man is in every respect a true placental." He has all the characteristics of structure and development that distinguish the placentals from the two lower divisions of the mammals, and, in fact, from all other animals. Among these characteristics we must especially notice the more advanced development of the brain. The fore-brain or cerebrum especially is much more developed in them than in the lower animals. The *corpus callosum*, which forms a sort of wide bridge connecting the two hemispheres of the cerebrum, is only fully formed in the placentals; it is very rudimentary in the marsupials and monotremes. It is true that the lowest placentals are not far removed from the marsupials in cerebral development; but within the placental group we can trace an unbroken gradation of progressive development of the brain, rising gradually from this lowest stage up to the elaborate psychic organ of the apes and man. The human soul—a physiological function of the brain—is in reality only a more advanced ape-soul.

The mammary glands of the placentals are provided with teats like those of the marsupials; but we never find in the placentals the pouch in which the latter carry and suckle their young. Nor have they the marsupial bones in the ventral wall at the anterior border of the pelvis, which the marsupials have in common with the monotremes, and which are formed by a partial ossification of the sinews of the inner oblique abdominal muscle. There are merely a few insignificant remnants of them in some of the carnivora. The placentals are also generally without the hook-shaped process at the angle of the lower jaw which is found in the marsupials.

However, the feature that characterises the placentals above all others, and that has given its name to the whole sub-class, is the formation of the placenta. We have already considered the formation and significance of this remarkable embryonic organ when we traced the development of the chorion and the allantois in the human embryo (pp. 375–385). The urinary sac or the allantois, the curious vesicle that grows out of the hind part of the gut, has essentially the same structure and function in the human embryo as in that of all the other amniotes (cf. Figs. 208–211). There is a quite secondary difference, on which great stress has wrongly been laid, in the fact that in man and the higher apes the original cavity of the allantois quickly degenerates, and the rudiment of it sticks out as a solid projection from the primitive gut. The thin wall of the allantois consists of the same two layers or membranes as the wall of the gut—the gut-gland layer within and the gut-fibre layer without. In the gut-fibre layer of the allantois there are large blood-vessels, which serve for the nutrition, and especially the respiration, of the embryo—the umbilical vessels (p. 399). In the reptiles and birds the allantois enlarges into a spacious sac, which encloses the embryo with the amnion, and does not combine with the outer fœtal membrane (the chorion). This is the case also with the lowest mammals, the oviparous monotremes and most of the marsupials. It is only in some of the later marsupials (peramelida) and all the placentals that the allantois developes into the distinctive and remarkable structure that we call the *placenta*.

The placenta is formed by the branches of the blood-vessels in the wall of the allantois growing into the hollow ectodermic tufts (villi) of the chorion, which run into corresponding depressions in the mucous membrane of the womb. The latter also is richly permeated with blood-vessels which bring the mother's blood to the embryo. As the partition in the chorion-villi between the maternal blood-vessels and those of the fœtus is extremely thin, there is a direct exchange of fluid between the two, and this is of the greatest importance in the nutrition of the young mammal. It is true that the maternal vessels do not entirely pass (by anastomosis) into the fœtal vessels, so that the two kinds of blood are simply mixed. But the partition between them is so thin that the nutritive fluid easily transudes through it. By means of this transudation or diosmosis the exchange of fluids takes place without difficulty. The larger the embryo is in the placentals, and the longer it remains in the womb, the more necessary it is to have special structures to meet its great consumption of food.

In this respect there is a very conspicuous difference between the lower and higher mammals. In the marsupials, in which the embryo is only a comparatively short time in the womb and is born in a very immature condition, the vascular arrangements in the yelk-sac and the allantois suffice for its nutrition, as we find them in the monotremes, birds, and reptiles. But in the placentals, where gestation lasts a long time, and the embryo reaches its full development under the protection of its enveloping membranes, there has to be a new mechanism for the direct supply of a large quantity of food, and this is admirably met by the formation of the placenta.

In order to understand clearly the formation of the placenta and the chief modifications of it in the various placentals, we must first glance again at the outer membranes of the mammal ovum. The reader will remember that the external envelope is formed at first, and even during gastrulation, by the *zona pellucida* and the thick albuminous membranes that are deposited on the outer side of it (Figs. 71–74). We gave the name of *prochorion* to these two external membranes, which afterwards coalesce. This prochorion quickly disappears (in the first week of development in man), and is replaced by the permanent outer membrane or *chorion*. But this is merely the "serous membrane" *(serolemma)*, the origin of which from the outer germinal layer of the blastula we have considered previously (cf. p. 373 and Figs. 223, 224). This is at first a smooth and thin membrane, enveloping the entire ovum, but it is presently covered with a quantity of small projections or villi (Figs. 207, 225, *chz*). These grow into the cavities of the uterine glands, into tubular depressions of the mucous lining of the womb, and thus attach the embryo to its wall. Like the whole of the chorion, its hollow villi consist of a thin stratum of cells that belongs to the horny plate, and a thin underlying layer of loose connective tissue (continuation of the parietal mesoblast). They soon develop to an extraordinary degree, growing and ramifying rapidly. New villi everywhere sprout out of the serolemma, and thus the whole of the outer surface of the ovum is soon (in the second week in the human embryo) clothed with a thick forest of very delicate villi (Plate XV. and Figs. 206, 207). Externally the villi are covered by a layer of maternal cells, the flat epithelium of the uterine glands. They combine in the first week of development.

Into these chorion-villi branches of the blood-vessels now penetrate from within, starting from the gut-fibre layer of the allantois, and bringing the blood of the fœtus through the umbilical vessels (Fig. 327 *chz*). On the other hand, a thick network of blood-vessels developes in the mucous membrane that clothes the inner surface of the womb, especially in the region of the depressions into which the chorion-villi penetrate *(plu)*. This net-work of arteries contains maternal blood, brought by the uterine vessels. As the connective tissue between the enlarged capillaries of the uterus disappears, wide cavities filled with maternal blood appear, and into these the chorion-villi of the embryo penetrate. The sum of these vessels of both kinds, that are so intimately correlated at this point, together with the connective and enveloping tissue, is the *placenta*. The placenta consists, therefore, properly speaking, of two different though intimately connected parts—the fœtal placenta (Fig. 327 *chz*) within and the maternal or uterine placenta *(plu)* without. The latter is made up of the mucous coat of the uterus and its blood-vessels, the former of the tufted chorion and the umbilical vessels of the embryo (cf. Fig. 212).

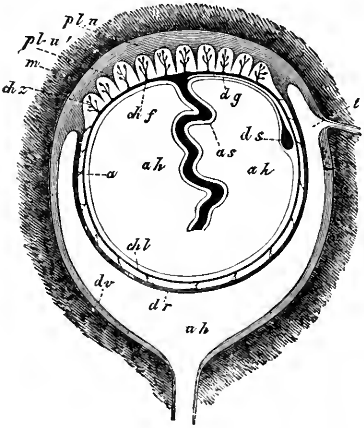


FIG. 327.—**Fœtal membranes of the human embryo** (diagrammatic). *m* the thick muscular wall of the womb. *plu* placenta [the inner layer *(plu')* of which penetrates into the chorion-villi *(chz)* with its processes]. *chf* tufted, *chl* smooth chorion. *a* amnion, *ah* amniotic cavity, *as* amniotic sheath of the umbilical cord (which passes under into the navel of the embryo—not given here), *dg* vitelline duct, *ds* yelk sac, *dv*, *dr* decidua (vera and reflexa). The uterine cavity *(uh)* opens below into the vagina and above on the right into an oviduct *(t)*. (From *Kölliker.*)

The manner in which these two kinds of vessels combine in the placenta, and the structure, form, and size of it, differ a good deal in the various placentals; to some extent they give us valuable data for the natural classification, and therefore the phylogeny, of the whole of this sub-class. On the ground of these differences we divide it into two principal sections: the lower placentals or *indecidua*, and the higher placentals or *deciduata*.

To the indecidua belong three important groups of mammals: the half-apes *(prosimiæ)*, the ungulates (tapirs, horses, pigs, ruminants, etc.), and the cetacea (dolphins and whales). In these indecidua the villi are distributed over the whole surface of the chorion (or its greater part), either singly or in groups. They are only loosely connected with the mucous coat of the uterus, so that the whole fœtal membrane with its villi can be easily withdrawn from the uterine depressions like a hand from a glove. There is no real coalescence of the two placentas at any part of the surface of contact. Hence at birth the fœtal placenta alone comes away; the uterine placenta is not torn away with it. In general, the mucous coat of the pregnant womb is very little changed, and suffers no loss of blood and no direct loss of substance at birth. In the cetacea, half-apes, and most of the ungulates the villi are regularly distributed over the chorion *(malloplacenta)*. But in most of the ruminants the branching villi join together to form a number of clusters or cotyledons *(cotyloplacenta)*.

The formation of the placenta is very different in the second and higher section of the placentals, the *deciduata*. Here again the whole surface of the chorion is thickly covered with the villi in the beginning. But they afterwards disappear from one part of the surface, and grow proportionately thicker on the other part. We thus get a differentiation between the smooth chorion *(chorion laeve*, Fig. 327 *chl)* and the thickly-tufted chorion *(chorion frondosum*, Fig. 327 *chf)*. The former has only a few small villi or none at all; the latter is thickly covered with large and well-developed villi; this alone now constitutes the placenta. In the great majority of the deciduata the placenta has the same shape as in man (Figs. 216, 219)—namely, a thick, circular disk like a cake; so we find in the insectivora, chiroptera, rodents, and apes. This *discoplacenta* lies on one side of the chorion. But in the sarcotheria (both the carnivora and the seals, *pinnipedia*) and in the elephant and several other deciduates we find a *zonoplacenta;* in these the rich mass of villi runs like a girdle round the middle of the ellipsoid chorion, the two poles of it being free from them.

Still more characteristic of the deciduates is the peculiar and very intimate connection between the chorion frondosum and the corresponding part of the mucous coat of the womb, which we must regard as a real coalescence of the two. The villi of the chorion push their branches into the blood-filled tissues of the coat of the uterus, and the vessels of each loop together so intimately that it is no longer possible to separate the fœtal from the maternal placenta; they form henceforth a compact and apparently simple placenta. In consequence of this coalescence, a whole piece of the lining of the womb comes away at birth with the fœtal membrane that is interlaced with it. This piece is called the "falling-away" membrane *(decidua)*. It is also called the serous (spongy) membrane, because it is pierced like a sieve or sponge. All the higher placentals that have this decidua are classed together as the "deciduates." The tearing away of the decidua at birth naturally causes the mother to lose a quantity of blood, which does not happen in the indecidua. The last part of the uterine coat has to be repaired by a new growth after birth in the deciduates. (Cf. Figs. 217–220, pp. 383–386.)

In the various orders of the deciduates the placenta differs considerably both in outer form and internal structure. The extensive investigations of the last ten years have shown that there is more variation in these respects among the higher mammals than was formerly supposed. The physiological work of this important embryonic organ, the nutrition of the fœtus during its long sojourn in the womb, is accomplished in the various groups of the placentals by very different and sometimes very elaborate structures. They have lately been fully described by Hans Strahl.

The phylogeny of the placenta has become more intelligible from the fact that we have found a number of transitional forms of it. Some of the marsupials *(perameles)* have the beginning of a placenta. In some of the half-apes *(tarsius)* a discoid placenta with decidua is developed. On the strength of these discoveries I have in the following table distinguished eight stages in the phylogeny of the human placenta. We have already seen (Chapter XV.) the chief results of them ; the special characteristics that distinguish the human discoplacenta, the formation of the *decidua reflexa* (also called *D. circumvallata* and *D. capsularis)*, the development of the umbilical cord from the ventral pedicle, etc., are shared by man with the anthropoid apes, but are not found in the lower apes (cf. pp. 382–385).

While the important results of comparative embryology have been throwing further light on the close blood-relationship of man and the anthropoid apes in the last few years (p. 399), the great advance of paleontology has at the same time been affording us a deeper insight into the stem-history of the placental group. In the seventh chapter of my *Systematic Phylogeny of the Vertebrates* I advanced the hypothesis that the placentals form a single stem with many branches, which has been evolved from an older group of the marsupials *(prodidelphia)*. The four great legions of the placentals—rodents, ungulates, carnassia, and primates—are sharply separated to-day by important features of organisation. But if we consider their extinct ancestors of the Tertiary period, the differences gradually disappear, the deeper we go in the cenozoic deposits; in the end we find that they vanish altogether. The primitive stem-forms of the rodents *(esthonychida)*, the ungulates *(chondylarthra)*, the carnassia *(ictopsida)*, and the primates *(lemuravida)* are so closely related at the beginning of the Tertiary period that we might group them together as different families of one order, the proplacentals *(mallotheria* or *prochoriata)*.

Hence the great majority of the placentals have no direct and close relationship to man, but only the legion of the *primates*. This is now generally divided into three orders—the half-apes *(prosimiæ)*, apes *(simiæ)*, and man *(anthropi)*. The half-apes are the stem-group, descending from the older *mallotheria* of the Cretaceous period. From them the apes

THIRTY-FIFTH TABLE

SYNOPSIS OF THE PHYLOGENY OF THE HUMAN PLACENTA

(Eight stages of evolution)

Stages I. and II.: Lower mammals.	III. and IV.: Lemurs.
V. and VI.: Lower primates.	VII. and VIII.: Higher primates.

I. Stage: **Monotrema** *(echidna, ornithorhyncus).* Oviparous earliest mammals, without placenta.	I. **Implacentalia ovipara.** The allantois remains a free urinary sac, filled with fluid, as in the sauropsids.
II. Stage: **Marsupialia.** Most living marsupials. Viviparous earlier mammals, without placenta.	II. **Implacentalia vivipara.** The allantois is free, as in the monotremes and sauropsids.
III. Stage: **Peramelida** *(perameles, dasyurus).* Part of the carnivorous marsupials.	III. **Semiplacenta avillosa.** The allantois coalesces at one part with the wall of the uterus (without chorion-villi), and forms an incipient placenta. No decidua.
IV. Stage: **Prosimiæ.** Most of the half-apes, and of the ungulates and cetacea (lemur, galago, pig, horse, dolphin, etc.).	IV. **Semiplacenta villosa** (malloplacenta). The allantois combines with the generally distributed chorion-villi. No decidua.
V. Stage: **Tarsiadæ.** Some of the half-apes *(tarsius).* Some of the insectivora *(centetes).*	V. **Discoplacenta primitiva.** The allantois begins to form a discoid placenta with decidua.
VI. Stage: **Platyrrhinæ.** American apes (western) (and probably all the older Tertiary, Eocene apes).	VI. **Discoplacenta dysmopitheca.** The allantois forms a discoid placenta with decidua, which is more advanced.
VII. Stage: **Cynopitheca.** Dog-faced apes (the tailed apes of the Old World, eastern apes).	VII. **Discoplacenta cynopitheca.** The allantois forms a double placenta, a larger dorsal (primary) and a small ventral (secondary) one.
VIII. Stage: **Anthropomorpha.** The man-like apes *(hylobates, satyrus, anthropithecus, gorilla)* and man *(homo).*	VIII. **Discoplacenta anthropoides.** The allantois does not form a vesicle, but a solid pedicle at the base and a decidua capsularis (or reflexa) in the outer part.

were evolved in the Tertiary period, and man was formed from these towards its close.

The half-apes or lemurs *(prosimiæ)* have few living representatives. But they are very interesting, and are the last survivors of a once extensive group. We find many fossil remains of them in the older Tertiary deposits of Europe and North America, in the Eocene and Miocene. We distinguish two sub-orders, the fossil *lemuravida* and the modern *lemurogona*. The earliest and most primitive forms of the lemuravida are the pachylemurs *(hypopsodina)*; they come next to the earliest placentals *(prochoriata)*, and have the typical full dentition, with forty-four teeth $\left(\frac{3\cdot1\cdot4\cdot3\cdot}{3\cdot1\cdot4\cdot3\cdot}\right)$. The necrolemurs (*adapida*, Fig. 328) have only forty teeth, and have lost an incisor in each jaw $\left(\frac{2\cdot1\cdot4\cdot3\cdot}{2\cdot1\cdot4\cdot3\cdot}\right)$. The dentition is still further reduced in the lemurogona *(autolemures)*, which usually have only thirty-six teeth $\left(\frac{2\cdot1\cdot3\cdot3\cdot}{2\cdot1\cdot3\cdot3\cdot}\right)$. These living survivors are scattered far over the southern part of the old world. Most of the species live in Madagascar, some in the Sunda Islands, others on the mainland of Asia and Africa. They are gloomy and melancholic animals; they live a quiet life, climbing trees, and eating fruit and insects. They are of different kinds. Some are closely related to the marsupials (especially the opossum). Others *(macrotarsi)* are nearer to the insectivora, others again *(chiromys)* to the rodents. Some of the lemurs *(brachytarsi)* approach closely to the true apes. The numerous fossil remains of half-apes and apes that have been recently found in the Tertiary deposits justify us in thinking that man's ancestors were represented

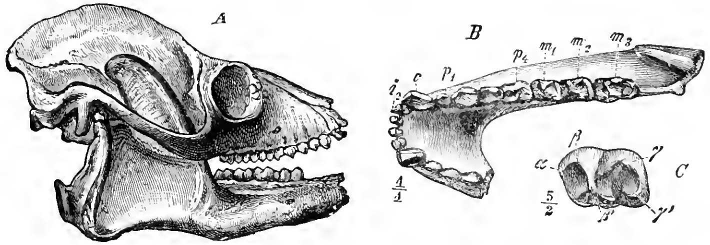


Fig. 328.—**Skull of a fossil lemur** *(adapis parisiensis)* from the Miocene at Quercy. *A* lateral view from the right, half natural size. *B* lower jaw. *C* lower molar, *i* incisors, *c* canines, *p* premolars, *m* molars.

by several different species during this long period. We may divide the earlier of them into two groups of prosimiæ: the *lemurovida* of the earlier Eocene (twenty-fourth stage) and the *lemurogona* of the later Tertiary (twenty-fifth stage). Some of these were almost as big as men, such as the diluvial lemurogonon *megaladapis* of Madagascar.

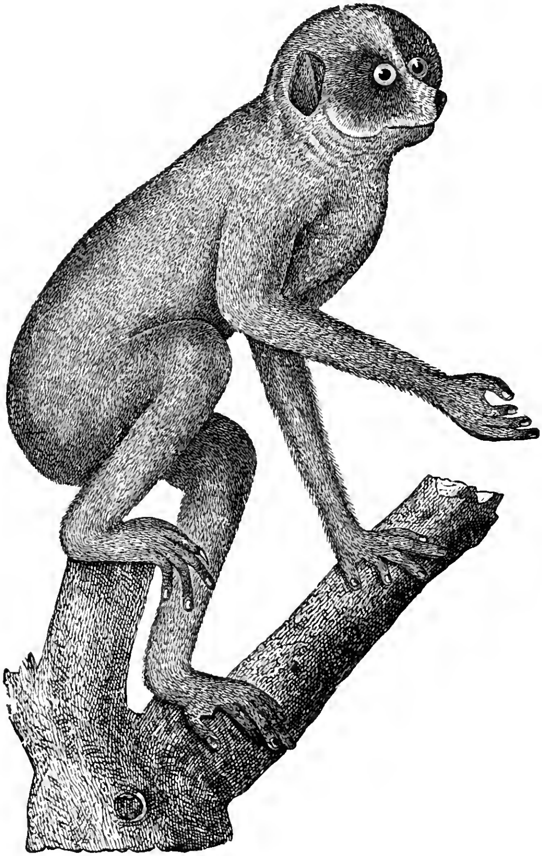


FIG. 329.—**The slender Lori** (*stenops gracilis*) of Ceylon, a tail-less lemur.

Next to the lemurs come the true apes (*simiæ*), the twenty-sixth stage in our ancestry. It has been beyond question for some time now that the apes approach nearest to man in every respect of all the animals. Just as the lowest apes come close to the lemurs, so the highest come next to man. When we carefully study the comparative anatomy of the apes and man, we can trace a gradual and uninterrupted advance in the organisation of the ape up to the purely human frame, and, after impartial examination of the "ape-problem" that has been discussed of late years with such passionate interest, we come infallibly to the important conclusion, first formulated by Huxley in 1863: "Whatever systems of organs we take, the comparison of their modifications in the series of apes leads to the same result: that the anatomic differences that separate man from the gorilla and chimpanzee are not as great as those that separate the gorilla from the lower apes." Translated into phylogenetic language, this "pithecometra-law," formulated in such masterly fashion by Huxley, is quite equivalent to the popular saying: "Man is descended from the apes."

In the very first exposition of his profound natural classification (1735) Linné placed the anthropoid mammals *(anthropomorpha)* at the head of the animal kingdom, with three genera: man *(homo)*, the ape *(simia)*, and the sloth *(bradypus)*. He afterwards called them the "primates"—the "lords" of the animal world; he then also separated the lemur from the true ape, and rejected the sloth. Later zoologists divided the order of primates. First the Göttingen anatomist, Blumenbach, founded a special order for man, which he called *bimana* ("two-handed"); in a second order he united the apes and lemurs under the name of *quadrumana* ("four-handed"); and a third order was formed of the distantly-related *chiroptera* (bats, etc.). The separation of the bimana and quadrumana was retained by Cuvier and most of the subsequent zoologists. It seems to be extremely important, but, as a matter of fact, it is totally wrong. This was first shown in 1863 by Huxley in his famous *Man's Place in Nature*. On the strength of careful comparative-anatomical research he proved that the apes are just as truly "two-handed" as man; or, if we prefer to reverse it, that man is as truly four-handed as the ape. He showed convincingly


FIG. 330.—**The white-nosed ape** *(cercopithecus petaurista)*.

that the ideas of hand and foot had been wrongly defined, and had been improperly based on physiological instead of morphological grounds. The circumstance that we oppose the thumb to the other four fingers in our hand, and so can grasp things, seemed to be a special distinction of the hand in contrast to the foot, in which the corresponding great toe cannot be opposed in this way to the others. But the apes can grasp with the hind-foot as well as the fore, and so were regarded as quadrumanous. However, the inability to grasp that we find in the foot of civilised man is a consequence of the habit of clothing it with narrow coverings for thousands

FIG. 331.—**The drill-baboon** *(cynocephalus leucophæus)*. (From *Brehm.*)

of years. Many of the bare-footed lower races of men, especially among the negroes, use the foot very freely in the same way as the hand. As a result of early habit and continued practice, they can grasp with the foot (in climbing trees, for instance) just as well as with the hand. Even new-born infants of our own race can grasp very strongly with the great toe, and hold a spoon with it as firmly as with the hand. Hence the physiological distinction between hand and foot can neither be pressed very far, nor has it a scientific basis. We must look to morphological characters. (Cf. Figs. 329–337 and Figs. 235–244.)

FIG. 332.—**Female chimpanzee** *(anthropithecus niger)*. (From *Brehm*.)

As a matter of fact, it is possible to draw such a sharp morphological distinction—a distinction based on anatomic structure—between the fore and hind extremity. In the formation both of the bony skeleton and of the muscles that are connected with the hand and foot before and behind there are material and constant differences; and these are found both in man and the age. For instance, the number and arrangement of the smaller bones of the hand and foot are quite different. There are similar constant differences in the muscles. The hind extremity always has three muscles (a short flexor muscle, a short extensor muscle, and a long calf-muscle) that are not found in the fore extremity. The arrangement of the muscles also is different before and behind. These characteristic differences between the fore and hind extremities are found in man as well as the ape. There can be no doubt, therefore, that the ape's foot deserves that name just as much as the human foot does, and that all true apes are just as "bimanous" as man. The common distinction of the apes as "quadrumanous" is altogether wrong morphologically.

But it may be asked whether, quite apart from this, we can find any other features that distinguish man more sharply from the ape than the various species of apes are distinguished from each other. Huxley gave so complete and demonstrative a reply to this question that the opposition still raised on many sides is absolutely without foundation. On the ground of careful comparative-anatomical research, Huxley proved that in all morphological respects the differences between the highest and lowest apes are greater than the corresponding differences between the highest apes and man. He thus restored Linné's order of the primates (excluding the bats), and divided it into three sub-orders, the first composed of the half-apes *(lemuridæ)*, the second of the true apes *(simiadæ)*, the third of men *(anthropidæ)*.

But, as we wish to proceed quite consistently and impartially on the laws of systematic logic, we may, on the strength of Huxley's own law, go a good deal farther in this division. As I showed in the *Generelle Morphologie*, we are justified in going at least one important step farther, and assigning man his natural place within one of the sections of the order of apes. All the features that characterise this group of apes are found in man, and not found in the other apes. We do not seem to be justified, therefore, in founding for man a special order distinct from the apes.

The order of the true apes *(simiæ or pitheca)*—excluding the lemurs—has long been divided into two principal groups, which also differ in their geographical distribution. One group *(hesperopitheca*, or western apes) live in America. The other group, to which man belongs, are the *eopitheca* or eastern apes; they are found in Asia and Africa, and formerly in Europe. All the eastern apes agree with man in the features that are chiefly used in zoological classification to distinguish between the two simian groups, especially in the dentition. The objection might be raised that the teeth are too subordinate an organ physiologically for us to lay stress on them in so important a question. But there is a good reason for it; it is with perfect justice that zoologists have for more than a century paid particular attention to the teeth in the systematic division and arrangement of the orders of mammals. The number, form, and arrangement of the teeth are much more faithfully inherited in the various orders than most other characters.

Hence the form of dentition in man is very important. In the fully-developed condition we have thirty-two teeth; of these eight are incisors, four canine, and twenty molars. The eight incisors *(dentes incisivi)*, in the middle of the jaws, have certain characteristic differences above and below. In the upper jaw the inner incisors are larger than the outer; in the lower jaw the inner are the smaller. Next to these, at each side of both jaws, is a canine (or "eye-tooth," *dens caninus)*, which is larger than the incisors. Sometimes it is very prominent in man, as it is in most apes and many of the other mammals, and forms a sort of tusk. Next to this there are five molars above and below on each side, the first two of which (the "pre-molars") are small, have only one root, and are included in the change of teeth; the three back ones are much larger, have two roots, and only come with the second teeth. The apes of the Old World, or all the living or fossil apes of Asia, Africa, and Europe, have the same dentition as man.

On the other hand, all the American apes have an additional pre-molar in each half of the jaw. They have six molars above and below on each side, or thirty-six teeth altogether. This characteristic difference between the eastern and western apes has been so faithfully inherited that it is very instructive for us. It is true that there seems to be an exception in the case of a small family of South American apes. The small silky apes *(arctopitheca* or *hapalidæ)*, which include the tamarin *(midas)* and the brush-monkey *(jacchus)*, have only five molars in each half of the jaw (instead of six), and so seem to be nearer to the eastern apes. But it is found, on closer examination, that they have three pre-molars, like all the western apes, and that only the last molar has been lost. Hence the apparent exception really confirms the above distinction.

Of the other features in which the two groups of apes differ, the structure of the nose is particularly instructive and conspicuous. All the eastern apes have the same type of nose as man—a comparatively narrow partition between the two halves, so that the nostrils run downwards. In some of them the nose protrudes as far as in man, and has the same characteristic structure. We have already alluded to the curious long-nosed apes which have a long, finely-curved nose (Plate XXV.). Most of the eastern apes have, it is true, rather flat noses, like, for instance, the white-nosed monkey (Fig. 330); but the nasal partition is thin and narrow in them all. The American apes have a different type of nose. The partition is very broad and thick at the bottom, and the wings of the nostrils are not developed, so that they point outwards instead of downwards. This difference in the form of the nose is so constantly inherited in both groups that the apes of the New World are called "flat-nosed" *(platyrrhinæ)*, and those of the Old World "narrow-nosed" *(catarrhinæ)*. The bony passage of the ear (at the bottom of which is the tympanum) is short and wide in all the platyrrhines, but long and narrow in all the catarrhines; and in man this difference also is significant.

This division of the apes into platyrrhines and catarrhines, on the ground of the above hereditary features, is now generally admitted in zoology, and receives strong support from the geographical distribution of the two groups in the east and west. It follows at once, as regards the phylogeny of the apes, that two divergent lines proceeded from the common stem-form of the ape-order in the early Tertiary period, one of which spread over the Old, the other over the New, World. It is certain that all the platyrrhines come of one stock, and also all the catarrhines; but the former are phylogenetically older, and must be regarded as the stem-group of the latter.

What can we deduce from this with regard to our own genealogy? Man has just the same characters, the same form of dentition, auditory passage, and nose, as all the catarrhines; in this he radically differs from the platyrrhines. We are thus forced to assign him a position among the eastern apes in the order of primates, or at least place him alongside of them. But it follows phylogenetically that man is a direct blood relative of the apes of the Old World, and can be traced to a common stem-form together with all the catarrhines. In his whole organisation and in his origin man is a true catarrhine; he originated in the Old World from an unknown, extinct group of the eastern apes. The apes of the New World, or the platyrrhines, form a divergent branch of our genealogical tree, and this is only distantly related at its root to the human race. We must assume, of course, that the earliest Eocene apes had the full dentition of the platyrrhines; hence we may regard this stem-group as a special stage (the twenty-sixth) in our ancestry, and deduce from it (as the twenty-seventh stage) the earliest catarrhines.

We have now reduced the circle of our nearest relatives to the small and comparatively scanty group that is represented by the sub-order of the catarrhines, and we are in a position to answer the question of man's place in this sub-order, and say whether we can deduce anything further from this position as to our immediate ancestors. In answering this question the comprehensive and able studies that Huxley gives of the comparative anatomy of man and the various catarrhines in his *Man's Place in Nature* are of great assistance to us. It is quite clear from these that the differences between man and the highest catarrhines (gorilla, chimpanzee, and orang) are in

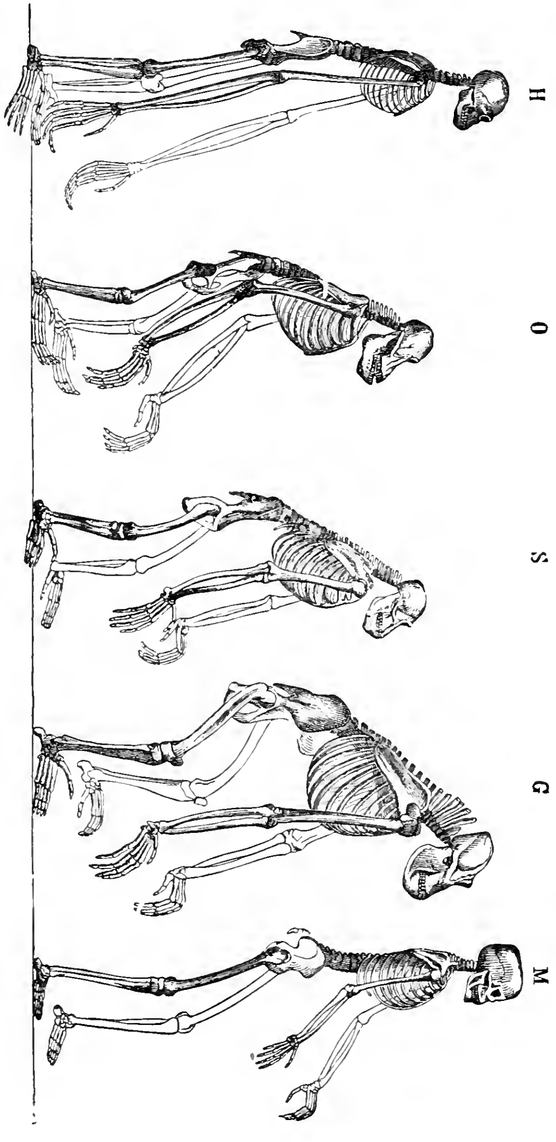


FIG. 333. Gibbon (*hylobates*).

FIG. 334. Orang (*satyrus*).

FIG. 335. Chimpanzee (*anthropithecus*).

FIG. 336. Gorilla (*gorilla*).

FIG. 337. Man (*homo*).

FIGS. 333-337.—**Skeleton of man** (Fig. 337) **and the four anthropoid genera**: Fig. 333. Gibbon. Fig. 334. Orang. Fig. 335. Chimpanzee. Fig. 336. Gorilla. (From *Huxley*.) Cf. Figs. 235-244.

every respect slighter than the corresponding differences between the highest and the lowest catarrhines (white-nosed monkey, macaco, baboon, etc.). In fact, within the small group of the tail-less anthropoid apes the differences between the various genera are not less than the differences between them and man. This is seen by a glance at the skeletons that Huxley has put together (Figs. 333-337). Whether we take the skull or the vertebral column or the ribs or the fore or hind limbs, or whether we extend the comparison to the muscles, blood-vessels, brain, placenta, etc., we always reach the same result on impartial examination—that man is not more different from the other catarrhines than the extreme forms of them (for instance, the gorilla and baboon) differ from each other. We may now, therefore, complete the Huxleian law we have already quoted with the following thesis : " Whatever system of organs we take, a comparison of their modifications in the series of catarrhines always leads to the same conclusion : the anatomic differences that separate man from the most advanced catarrhines (orang, gorilla, chimpanzee) are not as great as those that separate the latter from the lowest catarrhines (white-nosed monkey, macaco, baboon)."

We must, therefore, consider the descent of man from other catarrhines to be fully proved. Whatever further information on the comparative anatomy and ontogeny of the living catarrhines we may obtain in the future, it cannot possibly disturb this conclusion. Naturally, our catarrhine ancestors must have passed through a long series of different forms before the human type was produced. The chief advances that effected this " creation of man," or his differentiation from the nearest related catarrhines, were : the adoption of the erect posture, and the consequent greater differentiation of the fore and hind limbs, the evolution of articulate speech and its organ, the larynx, and the further development of the brain and its function, the soul ; sexual selection had a great influence in this, as Darwin showed in his famous work.

With an eye to these advances we can distinguish at least four important stages in our simian ancestry, which represent prominent points in the historical process of the making of man. We may take, after the lemurs, the earliest and lowest platyrrhines of South America, with thirty-six teeth, as the twenty-sixth stage of our genealogy ; they were developed from the lemurs by a peculiar modification of the brain, teeth, nose, and fingers. From these Eocene stem-apes were formed the earliest catarrhines or eastern apes, with the human dentition (thirty-two teeth), by modification of the nose, lengthening of the bony channel of the ear, and the loss of four pre-molars. These oldest stem-forms of the whole catarrhine group were still thickly coated with hair, and had long tails—dog-faced apes *(cynopitheca)* or tailed apes (*menocerca*, Fig. 330). They lived during the Tertiary period, and are found fossilised in the Miocene. Of the actual tailed apes perhaps the nearest to them are the *semnopitheci.*[1]

If we take these semnopitheci as the twenty-seventh stage in our ancestry, we may put next to them, as the twenty-eighth, the tail-less anthropoid apes. This name is given to the most advanced and man-like of the existing catarrhines. They were developed from the other catarrhines by losing the tail and part of the hair, and by a higher development of the brain, which found expression in the enormous growth of the skull. Of this remarkable family there are only a few genera to-day, and we have already dealt with them (Chapter XV.)—the gibbon *(hylobates,* Fig. 235) and orang *(satyrus,* Figs. 420–430) in South-Eastern Asia and the Archipelago ; and the chimpanzee *(anthropithecus,* Figs. 239–241) and gorilla *(gorilla,* Figs. 242–244) in Equatorial Africa.

The great interest that every thoughtful man takes in these nearest relatives of ours has found expression recently in a fairly large literature. The most distinguished of these for impartial treatment of the question of affinity is Robert Hartmann's little work on *The Anthropoid Apes.* Hartmann

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[1] These semnopitheci particularly resemble man in the form of the nose and the hair (both of the head and beard).

divides the primate order into two families: (1) *Primarii* (man and the anthropoid apes); and (2) *Simianæ* (true apes, catarrhines and platyrrhines). Professor Klaatsch, of Heidelberg, has advanced a different view in his interesting and richly illustrated work on *The Origin and Development of the Human Race.* This is a substantial supplement to my *Anthropogeny,* in so far as it gives the chief results of modern research on the early history of man and civilisation. But when Klaatsch declares the descent of man from the apes to be "irrational, narrow-minded, and false," in the belief that we are thinking of some living species of ape, we must remind him that no competent scientist has ever held so narrow a view. All of us look merely—in the sense of Lamarck and Darwin—to the original unity (admitted by Klaatsch) of the primate stem. This common descent of all the primates (men, apes, and lemurs) from one primitive stem-form, from which the most far-reaching conclusions follow for the whole of anthropology and philosophy, is admitted by Klaatsch as well as by myself and all other competent zoologists who accept the theory of evolution in general. He says explicitly (p. 172): "The three anthropoid apes—gorilla, chimpanzee, and orang—seem to be branches from a common root, and this was not far from that of the gibbon and man." That is in the main the opinion that I have maintained (especially against Virchow) in a number of works ever since 1866. The hypothetical common ancestor of all the primates, which must have lived in the earliest Tertiary period (more probably in the Cretaceous), was called by me *archiprimus;* Klaatsch now calls it *primatoid.* Dubois has proposed the appropriate name of *prothylobates* for the common and much younger stem-form of the anthropomorpha (man and the anthropoid apes). The actual *hylobates* is nearer to it than the other three existing anthropoids. None of these can be said to be absolutely the most man-like. The gorilla comes next to man in the structure of the hand and foot, the chimpanzee in the chief features of the skull, the orang in brain development, and the gibbon in the formation of the chest. None of these existing anthropoid apes is among the direct ancestors of our race; they are scattered survivors of an ancient branch of the catarrhines, from which the human race developed in a particular direction.

Although man is directly connected with this anthropoid family and originates from it, we may assign an important intermediate form between the *prothylobates* and him (the twenty-ninth stage in our ancestry), the ape-men *(pithecanthropi).* I gave this name in the *History of Creation* to the "speechless primitive men" *(alali),* which were men in the ordinary sense as far as the general structure is concerned (especially in the differentiation of the limbs), but lacked one of the chief human characteristics, articulate speech and the higher intelligence that goes with it, and so had a less developed brain. The phylogenetic hypothesis of the organisation of this "ape-man" which I then advanced was brilliantly confirmed twenty-four years afterwards by the famous discovery of the fossil *pithecanthropus erectus* by Eugen Dubois (then military surgeon in Java, afterwards professor at Amsterdam). In 1892 he found at Trinil, in the residency of Madiun at Java, in Pliocene deposits, certain remains of a large and very man-like ape (roof of the skull, femur, and teeth), which he described as "an erect ape-man" and a survivor of a "stem-form of man" (Fig. 338). Naturally, the pithecanthropus excited the liveliest interest, as the long-sought transitional form between man and the ape: we seemed to have found "the missing link." There

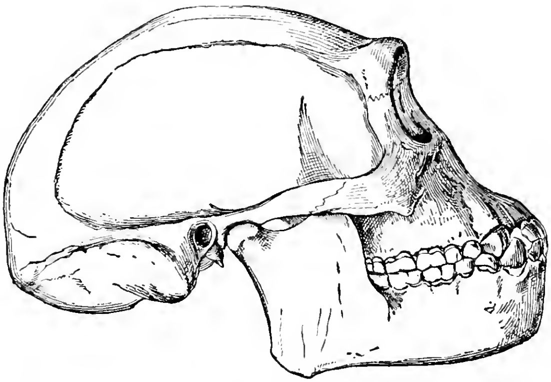


Fig. 338.—**Skull of the fossil ape-man of Java** *(pithecanthropus erectus),* restored by *Eugen Dubois.* (Cf. Plate XVII.)

were very interesting scientific discussions of it at the last three International Congresses of Zoology (Leyden, 1895, Cambridge 1898, and Berlin 1901). I took an active part in the discussion at Cambridge, and may refer the reader to the paper I read there on "The Present Position of Our Knowledge of the Origin of Man" (translated by Dr. Gadow with the title of *The Last Link).*

An extensive and valuable literature has grown up in the last ten years on the pithecanthropus and the pithecoid theory connected with it. A number of distinguished anthropologists, anatomists, paleontologists, and phylogenists have taken part in the controversy, and made use of the important data furnished by the new science of pre-historic research. Hermann Klaatsch has given a good summary of them, with many fine illustrations, in the above-mentioned work. I refer the reader to it as a valuable supplement to the present work, especially as I cannot go any further here into these anthropological and pre-historic questions. I will only repeat that I think he is wrong in the attitude of hostility that he affects to take up with regard to my own views on the descent of man from the apes.

The most powerful opponent of the pithecoid theory—and the theory of evolution in general—during the last thirty years (until his death in September, 1902) was the famous Berlin anatomist, Rudolf Virchow. In the speeches which he delivered every year at various congresses and meetings on this question, he was never tired of attacking the hated "ape theory." His constant categorical position was: "It is quite certain that man does not descend from the ape or any other animal." This has been repeated incessantly by opponents of the theory, especially theologians and philosophers. In the inaugural speech that he delivered in 1894 at the Anthropological Congress at Vienna, he said that "man might just as well have descended from a sheep or an elephant as from an ape." Absurd expressions like this only show that the famous pathological anatomist, who did so much for medicine in the establishment of cellular pathology, had not the requisite attainments in comparative anatomy and ontogeny, systematic zoology and paleontology, for sound judgment in the province of anthropology. The Strassburg anatomist, Gustav Schwalbe, deserved great praise for having the moral courage to oppose this dogmatic and ungrounded teaching of Virchow and showing its untenability. The recent admirable works of Schwalbe on the pithecanthropus, the earliest races of men, and the Neanderthal skull (1897–1901) will supply any candid and judicious reader with the empirical material with which he can convince himself of the baselessness of the erroneous dogmas of Virchow and his clerical friends (J. Ranke, J. Bumüller, etc.).

As the pithecanthropus walked erect, and his brain (judging from the capacity of his skull, Fig. 338) was midway between the lowest men and the anthropoid apes (Plate XVII., Fig. 2; Plates XXII., XXIII.), we must assume that the next great step in the advance from the pithecanthropus to man was the further development of human speech and reason.

Comparative philology has recently shown that human speech is polyphyletic in origin; that we must distinguish several (probably many) different primitive tongues that were developed independently. The evolution of language also teaches us (both from its ontogeny in the child and its phylogeny in the race) that human speech proper was only gradually developed after the rest of the body had attained its characteristic form. It is probable that language was not evolved until after the dispersal of the various species and races of men, and this probably took place at the commencement of the Quaternary or Diluvial period. The speechless ape-men or alali certainly existed towards the end of the Tertiary period, during the Pliocene, possibly even the Miocene, period.

The third, and last, stage of our animal ancestry is the true or speaking man *(homo)*, who was gradually evolved from the preceding stage by the advance of animal language into articulate human speech. As to the time and place of this real "creation of man" we can only express tentative opinions. It was probably during the Diluvial period in the hotter zone of the Old World, either on the mainland in tropical Africa or Asia, or on an earlier continent (Lemuria—now sunk below the waves of the Indian Ocean), which stretched from East Africa (Madagascar, Abyssinia) to East Asia (Sunda Islands, Further India). I have given fully in my *History of Creation* (chap. xxviii. and plate xxx.) the weighty reasons for claiming this descent of man from the anthropoid eastern apes, and shown how we may conceive the spread of the various races from this "Paradise" over the whole earth. I have also dealt fully with the relations of the various races and species of men to each other.

THIRTY-SIXTH TABLE

SYNOPSIS OF THE CHIEF SECTIONS OF OUR STEM-HISTORY

FIRST SECTION OF OUR PHYLOGENY.

Man's Invertebrate Ancestors.

First phylogenetic stage: **The Protists.**

Man's ancestors are unicellular protozoa, originally unnucleated monera like the chromacea, structureless green particles of plasm; afterwards real nucleated cells (first plasmodomous *protophyta*, like the palmella; then plasmophagous *protozoa*, like the amœbæ).

Second phylogenetic stage: **The Blastæads.**

Man's ancestors are round cœnobia or colonies of protozoa; they consist of a close association of many homogeneous cells, and thus are individuals of the second order. They resemble the round cell-communities of the magosphæræ and volvocina, equivalent to the ontogenetic blastula: hollow globules, the wall of which consists of a single layer of ciliated cells (blastoderm).

Third phylogenetic stage: **The Gastræads.**

Man's ancestors are gastræads, like the simplest of the actual metazoa (prophysema, olynthus, hydra, pemmatodiscus). Their body consists merely of a primitive gut, the wall of which is made up of the two primary germinal layers.

Fourth phylogenetic stage: **The Platodes.**

Man's ancestors have substantially the organisation of simple platodes (at first like the cryptocœlic platodaria, later like the rhabdocœlic turbellaria). The leaf-shaped bilateral-symmetrical body has only one gut-opening, and developes the first trace of a nervous centre from the ectoderm in the middle line of the back (Figs. 293, 294).

Fifth phylogenetic stage: **The Vermalia.**

Man's ancestors have substantially the organisation of unarticulated vermalia, at first gastrotricha (ichthydina), afterwards frontonia (nemertina, enteropneusta). Four secondary germinal layers develop, two middle layers arising between the limiting layers (cœloma). The dorsal ectoderm forms the vertical plate, acroganglion (Fig. 297).

Sixth phylogenetic stage: **The Prochordonia.**

Man's ancestors have substantially the organisation of a simple unarticulated chordonium (copelata and ascidian larvæ). The unsegmented chorda developes between the dorsal medullary tube and the ventral gut-tube. The simple cœlom-pouches divide by a frontal septum into two on each side: the dorsal pouch (episomite) forms a muscle-plate; the ventral pouch (hyposomite) forms a gonad. Head-gut with gill-clefts.

THIRTY-SEVENTH TABLE

SYNOPSIS OF THE CHIEF SECTIONS OF OUR EMBRYOLOGY

FIRST SECTION OF OUR ONTOGENY.

Man's Invertebrate Forms.

First ontogenetic stage: **The Protozoa stage.**

The human embryo is a simple round cell, the cytula or stem-cell (first segmentation-cell, or fecundated ovum). Unicellular stage (unnucleated during caryolysis, afterwards nucleated and amœboid).

Second ontogenetic stage: **The Blastula stage.**

The human embryo consists of a round cluster of simple cells—segmentation-cells—like a colony of protozoa (a cenobium of social protozoa). It is a cenogenetic modification of the globular blastula, a hollow ball, the wall of which consists of a single layer of cells (blastoderm). The corresponding pure palingenetic form is still found in the amphioxus (Fig. 257 *c*).

Third ontogenetic stage: **The Gastrula stage.**

The human embryo is a round epigastrula, the cenogenetically modified gastrula of the higher mammals. It is composed of two layers of cells, the two primary germinal layers. The corresponding palingenetic form (archigastrula) is still found in the amphioxus (Figs. 257–260).

Fourth ontogenetic stage: **The Neurula stage.**

The human embryo assumes the bilateral-symmetrical form, and developes the first trace of the medullary tube (with the neurenteric canal) from the ectoderm in the middle line of the back. This is found in palingenetic form in the amphioxus (Fig. 260).

Fifth ontogenetic stage: **The Cœlomula stage.**

The human embryo is an oval bilateral embryonic disk (blastodiscus), in which we distinguish the four secondary germinal layers. Between the two limiting layers or the primary germinal layers two middle layers (the parietal and visceral layers of the simple cœlom-pouches) have spread out from the primitive mouth (or primitive streak). The dorsal ectoderm forms the medullary plate.

Sixth ontogenetic stage: **The Chordula stage.**

The human embryo has the structure of a simple unarticulated chordonium, the nearest living relatives of which are the copelata (appendicularia) and the ascidian larvæ. The unsegmented chorda developes between the dorsal medullary tube and the ventral gut-tube. The simple cœlom-pouches divide by a frontal septum into two pouches on each side: the dorsal pouch ("stem-zone") forms a muscle-plate, the ventral pouch ("parietal zone") corresponds originally to a gonad. Head-gut with gill-clefts.

SECOND SECTION OF OUR PHYLOGENY.

Man's Vertebrate Ancestors.

Man's ancestors are vertebrates, and have the form of an articulated individual or chain of metamera. The skin-sense layer is differentiated into horny plate and medullary tube. The skin-fibre layer has divided into corium-plate, muscle-plate, and skeleton-plate. From the gut-fibre layer we get the heart with the blood-vessels and the muscular wall of the gut. The gut-gland layer forms the chorda and the visceral epithelium.

Seventh phylogenetic stage: **The Acrania.**

Man's ancestors are skull-less vertebrates, like the amphioxus. The body is a series of metamera, as several of the primitive segments are developed. The head contains in the ventral half the branchial gut, the trunk the hepatic gut. The medullary tube is still simple. No skull, jaws, or limbs.

Eighth phylogenetic stage: **The Cyclostoma.**

Man's ancestors are jaw-less craniotes (like the myxinoida and petromyzonta). The number of metamera increases. The fore-end of the medullary tube expands into a vesicle and forms the brain, which soon divides into five cerebral vesicles. In the sides of it appear the three higher sense-organs: nose, eyes, and auditory vesicles. No jaws, limbs, or floating bladder.

Ninth phylogenetic stage: **The Ichthyoda.**

Man's ancestors are fish-like craniotes: (1) Primitive fishes (selachii); (2) plated fishes (ganoida); (3) amphibian fishes (dipneusta); (4) mailed amphibia (stegocephala). The ancestors of this series develop two pairs of limbs: a pair of fore (breast-fins) and of hind (belly-fins) legs. The gill-arches are formed between the gill-clefts: the first pair form the maxillary arches (upper and lower jaws). The floating bladder (lung) and pancreas grow out of the gut.

Tenth phylogenetic stage: **The Amniotes.**

Man's ancestors are amniotes or gill-less vertebrates: (1) Primitive amniotes (proreptilia); (2) sauromammals; (3) primitive mammals (monotremes); (4) marsupials; (5) half-apes (prosimiæ); (6) western apes (platyrrhinæ); (7) eastern apes (catarrhinæ): at first tailed cynopitheca, then tail-less anthropoids; later speechless ape-men (alali); finally speaking man. The ancestors of these amniotes develop an amnion and allantois, and gradually assume the mammal, and finally the specifically human, form.

SECOND SECTION OF OUR ONTOGENY.

Man's Vertebrate Forms.

The human embryo represents an articulated individual or a series of metamera. The skin-sense layer is differentiated into horny plate and medullary tube. The skin-fibre layer has divided into corium-plate, muscle-plate, and skeleton-plate. From the gut-fibre layer we get the heart with the blood-vessels and the muscular wall of the gut. The gut-gland layer forms the chorda and the visceral epithelium.

Seventh ontogenetic stage : **The Acrania stage.**

The human embryo has substantially the organisation of a skull-less vertebrate, like the amphioxus. The body forms a series of metamera, as several of the primitive segments are differentiated. The head contains in the ventral half the branchial gut, and the trunk the hepatic gut. The medullary tube is still simple. No skull, jaws, or limbs.

Eighth ontogenetic stage : **The Cyclostoma stage.**

The human embryo has substantially the organisation of a jaw-less craniote (like the myxinoida and petromyzonta). The number of metamera increases, The fore-end of the medullary tube enlarges and forms a brain, which soon divides into five cerebral vesicles. At the sides of it appear the three higher sense-organs : olfactory pits, eyes, and auditory vesicles. No jaws, limbs, or lungs.

Ninth ontogenetic stage : **The Ichthyoda stage.**

The human embryo has substantially the organisation of a fish-like craniote. The two pairs of limbs appear in very rudimentary form, as fin-like buds : a pair of fore (breast-fins) and of hind (belly-fins) legs. Between the gill-clefts the gill-arches are formed : the first pair form the jaw-arches (upper and lower jaws). The lung (floating bladder) and pancreas grow out of the gut.

Tenth ontogenetic stage: **The Amniote stage.**

The human embryo has substantially the organisation of an amniote or gill-less vertebrate. The gill-clefts disappear or grow together. From the gill-arches are formed the jaws, hyoid bone, and the bones of the ear. The embryo is enveloped in two membranes (amnion and serolemma). The bladder developes from the body of the embryo, and forms the allantois (and afterwards, at a part of its periphery, the placenta). All the organs of the body gradually assume the mammal, and finally the specifically human, form.

THIRTY-EIGHTH TABLE

SYNOPSIS OF THE HUMAN SYSTEMS OF ORGANS AND THEIR DEVELOPMENT FROM THE GERMINAL LAYERS

Four Germinal Layers.	Systems of Organs.	Chief parts of the Systems of Organs.
I. **Sensory layer** (ectoblast). Ectoderm or epiblast. Skin-sense layer. —— Outer limiting layer.	1. **Epidermis** (product of the horny plate, ceratoblast).	1 a. Horny layer and mucous layers of the epidermis. 1 b. External appendages (hair, nails). 1 c. Epidermic glands (sudatory, sebaceous, mammary).
	2. **Nervous system** (product of the nerve-plate, neuroblast).	2 a. Central nervous system (brain and spinal marrow). 2 b. Peripheral nervous system (motor and sensory nerves).
	3. **Sense organs** (sensilla). Products of 1 and 2.	3 a. Tactile corpuscles and knobs. 3 b. Epithelium of the mouth. 3 c. Epithelium of the nasal cavity. 3 d. Primary optic vesicles. 3 e. Auscultory labyrinth.
II. **Muscular layer** (myoblast). Parietal mesoblast. Skin-fibre layer. —— Outer middle layer.	4. **Corium** (product of the cutis-plate).	4 a. Corium: Cutis and sub-cutis (parietal layer of the episomites). 4 b. Cutaneous skeleton (external bones).
	5. **Muscular system** (product of the muscle-plate, myocœl).	5 a. Muscles of the trunk. 5 b. Muscles of the limbs.
	6. **Skeletal system** (product of the skeleton-plate, scleroblast).	6 a. Skull and vertebral column (product of the chorda-sheath). 6 b. Skeleton of the limbs (secondary products of the hyposomites).
III. **Vascular layer** (angioblast). Visceral mesoblast. Gut-fibre layer. —— Inner middle layer.	7. **Renal system** (product of the middle plate).	7 a. Fore kidneys (pronephros). 7 b. Primitive kidneys (mesonephros). 7 c. Permanent kidneys (metanephros) [and the (ectodermic) prorenal duct].
	8. **Sexual system** (product of the sexual plate).	8 a. Sexual glands (gonades). 8 b. Sexual ducts (gonoducts). 8 c. Copulative organs.
	9. **Vascular system** (product of the entire mesoderm). (Mesenchyma.)	9 A. Ventral (venous) chief vessel (principal vein and heart). 9 B. Dorsal chief vessel (aorta). 9 C. Peripheral blood-vessels. 9 D. Lymphatic vessels.
	10. **Mesenteric system** (product of the visceral mesodermic layer).	10 a. Mesentery. 10 b. Muscles of the alimentary canal. 10 c. Visceral skeleton.
IV. **Glandular layer** (endoblast). Entoderm or hypoblast. Gut-gland layer. —— Inner limiting layer.	11. **Dorsal chorda** (product of the chordoblast).	11. Axial rod (notochorda), median dorsal streak of the wall of the primitive gut (complete only in the embryo).
	12. **Visceral epithelium** (product of the enteroblast).	12 a. Epithelia of the head-gut (gullet, gill-arches, larynx, lungs). 12 b. Epithelia of the trunk-gut (stomach, liver, pancreas, small intestine).

CHAPTER XXIV.

EVOLUTION OF THE NERVOUS SYSTEM

Animal and vegetal systems of organs. Their original relations to the primary germinal layers. Sensory apparatus. Its parts: originally only the ectoderm or cutaneous layer; afterwards skin differentiated from nervous system. Double function of the skin (protective and tactile organ). Epidermis and corium. Appendages of the epidermis: glands in the skin (sudorific, lachrymal, sebaceous, mammary), nails, and hair. The embryonic woolly coat. Hair of the head and beard. Influence of sexual selection. Structure of the nervous system. Motor and sensory nerves. Central marrow; brain and spinal marrow. Composition of the human brain (cerebrum and cerebellum). Comparative anatomy of the central marrow. Embryology of the medullary tube. Division of the medullary tube into brain and spinal marrow. Division of the simple cerebral vesicle into five parts: cerebrum, optic thalami, quadratum, cerebellum, pons Varolii. Variation in the formation of the five cerebral vesicles in the different classes of vertebrates. Development of the conducting marrow or peripheral nervous system. Psychological consequences.

The previous chapters have taught us how the human body as a whole developes from the first simple rudiment, a single layer of cells. The whole human race owes its origin, like the individual man, to a simple cell. The unicellular stem-form of the race is reproduced daily in the unicellular embryonic stage of the individual. We have now to consider in detail the evolution of the various parts that make up the human frame. I must, naturally, confine myself to the most general and principal outlines; to make a special study of the evolution of each organ and tissue is both beyond the scope of this work and probably beyond the anatomic capacity of most of my readers to appreciate. In tracing the evolution of the various organs we shall follow the method that has hitherto guided us, except that we shall now have to consider the ontogeny and phylogeny of the organs together. We have seen, in studying the evolution of the body as a whole, that phylogeny casts a light over the darker paths of ontogeny, and that we should be almost unable to find our way in it without the aid of the former. We shall have the same experience in the study of the organs in detail; and I shall be compelled to give simultaneously their ontogenetic and phylogenetic origin. The more we go into the details of organic development, and the more closely we follow the rise of the various parts, the more we see the inseparable connection of embryology and stem-history. The ontogeny of the organs can only be understood in the light of their phylogeny, just as we found of the embryology of the whole body. Each embryonic form is determined by a corresponding stem-form. This is true of details as well as of the whole.

We will consider first the animal and then the vegetal systems of organs of the body. The first group consists of the psychic and the motor apparatus. To the former belong the skin, the nervous system, and the sense organs. The motor apparatus is composed of the passive and the active organs of movement (the skeleton and the muscles). The second or vegetal group consists of the nutritive and the reproductive apparatus. To the nutritive apparatus belong the alimentary canal with all its appendages, the vascular system, and the renal system. The reproductive apparatus comprises the different organs of sex (embryonic glands, sexual ducts, and copulative organs).

As we know from previous Chapters (XI.–XIII.), the animal systems of organs (the organs of sensation and presentation) develop for the most part out of the *outer* primary germ-layer, or the cutaneous layer. On the other hand, the vegetal systems of organs arise for the most part from the *inner* primary germ-layer, the visceral layer. It is true that this antithesis of the animal and vegetal spheres of the body in man and all the higher animals is by no means rigid; several parts of the animal apparatus (for instance, the greater part of the muscles) are formed from cells that come originally from the entoderm; and a great part of the vegetative apparatus (for instance, the mouth-cavity and the gonoducts) are composed of cells that come from the ectoderm.

THIRTY-NINTH TABLE

SYNOPSIS OF THE APPARATUS OF ORGANS IN THE HUMAN BODY

(N.B.—The origin of the various organs from the four secondary germinal layers is indicated by the Roman numerals (I.–IV.): I. Skin-sense layer. II. Skin-fibre layer. III. Gut-fibre layer. IV. Gut-gland layer.)

A. Animal Systems of Organs.	a. **Sensory apparatus.** *Sensorium.*	1. **Skin.** (*Tegumentum.*)	Epidermis.	Epidermis I.	
			Corium.	Corium II.	
		2. **Central nervous system.**	Brain.	Encephalon.	I.
			Spinal marrow.	Medulla spinalis.	
			Spinal membranes.	Meninges II.	
		3. **Peripheral nervous system.**	Cerebral nerves.	Nervi cerebrales.	I.
			Spinal nerves.	Nervi spinales.	
			Intestinal nerves.	Nervi sympathetici.	
		4. **Sense-organs.** (*Sensilla.*)	Organ of touch (skin).	Org. tactus.	I. + II.
			Organ of taste (tongue).	Org. gustus.	
			Organ of smell (nose).	Org. olfactus.	
			Organ of sight (eyes).	Org. visus.	
			Organ of hearing (ears).	Org. auditus.	
	b. **Motor apparatus.** *Motorium.*	5. **Muscular system.** (Active organs of movement.)	Cutaneous muscles.	Musculi cutanei.	II. + III.
			Skeletal muscles.	Musculi skeleti.	
		6. **Skeletal system.** (Passive organs of movement.)	Vertebral column.	Vertebrarium.	
			Skull.	Cranium.	
			Skeleton of limbs.	Meloskeleton.	
B. Vegetal Systems of Organs.	c. **Nutritive apparatus.** *Nutritorium.*	7. **Alimentary system.** (*Gastralium.*)	Digestive organs.	O. digestiva.	III. + IV.
			Respiratory organs.	O. respiratoria.	
		8. **Vascular system.** (*Vasorium.*)	Body-cavity.	Cœloma II. + III.	
			Lymphatic vessels.	Vasa lymphatica.	II. + III.
			Blood-vessels.	Vasa sanguifera.	
			Heart.	Cor III. + IV.	
		9. **Renal system.** (*Organa urinaria.*)	Kidneys.	Renes II. + III.	
			Urinary ducts.	Ureteres I. + II.	
			Bladder.	Urocystis III. + IV.	
	d. **Reproductive apparatus.** *Propagatorium.*	10. **Sexual organs.** (*Organa sexualia.*)	Sexual glands.	Gonades.	II. + III.
			(A. Ovaries.)	(A. Ovaria.)	
			(B. Testicles.)	(B. Spermaria.)	
			Sexual ducts.	Gonaductus.	I. + II.
			(A. Oviducts.)	(A. Oviductus.)	
			(B. Spermaducts.)	(B. Spermaductus.)	
			Copulative organs.	Copulativa.	
			(A. Vagina.)	(A. Vagina.)	I. + II.
			(B. Penis.)	(B. Penis.)	

In the more advanced animal body there is so much interlacing and displacement of the various parts that it is often very difficult to indicate the sources of them. But, broadly speaking, we may take it as a positive and important fact that in man and the higher animals the chief part of the animal organs comes from the ectoderm, and the greater part of the vegetative organs from the entoderm. It was for this reason that Carl Ernst von Baer called the one the animal and the other the vegetative layer (see p. 41).

The solid foundation of this important thesis is the *gastrula*, the most instructive embryonic form in the animal world, which we still find in the same shape in the most diverse classes of animals. This form points demonstrably to a common stem-form of all the metazoa, the *gastræa;* in this long-extinct stem-form the whole body consisted throughout life of the two primary germinal layers, as is now the case temporarily in the gastrula; in the gastræa the simple cutaneous (skin) layer *actually* represented all the animal organs and functions, and the simple visceral (gut) layer all the vegetal organs and functions. This is the case with the modern gastræads (Fig. 287); and it is also the case *potentially* with the gastrula.

We shall easily see that the gastræa theory is thus able to throw a good deal of light, both morphologically and physiologically, on some of the chief features of embryonic development, if we take up first the consideration of the chief element in the animal sphere, the psychic apparatus or sensorium and its evolution. This apparatus consists of two very different parts, which seem at first to have very little connection with each other—the outer skin *(tegumentum* or *derma)*, with all its hairs, nails, sweat-glands, etc., and the nervous system. The latter comprises the central nervous system (brain and spinal cord), the peripheral cerebral and spinal nerves, and the sense-organs. In the fully-formed vertebrate body these two chief elements of the sensorium lie far apart, the skin being external to, and the central nervous system in the very centre of, the body. The one is only connected with the other by a section of the peripheral nervous system and the sense-organs. Nevertheless, as we know from human embryology, the medullary tube is formed from the cutaneous layer. The organs that discharge the most advanced functions of the animal body—the organs of the soul, or of psychic life—develop from the external skin.

This remarkable fact seems in itself to be so paradoxical and inexplicable that for a long time it was attempted to deny it. The most positive embryological observations were met with the false assertion that the central nervous system does not originate from the outermost germinal layer, but from a special underlying stratum of cells. However, the ontogenetic facts could not be suppressed; and now, when we regard them in the light of phylogeny, they seem to constitute a perfectly natural and necessary process. If we reflect on the historical evolution of the psychic and sensory functions, we are forced to conclude that the cells which accomplish them must originally have been located on the outer surface of the body. Only elementary organs in this superficial position could directly receive the influences of the environment. Afterwards, under the influence of natural selection, the cellular group in the skin which was specifically "sensitive" withdrew into the inner and more protected part of the body, and formed there the foundation of a central nervous organ. As a result of increased differentiation, the skin and the central nervous system became further and further separated, and in the end the two were only permanently connected by the afferent peripheral sensory nerves.

The observations of the comparative anatomist are in complete accord with this view. He tells us that large numbers of the lower animals have no nervous system, though they exercise the functions of sensation and will like the higher animals. In the unicellular protozoa, which do not form germinal layers, there is, of course, neither nervous system nor skin. But in the second division of the animal kingdom also, the metazoa, there is at first no nervous system. Its functions are represented by the simple cell-layer of the ectoderm, which the lower metazoa have inherited from the gastræa (Fig. 339 *e*). We find this in the lowest zoophytes—the gastræads, physemaria, and sponges (Figs. 287–292). The lowest cnidaria (the hydroid polyps) also are little superior to the gastræads in structure. Their vegetative functions are accomplished by the simple visceral layer, and their animal functions by the simple cutaneous layer. In these cases the simple cell-layer of the ectoderm is at once skin, locomotive apparatus, and nervous system.

When we come to the higher metazoa, in which the sensory functions and their organs are more advanced, we find a division of labour among the ectodermic cells. Groups of sensitive nerve cells separate from the ordinary epidermic cells; they retire into the more protected tissue of the mesodermic under-skin, and form special neural ganglia there. Even in the platodes, especially the *turbellaria*, we find an independent nervous system, which has separated from the outer skin. This is the "upper pharyngeal ganglion," or *acroganglion*, situated above the gullet (Fig. 341 *g*). From this rudimentary structure has been developed the elaborate central nervous system of the higher animals. In some of the higher worms, such as the rain-worm, the first rudiment of the central nervous system (Fig. 340 *n*) is a local thickening of the skin-sense layer *(hs)*, which afterwards separates altogether from the horny plate. In the earliest platodes *(cryptocœla)* and vermalia *(gastrotricha)* the acroganglion remains in the epidermis. But the medullary tube of the vertebrates originates in the same way. Our embryology has taught us that this first structure of the central nervous system also developes originally from the outer germinal layer.

Let us now examine more closely the evolution of the human skin, with its various appendages, the hairs and glands. This external covering has, physiologically, a double and important part to play. It is, in the first place, the common integument that covers the whole surface of the body, and forms a protective envelope for the other organs. As such it also effects a certain exchange of matter between the body and the surrounding atmosphere (exhalation, perspiration). In the second place, it is the earliest and original sense-organ, the common organ of feeling that experiences the sensation of the temperature of the environment and the pressure or resistance of bodies that come into contact.

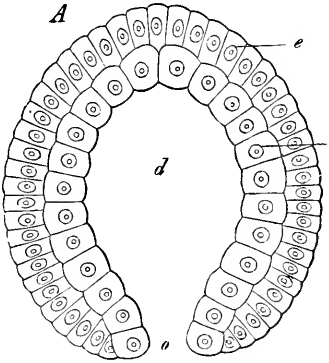
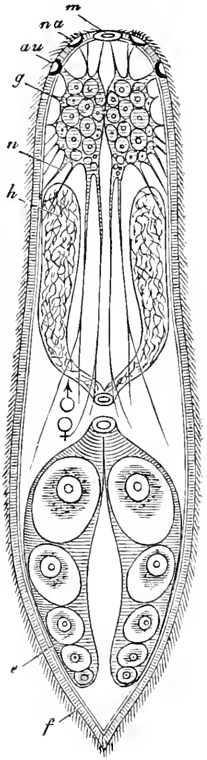


FIG. 339.



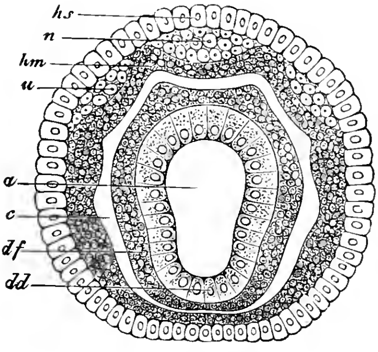


FIG. 340.

FIG 341.

FIG. 339.—**Gastrula of gastrophysema** (class of the gastræads, p. 518). *e* ectoderm, *i* entoderm, *d* primitive gut, *o* primitive mouth.

FIG. 340.—**Transverse section of the embryo of a rain-worm.** *hs* skin-sense layer, *hm* skin-fibre layer, *df* gut-fibre layer, *dd* gut-gland layer, *a* visceral cavity, *c* body-cavity or cœloma, *n* neural ganglia, *u* primitive kidneys.

FIG. 341.—**A turbellarian** (*rhabdocœlum*). From the brain or upper pharyngeal ganglion (*g*) nerves (*n*) radiate, and proceed to the skin (*f*), the eyes (*au*), the olfactory organ (*na*), and the mouth (*m*). *h* testicles, *e* ovaries. (Diagram.)

The human skin (like that of all the higher animals) is composed of two layers, the outer and the inner or underlying skin. The outer skin, or *epidermis*, consists of simple ectodermic cells, and contains no blood-vessels (Fig. 342 *a*, *b*). It developes from the outer germinal layer, or skin-sense layer.

The underlying skin *(corium* or *hypodermis)* consists chiefly of connective tissue, contains numerous blood-vessels and nerves, and has a totally different origin. It comes from the outermost parietal stratum of the middle germinal layer, or the skin-fibre layer. The corium is much thicker than the epidermis. In its deeper strata (the *subcutis*) there are clusters of fat-cells (Fig. 342 *h*). Its uppermost stratum (the cutis proper, or the papillary stratum) forms, over almost the whole surface of the body, a number of conical microscopic papillæ (something like warts), which push into the overlying epidermis *(c)*. These tactile or sensory particles contain the finest sensory organs of the skin, the touch-corpuscles. Others contain merely end-loops of the blood-vessels that nourish the skin *(c, d)*. The various parts of the corium arise by division of labour from the originally homogeneous cells of the cutis-plate, the outermost lamina of the mesodermic skin-fibre layer (Fig. 150 *hpr*, Figs. 168, 169 *cp;* Plates VI. and VII., *l*).[1]

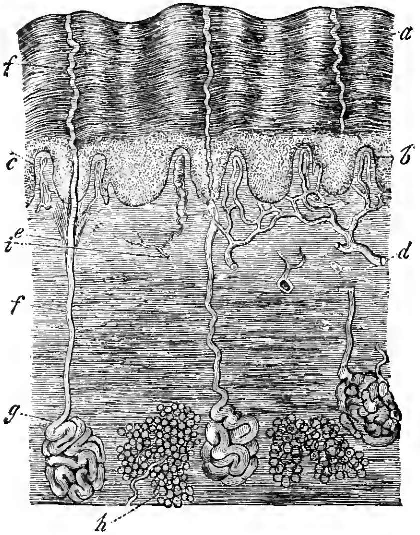


FIG. 342.—**The human skin in vertical section** (from *Ecker*), highly magnified. *a* horny layer of the epidermis, *b* mucous layer of the epidermis, *c* papillæ of the corium, *d* blood-vessels of same, *ef* ducts of the sweat glands *(g)*, *h* fat glands in the corium, *i* nerve, passing into a tactile corpuscle above.

In the same way, all the parts and appendages of the epidermis develop by differentiation from the homogeneous cells of the horny plate (Fig. 343). At an early stage the simple cellular layer of this horny plate divides into two. The inner and softer stratum (Fig. 342 *b*) is known as the

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[1] The cutis-plate is the connective organ, in which the cutaneous skeleton of the vertebrate is formed.

mucous stratum, the outer and harder *(a)* as the horny (corneous) stratum. This horny layer is being constantly used up and rubbed away at the surface; new layers of cells grow up in their place out of the underlying mucous stratum. At first the epidermis is a simple covering of the surface of the body. Afterwards various appendages develop from it, some internally, others externally. The internal appendages are the cutaneous glands—sudoriferous, sebaceous, etc. The external appendages are the hairs and nails.

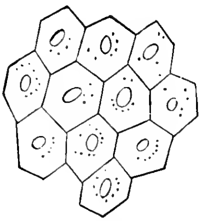


FIG. 343.—**Epidermic cells** of a human embryo of two months. (From *Kölliker*.)

The cutaneous glands are originally merely solid cone-shaped growths of the epidermis, which sink into the underlying corium (Fig. 344, *1*). Afterwards a canal *(2, 3)* is formed inside them, either by the softening and dissolution of the central cells or by the secretion of fluid internally. Some of the glands, such as the sudoriferous, do not ramify (Fig. 342 *efg*). These glands, which secrete the perspiration, are very long and have a spiral coil at the end, but they never ramify; so also the wax-glands of the ears. Most of the other cutaneous glands give out buds and ramify; thus, for instance, the lachrymal glands of the upper eye-lid that secrete tears (Fig. 344), and the sebaceous glands which secrete the fat in the skin and generally open into the hair-follicles. Sudoriferous and sebaceous glands are found only in mammals. But we find lachrymal glands in all the three classes of amniotes—reptiles, birds, and mammals. They are wanting in the lower, aquatic vertebrates.

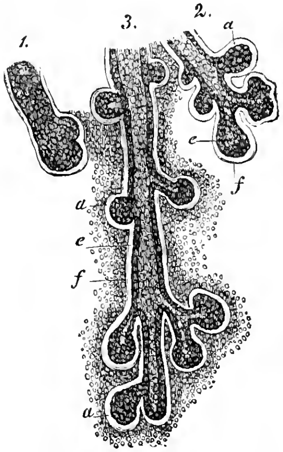


FIG. 344.—**Rudimentary lachrymal glands** from a human embryo of four months. (From *Kölliker*.) *1* earliest structure in the shape of a simple solid cone, *2* and *3* more advanced structures, ramifying and hollowing out. *a* solid buds, *e* cellular coat of the hollow buds, *f* structure of the fibrous envelope, which afterwards forms the corium about the glands

The mammary glands (Figs. 345 and 346) are very remarkable; they are found in all mammals, and in these alone. They secrete the milk for the feeding of the new-born mammal. In spite of their unusual size, these structures are nothing more than large sebaceous glands in the skin (Plate VII., Fig. 16 *md*). The milk is formed by the liquefaction of the fatty milk-cells inside the branching mammary-gland tubes (Fig. 345 *c*), in the same way as the skin-grease or hair-fat, by the solution of fatty cells inside the sebaceous glands. The outlets of the mammary glands enlarge and form sac-like mammary ducts *(b)*; these narrow again *(a)*, and open in the teats or nipples of the breast by sixteen to twenty-four fine apertures. The first structure of this large and elaborate gland is a very simple cone in the epidermis, which penetrates into the corium and ramifies. In the new-born infant it consists of twelve to eighteen radiating lobes (Fig. 346). These gradually ramify, their ducts become hollow and larger, and rich masses of fat accumulate between the lobes. Thus is formed the prominent female breast *(mamma)*, on the top of which rises the teat or nipple *(mammilla)*. The latter is only developed later on, when the mammary gland is fully formed; and this ontogenetic phenomenon is extremely interesting, because the earlier mammals (the stem-forms of the whole class) have no teats. In them the milk comes out through a flat portion of the ventral skin that is pierced like a sieve, as we still find in the lowest living mammals, the oviparous monotremes of Australia. The young animal licks the milk from the mother instead of sucking it. We may call the monotremes "teat-less" *(amasta)*. In many of the lower mammals we find a number of milk-glands at different parts of the ventral surface. In the human female there are usually only two pairs of glands, at the breast; and it is the same with the apes, bats, elephants, and several other mammals. Sometimes, however, we find two successive pairs of glands (or even more) in the human female. Some women have four or five pairs of breasts, like pigs and hedgehogs (Fig. 106). This polymastism points back to an older stem-form. We often find these accessory breasts in the male also (Fig. 106 *D*). Sometimes, moreover, the normal mammary glands are fully developed and can suckle in the male; but as a rule they are merely rudimentary organs without functions in the male. We have already (Chapter XI.) dealt with this remarkable and interesting instance of atavism.

While the cutaneous glands are inner growths of the epidermis, the appendages which we call hairs and nails are external local growths in it. The nails *(ungues)* which form important protective structures on the back of the most sensitive parts of our limbs, the tips of the fingers and toes, are horny growths of the epidermis, which we share with the apes. The lower mammals usually have claws instead of them; the ungulates, hoofs. The stem-form of the mammals certainly had claws; we find them in a rudimentary form even in the salamander. The horny claws are highly developed in most of the reptiles (Fig. 318, p. 592), and the mammals have inherited them from the earliest representatives of this class, the stem-reptiles *(tocosauria)*. Like the hoofs *(ungulæ)* of the ungulates, the nails of apes and men have been evolved from the claws of the older mammals. In

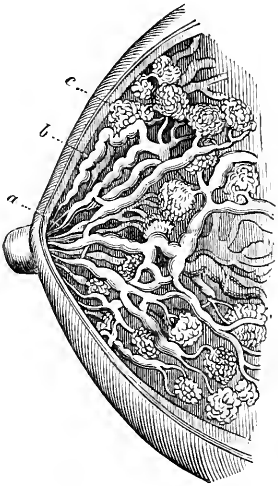


FIG. 345.

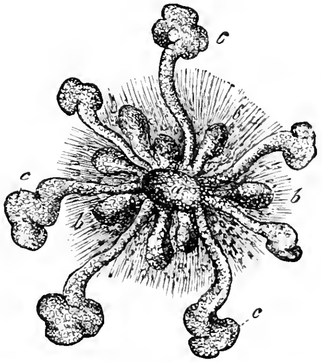


FIG. 346.

FIG. 345.—**The female breast** *(mamma)* in vertical section. *c* racemose glandular lobes, *b* enlarged milk-ducts, *a* narrower outlets, which open into the nipple. (From *H. Meyer.*)

FIG. 346.—**Mammary gland of a new-born infant.** *a* original central gland, *b* small and *c* large buds of same. (From *Langer.*)

the human embryo the first rudiment of the nails is found (between the horny and the mucous stratum of the epidermis) in the fourth month. But their edges do not penetrate through until the end of the sixth month.

The most interesting and important appendages of the epidermis are the hairs; on account of their peculiar composition and origin we must regard them as highly characteristic of the whole mammalian class. It is true that we also find hairs in many of the lower animals, such as insects and worms. But these hairs, like the hairs of plants, are thread-like appendages of the surface, and differ entirely from the hairs of the mammals in the details of their structure and development. Hence Oken rightly called the mammals "hairy animals." The human hairs, like those of all the other mammals, are solely composed of specially differentiated and distributed epidermic cells. In their rudimentary condition in the embryo they are solid, conical growths of the epiderms into the underlying corium, similar to the growths of the sebaceous and sudoriferous glands. As in the case of the latter, the simple cone is composed at first of ordinary epidermic cells. Inside this cone a central firmer mass of cells presently differentiates from the rest. This grows much longer, separates from the surrounding mass of cells (the root-sheath), and finally penetrates outwards and rises above the surface as the shaft of the hair. The part that sinks deepest into the skin (the "fundus" of the "follicle") is the root of the hair, clothed with its sheath. The first hairs break out in the human embryo at the end of the fifth and beginning of the sixth month.

The embryology of the hairs is known in all its details, but there are two different views as to their phylogeny. On the older view the hairs of the mammals are equivalent or homologous to the feathers of the bird or the horny scales of the reptile. As we deduce all three classes of amniotes from a common stem-group, we must assume that these Permian stem-reptiles *(tocosauria)* had a complete scaly coat, inherited from their Carboniferous ancestors, the mailed amphibia *(stegocephala)*; the bony scales of their corium *(pholides)* were covered with horny scales *(lepides)*. In passing from aquatic to terrestrial life the horny scales were further developed, and the bony scales degenerated in most of the reptiles. As regards the bird's feathers, it is certain that they are modifications of the horny scales of their reptilian ancestors. But it is otherwise with the hairs of the mammals. In their case the hypothesis has lately been advanced on the strength of very extensive research, especially by Friedrich Maurer, that they have been evolved from the cutaneous sense-organs of amphibian ancestors by modification of functions ; the epidermic structure is very similar in both in its embryonic rudiments. This modern view, which had the support of the greatest expert on the vertebrates, Carl Gegenbaur, can be harmonised with the older theory to an extent, in the sense that both formations, scales and hairs, were very closely connected originally. Probably the conical budding of the skin-sense layer grew up *under the protection of the horny scale*, and became an organ of touch subsequently by the cornification of the hairs ; many hairs are still sensory organs (tactile hairs on the muzzle and cheeks of many mammals : pubic hairs).

This middle position of the genetic connection of scales and hairs was advanced in my *Systematic Phylogeny of the Vertebrates* (p. 433). It is confirmed by the similar arrangement of the two cutaneous formations. As Maurer pointed out, the hairs, as well as the cutaneous sense-organs and the scales, are at first arranged in regular longitudinal series, and they afterwards break into alternate groups. In the embryo of a bear 2.5 cm. long, which I owe to the kindness of Herr von Schmertzing (of Arva Varallia, Hungary), the back is covered with sixteen to twenty alternating longitudinal rows of scaly protuberances (Fig. 347). They are at the same time arranged in regular transverse rows, which converge at an acute angle from both sides towards the middle of the back. The tip of the scale-like wart is turned inwards. Between these larger hard scales (or groups of hairs) we find numbers of rudimentary smaller hairs.

The human embryo is, as a rule, entirely clothed with a thick coat of fine wool during the last three or four weeks of gestation. This embryonic woollen coat *(lanugo)* generally disappears in part during the last weeks of fœtal life; but in any case, as a rule, it is lost immediately after birth, and is replaced by the thinner coat of the permanent hair. These permanent hairs grow out of hair-follicles, which are formed from the root-sheaths of the disappearing wool-fibres. The embryonic wool-coat usually, in the case of the human embryo, covers the whole body, with the exception of the palms of the hands and soles of the feet. These parts are always bare, as in the case of apes and of most other mammals. Sometimes the wool-coat of the embryo has a striking effect, by its colour, on the later permanent hair-coat. Hence it happens occasionally, for instance, among our Indo-Germanic races, that children of blond parents seem—to the dismay of the

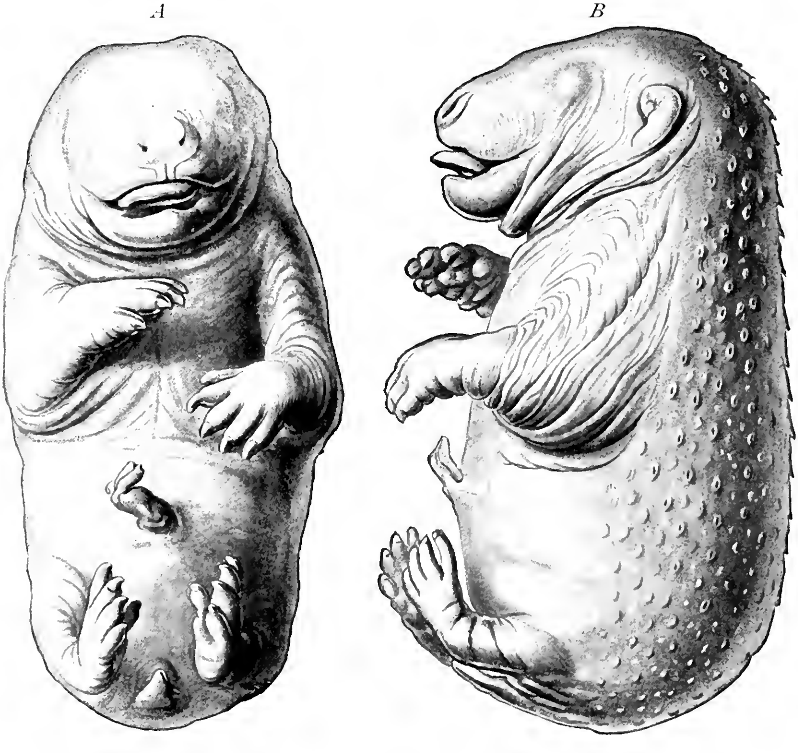


FIG. 347.—**Embryo of a bear** *(ursus arctos)* forty-five mm. long, twenty mm. broad, twice natural size. *A* seen from ventral side, *B* from the left.

latter—to be covered at birth with a dark brown or even a black woolly coat. Not until this has disappeared do we see the permanent blond hair which the child has inherited. Sometimes the darker coat remains for weeks, and even months, after birth. This remarkable woolly coat of the human embryo is a legacy from the apes, our ancient long-haired ancestors.

It is not less noteworthy that many of the higher apes approach man in the thinness of the hair on various parts of the body. With most of the apes, especially the higher catarrhines (or narrow-nosed apes), the face is mostly, or entirely, bare, or at least it has hair no longer or thicker than that of man. In their case, too, the back of the head is usually provided with a thicker growth of hair; this is lacking, however, in the case of the bald-headed chimpanzee (*Anthropithecus calvus*). The males of many species of apes have a considerable beard on the cheeks and chin; this sign of the masculine sex has been acquired by sexual selection. Many species of apes have a very thin covering of hair on the breast and the upper side of the limbs—much thinner than on the back or the under side of the limbs. On the other hand, we are often astonished to find tufts of hair on the shoulders, back, and extremities of members of our Indo-Germanic and of the Semitic races. Exceptional hair on the face, as on the whole body, is hereditary in certain families of hairy men. The quantity and the quality of the hair on head and chin are also conspicuously transmitted in families. These extraordinary variations in the total and partial hairy coat of the body, which are so noticeable, not only in comparing different races of men, but also in comparing different families of the same race, can only be explained on the assumption that in man the hairy coat is, on the whole, a rudimentary organ, a useless inheritance from the more thickly-coated apes. In this man resembles the elephant, rhinoceros, hippopotamus, whale, and other mammals of various orders, which have also, almost entirely or for the most part, lost their hairy coats by adaptation.

The particular process of adaptation by which man lost the growth of hair on most parts of his body, and retained or augmented it at some points, was most probably sexual selection. As Darwin luminously showed in his *Descent of Man,* sexual selection has been very active in this respect. As the male anthropoid apes chose the females with the least hair, and the females favoured the males with the finest growths on chin and head, the general coating of the body gradually degenerated, and the hair of the beard and head was more strongly developed. The growth of hair at other parts of the body (arm-pit, pubic region) was also probably due to sexual selection. Moreover, changes of climate, or habits, and other adaptations unknown to us, may have assisted the disappearance of the hairy coat.

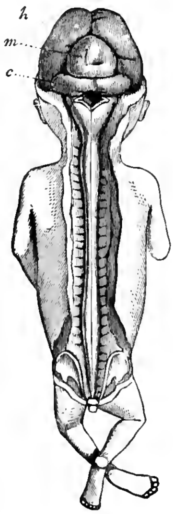
The fact that our coat of hair is inherited directly from the anthropoid apes is proved in an interesting way, according to Darwin, by the direction of the rudimentary hairs on our arms, which cannot be explained in any other way. Both on the upper and the lower part of the arm they point towards the elbow. Here they meet at an obtuse angle. This curious arrangement is found only in the anthropoid apes—gorilla, chimpanzee, orang, and several species of gibbons—besides man (Figs. 235, 241). In other species of gibbon the hairs are pointed towards the hand both in the upper and lower arm, as in the rest of the mammals. We can easily explain this remarkable peculiarity of the anthropoids and man on the theory that our common ancestors were accustomed (as the anthropoid apes are to-day) to place their hands over their heads, or across a branch above their heads, during rain. In this position, the fact that the hairs point downwards helps the rain to run off. Thus the direction of the hair on the lower part of our arm reminds us to-day of that useful custom of our anthropoid ancestors.

Comparative anatomy and embryology, after careful investigation of the skin and its appendages, discover quite a number of these important indications that it has been directly inherited from the apes. The skin and hair have been handed on to us by the anthropoid apes, which had inherited them from the lower apes, and these in turn from the earlier mammals. The same must be said of the other important system of organs that developes from the skin-sense layer—the nervous system and the sense-organs. This elaborate system, which accomplishes the most advanced vital functions, was inherited from the apes and, through them, from the lower mammals.

The nervous system in man and all the other vertebrates is, when fully formed, an extremely complex apparatus, that we may compare, in anatomic structure and physiological function, with an extensive telegraphic system. The chief station of the system is the central marrow or central nervous system, the innumerable ganglionic cells or *neurona* (Fig. 9) of which are connected by branching processes with each other and with numbers of very fine conducting wires. The latter are the peripheral and ubiquitous nerve-fibres; with their terminal apparatus, the sense-organs, etc., they constitute the conducting marrow or peripheral nervous system. Some of them—the sensory nerve-fibres—conduct the impressions from the skin and other sense-organs to the central marrow; others—the motor nerve-fibres—convey the commands of the will to the muscles.

The central nervous system or central marrow *(medulla centralis)* is the real organ of psychic action in the narrower sense. However we conceive the intimate connection of this organ and its functions, it is certain that its characteristic actions, which we call sensation, will, and thought, are inseparably dependent on the normal development of the material organ in man and all the higher animals. We must, therefore, pay particular attention to the evolution of the latter. As it can give us most important information regarding the nature of the "soul," it should be full of interest. If the central marrow developes in just the same way in the human embryo as in the embryo of the other mammals, the evolution of the human psychic organ from the central organ of the other mammals, and through them from the lower vertebrates, must be beyond question. No one can doubt the momentous bearing of these embryonic phenomena.

In order to understand them fully we must first say a word or two of the general form and the anatomic composition of the mature human central marrow. (Cf. Tables XL. and XLI.) Like the central nervous system of all the other craniotes, it consists of two parts, the head-marrow or brain *(medulla capitis* or *encephalon)* and the spinal-marrow *(medulla spinalis* or *notomyelon)*. The one is enclosed in the bony skull, the other in the bony vertebral canal, which is formed of a series of superimposed vertebræ of the shape of seal-rings. (Plate VII., Fig. 16 *m*.) Twelve pairs of cerebral nerves proceed from the brain, and thirty-one pairs of spinal nerves from the spinal cord, to the rest of the body (Fig. 186). On general anatomic investigation the spinal marrow is found to be a cylindrical cord, with a spindle-shaped bulb both in the region of the neck above (at the last cervical vertebra) and in the region of the loins (at the first lumbar vertebra) below (Fig. 349). At the cervical bulb the strong nerves of the upper limbs, and at the lumbar bulb those of the lower limbs, proceed from the spinal cord. Above, the latter passes into the brain through the medulla oblongata (Fig. 349 *mo*). The spinal cord seems to be a thick mass of nervous matter, but it has a narrow canal at its axis, which passes into the further cerebral ventricles above, and is filled, like these, with a clear fluid.



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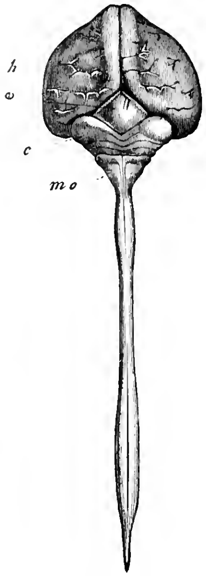


FIG. 349.

FIG. 348.—**Human embryo,** three months old, natural size, from the dorsal side: brain and spinal cord exposed. (From *Kölliker.*) *h* cerebral hemispheres (fore brain), *m* corpora quadrigemina (middle brain), *c* cerebellum (hind brain): under the latter is the triangular medulla oblongata (after-brain).

FIG. 349.—**Central marrow of a human embryo,** four months old, natural size, from the back. (From *Kölliker.*) *h* large hemispheres, *v* quadrigemina, *c* cerebellum, *mo* medulla oblongata: underneath it the spinal cord.

The brain is a large nerve-mass, occupying the greater part of the skull, of most elaborate structure. On general examination it divides into two parts, the cerebrum and cerebellum. The cerebrum lies in front and above, and has the familiar characteristic convolutions and furrows on its surface (Figs. 350, 351; Plates XXII. and XXIII.). On the upper side it is divided by a deep longitudinal fissure into two halves, the cerebral hemispheres; these are connected by the *corpus callosum*. The large cerebrum is separated from the small cerebellum by a deep transverse furrow. The latter lies behind and below, and has also numbers of furrows, but much finer and more regular, with convolutions between, at its surface. The cerebellum also is divided by a longitudinal fissure into two halves, the "small hemispheres"; these are connected by a vermiform piece, the *vermis cerebelli*, above, and by the broad pons Varolii below (Fig. 350 *VI.*).

But comparative anatomy and ontogeny teach us that in man and all the other craniotes the brain is at first composed, not of these two, but of three, and afterwards five, consecutive parts. These are found in just the same form—as five consecutive vesicles—in the embryo of all the craniotes, from the cyclostoma and fishes to man. But, however much they agree in their rudimentary condition, they differ considerably afterwards. In man and the higher mammals the first of these ventricles, the cerebrum, grows so much that in its mature condition it is by far the largest and heaviest part of the brain. To it belong not only the large hemispheres, but also the corpus callosum that unites them, the olfactory lobes, from which the olfactory nerves start, and most of the structures that are found at the roof and bottom of the large lateral ventricles inside the two hemispheres, such as the *corpora striata*. On the other hand, the *optic thalami*, which lie between the latter, belong to the second division, which developes from the "intermediate brain"; to the same section belong the single third cerebral ventricle and the structures that are known as the corpora geniculata, the infundibulum, and the pineal gland. Behind these parts we find, between the cerebrum and cerebellum, a small ganglion composed of two prominences, which is called the *corpus quadrigeminum* on account of a superficial transverse fissure cutting across (Figs. 348 *m*, 349 *v*). Although this quadrigeminum is very insignificant in man and the higher mammals, it forms a special third section, greatly developed in the lower vertebrates, the "middle brain." The fourth section is the "hind-brain" or little brain (cerebellum) in the narrower sense, with the single median part, the *vermis*, and the pair of lateral parts, the "small hemispheres" (Fig. 349 *c*). Finally, we have the fifth and last section, the *medulla oblongata* (Fig. 349 *mo*), which contains the single fourth cerebral cavity and the contiguous parts (pyramids, olivary bodies, corpora restiformia). The medulla oblongata passes straight into the medulla spinalis (spinal cord). The narrow central canal of the spinal cord continues above into the quadrangular fourth cerebral cavity of the medulla oblongata, the floor of which is the quadrangular depression. From here a narrow duct, called "the aqueduct of Sylvius," passes through the

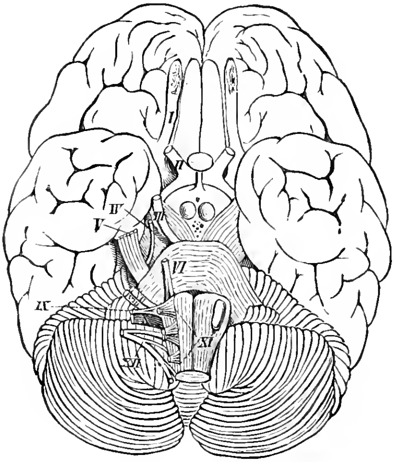


FIG. 350.

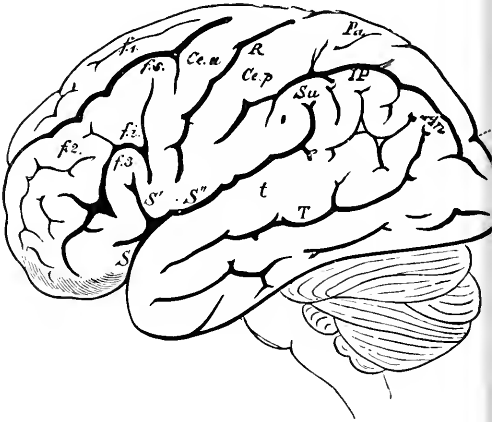


FIG. 351.

FIG. 350.—**The human brain,** seen from below. (From *H. Meyer.*) Above (in front) is the cerebrum with its extensive branching furrows; below (behind) the cerebellum with its narrow parallel furrows. The Roman numbers indicate the roots of the twelve pairs of cerebral nerves in a series towards the rear.

FIG. 351.—**The human brain,** seen from the left. (From *H. Meyer.*) The furrows of the cerebrum are indicated by thick, and those of the cerebellum by finer lines. Under the latter we can see the medulla oblongata. f_1-f_2 frontal convolutions, *C* central convolutions, *S* fissure of Sylvius, *T* temporal furrow, *Pa* parietal lobes, *An* angular gyrus, *Po* parieto-occipital fissure.

corpus quadrigeminum to the third cerebral ventricle, which lies between the two optic thalami; and this in turn is connected with the pairs of lateral ventricles which lie to the right and left in the large hemispheres. Thus all the cavities of the central marrow are directly interconnected. All these parts of the brain have an infinitely complex structure in detail, but we cannot go into this. Although it is much more elaborate in man and the higher vertebrates than in the lower classes, it developes in them all from the same rudimentary structure, the five simple cerebral vesicles of the embryonic brain. (Cf. Plates VIII.–XIII.)

But before we consider the development of the complicated structure of the brain from this simple series of vesicles, let us glance for a moment at the lower animals, which have no brain. Even in the skull-less vertebrates, the amphioxus, we find no independent brain, as we have seen. The whole central marrow is merely a simple cylindrical cord which runs the length of the body, and ends equally simply at both extremities—a plain medullary tube (Plate XIX., Fig. 15 *m*). All that we can discover is a small vesicular bulb at the foremost part of the tube, a degenerate rudiment of a primitive brain *(archencephalon)*. We meet the same simple medullary tube in the first structure of the ascidian larva (Plate XVIII., Fig. 5 *m*), in the same characteristic position, above the chorda. On closer examination we find here also a small vesicular swelling at the fore end of the tube, the first trace of a differentiation of it into brain *(m_1)* and spinal cord *(m)*. It is probable that this differentiation was more advanced in the extinct provertebrates, and the brain-bulb more pronounced (Figs. 101–105). The brain is phylogenetically older than the spinal cord, as the trunk was not developed until after the head. If we consider the undeniable affinity of the ascidiæ to the vermalia, and remember that we can trace all the chordonia to lower vermalia, it seems probable that the simple central marrow of the former is equivalent to the simple nervous ganglion, which lies above the gullet in the lower worms, and has long been known as the "upper pharyngeal ganglion" *(ganglion pharyngeum superius)*;

it would be better to call it the primitive or vertical brain (acroganglion). In the turbellaria and rotifers the nervous system consists merely of a simple pair of ganglia, which lie on the dorsal side of the body, and from which nerve-fibres radiate to the various parts of the body (Fig. 341 *g*, *n*). In the lowest and earliest platodes, the platodaria or cryptocœla (Fig. 293), this acroganglion is not yet separated from its source, the skin-sense layer, but represents a local swelling of it, an epidermic "vertical plate" *(acroplatea)*.

Probably this upper pharyngeal ganglion of the lower worms is the structure from which the complex central marrow of the higher animals has been evolved. The medullary tube of the chordonia has been formed by the lengthening of the vertical brain on the dorsal side. In all the other animals the central nervous system has been developed in a totally different way from the upper pharyngeal ganglion; in the articulates, especially, a pharyngeal ring, with ventral marrow, has been added. The molluscs also have a pharyngeal ring, but it is not found in the vertebrates. In these the central marrow has been prolonged down the dorsal side; in the articulates down the ventral side. This fact proves of itself that there is no direct relationship between the vertebrates and the articulates. The unfortunate attempts to derive the dorsal marrow of the former from the ventral marrow of the latter have totally failed (cf. pp. 331, 526–30).

When we examine the embryology of the human nervous system, we must start from the important fact, which we have already seen, that the first structure of it in man and all the higher vertebrates is the simple medullary tube, and that this separates from the outer germinal layer in the middle line of the sole-shaped embryonic shield. As the reader will remember, the straight medullary furrow first appears in the middle of the sandal-shaped embryonic shield (Plates IV. and V.). At each side of it the parallel borders curve over in the form of dorsal or medullary swellings. These bend together with their free borders, and thus form the closed medullary tube (Figs. 139–142). At first this tube lies directly underneath the horny plate; but it afterwards travels inwards, the upper edges of the provertebral plates growing together between the horny plate and the tube, joining above the latter, and forming a completely closed canal. As Gegenbaur very properly observes, "this gradual imbedding in the inner part of the body is a process acquired with the progressive differentiation and the higher potentiality that this secures; by this process the organ of greater value to the organism is buried within the frame." (Cf. Figs. 148–151 and Plates VI. and VII.)

It must seem to every thoughtful and impartial man a momentous fact that our psychic organ (like that of all the other craniotes) is formed in just the same way and in the same primitive shape in which we find it permanently in the amphioxus. In the cyclostoma—a stage above the acrania—the fore end of the cylindrical medullary tube begins early to expand into a pear-shaped vesicle; this is the first outline of an independent brain (Plate XIX., Fig. 116 m_1). In this way the central marrow of the vertebrates divides clearly into its two chief sections, brain (m_1) and spinal cord (m_2), corresponding to the two chief sections of the body, the head and trunk. We find the first faint trace of this important differentiation in the amphioxus, and still more in the ascidian larva (Plate XVIII., Fig. 5).

The simple vesicular form of the brain, which persists for some time in the cyclostoma, is found also at first in all the higher vertebrates (Fig. 352 *hb*). But in these it soon passes away, the one vesicle being divided into several successive parts by transverse constrictions. There are first two of these constrictions, dividing the brain into three consecutive vesicles (fore brain, middle brain, and hind brain, Fig. 353 *v*, *m*, *h*). Then the first and third are sub-divided by fresh constrictions, and thus we get five successive sections (Fig. 354; cf. Plate VII., Figs. 13–16, and Plates VIII.–XIII., second row). These five cerebral vesicles, which are found in the same form in the embryo of all the craniotes, were first clearly recognised by Baer, and received from him the following names: (1) Fore brain (*v*); (2) intermediate brain *(z)*; (3) middle brain *(m)*; (4) hind brain *(h)*; and (5) after brain *(n)*.

Comparative anatomy and ontogeny have recently shown that the first three vesicles belong to the primitive brain proper *(archencephalon)*; its typical structure differs from the contiguous after-brain *(metencephalon)*, which approaches more to the spinal cord. The fourth and fifth vesicles are really only

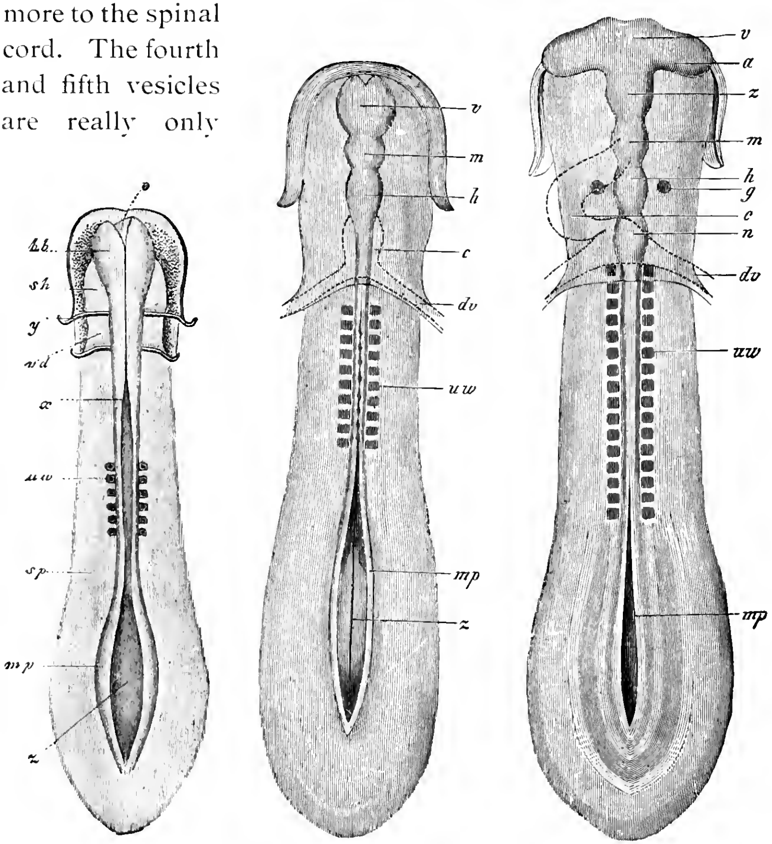


Fig. 352. Fig. 353. Fig. 354.

Figs. 352-354.—**Sole-shaped embryonic shield of the chick,** in three successive stages of development, dorsal view, magnified about twenty times, slightly diagrammatic. Fig. 352 with six pairs of provertebræ. Brain a simple vesicle *(hb)*. Medullary furrow still wide open from *x*; much enlarged behind at *z*. *mp* medullary plates, *sp* lateral plates, *y* limit of pharynx *(sh)* and fore gut *(vd)*. Fig. 353 with ten pairs of provertebræ. Brain divided into three vesicles: *v* fore brain, *m* middle brain, *h* hind brain, *c* heart, *dv* vitelline veins. Medullary furrow still wide open behind *(z)*. *mp* medullary plates. Fig. 354 with sixteen pairs of provertebræ. Brain divided into five vesicles: *v* fore brain, *z* intermediate brain, *m* middle brain, *h* hind brain, *n* after brain. *a* optic vesicles, *g* auditory vesicles, *c* heart, *dv* vitelline veins, *mp* medullary plate, *uw* provertebræ.

different parts of one after-brain; the hind-brain (= cerebellum) is its dorsal, and the medulla oblongata its ventral part (cf. Table XLI.). It is from the basis of the latter alone that the ten pairs of true cerebral nerves (3–12), which are formed on the model of the spinal nerves (*trigeminus*-group, 3–8, in front of the labyrinth of the ear, *vagus*-group, 9–12, behind it), proceed. The "first two cerebral nerves" (I. *olfactorius*, of smell, II. *opticus*, of sight) are of a totally different character and origin; they develop as direct processes of the primitive brain (the olfactory from the fore brain, and the optic from the intermediate brain).

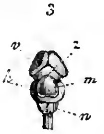


FIG. 355.

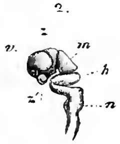


FIG. 356.

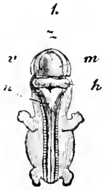


FIG. 357.

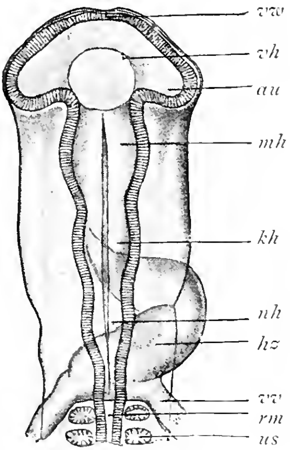


FIG. 358.

FIGS. 355–357.—**Central marrow of the human embryo** from the seventh week, two cm. long. (From *Kölliker.*) Fig. 357 back view of the whole embryo: brain and spinal cord exposed. Fig. 356 the brain with the uppermost part of the cord, from the left. Fig. 355 the brain from above. *v* fore brain, *z* intermediate brain, *m* middle brain, *h* hind brain, *n* after brain.

FIG. 358.—**Head of a chick-embryo** (hatched fifty-eight hours), from the back, magnified forty times. (From *Mihalkovics.*) *vw* anterior wall of the fore brain, *vh* its ventricle, *au* optic vesicles, *mh* middle brain, *kh* hind brain, *nh* after brain, *hz* heart (seen from below), *vv* vitelline veins, *us* primitive segment, *rm* spinal cord.

In all the craniotes, from the cyclostoma up to man, the same parts develop from these five original cerebral vesicles, though in very different ways. The first vesicle, the fore brain (*prosencephalon, v*), forms by far the largest part of the cerebrum—namely, the large hemispheres, the olfactory lobes, the corpora striata, the callosum, and the fornix. From the second vesicle, the intermediate brain (*deutencephalon, z*), originate especially the optic thalami, the other parts that surround the third cerebral ventricle, and the infundibulum and pineal gland. The third vesicle, the middle brain *(mesencephalon, m)*, produces the corpora quadrigemina and the aqueduct of Sylvius. From the fourth vesicle, the hind brain *(metencephalon, h)*, developes the greater part of the cerebellum—namely, the *vermis* and the two small hemispheres. Finally, the fifth vesicle, the after brain *(epencephalon, n)*, forms the medulla oblongata, with the quadrangular pit (the floor of the fourth ventricle), the pyramids, olivary bodies, etc.

We must certainly regard it as a comparative-anatomical and ontogenetic fact of the greatest significance that in all the craniotes, from the lowest cyclostomes and fishes up to the apes and man, the brain developes in just the same way in the embryo. The first rudiment of it is always a simple vesicular enlargement of the fore end of the medullary tube. In every case, first three, then five, vesicles develop from this bulb, and the permanent brain with all its complex anatomic structures, of so great a variety in the various classes of vertebrates, is formed from the five primitive vesicles. When we compare the mature brain of a fish, an amphibian, a reptile, a bird, and a mammal, it seems incredible that we can trace the various parts of these organs, that differ so much internally and externally, to common types. Yet all these different craniote brains have started with the same rudimentary structure. To convince ourselves of this we have only to compare the corresponding stages of development of the embryos of these different animals. (Plates VIII.–XIII., second row.)

This comparison is extremely instructive. If we extend it through the whole series of the craniotes, we soon discover this interesting fact: In the cyclostomes (the myxinoida and petromyzonta), which we have recognised as the lowest and earliest craniotes, the whole brain remains throughout life at a very low stage, which is very brief and passing in the embryos of the higher craniotes; they retain the five original sections of the brain unchanged. In the fishes we find an essential and considerable modification of the five vesicles; it is clearly the brain of the selachii in the first place, and subsequently the brain of the ganoids, from which the brain of the rest of the fishes on the one hand and of the dipneusts and amphibia, and through these of the higher vertebrates, on the other hand, must be derived. In the fishes and amphibia (Fig. 361) there is a preponderant development of the middle brain, and also the after-brain, the first, second, and fourth sections remaining very primitive. It is just the reverse in the higher vertebrates, in which the first and third sections, the cerebrum and cerebellum, are exceptionally developed; while the middle brain and after-brain remain small. The corpora quadrigemina are mostly covered by the cerebrum, and the oblongata by the cerebellum. But we find a number of stages of development within the higher vertebrates themselves. From the amphibia upwards the brain (and with it the psychic life) developes in two different directions; one of these is followed

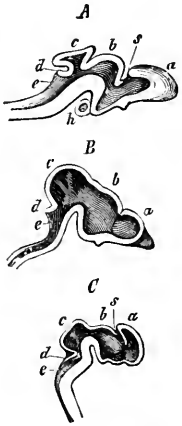


FIG. 359.

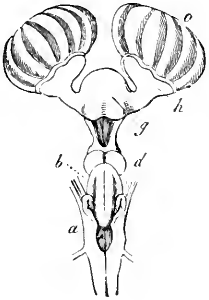


FIG. 360.

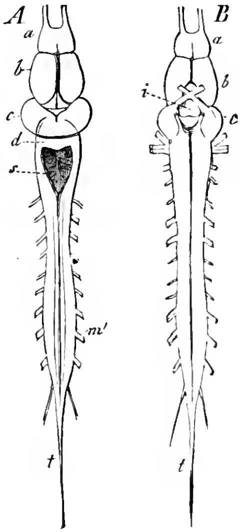


FIG. 361.

FIG. 359.—**Brain of three craniote embryos** in vertical section. *A* of a shark (*heptarchus*), *B* of a serpent (*coluber*), *C* of a goat (*capra*). *a* fore brain, *b* intermediate brain, *c* middle brain, *d* hind brain, *e* after brain, *s* primitive cleft. (From *Gegenbaur*.)

FIG. 360.—**Brain of a shark** (*scyllium*), back view. *g* fore-brain, *h* olfactory lobes, which send the large olfactory nerves to the nasal capsule (*o*), *d* intermediate brain, *b* middle brain; behind this the insignificant structure of the hind brain, *a* after brain. (From *Gegenbaur*.)

FIG. 361.—**Brain and spinal cord of the frog.** *A* from the dorsal, *B* from the ventral side. *a* olfactory lobes before the (*b*) fore brain, *i* infundibulum at the base of the intermediate brain, *c* middle brain, *d* hind brain, *s* quadrangular pit in the after brain, *m* spinal cord (very short in the frog), *m'* roots of the spinal nerves, *t* terminal fibres of the spinal cord. (From *Gegenbaur*.)

by the reptiles and birds, and the other by the mammals. The development of the first section, the fore brain, is particularly characteristic of the mammals. It is only in them that the cerebrum becomes so large as to cover all the other parts of the brain (Figs. 351, 362–365).

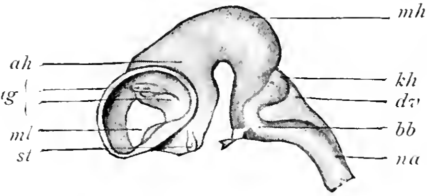


FIG. 362.

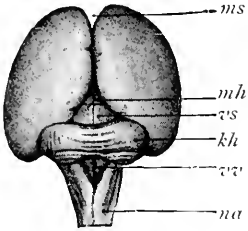


FIG. 363.

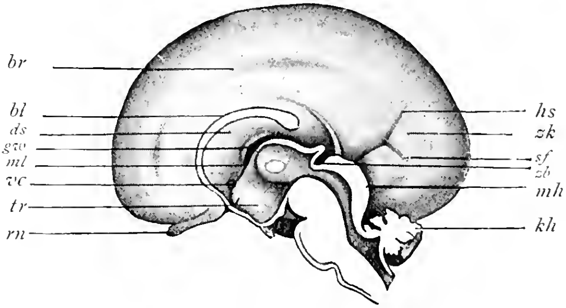


FIG. 364.

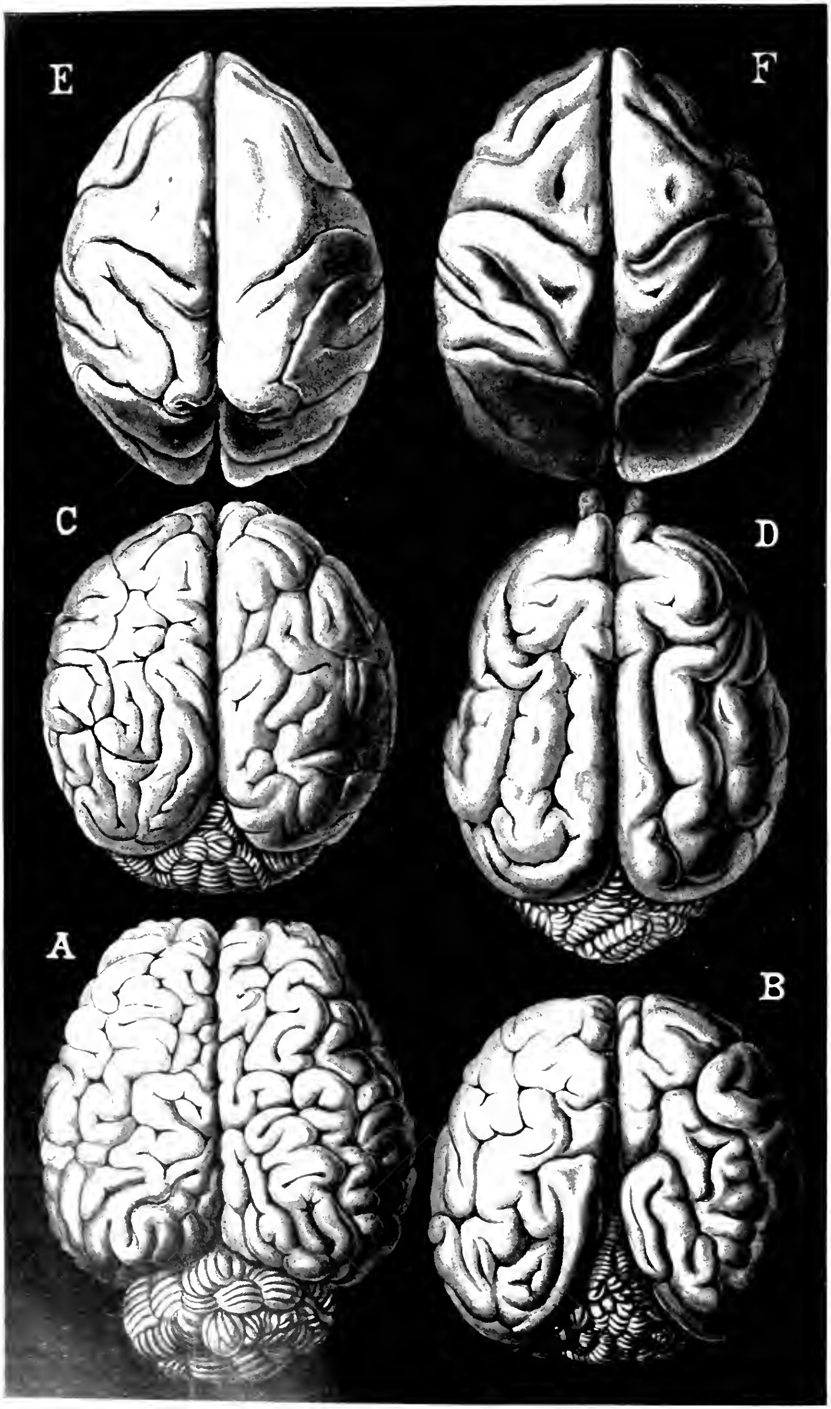
FIG. 362.—**Brain of an ox-embryo,** five cm. in length. (From *Mihalkovics*, magnified three times.) Left view; the lateral wall of the left hemisphere has been removed. *st* corpora striata, *ml* Monro-foramen, *ag* arterial plexus, *ah* Ammon's horn, *mh* middle brain, *kh* cerebellum, *dv* roof of the fourth ventricle, *bb* pons varolii, *na* medulla oblongata.

FIG. 363.—**Brain of a human embryo,** twelve weeks old. (From *Mihalkovics*, natural size.) Seen from behind and above. *ms* mantle-furrow, *mh* corpora quadrigemina (middle brain), *vs* anterior medullary ala, *kh* cerebellum, *vv* fourth ventricle, *na* medulla oblongata.

FIG. 364.—**Brain of a human embryo,** twenty-four weeks old, halved in the median plane: right hemisphere seen from inside. (From *Mihalkovics*, natural size.) *rn* olfactory nerve, *tr* funnel of the intermediate brain, *vc* anterior commissure, *ml* Monro-foramen, *gw* fornix, *ds* transparent sheath, *bl* corpus callosum, *br* fissure at its border, *hs* occipital fissure, *zh* cuneus, *sf* occipital transverse fissure, *zb* pineal gland, *mh* corpora quadrigemina, *kh* cerebellum.

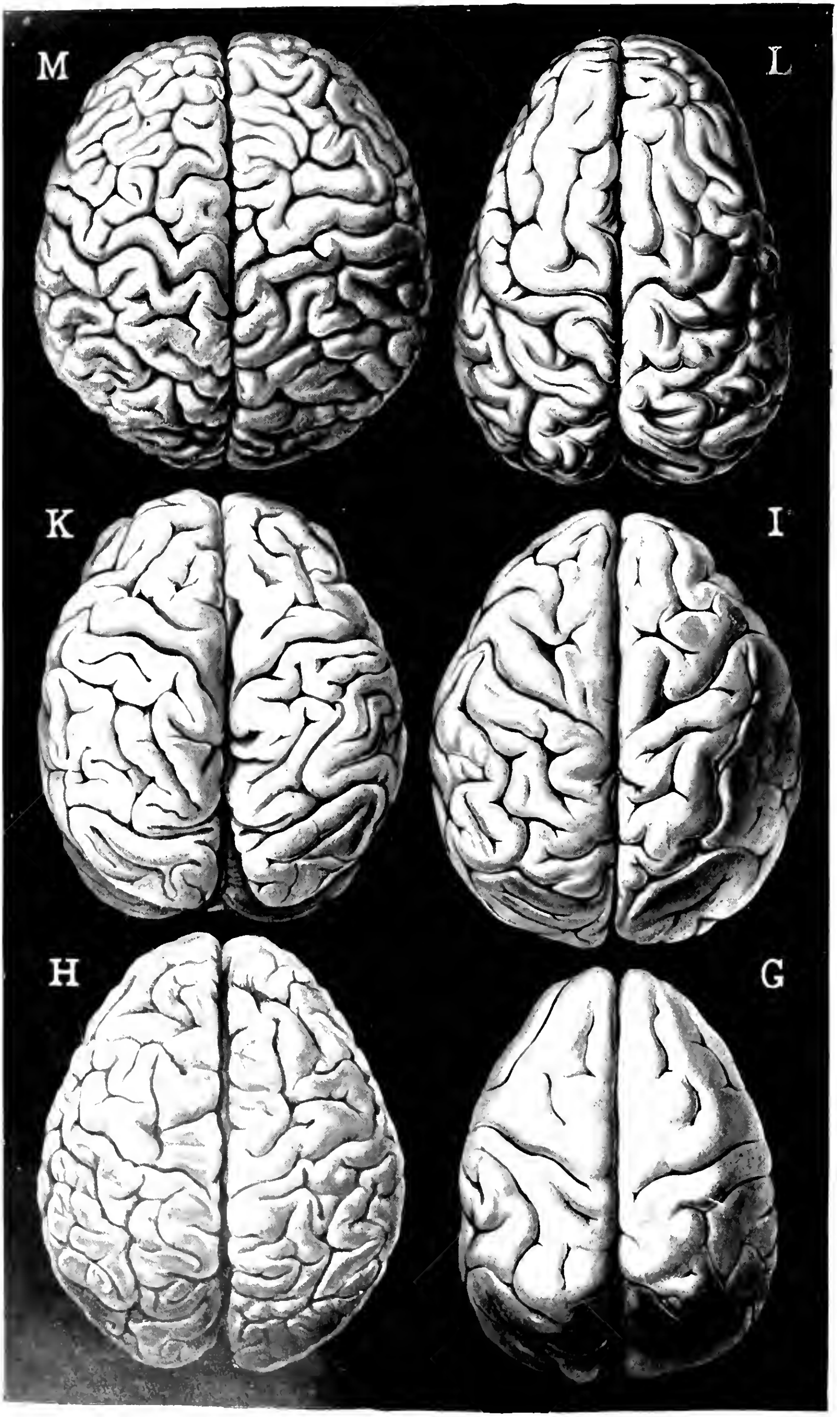
There are also notable variations in the relative position of the cerebral vesicles. In the lower craniotes they lie originally almost in the same plane. When we examine the brain laterally, we can cut through all five vesicles with a straight line. But in the amniotes there is a considerable

MAMMAL BRAINS



A Giraffe B Seal C Dolphin
D Lion E Semnopithecus F Cercopithecus

MAMMAL BRAINS



G Gibbon H Chimpanzee I Orang
K Gorilla L Bushman M Teuton

curve in the brain along with the bending of the head and neck; the whole of the upper dorsal surface of the brain developes much more than the under ventral surface. This causes a curve, so that the parts come to lie as follows: The fore brain is right in front and below, the intermediate brain a little higher, and the middle brain highest of all; the hind brain lies a little lower, and the after brain lower still. We find this only in the amniotes—the reptiles, birds, and mammals. (Cf. Plates I. and XXIV., and VIII.–XIII.)

Thus, while the brain of the mammals agrees a good deal in general growth with that of the birds and reptiles, there are some striking differences between the two. In the sauropsids (birds and reptiles, Plates VIII.–X.) the middle brain *(m)* and the middle part of the hind brain are well developed. In the mammals (Plates XI.–XIII.) these parts do not grow, and the fore-brain developes so much that it overlies the other vesicles. As it continues to grow towards the rear, it at last covers the whole of the rest of the brain, and also encloses the middle parts from the sides (Figs. 362–364). This process is of great importance, because the fore brain is the organ of the higher psychic life, and in it those functions of the nerve-cells are discharged which we sum up in the word "soul." The highest achievements of the animal body—the wonderful manifestations of consciousness and the complex molecular processes of thought—have their seat in the fore brain. We can remove the large hemispheres, piece by piece, from the mammal without killing it, and we then see how the higher functions of consciousness, thought, will, and sensation are gradually destroyed, and in the end completely extinguished. If the animal is fed artificially, it may be kept alive for a long time, as the destruction of the psychic organs by no means involves the extinction of the faculties of digestion, respiration, circulation, urination—in a word, the vegetative functions. It is only conscious sensation, voluntary movement, thought, and the combination of various higher psychic functions that are affected.

The fore brain, the organ of these functions, only attains this high level of development in the more advanced placentals, and thus we have the simple explanation of the intellectual superiority of the higher mammals. The soul of most of the lower placentals is not much above that of the reptiles, but among the higher placentals we find an uninterrupted gradation of mental power up to the apes and man. In harmony with this we find an astonishing variation in the degree of development of their fore brain not only qualitatively, but also quantitatively. The mass and weight of the brain are much greater in modern mammals, and the differentiation of its various parts more important, than in their extinct Tertiary ancestors. This can be shown paleontologically in any particular order. The brains of the living ungulates are (relatively to the size of the body) four to six times (in the highest groups even eight times) as large as those of their earlier Tertiary ancestors, the well-preserved skulls of which enable us to determine the size and weight of the brain.

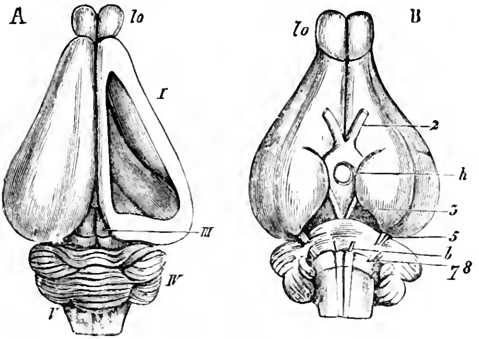


Fig. 365.—**Brain of the hare.** *A* from the dorsal, *B* from the ventral side. *lo* olfactory lobes, *I* fore brain, *h* hypophysis at the base of the intermediate brain, *III* middle brain, *IV* hind brain, *V* after brain, *2* optic nerve, *3* oculomotor nerve, *5–8* cerebral nerves. In *A* the roof of the right hemisphere *(I)* is removed, so that we can see the corpora striata in its lateral ventricle. (From *Gegenbaur*.)

In the lower mammals the surface of the cerebral hemispheres is quite smooth and level, as in the hare (Fig. 365). Moreover, the fore brain remains so small that it does not cover the middle brain. At a stage higher the middle brain is covered, but the hind brain remains free. Finally, in the apes and man, the latter also is covered by the fore brain. We can trace a similar gradual development in the fissures and convolutions that are found on the surface of the cerebrum of the higher mammals (Figs. 350, 351). If we compare different groups of mammals in regard to these fissures and convolutions, we find that their development proceeds step by step with the advance of mental life.

Of late years great attention has been paid to this special branch of cerebral anatomy, and very striking individual differences have been detected within the limits of the human race. In all human beings of special gifts and high intelligence the convolutions and fissures are much more developed than in the average man ; and they are more developed in the latter than in idiots and others of low mental capacity. There is a similar gradation among the mammals in the internal structure of the fore brain. In particular the corpus callosum, that unites the two cerebral hemispheres, is only developed in the placentals. Other structures—for instance, in the lateral ventricles—that seem at first to be peculiar to man, are also found in the higher apes, and these alone. It was long thought that man had certain distinctive organs in his cerebrum which were not found in any other animal. But careful examination has discovered that this is not the case, but that the characteristic features of the human brain are found in a rudimentary form in the lower apes, and are more or less fully developed in the higher apes. Huxley has convincingly shown, in his *Man's Place in Nature* (1863), that the differences in the formation of the brain within the ape-group constitute a deeper gulf between the lower and higher apes than between the higher apes and man.

The comparative anatomy and physiology of the brain of the higher and lower mammals are very instructive, and give important information in connection with the chief questions of psychology. This is seen in the comparison of the twelve mammal brains that I have represented—lower apes and other placentals on Plate XXII., and anthropoid apes and man on Plate XXIII. The twelve figures represent the brain as seen from above, reduced to the same size ; we see the various convolutions *(gyri)* and fisures *(sulci)* that distinguish so conspicuously the cerebral cortex in these higher mammals. This grey cortex (or mantle) of the brain is the great psychic organ in the narrower sense, the instrument of all higher mental action; when it is destroyed the mental functions are extinguished.

The central marrow (brain and spinal cord) developes from the medullary tube in man just as in all the other mammals, and the same applies to the conducting marrow or "peripheral nervous system." It consists of the *sensory* nerves, which conduct centripetally the impressions from the skin and the sense-organs to the central marrow, and of the *motor* nerves, which convey centrifugally the movements of the will from the central marrow to the muscles. All these peripheral nerves grow out of the medullary tube (Fig. 366), and are, like it, products of the skin-sense layer. The spinal ganglia (Fig. 367 *spg*) proceed from a dorsal region of the medullary tube, which grows upwards from its upper end between it and the horny plate, and enlarges in the middle of each primitive segment into a spinal ganglion. The intestinal ganglia of the sympathetic system are merely isolated parts of these spinal ganglia. Thus, while the whole nervous apparatus is ectodermal in origin, its connective-tissue envelopes are formed from the skin-fibre layer—especially the medullary membranes *(meninges)*. We can clearly understand the ontogenesis of the peripheral nerves and their original connection with the central marrow on the one hand, and with the sense-organs and muscles on the other, when we remember its causal relation to their phylogenesis, in the light of the biogenetic law.

The complete agreement in the structure and development of the psychic organs which we find between man and the highest mammals, and which can only be explained by their common origin, is of profound importance in the monistic psychology. This is only seen in its full light when we compare these morphological facts with the corresponding physiological phenomena, and remember that every psychic action requires the complete and normal condition of the correlative brain structure for its full and normal exercise. The very complex molecular movements inside the neural cells, which we describe comprehensively as "the life of the soul," can no more exist in the vertebrate, and therefore in man, than the circulation without the heart and blood. And as the central marrow developes in man from the same medullary tube as that of the other vertebrates, and as man shares the characteristic structure of his cerebrum (the organ

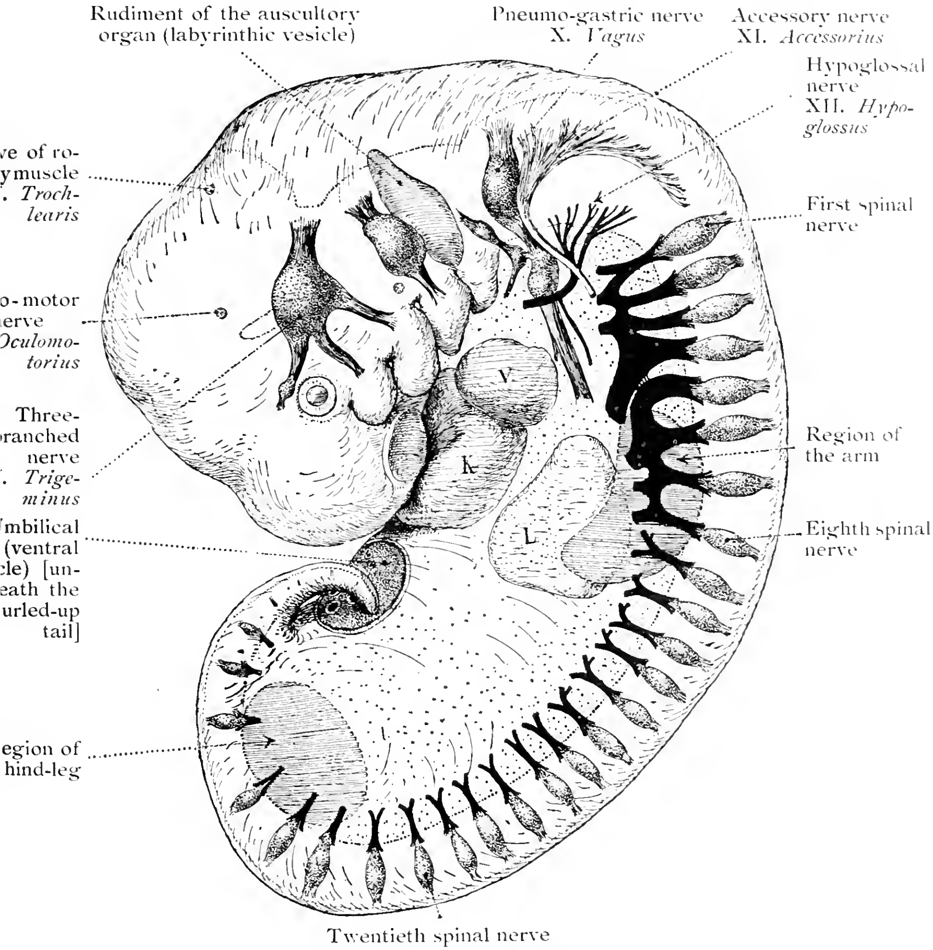


FIG. 366.—**Human embryo of the fourth week** (twenty-six days old), six mm. long, magnified twenty times. (From *Moll.*) The rudiments of the cerebral nerves and the roots of the spinal nerves are especially to be noticed. Underneath the four gill-arches (on the left) we see the heart (with auricle, *V*, and ventricle, *K*), underneath it the liver *(L)*. Between the labyrinthic vesicle and the semilunar ganglion *(ganglion semilunare)* of the large trigeminal cerebral nerve (V.) the root of the acoustic nerve (*acusticus*, VIII.) can be seen, connected with the motor nerves of the face *(facialis*, VII.); the two together originally formed the nerves of the arch of the tongue-bone *(N acustico-facialis)*. Between the labyrinthic vesicle and the large pneumogastric (*vagus*, X.) is the glossopharyngeal nerve *(glossopharyngeus*, IX.).

of thought) with the anthropoid apes, his psychic life also must have the same origin as theirs.

If we appreciate the full weight of these morphological and physiological facts, and put a proper phylogenetic interpretation on the observations of embryology, we see that the older idea of the personal immortality of the human soul is scientifically untenable. Death puts an end, in man as in any other vertebrate, to the physiological function of the cerebral neurona, the countless microscopic ganglionic cells, the collective activity of which is known as "the soul." I have shown this fully in the eleventh chapter of my *Riddle of the Universe*.

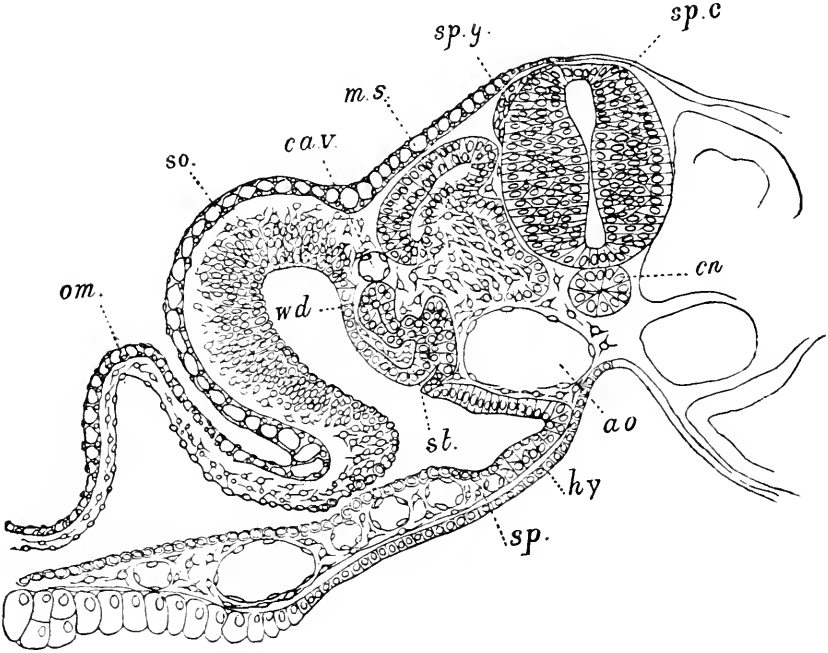


Fig. 367.—**Transverse section of a duck-embryo,** with twenty-four primitive segments. (From *Balfour.*) The spinal ganglia *(spg)* sprout out from a dorsal lateral part of the medullary tube *(spc)* between it and the horny plate. *ch* chorda, *ao* double aorta, *hy* gut-gland layer, *sp* gut-fibre layer, with sections of blood-vessels, *ms* muscle-plate, in the dorsal wall of the myocœl (episomite). Under the cardinal vein *(cav)* is the prorenal duct *(wd)* and a segmental prorenal canal *(st)*. The skin-fibre layer of the body-wall *(so)* continues into the amniotic fold *(om)*. Between the four secondary germinal layers and the structures that arise from them embryonic connective substance is developed with stellate cells and rudimentary vessels (Hertwig's "mesenchyma").

FORTIETH TABLE

SYNOPSIS OF THE DEVELOPMENT OF THE SKIN AND NERVOUS SYSTEM

XL. A.: The Skin.

Skin (Derma or Integumentum).	I. **Epidermis.** Product of the skin-sense layer.	I. A. Horny layer of the epidermis. (*Stratum corneum.*) I. B. Mucous layer of the epidermis. (*Stratum mucosum.*)	Hairs. Nails. Sudoriferous glands. Lachrymal glands. Sebaceous glands. Mammary glands.
	II. **Corium.** Product of the skin-fibre layer.	II. A. Fibrous layer of the corium. (*Cutis.*) II. B. Fatty layer of the corium. (*Subcutis.*)	Connective tissue. Fatty tissue. Smooth muscles. Blood-vessels and Lymph-vessels of the corium.

XL. B.: The Nervous System.

B a. **Central marrow** or central nervous system. **Medulla centralis.** Product of the skin-sense layer (ectoderm).	I. **Fore-brain.** *Prosencephalon.*	Large hemispheres.	*Hemisphæræ cerebri.*
		Olfactory lobes.	*Lobi olfactorii.*
		Lateral ventricles.	*Ventriculi laterales.*
		Corpora striata.	*Corpora striata.*
		Corpus callosum.	*Corpus callosum.*
	II. **Intermediate brain.** *Deutencephalon.*	Optic thalami.	*Thalami optici.*
		Third ventricle.	*Ventriculus tertius.*
		Pineal gland.	*Conarium (epiphysis).*
		Infundibulum.	*Infundibulum.*
	III. **Middle brain.** *Mesencephalon.*	Corpus quadrigeminum (or bigeminum).	*Corpus bigeminum.*
		Aqueduct of Sylvius.	*Aequæductus Sylvii.*
		Crura cerebri.	*Pedunculi cerebri.*
	IV. **Hind brain.** *Pontencephalon.*	Small hemispheres.	*Hemisphæræ cerebelli.*
		Vermis.	*Vermis cerebelli.*
		Pons Varolii.	*Pons Varolii.*
	V. **After brain.** *Rhombencephalon.*	Pyramidal bodies.	*Corpora pyramidalia.*
		Olivary bodies.	*Corpora olivaria.*
		Restiform bodies.	*Corpora restiformia.*
		Fourth ventricle.	*Ventriculus quartus.*
	VI. **Spinal cord.**	*Notomyelon.*	*Medulla spinalis.*
B b. **Medullary membranes.** (Meninges.) Product of the mesoderm.	Enveloping membranes with the blood-vessels of the central marrow.	1. Soft membrane.	*Pia mater.*
		2. Middle membrane.	*Arachnoidea.*
		3. Hard membrane.	*Dura mater.*
		(Products of the skin-fibre layer.)	
B c. **Conducting marrow** or peripheral nervous system. Product of the ectoderm.		1. Cerebral nerves.	*Nervi cerebrales.*
		2. Spinal nerves.	*Nervi spinales.*
		3. Sympathetic nerves.	*Nervi sympathici.*

FORTY-FIRST TABLE

SYNOPSIS OF THE CHIEF PHYLOGENETIC SECTIONS OF THE HUMAN NERVOUS SYSTEM AND ITS CONSTITUENTS

The Three Phylogenetic Sections of the Central Marrow.	**The Five Cerebral Vesicles. Products of the Spinal Cord.**	**Chief Groups of Nerves.**	**Peripheral Nerves.**
First section: **Primitive brain, Archencephalon.** Central organ of the dorsal part of the head: the sense-region (nose and eyes). (Cerebral type.)	I. Fore brain. **Prosencephalon** (with lateral ventricles).	Originally only olfactory brain. *Rhinencephalon* (afterwards brain-mantle *pallium*.)	1. *Olfactorius (lobus).* Olfactory nerve.
	II. Intermediate brain. **Deutencephalon** (with the third ventricle).	A pair of optic vesicles (ventral). A single occipital eye (dorsal). Rudimentary.	2a. *Opticus.* Double optic nerve (ventral). 2b. *Epiphysis.* Pineal gland. Single optic nerve (dorsal).
	III. Middle brain. **Mesencephalon** (with aqueduct of Sylvius).	Crura cerebri (ventral). Quadrigemina (dorsal).	
Second section: **After brain, Metencephalon.** Central organ of the vertebral part of the head: The gill-region (jaw and gill-arches). (Spinal type.)	IV. Hind brain. **Pontencephalon.** *Cerebellum.* (Dorsal.)	Preotic or trigeminal group. Third to eighth cerebral nerves.	3. Oculomotorius. 4. Trochlearis. 5. Trigeminus. 6. Abducens. 7. Facialis. 8. Acusticus.
	V. After brain. **Rhombencephalon.** *Medulla oblongata.* (Ventral.)	Postotic or vagus group. Ninth to twelfth cerebral nerves.	9. Glossopharyngeus. 10. Vagus. 11. Accessorius. 12. Hypoglossus.
Third section: **Spinal cord, Notomyelon.** *(Medulla spinalis.)* Central organ of the trunk. (Spinal type.)	VI. Trunk nervous system. **Spinalium** (for the skin and muscles of the trunk).	A. Motor roots (ventral). B. Sensory roots (dorsal).	Spinal nerves, a pair at each segment of the trunk (each rising from two roots).
	VII. Intestinal nervous system. **Sympathicus** (for the nutritive and sexual organs).	A. Double series of segmental ganglia, starting from spinal ganglia. B. Irregular plexus of intestinal nerves.	A. Terminal cord of the *sympathicus.* B. Plexus intestinales of the *sympathicus.*

FORTY-SECOND TABLE

SYNOPSIS OF THE CHIEF PERIODS OF THE STEM-HISTORY OF THE HUMAN SKIN

I. Period : **Gastræad-skin.**

The whole skin (including the not yet differentiated nervous system) consists of a single stratum of ciliated cells (the ectoderm or primary skin-layer), as we find still in the gastrula of the amphioxus.

II. Period : **Platode-skin.**

The skin consists of two different strata or secondary germinal layers, the skin-sense layer (with rudimentary nervous system) and skin-fibre layer (rudimentary corium).

III. Period : **Vermalian-skin.**

The skin-sense layer has divided into horny plate (epidermis) and central marrow. The skin-fibre layer has divided into corium-plate and the underlying cutaneous muscular tube.

IV. Period : **Acrania-skin.**

The horny plate is still a single stratum of cells, a simple epidermis. The corium is a thin cutis-plate (parietal layer of the cœlom-pouches), separated from the muscle-plate, as in amphioxus.

V. Period : **Cyclostoma-skin.**

The epidermis is a many-layered, soft, mucous cell-stratum, with sensory cells and unicellular glands (cup-cells). The corium divides into cutis and sub-cutis.

VI. Period : **Fish-skin.**

The epidermis remains simple. The corium forms placoid scales or bony tablets (cutaneous teeth), at first as in the selachii, afterwards as in the ganoids. (Silurian period.)

VII. Period : **Amphibian-skin.**

The epidermis divides into outer horny layer and inner mucous layer. The tips of the toes develop horny sheaths (first rudiment of the claws or nails). (Carboniferous period.)

VIII. Period : **Reptilian-skin.**

The cornification of the epidermis continues (horny scales), but the bony scales of the corium atrophy (hatteria, tocosauria). (Permian period.)

IX. Period : **Mammal-skin.**

The epidermis forms the appendages that are peculiar to the mammals : hairs, sweat, fat, and milk-glands. (Triassic.)

X. Period : **Ape-skin.**

The hair assumes the special form of the primate-coat ; the claws are converted into nails. (Tertiary period.)

FORTY-THIRD TABLE

SYNOPSIS OF THE CHIEF PERIODS IN THE STEM-HISTORY OF THE HUMAN NERVOUS SYSTEM

I. Period: **Gastræad-marrow.**

The nervous system is not yet differentiated from the skin, and is represented together with this by the simple cell-layer of the ectoderm or outer germinal layer; as is still the case in the gastrula of the amphioxus.

II. Period: **Platodaria-marrow.**

The nervous system separates from the skin, or vertical plate *(acroplatea)*, differentiating above the gullet from the rest of the horny plate, as in the platodaria (the lowest modern platodes: cryptocœla), and the gastrotricha (the lowest vermalia).

III. Period: **Vermalian-marrow.**

The vertical plate separates from its starting-point, the ectoderm, and passes into the underlying cutis-plate, the uppermost stratum of the mesoderm; here it forms the *acroganglion*, or pharyngeal brain, a single or double nervous ganglion above the gullet; as is still found in the platodes and the earlier vermalia.

IV. Period: **Enteropneust-marrow.**

The acroganglion lengthens on the dorsal side of the bilateral worm-like body, and forms a dorsal medullary plate in the middle line. This epidermic medullary plate grows deeper in the dorsal middle line, and forms a longitudinal medullary groove.

V. Period: **Prochordonia-marrow.**

As the parallel edges of the dorsal medullary plate rise up in the shape of medullary ridges, then bend towards each other, and unite above, a dorsal medullary tube is formed above the chorda (in the hypothetic chordæa, which is reproduced by heredity in the embryonic *chordula)*.

VI. Period: **Acrania-marrow.**

The simple medullary tube divides into two parts, a capital marrow and dorsal marrow. The capital marrow is a simple pear-shaped bulb (primitive or rudimentary brain), at the fore end of the long cylindrical spinal cord.

VII. Period: **Cyclostoma-marrow.**

The simple vesicular rudiment of the brain divides into three, then in four or five successive vesicles of simple structure: (1) cerebrum, (2) intermediate brain, (3) middle brain, (4) cerebellum, (5) after brain.

VIII. Period: **Selachii-marrow.**

The five cerebral vesicles differentiate during the Silurian period into the same form in which we find them permanently in the selachii; they afterwards assume the form of the ganoid-brain (crossopterygii).

IX. Period: **Amphibian-marrow.**

The differentiation of the five vesicles proceeds during the Devonian period, and reaches the dipneust-stage, and afterwards the stage that still characterises the amphibian brain.

X. Period: **Reptilian-marrow.**

The amphibian brain (stegocephala) passes into that of the earliest reptiles (tocosauria), and this into the brain of the sauromammals. The former probably took place during the Carboniferous period, the latter during the Permian.

XI. Period: **Mammal-marrow.**

During the Mesozoic age the brain acquires the features that characterise the mammals. We may distinguish the following subordinate stages of development: (1) monotreme brain, (2) marsupial brain, (3) prosimian brain, (4) simian brain, (5) anthropoid brain, (6) pithecanthropus brain, (7) human brain.

CHAPTER XXV.

EVOLUTION OF THE SENSE-ORGANS

Origin of the purposively constructed sense-organs without preconceived aim, by natural selection. The six sensory organs and eight functions. First origin of all the sense-organs from the outer skin (the skin-sense layer). Organs of the sense of pressure, warmth, sex, and taste. Structure of the olfactory organ. The blind olfactory pits of the fishes. The nasal furrows are changed into nasal canals. Separation of the nasal cavity and mouth cavity by the palate. Structure of the eye. The primary optic vesicles (folds of the intermediate brain with pedicles). Invagination of them by the lenticular sacs differentiated from the horny plate. Invagination of the lens. Vascular and fibrous capsule of the pupil. Eye-lids. Structure of the ear. Auscultory apparatus; labyrinth and acoustic nerve. Origin of the labyrinth from the primitive auscultory vesicle (by severance from the horny plate). Apparatus for conducting sound: tympanic cavity, bones, and tympanum. Origin of them from the first gill-cleft and contiguous parts. Rudimentary external ear. The rudimentary muscles of the shell of the human ear.

THE sense-organs are indubitably among the most important and interesting parts of the human body; they are the organs by means of which we obtain our knowledge of objects in the surrounding world. *Nihil est in intellectu quod non prius fuerit in sensu.* They are the first sources of the life of the soul. There is no other part of the body in which we discover such elaborate anatomical structures, co-operating with a definite purpose; and there is no other organ in which the wonderful and purposive structure seems so clearly to compel us to admit a Creator and a preconceived plan. Hence we find special efforts made by dualists to draw our attention here to the "wisdom of the Creator" and the design visible in his works. As a matter of fact, you will discover, on mature reflection, that on this theory the Creator is at bottom only playing the part of a clever mechanic or watch-maker; all these familiar teleological ideas of Creator and creation are based, in the long run, on a similar childlike anthropomorphism.

However, we must grant that at the first glance the teleological theory seems to give the simplest and most satisfactory explanation of these purposive structures. If we merely examine the structure and functions of the most advanced sense-organs, it seems impossible to explain them without postulating a creative act. Yet evolution shows us quite clearly that this popular idea is totally wrong. With its assistance we discover that the purposive and remarkable sense-organs were developed, like all other organs, without any preconceived design—developed by the same mechanical process of natural selection, the same constant correlation of adaptation and heredity, by which the other purposive structures in the animal frame were slowly and gradually brought forth in the struggle for life.

Like most other vertebrates, man has six sensory organs, which serve for eight different classes of sensations. The skin serves for sensations of pressure (resistance) and temperature (warmth and cold). This is the oldest, lowest, and vaguest of the sense-organs; it is distributed over the surface of the body. The other sensory activities are localised. The sexual sense is bound up with the skin of the external sexual organs, the sense of taste with the mucous lining of the mouth (tongue and palate), and the sense of smell with the mucous lining of the nasal cavity. For the two most advanced and most highly differentiated sensory functions there are special and very elaborate mechanical structures—the eye for the sense of sight, and the ear for the sense of hearing and space (equilibrium).

Comparative anatomy and physiology teach us that there are no differentiated sense-organs in the lower animals; all their sensations are received by the surface of the skin. The undifferentiated skin-layer or ectoderm of the gastræa is the simple stratum of cells from which the differentiated sense-organs of all the metazoa (including the vertebrates) have been evolved. Starting from the assumption that necessarily only the superficial parts of the body, which are in direct touch with the outer world, could be concerned in the origin of sensations, we can see at once that the sense-organs also must have arisen there. This is really the case. The chief part of all the sense-organs originates from the skin-sense layer, partly directly from the horny plate, partly from the brain, the foremost part of the medullary tube, after it has separated from the horny plate. If we compare the embryonic development of the various sense-organs, we see that they all make their appearance in the simplest conceivable form ; the wonderful contrivances that make the higher sense-organs among the most remarkable and elaborate structures in the body develop only gradually. In the phylogenetic explanation of them comparative anatomy and ontogeny achieve their greatest triumphs. But at first all the sense-organs are merely parts of the skin in which sensory nerves expand. These nerves themselves were originally of a homogeneous character. The different functions or specific energies of the differentiated sense-nerves were only gradually developed in the division of labour. At the same time, their simple terminal expansions in the skin were converted into extremely complex organs.

The great instructiveness of these historical facts in connection with the life of the soul is not difficult to see. The whole philosophy of the future will be transformed as soon as psychology takes cognisance of these genetic phenomena and makes them the basis of its speculations. When we examine impartially the manuals of psychology that have been published by the most distinguished speculative philosophers and are still widely distributed, we are astonished at the naïvety with which the authors raise their airy metaphysical speculations, regardless of the momentous embryological facts that completely refute them. Yet the science of evolution, in conjunction with the great advance of the comparative anatomy and physiology of the sense-organs, provides the one sound empirical basis of a natural psychology.

In respect of the terminal expansions of the sensory nerves, we can distribute the human sense-organs in three groups, which correspond to three stages of development. The first group comprises those organs the nerves of which spread out quite simply in the free surface of the skin itself (organs of the sense of pressure, warmth, and sex). In the second group the nerves spread out in the mucous coat of cavities which are at first depressions in or invaginations of the skin (organs of the sense of smell and taste). The third group is formed of the very elaborate organs, the nerves of which spread out in an internal vesicle, separated from the skin (organs of the sense of sight, hearing, and space). The following table will give a better idea of this remarkable genetic relation :—

Three Groups of Sensilla.	**Differentiated Sense-organs.**	**Special Sense-nerves.**	**Sensory Functions.**
A. Sense-organs, the nerves of which spread out terminally in the surface of the skin.	I. Skin (epidermis and corium).	I. Cutaneous nerves. *(Nervi cutanei.)*	1. Sense of pressure. 2. Sense of warmth.
	II. External sexual organs (penis and clitoris).	II. Sexual nerves. *(Nervi pudendi.)*	3. Sense of sex.
B. Sense-organs, the nerves of which expand terminally in hollowed-out depressions of the skin.	III. Mucous coat of the mouth (tongue and palate).	III. Nerves of taste. *(Nervus glosso-pharyngeus.)*	4. Sense of taste.
	IV. Mucous lining of the nasal cavity.	IV. Olfactory nerve. *(N. olfactorius.)*	5. Sense of smell.
C. Sense-organs, the nerves of which expand terminally in vesicles that are separated from the skin.	V. Eye.	V. Optic nerve. *(N. opticus.)*	6. Sense of sight.
	VI. Ear.	VI. Auscultory nerve. *(N. acusticus.)*	7. Sense of hearing. 8. Sense of taste.

There is little to be said of the development of the lower sense-organs. We have already considered (p. 647) the organ of touch and temperature in the skin. I need only add that in the corium of man and all the higher vertebrates countless microscopic sense-organs develop, but the precise relation of these to the sensations of pressure or resistance, of warmth and cold, has not yet been explained. Organs of this kind, in or on which sensory cutaneous nerves terminate, are the "tactile corpuscles" (or the Pacinian corpuscles) and end-bulbs. We find similar corpuscles in the organs of the sexual sense, the male penis and the female clitoris; they are processes of the skin, the development of which we will consider later (together with the rest of the sexual parts, Chapter XXIX.). The evolution of the organ of taste, the tongue and palate, will also be treated later, together with that of the alimentary canal to which these parts belong (Chapter XXVII.). I will only point out for the present that the mucous coat of the tongue and palate, in which the gustatory nerve ends, originates from a part of the outer skin. As we have seen, the whole of the mouth-cavity is formed, not as a part of the gut-tube proper, but as a pit-like fold in the outer skin (p. 319). Its mucous lining is therefore formed, not from the visceral, but from the cutaneous layer, and the taste-cells at the surface of the tongue and palate are not products of the gut-fibre layer, but of the skin-sense layer.

This applies also to the mucous lining of the olfactory organ, the nose. However, the development of this organ is much more interesting. Although the nose seems superficially to be simple and single, it really consists, in man and all other gnathostomes, of two completely separated halves, the right and left cavities. They are divided by a vertical partition, so that the right nostril leads into the right cavity alone and the left nostril into the left cavity. They open internally (and separately) by the posterior nasal apertures into the pharynx, so that we can get direct into the gullet through the nasal passages without touching the mouth. This is the way the air usually passes in respiration; the mouth being closed, it goes through the nose into the gullet, and through the larynx and bronchial tubes into the lungs. The nasal cavities are separated from the mouth by the horizontal bony palate, to which is attached behind (as a dependent process) the soft palate with the uvula. In the upper and hinder parts of the nasal cavities the olfactory nerve, the first pair of cerebral nerves, expands in the mucous coat which clothes them. The terminal branches of it spread partly over the septum (partition), partly on the side-walls of the internal cavities, to which are attached the turbinated bones. These bones are much more developed in many of the higher mammals than in man, but there are three of them in all mammals. The sensation of smell arises by the passage of a current of air containing odorous matter over the mucous lining of the cavities, and stimulating the olfactory cells of the nerve-endings.

Man has all the features which distinguish the olfactory organ of the mammals from that of the lower vertebrates. In all essential points the human nose entirely resembles that of the catarrhine apes, some of which have quite a human external nose (compare the face of the long-nosed apes, Plate XXV.). However, the first structure of the olfactory organ in the human embryo gives no indication of the future ample proportions of our catarrhine nose. It has the form in which we find it permanently in the fishes—a couple of simple depressions in the skin at the outer surface of the head. We find these blind olfactory pits in all the fishes; sometimes they lie near the eyes, sometimes more forward at the point of the muzzle, sometimes lower down, near the mouth (Fig. 303).

This first rudimentary structure of the double nose is the same in all the gnathostomes or amphirrhines; it has no connection with the primitive mouth. But even in a section of the fishes a connection of this kind begins to make its appearance, a furrow in the surface of the skin running from each side of the nasal pit to the nearest corner of the mouth. This furrow, the nasal groove or furrow (Fig. 368 *r*), is very important. In many of the sharks, such as the *scyllium*, a special process of the frontal skin, the nasal fold or internal nasal process, is formed internally over the groove *(n, n')*. In contrast to this the outer edge of the furrow rises in an "external nasal process." As the two processes meet and coalesce over the nasal groove in the dipneusts and amphibia, it is converted into a canal, the nasal canal. Henceforth we can penetrate from the external pits through the nasal canals direct into the mouth, which has been formed quite independently. In the dipneusts and the lower amphibia the internal aperture of the nasal canals lies in front (behind the lips); in the higher amphibia it is right behind. Finally, in the three higher classes of vertebrates the primary mouth-cavity is divided by the formation of the horizontal palate-roof into two distinct cavities—the upper (secondary) nasal cavity and the lower (secondary) mouth-cavity. The nasal cavity in turn is divided by the construction of the vertical septum into two halves—right and left.

Comparative anatomy shows us to-day, in the series of the double-nosed vertebrates, from the fishes up to man, all the different stages in the development of the nose, which the advanced olfactory organ of the higher mammals has passed through at various periods in the course of its phylogeny. It first appears in the embryo of man and the higher vertebrates, in which the double fish-nose persists throughout life (cf. Plates I., VIII.–XIII., XXIV.). At an early stage, before there is any trace of the characteristic human face, a pair of small pits are formed in the head over the original mouth-cavity; these were first discovered by Baer, and rightly called the "olfactory pits" (Figs. 369 *n*, 370 *n*). These primitive nasal pits are quite separate from the rudimentary mouth, which also originates as a pit-like depression in the skin, in front of the blind fore end of the gut. Both the pair of nasal pits and the single mouth-pit (Fig. 373 *m*) are clothed with the horny plate. The original separation of the former from the latter is, however, presently abolished, a process forming above the mouth-pit—the "frontal process" (Rathke's "nasal process of the frontal wall," Fig. 372 *st*). Its outer edge rises to the right and left in the shape of two lateral processes; these are the inner nasal processes or folds *(in)*. Opposite to these a parallel ridge is formed on either side between the eye and the nasal pit; these are the outer

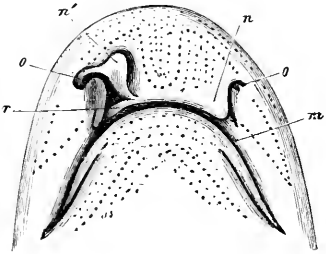


FIG. 368.—**Head of a shark** *(scyllium)*, from the ventral side. *m* mouth, *o* olfactory pits, *r* nasal groove, *n* nasal fold in natural position, *n'* nasal fold drawn up. (The dots are openings of the mucous canals.) (From *Gegenbaur*.)

nasal processes, or Rathke's "nasal roofs" *(an)*. Thus between the inner and outer nasal processes a groove-like depression is formed on either side, which leads from the nasal pit towards the mouth-pit *(m)*; this groove is, as the reader will guess, the same nasal furrow or groove that we have already seen in the shark (Fig. 367 *r*). As the parallel edges of the inner and outer nasal processes bend towards each other and join above the nasal groove, this is converted into a tube, the primitive nasal canal. Hence the nose of man and all the other amniotes consists at this embryonic stage of a couple of narrow tubes, the nasal canals, which lead from the outer surface of the forehead into the

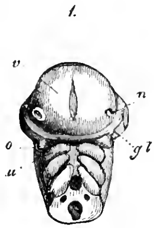


FIG. 369.

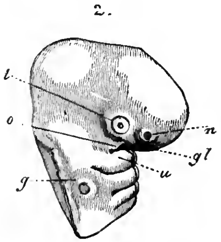


FIG. 370.

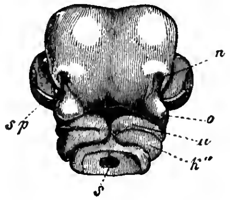


FIG. 371.

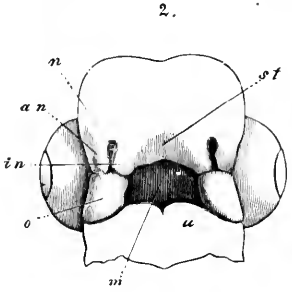


FIG. 373.

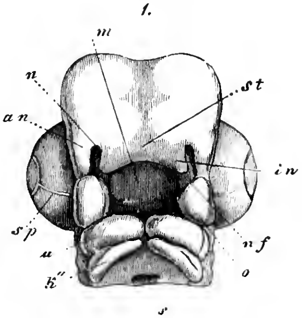


FIG. 372.

FIGS. 369 and 370.—**Head of a chick embryo,** three days old: 369 front view, 370 from the right. *n* rudimentary nose (olfactory pits), *l* rudimentary eyes (optic pits), *g* rudimentary ear (auscultory pit), *v* fore brain, *gl* eye-cleft, *o* process of upper jaw, *u* process of lower jaw of the first gill-arch.

FIG. 371.—**Head of a chick embryo,** four days old, from below. *n* nasal pit, *o* upper-jaw process of the first gill-arch, *u* lower-jaw process of same, *k''* second gill-arch, *sp* choroid fissure of eye, *s* gullet.

FIGS. 372 and 373.—**Heads of chick embryos:** 372 from the end of the fourth, 373 from the beginning of the fifth week. Letters as in Fig. 371, except: *in* inner, *an* outer, nasal process, *nf* nasal furrow, *st* frontal process, *m* mouth. (From *Kölliker*.) Figs. 369–373 are magnified to the same extent.

rudimentary mouth. This transitory condition resembles that in which we find the nose permanently in the dipneusts and amphibia.

A cone-shaped structure, which grows from below towards the lower ends of the two nasal processes and joins with them, plays an important part in the conversion of the open nasal groove into the closed canal. This is the upper-jaw process (Figs. 369–373 *o*). Below the mouth-pit are the gill-arches, which are separated by the gill-clefts. The first of these gill-arches, and the most important for our purpose, which we may call the maxillary (jaw) arch, forms the skeleton of the jaws. Above at the basis a small process grows out of this first gill-arch; this is the upper-jaw process. The first gill-arch itself developes a cartilage at one of its inner sides, the "Meckel cartilage" (named after its discoverer), on the outer surface of which the lower jaw is formed (Figs. 369–373 *u*). The upper-jaw process forms the chief part of the skeleton of that jaw, the palate bone and the pterygoid bone. On its outer side is afterwards formed the upper-jaw bone in the narrower sense, while the middle part of the skeleton of the upper jaw, the intermaxillary, developes from the foremost part of the frontal process. (Cf. the embryology of the face on Plates I., VIII.–XIII., and XXIV.)

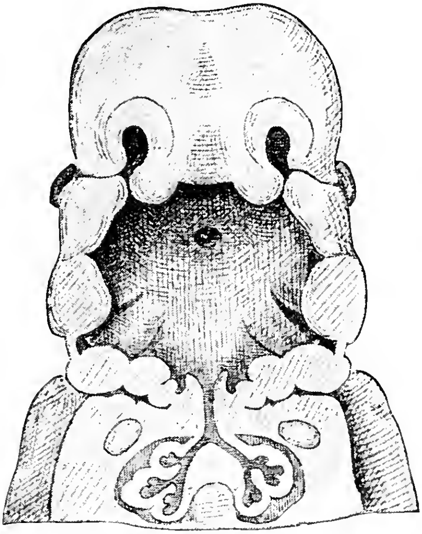


FIG. 374.—**Frontal section of the mouth and throat of a human embryo,** neck 11.5 mm. long. "Invented" by *Wilhelm His.* The vertical section (in the frontal plane, from left to right) is so constructed that we see the nasal pits in the upper third of the figure and the eyes at the sides; in the middle third the primitive gullet with the gill-clefts (gill-arches in section); in the lower third the pectoral cavity with the bronchial tubes and the rudimentary lungs.

The two upper-jaw processes are of great importance in the further development of the face. From them is formed, growing into the primitive mouth-cavity, the important horizontal partition (the palate) that divides the former into two distinct cavities. The upper cavity, into which the nasal canals open, now developes into the nasal cavity, the air-passage and the organ of smell. The lower cavity forms the permanent secondary mouth (Fig. 375 *m*), the food-passage and the organ of taste. Both the upper and lower cavities open behind into the gullet (pharynx). The hard palate that separates them is formed by the joining of two lateral halves, the horizontal plates of the two upper-jaw processes, or the palate-plates *(p)*. When these do not, sometimes, completely join in the middle, a longitudinal cleft remains, through which we can penetrate from the mouth straight into the nasal cavity. This is the malformation known as "wolf's-throat." "Hare-lip" is a lesser form of the same defect.

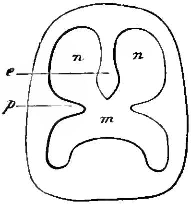


FIG. 375.—**Diagrammatic section of the mouth-nose cavity.** While the palate-plates *(p)* divide the original mouth-cavity into the lower secondary mouth *(m)* and the upper nasal cavity, the latter in turn is divided by the vertical septum *(e)* into two halves *(n, n)*. (From *Gegenbaur*.)

At the same time as the horizontal partition of the hard palate a vertical partition is formed by which the simple nasal cavity is divided into two sections—a right and left half (Fig. 375 *n*, *n*). The vertical nasal septum *(e)* is developed from the middle layer of the frontal process; from it arise by ossification the vertical lamella of the cribriform bone above, the large bony vertical partition (the *vomer*) below, and the intermaxillary bone in front. Goethe was the first to point out that the latter developes as an independent bone between the two halves of the upper jaw in man just as in the other craniotes. The vertical nasal partition joins eventually with the horizontal palate. The two nasal cavities are now just as completely separated from each other as from the mouth. The three cavities, however, open behind into the gullet or throat.

The double nose has now acquired the characteristic form that man shares with the other mammals. Its further

LONG-NOSED APE. NASALIS LARVATUS.

Lith. Anst. v. E. Giltsch, Jena.

1. 2 Embryo. 3. 4 Female. 5–9 Male.

development is easy to follow ; it is restricted to the formation of the inner and outer processes of the walls of the two cavities. Inside them the turbinated bones—spongy bones on which the olfactory mucous membrane is spread—are developed. The first cerebral nerve, the olfactory nerve, comes down from the cerebrum, and covers with its fine branchlets the roof of the two cavities, and spreads over the mucous coat. At the same time there are formed, by folding of the nasal mucous membrane, the accessory nasal cavities (afterwards filled with air), which are openly connected with the nasal cavities (frontal cavities, cuneiform cavities, maxillary cavities, etc.). In this characteristic development they are found exclusively in the mammals.

The external nose is not formed until long after all these essential parts of the internal organ of smell. The first traces of it in the human embryo are found about the middle of the second month (Figs. 376–379). As can be seen in any human embryo during the first month, there is at first no trace of the external nose. It only developes afterwards from the foremost nasal part of the primitive skull, growing forwards from behind. The characteristically human nose is formed very late. Much stress is at times laid on this organ as an exclusive privilege of man. But there are apes that have similar noses, such as the long-nosed ape (Plate XXV.). The ontogeny of its large mobile nose is very instructive for man, whose external nose has assumed such a handsome shape.

But, however much of an ornament the nose may be, it remains very ape-like in many of the lower races. In most of the apes the external nose is not much developed. It is especially noteworthy that, as we have seen, in the apes of the Old World, the catarrhines, the nasal partition is as narrow as in man, whereas in the apes of the New World it is very broad at the bottom, and so forces the nostrils outwards (platyrrhines). The muscles of the external nose are very strongly developed in those mammals in which it is converted into a grubbing or prehensile organ, or snout (pig, mole, elephant, etc.).

FORTY-FOURTH TABLE

SYNOPSIS OF THE PHYLOGENY OF THE HUMAN NOSE

I. Period: **Earlier primitive-fish nose.**

This nose is formed of a couple of simple cutaneous pits (olfactory pits), at the surface of the head (as it is still permanently in the lower selachii).

II. Period: **Later primitive-fish nose.**

The blind olfactory pits are connected by a furrow (nasal groove) at each side with the corners of the mouth (as we still find permanently in the higher selachii).

III. Period: **Dipneust nose.**

The two nasal grooves are converted, by the joining of their edges, into the primary nasal canals, which open into the front of the primary mouth (permanent in the dipneusts).

IV. Period: **Amphibian nose.**

The inner apertures of the nasal canals go further back in the mouth, so that they are bordered by the solid skeletal parts of the jaws (permanent in the higher amphibia).

V. Period: **Earlier reptilian nose.**

The primary mouth, into which the nasal canals open, is divided, through the formation of a horizontal partition (the palate), into an upper nasal cavity and a lower (secondary) mouth-cavity (in the earliest amniotes, the proreptiles).

VI. Period: **Later reptilian nose.**

The simple nasal cavity is divided by the formation of a vertical partition (the *vomer*) into two separate cavities, each of which occupies the nasal canal on its side (as in most of the amniotes). The nasal meatus are divided.

VII. Period: **Earlier mammalian nose.**

The nasal cavities spread downward and backwards, while at their roof the cribriform bone forms cellular folds and olfactory bulbs—the cribriform labyrinth.

VIII. Period: **Later mammalian nose.**

In the two nasal cavities there is a further development of the olfactory bulbs in the cribriform labyrinth (middle and upper meatus), and an external nose begins to appear.

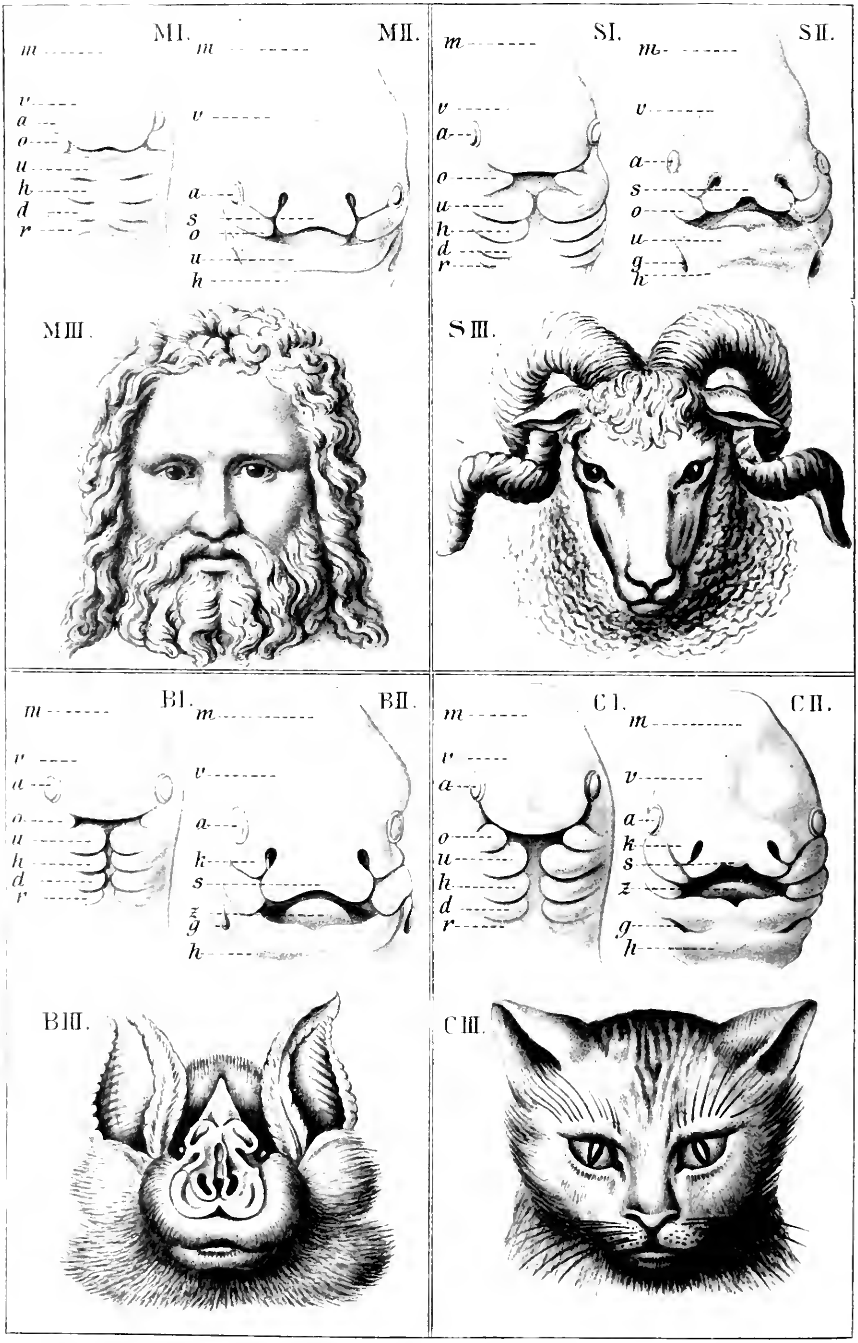
IX. Period: **Western ape (platyrrhine) nose.**

As the olfactory function loses its importance, there is a partial atrophy of the olfactory bulbs (in the primate stem-forms). The nasal septum is broad.

X. Period: **Eastern ape (catarrhine) nose.**

The nasal septum is narrow and long: the nostrils point downwards. The internal and external noses attain their characteristic form in the catarrhines and man.

THE EMBRYONIC DEVELOPMENT OF THE FACE



M. MAN.　B. BAT.　C. CAT.　S. SHEEP.

[illegible] Dorn & Meyenbach [illegible]

The evolution of the eye is not less interesting and instructive than that of the nose. Although this noblest of the sensory organs is one of the most elaborate and purposive on account of its optic perfection and remarkable structure, it nevertheless developes, without preconceived design, from a simple process of the outer germinal layer.

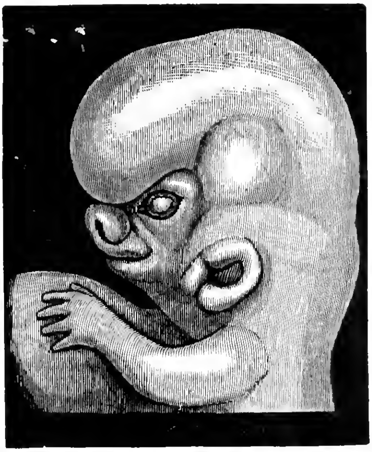


Fig. 376.

Fig. 377.

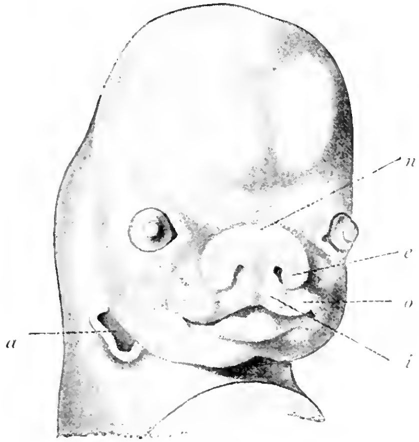


Fig. 378.

Fig. 379.

Figs. 376 and 377.—**Upper part of the body of a human embryo,** sixteen mm. long, of the sixth week; Fig. 376 from the left, Fig. 377 from the front. The origin of the nose and the upper lip from two lateral and originally separate halves can be clearly seen. Nose and upper lip are large in proportion to the rest of the face, and especially to the lower lip. (From *Kollmann.*)

Fig. 378.—**Face of a human embryo,** seven weeks old. (From *Kollmann.*) Joining of the nasal processes (*e* outer, *i* inner) with the upper-jaw process (*o*), *n* nasal wall, *a* ear-opening.

Fig. 379.—**Face of a human embryo,** eight weeks old. (From *Ecker.*) (Cf. Plate I. (frontispiece) and Plate XXIV.)

The fully-formed human eye is a round capsule, the eye-ball *(bulbus,* Fig. 380). This lies in the bony cavity of the skull, surrounded by protective fat and motor muscles. The greater part of it is taken up with a semi-fluid, transparent gelatinous substance, the *corpus vitreum.* The crystalline lens is fitted into the anterior surface of the ball (Fig. 380 *l*). It is a lenticular, biconvex, transparent body, the most important of the refractive media in the eye. Of this group we have, besides the corpus vitreum and the lens, the watery fluid *(humor aqueous)* that is found in front of the lens (at the letter *m* in Fig. 380). These three transparent refractive media, by which the rays of light that enter the eye are broken up and re-focussed, are enclosed in a solid round capsule, composed of several different coats, something like the concentric layers of an onion.

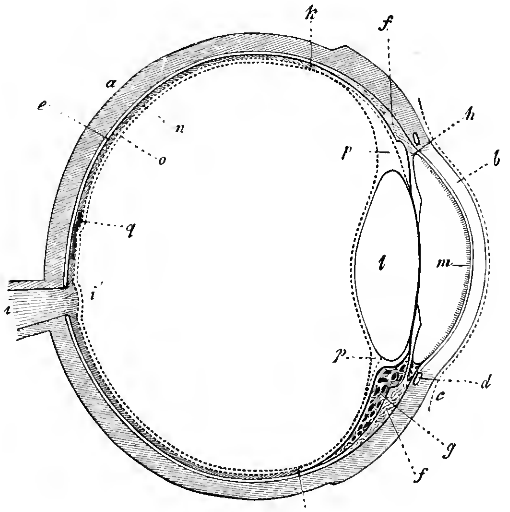


Fig. 380.—**The human eye** in section. *a* sclerotic coat *(sclerotica)*, *b* cornea, *c* conjunctiva, *d* circular veins of the iris, *e* choroid coat *(choreoidea)*, *f* ciliary muscle, *g* corona ciliaris, *h* iris, *i* optic nerve, *k* anterior border of the retina, *l* crystalline lens, *m* inner covering of the cornea (aqueous membrane; *membrana* Descemeti), *n* pigment membrane *(pigmentea)*, *o* retina, *p* Petit's canal, *q* yellow spot of the retina. (From *Helmholtz.*)

The outermost and thickest of these envelopes is the white *sclerotic coat* of the eye. It consists of tough white connective tissue. In front of the lens a circular, strongly-curved, transparent plate is fitted into the sclerotic, like the glass of a watch — the *cornea (b).* At its outer surface the cornea is covered with a very thin layer of the epidermis; this is known as the *conjunctiva.* It goes from the cornea over the inner surface of the eye-lids, the upper and lower folds which we draw over the eye in closing it. At the inner corner of the eye we have a rudimentary organ in the shape of the relic of a third (inner) eye-lid, which is greatly developed, as "nictitating membrane," in the lower vertebrates (p. 86). Underneath the upper eye-lid are the lachrymal glands, the product of which, the lachrymal fluid, keeps the outer surface of the eye smooth and clean.

Immediately under the sclerotic we find a very delicate, dark-red membrane, very rich in blood-vessels—the *choroid coat (choreoidea)*—and inside this the *retina (o)*, the expansion of the optic nerve *(i)*. The latter is the second cerebral nerve. It proceeds from the optic thalami (the second cerebral vesicle) to the eye, penetrates its outer envelopes, and then spreads out like a net between the choroid and the corpus vitreum. Between the retina and the choroid there is a very delicate membrane, which is usually (but wrongly) associated with the latter. This is the black pigment-membrane *(pigmentosa, lamina pigmenti, n)*, or "black carpet" *(tapetum nigrum)*. It consists of a single stratum of graceful, hexagonal, regularly-joined cells, full of granules of black colouring matter. This pigment membrane clothes, not only the inner surface of the choroid proper, but also the hind surface of its anterior muscular continuation, which covers the edge of the lens in front as a circular membrane, and arrests the rays of light at the sides. This is the well-known *iris* of the eye *(h)*, coloured differently in different individuals (blue, grey, brown, etc.); it forms the anterior border of the choroid. The circular opening that is left in the middle is the *pupil*, through which the rays of light penetrate into the eye. At the point where the iris leaves the anterior border of the choroid proper the latter is very thick, and forms a delicate crown of folds *(g)*, which surrounds the edge of the lens with about seventy large and many smaller rays *(corona ciliaris)*.

At a very early stage a couple of pear-shaped vesicles develop from the foremost part of the first cerebral vesicle in the embryo of man and the other craniotes (Figs. 354 *a*, 358 *au*). These growths are the primary optic vesicles.

They are at first directed outwards and forwards, but presently grow downward, so that, after the complete separation of the five cerebral vesicles, they lie at the base of the intermediate brain. The inner cavities of these pear-shaped vesicles, which soon attain a considerable size, are openly connected with the ventricle of the intermediate brain by their hollow stems. They are covered externally by the epidermis. At the point where this comes into direct contact with the most curved part of the primary optic vesicle there is a thickening *(l)* and also a depression *(o)* of the horny plate (Fig. 381, *I*). This pit, which we may call the lens-pit, is converted into a closed sac, the thick-walled lens-vesicle *(2, l)*, the thick edges of the pit joining together above it. In the same way in which the medullary tube separates from the outer germinal layer, we now see this lens-sac sever itself entirely from the horny plate *(h)*, its source of origin. The hollowing-out of the sac is afterwards filled with the cells of its thick walls, and thus we get the solid crystalline lens. This is, therefore, a purely epidermic structure. Together with the lens the small underlying piece of corium-plate also separates from the skin. This piece then encloses the lens in the shape of a richly vascular sac *(capsula vasculosa lentis)*. Its anterior part at first encloses the pupil as the pupillary membrane *(membrana pupillaris)*. Its posterior part is called the caspsulo-pupillary membrane. This capsule afterwards disappears; it merely serves for the nutrition of the growing lens. The later permanent capsule has no vessels, and is a structureless secretion of the lenticular cells.

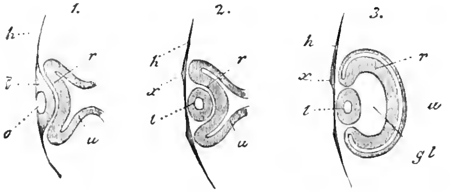


FIG. 381.—**Eye of the chick embryo** in longitudinal section (*1.* from an embryo sixty-five hours old; *2.* from a somewhat older embryo; *3.* from an embryo four days old). *h* horny plate, *o* lens-pit, *l* lens (in *1.* still part of the epidermis, in *2.* and *3.* separated from it), *x* thickening of the horny plate at the point where the lens has severed itself, *gl* corpus vitreum, *r* retina, *u* pigment membrane. (From *Remak.*)

As the lens thus separates from the corneous plate and grows inwards, it necessarily hollows out the contiguous primary optic vesicle (Fig. 381, *1–3*). This is done in just the same way as the invagination of the blastula, which gives rise to the gastrula in the amphioxus (Fig. 257 *C–F*). In both cases the hollowing of the closed vesicle on one side goes so far that at last the inner, folded part touches the outer, not folded part, and the cavity disappears. As in the gastrula the first part is converted into the entoderm and the latter into the ectoderm, so in the invagination of the primary optic vesicle the retina *(r)* is formed from the first (inner) part, and the black pigment membrane *(u)* from the latter (outer, non-invaginated) part. The hollow stem of the primary optic vesicle is converted into the optic nerve.

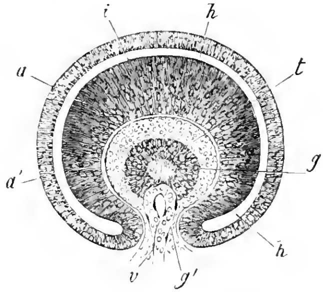


Fig. 382.—**Horizontal transverse section of the eye of a human embryo,** four weeks old (magnified one hundred times). (From *Kölliker.*) *t* lens (the dark wall of which is as thick as the diameter of the central cavity), *g* corpus vitreum (connected by a stem, *g*, with the corium), *v* vascular loop (pressing behind the lens inside the corpus vitreum by means of this stem *g*), *i* retina (inner thicker, invaginated layer of the primary optic vesicle), *a* pigment membrane (outer, thin, non-invaginated layer of same), *h* space between retina and pigment membrane (remainder of the cavity of the primary optic vesicle).

The lens *(l)*, which has so important a part in this process, lies at first directly on the invaginated part, or the retina *(r)*. But they soon separate, a new structure, the corpus vitreum *(gl)*, growing between them. While the lenticular sac is being detached and is causing the invagination of the primary optic vesicle, another invagination is taking place from below; this proceeds from the superficial part of the skin-fibre layer—the corium of the head. Behind and under the lens a last-shaped process rises from the cutis-plate (Fig. 382 *g*), hollows out the cup-shaped optic vesicle from below, and presses between the lens *(l)* and the retina *(i)*. In this way the optic vesicle acquires the form of a hood. The opening of the hood, which corresponds to the face, is occupied by the lens. But the opening in which the neck would be found corresponds to the invagination by which the corium grows between the lens and the retina (the inner wall of the hood). The space inside this *secondary* optic vesicle is mostly taken up with the corpus vitreum, which corresponds to the head covered by the hood. The hood itself is really double ; the inner hood is the retina, the outer one (immediately enclosing this) the pigment membrane. This illustration will help the reader to form a clear idea of the rather obscure process of invagination. The corpus vitreum is at first very insignificant (Fig. 382 *g)*, and the retina disproportionately thick *(i)*. But the latter grows thinner as the former extends, and at last has the appearance of a very delicate membrane of the thick, almost round, corpus vitreum, which fills the greater part of the secondary optic vesicle. The outermost layer of the corpus vitreum is a capsule with a large number of blood-vessels, which afterwards disappear.

The opening by which the last-shaped structure of the corpus vitreum grows up between the lens and retina from below naturally involves an interruption of the continuity of the retina and pigment membrane. This breach, which appears on the inner surface of the choroid as a pigmentless streak, has been wrongly called the "choroid fissure," though the real choroid is not interrupted at all here (Figs. 371 *sp*, 372 *sp*). A narrow process of the corpus vitreum pushes inward to the lower surface of the optic nerve, and hollows this out in the same way as the primary optic vesicle. In this way the hollow cylindrical optic nerve (the stem of the vesicle) is converted into a groove open below. The folded lower surface lies on the upper non-invaginated surface of the hollow stem, and this does away with its cavity, which hitherto maintained an open connection between the ventricle of the intermediate brain and the primary optic vesicle. The edges of the groove then grow towards each other, enclose the process of the corium-plate, and join underneath it. The process thus finds its way into the axis of the solid secondary optic nerve ; it becomes the cord of connective tissue, which conducts the central vessels of the retina *(vasa centralia retinæ)*.

FORTY-FIFTH TABLE

SYNOPSIS OF THE EMBRYONIC DEVELOPMENT OF THE HUMAN EYE

I. The parts of the Eye that develop from the Ectoderm, the Outer Germinal Layer.

A. **Products of the medullary plate.**	1. Stem of the primary vesicle.	1. Optic nerve.	*Nervus opticus.*
	2. Inner (invaginated) part of the primary vesicle.	2. Retina.	*Retina.*
	3. Outer (non-invaginated) part of the primary vesicle.	3. Pigment membrane or coloured carpet.	*Pigmentosa (lamina pigmenti) (tapetum nigrum).*
B. **Products of the horny plate.**	4. Separated sac of the horny plate.	4. Crystalline lens.	*Lens crystallina.*
	5. Outer epidermic covering.	5. Conjunctiva.	*Conjunctiva.*
	6. Involutions of the epidermic covering.	6. Lachrymal glands.	*Glandulæ lacrymales.*

II. The parts of the Eye that develop from the Mesoderm, the Middle Germinal Layer.

C. **Products of the corium.**	7, 8. Last-shaped process of the corium at the under side of the primary vesicle.	7. Corpus vitreum. 8. Vascular capsule of the corpus vitreum.	*Corpus vitreum.* *Capsula vasculosa corporis vitrei.*
	9. Continuation of the corium-process.	9. Central vessels of the retina.	*Vasa centralia retinæ.*
	10. Pupillary membrane with capsule.	10. Vascular capsule of the lens.	*Capsula vasculosa lentis crystallinæ.*
	11. Corium folds.	11. Eye-lids.	*Palpebræ.*
D. **Products of the head-plate.**	12, 13. Vascular capsule of the eye-ball. (*Capsula vasculosa bulbi.*)	12. Choroid coat. 13. Iris.	*Choreoidea.* *Iris.*
	14, 15. Fibrous capsule of the eye-ball. (*Capsula fibrosa bulbi.*)	14. Sclerotic coat. 15. Cornea.	*Sclerotica.* *Cornea.*

Finally, a complete fibrous envelope, the fibrous capsule of the eye-ball, is formed about the secondary optic vesicle and its stem (the secondary optic nerve). It originates from the part of the head-plates which immediately encloses the eye. This fibrous envelope takes the form of a closed round vesicle, surrounding the whole of the ball and pushing between the lens and the horny plate at its outer side. The round wall of the capsule soon divides into two different membranes by surface-cleavage. The inner membrane becomes the choroid or vascular coat, and in front the ciliary corona and iris. The outer membrane is converted into the white protective or sclerotic coat—in front, the transparent cornea. The eye is now formed in all its essential parts. The further development—the complicated differentiation and composition of the various parts—is a matter of detail.

The chief point in this remarkable evolution of the eye is the circumstance that the optic nerve, the retina, and the pigment membrane originate really from a part of the brain—an outgrowth of the intermediate brain—while the lens, the chief refractive body, developes from the outer skin. From the skin—the horny plate—also arises the delicate conjunctiva, which afterwards covers the outer surface of the eye-ball. The lachrymal glands are ramified growths from the conjunctiva (Fig. 344). All these important parts of the eye are products of the outer germinal layer. The remaining parts—the corpus vitreum (with the vascular capsule of the lens), the choroid (with the iris), and the sclerotic (with the cornea)—are formed from the middle germinal layer.

The outer protection of the eye, the eye-lids, are merely folds of the skin, which are formed in the third month of human embryonic life. In the fourth month the upper eye-lid reaches the lower, and the eye remains covered with them until birth. (Plates VIII.–XIII.) As a rule, they open wide shortly before birth (sometimes only after birth). Our craniote ancestors had a third eye-lid, the nictitating membrane, which was drawn over the eye from its inner angle. It is still found in many of the selachii and amniotes.

In the apes and man it has degenerated, and there is now only a small relic of it at the inner corner of the eye, the semilunar fold, a useless rudimentary organ (cf. p. 86). The apes and man have also lost the Harderian gland that opened under the nictitating membrane; we find this in the rest of the mammals, and the birds, reptiles, and amphibia.

The peculiar embryonic development of the vertebrate eye does not enable us to draw any definite conclusions as to its obscure phylogeny; it is clearly cenogenetic to a great extent, or obscured by the reduction and curtailment of its original features. It is probable that many of the earlier stages of its phylogeny have disappeared without leaving a trace. It can only be said positively that the peculiar ontogeny of the complicated optic apparatus in man follows just the same laws as in all the other vertebrates. Their eye is a part of the fore brain, which has grown forward towards the skin, not an original cutaneous sense-organ, as in the invertebrates.

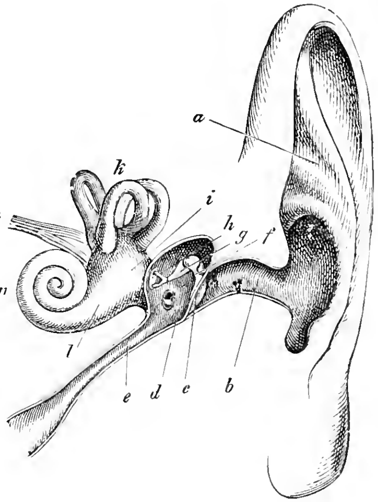


FIG. 383.—**The human ear** (left ear, seen from the front, natural size). *a* shell of ear, *b* external passage, *c* tympanum, *d* tympanic cavity, *e* Eustachian tube, *f*, *g*, *h* the three bones of the ear (*f* hammer, *g* anvil, *h* stirrup), *i* utricle, *k* the three semi-circular canals, *l* the sacculus, *m* cochlea, *n* auscultory nerve.

The vertebrate ear resembles the eye and nose in many important respects, but is different in others, in its development. The auscultory organ in the fully-developed man is like that of the other mammals, and especially the apes, in the main features. As in them, it consists of two chief parts—an apparatus for conducting sound (external and middle ear) and an apparatus for the sensation of sound (internal ear). The external ear opens in the shell at the side of the head (Fig. 383 *a*, Plates XXVI. and XXVII.). From this point the external passage *(b)*, about an inch in length, leads into the head. The inner end of it is closed by the tympanum, a vertical, but not quite upright, thin membrane of an oval shape *(c)*. This tympanum separates the external passage from the tympanic cavity *(cavum tympani, d)*. This is a small cavity, filled with air, in the temporal bone ; it is connected with the mouth by a special tube. This tube is rather longer, but much narrower, than the outer passage, leads inwards obliquely from the anterior wall of the tympanic cavity, and opens in the throat below, behind the nasal openings. It is called the Eustachian tube *(tuba Eustachia, e)*; it serves to equalise the pressure of the air within the tympanic cavity and the outer atmosphere that enters by the external passage. Both the Eustachian tube and the tympanic cavity are lined with a thin mucous coat, which is a direct continuation of the mucous lining of the throat. Inside the tympanic cavity there are three small bones which are known (from their shape) as the hammer, anvil, and stirrup (Fig. 383, *f*, *g*, *h*). The hammer *(f)* is the outermost, next to the tympanum. The anvil *(g)* fits between the other two, above and inside the hammer. The stirrup *(h)* lies inside the anvil, and touches with its base the outer wall of the internal ear, or auscultory vesicle. All these parts of the external and middle ear belong to the apparatus for conducting sound. Their chief task is to convey the waves of sound through the thick wall of the head to the inner-lying auscultory vesicle. They are not found at all in the fishes. In these the waves of sound are conveyed directly by the wall of the head to the auscultory vesicle.

The internal apparatus for the sensation of sound, which receives the waves of sound from the conducting apparatus, consists in man and all other mammals of a closed auscultory vesicle filled with fluid and an auscultory nerve, the ends of which expand over the wall of this vesicle. The vibrations of the sound-waves are conveyed by these media to the nerve-endings. In the labyrinthic water that fills the auscultory vesicle there are small stones at the points of entry of the acoustic nerves, which are composed of groups of microscopic calcareous crystals (otoliths). The auscultory organ of most of the invertebrates has substantially the same composition. It usually consists of a closed vesicle, filled with fluid, and containing otoliths, with the acoustic nerve expanding on its wall. But, while the auditory vesicle is usually of a simple round or oval shape in the invertebrates, it has in the vertebrates a special and curious structure, the labyrinth. This thin-membraned labyrinth is enclosed in a bony capsule of the same shape, the osseous labyrinth (Fig. 384), and this lies in the middle of the petrous bone of the skull. The labyrinth is divided into two vesicles in all the gnathostomes. The larger one is called the *utriculus*, and has three arched appendages, called the "semi-circular canals" *(c, d, e)*. The smaller vesicle is called the *sacculus*, and is connected with a peculiar appendage, with (in man and the higher mammals) a spiral form something like a snail's shell, and therefore called the *cochlea* (=snail, *b*). On the thin wall of this delicate labyrinth the acoustic nerve, which comes from the after-brain, spreads out in most elaborate fashion. It divides into two main branches—a cochlear nerve (for the cochlea) and a vestibular nerve (for the rest of the labyrinth). The former seems to have more to do with the quality, the latter with the quantity, of the acoustic sensations. Through the cochlear nerves we learn the height and timbre, through the vestibular nerves the intensity, of tones.

FIG. 384.

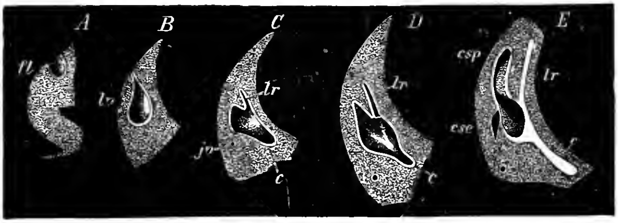


FIG. 385.

FIG. 384.—**The bony labyrinth of the human ear** (left side). *a* vestibulum, *b* cochlea, *c* upper canal, *d* posterior canal, *e* outer canal, *f* oval fenestra, *g* round fenestra. (From *Meyer.*)

FIG. 385.—**Development of the auscultory labyrinth** of the chick, in five successive stages (*A–E*). (Vertical transverse sections of the skull.) *fl* auscultory pits, *lv* auscultory vesicles, *lr* labryrinthic appendage, *c* rudimentary cochlea, *csp* posterior canal, *cse* external canal, *jv* jugular vein. (From *Reissner.*)

The first structure of this highly elaborate organ is very simple in the embryo of man and all the other craniotes; it is a pit-like depression in the skin. At the back part of the head at both sides, near the after brain, a small thickening of the horny plate is formed at the upper end of the second gill-cleft (Figs. 385 *A fl*, 387 *g*). This sinks into a sort of pit, and severs from the epidermis, just as the lens of the eye does. In this way is formed at each side, directly under the horny plate of the back part of the head, a small vesicle filled with fluid, the primitive auscultory vesicle, or the primary labyrinth (Plates VIII.–XIII. *o*). As it separates from its source, the horny plate, and presses inwards and backwards into the skull, it changes from round to pear-shaped (Figs. 385 *B lv*, 388 *o*). The outer part of it is lengthened into a thin stem, which at first still opens outwards by a narrow canal (cf. Fig. 210 *f*). This is the labyrinthic appendage (*recessus labyrinthi*, Fig. 385 *lr*). In the lower vertebrates it developes into a special cavity filled with calcareous crystals, which remains open permanently in some of the primitive fishes, and opens outwards in the upper part of the skull (*ductus endolymphaticus*). But in the mammals the labyrinthic appendage degenerates. In these it has only a phylogenetic interest as a rudimentary organ, with no actual

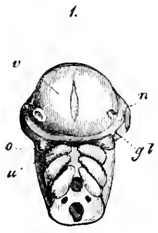


Fig. 386.

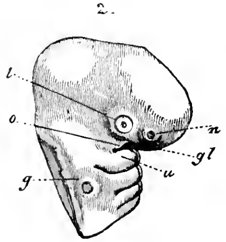


Fig. 387.

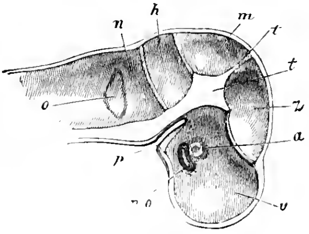


Fig. 388.

Figs. 386 and 387.—**Head of a chick embryo,** three days old; 386 front view, 387 from the right. *n* rudimentary nose (olfactory pit), *l* rudimentary eye (optic pit), *g* rudimentary ear (auscultory pit), *v* fore-brain, *gl* eye-fissure, *o* upper-jaw process, *u* lower-jaw process of the first gill-arch. (From *Kölliker*.)

Fig. 388.—**Primitive skull of the human embryo,** four weeks old, vertical section, left half seen internally. *v*, *z*, *m*, *h*, *n* the five pits of the cranial cavity, in which the five cerebral vesicles lie (fore, intermediate, middle, hind, and after brains), *o* pear-shaped primary auscultory vesicle (appearing through), *a* eye (appearing through), *no* optic nerve, *p* canal of the hypophysis, *t* central prominence of the skull. (From *Kölliker*.)

physiological significance. The useless relic of it passes through the wall of the petrous bone in the shape of a narrow canal, and is called the vestibular aqueduct *(aquæductus vestibuli)*.

It is only the inner and lower bulbous part of the separated auscultory vesicle that developes into the highly complex and differentiated structure that is afterwards known as the secondary labyrinth. This vesicle divides at an early stage into an upper and larger and a lower and smaller section. From the one we get the *utriculus* with the semi-circular canals; from the other the *sacculus* and the cochlea (Fig. 385 *c*). The canals are formed in the shape of simple pouch-like involutions of the utricle *(cse* and *csp)*. The edges join together in the middle part of each fold, and separate from the utricle, the two ends remaining in open connection with its cavity. All the gnathostomes have these three canals like man, whereas among the cyclostomes the lampreys have only two and the myxinoides only one. The very complex structure of the cochlea, one of the most elaborate and wonderful outcomes of adaptation in the mammal body, developes originally in very simple fashion as a flask-like projection from the sacculus. As Hasse and Retzius have pointed out, we find the successive ontogenetic stages of its growth represented permanently in the series of the higher vertebrates. The cochlea is wanting even in the monotremes, and is restricted to the rest of the mammals and man.

The auscultory nerve *(nervus acusticus)*, or eighth cerebral nerve, expands with one branch in the cochlea, and with the other in the remaining parts of the labyrinth. This nerve is, as Gegenbaur has shown, the sensory dorsal branch of a cerebro-spinal nerve, the motor ventral branch of which acts for the muscles of the face *(nervus facialis)*. It has therefore originated phylogenetically from an ordinary cutaneous nerve, and so is of quite different origin from the optic and olfactory nerves, which both represent direct outgrowths of the brain. In this respect the auscultory organ is essentially different from the organs of sight and smell. The acoustic nerve is formed from ectodermic cells of the hind brain, and developes

FORTY-SIXTH TABLE

SYNOPSIS OF THE PHYLOGENY OF THE HUMAN EAR

I. **Period.**—The auscultory nerve is an ordinary sensory nerve, spreading out over an auscultory plate, a special part of the skin of the head with differentiated horny plate.

II. **Period.**—The auscultory plate forms a sort of pit in the skin, which opens outwards (by the labyrinthic appendage).

III. **Period.**—The auscultory pit has separated from the horny plate in the shape of a vesicle filled with fluid. An otolith is formed in this by calcareous secretion. The labyrinthic appendage becomes rudimentary *(aquæductus vestibuli)*.

IV. **Period.**—The auscultory vesicle divides into two connected parts—the utriculus and sacculus. A special branch of the acoustic nerve goes to each vesicle.

V. **Period.**—Three circular canals develop from the utricle (as in all the gnathostomes).

VI. **Period.**—The cochlea developes from the sacculus (very insignificant in the fishes and amphibia, only developing as an independent part in the amniotes).

VII. **Period.**—The first gill-cleft (the "squirting-hole" of the selachii) is converted into the tympanic cavity and Eustachian tube; the former is closed without by the tympanum (amphibia).

VIII. **Period.**—From the uppermost piece of the second gill-arch a rod-shaped auscultory bone (columella) is developed internally, and this connects the labyrinth with the tympanum (amphibia, reptiles).

IX. **Period.**—The columella of the reptiles is converted into the stirrup of the mammals, the quadrate bone of the former into the anvil of the latter, and the prominent joint of the lower jaw into the hammer. Thus the hammer and anvil are formed from the first, the stirrup from the second, gill-arch.

X. **Period.**—The external ear, the bony passage, and the cartilage of the pinna develop from the hyoid-bone arch (second gill-arch). The pinna is pointed and mobile (as in most of the lower mammals).

XI. **Period.**—The pinna of the ear and its muscles fall into disuse and become a rudimentary organ. It is no longer pointed, but has a folded border and a lobe (in the anthropoid apes and man).

FORTY-SEVENTH TABLE

SYNOPSIS OF THE DEVELOPMENT OF THE PARTS OF THE HUMAN EAR

I. Parts of the Internal Ear.
Apparatus of the Sensation of Sound.

A. **Products of the horny plate.**	1. Stem of the primary auscultory vesicle.	1. Aqueduct of the vestibule (ductus endolymphaticus).	*Aquæductus vestibuli* or *recessus labyrinthi.*
	2, 3. Upper part of the primary vesicle.	2. Utricle. 3. Three semicircular canals.	*Utriculus.* *Canales semicirculares.*
	4, 5. Under part of the primary vesicle.	4. Sacculus. 5. Cochlea.	*Sacculus.* *Cochlea.*
B. **Products of the medullary plate.**	6. Nervous structure at the last part of the hind brain.	6. Auscultory nerve.	*Nervus acusticus.*
C. **Products of the head-plate.**	7. Bony envelope of the membranous labyrinth.	7. Bony labyrinth.	*Labyrinthus osseus.*
	8. Bony covering of the whole internal ear.	8. Petrous bone.	*Os petrosum.*

II. Parts of the Middle and External Ear.
Apparatus for Conducting Sound.

D. **Products of the first gill-cleft.**	9. Inner part of the first gill-cleft.	9. Eustachian tube.	*Tuba Eustachii.*
	10. Middle part of the first gill-cleft.	10. Tympanic cavity.	*Cavum tympani.*
	11. Last part of the first gill-cleft.	11. Tympanic membrane.	*Membrana tympani.*
E. **Products of the first two gill-arches.**	12. Uppermost part of the second gill-arch.	12. Stirrup (first auscultory bone).	*Stapes* (= *columella*).
	13. Uppermost part of the first gill-arch.	13. Anvil (second auscultory bone).	*Incus.*
	14. Middle part of the first gill-arch.	14. Hammer (third auscultory bone).	*Malleus.*
F. **Products of the head-plate.**	15. Tympanic ring (annulus tympanicus).	15. Outer bony passage.	*Meatus auditorius osseus.*
	16. Ring-shaped fold of the skin at the last part of the first gill-arch.	16. Shell of ear. 17. Rudimentary muscles of ear.	*Concha auris.* *Musculi conchæ.*

from the nervous structure that appears at its dorsal limit (Fig. 387 *spg)*. On the other hand, all the membranous, cartilaginous, and osseus coverings of the labyrinth are formed from the mesodermic head-plates.

The apparatus for conducting sound which we find in the external and middle ear of mammals developes quite separately from the apparatus for the sensation of sound. It is both phylogenetically and ontogenetically an independent secondary formation, a later accession to the primary internal ear. Nevertheless, its development is not less interesting, and is explained with the same ease by comparative anatomy. In all the fishes and in the lowest vertebrates there is no special apparatus for conducting sound, no external or middle ear; they have only a labyrinth, an internal ear, which lies within the skull. They are without the tympanum and tympanic cavity, and all its appendages. From many observations made in the last few decades it seems that many of the fishes (if not all) cannot distinguish tones; their labyrinth seems to be chiefly (if not exclusively) an organ for the sense of space (or equilibrium). If it is destroyed, the fishes lose their balance and fall. In the opinion of recent physiologists this applies also to many of the invertebrates (including the nearer ancestors of the vertebrates). The round vesicles which are considered to be their auscultory vesicles, and which contain an otolith, are supposed to be merely organs of the sense of space ("static vesicles or statocysts").

The middle ear makes its first appearance in the amphibian class, where we find a tympanum, tympanic cavity, and Eustachian tube; these animals, and all terrestrial vertebrates, certainly have the faculty of hearing. All these essential parts of the middle ear originate from the first gill-cleft and its surrounding part; in the selachii this remains throughout life an open squirting-hole, and lies between the first and second gill-arch. In the embryo of the higher vertebrates it closes up in the centre, and thus forms the tympanic membrane. The outlying remainder of the first gill-cleft is the rudiment of the external meatus. From its inner part we get the tympanic cavity, and, further inward still, the Eustachian tube. Connected with this is the development of the three bones of the mammal ear from the first two gill-arches; the hammer and anvil are formed from the first, the stirrup from the upper end of the second, gill-arch.

The formation of these three bones is very remarkable, as it involves a most curious phyletic metamorphosis of the maxillary joint. The stirrup alone corresponds to the columella of our reptilian ancestors. The anvil has been formed from their quadrate bone, and the hammer from the joint of their lower jaw. The original joint of the jaw in the reptiles and amphibia has been converted in the mammals into the joint between the anvil and hammer. The maxillary joint in the mammal is a new formation, developing between the dental part and the joint part (articulare) of the lower jaw of their reptilian ancestors.

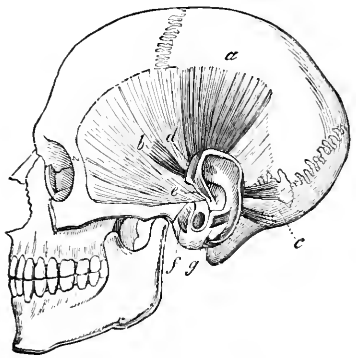
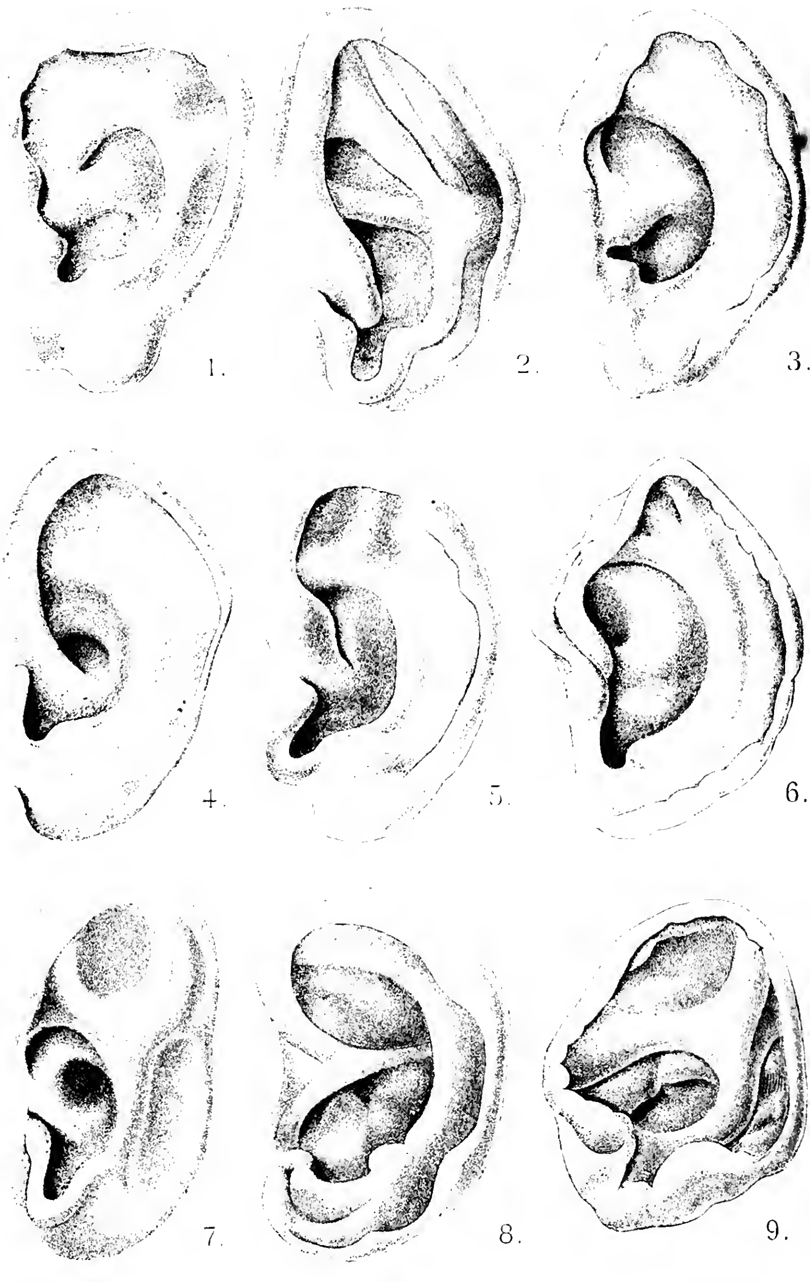


FIG. 389.—**The rudimentary muscles of the ear** in the human skull. *a* raising muscle (*M. attollens*), *b* drawing muscle (*M. attrahens*), *c* withdrawing muscle (*M. retrahens*), *d* large muscle of the helix (*M. helicis major*), *e* small muscle of the helix (*M. helicis minor*), *f* muscle of the angle of the ear (*M. tragicus*), *g* anti-angular muscle (*M. antitragicus*). (From *H. Meyer*.)

Finally, the shell (pinna or concha) and external meatus (passage to the tympanum) of the outer ear are developed in a very simple fashion from the skin that borders the external aperture of the first gill-cleft. The shell rises in the shape of a circular fold of the skin, in which cartilage and muscles are afterwards formed (Figs. 376 and 378). This organ is only found in the mammalian class. It is very rudimentary in the lowest section, the monotremes. In the others it is found at very different stages of development, and sometimes of degeneration. It is degenerate in most of the aquatic mammals. The majority of them have lost it altogether—for instance, the walruses and whales and most of the seals. On the other hand, the pinna is well developed in the great majority of the marsupials and placentals; it receives and collects the waves of sound, and is equipped with a very elaborate muscular apparatus, by means of which the pinna can be turned freely in any direction and its shape be altered. It is well known how readily domestic animals—horses, cows, dogs, hares, etc.—point their ears and move them in different directions. Most of the apes do the same, and our earlier ape ancestors were also able to do it. But our later simian ancestors, which we have in common with the anthropoid apes, abandoned the use of these muscles, and they gradually became rudimentary and useless. However, we possess them still (Fig. 389). In fact, some men can still move their ears a little backward and forward by means of the drawing and withdrawing muscles *(b* and *c);* with practice this faculty can be much improved. But no man can now lift up his ears by the raising muscle *(a)*, or change the shape of them by the small inner muscles *(d, e, f, g)*. These muscles were very useful to our ancestors, but are of no consequence to us. This applies to most of the anthropoid apes as well.

We also share with the higher anthropoid apes (gorilla, chimpanzee, and orang) the characteristic form of the human outer ear, especially the folded border, the helix, and the lobe (Plates XXVI. and XXVII.). The lower apes have pointed ears, without folded border or lobe, like the other mammals. But Darwin has shown that at the upper part of the folded border there is in many men a small pointed process, which most of us do not possess. In some individuals this process is well developed (Figs. 12 and 15). It can only be explained as the relic of the original point of the ear, which has been turned inwards in consequence of the curving of the edge. If we compare the pinna of man and the various apes in this respect, we find that they present a connected series of degenerate structures. In the common catarrhine ancestors of the anthropoids and man the degeneration set in with the folding together of the pinna. This brought about the helix of the ear, in which we find the significant angle which represents the relic of the salient point of the ear in our earlier simian ancestors. Here again,



Lith Anst v A Giltsch.

EAR-MUSCLES OF APES.

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ckel del.

HUMAN-EAR MUSCLES.

therefore, comparative anatomy enables us to trace with certainty the human ear to the similar, but more developed, organ of the lower mammals. At the same time, comparative physiology shows that it was a more or less useful implement in the latter, but is quite useless in the anthropoids and man. The conducting of the sound has scarcely been affected by the loss of the pinna. We have also in this the explanation of the extraordinary variety in the shape and size of the shell of the ear in different men; in this it resembles other rudimentary organs.

The cartilages that form the supporting skeleton of the pinna and determine the shape of its folds are originally connected with the cartilage of the external meatus, and have been developed, together with it, from the uppermost part of the hyoid (tongue) bone arch (the second gill-arch, *hyoideum*); this was shown by Georg Ruge (1897) in the auricula of the monotremes. Gustav Schwalbe (1897) has dealt with the many interesting phylogenetic questions that are raised by the comparative study of the pinna; he showed that the zone of the folds (the upper and hind half of the auricula, with the point) is much more variable than the zone of prominences (the lower and anterior part). Robert Wiederscheim gives further particulars of this in his interesting *Man's Structure as a Witness to his Past* (1902).

On Plates XXVI. and XXVII. the shells of the left ears of eighteen anthropomorphic individuals are presented and reduced to the same size. A thorough and impartial comparison of them shows convincingly that the characteristic shape both of the whole pinna and of its various parts is just as changeable in the anthropoid apes (Plate XXVI.) as in man (XXVII.): Figs. 1–3, gorilla; Figs. 4–6, chimpanzee; Figs. 7–8, orang; Fig. 9, gibbon; Fig. 10, a Bushman; Figs. 11–18, various Europeans (Fig. 13 a Swede; 14, a Jena woman; 16, the musician Humperdink; 17, the musician Richard Strauss). In large assemblies, when our mental interest is fatigued by long conversation or speeches, it is stimulating to compare the ears of the people, which are extraordinarily varied both in the general form and in detail.

CHAPTER XXVI.

EVOLUTION OF THE ORGANS OF MOVEMENT

The vertebrate motorium. Composition of it from passive and active organs of movement (skeleton and muscles). The significance of the internal skeleton in the vertebrate. Structure of the vertebral column. Structure and number of the vertebræ. Ribs and breast-bone. Embryology of the vertebral column. Chorda and perichorda (chorda-sheath). Muscle-plates of the primitive segments. Metamerism. Cartilaginous and osseus vertebræ. Intervertebral sheaths. Skeleton of the head (skull and gill-arches). Vertebral theory of the skull: Goethe and Oken, Huxley and Gegenbaur. Primordial skull (cranium). Its composition from at least nine combined metamera. Phyletic and exact craniology. Gill-arches (head-ribs). Skeleton of the two pairs of limbs. Origin of the five-toed walking foot from the many-toed fin. The primitive fin of the selachii: archipterygium of Gegenbaur. Transition of the feathered and double-lined fin into the half-feathered and single-lined fin. Degeneration of the fin-radii or toes. Polydactylism and pentadactylism. Comparison of the fore legs (breast fins) and the hind legs (belly fins). Shoulder zone and pelvic zone. Embryology of the limbs. Development of the muscles. Muscles of the skin and of the skeleton.

THE peculiar structure of the locomotive apparatus is one of the features that are most distinctive of the vertebrate stem. The chief part of this apparatus is formed, as in all the higher animals, by the active organs of movement, the muscles; in consequence of their contractibility they have the power to draw up and shorten themselves. This effects the movement of the various parts of the body, and thus the whole body is conveyed from place to place. But the arrangement of these muscles and their relation to the solid skeleton are different in the vertebrates from the invertebrates.

In most of the lower animals, especially the platodes and vermalia, we find that the muscles form a simple, thin layer of flesh immediately underneath the skin. This muscular layer is very closely connected with the skin itself; it is the same in the mollusc stem. Even in the large division of the articulates, the classes of crabs, spiders, myriapods, and insects, we find a similar feature, with the difference that in this case the skin forms a solid armour—a rigid cutaneous skeleton made of chitine (and often also of carbonate of lime). This external chitine coat undergoes a very elaborate articulation both on the trunk and the limbs of the articulates, and in consequence the muscular system also, the contractile fibres of which are attached inside the chitine tubes, is highly articulated. The vertebrates form a direct contrast to this. In these alone a solid internal skeleton is developed, of cartilage or bone, to which the muscles are attached. This bony skeleton is a complex lever apparatus, or *passive* apparatus of movement. Its rigid parts, the arms of the levers, or the bones, are brought together by the actively mobile muscles, as if by drawing-ropes. This admirable locomotorium, especially its solid central axis, the vertebral column, is a special feature of the vertebrates, and has given the name to the group.

However, the internal skeleton has had so many different developments in the various classes of vertebrates, in spite of their agreement in the first rudiment, and has become so elaborate a mechanism in the higher sections, that comparative anatomy found a rich mine in this subject. This was appreciated by the older natural philosophy at the beginning of the the nineteenth century, which gladly devoted itself to the study. The science which we now call "comparative anatomy," in the higher philosophic sense, has reaped its finest harvest in this department. Modern comparative anatomy has made a more thorough study of the vertebrate skeleton, and been more successful in gathering the laws of its structure, than it has done with any other system of organs in the body. Here, more than anywhere else, applies the famous couplet in which Goethe summed up the general results of his morphological investigations :—

> "All forms are similar, yet none is like the other ;
> Thus does the harmony point to a hidden law."

To-day, when we have detected this "hidden law" and solved this "sacred problem" by the theory of evolution, when we explain the likeness of forms by heredity and their unlikeness by adaptation, we find no weapons in the vast arsenal of comparative anatomy that more effectively support the truth of evolution than the comparison of the internal skeleton in the various vertebrates. Hence we shall be prepared to find that it has also a special importance in connection with our anthropogeny. The internal skeleton of the vertebrates is one of those organs as to the phylogeny of which we obtain far more important and abundant data from comparative anatomy than from embryology.

There is no other system of organs in which the observer has so clear and convincing a view of the *necessity* of the phylogenetic connection of related yet dissimilar forms as he has in the internal skeleton of the vertebrates. When we compare the bony skeleton of man with that of the other mammals, and this in turn with that of the lower vertebrates, we have in this alone sufficient evidence of the phyletic relationship of all the vertebrates. The parts that make up his bony skeleton are, it is true, different in their form ; but they have just the same characteristic arrangement and connection as in the other mammals. If we, then, further compare the anatomic features of the skeleton from the mammals downwards, we find everywhere an unbroken and direct connection between the manifold and, at first sight, very different structures, and we can in the end trace them all to the same simple type. From this alone every supporter of the theory of evolution will conclude with perfect confidence that all the vertebrates (including man) descend from a common stem-form, a primitive vertebrate. The morphological features of the internal skeleton and of the closely correlated muscular system are such as to make the idea of a polyphyletic origin —a descent from several different root-forms—quite inconceivable. On mature reflection it is impossible to think that the vertebral column with its various appendages, or the skeleton of the limbs with its highly differentiated parts, was evolved more than once in the course of organic history, and that the different vertebrates can therefore be traced to several distinct lines of invertebrate ancestors. Comparative anatomy and ontogeny irresistibly impel us to the monophyletic conviction that the human race is the youngest branch of the vast stem of which all the other vertebrates are collateral branches.

FORTY-EIGHTH TABLE

SYNOPSIS OF THE COMPOSITION OF THE HUMAN SKELETON

A. Central or Axial Skeleton. Chordaskeleton.

Aa.: Vertebræ and Upper Vertebral Arches.

1. Skull (*cranium*).	1a. Prevertebral skull. 1b. Vertebral skull.
2. Vertebral column (*vertebrarium*).	7 Cervical vertebræ. 12 Dorsal vertebræ. 5 Lumbar vertebræ. 5 Sacral vertebræ. 4 Caudal vertebræ.

Ab.: Lower Vertebral Arches.

1. Products of the gill-arches.	*Producta arcuum branchialium.*
2. Ribs and breast-bone.	*Costæ et sternum.*

B. Zone-skeleton of the Limbs.

Ba.: Zone-skeleton of the Fore Legs: Shoulder-zone (*Scapulozona*).

1. Shoulder-blade.	*Scapula.*
[2. Primitive clavicle.	*Procoracoides.* †]
[3. Tearing bone.	*Coracoides.* †]
4. Clavicle.	*Clavicula.*

Bb.: Zone-skeleton of the Hind Legs: Pelvic Zone (*Pelycozona*).

1. Iliac bone.	*Os ilium.*
2. Pubic bone.	*Os pubis.*
3. Ischial bone.	*Os ischii.*

C. Skeleton of the Limbs. Meloskeleton.

Ca.: Limb-skeleton of the Fore Legs (*carpomela*).

I. First section: Upper arm.

1. Humerus. *Humerus.*

II. Second section: Lower arm.

2. Radius. *Radius.*
3. Ulna. *Ulna.*

III. Third section: Hand.

III. A. Wrist. Original parts.	*Carpus.* Modified parts.
a. Radiale	= *Scaphoideum.*
b. Intermedium	= *Lunatum.*
c. Ulnare	= *Triquetrum.*
d. Centrale.	= *Centrale.*
e. Carpale I.	= *Trapezium.*
f. Carpale II.	= *Trapezoides.*
g. Carpale III.	= *Capitatum.*
h. Carpale IV. + V.	= *Hamatum.*

III. B. Middle hand *Metacarpus* (5).

III. C. Five fingers: *Digiti* (14 bones: *Phalanges*).

Cb.: Limb-skeleton of the Hind Legs (*tarsomela*).

I. First section: Thigh.

1. Thigh-bone. *Femur.*

II. Second section: Lower leg.

2. Shin-bone. *Tibia.*
3. Fibula. *Fibula.*

III. Third section: Foot.

III. A. Ankle. Original parts.	*Tarsus.* Modified parts.
a. Tibiale b. Intermedium	= *Astragalus.*
c. Fibulare	= *Calcaneus.*
d. Centrale	= *Naviculare.*
e. Tarsale I.	= *Cuneiforme I.*
f. Tarsale II.	= *Cuneiforme II.*
g. Tarsale III.	= *Cuneiforme III.*
h. Tarsale IV. + V.	= *Cuboides.*

III. B. Middle foot *Metatarsus* (5).

III. C. Five toes: *Digiti* (14 bones: *Phalanges*).

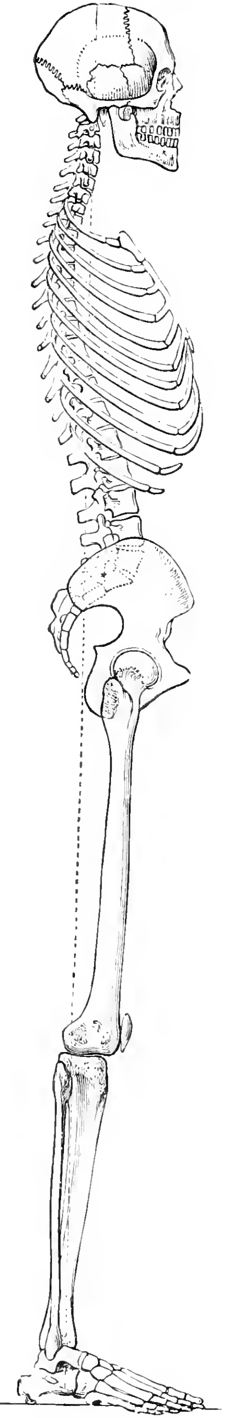


FIG. 390.

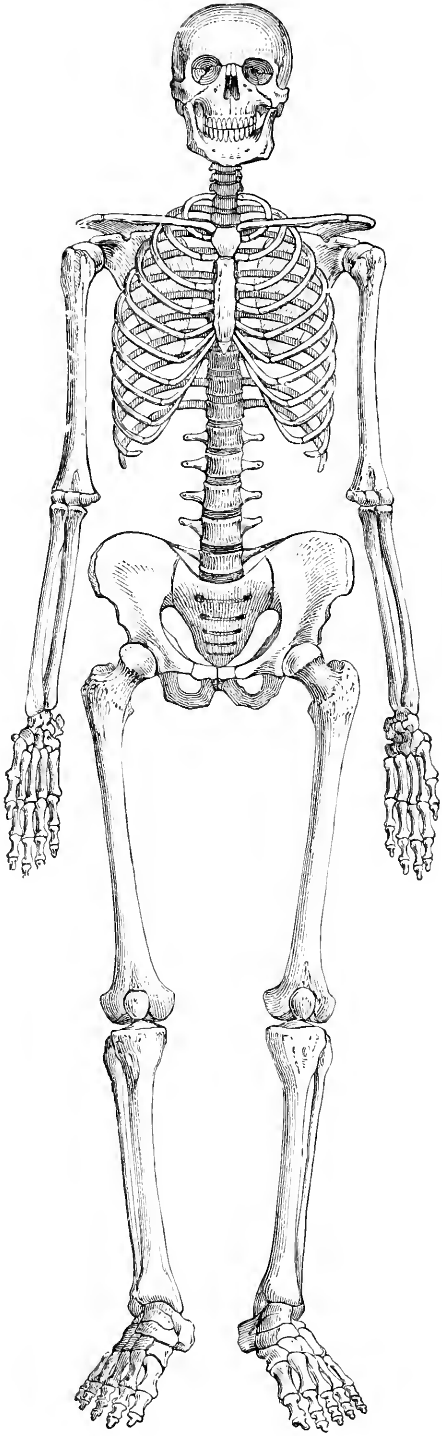


FIG. 391.

In order to get a clear idea of the chief features of the development of the human skeleton, we must first examine its composition in the adult frame (cf. Table XLVIII. and Fig. 390, the human skeleton seen from the right ; Fig. 391, front view of the whole skeleton). As in all other mammals, we distinguish first between the axial or dorsal skeleton and the skeleton of the limbs. The axial skeleton consists of the vertebral column (the skeleton of the trunk) and the skull (skeleton of the head) ; the latter is a peculiarly modified part of the former. As appendages of the vertebral column we have the ribs, and of the skull we have the hyoid bone, the lower jaw, and the other products of the gill-arches.

The skeleton of the limbs *(meloskeleton)* or extremities is composed of two groups of parts—the skeleton of the extremities proper *(podoskeleton)* and the zone-skeleton which connects these with the vertebral column *(zonoskeleton)*. The zone-skeleton of the arms (or fore legs, *carpomela)* is the shoulder-zone *(scapulozona)*; the zone-skeleton of the legs (or hind legs, *tarsomela)* is the pelvic zone *(pelycozona)*.

The vertebral column *(columna vertebralis* or *vertebrarium*, Fig. 392) in man is composed of thirty-three to thirty-five ring-shaped bones in a continuous series (above each other, in man's upright position). These *vertebræ* are separated from each other by elastic ligaments *(ligamenta intervertebralia)*, and at the same time connected by joints, so that the whole column forms a firm and solid, but flexible and elastic, axial skeleton, moving freely in all directions. The vertebræ differ in shape and connection at the various parts of the trunk, and we distinguish the following groups in the series, beginning at the top: Seven cervical vertebræ, twelve

FIG. 392.—**The human vertebral column** (standing upright, from the right side). (From *H. Meyer.*)

dorsal vertebræ, five lumbar vertebræ, five sacral vertebræ, and four to six caudal vertebræ. The uppermost, or those next to the skull, are the cervical vertebræ (Fig. 393); they have a hole in each of the lateral processes. There are seven of these vertebræ in man and almost all the other mammals, even if the neck is as long as that of the camel or giraffe, or as short as that of the mole or hedge-hog. This constant number, which has few exceptions (due to adaptation), is a strong proof of the common descent of the mammals; it can only be explained by faithful heredity from a common stem-form, a primitive mammal with seven cervical vertebræ. If each species had been created separately, it would have been better to have given the long-necked mammals more, and the short-necked animals less, cervical vertebræ. Next to these come the dorsal (or pectoral) vertebræ, which number twelve to thirteen (usually twelve) in man and most of the other mammals. Each dorsal vertebra (Fig. 394) has at the side, connected by joints, a couple of ribs, long bony arches that lie in and protect the wall of the chest. The twelve pairs of ribs, together with the connecting intercostal muscles and the sternum, which joins the ends of the right and left ribs in front, form the chest *(thorax)*. In this strong and elastic frame are the lungs, and between them the heart. Next to the dorsal vertebræ comes a short but stronger section of the column, formed of five large vertebræ. These are the lumbar vertebræ (Fig. 395); they have no ribs and no holes in the transverse processes. To these succeeds the sacral bone, which is fitted between the two halves of the

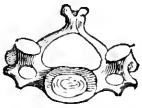


FIG. 393.

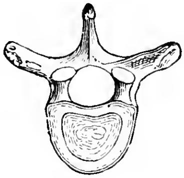


FIG. 394.

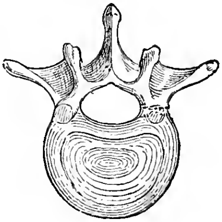


FIG. 395.

FIG. 393.—**The third cervical vertebra** in man.
FIG. 394.—**The sixth dorsal vertebra** in man.
FIG. 395.—**The second lumbar vertebra** in man.

pelvic zone. The sacrum is formed of five vertebræ, completely blended together. Finally, we have at the end a small rudimentary caudal column, the *coccyx*. This consists of a varying number (usually four, more rarely three, or five to six) of small degenerated vertebræ, and is a useless rudimentary organ with no actual physiological significance. Morphologically, however, it is of great interest as an irrefragable proof of the descent of man and the anthropoids from long-tailed apes. On no other theory can we explain the existence of this rudimentary tail. In the earlier stages of development the tail of the human embryo protrudes considerably (Plate XIII., M. II). It afterwards atrophies; but the relic of the atrophied caudal vertebræ and of the rudimentary muscles that once moved it remains permanently. Sometimes, in fact, the external tail is preserved (Fig. 195, p. 369). The older anatomists say that the tail is usually one vertebra longer in the human female than in the male (or four against five); Steinbach says it is the reverse.

	Number of Vertebræ in different Catarrhines.	Cervical.	Dorsal.	Lumbar.	Sacral.	Caudal.	Total.
Tail-less.	Man (Figs. 337, 392)	7	12	5	5	4	33
	Orang (Figs. 236–238)	7	12	5	4	3	31
	Gibbon (Figs. 235, 333)	7	13	5	4	3	32
	Gorilla (Figs. 242–4, 336)	7	13	4	4	5	33
	Chimpanzee (Figs. 239–241)	7	14	4	4	5	34
Tailed.	Mandril (*mormon choras*)	7	13	6	3	5	34
	Drill (*mormon leucophæus*)	7	12	7	3	8	37
	Rhesus (*inuus rhesus*)	7	12	7	2	18	46
	Sphinx (*papio sphinx*)	7	13	6	3	24	53
	Simpai (*semnopithecus melas*)	7	12	7	3	31	60

In the human vertebral column there are usually thirty-three vertebræ. It is interesting to find, however, that the number often changes, one or two vertebræ dropping out or an additional one appearing. Often, also, a mobile rib is formed at the last cervical or the first lumbar vertebra, so that there are then thirteen dorsal vertebræ besides six cervical or four lumbar. In this way the contiguous vertebræ of the various sections of the column may take each other's places. On the other hand, the preceding table of the vertebræ of various tailed and tail-less catarrhines shows how great a variation there may be in the number even within the limits of one family.

In order to understand the embryology of the human vertebral column we must first carefully consider the shape and connection of the vertebræ. Each vertebra has, in general, the shape of a seal-ring (Figs. 393–395). The thicker portion, which is turned towards the ventral side, is called the body of the vertebra, and forms a short osseus disk ; the thinner part forms a semi-circular arch, the *vertebral arch*, and is turned towards the back. The arches of the successive vertebræ are connected by thin intercrural ligaments in such a way that the cavity they collectively enclose represents a long canal. In this vertebral canal we find the trunk part of the central nervous system, the spinal cord. Its head part, the brain, is enclosed by the skull, and the skull itself is merely the uppermost part of the vertebral column, distinctively modified. The base or ventral side of the vesicular cranial capsule corresponds originally to a number of developed vertebral bodies ; its vault or dorsal side to their combined upper vertebral arches.

While the solid, massive bodies of the vertebræ represent the real central axis of the skeleton, the dorsal arches serve to protect the central marrow they enclose. But similar arches develop on the ventral side for the protection of the viscera in the breast and belly. These lower or ventral vertebral arches, proceeding from the ventral side of the vertebral bodies, form, in many of the lower vertebrates, a canal in which the large blood-vessels are enclosed on the lower surface of the vertebral column (aorta and caudal vein). In the higher vertebrates the majority of these vertebral arches are lost or become rudimentary. But at the thoracic section of the column they develop into independent strong osseous arches, the ribs *(costæ)*. In reality the ribs are merely large and independent lower vertebral arches, which have lost their original connection with the vertebral bodies. The branchial arches have the same origin; they are really "head-ribs," or lower arches of cranial vertebræ, generally corresponding to the ribs of the vertebral column. Moreover, the way in which the right and left halves of the arches are connected on the ventral side is the same in both cases. The chest is closed in front by the insertion of the breast-bone *(sternum)* between the front ribs; this is a single bone that forms originally from two lateral halves. The gill pannier is also closed in front by the insertion between the right and left halves of the branchial arches of a single connecting piece—the hyoid body *(copula lingualis,* or *basis hyoidis).*

If we turn from this anatomic survey of the composition of the column to the question of its development, I may refer the reader to earlier pages with regard to the first and most important points (pp. 332–336). It will be remembered that in the human embryo and that of the other vertebrates we find at first, instead of the segmented column, only a simple unarticulated cartilaginous rod. This solid but flexible and elastic rod is the axial rod (or the *chorda dorsalis).* In the lowest vertebrate, the amphioxus, it retains this simple form throughout life, and permanently represents the whole internal skeleton (Fig. 245 *i*). In the tunicates, also, the nearest invertebrate relatives of the vertebrates, we meet the same chorda—transitorily in the passing larva-tail of the ascidia (Plate XVIII., Figs. 6–13 *ch*), permanently in the copelata (Fig. 276 *c*). Undoubtedly both the tunicates and acrania have inherited the chorda from a common unsegmented stem-form; and these ancient, long-extinct ancestors of all the chordonia are our hypothetical prochordonia.

Long before there is any trace of the skull, limbs, etc., in the embryo of man or any of the higher vertebrates—at the early stage in which the whole body is merely a sole-shaped embryonic shield—there appears in the middle line of the shield, directly under the ectoblastic medullary furrow, the simple endoblastic chorda. (Cf. Figs. 128–156 *ch*, Plates

VI. and VII. *ch.*) It follows the long axis of the body in the shape of a cylindrical axial rod of elastic but firm composition, equally pointed at both ends. In every case the chorda originates from the dorsal wall of the primitive gut; the cells that compose it (Fig. 396 *b*) belong to the entoderm (Figs. 251–262). At an early stage the chorda developes a homogeneous cuticula, a transparent structureless sheath, which is secreted from its cells (Fig. 396 *a*). This *chordalemma* is often called the "inner chorda-sheath," and must not be confused with the real external-sheath, the mesoblastic perichorda.

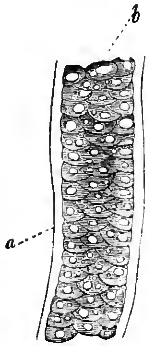


FIG. 396. — **A piece of the axial rod** (*chorda dorsalis*), from a sheep embryo. *a* cuticular sheath, *b* cells. (From *Kölliker.*)

But this unsegmented primary axial skeleton is soon replaced by the segmented secondary axial skeleton, which we know as the vertebral column. The provertebral cords or plates (Fig. 132 *s*) differentiate from the innermost, median part of the visceral layer of the cœlom-pouches at each side of the chorda. As they grow round the chorda and enclose it they form the skeletal plate or skeletogenetic layer—that is to say, the skeleton-forming stratum of cells, which provides the mobile foundation of the permanent vertebral column and skull (sclero-blast). In the head-half of the embryo the skeletal plate remains a continuous, simple, undivided layer of tissue, and presently enlarges into a thin-walled capsule enclosing the brain, the primordial skull. In the trunk-half the provertebral plate divides into a number of homogeneous, cubical, successive pieces; these are the several primitive vertebræ. They are not numerous at first, but soon increase as the embryo grows longer (Figs. 352–354). The first and earliest provertebræ are the foremost cervical vertebræ; after these come the next cervical, then the dorsal, and so on. The caudal vertebræ are the last to appear. This successive ontogenetic growth of the vertebral column from the front part is explained phylogenetically by regarding the much-articulated vertebrate as a secondary product, evolved by the increasing formation of metamera from an originally unsegmented stem-form.

As I have often pointed out already, this vertebration, or internal formation of metamera, is very important in connection with the higher morphological and physiological development of the vertebrates (cf. p. 331). This internal articulation, quite different from the external articulation of the articulates, is by no means restricted to the vertebral column, but affects to the same extent the muscular, nervous, vascular systems, etc. It first influences the muscular system, and only appears later on in the skeletal system. In reality, each primitive vertebra is much more than the mere rudiment of a coming vertebra. It is only the innermost part of it, next to the chorda and the medullary tube, the *sclerotome*, that is used in the formation of vertebræ; its chief mass forms the muscle-plate (*myotome*). We have already seen how the vertebræ proper are formed from the skeleton-plate of the provertebra. The originally separate halves of each provertebra, to the right and left of the chorda, join together. The ventral edges of each half, underneath the medullary tube, enclose the chorda, and thus form the base of the vertebral body. The dorsal edges, which unite *above* the medullary tube, form the first structure of the upper vertebral arch. (Cf. Figs. 148–151, and Plate VI., Figs. 3–8.)

In all the craniotes the soft, indifferent cells of the mesoderm, which originally compose the skeletal plate, are afterwards converted for the most part into cartilaginous cells, and these secrete a firm and elastic intercellular substance between them, and form cartilaginous tissue. Like most of the other parts of the skeleton, the membranous rudiments of the vertebræ soon pass into a cartilaginous state, and in the higher vertebrates this is afterwards replaced by the hard osseous tissue with its characteristic stellate cells (Fig. 6, p. 101). The primary axial skeleton remains a simple chorda throughout life in the acrania, the cyclostomes, and the lowest fishes. In most of the other vertebrates the chorda is more or less replaced by the cartilaginous tissue of the secondary perichorda that grows round it. In the lower craniotes (especially the fishes) a more or less considerable part of the chorda is preserved in the bodies of the vertebræ. In the mammals it disappears for the most part. By the end of the second month in the human embryo the chorda is merely a slender thread, running through the axis of the thick, cartilaginous vertebral column (Figs. 194 *ch*, 397 *ch*). In the cartilaginous vertebral bodies themselves, which afterwards ossify, the slender remnant of the chorda presently disappears (Fig. 398 *ch*). But in the elastic intervertebral disks, which develop from the skeletal plate between each pair of vertebral bodies (Fig. 397 *li*), a relic of the chorda remains permanently. In the new-born child there is a large pear-shaped cavity in each intervertebral disk, filled with a gelatinous mass of cells (Fig. 399 *a*). Though less sharply defined, this gelatinous nucleus of the elastic cartilaginous disks persists throughout life in the mammals, but in the birds and most reptiles the last trace of the chorda disappears. In the subsequent ossification of the cartilaginous vertebra the first deposit of bony matter ("first osseous nucleus") takes place in the vertebral body immediately round

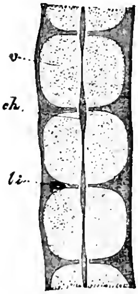


FIG. 397.

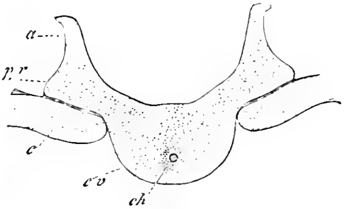


FIG. 398.

FIG. 397.—**Three dorsal vertebræ,** from a human embryo, eight weeks old, in lateral longitudinal section. *v* cartilaginous vertebral body, *li* intervertebral disks, *ch* chorda. (From *Kölliker*.)

FIG. 398.—**A dorsal vertebra** of the same embryo, in lateral transverse section. *cv* cartilaginous vertebral body, *ch* chorda, *pr* transverse process, *a* vertebral arch (upper arch), *c* upper end of the rib (lower arch). (From *Kölliker*.)

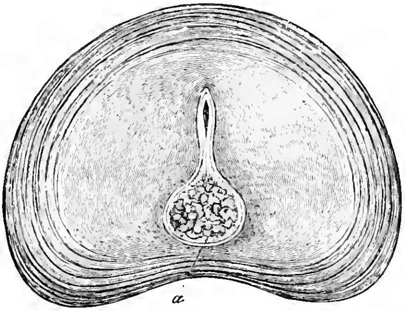


FIG. 399.—**Intervertebral disk** of a new-born infant, transverse section. *a* rest of the chorda. (From *Kölliker*.)

the remainder of the chorda, and soon displaces it altogether. Then there is a special osseous nucleus formed in each half of the vertebral arch. The ossification does not reach the point at which the three nuclei are joined until after birth. In the first year the two osseous halves of the arches unite; but it is much later—in the second to the eighth year—that they connect with the osseous vertebral bodies.

The bony skull *(cranium)*, the head-part of the secondary axial skeleton, developes in just the same way as the vertebral column. The skull forms a bony envelope for the brain, just as the vertebral canal does for the spinal cord; and as the brain is only a peculiarly differentiated part of the head, while the spinal cord represents the longer trunk-section of the originally homogeneous medullary tube, we shall expect to find that the osseous coat of the one is a special modification of the osseous envelope of the other. When we examine the adult human skull in itself (Fig 400), it is difficult to conceive how it can be merely the modified fore part of the vertebral column. It is an elaborate and extensive bony structure, composed of no less than twenty bones of different shapes and sizes. Seven of them form the spacious shell that surrounds the brain, in which we distinguish the solid ventral base *(basis cranii)* below and the curved dorsal vault *(fornix cranii)* above. The other thirteen bones form the facial skull, which is especially the bony envelope of the higher sense-organs, and at the same time, as the maxillary skeleton, encloses the entrance of the elementary canal. The lower jaw is articulated at the base of the skull (usually regarded as the XXI. cranial bone). Behind the lower jaw we find the hyoid bone at the root of the tongue, also formed from the gill-arches, and a part of the lower arches that have developed as "head-ribs" from the ventral side of the base of the cranium.

Although the fully-developed skull of the higher vertebrates, with its peculiar shape, its enormous size, and its complex composition, seems to have nothing in common with the ordinary vertebræ, nevertheless even the older comparative anatomists came to recognise at the end of the eighteenth century that it is really nothing else originally than a series of modified vertebræ. When Goethe in 1790 "picked up the skull of a slain victim from the sand of the Jewish cemetery at Venice, he noticed at once that the bones of the face also could be traced to vertebræ (like the three hindmost cranial vertebræ)." And when Oken (without knowing anything of Goethe's discovery) found at

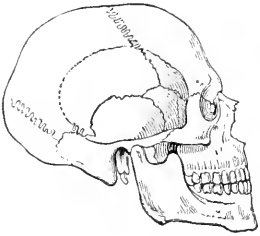


Fig. 400.

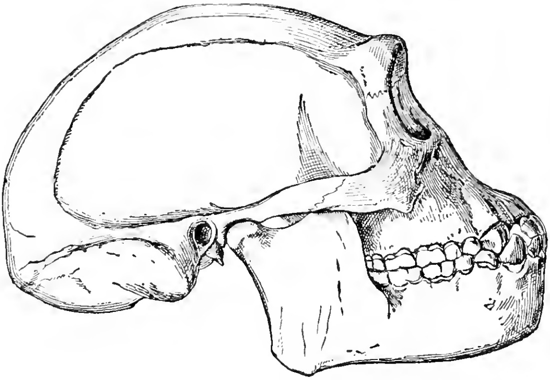


Fig. 401.

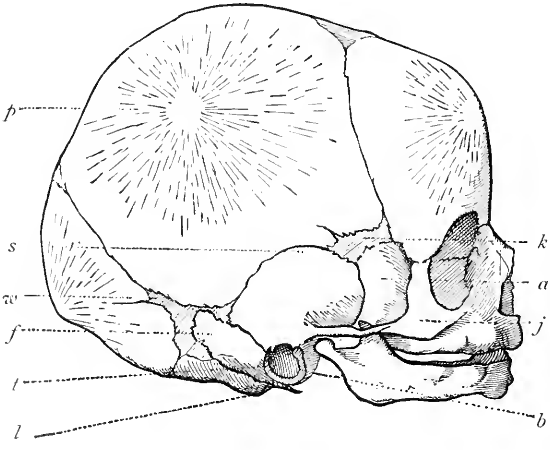


Fig. 402.

Fig. 400.—**Human Skull.** (Cf. Plate XVII.)

Fig. 401.—**Skull of the fossil ape-man of Java** *(pithecanthropus erectus)*, restored by *Eugen Dubois*. (Cf. Plate XVII.)

Fig. 402.—**Skull of new-born child.** (From *Kollmann*.) Above, in the three bones of the roof of the skull, we see the lines that radiate from the central points of ossification; in front, the frontal bone; behind, the occipital bone; between the two the large parietal bone, *p*. *s* the scurf bone, *w* mastoid fontanelle, *f* petrous bone, *t* tympanic bone, *l* lateral part, *b* bulla, *j* cheek-bone, *a* large wing of cuneiform bone, *k* fontanelle of cuneiform bone.

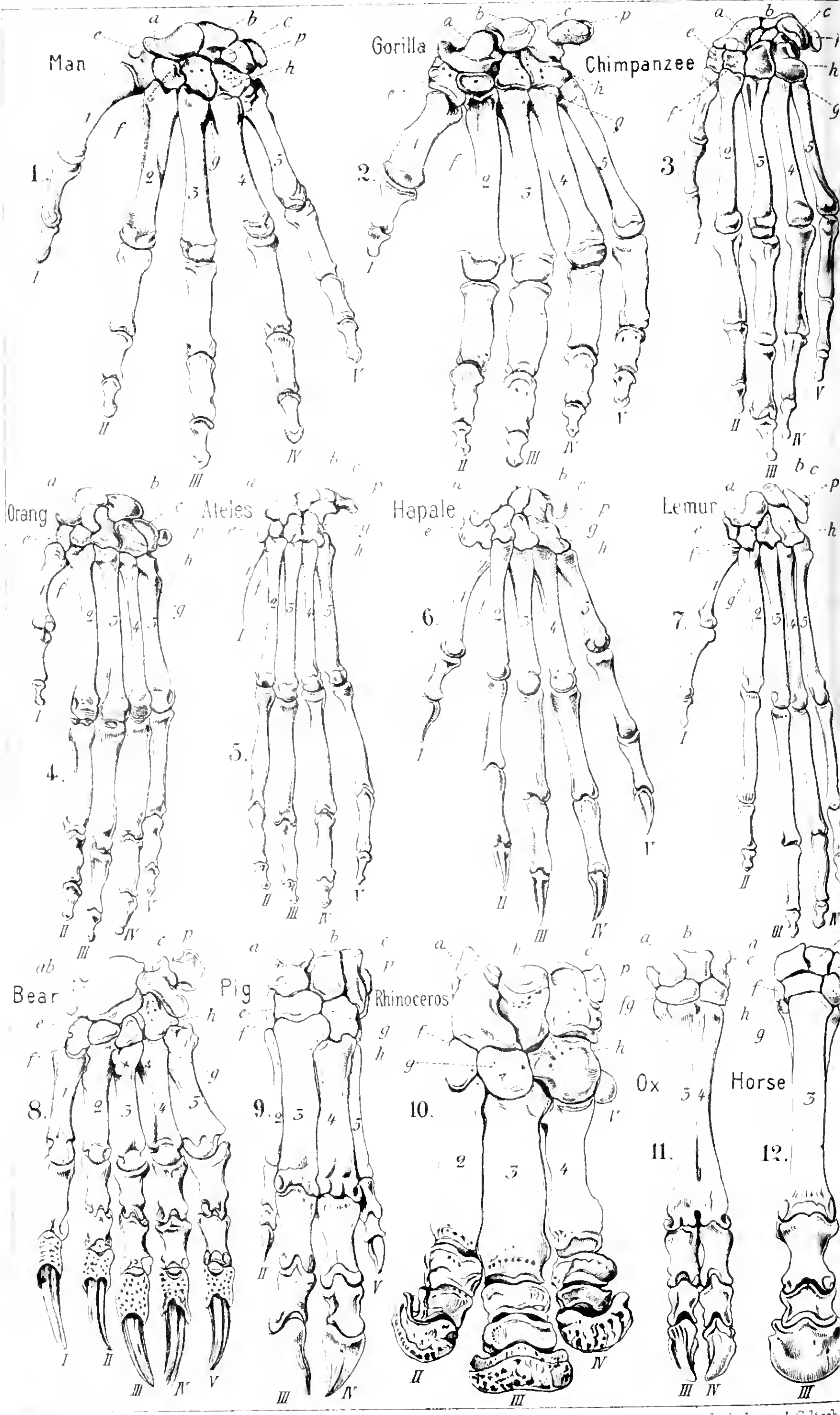
llenstein "a fine bleached skull of a hind, the thought flashed across him like lightning: 'It is a vertebral column.'"

This famous vertebral theory of the skull has interested the most distinguished zoologists for more than a century; the chief representatives of comparative anatomy have devoted their highest powers to the solution of the problem, and the interest has spread far beyond their circle. But it was not until 1872 that it was happily solved, after seven years' labour, by the comparative anatomist who surpassed all other experts of this science in the second half of the nineteenth century by the richness of his empirical knowledge and the acuteness and depth of his philosophic speculations. Carl Gegenbaur has shown, in his classic *Studies of the Comparative Anatomy of the Vertebrates* (third section), that we find the most solid foundation for the vertebral theory of the skull in the head-skeleton of the selachii. Earlier anatomists had wrongly started from the mammal skull, and had compared the several bones that compose it with the several parts of the vertebra (Fig. 402); they thought they could prove in this way that the fully-formed mammal skull was made of from three to six vertebræ. The hindmost of these cranial vertebræ was supposed to be the occipital bone ("occipital vertebra"). A second (the "parietal vertebra") was believed to have given the hind cheek bone and the parietal bones; a third (the "frontal vertebra") the front cheek bone and the frontal bone. Thus it was thought possible to trace the elements of former cranial vertebræ in the bones of the facial skull. But the able English anatomist, Huxley, pointed out that this bony skull originated in the embryo from a simple cartilaginous capsule, and in this there was no trace whatever of composition of vertebra-like parts. This applies permanently to the skull of the lowest and oldest craniotes, the cyclostomes and selachii. In these the skull remains throughout life a very simple cartilaginous capsule, an unsegmented primordial cranium. If the older theory of the skull, as it was advanced by most comparative anatomists after Goethe and Oken, were correct, the composition of the primordial cranium from a series of separate cranial vertebræ ought to be perfectly clear in the lowest craniotes and in the embryo of the higher craniotes.

The older theory was thus refuted by this simple and obvious fact, which was first pointed out by Huxley. Nevertheless, the fundamental idea of it—the belief that the skull is formed from the head-part of the perichordal axial skeleton, just as the brain is from the simple medullary tube, by differentiation and modification—remained. The work now was to discover the proper way of supplying this philosophic theory with an empirical foundation, and it was reserved for Gegenbaur to achieve this. He first opened out the phylogenetic path which here, as in all morphological questions, leads most confidently to the goal. He showed that the primitive fishes (Figs. 302–305), the ancestors of all the gnathostomes, still preserve permanently in the form of their skull the structure out of which the transformed skull of the higher vertebrates, including man, has been evolved. He further showed that the branchial arches of the selachii prove that their skull originally consisted of a large number of (at least nine or ten) provertebræ, and that the cerebral nerves that proceed from the base of the brain entirely confirm this. These cerebral nerves are (with the exception of the first and second pair, the olfactory and optic nerves) merely modifications of spinal nerves, and are essentially similar to them in their peripheral expansion. The comparative anatomy of these cerebral nerves, their origin and their expansion, furnishes one of the strongest arguments for the new vertebral theory of the skull.

We have not space here to go into the details of Gegenbaur's theory of the skull. I must be content to refer the reader to the great work I have mentioned, in which it is thoroughly established from the empirico-philosophical point of view. He has also given a comprehensive and up-to-date treatment of the subject in his *Comparative Anatomy of the Vertebrates* (1898). Gegenbaur indicates as original "cranial ribs," or "lower arches of the cranial vertebræ," at each side of the head of the selachii (Fig. 403), the following pairs of

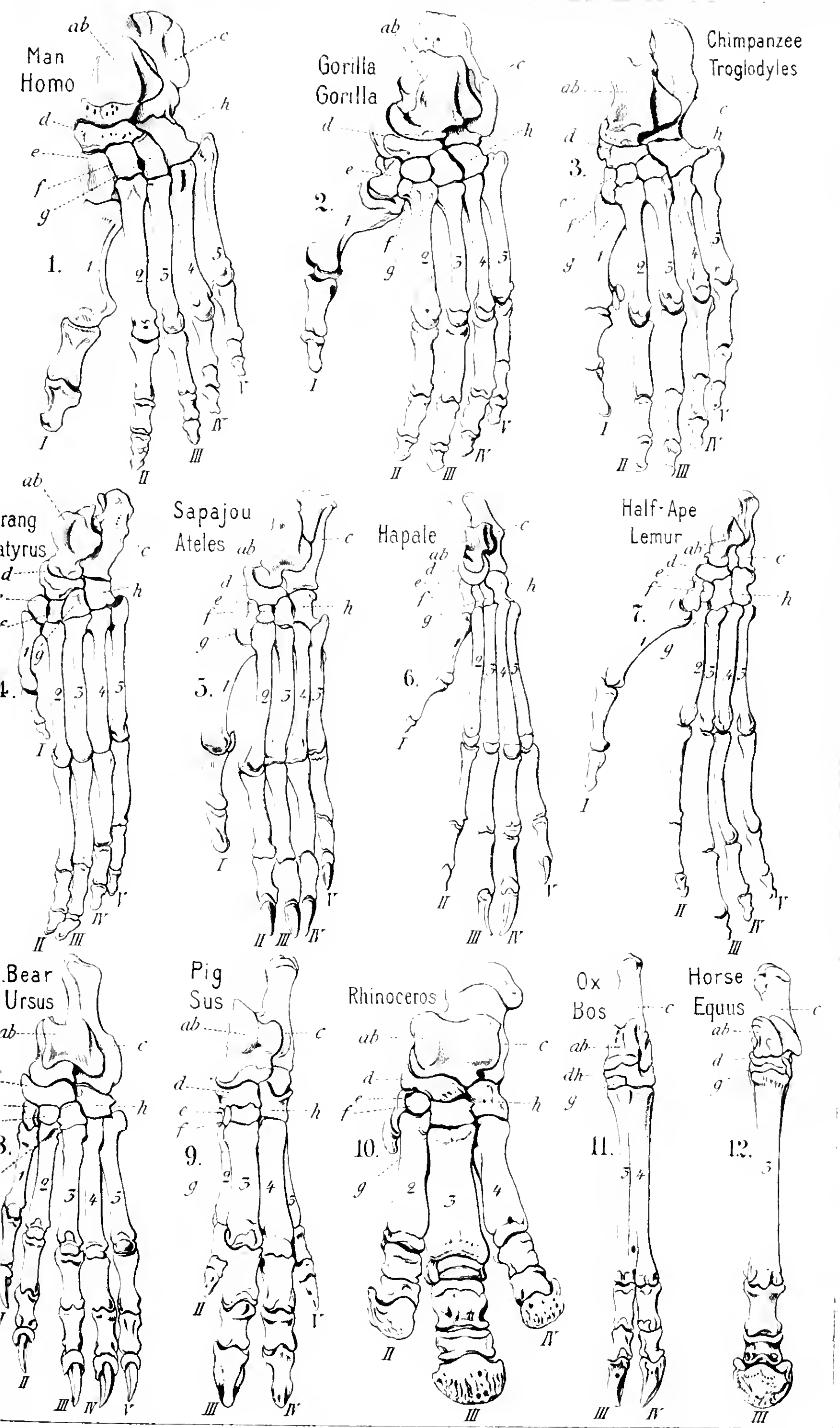
BONES OF HAND



Lith. Anst. v. A. Giltsch

HAND OF TWELVE MAMMALS

BONES OF FOOT



Huxley.

Lith. Anst. v. A. Giltsch, Jena.

FOOT OF TWELVE MAMMALS

arches: *I* and *II*, two lip-cartilages, the anterior *(a)* of which is composed of an upper piece only, the posterior *(bc)* from an upper and lower piece; *III*, the maxillary arches, also consisting of two pieces on each side—the primitive upper jaw *(os palato-quadratum, o)* and the primitive lower jaw *(u)*; *IV*, the hyaloid bone *(II)*; finally, *V–X*, six branchial arches in the narrower sense *(III–VIII)*. From the anatomic features of these nine to ten cranial ribs or "lower vertebral arches" and the cranial nerves that spread over them, it is clear that the apparently simple cartilaginous primitive skull of the selachii was originally formed from so many (at least nine) somites or provertebræ. The blending of these primitive segments into a single capsule is, however, so ancient that, in virtue of the law of curtailed heredity, the original division seems to have disappeared; in the embryonic development it is very difficult to detect it in isolated traces, and in some respects quite impossible. It is claimed that several (three to six) traces of provertebræ have been discovered in the anterior (prechordal) part of the selachii-skull; this would bring up the number of cranial somites to twelve or sixteen, or even more.

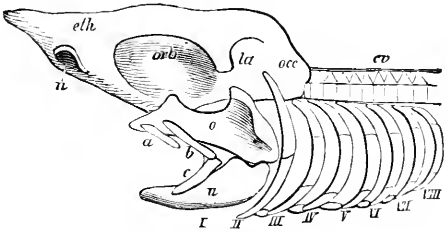


FIG. 403.—**Head-skeleton of a primitive fish.** *n* nasal pit, *eth* cribriform bone region, *orb* orbit of eye, *la* wall of auscultory labyrinth, *occ* occipital region of primitive skull, *cv* vertebral column, *a* fore, *bc* hind lip-cartilage, *o* primitive upper jaw *(palato-quadratum)*, *u* primitive lower jaw, *II* hyaloid bone, *III–VIII* first to sixth branchial arches. (From *Gegenbaur.*)

In the primitive skull of man (Fig. 404) and the higher vertebrates, which has been evolved from that of the selachii, five consecutive sections are discoverable at a certain early period of development, and one might be induced to trace these to five primitive vertebræ; but these sections are due entirely to adaptation to the five primitive cerebral vesicles, and correspond, like these, to a large number of metamera. That we have in the primitive skull of the mammals a greatly modified and transformed organ, and not at all a primitive formation, is clear from the circumstance that its original soft membranous form only assumes the cartilaginous character for the most part at the base and the sides, and remains membranous at the roof. At this part the bones of the subsequent osseous skull develop as external coverings over the membranous structure, without an intermediate cartilaginous stage, as there is at the base of the skull. Thus a large part of the cranial bones develop originally as covering bones from the corium, and only secondarily come into close touch with the primitive skull (Fig. 402). We have previously seen how this very rudimentary beginning of the skull in man is formed ontogenetically from the "head-plates," and thus the fore end of the chorda is enclosed in the base of the skull. (Cf. Fig. 230; also Fig. 213 *k*, pp. 314, 335, 344, and Fig. 172, p. 342.)

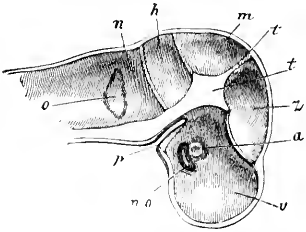


FIG. 404.—**Primitive skull of the human embryo,** four weeks old, vertical section, the left half seen internally. *v*, *z*, *m*, *h*, *n* the five depressions in the cranial cavity in which are found the five cerebral vesicles (fore, intermediate, middle, hind, and after brain), *o* pear-shaped primary auscultory vesicle (seen through), *no* optic nerve, *p* canal of the hypophysis, *t* middle cranial prominences. (From *Kölliker*.)

The phylogeny of the skull has made great progress during the last three decades through the joint attainments of comparative anatomy, ontogeny, and paleontology. By the judicious and comprehensive application of the phylogenetic method (in the sense of Gegenbaur) we have found the key to the great and important problems that arise from the thorough comparative study of the skull. Another school of research, the school of what is called "exact craniology" (in the sense of Virchow), has, meantime, made fruitless efforts to obtain this result. We may gratefully acknowledge all that this descriptive school has done in the way of accurately describing the various forms and measurements of the human skull, as compared with those of other mammals. But the vast empirical material that it has accumulated in its extensive literature is mere dead and sterile erudition until it is vivified and illumined by phylogenetic speculation.

The names of the two great anatomists who died recently—Rudolf Virchow in September, 1902, and his pupil, Carl Gegenbaur, in June, 1903—stand very characteristically in this broad field of craniology for the opposition between the older, descriptive science and the new, phylogenetic study. Virchow confined himself to the most careful analysis of large numbers of human skulls and those of anthropoid mammals. He saw only the differences between them, and sought to express this in figures; he knew nothing of the cranial structures of the lower vertebrates, and their phyletic connection with the higher. Gegenbaur, on the other hand, took in with one glance the whole broad province of craniology, from the lowest and earliest to the highest and most recent vertebrates; by intelligent synthesis (in the sense of Goethe and Johannes Müller) he recognised the common type that lies at the base of these innumerable forms of skull, and proved that they are all only variations of one and the same model; he showed, further, that the human skull, like that of all the gnathostome vertebrates, can be traced to the simple primordial skull of the earliest Silurian selachii (Fig. 403).

How little capable Virchow was of appreciating these great discoveries of Gegenbaur's is clear from his obstinate opposition, to the close of his life, to the evolutionary theory. Without adducing a single solid reason, or offering any alternative explanation, he rejected it as an unproved hypothesis. He played a most unfortunate part in the controversy as to the significance of the fossil human skulls of Spy and Neanderthal, and the comparison of them with the skull of the pithecanthropus (Fig. 401). All the interesting features of these skulls that clearly indicated the transition from the anthropoid to the man were declared by Virchow to be chance pathological variations. He said that the roof of the skull of pithecanthropus (Fig. 405, *3*) must have belonged to an ape, because so pronounced an *orbital stricture* (the horizontal constriction between the outer edge of the eye-orbit and the temples) is not found in any human being. Immediately afterwards Nehring showed in the skull of a Brasilian Indian (Fig. 405, *2*), found in the

Sambaquis of Santos, that this stricture can be even deeper in man than in many of the apes. It is very instructive in this connection to compare the roofs of the skulls (seen from above) of different primates. I have, therefore, arranged nine such skulls in Fig. 405, and reduced them to a common size. Fig. *1* an advanced European (Aryan), Fig. *2* a Brazilian from the Sambaquis (diluvial mussel-formations), Fig. *3* the Pliocene ape-man of Java *(pithecanthropus)*, Figs. *4* and *5* African anthropoid apes (gorilla and chimpanzee), Figs. *6* and *7* Asiatic anthropoids (orang and gibbon), Figs. *8* and *9* tailed dog-faced apes (presbytis and baboon). On Plate XVII. (frontispiece to this volume) I have put together the skulls of eight other primates (in profile from the right). An impartial examination of them shows at once that Huxley's pithecometra-principle applies here (p. 399).

We turn now to the branchial arches, which were regarded even by the earlier natural philosophers as "head-ribs." (Cf. Plates VIII.–XIII., I., and XXIV., and Figs. 178–186.) Of the four original gill-arches of the mammals the first lies between the primitive mouth and the first gill-cleft. From the base of this arch is formed the upper-jaw process, which joins with the inner and outer nasal processes on each side, in the manner we have previously explained, and forms the chief parts of the skeleton of the upper jaw (palate bone, pterygoid bone, etc.). (Cf. p. 687.) The remainder of the first branchial arch, which is now called, by way of contrast, the "upper-jaw process," forms from its base two of the ear-ossicles (hammer and anvil), and as to the rest is converted into a long strip of cartilage that is known, after its discoverer, as "Meckel's cartilage," or the *promandibula*. At the outer surface of the latter is formed from the cellular matter of the corium, as covering or accessory bone, the permanent bony lower jaw. From the first part or base of the second branchial arch we get, in the mammals, the third ossicle of the ear, the stirrup; and from the succeeding parts we get (in this order) the muscle of the stapes, the styloid process of the temporal bone, the styloid-hyoid ligament, and the little horn of the hyoid bone. The third branchial arch is only cartilaginous at the foremost part, and here the body of

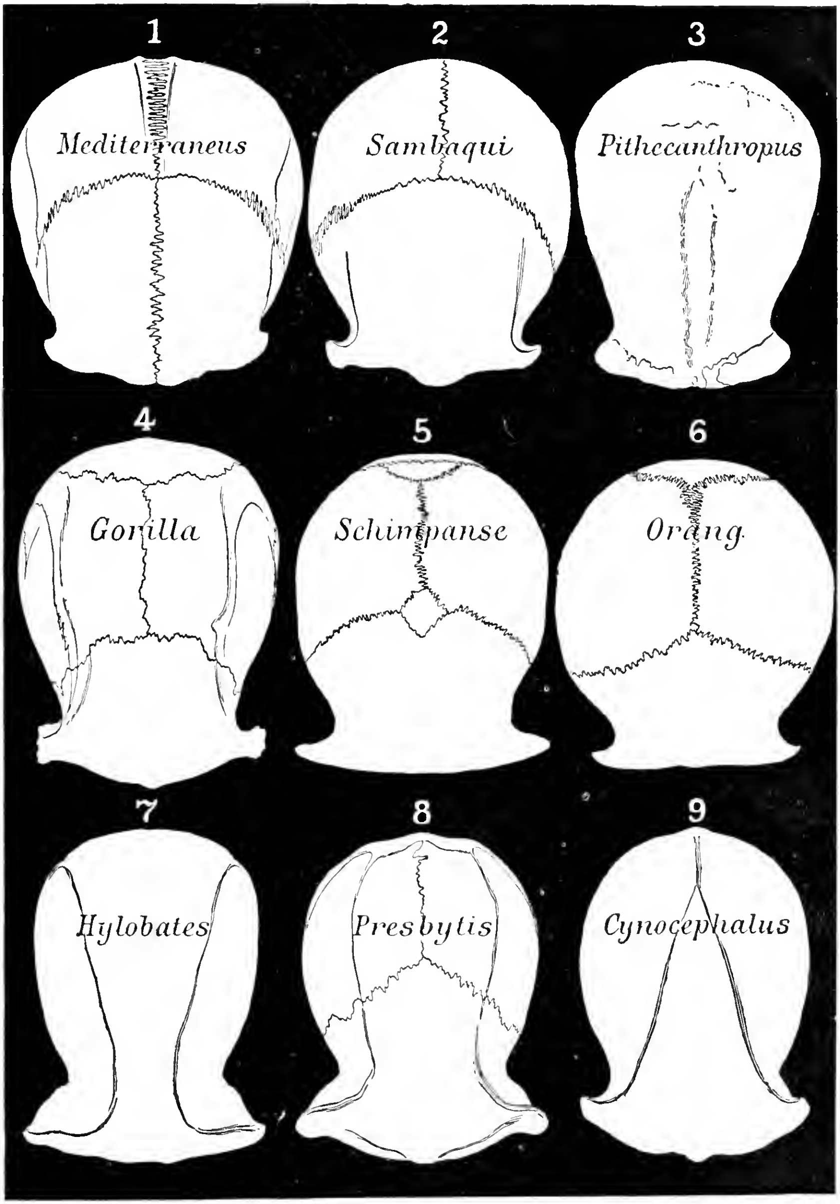


Fig. 405.—**Roofs of the skulls of nine primates** *(catarrhines)*, seen from above and reduced to a common size. *1* European, *2* Brasilian, *3* Anthropithecus, *4* Gorilla, *5* Chimpanzee, *6* Orang, *7* Gibbon, *8* Semnopithecus, *9* Baboon.

the hyoid bone *(copula hyoidea)* and its larger horn are formed at each side by the junction of its two halves. The fourth branchial arch is only found transitorily in the mammal embryo as a rudimentary organ, and does not develop special parts; and there is no trace in the embryo of the higher vertebrates of the posterior branchial arches (fifth and sixth pair), which are permanent in the selachii. They have been lost long ago. Moreover, the four gill-clefts of the human embryo are only interesting as rudimentary organs, and they soon close up and disappear. The first alone (between the first and second branchial arches) has any permanent significance; from it are developed the tympanic cavity and the Eustachian tube. (Cf. Figs. 383, 387.)

Carl Gegenbaur was the first to open our eyes to the true meaning of the skull and its relation to the vertebral column by his masterly *Studies of the Comparative Anatomy of the Vertebrates*, and the same scientist solved the no less interesting and difficult problem of tracing the skeleton of the limbs of the vertebrates to a common phylogenetic type. Few parts of the vertebrate body have undergone such infinitely varied modifications in regard to size, shape, and adaptation of structure as the limbs or extremities; yet we are in a position to reduce them all to the same hereditary standard. We may generally distinguish three groups among the vertebrates in relation to the formation of their limbs (p. 576). The lowest and earliest vertebrates, the acrania and gnathostomes, had, like their invertebrate ancestors, no pairs of limbs, as we see in the amphioxus and the cyclostomes to-day *(adactylia,* Figs. 245, 301). The second group is formed of the two classes of the true fishes and the dipneusts; here there are always two pairs of limbs at first, in the shape of many-toed fins—one pair of breast fins or fore legs, and one pair of belly-fins or hind legs *(polydactylia,* Figs. 302–313). The third group comprises the four higher classes of vertebrates—the amphibia, reptiles, birds, and mammals; in these quadrupeds *(quadrupeda* or *tetrapoda)* there are at first the same two pairs of limbs, but in the shape of five-toed feet. Frequently we find less than five toes, and sometimes the feet are wholly atrophied (as in the serpents). But the original stem-form of the group had five toes or fingers before and behind (*pentadactylia*, Figs. 317–319).

It also follows phylogenetically from the comparative anatomy of the limbs that they were first evolved in the earliest fishes, the selachii. From these they have been inherited by all the higher vertebrates, first as polydactyle fins, afterwards as pentadactyle feet. The foremost extremity, the breast-fin or fore limb, was originally just the same in structure as the belly-fin or hind limb. In both we can distinguish the inner zone by which the limb is attached to the vertebral column from the extending limb itself—in front the shoulder-zone, behind the pelvic zone.

The true primitive form of the pairs of limbs, such as they were found in the primitive fishes of the Silurian period, is preserved for us in the Australian dipneust, the remarkable *ceratodus* (Fig. 311). Both the breast-fin and the belly-fin are flat oval paddles in which we find a biserial cartilaginous skeleton (Fig. 406). This consists, firstly, of a much segmented fin-rod or "stem" (*A*, *B*), which runs through the fin from base to tip; and secondly of a double row of thin articulated fin-radii (*r*, *r*), which are attached to both sides of the fin-rod, like the feathers of a feathered leaf. This primitive fin, which Gegenbaur first recognised and called archipterygium, is attached to the vertebral column by a simple zone in the shape of a cartilaginous arch. It has probably originated from the branchial arches.[1]

We find the same biserial primitive fin more or less preserved in the fossilised remains of the earliest selachii (Fig. 292), ganoids (Fig. 297), and dipneusts (Fig. 310). It is also found in modified form in some of the actual sharks and pikes. But in the majority of the selachii it has already degenerated to the extent that the radii on one side of the fin-rod have been partly or entirely lost, and are retained only

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[1] While Gegenbaur derives the fins from two pairs of posterior separated branchial arches, Balfour holds that they have been developed from segments of a pair of originally continuous lateral fins or folds of the skin.

on the other (Fig. 407). We thus get the uniserial fin, which has been transmitted from the selachii to the rest of the fishes (Fig. 408).

Gegenbaur has shown how the five-toed leg of the amphibia, that has been inherited by the three classes of amniotes, was evolved from the uniserial fish-fin.[1] In the dipneust ancestors of the amphibia the radii gradually atrophy,

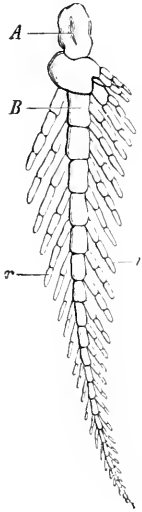

FIG. 406.

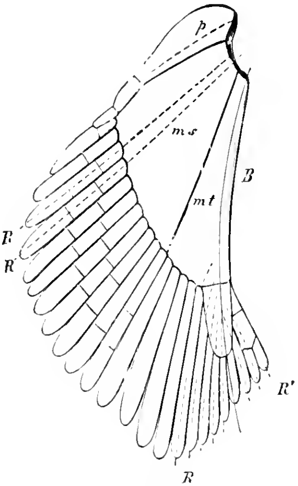

FIG. 407.

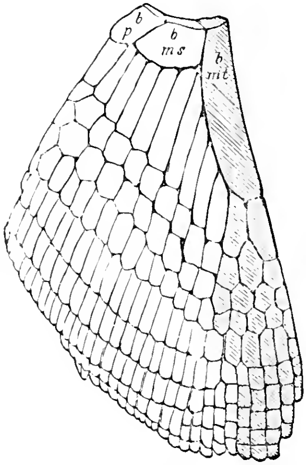

FIG. 408.

FIG. 406.—**Skeleton of the breast-fin of ceratodus** (archipterygium or biserial feathered skeleton). *A*, *B*, cartilaginous series of the fin-stem. *rr* cartilaginous fin-radii. (From *Günther.*)

FIG. 407.—**Skeleton of the breast-fin of an early selachius** *(acanthias).* The radii of the median fin-border *(B)* have disappeared for the most part; a few only *(R)* are left. *R*, *R*, radii of the lateral fin-border, *mt* metapterygium, *ms* mesopterygium, *p* propterygium. (From *Gegenbaur.*)

FIG. 408.—**Skeleton of the breast-fin of a young selachius.** The radii of the median fin-border have wholly disappeared. The shaded part on the right is the section that persists in the five-fingered hand of the higher vertebrates. (*b* the three basal pieces of the fin: *mt* metapterygium, rudiment of the humerus, *ms* mesopterygium, *p* propterygium.) (From *Gegenbaur.*)

and are lost, for the most part, on the other side of the fin-rod as well (the lighter cartilages in Fig. 408). Only the four lowest radii (shaded in the illustration) are preserved; and these are the four inner toes of the foot (first to fourth). The

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[1] The pentadactyl limb of the four higher classes of vertebrates is now explained in the sense that the original fin-rod passes along its outer (ulnar or fibular) side, and ends in the fifth toe. It was formerly believed to go along the inner (radial or tibial) side, and end in the first toe, as Fig. 409 shows.

little or fifth toe is developed from the lower end of the fin-rod. From the middle and upper part of the fin-rod was developed the long stem of the limb—the important radius and ulna (Fig. 409 *r* and *u*) and humerus *(h)* of the higher vertebrates.

In this way the five-toed foot of the amphibia, which we first meet in the Carboniferous stegocephala (Fig. 314), and which was inherited from them by the reptiles on one side and the mammals on the other, was formed by gradual degeneration and differentiation from the many-toed fish-fin (Fig. 411). The reduction of the radii to four was accompanied by a further differentiation of the fin-rod, its transverse segmentation into upper and lower halves, and the formation of the zone of the limb, which is composed originally of three limbs before and behind in the higher vertebrates. The simple arch of the original shoulder-zone divides on each side into an upper (dorsal) piece, the shoulder-blade *(scapula)*, and a lower (ventral) piece; the anterior part of the latter forms the primitive clavicle *(procoracoideum)*, and the posterior part the raven-bone *(coracoideum)*. In the same

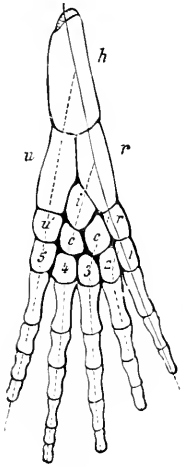

FIG. 409.

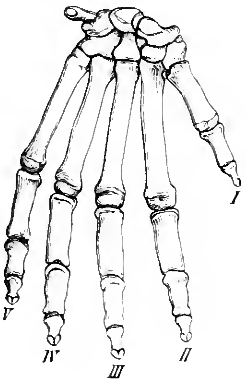

FIG. 410.

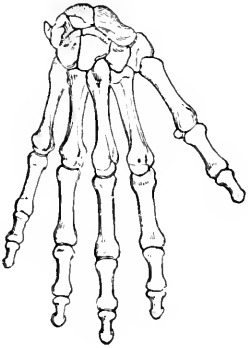

FIG. 411.

FIG. 409.—**Skeleton of the fore leg of an amphibian.** *h* upper-arm (humerus), *ru* lower arm (*r* radius, *u* ulna), *rcicu'* wrist-bones of first series (*r* radiale, *i* intermedium, *c* centrale, *u'* ulnare). *1, 2, 3, 4, 5* wrist-bones of the second series. (From *Gegenbaur.*)

FIG. 410.—**Skeleton of gorilla's hand.** (From *Huxley.*)

FIG. 411.—**Skeleton of human hand,** back. (From *Meyer.*)

way the simple arch of the pelvic zone breaks up into an upper (dorsal) piece, the iliac-bone *(os ilium)*, and a lower (ventral) piece; the anterior part of the latter forms the pubic bone *(os pubis)*, and the posterior the ischial bone *(os ischii)*. Table XLVIII. shows how these three parts of the pelvic zone correspond to those of the scapular zone. The latter has also a fourth bone (originally a covering bone in the skin) in the secondary clavicle *(clavicula)*, which is not found in the former.

There is also a complete agreement between the fore and hind limb in the stem or shaft. The first section of the stem is supported by a single strong bone—the humerus in the fore, the femur in the hind limb. The second section contains two bones: in front the radius *(r)* and ulna *(u)*, behind the tibia and fibula. (Cf. the skeletons in Figs. 314, 319, 324, 333–337, and 420.) The succeeding numerous small bones of the wrist *(carpus)* and ankle *(tarsus)* are also similarly arranged in the fore and hind extremities, and so are the five bones of the middle-hand *(metacarpus)* and middle-foot *(metatarsus)*. Finally, it is the same with the toes themselves, which have a similar characteristic composition from a series of bony pieces before and behind. We find *homodynamism* in all the parts of the fore leg *(carpomela)* and the hind leg *(tarsomela)*.[1]

When we thus learn from comparative anatomy that the skeleton of the human limbs is composed of just the same bones, put together in the same way, as the skeleton in the four high classes of vertebrates, we may at once infer a common descent of them from a single stem-form. This stem-form was the earliest amphibium that had five toes on each foot. It is particularly the outer parts of the limbs that have been modified by adaptation to different conditions. We need only recall the immense variations they offer within the mammal class. We have the slender legs of the deer and the strong springing legs of the kangaroo, the climbing feet

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[1] Homodynamism is the special kind of homology, or the morphological equivalence, that we find in the segments of parts of the body lying consecutively in its long axis.

of the sloth and the digging feet of the mole, the fins of the whale and the wings of the bat. It will readily be granted that these organs of locomotion differ as much in regard to size, shape, and special function as can be conceived. Nevertheless, the bony skeleton is substantially the same in every case. In the different limbs we always find the same characteristic bones in essentially the same, rigidly hereditary connection; this is as splendid a proof of the theory of evolution as comparative anatomy can discover in any organ of the body. (Cf. Plates XXVIII. and XXIX.) It is true that the skeleton of the limbs of the various mammals undergoes many distortions and degenerations besides the special adaptations (Fig. 412). Thus we find the first finger or the thumb atrophied in the fore-foot (or hand) of the dog (II). It has entirely disappeared in the pig (III) and tapir (V). In the ruminants (such as the ox, Fig. IV) the second and fifth toes are also atrophied, and only the third and fourth are well developed (Fig. VI, 3). Nevertheless, all these different fore-feet, as well as the hand of the ape (Fig. 410) and of man (Fig. 411), were originally developed from a common pentadactyle stem-form. This is proved by the rudiments of the degenerated toes, and by the similarity of the arrangement of the wrist-bones in all the pentanomes (Fig. 412 *a–p*). Compare also the carpomela on Plates XXVIII. and the tarsomela on Plate XXIX., and p. 579.

If we candidly compare the bony skeleton of the human arm and hand with that of the nearest anthropoid apes, we find an almost perfect identity. This is especially true of the chimpanzee. In regard to the proportions of the various parts, the lowest living races of men (the Veddahs of Ceylon, Fig. 414) are midway between the chimpanzee (Fig. 413) and the European (Fig. 415). More considerable are the differences in structure and the proportions of the various parts between the different genera of anthropoid apes (Figs. 333–337); and still greater is the morphological distance between these and the lowest apes (the *cynopitheca*). Here, again, impartial and thorough anatomic comparison confirms the accuracy of Huxley's pithecometra principle (p. 399).

The complete unity of structure which is thus revealed by the comparative anatomy of the limbs is fully confirmed by their embryology. This is originally just the same, not only in all the mammals, but in the tetrapods or pentadactyle vertebrates generally, from the earliest amphibia up to man. However different the extremities of the four-footed craniotes may be in their adult state, they all develop from the same rudimentary structure (cf. Plates VIII.–XIII.; *f* fore-leg, *b* hind-leg). In every case the first trace of the limb in the embryo is a very simple protuberance that grows out of the side of the hyposoma. The cells that compose it belong to the skin-fibre layer. The surface is covered with the horny plate, and this is thickened a little at the tip of the protuberance (Plate VI., Fig. 8 *x*). The two anterior protuberances appear a little earlier than the hind ones. These simple structures develop directly into fins in the fishes and dipneusts by differentiation of their cells. In the higher classes of vertebrates each of the four takes the shape in its further growth of a leaf with a stalk, the inner half becoming narrower and thicker and the outer half broader and thinner. The inner half (the stalk of the leaf) then divides into two

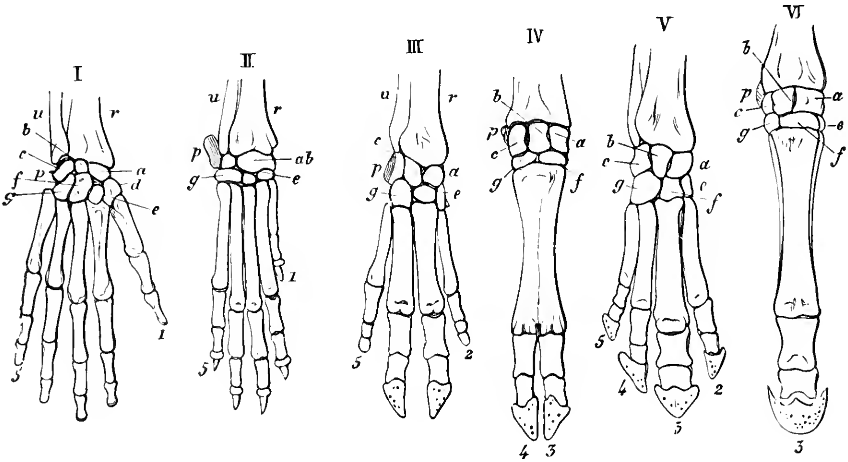

FIG. 412.—**Skeleton of the hand or fore foot** of six mammals. *I* man, *II* dog, *III* pig, *IV* ox, *V* tapir, *VI* horse. *r* radius, *u* ulna, *a* scaphoideum, *b* lunare, *c* triquetrum, *d* trapezium, *e* trapezoid, *f* capitatum, *g* hamatum, *p* pisiforme. *1* thumb, *2* index finger, *3* middle finger, *4* ring finger, *5* little finger. (From *Gegenbaur.*)

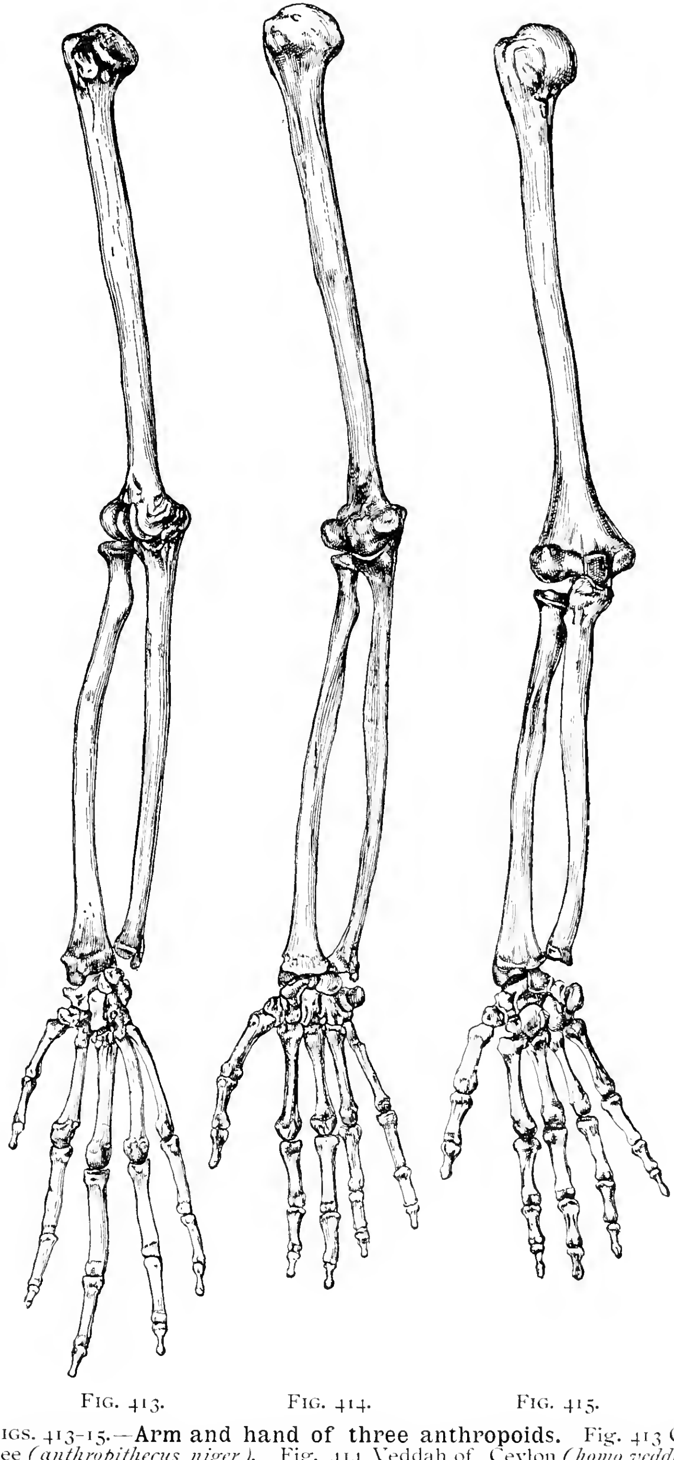

FIG. 413. FIG. 414. FIG. 415.

FIGS. 413-15.—**Arm and hand of three anthropoids.** Fig. 413 Chimpanzee *(anthropithecus niger)*. Fig. 414 Veddah of Ceylon *(homo veddalis)*. Fig. 415 European *(homo mediterraneus)*. (From *Paul* and *Fritz Sarasin*.)

sections—the upper and lower parts of the limb. Afterwards four shallow indentations are formed at the free edge of the leaf, and gradually deepen; these are the intervals between the five toes (Fig. 185). The toes soon make their appearance. But at first all five toes, both of fore and hind feet, are connected by a thin membrane like a swimming-web; they remind us of the original shaping of the foot as a paddling fin. The further development of the limbs from this rudimentary structure takes place in the same way in all the vertebrates according to the laws of heredity; certain groups of the cells of the skin-fibre layer form connective tissue, other groups cartilage, and so on. Muscles, nerves, and blood-vessels grow like peripheral buds from the central structure of the stem (muscle-plates, medullary tube, vascular stems) into the limbs. Like the vertebral column and the skull, the skeletal parts of the limbs are first formed from soft, indifferent cell-groups of the skin-fibre layer. These are afterwards converted into cartilages, and from these we finally get the permanent bones.[1]

The embryonic development of the muscles, or *active* organs of locomotion, is not less interesting than that of the skeleton, or *passive* organs. The two are most closely correlated; and in the phylogeny of both comparative anatomy is more instructive than embryology. The successful research into the comparative myology of the vertebrates of Max Fürbringer, Georg Ruge, Hans Gadow, L. Testut, etc., has shown of late how rich a harvest awaits the workers in this field. But the comparative anatomy and ontogeny of the muscular system are much more difficult and inaccessible, and consequently have hitherto been less studied. We can therefore only draw some general phylogenetic conclusions therefrom.

It is incontestable that the musculature of the vertebrates has been evolved from that of lower invertebrates; and among these we have to consider especially the unarticulated vermalia. They have a simple cutaneous muscular layer,

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[1] But the bones of the human body do not all pass through a cartilaginous stage.

developing from the mesoderm. This was afterwards replaced by a pair of internal lateral muscles, that developed from the middle wall of the cœlom-pouches ; we still find the first rudiments of the muscles arising from the muscle-plate of these in the embryos of all the vertebrates (cf. Plates VI., VII. *mp*, and Figs. 268–275, 361, 362 *mp*). In the unarticulated stem-forms of the chordonia, which we have called the prochordonia, the two cœlom-pouches, and therefore also the muscle-plates of their walls, were not yet segmented. A great advance was made in the articulation of them, as we have followed it step by step in the amphioxus (Figs. 267–272). This metamerism of the muscles was the momentous historical process with which vertebration, and the development of the vertebrate stem, began. The articulation of the skeleton came after this

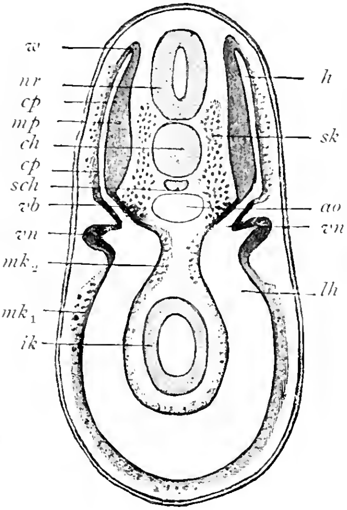

FIG. 416.

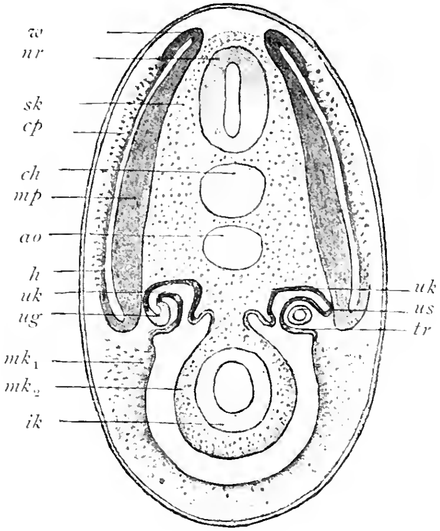

FIG. 417.

FIGS. 416 and 417.—**Transverse sections of shark-embryos** (through the prorenal region). (From *Wijhe* and *Hertwig*.) In Fig. 417 the dorsal primitive-segment cavities (*h*) are already separated from the body-cavity (*lh*), but a little earlier (in Fig. 416) they are still connected. *nr* neural tube, *ch* chorda, *sch* subchordal string, *ao* aorta, *sk* skeletal plate, *mp* muscular plate, *cp* cutis plate, *w* connection of latter (zone of growth), *vn* pronephridia, *ug* prorenal duct, *uk* prorenal canals, *us* point of separation of same, *tr* prorenal funnel, *mk* middle germinal layer (mk_1 parietal, mk_2 visceral), *ik* inner germinal layer (gut-gland layer).

articulation of the muscular system, and the two entered into very close correlation.

The episomites or dorsal cœlom-pouches of the acrania, cyclostomes, and selachii (Fig. 416 *h*) first develop from their inner or median wall (from the cell-layer that lies directly on the skeletal plate [*sk*] and the medullary tube [*nr*]) a strong muscle-plate (*mp*). By dorsal growth (*w*) it also reaches the external or parietal wall of the cœlom-pouches, and proceeds from the dorsal to the ventral wall. From these segmental muscle-plates, which are chiefly concerned in the metamerism of the vertebrates, proceed the lateral muscles of the stem, as we find in the simplest form in the amphioxus (Fig. 236). By the formation of a horizontal frontal septum they divide on each side into an upper and a lower series of myotomes, dorsal and ventral lateral muscles. This is seen with typical regularity in the transverse section of the tail of a fish (Fig. 418). From these earlier lateral muscles of the trunk develop the greater part of the subsequent muscles of the trunk, and also the much later "muscular buds" of the limbs.[1]

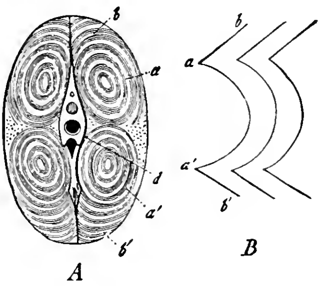

FIG. 418.—**Transverse section of a fish's tail** (from the tunny). (From *Johannes Müller.*) *a* upper (dorsal) lateral muscles, *a'*, *b'* lower (ventral) lateral muscles, *d* vertebral bodies, *b* sections of incomplete conical mantle, *B* attachment lines of the intermuscular ligaments (from the side).

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[1] The ontogeny of the muscles is mostly cenogenetic. The greater part of the muscles of the head (or the visceral muscles) belong originally to the hyposoma of the vertebrate organism, and develop from the wall of the hyposomites or ventral cœlom-pouches. This also applies originally to the primary muscles of the limbs, as these too belong phylogenetically to the hyposoma. (Cf. Chapter XIV.)

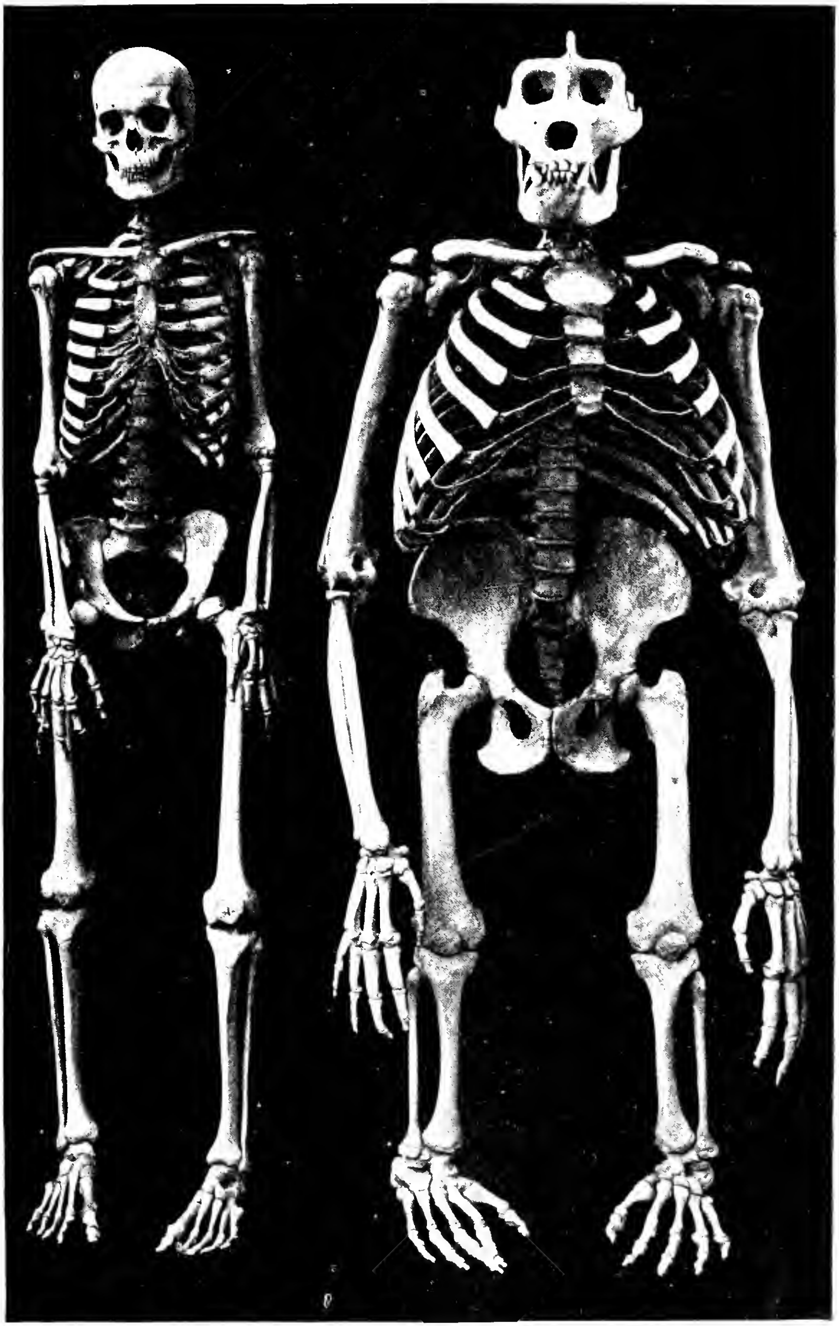

FIG. 419.   FIG. 420.

FIG. 419.—Human skeleton. (Cf. Fig. 391.)
FIG. 420.—Skeleton of the giant gorilla. (Cf. Figs. 243, 244.)

FORTY-NINTH TABLE

SYNOPSIS OF THE PHYLOGENY OF THE HUMAN SKELETON

1. First period: **Prochordonia-skeleton.**

The skeleton is formed solely by the chorda dorsalis.

2. Second period: **Acrania-skeleton.**

A mesodermic perichorda is formed about the chorda; its dorsal continuation forms an envelope for the medullary tube.

3. Third period: **Cyclostoma-skeleton.**

At the anterior end of the chorda a cartilaginous primordial skull is formed from the perichorda. An external cartilaginous branchial skeleton is formed about the gills.

4. Fourth period: **Proselachii-skeleton.**

A primitive vertebral column is formed about the chorda. Remnants of the external branchial skeleton persist beside the internal. Two pairs of limbs with biserial skeleton appear.

5. Fifth period: **Selachii-skeleton.**

The anterior branchial arches are converted into labial cartilages and mandibular arches. The external branchial skeleton is lost.

6. Sixth period: **Ganoid-skeleton.**

The vertebral bodies are formed. The cranium is partly ossified; also the scapular and pelvic zones. The skeleton of the two pairs of fins becomes uniserial.

7. Seventh period: **Dipneust-skeleton.**

The ossification of the facial skull and the limbs advances (paladipneusta).

8. Eighth period: **Amphibia-skeleton.**

The branchial arches are converted into parts of the hyoid bone and the mandibular apparatus. On the uniserial skeleton of the fins the radii are reduced to four, thus giving rise to the pentadactyle foot (stegocephala).

9. Ninth period: **Reptile-skeleton.**

The bony skull developes further; the bony palate separates the mouth and nasal cavities (proreptilia).

10. Tenth period: **Monotreme-skeleton.**

Vertebral column and skull, especially mandibular apparatus and the skeleton of the limbs, attain the characteristic mammalian features.

11. Eleventh period: **Marsupial-skeleton.**

The coracoid bone at the scapular zone degenerates, and its relic blends with the scapula.

12. Twelfth period: **Prosimian-skeleton.**

The marsupial bones are lost. The limbs are adapted to climbing.

13. Thirteenth period: **Anthropoid-skeleton.**

The skeleton assumes the form that is peculiar to man and the anthropoids.

FIFTIETH TABLE

SYNOPSIS OF THE PHYLOGENY OF THE HUMAN MUSCLES

1. First period: **Platode-muscles** *(turbellaria)*.

A simple primary cutaneous muscular layer developes from the mesoderm, directly underneath the skin.

2. Second period: **Vermalia-muscles** *(prochordonia)*.

From the wall of the two cœlom-pouches a couple of simple unsegmented stem-muscles are developed.

3. Third period: **Acrania-muscles** *(amphioxus)*.

By the segmentation of the cœlom-pouches the simple stem-muscles break up into a double row of muscular segments, separated by connective-tissue membranes or myocommata: lateral muscles.

4. Fourth period: **Cyclostome-muscles** *(petromyzon)*.

By the formation of the horizontal frontal septum each lateral muscle divides into a dorsal and vental lateral muscle.

5. Fifth period: **Fish-muscles** *(selachii)*.

To the trunk-muscles of the cyclostomes are added the visceral muscles of the branchial arches and the muscular apparatus of the pairs of fins. Three different stages of their development from hyposomites are seen in the selachii, ganoids, and dipneusts.

6. Sixth period: **Amphibia-muscles** *(stegocephala)*.

With the transformation of the polydactyle fin into the pentadactyle foot we get a manifold articulation of the muscles of the limbs, corresponding to the differentiation of their skeleton.

7. Seventh period: **Reptile-muscles** *(hatteria)*.

As a branch of the amphibia becomes the stem-form of the amniotes, and abandons branchial respiration, there is atrophy of the branchial muscles and a further development of the pulmonary.

8. Eighth period: **Mammal-muscles** *(echidna)*.

As the mandibular apparatus of the proreptiles changes into that of the promammals, the skull enters into close connection with the mandibular-palate apparatus. The muscles that served for the working of these skeletal parts undergo a corresponding change. The diaphragm becomes fully formed.

9. Ninth period: **Simian-muscles** *(semnopithecus)*.

By the adaptation of the lemurs and apes to arboreal habits the muscles inherited from their earlier mammal ancestors suffer those modifications (especially in the limbs) that characterise the primates.

10. Tenth period: **Anthropoid-muscles** *(gorilla)*.

As the anthropoid apes adopt the upright position we get the differentiation in the structure of the limbs (skeleton and muscles) that characterises man and the anthropoids.

CHAPTER XXVII.

THE EVOLUTION OF THE ALIMENTARY SYSTEM

Primitive gut and primitive mouth of the gastrula. Its homology in all the metazoa. General survey of the structure of the adult human alimentary canal. Mouth. Pharynx. Œsophagus. Trachea and lungs. Larynx. Stomach. Small intestine. Liver and duodenum. Pancreas. Large intestine. Rectum. The first trace of the rudimentary gut-tube. Gastrula of the amphioxus and the craniotes. Severance of the embryo from the embryonic vesicle (gastrocystis). Primitive gut and permanent gut. Secondary formation of mouth and anus from the skin. Origin of the visceral epithelium from the gut-gland layer, and of all other parts of the gut from the gut-fibre layer. Simple gastric tube of the gastræads. Platodes and helmintha. Division of the primitive gut-tube into respiratory and digestive gut. Head-gut (branchial gut) and trunk-gut (hepatic gut) in the enteropneusts, the amphioxus, and the ascidian. Origin and significance of the gill-clefts. Their disappearance. Branchial arches and mandibular skeleton. Formation of the teeth. Origin of the lungs from the floating bladder of the fishes. Hypobranchial groove. Differentiation of the stomach. Origin of the liver and the pancreas. Differentiation of the small and large intestines. Bladder. Cloaca.

THE chief of the vegetal organs of the human frame, to the evolution of which we now turn our attention, is the alimentary canal. The gut is the oldest of all the organs of the metazoic body, and it leads us back to the earliest age of organological differentiation—to the first section of the Laurentian period. As we have already seen, the result of the first division of labour among the homogeneous cells of the earliest multicellular animal body was the formation of an alimentary cavity. The first duty and first need of every organism is self-preservation. This is met by the functions of the nutrition and the covering of the body. When, therefore, in the primitive globular *blastæa* (the phylogenetic existence of which is proved to-day by the embryonic form of the *blastula*) the homogeneous blastodermic cells began to effect a division of labour, they had first to meet this twofold need. One half were converted into alimentary cells and enclosed a digestive cavity, the gut. The other half became covering cells, and formed an envelope round the alimentary tube and about the whole body. Thus arose the primary germinal layers—the inner, alimentary, or vegetal layer, and the outer, covering, or animal layer. (Cf. p. 312–19.)

When we try to construct an animal frame of the simplest conceivable type, that has some such primitive alimentary canal and the two primary layers constituting its wall, we inevitably come to the very remarkable embryonic form of the gastrula, which we have found with extraordinary persistence throughout the whole range of animals, with the exception of the unicellulars—in the sponges, cnidaria, platodes, vermalia, molluscs, articulates, echinoderms, tunicates, and vertebrates. In all these stems the gastrula recurs in the same very simple form (Fig. 421). Its whole body is really only a double-walled gastric sac; the rudimentary body-cavity is the digestive cavity, the primitive gut *(progaster, g)*; its simple opening is the primitive mouth *(prostoma, o)*; it is at once mouth and anus. The two strata of cells that compose its wall are the primary germinal layers: the inner or vegetal is the gut-layer *(entoderma* or *endoblast, i)*; the

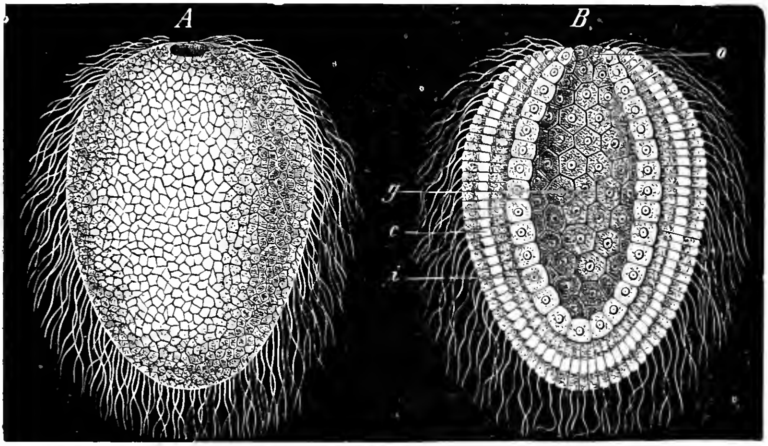

FIG. 421.—**Gastrula of a sponge** *(olynthus)*. *A* from without, *B* longitudinal section through the axis. *g* primitive gut *(progaster* or *archenteron)*, *o* primitive mouth *(prostoma* or *blastoporus)*, *i* gut-layer *(entoderm)*, *c* skin-layer *(ectoderm)*.

outer, nutritive, animal layer (also the agent of locomotion through its vibratory hairs) is the skin-layer (*ectoderma* or *ectoblast*, *e*). It is certainly a remarkable fact that the gastrula is found in various animals as a larva-stage in their individual development, and that this gastrula, though much disguised by cenogenetic modifications, has everywhere essentially the same palingenetic structure (Figs. 32–37). The elaborate alimentary canal of the higher animals developes ontogenetically from the same simple primitive gut of the *gastrula*.

When I first advanced this gastræa theory in 1872, in my *Monograph on the Sponges*, and claimed that the primitive gut and its aperture, the primitive mouth, were the common primitive organs of all the metazoa, my opinion met with the most lively opposition. However, it is now accepted by nearly all zoologists, after a long and stubborn contest. It was first supported and partly modified by Professor Ray-Lankester; he proposed three years afterwards (in his essay on the development of the molluscs, 1875) to give the name of *archenteron* to the primitive gut and *blastoporus* to the primitive mouth. These names are very frequently used. From the homology of the primitive gut we deduce two important conclusions in connection with phylogeny—one of a general and one of a specific character. The general one is the inductive conclusion, and runs: The very varied alimentary canal of the different metazoa has been developed phylogenetically from one and the same very simple primitive gut of the gastræa, the common stem-form that is still reproduced by the gastrula in accordance with the biogenetic law. The interesting *gastræads* of our day (Fig. 287) retain permanently this primitive type of the metazoa. Our special conclusion is deductive, and runs: The human alimentary canal, as a whole, is homologous to that of all other animals; it has the same original significance, and has proceeded historically from the same gastræa-type (Fig. 287).

Before we follow the development of the human alimentary canal in detail, it is necessary to say a word about the general features of its composition in the fully-developed man.

(Cf. Table LI., and Plates VI. and VII.) The mature alimentary canal in man is constructed in all its main features like that of all the higher mammals, and particularly resembles that of the catarrhines, the narrow-nosed apes of the Old World. The entrance into it is the mouth (Plate VII., Fig. 16 *o*). Food and drink enter by it into the mouth-cavity, at the base of which is the tongue. It is armed with thirty-two teeth, fixed in rows in the upper and lower jaws. As we have seen, our dentition is exactly the same as that of the catarrhines, and differs from that of all other animals (p. 625). Above the mouth-cavity is the double nasal cavity; they are separated by the palate-wall. But we saw that this separation is not there from the first, and that originally there is a common mouth-nasal cavity in the embryo; and this is only divided afterwards by the hard palate into two—the nasal cavity above and that of the mouth below (Fig. 374). The nasal cavity is connected with certain air-filled osseous cavities—mandibular cavities in the upper jaw, frontal cavities in the frontal bone, and cuneiform cavities in the cuneiform bone. Into the mouth open a number of glands of different kinds, especially several small mucous glands and the three larger pairs of salivary glands.

At the back the cavity of the mouth is half closed by the vertical curtain that we call the soft palate, in the middle of which is the uvula. A glance into a mirror with the mouth wide open will show its shape. The uvula is interesting because, besides man, it is only found in the ape. At each side of the soft palate are the tonsils. Through the curved opening that we find underneath the soft palate we penetrate into the gullet or pharynx behind the mouth-cavity (Plate VII., Fig. 16 *sh*). Into this opens on either side a narrow canal (the Eustachian tube), through which we can get direct into the tympanic cavity of the ear (Fig. 383 *e*). The pharynx is continued in a long, narrow tube, the œsophagus *(sr)*. By this the food passes into the stomach when masticated and swallowed. Into the gullet also opens, right above, the trachea *(lr)*, that leads to the lungs. The entrance to it is covered by the epiglottis, over which the food slides. The cartilaginous epiglottis is found only in the mammals, and has developed from the fourth branchial arch of the fishes and amphibia. The respiratory organs, or lungs (Plate VI., Fig. 9 *lu*), are found, in man and all the mammals, to the right and left in the pectoral cavity, with the heart between them (Fig. 9 *hr; hl*). At the upper end of the trachea there is, under the epiglottis, a specially differentiated part, strengthened by a cartilaginous skeleton, the larynx. This important organ of human speech also developes from a part of the alimentary canal. In front of the larynx is the thyroid gland *(thyreoidea)*, which sometimes enlarges and forms goitre *(struma)*.

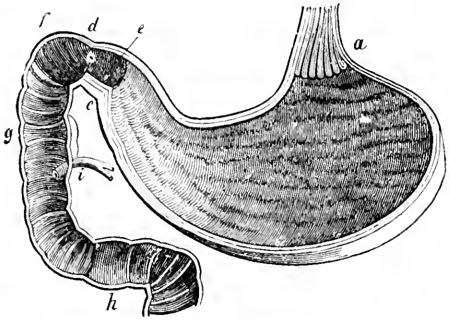

FIG. 422.—**Human stomach and duodenum,** longitudinal section. *a* cardia (end of œsophagus), *b* fundus (blind sac of the left side), *c* pylorus-fold, *d* pylorus-valves, *e* pylorus-cavity, *fgh* duodenum, *i* entrance of the gall-duct and the pancreatic duct. (From *Meyer*.)

The œsophagus descends into the pectoral cavity along the vertebral column, behind the lungs and the heart, pierces the diaphragm, and enters the visceral cavity. The diaphragm (Plate VII., Fig. 16 *z*) is a membrano-muscular partition that completely separates the thoracic (c') from the abdominal (c'') cavity in all the mammals (and these alone). This separation is not found in the beginning; there is at first a common breast-belly cavity, the cœloma or pleuroperitoneal cavity. The diaphragm is formed later on as a muscular horizontal partition between the thoracic and abdominal cavities. It then completely separates the two cavities, and is only pierced by several organs that pass from the one to the other. One of the chief of these organs is the œsophagus. After this has passed through the diaphragm, it expands into the gastric sac in which digestion chiefly takes place. The stomach of the adult man (Fig. 422, Plate VII., Fig. 16 *mg*) is a long, somewhat oblique sac, expanding on the left into a blind sac, the fundus of the stomach *(b')*, but narrows on the right, and passes at the pylorus *(e)* into the small intestine. At this point there is a valve, the pyloric valve *(d)*, between the two sections of the canal; it opens only when the pulpy food passes from the stomach into the intestine. In man and the higher vertebrates the stomach itself is the chief organ of digestion, and is especially occupied with the solution of the food; this is not the case in many of the lower vertebrates, which have no stomach, and discharge its function by a part of the gut farther on. The muscular wall of the stomach is comparatively thick; it has externally strong muscles that accomplish the digestive movements, and internally a large quantity of small glands, the peptic glands, which secrete the gastric juice.

Next to the stomach comes the longest section of the alimentary canal, the middle gut or small intestine *(chylogaster)*. Its chief function is to absorb the peptonised fluid mass of food, or the chyle, and it is sub-divided into several sections, of which the first (next to the stomach) is called the duodenum (Fig. 422, *fgh*). It is a short, horseshoe-shaped loop of the gut. The largest glands of the alimentary canal open into it—the liver *(hepar)*, the chief digestive gland, that secretes the gall, and the pancreas, which secretes the pancreatic juice. The two glands pour their secretions, the bile and pancreatic juice, close together into the duodenum *(i)*. The opening of the gall-duct is of particular phylogenetic importance, as it is the same in all the vertebrates, and indicates the principal point of the hepatic or trunk-gut (Gegenbaur). The liver, phylogenetically older than the stomach, is a large gland, rich in blood, in the adult man, immediately under the diaphragm on the left side, and separated by it from the lungs (Plate VII., Fig. 16 *lb*). The pancreas lies a little further back and more to the left (Fig. 16 *p*). The remaining part of the small intestine is so long that it has to coil itself in many folds in order to find room in the narrow space of the abdominal cavity. It is divided into the jejunum above and the ileum below. In the last section of it is the part of the small intestine at which in the embryo the yelk-sac opens into the gut (Plate VII., Fig. 15 *dd*). This long and thin intestine then passes into the large intestine, from which it is cut off by a special valve. Immediately behind this "Bauhin-valve" the first part of the large intestine forms a wide, pouch-like structure, the cœcum. The atrophied end of the cœcum is the famous rudimentary organ, the vermiform appendix *(processus vermiformis*, p. 87). The large intestine *(colon)* consists of three parts—an ascending part on the right, a transverse middle part, and a descending part on the left. The latter finally passes through an S-shaped bend into the last section of the alimentary canal, the rectum, which opens behind by the anus (Plate VII., Fig. 16 *a*). Both the large and small intestines are equipped with numbers of small glands, which secrete mucous and other fluids.

For the greater part of its length the alimentary canal is attached to the inner dorsal surface of the abdominal cavity, or to the lower surface of the vertebral column. The fixing is accomplished by means of the thin membranous plate that we call the mesentery, and that developes immediately under the chorda from the gut-fibre layer, at the point where it bends into the outer plate of the lateral layer, the skin-fibre layer (Figs. 148–151 ; Plate VI., Fig. 8 *t*). This point is known as the middle plate (Fig. 141 *mp*). The mesentery is very short at first (Plate VII., Fig. 14 *g*) ; but in the middle of the alimentary canal it presently lengthens considerably, and forms a thin, transparent, membranous plate, which has to grow in proportion as the loops of the gut remove from their original point of attachment to the vertebral column. In this mesenteric plate we find the blood-vessels, lymph-vessels, and nerves that reach the alimentary canal.

Although the fully-formed alimentary canal is thus a very elaborate organ, and although in detail it has a quantity of complex structural features into which we cannot enter here, nevertheless the whole complicated structure has been historically evolved from the very simple form of the primitive gut that we find in our gastræad ancestors, and that every gastrula brings before us to-day. We have already pointed out (Chapter IX.) how the epigastrula of the mammals (Fig. 70) can be reduced to the original type of the bell-gastrula, which is now preserved by the amphioxus alone (Fig. 258). Like the latter, the human gastrula and that of all other mammals must be regarded as the ontogenetic reproduction of the phylogenetic form that we call the gastræa, and in which the whole body is nothing but a double-walled gastric sac.

The peculiar way in which man's complex alimentary canal developes from the simple gastrula, and which is like that of the other mammals, can only be properly understood when it is examined in the light of phylogeny. In compliance with this we must distinguish between the original, primary gut of the acrania and the modified secondary gut of the craniotes. The gut of the amphioxus (the representative of the acrania) does not form a yelk-sac, and developes palingenetically from the whole of the primitive gut of the gastrula. On the other hand, the gut of the craniotes has a modified cenogenetic development, and quickly divides into two parts—the permanent secondary gut *(metagaster)*, from which alone the various parts of the differentiated enteric system are developed, and the transitory yelk-sac, which is merely a kind of food-store for the developing fœtus *(lecithoma*, Fig. 108). The yelk-sac is most developed in the selachii, teleostei, reptiles, and birds. It atrophies in the mammals, especially in most of the placentals. The peculiar gut-development of the cyclostomes, ganoids, dipneusts, and amphibia is an intermediate form between the palingenetic type of the acrania and the cenogenetic embryology of the amniotes.

We already know from embryology the manner in which the gut developes in the embryo of man and the other mammals. From the gastrula is first formed the spherical embryonic vesicle filled with fluid (*gastrocystis*, Fig. 109). In the dorsal wall of this the sole-shaped embryonic shield is developed, and on the under-side of this a shallow groove appears in the middle line, the first trace of the later, secondary alimentary tube. The gut-groove becomes deeper and deeper, and its edges bend towards each other, and finally form a tube (Fig. 108). The wall of this secondary tube consists of two membranes, the inner gut-gland layer and the outer gut-fibre layer. The tube is quite closed at first, and merely has an opening in the middle of its lower wall by which it communicates with the embryonic vesicle (Plate VII., Fig. 14). The latter becomes smaller and smaller as the development of the alimentary canal proceeds. At first the tube seems to be a small appendage at one side of the large vesicle (Fig. 209); afterwards it is the remnant of the vesicle that looks like an insignificant appendage of the large alimentary canal. This appendage is the yelk-sac or umbilical vesicle. In time it loses all significance and shrivels up, the original central opening in the gut being closed and the intestinal navel being formed at the point (cf. Figs. 221–225).

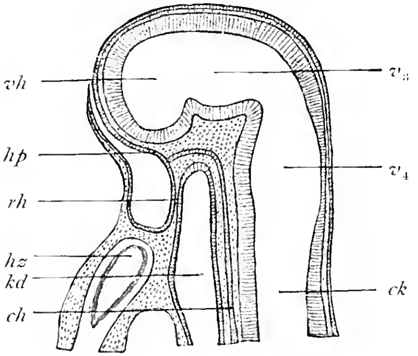

Fig. 423.—**Median section of the head of a hare-embryo,** six mm. in length. (From *Mihalcovics*.) The deep mouth-cleft *(hp)* is separated by the membrane of the throat *(rh)* from the blind cavity of the head-gut *(kd)*. *hz* heart, *ch* chorda, *hp* the point at which the hypophysis developes from the mouth-cleft, *vh* ventricle of the cerebrum, v_3 third ventricle (intermediate brain), v_4 fourth ventricle (hind brain), *ck* spinal canal.

As we have seen, this simple cylindrical gut-tube is at first completely closed before and behind in man and in the vertebrates generally (Fig. 153; Plate VII., Fig. 14); the permanent openings of the alimentary canal, the mouth and anus, are only formed later on, and from the outer skin. A mouth-pit appears in the skin in front (Fig. 423 *hp*), and this grows towards the blind fore end of the cavity of the head-gut *(kd)*, and at length breaks into it. In the same way a shallow anus-pit is formed in the skin behind, which grows deeper and deeper, advances towards the blind hinder end of the pelvic gut, and at last connects with it. There is at first, both before and behind, a thin partition between the external cutaneous pit and the blind end of the gut—the throat-membrane in front and the anus-membrane behind; these disappear when the connection takes place.

Directly in front of the anus-opening the allantois developes from the hind gut; this is the important embryonic structure that forms into the placenta in the placentals (including man, Fig. 211 *p;* Plate VII., Fig. 14 *al*). In this more advanced form the human alimentary canal (and that of all the other mammals) is a slightly bent, cylindrical tube, with an opening at each end, and two appendages growing from its lower wall: the anterior one is the umbilical vesicle or yelk-sac, and the posterior the allantois or uninary sac (Fig. 224).

The thin wall of this simple alimentary tube and its ventral appendages is found, on microscopic examination, to consist of two strata of cells. The inner stratum, lining the entire cavity, consists of larger and darker cells, and is the gut-gland layer. The outer stratum consists of smaller and lighter cells, and is the gut-fibre layer. The only exception is in the cavities of the mouth and anus, because these originate from the skin. The inner coat of the mouth-cavity is not provided by the gut-gland layer, but by the skin-sense layer; and its muscular substratum is provided, not by the gut-fibre, but the skin-fibre, layer. It is the same with the wall of the small anus-cavity (Plate VII., Fig. 15).

If it is asked how these constituent layers of the primitive gut-wall are related to the various tissues and organs that we find afterwards in the fully-developed system, the answer is very simple. It can be put in a single sentence. The epithelium of the gut—that is to say, the internal soft stratum of cells that lines the cavity of the alimentary canal and all its appendages, and is immediately occupied with the processes of nutrition, is formed solely from the gut-gland layer; all other tissues and organs that belong to the alimentary canal and its appendages originate from the gut-fibre layer. From the latter is also developed the whole of the outer envelope of the gut and its appendages; the fibrous connective tissue and the smooth muscles that compose its muscular layer, the cartilages that support it (such as the cartilages of the larynx and the trachea), the blood-vessels and lymph-vessels that absorb the nutritive fluid from the intestines—in a word, all that there is in the alimentary system besides the epithelium of the gut. From the same layer we also get the whole of the mesentery, with all the organs embedded in it—the heart, the large blood-vessels of the body, etc. (Cf. p. 638 and Plate VII., Fig. 16.)

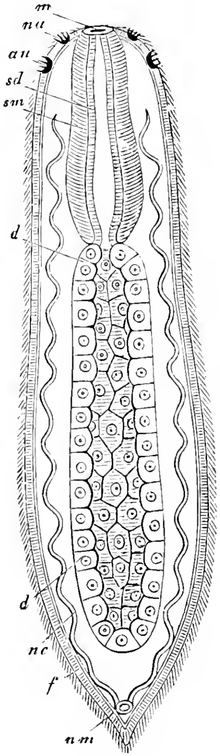

Fig. 424.

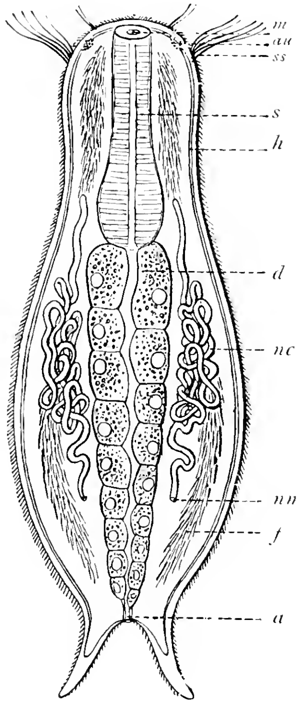

Fig. 425.

Fig. 424.—**A simple turbellarian** (*rhabdocœlum*). *m* mouth, *s* gullet, *sd* gullet-epithelium, *sm* gullet-muscles, *d* stomach, *nc* renal canals, *nm* renal aperture, *au* eye, *na* olfactory pit. (Diagrammatic.)

Fig. 425.—**Chætonotus, one of the simplest vermalian forms,** of the group of the gastrotricha. *m* mouth, *s* gullet, *d* gut, *a* anus, *ss* sensory hairs, *au* eyes, *ms* muscular cells, *h* skin, *f* ciliated ligaments of the ventral surface, *nc* nephridia (water-vessels or excretory organs), *nm* opening of same.

Let us now leave this original structure of the mammal gut for a moment, in order to compare it with the alimentary canal of the lower vertebrates, and of those invertebrates that we have recognised as man's ancestors. We find, first of all, in the lowest metazoa, the gastræads, that the gut remains permanently in the very simple form in which we find it transitorily in the palingenetic gastrula of the other animals; it is thus in the gastremaria *(pemmatodiscus)*, the physemaria *(prophysema)*, the simplest sponges *(olynthus)*, the fresh-water polyps *(hydra)*, and the *ascula*-embryos of many other cœlenteria (Figs. 287–292). Even in the simplest forms of the platodes, the rhabdocœla (Fig. 424), the gut is still a simple straight tube, lined with the entoderm; but with the important difference that in this case its single opening, the primitive mouth *(m)*, has formed a muscular gullet *(sd)* by invagination of the skin.

We have the same simple form in the gut of the lowest vermalia (gastrotricha, Fig. 425, nematodes, sagitta, etc.). But in these a second important opening of the gut has been formed at the opposite end to the mouth, the anus (Fig. 425 *a*).

We see a great advance in the structure of the vermalian gut in the remarkable *balanoglossus* (Fig. 426), the sole survivor of the enteropneust class. Here we have the first appearance of the division of the alimentary tube into two sections that characterises the chordonia. The fore half, the head-gut *(cephalogaster)*, becomes the organ of respiration (branchial gut, Fig. 426 *k*); the hind half, the trunk-gut *(truncogaster)*, alone acts as digestive organ (hepatic gut, *d*). The morphological and physiological differentiation of these two parts of the gut in the enteropneust is just the same as in all the tunicates and vertebrates; it is the more important, as in every case there are at first only a pair of gill-clefts in the head-gut, and as the middle line of its ventral wall has a ciliated glandular groove in all three groups (Fig. 300).

It is particularly interesting and instructive in this connection to compare the enteropneusts with the ascidia and the amphioxus (Figs. 427, 428)—the remarkable animals that

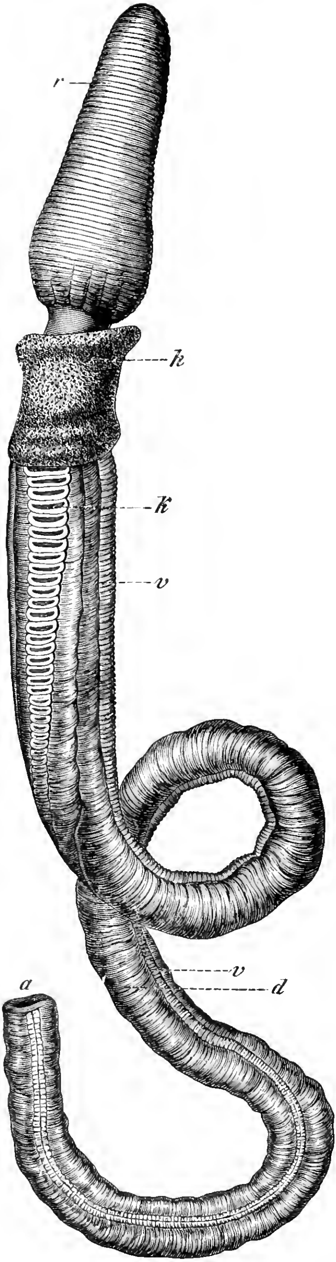

FIG. 426.

FIG. 426.—**A young enteropneust** *(balanoglossus).* (From *Alexander Agassiz.*) *r* acorn-shaped snout, *h* neck, *k* branchial clefts and arches of the fore gut, in long rows on each side, *d* digestive hind gut, occupying the greater part of the body cavity, *v* intestinal vein or ventral vessel, lying between two parallel folds of the skin, *a* anus.

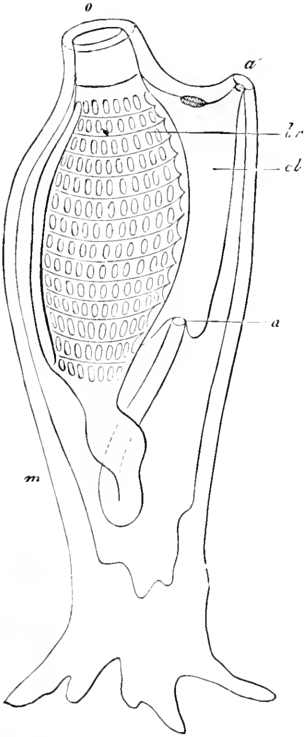

FIG. 427.

FIG. 427.—**Organisation of an ascidian** (left view as in Plate XIX., Fig. 14); the back is turned to the right, the belly to the left, the mouth *(o)* above; at the tail-end the ascidian is attached. The branchial gut *(br)*, pierced by a number of clefts, continues in the digestive gut below. The rectum opens at the anus *(a)* into the mantle-cavity *(cl)*, from which the excrements are ejected with the breathing-water through the branchial pore or cloaca *(a')*. *m* mantle. (From *Gegenbaur.*)

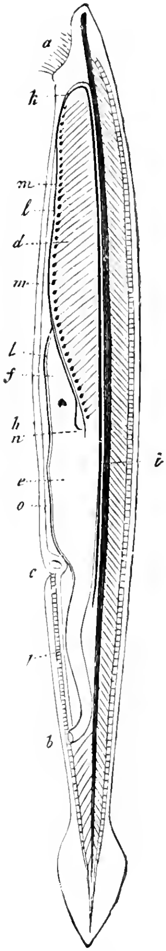

FIG. 428.

FIG. 428.—**The lancelet** *(amphioxus lanceolatus)*, twice natural size, seen from the left (the long axis is vertical; the mouth is above, the tail-end below, as in Plate XIX., Fig. 15). *a* mouth, surrounded by threads of beard, *b* anus, *c* branchial pore, *d* gill pannier, *e* stomach, *f* liver, *g* small intestine, *h* branchial cavity, *i* chorda (axial rod), underneath it the aorta, *k* aortic arches, *l* trunk of the branchial artery, *m* bulbs on its branches, *n* vena cava, *o* intestinal vein.

form the connecting link between the invertebrates and the vertebrates. In both forms the gut is of substantially the same construction; the anterior section forms the respiratory branchial gut, the posterior the digestive hepatic gut. In both it developes palingenetically from the primitive gut of the gastrula (Plate XVIII., Figs. 4, 10), and in both the hinder end of the medullary tube covers the primitive mouth to such an extent that the remarkable medullary intestinal duct is formed, the passing communication between the neural and intestinal tubes *(canalis neurentericus*, Figs. 86, 88 *ne)*. In the vicinity of the closed primitive mouth, possibly in its place, the later anus is developed. In the same way the mouth is a fresh formation in the amphioxus and the ascidian. It is the same with the human mouth and that of the craniotes generally. The secondary formation of the mouth in the chordonia is probably connected with the development of the gill-clefts which are formed in the gut-wall immediately behind the mouth. In this way the anterior section of the gut is converted into a respiratory organ. I have already pointed out that this modification is distinctive of the vertebrates and tunicates. The phylogenetic appearance of the gill-clefts indicates the commencement of a new epoch in the stem-history of the vertebrates.

Moreover, in the further ontogenetic development of the alimentary canal in the human embryo the appearance of the gill-clefts is the most important process. At a very early stage the gullet-wall joins with the external body-wall in the head of the human embryo, and this is followed by the formation of four clefts, which lead directly into the gullet from without, on the right and left sides of the neck, behind the mouth. These are the gill or gullet-clefts, and the partitions that separate them are the gill or gullet-arches (Fig. 181, Plates I. and XXIV., and Plate VII., Fig. 15 *ks*).

These are most interesting embryonic structures. They show us that all the higher vertebrates reproduce in their earlier

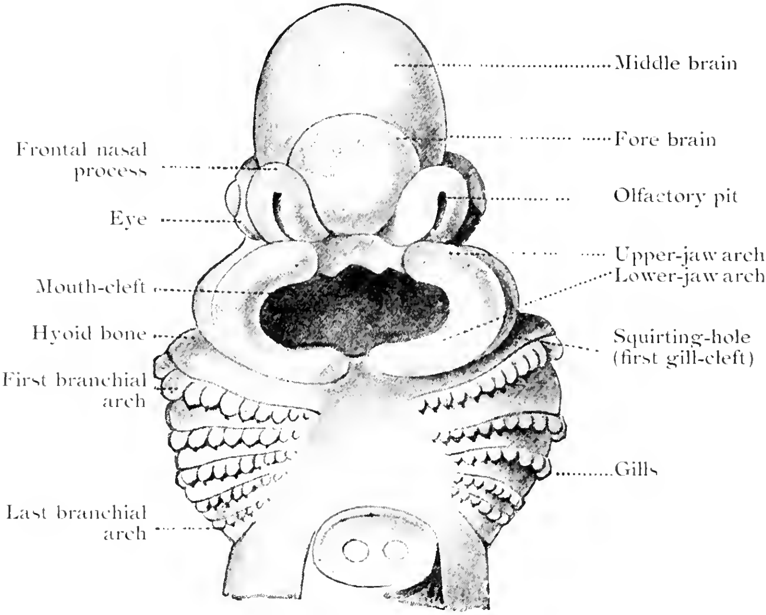

FIG. 429.—**Head of a shark-embryo** *(pristiurus)*, eight mm. in length, magnified twenty times. (From *Parker*.) Left view.

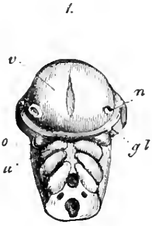

FIG. 430.

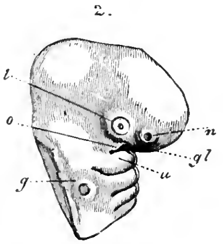

FIG. 431.

FIGS. 430 and 431.—**Head of a chick-embryo,** three days old. Fig. 430 from the front, Fig. 431 from the right. *n* rudimentary nose (olfactory pit), *l* rudimentary eye (optic pit, lenticular cavity), *g* rudimentary ear (auscultory pit), *v* fore brain, *gl* eye-clefts. Of the three pairs of branchial arches the first has been converted into an upper-jaw process *(o)* and a lower-jaw process *(u)*. (From *Kölliker*.)

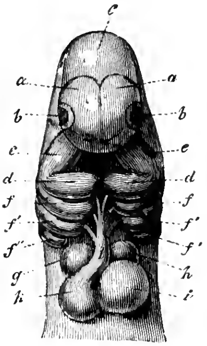

FIG. 432.

FIG. 432.—**Head of a dog-embryo,** from the front. *a* the lateral halves of the foremost cerebral vesicle, *b* rudimentary eyes, *c* middle cerebral vesicle, *de* first pair of branchial arches (*e* upper-jaw process, *d* lower-jaw process), *f, f,' f''* second, third, and fourth pairs of branchial arches, *gkih* heart (*g* right, *h* left auricle; *i* left, *k* right ventricle), *l* source of the aorta with three pairs of aortic arches, which go to the branchial arches. (From *Bischoff*.)

stages, in harmony with the biogenetic law, the process that had so important a part in the rise of the whole chordonia-stem. This process was the differentiation of the gut into two sections—an anterior respiratory section, the branchial gut, that was restricted to breathing (head-gut, *cephalogaster*, or *branchienteron)*, and a posterior digestive section, the hepatic gut (trunk-gut, *truncogaster*, or *hepatenteron)*. As we find this highly characteristic differentiation of the gut into two physiologically quite different sections in all the vertebrates and all the tunicates, we may conclude that it was also found in their common ancestors, the prochordonia—especially as even the enteropneusts have it. (Cf. pp. 260, 348, 548, and Figs. 426–428.) It is entirely wanting in all the other invertebrates.

There is at first only one pair of gill-clefts in the amphioxus, as in the ascidia and enteropneusts ; and the copelata (p. 466) have only one pair throughout life. But the number presently increases in the former. In the craniotes, however, it decreases still further. The cyclostomes have six to eight pairs (Fig. 301) ; some of the selachii six to seven pairs, most of the fishes only four to five pairs. In the embryo of man, and the higher vertebrates generally, where they make an appearance at an early stage, only three to four pairs are developed. In the fishes they remain throughout life, and form an exit for the water taken in at the mouth (Figs. 303–305; Plate VII., Fig. 13 *ks*). But they are partly lost in the amphibia, and entirely in the higher vertebrates. In these nothing is left but a relic of the first gill-cleft. This is formed into a part of the auscultory organ ; from it are developed the external meatus, the tympanic cavity, and the Eustachian tube. We have already considered these remarkable structures, and need only point here to the interesting fact that our middle and external ear is a modified inheritance from the fishes. The branchial arches also, which separate the clefts, develop into very different parts. In the fishes they remain gill-arches, supporting the respiratory gill-leaves. It is the same with the lowest amphibia, but in the higher amphibia they undergo various modifications; and in the three higher classes of vertebrates (including man) the hyoid bone and the ossicles of the ear develop from them. (Cf. pp. 704 and 707, and Plates VIII.–XIII.)

From the first gill-arch, from the inner surface of which the muscular tongue proceeds, we get the first structure of the maxillary skeleton—the upper and lower jaw, which surround the mouth and support the teeth. These important parts are wholly wanting in the two lowest classes of vertebrates, the acrania and cyclostoma. They appear first in the earliest selachii (Figs. 302–305), and have been transmitted from this stem-group of the gnathostomes to the higher vertebrates. Hence the original formation of the skeleton of the mouth can be traced to these primitive fishes, from which we have inherited it. The formation of teeth proceeds from the skin that clothes the jaws. As the whole mouth-cavity originates from the outer integument (Fig. 423), the teeth also must come from it. As a fact, this is found to be the case on microscopic examination of the development and finer structure of the teeth. The scales of the fishes, especially of the shark type (Fig. 433), are in the same position as their teeth in this respect (Fig. 306). The osseous matter of the tooth (dentine) developes from the corium; its enamel covering is a secretion of the epidermis that covers the corium. It is the same with the cutaneous teeth or placoid scales of the selachii. At first the whole of the mouth was armed with these cutaneous teeth in the selachii and in the earliest amphibia. Afterwards the formation of them was restricted to the edges of the jaws.

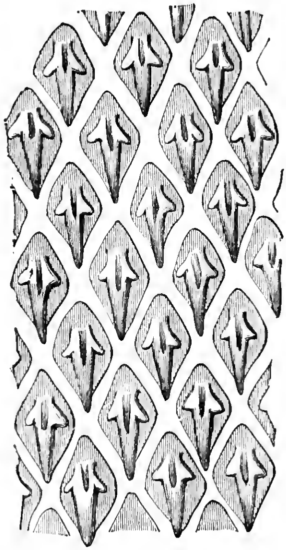

FIG. 433.—**Scales or cutaneous teeth of a shark** (*centrophorus calceus*). A three-pointed tooth rises obliquely on each of the quadrangular bony plates that lie in the corium. (From *Gegenbaur*.)

FIFTY-FIRST TABLE

SYNOPSIS OF THE FORMATION OF THE HUMAN ALIMENTARY SYSTEM

(N.B.—The parts marked thus † are invaginations of the gut.)

I. First section of the alimentary system: **Head-gut** (*cephalogaster*) or **respiratory gut** (*tractus respiratorius*) = **Branchial gut** (*branchienteron*).	1. **Mouth cavity (cavum oris).**	Mouth.	*Rima oris.*	Gut-epithelia formed from **Ectoderm** (horny plate).
		Lips.	*Labia.*	
		Jaws.	*Maxillæ.*	
		Teeth.	*Dentes.*	
		Tongue (part).	*Lingua.*	
		†Salivary glands.	*Glandulæ salivales.*	
		Soft palate.	*Velum palatinum.*	
		Uvula.	*Uvula.*	
	2. **Nasal cavity (cavum nasi).**	Nasal passages.	*Meatus narium.*	
		†Jaw-cavities.	*Sinus maxillares.*	
		†Frontal cavities.	*Sinus frontales.*	
		†Cribriform-bone cavities.	*Sinus ethmoidales.*	
	3. **Pharyngeal cavity (cavum pharyngis).**	Throat.	*Isthmus faucium.*	Gut-epithelia formed from the **Entoderm** (gut-gland layer) (with the exception of the anus, formed from the horny plate).
		Tonsils.	*Tonsillæ.*	
		Pharynx.	*Pharynx.*	
		†Eustachian tube.	*Tuba Eustachii.*	
		†Tympanic cavity.	*Cavum tympani.*	
		Hyoid bone.	*Os hyoides.*	
		†Thyroid gland.	*Thyreoidea.*	
		†Thymus gland.	*Thymus.*	
	4. **Pulmonary cavity (cavum pulmonis).**	†Larynx.	*Larynx.*	
		†Trachea.	*Trachea.*	
		†Lungs.	*Pulmones.*	
II. Second section of the alimentary system: **Trunk-gut** (*truncogaster*) or **digestive gut** (*tractus digestivus*) = **Hepatic gut** (*cholenteron*).	5. **Fore gut (prosogaster).**	Œsophagus.	*Œsophagus.*	
		Cardia.	*Cardia.*	
		Stomach.	*Stomachus.*	
		Pylorus.	*Pylorus.*	
	6. **Middle gut (mesogaster).**	Duodenum.	*Duodenum.*	
		†Liver.	*Hepar.*	
		†Pancreas.	*Pancreas.*	
		Jejunum.	*Jejunum.*	
		Ileum.	*Ileum.*	
		(†Yelk sac or umbilical vesicle.)	(*Vesicula umbilicalis.*)	
	7. **Hind gut (telogaster).**	Colon.	*Colon.*	
		†Cœcum.	*Cæcum.*	
		Vermiform appendix.	*Processus vermiformis.*	
		Rectum.	*Rectum.*	
		Anus.	*Anus.*	
	8. **Urinary gut (urogaster).**	(†Urinary sac.)	(*Allantois.*)	
		†Urethra.	*Urethra.*	
		†Bladder.	*Urocystis.*	

Hence our human teeth are, in relation to their original source, modified fish-scales. For the same reason we must regard the salivary glands, which open into the mouth, as epidermic glands, as they are formed, not from the glandular layer of the gut like the rest of the alimentary glands, but from the epidermis, from the horny plate of the outer germinal layer. Naturally, in harmony with this evolution of the mouth, the salivary glands belong genetically to one series with the sudoriferous, sebaceous, and mammary glands.

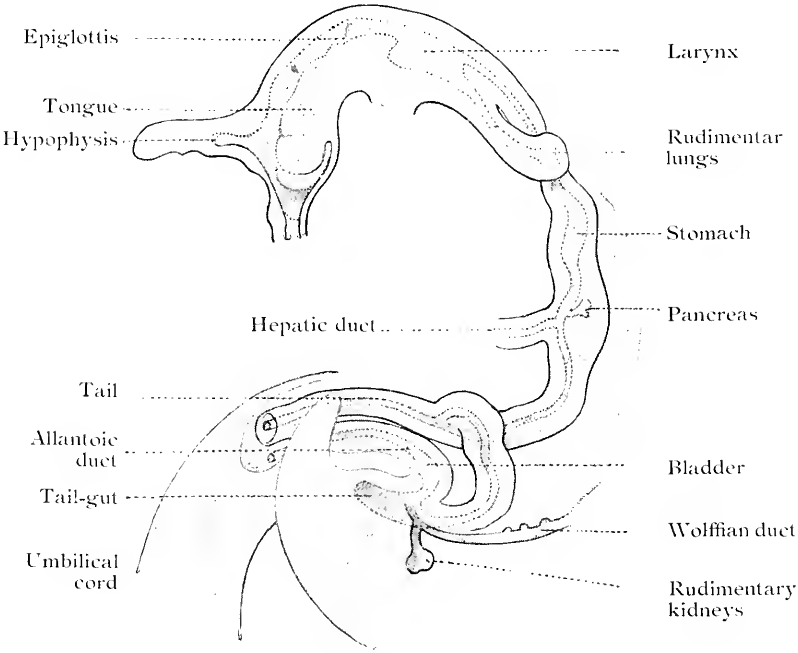

FIG. 434.—**Gut of a human embryo,** 4.1 mm. long, magnified fifteen times. (From *His.*)

Thus the human alimentary canal is as simple as the primitive gut of the gastrula in its original structure. Later it resembles the gut of the earliest vermalia (gastrotricha). It then divides into two sections, a fore or branchial gut and a hind or hepatic gut, like the alimentary canal of the balanoglossus, the ascidian, and the amphioxus. The formation of the jaws and the branchial arches changes it into a real fish-gut *(selachii)*. But the branchial gut, the one reminiscence of our fish-ancestors, is afterwards atrophied as such. The parts of it that remain are converted into entirely different structures.

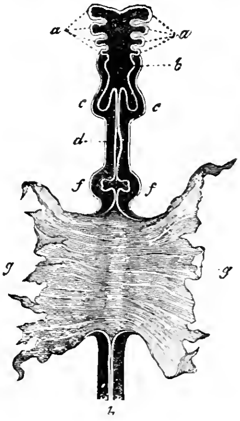

FIG. 435.

FIG. 436.

FIG. 435.—**Gut of a dog-embryo** (shown in Fig. 210, from *Bischoff)*, seen from the ventral side. *a* gill-arches (four pairs), *b* rudiments of pharynx and larynx, *c* lungs, *d* stomach, *f* liver, *g* walls of the open yelk-sac (into which the middle gut opens with a wide aperture), *h* rectum.

FIG. 436.—**The same gut** seen from the right. *a* lungs, *b* stomach, *c* liver, *d* yelk-sac, *e* rectum. (Cf. p. 379.)

But, although the anterior section of our alimentary canal thus entirely loses its original character of branchial gut, it retains the physiological significance of respiratory gut. We are now astonished to find that the permanent respiratory organ of the higher vertebrates, the air-breathing lung, is developed from this first part of the alimentary canal. Our lungs, trachea, and larynx are formed from the ventral wall of the branchial gut. The whole of the respiratory apparatus, which occupies the greater part of the pectoral cavity in the adult man, is at first merely a small pair of vesicles or sacs, which grow out of the floor of the head-gut immediately behind the gills (Figs. 436 *c*, 440 *l;* Plate VII., Figs. 13, 15, 16 *lu*). These vesicles are found in all the vertebrates except the two lowest classes, the acrania and cyclostomes. But in the lower vertebrates they do not develop into lungs, but into a large air-filled bladder, which occupies a good deal of the body-cavity and has a quite different purport. It serves, not for breathing, but to effect vertical swimming movements, and so is a sort of hydrostatic apparatus—the floating bladder of the fishes *(nectocystis*, p. 561). However, the human lungs, and those of all air-breathing vertebrates, develop from the same simple vesicular appendage of the head-gut that becomes the floating bladder in the fishes.

At first this bladder has no respiratory function, but merely acts as hydrostatic apparatus for the purpose of increasing or lessening the specific gravity of the body. The fishes, which have a fully-developed floating bladder, can press it together, and thus condense the air it contains. The air also escapes sometimes from the alimentary canal through an air-duct that connects the floating bladder with the pharynx, and is ejected by the mouth. This lessens the size of the bladder, and so the fish becomes heavier and sinks. When it wishes to rise again, the bladder is expanded by relaxing the pressure. In many of the crossopterygii the wall of the bladder is covered with bony plates, as in the Triassic *undina* (Fig. 307).

This hydrostatic apparatus begins in the dipneusts to change into a respiratory organ; the blood-vessels in the wall of the bladder now no longer merely secrete air themselves, but also take in fresh air through the air-duct. This process reaches its full development in the amphibia. In these the floating bladder has turned into lungs, and the air-passage into a trachea. The lungs of the amphibia have been transmitted to the three higher classes of vertebrates. In the lowest amphibia the lungs on either side are still very simple transparent sacs with thin walls, as in the common water-salamander, the triton. It still entirely resembles the floating bladder of the fishes. It is true that the amphibia have two lungs, right and left. But the floating bladder is also double in many of the fishes (such as the early ganoids), and divides into right and left halves. On the other hand, the lung is single in ceratodus (Fig. 311).

In the human embryo and that of all the other amniotes the lungs develop from the hind part of the ventral wall of the head-gut (Fig. 437). Immediately behind the single structure of the thyroid gland a median groove, the rudiment of the trachea, is detached from the gullet. From its hinder end a couple of vesicles develop—the simple tubular rudiments of the right and left lungs. They afterwards increase considerably in size, fill the greater part of the thoracic cavity, and take the heart between them (Plate VII., Figs. 13–16). Even in the frogs we find that the simple sac has developed into a spongy body of peculiar froth-like tissue. The originally short connection of the pulmonary sacs with the head-gut extends into a long, thin tube. This is the wind-pipe (trachea); it opens into the gullet above, and divides below into two branches which go to the two lungs. In the wall of the trachea circular cartilages develop, and these keep it open. At its upper end, underneath its pharyngeal opening, the larynx is formed—the organ of voice and speech. The larynx is found at various stages of development in the amphibia, and comparative anatomists are in a position to trace the progressive growth of this important organ from the rudimentary structure of the lower amphibia up to the elaborate and delicate vocal apparatus that we have in the larynx of man and of the birds.

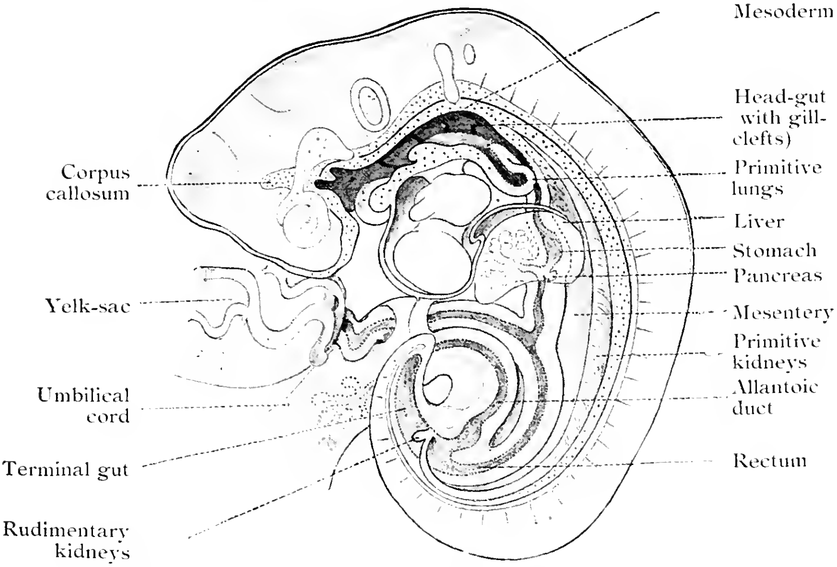

FIG. 437.—**Longitudinal section of a human embryo** of the fourth week, five mm. in length, magnified fifteen times. (From *Kollmann*.)

However varied may be the development of this organ of voice and respiration in the higher vertebrates, it always comes from the same original rudimentary structure—the ventral groove in the hind part of the head-gut. Thus from this respiratory gut we get two kinds of breathing apparatus in the vertebrates: firstly, the primary, earlier, water-breathing apparatus, the gill-crate, the original function of which has been lost altogether in the three higher classes of vertebrates; secondly, the secondary, later air-breathing apparatus, which acts as floating bladder alone in the fishes, but as lungs from the dipneusts upwards.

We must refer here to an interesting rudimentary organ of the respiratory gut, the thyroid gland *(thyreoidea)*, the large gland in front of the larynx, that lies below the "Adam's apple," and is often especially developed in the male sex. It has a certain function—not yet fully understood—in the nutrition of the body, and arises in the embryo by constriction from the lower wall of the pharynx. In many mining districts the thyroid gland is peculiarly liable to morbid enlargement, and then forms the goitre that hangs at the front of the neck *(struma)*. But it is much more interesting phylogenetically. As Wilhelm Müller, of Jena, has shown, this rudimentary organ is the last relic of the hypobranchial groove, which we considered in a previous chapter, and which runs in the middle line of the gill-crate in the ascidian and amphioxus, and conveys food to the stomach. (Cf. p. 424, Fig. 300, and Plate XIX., Figs. 14–16 *y*.) We still find it in its original character in the larvæ of the cyclostomes (Figs. 438 and 439).

The second section of the alimentary canal, the trunk or hepatic gut *(truncogaster)*, undergoes not less important modifications among our vertebrate ancestors than the first section. In tracing the further development of this digestive part of the gut, we find that most complex and elaborate organs originate from a very rudimentary original structure. For clearness we may divide the digestive gut into three sections: the fore gut (with œsophagus and stomach), the middle gut (duodenum, with liver, pancreas, jejunum, and ileum), and the hind gut (colon and rectum). Here again we find vesicular growths or appendages of the originally simple gut developing into a variety of organs. Two of these embryonic structures are already known to us: the yelk-sac, which hangs from the middle of the gut (Fig. 440 *c*), and the allantois, which grows from the hind section of the pelvic gut in the shape of a large sac-like growth *(u)*. The two large glands that open into the duodenum, the liver *(h)* and pancreas, are growths from the middle and most important part of the trunk-gut.

Immediately behind the vesicular rudiments of the lungs (Fig. 440 *l*) comes the section of the alimentary canal that forms the stomach (Figs. 435 *d*, 436 *b*). This sac-shaped organ, which is chiefly responsible for the solution and digestion of the food, has not in the lower vertebrates the great physiological importance and the complex character that it has in the higher. In the acrania and cyclostomes and the earlier fishes we can scarcely distinguish a real stomach; it is represented merely by the short piece from the branchial to the hepatic gut. In some of the other fishes also the stomach is only a very simple spindle-shaped enlargement at the beginning of the digestive section of the gut, running straight from front to back in the median plane of the body, underneath the vertebral column. In the mammals

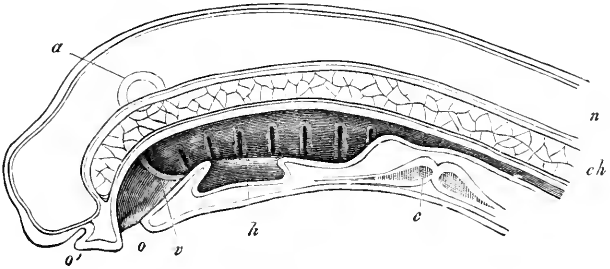

FIG. 438.

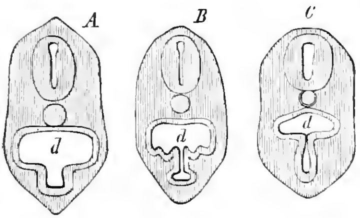

FIG. 439.

FIG. 438.—**Median section of the head of a petromyzon-larva.** (From *Gegenbaur.*) *h* hypobranchial groove (above it in the gullet we see the internal openings of the seven gill-clefts), *v* velum, *o* mouth, *c* heart, *a* auditory vesicle, *n* neural tube, *ch* chorda.

FIG. 439.—**Transverse section of the head of a petromyzon-larva.** (From *Gegenbaur.*) Beneath the pharynx *(d)* we see the hypobranchial groove; above it the chorda and neural tube. *A*, *B*, *C* stages of constriction.

its first structure is just as rudimentary as it is permanently in the preceding. But its various parts soon begin to develop. As the left side of the spindle-shaped sac grows much more quickly than the right, and as it turns considerably on its axis at the same time, it soon comes to lie obliquely. The upper end is more to the left, and the lower end more to the right. The foremost end draws up into the longer and narrower canal of the œsophagus. Underneath this on the left the blind sac (fundus) of the stomach bulges out, and thus the later form gradually developes (Figs. 422, 441 *e*). The original longitudinal axis becomes oblique, sinking below to the left and rising to the right, and approaches nearer and nearer to a transverse position. In the outer layer of the stomach-wall the powerful muscles that accomplish the digestive movements develop from the gut-fibre layer. In the inner layer a number of small glandular tubes are formed from the gut-gland layer; these are the peptic glands that secrete the gastric juice. At the lower end of the gastric sac is developed the valve that separates it from the duodenum (the pylorus, Fig. 422 *d*).

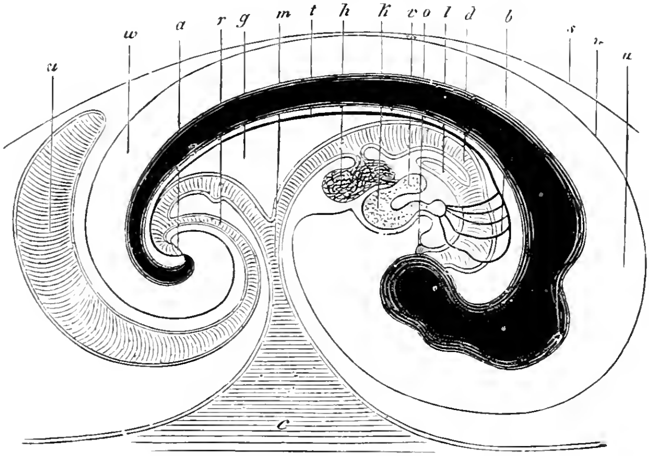

FIG. 440.—**Longitudinal section of the embryo of a chick** (of the fifth day). *d* gut, *o* mouth, *a* anus, *l* lungs, *h* liver, *g* mesentery, *v* auricle of heart, *k* ventricle, *b* arterial arches, *t* aorta, *c* yelk-sac, *m* vitelline duct, *u* allantois, *r* allantoic pedicle, *n* amnion, *w* amniotic cavity, *s* serous membrane. (From *Baer*.)

Underneath the stomach there now developes the disproportionately long stretch of the small intestine. The development of this section is very simple, and consists essentially in an extremely rapid and considerable growth lengthways. It is at first very short, quite straight, and simple. But immediately behind the stomach we find at an early stage a horseshoe-shaped bend and loop of the gut, in connection with the severance of the alimentary canal from the yelk-sac and the development of the first mesentery. (Cf. Plate VII., Fig. 14 *g*, and Fig. 211.) Like a small umbilical rupture, a horseshoe loop of the gut proceeds from the ventral opening of the embryo, before the closing of the ventral wall (Fig. 211 *m*); and into the curve of this the yelk-sac or umbilical vesicle *(n)* opens. The thin delicate membrane that fastens this loop to the ventral side of the vertebral column, and fills the inner bend of the horseshoe formation, is the first rudiment of the mesentery (Fig. 440 *g*). The most projecting part of the loop, into which the vitelline sac opens (Fig. 441 *x*), and which is afterwards closed by the intestinal navel, corresponds to the later ileum. We find at an early stage a considerable growth of the small intestine; it is thus forced to coil itself in a number of loops. The various sections that we have to distinguish in it are differentiated in a very simple way—the duodenum (next

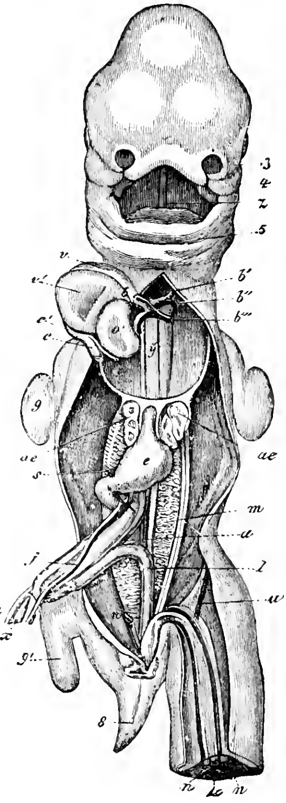

FIG. 441.—**Human embryo, five weeks old,** from the ventral side, opened (magnified). The pectoral and ventral walls and the liver are removed. *3* external nasal process, *4* upper jaw, *5* lower jaw, *z* tongue, *v* right and *v'* left ventricle of heart, *o'* left auricle, *q* source of the aorta, *b'*, *b''*, *b'''* first, second, and third aortic arches, *c*, *c'*, *c''* venae cavae, *ae* lungs (*y* pulmonary arteries), *e* stomach, *m* pronephridia (*j* left vitelline veins, *s* portal artery, *a* right vitelline artery, *n* umbilical artery, *u* umbilical vein), *x* vitelline duct, *i* rectum, *8* tail, *9* fore legs (carpomela), *9'* hind legs (tarsomela). (From *Coste*.)

to the stomach), the succeeding long jejunum, and the last section of the small intestine, the ileum.

From the duodenum are developed the two large glands that we have already mentioned—the liver and pancreas. The liver appears first in the shape of two small sacs, that are found to the right and left immediately behind the stomach (Figs. 435 *f*, 436 *c*). In many of the lower vertebrates they remain separate for a long time (in the myxinoides throughout life), or are only imperfectly joined. In the higher vertebrates they soon blend more or less completely to form a single large organ. The gut-gland layer, which lines the hollow tubular rudiments of the liver, sends a number of branching shoots into the enveloping gut-fibre layer. As these solid shoots (rows of glandular cells) continue to ramify, and their branches join each other, we get the peculiar reticular quality of the mature liver. The hepatic cells, the organs that secrete the bile, all develop from the gut-gland layer. But the connective-tissue fibrous mass that binds this large network of cells into a compact organ and surrounds the whole originates from the gut-fibre layer. From the latter also come the large blood-vessels that permeate the liver and interlace their innumerable branches, connected into a network, with the network of the hepatic cells. The biliary canals that pass through the whole of the liver, and collect the bile and conduct it to the gut, are formed as intercellular passages in the axis of the solid strings of cells. They all open into the two primitive chief biliary ducts, which develop from the base of the original outgrowths from the gut. In man and many other vertebrates they afterwards blend into a single biliary duct, which opens inside the ascending part of the duodenum. The gall-bladder developes as a hollow outgrowth from the right original biliary duct. The growth of the liver is very brisk at first. In the human embryo it grows so much in the second month of development that in the third it occupies by far the greater part of the body-cavity (Fig. 442). At first the two halves develop equally; afterwards the left falls far behind the right. In consequence of the unsymmetrical development and turning of the stomach and other abdominal viscera, the whole liver is now pushed to the right ride. Although the liver does not afterwards grow so disproportionately, it is comparatively larger in the embryo at the end of pregnancy than in the adult. Its weight relatively to that of the whole body is 1 : 36 in the adult, and 1 : 18 in the embryo. Hence it is very important physiologically during embryonic life; it is chiefly concerned in the formation of blood, not so much in the secretion of bile.

Immediately behind the liver a second large visceral gland developes from the duodenum, the pancreas. It is wanting in most of the lowest classes of vertebrates, and is first found in the fishes. This organ also is an outgrowth from the gut. The gut-gland layer puts out a number of solid branching shoots, and these gradually become hollow. Like the salivary glands in the mouth, the pancreas developes into a large and very complex racemose gland. Its outlet, the pancreatic duct, which conveys the pancreatic juice into the duodenum, seems to be simple and single at first. It often becomes double subsequently.

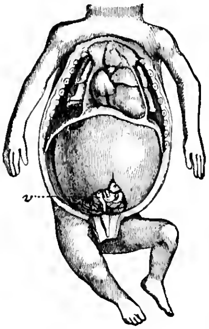

Fig. 442.—**Thoracic and abdominal viscera** of a human embryo of twelve weeks, natural size. (From *Kölliker*.) The head is omitted. Ventral and pectoral walls are removed. The greater part of the body-cavity is taken up with the liver, from the middle part of which the cœcum and the vermiform appendix protrude. Above the diaphragm, in the middle, is the conical heart; to the right and left of it are the two small lungs.

The last section of the alimentary canal, the large intestine, is at first in the embryo a very simple, short, and straight tube, which opens behind by the anus. It remains thus throughout life in the lower vertebrates. But it grows considerably in the mammals, coils into various folds, and divides into two sections, the first and longer of which is the colon, and the second the rectum. At the beginning of the colon there is a valve *(valvula Bauhini)* that separates it from the small intestine. Immediately behind this there is a sac-like growth, which enlarges into the cœcum (Fig. 442 *v*).

In the plant-eating mammals this is very large, but it is very small or completely atrophied in the flesh-eaters. In man, and most of the apes, only the first portion of the cœcum is wide ; the blind end-part of it is very narrow, and seems later to be merely a useless appendage of the former. This "vermiform appendage" *(appendix vermiformis)* is very interesting in dystelology as a rudimentary organ. The only significance of it in man is that not infrequently a cherry-stone or some other hard and indigestible matter penetrates into its narrow cavity, and by setting up inflammation and suppuration causes the death of otherwise sound men. Teleology has great difficulty in giving a rational explanation of, and attributing to a beneficent Providence, this dreaded appendicitis. In our plant-eating ancestors this rudimentary organ was much larger and had a useful function.

Finally, we have important appendages of the alimentary tube in the bladder and urethra, which belong to the alimentary system in their development and morphological value. These urinary organs, acting as reservoir and duct for the urine excreted by the kidneys, originate from the innermost part of the allantoic pedicle. The allantois is a sac-shaped outgrowth from the fore wall of the last section of the gut (Fig. 440 *u*). In the dipneusts and amphibia, in which this blind sac first makes its appearance, it remains within the body-cavity, and functions entirely as bladder. But in all the amniotes it grows far outside of the body-cavity of the embryo, and forms the large embryonic "primitive bladder," from which the placenta developes in the higher mammals. This is lost at birth. But the long stalk or pedicle of the allantois *(r)* remains, and forms with its upper part the middle vesico-umbilical ligament *(ligamentum vesico-umbilicale medium)*, a rudimentary organ that goes in the shape of a solid string from the vertex of the bladder to the navel. The lowest part of the allantoic pedicle (or the "urachus") remains hollow, and forms the bladder. At first this opens into the last section of the gut in man as in the lower vertebrates ; thus there is a real cloaca, which takes off both urine and excrements. But among the mammals this cloaca is only permanent in the monotremes, as it is in all the birds, reptiles, and amphibia. In all the other mammals (marsupials and placentals) a transverse partition is afterwards formed, and this separates the uro-genital aperture in front from the anus-opening behind. (Cf. p. 376 and Chapter XXIX.)

When we survey the whole development of the alimentary system, in conjunction with that of the vascular system, and trace the long gradation from the gastræa up to man, we find plenty of proofs of the solidity of the biogenetic law. The whole trophesis—that is to say, the anatomy and physiology of the whole nutritive apparatus—reveals to us the various stages that are of interest for anthropogeny.

FIFTY-SECOND TABLE

SYNOPSIS OF THE PHYLOGENY OF TROPHESIS

(The chief stages in the stem-history of the human apparatus of nutrition).

I. First section: **Nutritive apparatus of the protists.**

The unicellular organism has no gut, no tissues, and no organs (or organella).

1. First stage: **Trophesis of the chromacea.**

The protophytic organism is a homogeneous moneron, a simple granule of plasm with plasmodomous function (*chroococcus*, p. 502).

2. Second stage: **Trophesis of the algaria.**

The vegetal moneron (1) has been converted into a simple cell by differentiation of internal nucleus and external cell-body (*cytoplasm*) (*palmella*, p. 505).

3. Third stage: **Trophesis of the protozoa.**

By metasitism (p. 508) the plasmophagous protozoa has been evolved from the plasmodomous protophyton (2) (*amœbina*, p. 506).

4. Fourth stage: **Trophesis of the cenobia.**

By a permanent conjunction of social protozoa (3) are formed blastæads, cell-communities in the form of hollow balls, the wall of which is a single stratum of cells, the blastoderm (*catallacta*, p. 514).

II. Second section: **Nutritive apparatus of the cœlenteria.**

The multicellular organism has a simple alimentary system, with one opening (primitive gut and primitive mouth). No body-cavity.

5. Fifth stage: **Trophesis of the gastræads.**

The primitive gut (*progaster*) is a simple cavity, lined with the ectoderm, opening by the primitive mouth (*gastremaria*, p. 518).

6. Sixth stage: **Trophesis of the platodes.**

The invagination of the primitive mouth gives rise to a second gut-chamber, the ectodermic gullet. A pair of ectodermic nephridia are developed from a pair of cutaneous glands (*turbellaria*, p. 536).

III. Third section: **Nutritive apparatus of the vermalia.**

The alimentary canal has two openings (mouth and anus), and separates from the surrounding body-cavity (*cœloma*).

7. Seventh stage: **Trophesis of the rotatoria.**

The primitive gut of the platodes changes, by the formation of the second aperture, into the gut of the gastrotricha (p. 542); the constriction of a couple of cœlom-pouches gives rise to the *enterocœl* (*chætognatha*, p. 224).

8. Eighth stage: **Trophesis of the nemertina.**

The vascular system makes its appearance, with two communicating median tubes in the gut-wall (*nemertina*, p. 544).

9. Ninth stage: **Trophesis of the enteropneusts.**

The alimentary canal divides into head-gut (with gill-clefts) and trunk-gut (with liver) (*balanoglossus*, p. 545).

10. Tenth stage: **Trophesis of the prochordonia.**

In the head-gut the ventral hypobranchial groove is formed above and the dorsal epibranchial groove (*chorda*) below (*copelata*, p. 466).

IV. Fourth section: **Nutritive apparatus of the vertebrates.**

The alimentary canal, hitherto unsegmented, undergoes in the head-gut the vertebral metamerism that distinguishes the vertebrates from their invertebrate ancestors; so also the vascular system and the segmental renal system.

11. Eleventh stage: **Trophesis of the acrania.**

The branchial gut contains numbers of metamerous gill-clefts and corresponding blood-vessels. The nephridia are multiplied segmentally.

12. Twelfth stage: **Trophesis of the craniotes.**

The various sections of the alimentary system undergo a manifold and characteristic articulation, advancing by many stages (Table LIII.); so also the vascular system (Table LV.) and the renal system (Table LVI.).

FIFTY-THIRD TABLE

SYNOPSIS OF THE STEM-HISTORY OF THE HUMAN ALIMENTARY SYSTEM

I. First period: **Gastread-gut.**

The whole alimentary system is a simple primitive gut with primitive mouth.

II. Second period: **Rhabdocœla-gut.**

The primitive mouth forms a muscular gullet by invagination.

III. Third period: **Vermalia-gut.**

The gut receives a second aperture at its blind end: anus.

IV. Fourth period: **Enteropneust-gut.**

The gut-tube divides into two sections: the respiratory (branchial) gut in front, and the digestive (hepatic) gut behind.

V. Fifth period: **Prochordonia-gut.**

The ventral furrow of the branchial gut becomes the hypobranchial groove.

VI. Sixth period: **Acrania-gut.**

The gill-arches form between the segmental gill-clefts.

VII. Seventh period: **Cyclostoma-gut.**

The thyroid gland developes from the hypobranchial groove. The simple blind hepatic sac becomes the compact hepatic gland.

VIII. Eighth period: **Selachii-gut.**

Between the gill-clefts cartilaginous inner gill-arches are formed: the foremost of them form the cartilages of the lips and the skeleton of the jaws. The pancreas is formed.

IX. Ninth period: **Ganoid-gut.**

The partitions between the separate gill-pouches disappear. The floating bladder developes from the gullet.

X. Tenth period: **Dipneust-gut.**

The floating bladder is converted into lungs, its air-duct into the trachea. The mouth and nasal pits are connected.

XI. Eleventh period: **Amphibia-gut.**

The gill-clefts close up. The gills are lost. From the upper end of the trachea the larynx is developed. The bladder is formed from the hind gut.

XII. Twelfth period: **Reptilia-gut.**

The gills have entirely disappeared. Breathing is exclusively pulmonary. The primitive mouth-nasal cavity is divided by the horizontal palate into the lower mouth-cavity and the upper nasal cavity. The allantois is formed from the bladder.

XIII. Thirteenth period: **Monotreme-gut.**

The tongue is metamorphosed: a new tongue is developed from the hindmost part of the lower tongue. Three pairs of salivary glands make their appearance.

XIV. Fourteenth period: **Marsupial-gut.**

The cloaca is divided by a partition into a uro-genital passage in front and rectum with anus behind.

XV. Fifteenth period: **Catarrhine-gut.**

All parts of the alimentary system, especially the teeth, attain the distinctive characters that man shares with the catarrhine apes.

CHAPTER XXVIII.

EVOLUTION OF THE VASCULAR SYSTEM

Composition and function of the vascular system. Red and white blood. Rhodocytes and leucocytes. Origin from the entoderm and mesoderm. Vascular layer. Lacunoma. First development of the vessels. Eating yelk-cells: merocytes. Their pseudopodia. Their origin. Theory of parablasts and of mesenchym. Histological similarity and genetic independence of the two groups of mesenchyms: lymphoids and connectives. Secondary and polyphyletic origin of both groups from mesenchymic organs. Outer mesenchymic membranes of the tunicates. Absence of blood-vessels in the lower animals. Gradual formation of the vascular system. Blood-vessels of the nemertines and annelids. Branchial vessels of the balanoglossus. Heart of the tunicates. Degeneration of the heart in the amphioxus. Advance of the vascular system in the cyclostomes and fishes. Division of the larger and smaller circulation in the higher vertebrates. Origin and metamorphosis of the heart in the advancing series of vertebrates. Mesocardium. Cardiocœl. Severance of the pericardium from the pleural cavities. Diaphragm. Passage of the heart and pericardium from the head to the trunk. Double structure of the heart in the amniotes cenogenetic.

THE use that we have hitherto made in organogeny of our biogenetic law will give the reader an idea how far we may trust its guidance in phylogenetic investigation. This differs considerably in the various systems of organs; the reason is that heredity and variability have a very different range in these systems. While some of them faithfully preserve the original palingenetic development inherited from earlier animal ancestors, others show little trace of this rigid heredity; they are rather disposed to follow new and divergent *cenogenetic* lines of development in consequence of adaptation. The organs of the first kind represent the *conservative* element in the multicellular state of the human frame, while the latter represent the *progressive* element. The course of historic development is a result of the correlation of the two tendencies.

It is only in the conservative organs, in which heredity preponderates over adaptation, that we can use ontogeny directly for phylogenetic purposes, and deduce the former changes of the stem-forms from the *palingenetic* changes in the embryonic forms. In the progressive organs, in which adaptation prevails over heredity, the original course of development has been so much distorted and curtailed that we learn very little with confidence from the *cenogenetic* phenomena as to their stem-history. Here we need the help of comparative anatomy, which often yields much more important phylogenetic information than ontogeny. Hence it is clearly most imperative to keep both sides of it constantly in view if we are to make a just and proper application of the biogenetic law. The first half of this great law of evolution opens to us the path of phylogeny, in teaching us how to gather the course of the stem-history from that of the embryonic development of the individual; the embryonic form reproduces by heredity the corresponding stem-form *(palingenesis)*. But the other half restricts this principle, and warns us to be cautious in applying it. It shows that the original reproduction of the phylogenesis in the ontogenesis has been much modified and curtailed in the course of millions of years; the embryonic form has diverged, through adaptation, from the corresponding stem-form *(cenogenesis)*. The greater this divergence is the more we are compelled to seek the aid of comparative anatomy in our phylogenetic studies.

There is perhaps no other system of organs in the human body in which this is more necessary than in that of which we are now going to consider the obscure development—the vascular system, or apparatus of circulation *(vasorium)*. If we were to draw our conclusions as to the original features in our earlier animal ancestors solely from the phenomena of the development of this system in the embryo of man and the other higher vertebrates, we should be wholly misled. By a number of important embryonic adaptations, the chief of which is the formation of an extensive food-yelk, the original course of the development of the vascular system has been so much falsified and curtailed in the higher vertebrates that little or nothing now remains in their embryology of some of the principal phylogenetic features. We should be quite unable to explain these if comparative anatomy and ontogeny did not come to our assistance.

The vascular system *(vasorium)* in man and all the craniotes is an elaborate apparatus of cavities filled with juices or cell-containing fluids. These "vessels" *(vascula)* play an important part in the nutrition of the body. They partly conduct the nutritive red blood to the various parts of the body (blood-vessels); partly absorb from the gut the white chyle formed in digestion (chyle-vessels); and partly collect the used-up juices and convey them away from the tissues (lymphatic vessels). With the latter are connected the large serous cavities of the body, especially the body-cavity, or cœloma. The lymphatic vessels conduct both the colourless lymph and the white chyle into the venous part of the circulation. The lymphatic glands act as producers of new blood-cells, and with them is associated the spleen. The centre of movement for the regular circulation of the fluids is the heart, a strong muscular sac, which contracts regularly and is equipped with valves like a pump. This constant and steady circulation of the blood makes possible the complex metabolism of the higher animals.

But, however important the vascular system may be to the more advanced and larger and highly-differentiated animals, it is not at all so indispensable an element of animal life as is commonly supposed. The older science of medicine regarded the blood as the real source of life, and "humoral pathology" traced most diseases to "bad mixture of the blood." Moreover, even in the still prevalent confused notions of heredity the blood plays the chief part. People speak generally of full blood, half blood, etc., and imagine that the hereditary transmission of certain morphological and physiological characters "lies in the blood." The incorrectness of these ideas is clearly seen from the fact that in the act of generation the blood of the parents is not directly transmitted to the offspring, nor does the embryo possess blood in its early stages. We have already seen that not only the differentiation of the four secondary germinal layers, but also the first structures of the principal organs in the embryo of all the vertebrates, take place long before there is any trace of the vascular system—the heart and the blood. In accordance with this ontogenetic fact, we must regard the vascular system as one of the latest organs from the phylogenetic point of view, just as we have found the alimentary canal to be one of the earliest. In any case, the vascular system is much later than the alimentary.

When we fully appreciate both parts of the biogenetic law we can draw an approximate conclusion from the ontogenetic succession of the various organs in the animal embryo as regards their phylogenetic succession in the evolutionary series of our ancestors. In my *Gastræa Theory* (1873) I made the first attempt to establish in this sense "the phylogenetic significance of the ontogenetic succession of systems of organs." It must be observed, however, that this is not uniform in the higher animal stems. In the vertebrate stem (which includes our own ancestors) the series of systems of organs may be described, with a fair amount of confidence, as follows:—I. Cutaneous system *(A)* and alimentary system *(B)*; II. Sexual system *(C)*; III. Nervous system *(D)* and muscular system *(E)*; IV. Renal system *(F)*; V. Vascular system *(G)*; VI. Skeletal system *(H)*.

In the same way it is possible to distinguish a phylogenetic succession among the various tissues of the body corresponding to the succession of their development in the embryo. At first we have only *epithelia,* or simple strata of cells—the blastoderm and the two primary germinal layers that proceed from it by gastrulation. Moreover, the two middle layers, from which the various tissues are afterwards formed, are at first (as walls of the cœlom-pouches) simple epithelia. In contrast to these primary tissues all the rest are regarded as later and secondary, or as *apothelia*. Of these we may distinguish two groups, the neuro-muscular tissues and the mesenchymic tissues (connectives and lymphoids). In the amphioxus, which here again gives us most important phylogenetic indications, the apothelia retain their original character for a long time; the mesenchym (blood and connective tissues) is very slightly developed in it. The classification of the tissues from this point of view will be found in my *Origin and Development of Animal Tissues* (1884).

"The blood is a very special fluid." The important nutritive fluid that circulates as blood and lymph in the elaborate canals of our vascular system is not a clear, simple fluid, but a very complex chemical juice with millions of cells floating in it. These blood-cells are just as important in the complicated life of the higher animal body as the circulation of money is to the commerce of a civilised community. Just as the citizens meet their needs most conveniently by means of a financial circulation, so the various tissue-cells, the microscopic citizens of the multicellular human body, have their food conveyed to them best by the circulating cells in the blood. These blood cells *(hæmocytes)* are of two kinds in man and all the other craniotes—red cells *(rhodocytes* or *erythrocytes)* and colourless or lymph cells *(leucocytes)*. The red colour of the blood is caused by the great accumulation of the former, the others circulating among them in much smaller quantity. When the colourless cells increase at the expense of the red we get anæmia (or chlorosis).

The lymph-cells *(leucocytes)*, commonly called the "white corpuscles" of the blood, are phylogenetically older and more widely distributed in the animal world than the red. The great majority of the invertebrates that have acquired an independent vascular system, or a nutritive circulatory apparatus, have only colourless lymph-cells in the circulating fluid. There is an exception in the nemertines (Fig. 443) and some groups of annelids. When we examine the colourless blood of a river-crab or a snail (Fig. 443) under a high power of the microscope, we find in each drop numbers of mobile leucocytes, which behave morphologically and physiologically just like independent amœbæ (Fig. 17). Like these unicellular protozoa, the colourless blood-cells creep slowly about, their unshapely plasma-body constantly changing its form, and stretching out finger-like processes first in one direction, then another. Like the amœbæ, they take particles into their cell-body. On account of this feature these amœboid plastids are called "eating cells" *(phagocytes)*, and on account of their motions "travelling cells" *(planocytes)*. It has been shown by the discoveries of the last few decades that these leucocytes are of the greatest physiological and pathological consequence to the organism. They can absorb either solid or dissolved particles from the wall of the gut, and convey them to the blood in the chyle; they can absorb and remove unusable matter from the tissues. When they pass in large quantities through the fine pores of the capillaries and accumulate at irritated spots, they cause inflammation. They can consume and destroy bacteria, the dreaded vehicles of infectious diseases; but they can also transport these injurious monera to fresh regions, and so extend the sphere of infection. It is probable that the sensitive and travelling leucocytes of our invertebrate ancestors have powerfully co-operated for millions of years in the phylogenesis of the advancing animal organisation.

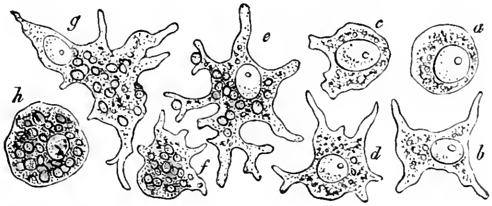

Fig. 443.—**Eating lymph-cells from the blood of a sea-snail** *(thetis)*. (Cf. p. 121.) Each of the colourless blood-cells may assume in succession the eight forms in Fig. *a–h*.

The red blood-cells *(rhodocytes* or *erythrocytes)* have a much more restricted sphere of distribution and activity. But they also are very important in connection with certain functions of the craniote organism, especially the exchange of gases or respiration. The cells of the dark red, carbonised or venous, blood, which have absorbed carbonic acid from the animal tissues, give this off in the respiratory organs; they receive instead of it fresh oxygen, and thus bring about the bright red colour that distinguishes oxydised or arterial blood. The red colouring matter of the blood *(hæmoglobin)* is regularly distributed in the pores of their protoplasm. The red cells of most of the vertebrates are elliptical flat disks, and enclose a nucleus of the same shape; they differ a good deal in size (Fig. 444). The mammals are distinguished from the other vertebrates by the circular form of their biconcave red cells and by the absence of a nucleus (Fig. 1); only a few genera still have the elliptic form inherited from the reptiles (Fig. 2). In the embryos of the mammals the red cells have a nucleus and the power of increasing by cleavage (Fig. 10).

The origin of the blood-cells and the vessels in the embryo, and their relation to the germinal layers and tissues, are among the most difficult problems of ontogeny—those obscure questions on which the most divergent opinions are still advanced by the most competent scientists. In general, it is certain that the greater part of the cells that compose the vessels and their contents come from the mesoderm—in fact, from the gut-fibre layer; it was on this account that Baer gave the name of "vascular layer" to this visceral layer of the cœloma. But other important observers say that a part of these cells come from other germinal layers, especially from the gut-gland layer. It seems to be true that blood-cells

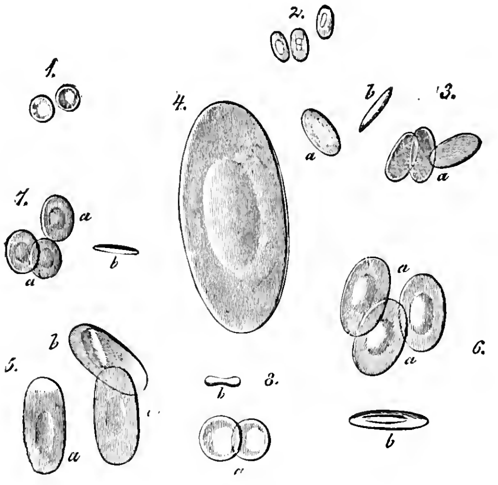

FIG. 444.

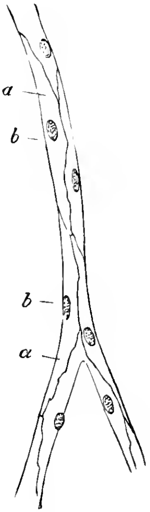

FIG. 445.

FIG 444.—**Red blood-cells of various vertebrates** (equally magnified). *1.* of man, *2.* camel, *3.* dove, *4.* proteus, *5.* water-salamander *(triton)*, *6.* frog, *7.* merlin *(cobitis)*, *8.* lamprey *(petromyzon)*. *a* surface-view, *b* edge-view. (From *Wagner*.)

FIG. 445.—**Vascular tissues or endothelium** *(vasalium)*. A capillary from the mesentery. *a* vascular cells, *b* their nuclei.

may be formed from the cells of the entoderm before the development of the mesoderm. If we examine sections of chickens, the earliest and most familiar subjects of embryology, we find at an early stage the "primitive aortas" we have already described (Fig. 446 *ao*) in the ventral angle between the episoma *(Pv)* and hyposoma *(Sp)*. The thin wall of these first vessels of the amniote embryo consists of flat cells *(endothelia* or *vascular epithelia)*; the fluid within already contains numbers of red blood-cells; both have been developed from the gut-fibre layer. It is the same with the vessels of the germinative area (Fig. 446 *v*), which lie on the entodermic membrane of the yelk-sac *(c)*. These features are seen still more clearly in the transverse section of the duck-embryo in Fig. 157 (p. 322). In this we see clearly how a number of stellate cells proceed from the "vascular layer" or visceral layer of the splanchnopleura, and spread in all directions in the "primary body-cavity"—*i.e.*, in the spaces between the germinal layers *(lacunoma)*. A part of these travelling cells come together and line the wall of the larger spaces, and thus form the first vessels; others enter into the cavity, live in the fluid that fills it, and multiply by cleavage—the first blood-cells.

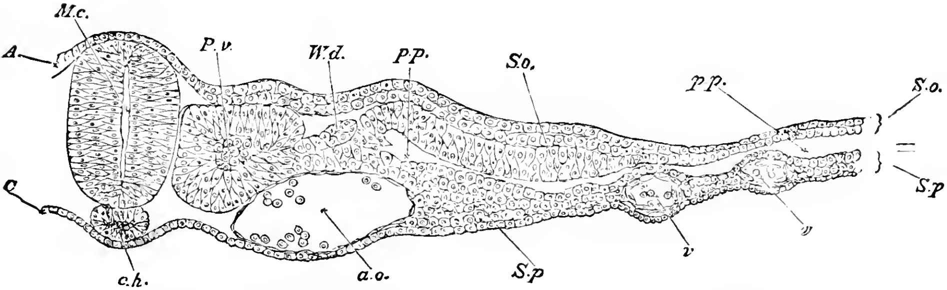

FIG. 446.—**Transverse section of the trunk of a chick-embryo,** forty-five hours old. (From *Balfour.*) *A* ectoderm (horny-plate), *Mc* medullary tube, *ch* chorda, *C* entoderm (gut-gland layer), *Pv* primitive segment (episomite), *Wd* prorenal duct, *pp* cœloma (secondary body-cavity), *So* skin-fibre layer, *Sp* gut-fibre layer, *v* blood-vessels in latter, *ao* primitive aortas, containing red blood-cells.

But, besides these mesodermic cells of the "vascular layer" proper, other travelling cells, of which the origin and purport are still obscure, take part in the formation of blood in the meroblastic vertebrates (especially fishes). The chief of these are those that Rückert has most aptly denominated "merocytes." These "eating yelk-cells" are found in large numbers in the food-yelk of the selachii, especially in the yelk-wall—the border zone of the germinal disk in which the embryonic vascular net is first developed. The nuclei of the merocytes become ten times as large as the ordinary cell-nucleus, and are distinguished by their strong capacity for taking colour, or their special richness in chromatin. Their protoplasmic body resembles the stellate cells of osseous tissue (astrocytes), and behaves just like a rhizopod (such as gromia); it sends out numbers of stellate processes all round, which ramify and stretch into the surrounding food-yelk. These variable and very mobile processes, the pseudopodia of the merocytes, serve both for locomotion and for getting food; as in the real rhizopods, they surround the solid particles of food (granules and plates of yelk), and accumulate round their nucleus the food they have received and digested. Hence we may regard them both as eating-cells *(phagocytes)* and travelling-cells *(planocytes)*. Their lively nucleus divides quickly and often repeatedly, so that a number of new nuclei are formed in a short time; as each fresh nucleus surrounds itself with a mantle of protoplasm, it provides a new cell for the construction of the embryo.

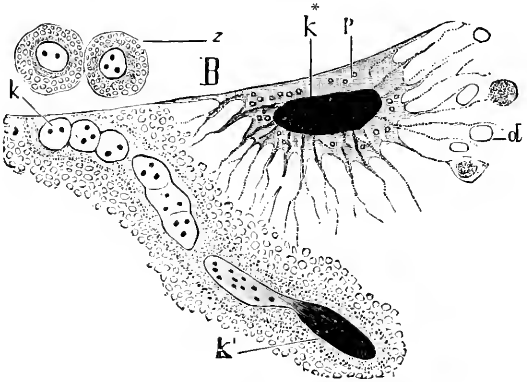

FIG. 447.—**Merocytes of a shark-embryo,** rhizopod-like yelk-cells underneath the embryonic cavity *(B)*. (From *Rückert*.) *z* two embryonic cells, *k* nuclei of the merocytes, which wander about in the yelk and eat small yelk-plates *(d)*, *k* smaller, more superficial, lighter nuclei, *k'* a deeper nucleus, in the act of cleavage, *k** chromatin-filled border-nucleus, freed from the surrounding yelk in order to show the numerous pseudopodia of the protoplasmic cell-body.

Some of these embryonic cells are used merely for the growth of the entoderm; others for the formation of blood-cells. "As the merocytes on the one hand continually absorb fresh food from the yelk, and on the other hand steadily yield it up in the form of cells to the germinal layers of the growing embryo, they form an important connecting link between these and the yelk" (Rückert). Many other fishes, as well as the reptiles and birds, behave like the selachii in this respect.

The origin of the merocytes is still obscure. Some embryologists trace them directly to the inner germinal layer, and think a part of the entodermic cells permanently originate from it and multiply (Rückert, Hoffmann, etc.). Others believe that they came from a special stratum of cells that has been formed at the periphery of the germinal disk between the primary germinal layers, and may be conceived as a peripheral mesoderm (the *acroblast* of Kollmann, *hæmoblast* of Rauber, etc.). A third view was advanced by His in 1868, and was made the foundation of his famous "parablast-theory." According to this much-admired theory, all the cells that compose the vascular and skeletal systems (connective, cartilage, bones, etc.) do not belong to the sexually generated embryo, but are foreign parthenogenetic accessions, developed by "virginal conception" from the follicle-cells of the maternal ovary. Thus every vertebrate (including man) is a double entity, and is formed by *symbiosis*, or by the coalescence of two entirely different animals. Although this contradictory parablast-theory and the other pseudo-mechanical theories of His had a great vogue for a decade, they are now almost universally abandoned (cf. p. 50, and my work on *Aims and Methods of Modern Embryology;* Jena, 1875).

In order to understand these yelk-cells and the first formation of blood in the vertebrate embryo we must, in my opinion, hold to the following principles:—1. The origin of the merocytes in the yelk and their function in the embryo of the meroblastic vertebrates is in all cases a cenogenetic phenomenon; because all meroblastic vertebrates descend from holoblastic ancestors, the palingenetic embryo of which has no independent food-yelk. 2. Hence the yelk-cells or merocytes of the more recent meroblastic vertebrates were represented in the earlier holoblastic by cells of the inner germ-layer or of the middle layer developed therefrom (yelk-cells in the ventral wall of the primitive gut of cyclostomes, ganoids, and amphibia). 3. The yelk-sac and germinative area are always parts of the embryo: the former can only be contrasted as peripheral embryonic organs to the permanent body *(menosoma)* of the latter. 4. As the mesoderm comes from the entoderm in all vertebrates, it is of secondary interest in connection with the question of the origin of the blood-cells whether they all develop from the former ("vascular layer") or come partly from the latter. 5. As the primitive blood or lymph-cells are real travelling cells, they may pass at a very early stage from their source in the germinal layer, and spread in very distant parts of the embryo.

People often wrongly confuse with the parablast theory of His the later mesenchym theory of Hertwig, which this distinguished embryologist established in his *Cœlom Theory*, and further developed in his *Manual of Embryology*. The name "mesenchym" (=intermediate germ or layer) is given by Hertwig to all the embryonic structures that develop from the epithelial four secondary germinal layers, not directly or by involution, but by the withdrawal of some of their cells from their epithelial connection; as these amœboid cells penetrate everywhere into the pores and spaces between the four secondary germinal layers and multiply, they give rise to various organs in very distant parts of the body. As a rule, the mesenchymic cells secrete large quantities of intercellular matter between them; this is fluid and amorphous in the blood, solid and with definite form in the connective substance (Fig. 449). The viscous gelatinous tissue (Fig. 448) is an intermediate form between the two. Hertwig has, in his very suggestive mesenchym theory, opposed the two large tissue groups of "connective substances" and "blood substances" *(lymphoids)* to all the other embryonic structures, and has accordingly separated "the organs of the intermediate layer or mesenchym" as a special group from all the other parts of the body (the "organs of the inner, middle, and outer germinal layers"). This gave his theory a superficial resemblance to the erroneous parablast theory of His. The radical difference between the two theories is seen at once when we remember that, according to the former, all the cells of the embryo come from the original stem-cell *(cytula)*, whereas, according to the latter, they have two different sources, and are only secondarily united by symbiosis (p. 50).

The mesenchym theory has, like the parablast theory, had a very mixed reception, and provoked an extensive literature. In appreciating it we should keep the following principles in view:—1. The various mesenchymic structures can only be classed together as a unity in the histological sense, as embryonic structures that arise by the secretion of intercellular matter between travelling cells. 2. As these travelling cells always come gradually from the group of one of the epithelial germinal layers, they must be subordinated to these layers, and cannot be regarded as equivalent or co-ordinate structures. 3. The two chief groups of embryonic mesenchyms, the lymphoids ("blood-tissues") and connectives, are very much alike histologically and ontogenetically, and are apparently connected by intermediate stages (for instance, "gelatinous tissue," Fig. 448); but physiologically and phylogenetically they differ altogether. 4. The lymphoid organs (lymph and blood, lymphatic and blood-vessels) do not originate from a continuous "vascular layer," but develop from a number of originally separate local structures (each from a localised group of travelling cells, a "colony of

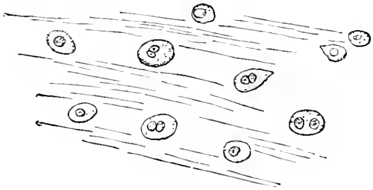

FIG. 448.

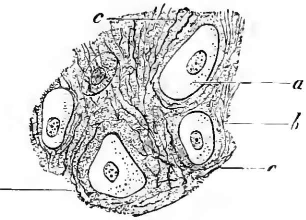

FIG. 449.

FIG. 448.—**Gelatinous tissue from the corpus vitreum of an embryo of four months.** Round cells in gelatinous intercellular matter.

FIG. 449.—**Cartilaginous tissue from the reticular cartilage of the shell of the ear.** *a* cells, *b* intercellular matter, *c* fibres in preceding. (From *Frey*.)

planocytes"); these "islands of blood" only unite subsequently for the formation of *vessels*, and these in turn do not join to form a vascular *system* until much later; the central organs of the system are phyletically younger than the peripheral parts (spaces between the germinal layers). 5. The connective organs of vertebrates originate from definite germinal plates *(blastoplates)—i.e.*, from epithelial parts of the germinal layers (the two middle layers), which are just as much morphologically definite organs as the various embryonic organs of the inner and outer layers; thus the corium developes from a cutis-plate, the axial skeleton from a skeletal plate, and the gut-fibre wall from a mesenteric plate (Figs. 169-172; Plate VI., Fig. 5). 6. The simplest and most original forms of these connective organs (cutis-plate, skeletal plate, and mesenteric plate) are, permanently in the acrania *(amphioxus)*, and for a time in the embryos of the craniotes *(selachii)*, simple one-layered epithelia; it is only later that the mesenchymic tissues of the connectives develop from the latter. 7. All these fundamental structures of the connectives are at first free from blood-vessels, and have nothing to do with their independent beginnings. 8. Hence, in the vertebrates there is no "blood-connective embryo" ("parablast" or "desmohæmoblast"), no one rudimentary structure of the lymphoids and connectives.

The studies of the structure of the amphioxus that Hatschek published in 1888 in the *Anatomischer Anzeiger*, and those of Rabl on the differentiation of the mesoderm, give an important support to this conception of the mesenchym. The independence they establish of the two sets of mesenchymic structures, the lymphoids and connectives, is first proved ontogenetically; and to this is added proof of their phylogenetic independence. As a fact, comparative anatomy and ontogeny teach that the two sets of mesenchymic organs have been evolved independently of each other and polyphyletically. Large connectives (mesodermic supporting tissue and skeletons) are developed in various stems of the cœlenteria (sponges, corals, platodes), though these show no trace of lymphoids. So also we find planocytes in the embryos and larvæ of the vermalia, echinoderms (Fig. 450), and other cœlomaria, long before blood-vessels develop. On the other hand, blood may be formed in the primary body-cavity (by the migration of planocytes) without any formation of connectives (various vermalia).

The tunicates have a very remarkable external mesenchymic envelope in their characteristic mantle, which encloses the whole of the rest of the body. In the lower and older animals of this stem the tunica is a structureless cellulose envelope, a *cuticula*, secreted from the superficial stratum of the ectoderm, the horny plate or epidermis. But in the higher and later tunicates planocytes slip from the latter into the former, multiply, and secrete fresh masses of cellulose between them ; the external cuticula is thus converted into a mesenchymic envelope, the many metamorphoses of which correspond entirely to those of the ordinary internal connective tissue (cf. pp. 435, 468). When this connective-tunica becomes thicker, processes grow into it from the underlying skin with blood-vessels. So in the vertebrates secondary blood-vessels proceed into the various connective organs, just as into all the other organs of the body.

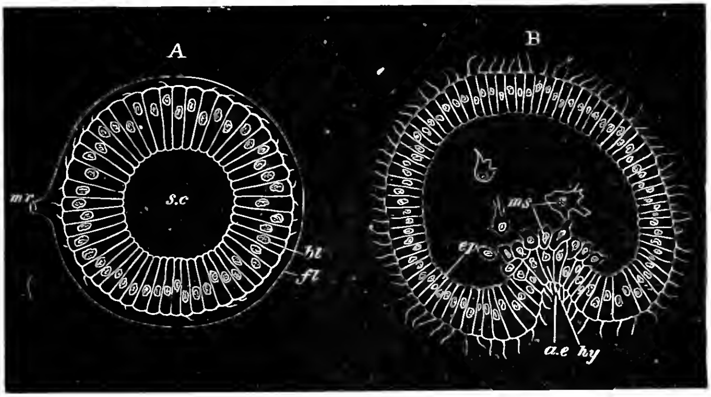

FIG. 450.—**Blastula of a holoturian** *(A)*. *B* The same at the beginning of gastrulation. Diagrammatic section, from *Selenka*. During the invagination *(B)* of the blastula *(A)* amœboid cells (planocytes) migrate into the gelatinous matter of the embryonic cavity (blastocœl or primary body-cavity, *sc*), and form there a primitive mesoderm *(ms)*. *bl* blastoderm, *ep* ectoderm, *hy* entoderm, *ae* primitive gut, *fl* blastolemma (structureless embryonic membrane), *mr* micropyle.

Half of the twelve stems of the animal world that we have distinguished (p. 538) have no blood-vessels (I.–VI. phylon). They make their first appearance in the vermalia. Their earliest source is the primary body-cavity, the simple space between the two primary germinal layers, which is either a relic of the segmentation-cavity (blastocœl, Fig. 450), or is a subsequent formation (schizocœl). Amœboid planocytes, which migrate from the entoderm and reach this fluid-filled primary cavity (protocœl), live and multiply there, and form the first colourless blood-cells (primary leucocytes). We find the vascular system in this very simple form to-day in the bryozoa, rotatoria, nematoda, and other lower vermalia.

The first step in the improvement of this primitive vascular system is the formation of larger canals or blood-conducting tubes. The spaces filled with blood, the relics of the primary body-cavity, receive a special wall. "Blood-vessels" of this kind (in the narrower sense) are found among the higher worms in various forms, sometimes very simple, at other times very complex. The form that was probably the incipient structure of the elaborate vascular system of the vertebrates (and of the articulates) is found in two primordial principal vessels—a dorsal vessel in the middle line of the dorsal wall of the gut, and a ventral vessel that runs from front to rear in the middle line of its ventral wall. From the dorsal vessel is evolved the aorta (or principal artery), from the ventral vessel the principal or subintestinal vein. The two vessels are connected in front and behind by a loop that runs round the gut. The blood contained in the two tubes is propelled by their peristaltic contractions.

The earliest vermalia in which we first find this independent vascular system are the nemertina (Fig. 451). As a rule, they have three parallel longitudinal vessels connected by loops, a single dorsal vessel above the gut and a pair of lateral vessels to the right and left. In some of the nemertina the blood is already coloured, and the red colouring matter is real hæmoglobin, connected with elliptical discoid cells, as in the vertebrates. The further evolution of this rudimentary vascular system can be gathered from the class of the annelids in which we find it at various stages of development. First, a number of transverse connections are formed between the dorsal and ventral vessels, which pass round the gut ring-wise (Fig. 452). Other vessels grow into the body-wall and ramify in order to convey blood to it. In addition to the two large vessels of the middle plane there are often two lateral vessels, one to the right and one to the left; as, for instance, in the leech. There are four of these parallel longitudinal vessels in the enteropneusts (*balanoglossus*, Fig. 299). In these important vermalia the foremost section of the gut has already been converted into a gill-crate, and the vascular arches that rise in the wall of this from the ventral to the dorsal vessel have become branchial vessels.

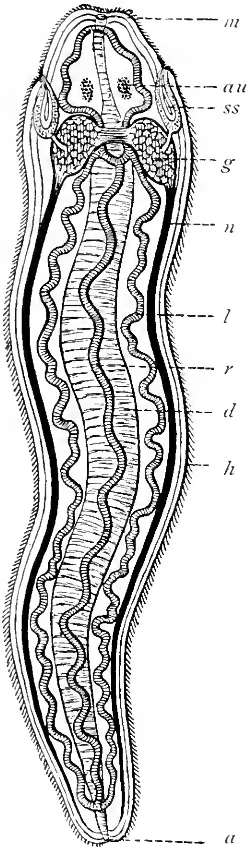

Fig. 451.

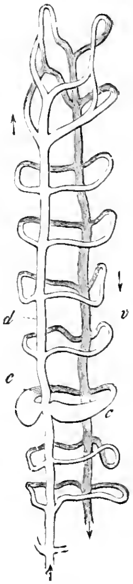

Fig. 452.

Fig. 451.—**A simple nemertine.** *m* mouth, *d* gut, *a* anus, *g* brain, *n* nerves, *h* ciliary coat, *ss* sensory pits (head-clefts), *au* eyes, *r* dorsal vessel, *l* lateral vessels. (Diagram.)

Fig. 452.—**Vascular system of an annelid** (*sænuris*), foremost section. *d* dorsal vessel, *v* ventral vessel, *c* transverse connection of two (enlarged in shape of heart). The arrows indicate the direction of the flow of blood. (From *Gegenbaur*.)

We have a further important advance in the tunicates, which we have recognised as the nearest blood-relatives of our early vertebrate ancestors. Here we find for the first time a real heart—*i.e.*, a central organ of circulation, driving the blood into the vessels by the regular contractions of its muscular wall. It is of a very rudimentary character, a spindle-shaped tube, passing at both ends into a principal vessel (Fig. 256; Plate XIX., Fig. 14 *hz*). By its original position behind the gill-crate, on the ventral side of the tunicates (sometimes more, sometimes less, forward), the heart shows clearly that it has been formed by the local enlargement of a section of the ventral vessel. We have already noticed the remarkable alternation of the direction of the blood-stream, the heart driving it first from one end, then from the other (p. 438). This is very instructive, because in most of the worms (even the enteropneust) the blood in the dorsal vessel travels from back to front, but in the vertebrates in the opposite direction. As the ascidian-heart alternates steadily from one direction to the other, it shows us permanently, in a sense, the phylogenetic transition from the earlier forward direction of the dorsal current (in the worms) to the new backward direction (in the vertebrates).

As the new direction became permanent in the earlier prochordonia, which gave rise to the vertebrate stem, the two vessels that proceed from either end of the tubular heart acquired a fixed function. The foremost section of the ventral vessel henceforth always conveys blood from the heart, and so acts as an artery; the hind section of the same vessel brings the blood from the body to the heart, and so becomes a vein. In view of their relation to the two sections of the gut, we may call the latter the intestinal vein and the former the branchial artery. The blood contained in both vessels, and also in the heart, is venous or carbonised blood—*i.e.*, rich in carbonic acid; on the other hand, the blood that passes from the gills into the dorsal vessel is provided with fresh oxygen—arterial or oxydised blood. The finest branches of the arteries and veins pass into each other in the tissues by means of a network of very fine, ventral, hair-like vessels, or capillaries (Fig. 445).

When we turn from the tunicates to the closely-related amphioxus we are astonished at first to find an apparent retrogression in the formation of the vascular system. As we have seen, the amphioxus has no real heart; its colourless blood is driven along in its vascular system by the principal vessel itself, which contracts regularly in its whole length (cf. Fig. 245). A dorsal vessel that lies above the gut (aorta) receives the arterial blood from the gills, and drives it into the body. Returning from here, the venous blood gathers in a ventral vessel under the gut (intestinal vein), and goes back to the gills. A number of branchial vascular arches, which effect respiration and rise in the wall of the branchial gut from belly to back, absorb oxygen from the water and give off carbonic acid; they connect the ventral with the dorsal vessel. As the same section of the ventral vessel, which also forms the heart in the craniotes, has developed in the ascidia into a simple tubular heart, we may regard the absence of this in the amphioxus as a result of degeneration, a return in this case to the earlier form of the vascular system, as we find it in many of the worms. We may assume that the acrania that really belong to our ancestral series did not share this retrogression, but inherited the one-chambered heart of the prochordonia, and transmitted it directly to the earliest craniotes (cf. the ideal primitive vertebrate, *prospondylus*, Figs. 101 and 103).

The further phylogenetic evolution of the vascular system is revealed to us by the comparative anatomy of the craniotes. At the lowest stage of this group, in the cyclostomes, we find for the first time the differentiation of the vasorium into two sections: a system of blood-vessels proper, which convey the *red* blood about the body, and a system of lymphatic vessels which absorb the colourless lymph from the tissues and convey it to the blood. The lymphatics that absorb from the gut and pour into the blood-stream the milky food-fluid formed by digestion are distinguished by the special name of "chyle-vessels." While the chyle is white on account of its high proportion of fatty particles, the lymph proper is colourless. Both chyle and lymph contain the colourless amœboid cells (leucocytes, Fig. 12) that we also find distributed in the blood as colourless blood-cells (or "white corpuscles"); but the blood also contains a much larger quantity of red cells, and these give its characteristic colour to the blood of the craniotes (rhodocytes, Fig. 444). The distinction between lymph, chyle, and blood-vessels which is found in all the craniotes may be regarded as an outcome of division of labour between various sections of our originally simple vascular system (or *hæmolymph system)*. In the gnathostomes the spleen makes its first appearance, an organ rich in blood, the chief function of which is the extensive formation of new colourless and red cells. It is not found in the acrania and cyclostomes, or any of the invertebrates. It has been transmitted from the earliest fishes to all the craniotes.

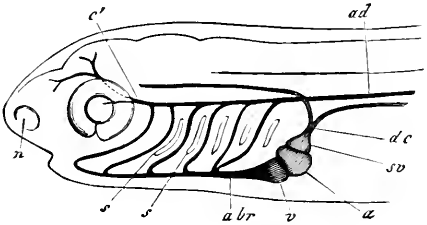

FIG. 453.—**Head of a fish-embryo,** with rudimentary vascular system, from the left. *dc* Cuvier's duct (juncture of the anterior and posterior principal veins), *sv* venous sinus (enlarged end of Cuvier's duct), *a* auricle, *v* ventricle, *abr* trunk of branchial artery, *s* gill-clefts (arterial arches between), *ad* aorta. *c* carotid artery, *n* nasal pit. (From *Gegenbaur.*)

The heart also, the central organ of circulation in all the craniotes, shows an advance in structure in the cyclostomes. The simple, spindle-shaped heart-tube, found in the same form in the embryo of all the craniotes, is divided into two sections or chambers in the cyclostomes, and these are separated by a pair of valves (Plate XIX., Fig. 16 *hv, hk*). The hind section, the auricle (or *atrium, hv)*, receives the venous blood from the body and passes it on to the anterior section, the ventricle *(ventriculus, hk)*. From this it is driven through the trunk of the branchial artery (the foremost section of the ventral vessel or principal vein) into the gills.

In the selachii an arterial cone *(conus arteriosus)* is developed from the foremost end of the ventricle, as a special division, cut off by valves. It passes into the enlarged base of the trunk of the branchial artery (Fig. 453 *abr*). On each side 5–7 arteries proceed from it. These rise between the gill-clefts *(s)* on the gill-arches, surround the gullet, and unite above into a common trunk-aorta, the continuation of which over the gut corresponds to the dorsal vessel of the worms. As the curved arteries on the gill-arches spread into a network of respiratory capillaries, they contain venous blood in their lower part (as arches of the branchial artery) and arterial blood in the upper part (as arches of the aorta). The junctures of the various aortic arches on the right and left are called the roots of the aorta. Of an originally large number of aortic arches there remain at first six, then (owing to degeneration of the fifth arch) only five pairs; and from these five pairs (Fig. 454) the chief parts of the arterial system develop in all the higher vertebrates.

The appearance of the lungs and the atmospheric respiration connected therewith, which we first meet in the dipneusts, is the next important step in vascular evolution. In the dipneusts the auricle of the heart is divided by an incomplete partition into two halves. Only the right auricle now receives the venous blood from the veins of the body. The left auricle receives the arterial blood from the pulmonary veins. The two auricles have a common opening into the simple ventricle, where the two kinds of blood mix, and are driven through the arterial cone or bulb into the arterial arches. From the last arterial arches the pulmonary arteries arise (Fig. 455 *p*). These force a part of the mixed blood into the lungs, the other part of it going through the aorta into the body.

From the dipneusts upwards we now trace a progressive development of the vascular system, which ends finally with the loss of branchial respiration and a complete separation of the two halves of the circulation. In the amphibia the partition between the two auricles is complete. In their earlier stages, as tadpoles (Fig. 316), they have still the branchial respiration and the circulation of the fishes, and their heart contains venous blood alone. Afterwards the lungs and pulmonary vessels are developed, and henceforth the ventricle of the heart contains mixed blood. In the reptiles the ventricle and its arterial cone begin to divide into two halves by a longitudinal partition, and this partition becomes complete in the higher reptiles and birds on the one hand, and the stem-forms of the mammals on the other. Henceforth, the right half of the heart contains only venous, and the left half only arterial, blood, as we find in all birds and mammals. The right auricle receives its carbonised or venous blood from the veins of the body, and the right ventricle drives it through the pulmonary arteries into the lungs. From here the blood returns, as oxydised or arterial blood, through the pulmonary veins to the left auricle, and is forced by the left ventricle into the arteries of the body. Between the pulmonary arteries and veins is the capillary system of the small or pulmonary circulation. Between the body-arteries and veins is the capillary system of the large or body-circulation. It is only in the two highest classes of vertebrates—the birds and mammals—that we find a complete division of the circulations. Moreover, this complete separation has been developed quite independently in the two classes, as the dissimilar formation of the aortas shows of itself. In the birds the *right* half of the fourth arterial arch has become the permanent arch (*arcus aortæ*,

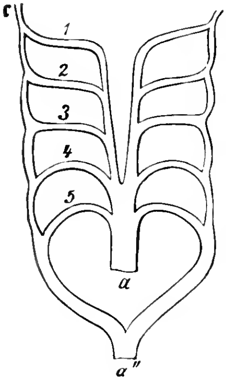

Fig. 454.

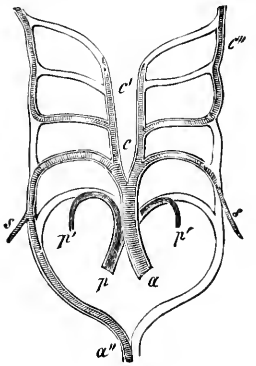

Fig. 455.

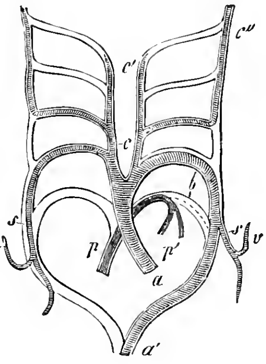

Fig. 456.

Fig. 454.—**The five arterial arches of the craniotes** *(1-5)* in their original disposition. *a* arterial cone or bulb, *a''* aorta-trunk, *c* carotid artery (foremost continuation of the roots of the aorta). (From *Rathke.*)

Fig. 455.—**The five arterial arches of the birds**; the lighter parts of the structure disappear; only the shaded parts remain. Letters as in Fig. 454. *s* subclavian arteries, *p* pulmonary artery, *p'* branches of same, *c'* outer carotid, *c''* inner carotid. (From *Rathke.*)

Fig. 456.—**The five arterial arches of mammals**; letters as in Fig. 455. *v* vertebral artery, *b* Botalli's duct (open in the embryo, closed afterwards). (From *Rathke.*)

Fig. 455). In the mammals this has been developed from the *left* half of the same fourth arch (Fig. 456).

If we compare the fully-developed arterial system of the various classes of craniotes, it shows a good deal of variety, yet it always proceeds from the same fundamental type. Its development is just the same in man as in the other mammals; in particular, the modification of the six pairs of arterial arches is the same in both (Figs. 457–460). At first there is only a single pair of arches, which lie on the inner surface of the first pair of gill-arches. Behind this there then develop a second and third pair of arches (lying on the inner side of the second and third gill-arches, Fig. 457). Finally, we get a fourth, fifth, and sixth pair. Of the six primitive arterial arches of the amniotes three soon pass away (the first, second, and fifth); of the remaining three, the third gives the carotids, the fourth the aortas, and the sixth (number 5 in Figs. 454 and 458) the pulmonary arteries.

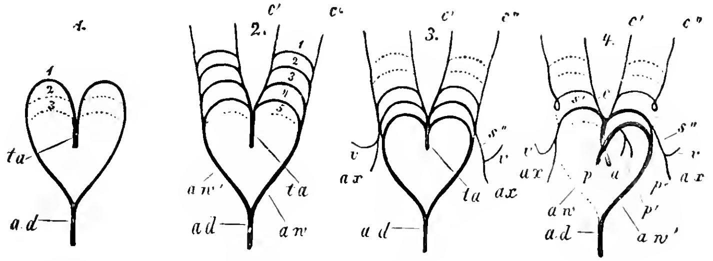

FIG. 457. FIG. 458. FIG. 459. FIG. 460.

FIGS. 457–460.—**Metamorphosis of the five arterial arches in the human embryo** (diagram from *Rathke.*) *la* arterial cone, *1*, *2*, *3*, *4*, *5* first to fifth pair of arteries, *ad* trunk of aorta, *aw* roots of aorta. In Fig. 457 only three, in Fig. 458 all five, of the aortic arches are given (the dotted ones not yet developed). In Fig. 459 the first two pairs have disappeared again. In Fig. 460 the permanent trunks of the artery are shown; the dotted parts disappear. *s* subclavian artery, *v* vertebral, *ax* axillary, *c* carotid (*c'* outer, *c''* inner carotid), *p* pulmonary.

The human heart also developes in just the same way as that of the other mammals (Fig. 468). We have already seen the first rudiments of its embryology, which in the main corresponds to its phylogeny (Figs. 229–234). We saw that the palingenetic form of the heart is a spindle-shaped thickening of the gut-fibre layer in the ventral wall of the head-gut (Fig. 229 *df*). The structure is then hollowed out, forms a simple tube, detaches from its place of origin, and henceforth lies freely in the cardiac cavity (Fig. 229 *c*). Presently the tube bends into the shape of an S, and turns spirally on an imaginary axis in such a way that the hind part comes to lie on the dorsal surface of the fore part. The united vitelline veins open into the posterior end. From the anterior end spring the aortic arches (Fig. 234).

This first structure of the human heart, enclosing a very simple cavity, corresponds to the tunicate-heart, and is a reproduction of that of the prochordonia, but it now divides into two, and subsequently into three, compartments; this reminds us for a time of the heart of the cyclostomes and fishes. The spiral turning and bending of the heart increases, and at the same time two transverse constrictions appear, dividing it externally into three sections (Figs. 461, 462). The foremost section, which is turned towards the ventral side, and from which the aortic arches rise, reproduces the arterial bulb *(conus arteriosus)* of the selachii. The middle section is a simple ventricle *(ventriculus)*; and the hindmost, the section turned towards the dorsal side, into which the vitelline veins

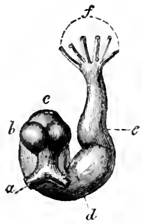

FIG. 461.

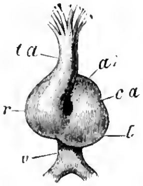

FIG. 462.

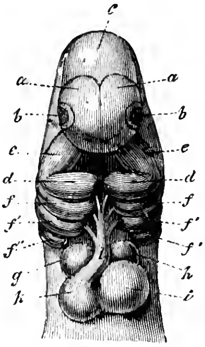

FIG. 463.

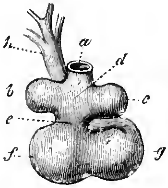

FIG. 464.

FIG. 461.—**Heart of a hare-embryo,** from behind. *a* vitelline veins, *b* auricles of the heart, *c* atrium, *d* ventricle, *e* arterial bulb, *f* base of the three pairs of arterial arches. (From *Bischoff.*)

FIG. 462.—**Heart of the same embryo** (Fig. 461), from the front. *v* vitelline veins, *a* auricle, *ca* auricular canal, *l* left ventricle, *r* right ventricle, *ta* arterial bulb. (From *Bischoff.*)

FIG. 463.—**Heart and head of a dog embryo,** from the front. *a* fore brain, *b* eyes, *c* middle brain, *d* primitive lower jaw, *e* primitive upper jaw, *f* gill-arches, *g* right auricle, *h* left auricle, *i* left ventricle, *k* right ventricle. (From *Bischoff.*)

FIG. 464.—**Heart of the same embryo,** from behind. *a* inosculation of the vitelline veins, *b* left auricle, *c* right auricle, *d* auricle, *e* auricular canal, *f* left ventricle, *g* right ventricle, *h* arterial bulb. (From *Bischoff.*)

inosculate, is a simple auricle (or *atrium*). The latter forms, like the simple atrium of the fish-heart, a pair of lateral dilatations, the auricles (*auriculæ*, Fig. 461 *b*); and the constriction between the atrium and ventricle is called the auricular canal (*canalis auricularis*, Fig. 462 *ca*). The heart of the human embryo is now a complete fish-heart.

In perfect harmony with its phylogeny, the embryonic development of the human heart shows a gradual transition from the fish-heart, through the amphibian and reptile, to the mammal form. The most important point in the transition is the formation of a longitudinal partition—incomplete at first, but afterwards complete—which separates all three divisions of the heart into right (venous) and left (arterial) halves (cf. Figs. 463–468). The atrium is separated into a right and left half, each of which absorbs the corresponding auricle; into the right auricle open the body-veins (upper and lower vena cava, Figs. 465 *c*, 467 *c*); the left auricle receives the pulmonary veins. In the same way a superficial interventricular furrow is soon seen in the ventricle (*sulcus interventricularis*, Fig. 466 *s*). This is the external sign of the internal partition, by which the ventricle is divided into two—a right venous and left arterial ventricle. Finally a longitudinal partition is formed in the third section of the primitive fish-like heart, the arterial bulb, externally indicated by a longitudinal furrow (Fig. 466 *af*). The cavity of the bulb is divided into two lateral halves, the pulmonary-artery bulb, that opens into the right ventricle, and the aorta-bulb, that opens into the left ventricle. When all the partitions are complete, the small (pulmonary) circulation is distinguished from the large (body) circulation; the motive centre of the former is the right half, and that of the latter the left half, of the heart (cf. Tables LV. and LVI.).

The heart of all the vertebrates belongs originally to the hyposoma of the head, and we accordingly find it in the embryo of man and all the other amniotes right in front on the under-side of the head; just as in the fishes it remains permanently in front of the gullet. It afterwards descends into the trunk, with the advance in the development of the neck and breast, and at last reaches the breast, between the two lungs. At first it lies symmetrically in the middle plane of the body, so that its long axis corresponds with that of the body (Plate VI., Fig. 9). In most of the mammals it remains permanently in this position. But in the apes the axis begins to be oblique, and the apex of the heart to move towards the left side. The displacement is greatest in the anthropoid apes—chimpanzee, gorilla, and orang—which resemble man in this.

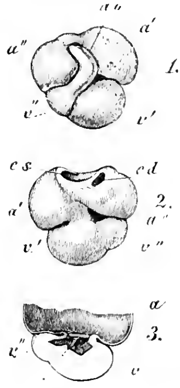

Fig. 465.

Fig. 466.

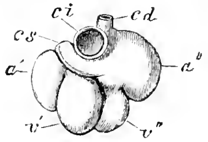

Fig. 467.

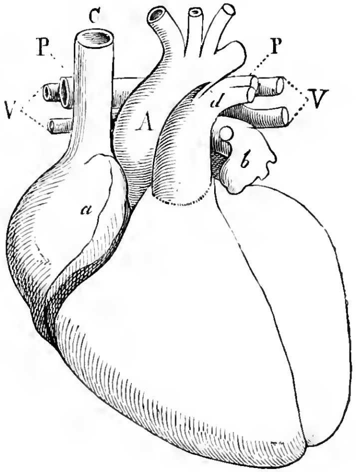

Fig. 468.

Fig. 465.—**Heart of a human embryo,** four weeks old; *1* front view, *2* back view, *3* opened, and upper half of the atrium removed. *a'* left auricle, *a''* right auricle, *v'* left ventricle, *v''* right ventricle, *ao* arterial bulb, *c* superior vena cava (*cd* right, *cs* left), *s* rudiment of the interventricular wall. (From *Kölliker.*)

Fig. 466.—**Heart of a human embryo,** six weeks old, front view. *r* right ventricle, *t* left ventricle, *s* furrow between ventricles, *ta* arterial bulb, *af* furrow on its surface; to right and left are the two large auricles. (From *Ecker.*)

Fig. 467.—**Heart of a human embryo,** eight weeks old, back view. *a'* left auricle, *a''* right auricle, *v'* left ventricle, *v''* right ventricle, *cd'* right superior vena cava, *ci* inferior vena cava. (From *Kölliker.*)

Fig. 468.—**Heart of the adult man,** fully developed, front view, natural position. *a* right auricle (underneath it the right ventricle), *b* left auricle (under it the left ventricle), *C* superior vena cava, *V* pulmonary veins, *P* pulmonary artery, *d* Botalli's duct, *A* aorta. (From *Meyer.*)

As the heart of all vertebrates is originally, in the light of phylogeny, only a local enlargement of the middle principal vein, it is in perfect accord with the biogenetic law that its first structure in the embryo is a simple spindle-shaped tube in the ventral wall of the head-gut. A thin membrane, standing vertically in the middle plane, the mesocardium, connects the ventral wall of the head-gut with the lower head-wall. As the cardiac tube extends and detaches from the gut-wall, it divides the mesocardium into an upper (dorsal) and lower (ventral) plate (usually called the *mesocardium anterius* and *posterius* in man, Fig. 469 *uhg*). The mesocardium divides two lateral cavities, Remak's "neck-cavities" (Fig. 469 *hh*). These cavities afterwards join and form the simple pericardial cavity, and are therefore called by Kölliker the "primitive pericardial cavities." Wilhelm His has given them the unsuitable name of "parietal cavities," which is just as unfortunate as so many other of his inventions —such as his "stem-zone" and "parietal-zone" for dorsal and ventral body. (Cf. pp. 50, 292, and 324.)

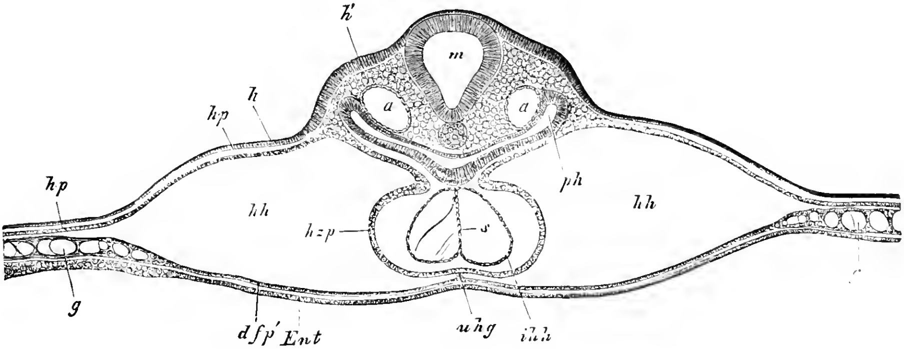

FIG. 469.—**Transverse section of the back of the head of a chick-embryo,** forty hours old. (From *Kölliker.*) *m* medulla oblongata, *ph* pharyngeal cavity (head-gut), *h* horny plate, *h′* thicker part of it, from which the auscultory pits afterwards develop, *hp* skin-fibre plate, *hh* cervical cavity (head-cœlom or cardiocœl), *hzp* cardiac plate (the outermost mesodermic wall of the heart), connected by the ventral mesocardium (*uhg*) with the gut-fibre layer or visceral cœlom-layer (*dfp′*), *Ent* entoderm, *ihh* inner (entodermic ?) wall of the heart; the two endothelial cardiac tubes are still separated by the cenogenetic septum (*s*) of the amniotes (cf. p. 806), *g* vessels.

The double cervical cavity of the amniotes is very interesting morphologically and phylogenetically; it corresponds to a part of the hyposomites of the head of the lower vertebrates—that part of the ventral cœlom-pouches which comes next to Van Wijhe's "visceral cavities" below. Each of the cavities still communicates freely behind with the two cœlom-pouches of the trunk; and, just as these afterwards coalesce into a simple body-cavity (the ventral mesentery disappearing), we find the same thing happening in the head. This simple primary pericardial cavity has been well called by Gegenbaur the "head-cœloma," and by Hertwig the "pericardial breast-cavity." As it now encloses the heart, it may also be called *cardiocœl.*

The cardiocœl, or head-cœlom, is often disproportionately large in the amniotes, the simple cardiac tube growing considerably and lying in several folds. This causes the ventral wall of the amniote embryo, between the head and the navel, to be pushed outwards as in rupture (cf. Fig. 192 *h* and Plates VIII.–XIII. *c*). A transverse fold of the ventral wall, which receives all the vein-trunks that open into the heart, grows up from below between the pericardium and the stomach, and forms a transverse partition *(septum transversum)*, which is the first structure of the primary diaphragm (Fig. 470 *d*). This important muscular partition, which completely separates the thoracic and abdominal cavities in the mammals alone, is still very imperfect here; the two cavities still communicate for a time by two narrow canals, His's "thoracic processes of the trunk-cavity." These canals, which belong to the dorsal part of the head-cœlom, and which we may call briefly *pleural ducts*, receive the two pulmonary sacs, which develop from the hind end of the ventral wall of the head-gut; they thus become the two pleural cavities. The dorsal pleural cavities separate entirely from the ventral "secondary pericardial cavity" and the ventral or peritoneal cavity that lies behind it.

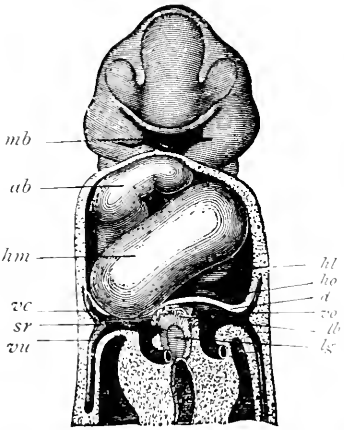

FIG. 470.—**Frontal section of a human embryo,** 2.15 mm. long in the neck, magnified forty times; "invented" by *Wilhelm His.* Seen from ventral side. *mb* mouth-fissure, surrounded by the branchial processes, *ab* bulbus of aorta, *hm* middle part of ventricle, *hl* left lateral part of same, *ho* auricle, *d* diaphragm, *vc* superior vena cava, *vu* umbilical vein, *vo* vitelline space, *lb* liver, *lg* hepatic duct.

The diaphragm makes its first appearance in the class of the amphibia (in the salamanders) as an insignificant muscular transverse fold of the ventral wall, which rises from the fore end of the transverse abdominal muscle *(musculus transversus abdominis)*, and grows between the pericardium and the liver. In the reptiles (tortoises and crocodiles) a later dorsal part is joined to this earlier ventral part of the rudimentary diaphragm, a pair of subvertebral muscles rising from the vertebral column and being added as "columns" to the transverse septum. But it was probably in the Permian sauromammals that the two originally separate parts were united, and the diaphragm became a complete partition between the thoracic and abdominal cavities in the mammals; as it considerably enlarges the chest-cavity when it contracts, it becomes an important respiratory muscle. The ontogeny of the diaphragm in man and the other mammals reproduces this phylogenetic process to-day, in accordance with the biogenetic law; in all the mammals the diaphragm is formed by the secondary conjunction of the two originally separate structures, the earlier ventral part *(diaphragma sternale)* and the later dorsal part *(diaphragma pleurale)*.

Sometimes the blending of the two diaphragmatic structures, and consequently the severance of the one pleural duct from the abdominal cavity, is not completed in man. This leads to a diaphragmatic rupture *(hernia diaphragmatica)*. The two cavities then remain in communication by an open pleural duct (or "thoracic process of the trunk-cavity"), and loops of the intestine may penetrate by this "rupture-opening" into the chest-cavity. This is one of those fatal mis-growths that show the great part that blind chance has in organic development.

Thus the thoracic cavity of the mammals, with its important contents, the heart and lungs, belongs originally to the *head-part* of the vertebrate body, and its inclusion in the trunk is secondary. This instructive and very interesting fact is entirely proved by the concordant evidence of comparative anatomy and ontogeny. The lungs are outgrowths of the head-gut; the heart developes from its inner wall.

The pleural sacs that enclose the lungs are dorsal parts of the head-cœlom, originating from the pleuroducts; the pericardium in which the heart afterwards lies is also double originally, being formed from ventral halves of the head-cœlom, which only combine at a later stage. When the lung of the air-breathing vertebrates issues from the head-cavity and enters the trunk-cavity, it follows the example of the floating bladder of the fishes, which also originates from the pharyngeal wall in the shape of a small pouch-like outgrowth, but soon grows so large that, in order to find room, it has to pass far behind into the trunk-cavity. To put it more precisely, the lung of the pentadactyles retains this hereditary growth-process of the fishes; for the hydrostatic floating bladder of the latter is the air-filled organ from which the air-breathing organ of the former has been evolved.

Here there is an interesting cenogenetic phenomenon in the formation of the heart of the higher vertebrates that deserves special notice. In its earliest form the heart is *double*, as recent observation has shown, in all the amniotes, and the simple spindle-shaped cardiac tube, which we took as our starting-point, is only formed at a later stage, when the two lateral tubes move backwards, touch each other, and at last combine in the middle line. In man, as in the hare, the two embryonic hearts are still far apart at the stage when there are already eight primitive segments (Fig. 471 *h*). So also the two cœlom-pouches of the head in which they lie (the two "cervical or parietal cavities") are still separated by a broad space. It is not until the permanent body of the embryo developes and detaches from the embryonic vesicle that the separate lateral structures join together, and finally combine in the middle line. As the median partition between the right and left cardiocœl disappears, the two cervical cavities freely communicate (Fig. 472), and form, on the ventral side of the amniote head, a horseshoe-shaped arch, the points of which advance backwards into the pleuroducts or pleural cavities, and from there into the two peritoneal sacs of the trunk. But even after the conjunction of the cervical cavities (Fig. 472) the two cardiac tubes remain separate at first; and even after they have united a delicate partition in the middle of the simple endothelial tube (Figs. 469 *s*, 473 *h*) indicates the original separation. This *cenogenetic* "primary cardiac septum" presently disappears, and has no relation to the subsequent permanent partition between the halves of the heart, which, as a heritage from the reptiles, has a great *palingenetic* importance.

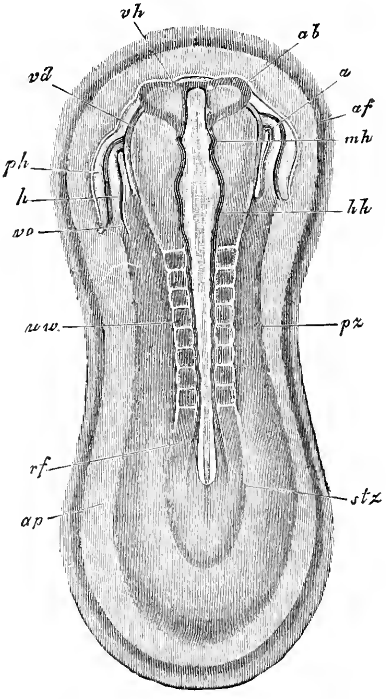

FIG. 471.—**Sandal-shaped embryonic shield of a hare,** nine days old. (From *Kölliker.*) (Dorsal view, from above.) *stz* stem-zone, or dorsal shield (with eight pairs of primitive segments), *pz* parietal or ventral zone, *ap* pellucid area, *af* amniotic fold, *h* heart, *ph* pericardial cavity, *vo* omphalo-mesenteric vein, *ab* optic vesicles, *vh* fore brain, *mh* middle brain, *hh* hind brain, *uw* primitive segment (primitive vertebra).

Thorough opponents of the biogenetic law, such as Wilhelm His and Viktor Hensen, have laid great stress on these and similar cenogenetic phenomena, and endeavoured to urge them as striking disproofs of the law. As in every other instance, careful, discriminating, comparative-morphological examination converts these supposed disproofs of evolution into strong arguments in its favour. In his excellent work, *On the Structure of the Heart in the Amphibia* (1886), Carl Rabl has shown how easily these curious cenogenetic facts can be explained by the secondary adaptation of the embryonic structure to the great extension of the food-yelk. As the heart of the amniote embryo is developed at a time when the gut-layer is still spread flat on the large vesicle and is not yet folded into the head-gut cavity in front, the halves of the heart are bound to appear separate, and can only unite in the middle after the formation of the cephalogaster

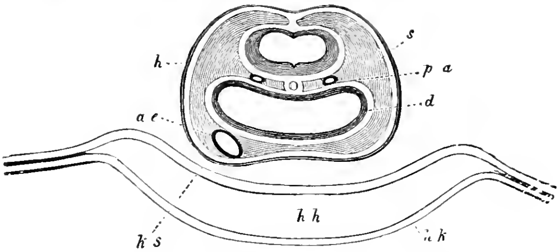

FIG. 472.—**Transverse section of the head of a chick-embryo,** thirty-six hours old. Underneath the medullary tube the two primitive aortas *(pa)* can be seen in the head plates *(s)* at each side of the chorda. Underneath the gullet *(d)* we see the aorta-end of the heart *(ae)*, *hh* cervical cavity or head cœlom, *hk* top of heart, *ks* head-sheath, amniotic fold, *h* horny plate. (From *Remak.*)

(head-gut). This secondary separation of the originally simple median rudimentary heart is the more instructive, as it is diphyletic, or has been evolved twice independently in the vertebrate stem. In the bony fishes, just as in the amniotes, the palingenetically simple embryonic heart divides into two lateral halves owing to the flat expansion of the discogastrula on the vitelline sac. All the earlier vertebrates—the cyclostomes, selachii, ganoids, and amphibia—have preserved the original single heart, in the middle of the ventral wall of the head-gut, unchanged down to the present day; thus it was *palingenetic* even in the earliest primitive craniotes (p. 562).

The embryology of all the other parts of the vascular system also gives us abundant and valuable data for the purposes of phylogeny. But as one needs a thorough knowledge of the intricate structure of the whole vascular system in man and the other vertebrates in order to follow this with profit, we cannot go into it further here. Moreover, many important features in the ontogeny of the vascular

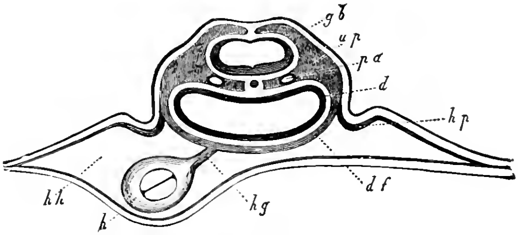

FIG. 473.—**Transverse section of the cardiac region of the same chick-embryo** (behind the preceding). In the cervical cavity *(hh)* the heart *(h)* is still connected by a mesocard *(hg)* with the gut-fibre layer *(pf)*. *d* gut-gland layer, *up* provertebral plates, *jb* rudimentary auditory vesicle in the horny plate, *hp* first rise of the amniotic fold. (From *Remak.*)

system are still very obscure and controverted. The characters of the embryonic circulation of the amniotes, which we have previously considered (Chapter XV.), are late acquisitions and entirely cenogenetic. (Cf. pp. 392–399; Figs. 229–234.)

FIFTY-FOURTH TABLE

SYSTEM OF THE TISSUES OF THE HUMAN BODY

I. First Chief Group: Epithelia. Primary Tissues.

I. A. **Primary epithelia** (of the two limiting layers).	1. **Dermal tissues** (*epithelium dermale*).	1a. Epidermis. 1b. Epidermic glands. 1c. Hairs and nails.	Ectoblast.
	2. **Gastric epithelium** (*epithelium gastrale*).	2a. Gut-epithelium. 2b. Gut-gland epithelium.	Endoblast.
I. B. **Secondary epithelia** (of the two middle layers).	3. **Cœlous epithelium** (*epithelium cœlomale*). (Mesoblast.)	3a. Germinal cœlom-epithelium (embryonic epithelium). 3b. Renal cœlom-epithelium (renal epithelium). 3c. Serous cœlom-epithelium (endothel of the body-cavity).	

II. Second Chief Group: Apothelia. Secondary Tissues.

II. A. **Neuro-muscular tissues** (apothelia without intercellular matter).	4. **Neural tissues** (*tela nervea*).	4a. Sensory cells. 4b. Ganglionic cells. 4c. Nerve-fibres.	Neuroblast.
	5. **Muscular tissues** (*tela muscularis*).	5a. Non-striated muscles. 5b. Striated muscles.	Myoblast.
II. B. **Mesenchymic tissues** (apothelia with intercellular matter).	6. **Skeletal tissues** (*tela skeletalis*).	6a. Cartilaginous tissues. 6b. Osseous tissues.	6 and 7 **Connectives** (*Tela connectiva*).
	7. **Filling tissues** (*tela maltharis*).	7a. Corium-tissues. 7b. Fat tissues. 7c. Gelatinous tissues.	
	8. **Blood-tissues** (*tela limphoides*).	8a. Rhodocytes (red blood-cells). 8b. Leucocytes (white blood-cells).	

FIFTY-FIFTH TABLE

SYNOPSIS OF THE CHIEF PERIODS OF THE STEM-HISTORY OF THE HUMAN VASCULAR SYSTEM (VASORIUM)

I. First period: **Vermalia-vasorium.**

Between the primary germinal layers vacuoles appear in the mesoderm (relics of the blastocœl or newly-formed schizocœl); leucocytes migrate into this primary body-cavity *(lacunoma)*.

II. Second period: **Nemertine-vasorium.**

As the lymph-filled spaces combine to form larger canals, the first real blood-vessels take shape—a dorsal vessel in the dorsal wall and a ventral vessel in the ventral wall of the gut. The two communicate by means of a number of circular vessels that pass round the gut.

III. Third period: **Enteropneust-vasorium.**

As the fore-half of the gut is converted into the branchial gut, the anterior section of the ventral vessel becomes the branchial artery and the anterior section of the dorsal vessel the branchial vein. Between the two a network of capillaries is developed.

IV. Fourth period: **Tunicate-vasorium.**

The section of the ventral vessel that lies next to the branchial gut dilates into a simple cardiac tube (ascidia).

V. Fifth period: **Acrania-vasorium.**

The ventral vessel (intestinal vein) forms a loop round the incipient hepatic tube—the first trace of a portal system.

VI. Sixth period: **Cyclostome-vasorium.**

The one-chambered heart divides into two compartments—anterior ventricle and posterior atrium. The vascular system differentiates into blood-vessels and lymphatics.

VII. Seventh period: **Selachii-vasorium.**

From the anterior section of the ventricle an arterial bulb is developed, and from this proceed, at first seven, afterwards six or five, pairs of arterial arches (as in the selachii).

VIII. Eighth period: **Dipneust-vasorium.**

From the last (sixth) pair of arterial arches the pulmonary arteries develop. The atrium divides into two halves.

IX. Ninth period: **Amphibia-vasorium.**

The branchial arteries gradually disappear with the gills. Right and left aortic arches remain.

X. Tenth period: **Reptile-vasorium.**

The ventricle is divided into two by a partition. Both aortic arches remain open.

XI. Eleventh period: **Mammal-vasorium.**

The small and large circulations are completely separated. The right aortic arch and Botalli's duct disappear. Lymphatic glands are formed.

FIFTY-SIXTH TABLE

SYNOPSIS OF THE CHIEF PERIODS OF THE STEM-HISTORY OF THE HUMAN HEART

I. First period: **Prochordonia-heart.**

The heart is a simple, spindle-shaped dilatation of the ventral vessel in the hind part of the ventral wall of the branchial gut. The circulation is at first regular in alternate directions (as in the tunicates).

II. Second period: **Acrania-heart.**

The heart resembles that of the prochordonia, but the circulation is constant in one direction, valves being developed and the contraction being always from rear to front. (In the amphioxus the heart has probably been lost by degeneration.)

III. Third period: **Cyclostoma-heart.**

The heart divides into two compartments, an atrium behind and a ventricle in front.

IV. Fourth period: **Selachii-heart.**

An arterial bulb *(conus arteriosus)* is developed from the anterior section of the ventricle, as in all the earlier fishes.

V. Fifth period: **Dipneust-heart.**

The atrium is divided, in consequence of pulmonary respiration, by an incomplete partition into right and left halves, as in the actual dipneusts.

VI. Sixth period: **Amphibia-heart.**

The partition between the right and left auricles is completed (as in the higher amphibia).

VII. Seventh period: **Proreptilian-heart.**

The ventricle is divided by an incomplete partition into right and left halves (as in most of the reptiles).

VIII. Eighth period: **Monotreme-heart.**

The partition between the right and left ventricles is completed (as in all the mammals).

IX. Ninth period: **Marsupial-heart.**

The valves between the ventricles and auricles (atrio-ventricular valves), with the connected tendons and papillary muscles, are differentiated from the muscular frame of the monotremes.

X. Tenth period: **Ape-heart.**

The chief axis of the heart in the middle line becomes oblique, the apex being drawn to the left (as in the apes and man).

CHAPTER XXIX.

EVOLUTION OF THE SEXUAL ORGANS

Reproduction and growth. Asexual reproduction: cleavage and gemmation. Sexual reproduction: union of two erotic cells—spermatozoon and ovum. Fecundation. Source of love: erotic chemotropism. Original hermaphrodism: later gonochorism. Origin of the gonidia from the germinal layers (cœlous epithelium). Progonidia. Hermaphroditic and gonochoristic cells. Segmental gonades of the lower vertebrates: their secondary conjunction. Ovaries and spermaries. Sexual ducts: oviduct and spermaduct. Origin of them from the prorenal ducts. Renal system of the vertebrates: three generations—pronephridia, mesonephridia, metanephridia. Longitudinal prorenal duct (nephroductus) and transverse segmental canals (nephridia). Pronephridia of the amphioxus. Mesonephridia of the myxinoides. Mesonephridia of the craniotes. Permanent kidneys (metanephridia) of the amniotes. Origin of the bladder from the allantois. Differentiation of the prorenal ducts. Müllerian duct (oviduct) and Wolffian duct (spermaduct). Migration of the germinative glands in the mammals. Formation of ova in the mammals (Graafian follicles). Origin of the external sexual organs. Phallus. Male and female copulative organs: penis and clitoris. Cloaca. Urogenital canal. Human hermaphrodism.

If we measure the importance of the systems of organs in the animal frame according to the richness and variety of their phenomena and the physiological interest that this implies, we must regard as one of the principal and most interesting systems the one which we are now going to examine—the system of the reproductive organs. Just as nutrition is the first and most urgent condition for the self-maintenance of the individual organism, so reproduction alone secures the maintenance of the species—or, rather, the maintenance of the long series of generations which the totality of the organic stem, the *phylon*, represents in their genealogical connection. No individual organism has the prerogative of immortality. To each is allotted only a brief span of personal development, an evanescent moment in the million-year course of the history of life.

Hence, reproduction and the correlative phenomenon, heredity, have long been regarded, together with nutrition, as the most important and fundamental functions of living things, and it has been attempted to distinguish them from "lifeless bodies" on this very score. As a matter of fact, this division is not so profound and thorough as it seems to be, and is generally supposed to be. If we examine carefully the nature of the reproductive process, we soon see that it can be reduced to a general property that is found in inorganic as well as organic bodies—growth. Reproduction is a nutrition and growth of the organism beyond the individual limit, which raises a part of it into the whole. This is most clearly seen when we study it in the simplest and lowest organisms, especially the monera (Figs. 277–279) and the unicellular amœbæ (Fig. 17). There the simple individual is a single plastid. As soon as it has reached a certain limit of size by continuous feeding and normal growth, it cannot pass it, but divides, by simple cleavage, into two equal halves. Each of these halves then continues its independent life, and grows on until it in turn reaches the limit of growth, and divides. In each of these acts of self-cleavage two new centres of attraction are formed for the particles of bodies, the foundations of the two new-formed individuals. There is no such thing as immortality even in these unicellulars. The individual as such is annihilated in the act of cleavage (cf. p. 142).

In many other protozoa reproduction takes place not by cleavage, but by budding (gemmation). In this case the growth that determines reproduction is not total (as in segmentation), but partial. Hence in gemmation also we may oppose the local growth-product, that becomes a new individual in the bud, as a child-organism to the parent-organism from which it is formed. The latter is older and larger than the former. In cleavage the two products are equal in age and morphological value. Next to gemmation we have, as other forms of asexual reproduction, the forming of embryonic buds and the forming of embryonic cells. But the latter leads us at once to sexual generation, the distinctive feature of which is the separation of the sexes. I have dealt fully with these various types of reproduction in my *Generelle*

Morphologie (vol. ii., pp. 32–71) and my *History of Creation* (chap. viii.).

The earliest ancestors of man and the higher animals had no faculty of sexual reproduction, but multiplied solely by asexual means—cleavage, gemmation, or the formation of embryonic buds or cells, as many protozoa still do. The differentiation of the sexes came at a later stage of phylogeny. We see this most plainly in the protists, in which the union of two individuals precedes the continuous cleavage of the unicellular organism (transitory conjugation and permanent copulation of the infusoria). We may say that in this case the growth (the condition of reproduction) is attained by the coalescence of two full-grown cells into a single, disproportionately large individual. At the same time, the mixture of the two plastids causes a rejuvenation of the plasm. At first the copulating cells are quite homogeneous; but natural selection soon brings about a certain contrast between them—larger female cells *(macrospores)* and smaller male cells *(microspores)*. It must be a great advantage in the struggle for life for the new individual to have inherited different qualities from the two cellular parents. The further advance of this contrast between the generating cells or gonidia led to sexual differentiation. One cell became the female ovum *(macrogonidion)*, and the other the male sperm-cell *(microgonidion)*. (Cf. p. 140).

The simplest forms of sexual reproduction among the living metazoa are seen in the gastræads (p. 518), the lower sponges, the common fresh-water polyp *(hydra)*, and other cœlenteria of the lowest rank. Prophysema (Fig. 288), olynthus (Fig. 292), hydra, etc., have very simple tubular bodies, the thin wall of which consists (as in the original gastrula) only of the two primary germinal layers. As soon as the body reaches sexual maturity, a number of the cells in its wall become female ova, and others male sperm-cells: the former become very large, as they accumulate a considerable quantity of yelk-granules in their protoplasm (Fig. 289 *e*); the latter are very small on account of their repeated cleavage, and change into mobile cone-shaped spermatozoa (Fig. 20). Both kinds of cells detach from their source of origin, the primary germinal layers, fall either into the surrounding water or into the cavity of the gut, and unite there by fusing together. This is the momentous process of fecundation, which we have examined in the seventh Chapter (cf. Figs. 23–29).

From these simplest forms of sexual propagation, as we can observe them to-day in the lowest zoophytes, the gastræads, sponges, and polyps, we gather most important data. In the first place, we learn that, properly speaking, nothing is required for sexual reproduction except the fusion or coalescence of two different cells—a female ovum and male sperm-cell. All other features, and all the very complex phenomena that accompany the sexual act in the higher animals, are of a subordinate and secondary character, and are later additions to this simple, primary process of copulation and fecundation. But if we bear in mind how extremely important a part this relation of the two sexes plays in the whole of organic nature, in the life of plants, of animals, and of man; how the mutual attraction of the sexes, love, is the mainspring of the most heterogeneous and remarkable processes—in fact, one of the chief mechanical causes of the highest development of life—we cannot too greatly emphasise this tracing of love to its source, the attractive force of two erotic cells.

Throughout the whole of living nature the greatest effects proceed from this very small cause. Consider the part that the flowers, the sexual organs of the flowering plants, play in nature; or the exuberance of wonderful phenomena that sexual selection produces in animal life; or the momentous influence of love in the life of man. In every case the fusion of two cells is the sole original motive power; in every case this invisible process profoundly affects the development of the most varied structures. We may say, indeed, that no other organic process can be compared to it for a moment in comprehensiveness and intensity of action. Are not the Semitic myth of Adam and Eve, the old Greek legend of Paris and Helena, and so many other famous traditions, only the poetic expression of the vast influence that love and sexual selection have exercised over the course of history ever since the differentiation of the sexes? All the other passions that agitate the heart of man are far outstripped in their joint influence by this sense-inflaming and mind-benumbing Eros. On the one hand, we look to love with gratitude as the source of the greatest artistic achievements—the noblest creations of poetry, plastic art, and music; we see in it the chief factor in the moral advance of humanity, the foundation of family life, and therefore of social advance. On the other hand, we dread it as the devouring flame that brings destruction on so many, and has caused more misery, vice, and crime than all the other evils of human life put together. So wonderful is love and so momentous its influence on the life of the soul, or on the different functions of the medullary tube, that here more than anywhere else the "supernatural" result seems to mock any attempt at natural explanation. Yet comparative evolution leads us clearly and indubitably to the first source of love—the affinity of two different erotic cells, the sperm-cell and ovum *(erotic chemotropism)*.[1]

The lowest metazoa throw light on this very simple origin of the intricate phenomena of reproduction, and they also teach us that the earliest sexual form was hermaphrodism, and that the separation of the sexes (by division of labour) is a secondary and later phenomenon. Hermaphrodism predominates in the most varied groups of the lower animals; each sexually-mature individual, each person, contains female and male sexual cells, and is therefore able to fertilise itself and reproduce. Thus we find ova and sperm-cells in the same individual, not only in the lowest zoophytes (gastræads, sponges, and many polyps), but also in many worms (leeches and rain-worms), many of the snails (the common garden and vineyard snails), all the tunicates, and many

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[1] The sensual perception (probably related to smell) of the two copulating sex-cells, which causes their mutual attraction, is a little understood, but very interesting, chemical function of the cell-soul (cf. p. 141 and *The Riddle of the Universe*, chap. ix.).

other invertebrate animals. All man's earlier invertebrate ancestors, from the gastræads up to the prochordonia, were hermaphrodites; possibly even the earliest acrania. We have an instructive proof of this in the remarkable circumstance that many genera of fishes are still hermaphrodites, and that it is occasionally found in the higher vertebrates of all classes (as atavism). We may conclude from this that gonochorism (separation of the sexes) was a later stage in our phylogeny. At first, male and female individuals differ only in the possession of one or other kind of gonades; in other respects they were identical, as we still find in the amphioxus and the cyclostomes. Afterwards, accessory organs (ducts, etc.) are associated with the primary sexual glands; and much later again sexual selection has given rise to the secondary sexual characters—those differences between the sexes which do not affect the sexual organs themselves, but other parts of the body (such as the man's beard or the woman's breast).

The third important fact that we learn from the lower zoophytes relates to the earliest origin of the two kinds of sexual cells. As in the gastræads (the lowest sponges and hydroids), in which we find the first beginnings of sexual differentiation, the whole body consists merely of the two primary germinal layers, it follows that the sexual cells also must have proceeded from the cells of these primary layers, either the inner or outer, or from both. This simple fact is extremely important, because the first trace of the ova as well as the spermatozoa is found in the middle germinal layer or mesoderm in the higher animals, especially the vertebrates. This arrangement is a later development from the preceding (in connection with the secondary formation of the mesoderm).

If we trace the phylogeny of the sexual organs in our earliest metazoa ancestors, as the comparative anatomy and ontogeny of the lowest cœlenteria *(cnidaria, platodaria)* exhibit it to us, we find that the first step in advance is the localisation of the gonidia, or the concentration of the two kinds of sexual cells scattered in the epithelium into definite groups. In the sponges and lowest hydropolyps isolated cells are detached from the cell-strata of the two primary germinal layers, and become free sexual cells; but in the cnidaria and platodes we find these associated in groups which we call sexual glands *(gonades)*. We can now for the first time speak of sexual organs in the morphological sense. The female germinative glands, which in this simplest form are merely groups of homogeneous cells, are the ovaries *(ovaria* or *oophora*, Fig. 341 *c)*. The male germinative glands, which also in their first form consist of a cluster of sperm-cells, are the testicles *(spermaria* or *testiculi*, Fig. 347 *h)*. In the medusæ, which descend, both ontogenetically and phylogenetically, from the more simply organised polyps, we find these simple sexual glands sometimes as gastric pouches, sometimes as outgrowths of the radial canals that proceed from the stomach. In the lower medusæ (craspedotes) both sorts of gonades originate from the ectoderm; in the higher medusæ (acraspeda) from the entoderm. The former develop from hydropolyps, the latter from scyphopolyps. Particularly interesting in connection with the question of the first origin of the gonades are the lowest forms of the platodes, the *cryptocœla* that

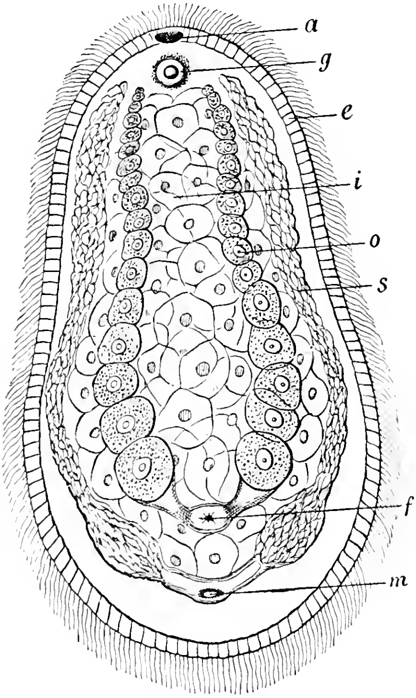


FIG. 474.—**Aphanostomum Langii** *(Haeckel)*, a primitive worm of the platodaria class, of the order of *cryptocœla* or *acœla*. This new species of the genus aphanostomum, named in honour of Professor *Arnold Lang*, of Zürich, was discovered at Ajaccio in Corsica in September, 1899 (creeping between fucoidea); it is two mm. long, one mm. broad, and of a violet colour. *a* mouth, *g* auditory vesicles (statocyst), *e* ectoderm, *i* entoderm ("digestive parenchym"), *o* ovaries, *s* spermaries, *f* female outlet, *m* male outlet.

have of late been separated as a special class *(platodaria)* from the turbellaria proper (Fig. 474). In these very primitive platodes the two pairs of sexual glands are merely two pairs of rows of differentiated cells in the entodermic wall of the primitive gut—two median ovaries *(o)* within, and two lateral spermaries *(s)* without. The mature sexual cells are ejected by the posterior outlets; the female *(f)* lies in front of the male *(m)*.

In the great majority of the bilateria or cœlomaria it is the mesoderm from which the gonades develop. Probably the first traces of them are the two large cells that appear at the edge of the primitive mouth (right and left), as a rule during gastrulation or immediately afterwards—the important promesoblasts, or "polar cells of the mesoderm," or "primitive cells of the middle germinal layer" (p. 454). In the real enterocœla, in which the mesoderm appears from the first in the shape of a couple of cœlom-pouches, these are very probably the original gonades (p. 456). This is seen very clearly in the arrow-worm *(sagitta)*, the interesting strongylarian, which teaches us so much from the typical simplicity of its epithelial histogeny—excluding the formation of mesenchyms. In the gastrula of sagitta (Fig. 475 *A*) we find at an early stage a couple of entodermic cells of an unusual size *(g)* at the base of the primitive gut *(ud)*. These primitive sexual cells *(progonidia)* are symmetrically placed to the right and left of the middle plane, like the two

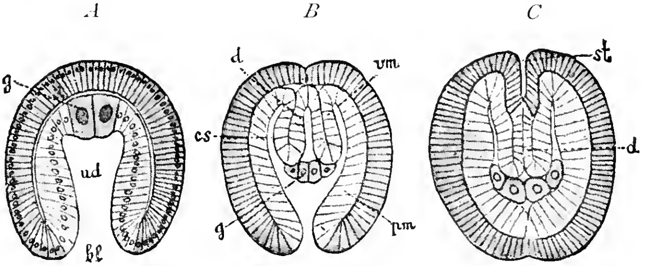


FIG. 475.—**Embryos of sagitta,** in three earlier stages of development. (From *Hertwig*.) *A* gastrula, *B* cœlomula with open primitive mouth, *C* the same with primitive mouth closed, *ud* primitive gut, *bl* primitive mouth, *g* progonidia (hermaphroditic primitive sexual cells), *cs* cœlom-pouches, *pm* parietal layer, *vm* visceral layer of same, *d* permanent gut (enteron), *st* mouth-pit (stomodæum).

promesoblasts of the bilateral gastrula of the amphioxus (Fig. 267 *p*, p. 456). A little outwards from them the two cœlom pouches *(B, cs)* are developed out of the primitive gut, and each progonidion divides into a male and a female sexual cell *(B, g)*. The two male cells (at first rather the larger) lie close together within, and are the parent-cells of the testicles *(prospermaria)*. The two female cells lie outwards from these, and are the parent-cells of the ovary *(protovaria)*. Afterwards, when the cœlom-pouches have detached from the permanent gut *(C, d)* and the primitive mouth *(A, bl)* is closed, the female cells advance towards the mouth *(C, st)*, and the male towards the rear. The foremost pair of ovaries are then separated by a transverse partition from the hind pair. Thus the first structures of the sexual glands of the sagitta are a couple of hermaphroditic entodermic cells; each of these divides into a male and a female cell; and these four gonochoristic cells are the parent-cells of the four sexual glands. Probably the two promesoblasts of the amphioxus-gastrula (Fig. 261) are also hermaphroditic primitive sexual cells in the same sense, inherited by this earliest vertebrate from its ancient bilateral gastræad ancestors.

The sexually-mature amphioxus is not hermaphroditic, as its nearest invertebrate relatives, the tunicates, are, and as the long-extinct pre-Silurian primitive vertebrate *(prospondylus*, Figs. 101–105) probably was. The actual lancelet has gonochoristic structures of a very interesting kind. As we saw in the anatomy of the amphioxus, we find the ovaries of the female and the spermaries of the male in the shape of twenty to thirty pairs of elliptical or roundish four-cornered sacs, which lie on either side of the gut on the parietal surface of the respiratory pore (Fig. 254 *g*). These gonades, at first segmentally distributed over the middle third of the body, are very interesting phylogenetically. Their ontogenetic development teaches us that they originate from the lower part of the ventral cœlom-pouches, the middle part of which forms the uppermost part of the prorenal canals. The metamerous gonades of the acrania are hyposomites of the trunk. According to the important discovery of Rückert (1888), the sexual glands of the earliest fishes, the selachii, are similarly arranged. They only unite afterwards to form a pair of simple gonades. These have been transmitted by heredity to all the rest of the craniotes. In every case they lie originally on each side of the mesentery, underneath the chorda, at the bottom of the body-cavity (Fig. 476 *g*). The first traces of them are found in the cœlom-epithelium, at the spot where the skin-fibre layer and gut-fibre layer meet in the middle of the mesenteric plate (Fig. 480 *mp*). At this point

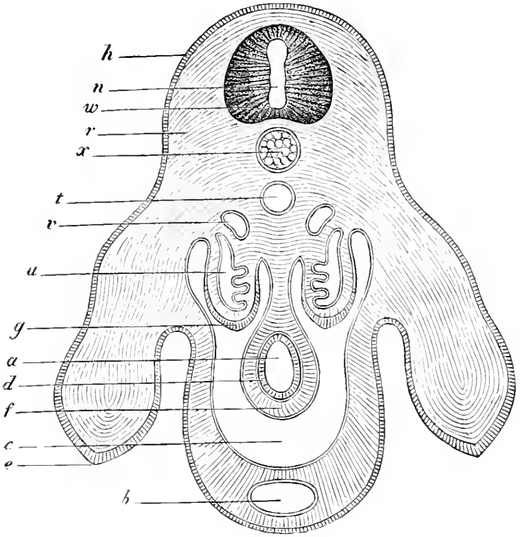


FIG. 476.

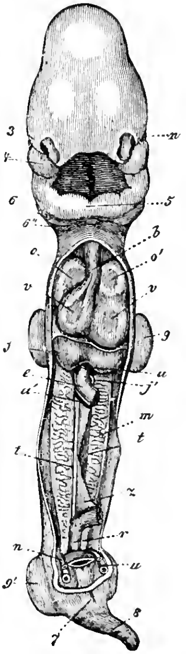


FIG. 477.

FIG. 476.—**Transverse section of the pelvic region and the hind legs of a chick embryo,** third day of incubation, magnified about forty times. *h* horny plate, *w* medullary tube, *n* medullary canal, *u* primitive kidneys, *x* chorda, *e* hind legs, *b* allantoic canal in the ventral wall, *t* aorta, *v* cardinal veins, *a* gut, *d* gut-gland layer, *f* gut-fibre layer, *g* embryonic epithelium, *r* dorsal muscles, *c* body-cavity. (From *Waldeyer.*)

FIG. 477.—**Human embryo,** four weeks old, seen from the ventral side, laid open. The breast and abdominal walls have been removed, so as to show the contents of the thoracic and abdominal cavities. All the appendages (amnion, allantois, yelk-sac) are also removed, and the middle part of the gut. *n* eye, *3* nose, *4* upper jaw, *5* lower jaw, *6* second, *6"* third branchial arch, *w* heart (*o* right, *o'* left auricle; *v* right, *v'* left ventricle), *b* source of aorta, *f* liver (*u* umbilical vein), *e* gut (with the vitelline artery, cut at *a'*), *f'* vitelline vein, *m* primitive kidneys, *t* rudimentary sexual glands, *r* rectum (cut through near the mesentery, *z*), *u* umbilical artery, *7* anus, *8* tail, *9* fore leg, *9'* hind leg. (From *Coste.*)

we observe at an early stage in all craniote embryos a small string-like cluster of cells, which we may call, with Waldeyer, the "germ epithelium," or (in harmony with the other plate-shaped rudimentary organs) the *sexual plate* (Fig. 476 *g;* Plate VI., Fig. 5 *k*). This germinal or sexual plate *(callus germinalis)* is found in the fifth week in the human embryo, in the shape of a couple of long whitish streaks, on the inner side of the primitive kidneys (Figs. 477 *t*, 483 *r*). The cells of this sexual plate *(lamella sexualis)* are distinguished by their cylindrical form and chemical composition from the rest of the cœlom-cells; they have a different purport from the flat cells which line the rest of the body-cavity. As the germ epithelium of the sexual plate becomes thicker, and supporting tissue grows into it from the mesoderm, it becomes a rudimentary sexual gland. This ventral gonad then developes into the ovary in the female craniotes, and the testicles in the male.

In the formation of the gonidia or erotic sexual cells and their conjunction at fecundation we have the sole essential features of sexual reproduction; but in the great majority of animals we find other organs taking part in it. The chief of these secondary sexual organs are the gonoducts, which serve to convey the mature sexual cells out of the body, and the copulative organs, which bring the fecundating male sperm into touch with the ovum-bearing female. The latter organs are, as a rule, only found in the higher animals, and are much less widely distributed than the gonoducts. But these also are secondary formations, and are wanting in many animals of the lower groups.

In the lower animals the mature sexual cells are generally ejected directly from the body. Sometimes they pass out immediately through the skin (hydra and many hydroids); sometimes they fall into the gastric cavity, and are evacuated by the mouth (gastræads, sponges, many medusæ, and corals); sometimes they fall into the body-cavity, and are ejected by a special pore *(porus genitalis)* in the ventral wall. The latter procedure is found in many of the worms, and also in the lowest vertebrates. Amphioxus has the peculiar feature that the mature sexual products fall first into the mantle-cavity ; from there they are either evacuated by the respiratory pore, or else they pass through the gill-clefts into the branchial gut, and so out by the mouth (p. 451). In the cyclostomes they fall into the body-cavity, and are ejected by a genital pore in its wall ; so also in some of the fishes. From these we gather the features of our earlier ancestors in this respect. On the other hand, in all the higher and most of the lower vertebrates (and most of the higher invertebrates) we find in both sexes special tubular passages of the sexual glands, which are called "gonoducts." In the female they conduct the ova from the ovary, and so are called "oviducts," or "Fallopian tubes." In the male they convey the spermatozoa away from the testicles, and are called "spermaducts," or *vasa deferentia.*

The original and genetic relation of these two kinds of ducts is just the same in man as in the rest of the higher vertebrates, and quite different from what we find in most of the invertebrates. In the latter, as a rule, the gonoducts develop directly from the embryonic glands or from the outer skin; but in the vertebrates an independent organic system is employed to convey the sexual products, and this had originally a totally different function—namely, the renal system of urinary organs. These organs have primarily the sole duty of removing unusable matter from the body in a fluid form. Their liquid excretory product, the urine, is either evacuated directly through the skin or through the last section of the gut. It is only at a later stage that the tubular urinary passages also convey the sexual products from the body. In this way they become "urogenital ducts." This remarkable secondary conjunction of the urinary and sexual organs into a common urogenital system is very characteristic of the gnathostomes, the six higher classes of vertebrates. It is wanting in the lower classes. In order to appreciate it fully, we must give a comparative glance at the structure of the urinary organs.

The renal or urinary system *(system uropoeticum)* is one of the oldest and most important systems of organs in the differentiated animal body, as I have pointed out on several previous occasions (cf. Chapter XVII.). We find it not only in the higher stems, but also very generally distributed in the earlier group of the vermalia. Here we meet it in the lowest worms, the rotatoria (gastrotricha, Fig. 425), and in the instructive stem of the platodes, that stands at the border between the cœlenteria and bilateria. Although these platodes have no real body-cavity, blood, vascular system, or anus, they have nearly always a renal system; it is only wanting in the lowest and oldest forms of the stem, the platodaria or cryptocœla (Fig. 474). It consists of a pair of simple or branching canals, which are lined with one layer of cells, absorb unusable juices from the tissue, and eject them by an outlet in the outer skin (Fig. 424 *nm*). Not only the free-living turbellaria, but also the parasitic suctoria, and even the still more degenerate tape-worms, which have lost their alimentary canal in consequence of their parasitic life, are equipped with these renal canals or nephridia. In the first embryonic structure they are merely a pair of simple cutaneous glands, depressions in the ectoderm. They are generally described as excretory organs in the worms, but formerly often as "water vessels." They may be conceived phylogenetically as largely-developed tubular cutaneous glands, formed by invagination of the cutaneous layer. According to another view, they owe their origin to a later rupture of the body-cavity outwards. In most of the vermalia each nephridium has an inner opening (with cilia) into the body-cavity and an outer one on the epidermis.

In these lowest, unsegmented worms, and in the unsegmented molluscs, there is only one pair of renal canals. They are more numerous in the higher articulates. In the annelids, the body of which is composed of a large number of joints or metamera, there is a pair of these pro-nephridia in each segment (hence they are called segmental canals or organs). Even here they are still simple tubes; on account of their coiled or looped form they are often called "looped canals." In most of the annelids, and many of the vermalia, we can distinguish three sections in the nephridium—an outer muscular duct, a glandular middle part, and an inner part that opens by a ciliated funnel into the body-cavity. This opening is furnished with whirling cilia, and can, therefore, take up the juices to be excreted directly from the body-cavity and convey them from the body. But in these worms the sexual cells, which develop in very primitive form on the inner surface of the body-cavity, also fall into it when mature, and are sucked up by the funnel-shaped inner ciliated openings of the renal canals, and ejected with the urine. Thus the urine-forming looped canals, or pronephridia, serve as oviducts in the female annelids and as spermaducts in the male.

The renal system of the vertebrates is similar to, yet materially different from, these segmental canals of the annelids. The peculiar development of it and its relations to the sexual organs are among the most difficult problems in the morphology of our stem. Although the solution had been anticipated by a number of distinguished scientists (Johannes Müller, Rathke, Wilhelm Müller, Fürbringer, etc.), it was not much advanced until the comparative-embryological discoveries of the last decade, especially the important studies of J. Rückert and J. Van Wijhe on the selachii, of Theodor Boveri on the amphioxus, and of Richard Semon on the ichthyophis. These well-directed comparative researches in the light of the theory of descent have enabled us to understand palingenetically a number of remarkable facts that had hitherto been regarded as very mysterious in the ontogeny of our urogenital system; and at the same time we have learned the cenogenetic meaning of many striking secondary divergences from the original type of structure.

If we examine briefly the vertebrate renal system from the phylogenetic point of view, as confirmed by these discoveries, we may distinguish three forms of it: (1) Fore kidneys or head-kidneys *(pronephros)*; (2) primitive or middle kidneys *(mesonephros)*; (3) permanent kidneys *(metanephros)*. These three systems of kidneys are not fundamentally and completely distinct, as earlier students (such as Semper) wrongly supposed; they represent three different generations of one and the same excretory apparatus; they correspond to three phylogenetic stages, and succeed each other in the stem-history of the vertebrates in such wise that each younger and more advanced generation developes farther behind in the body, and replaces the older and less advanced generation that preceded it in time and space. The *fore kidneys,* first accurately described by Wilhelm Müller in 1875 in the cyclostomes and ichthyoda, form the sole excretory organ of the acrania (amphioxus); they continue in the cyclostomes and some of the fishes, but are found only in slight traces and for a time in the embryos of the six other classes of vertebrates. The *primitive kidneys* are first found in the cyclostomes, behind the fore kidneys; they have been transmitted from the selachii to all the gnathostomes. In the *anamnia* they act permanently as urinary glands; in the *amniotes* their anterior part ("germinal kidneys") change into organs of the sexual apparatus, while the third generation developes from the end of their posterior part ("urinal kidneys")—the characteristic after or permanent kidneys of the three higher classes of vertebrates. The ontogenetic order in which the three renal systems succeed each other in the embryo of man and the higher vertebrates corresponds to their phylogenetic succession in the history of our stem, and, consequently, in the natural classification of the vertebrates.

As the segmental arrangement and structure of the kidneys—originally a pair of canals to each segment of the body—is just the same in the vertebrates as in the annelids, it has wrongly been inferred that there is a close affinity between the two stems (pp. 331, 528). This metamerism affords no proof whatever of such relationship; it merely corresponds to the general articulation of the body, which is also found in most of the other organs of the body, but is very different in the two groups. Moreover, in all the vertebrates the renal canals open on each side into a simple duct, the nephroduct; this is completely wanting in the annelids. In them each canal has an independent outlet in the skin.

As in the morphology of any other system of organs, so in the case of the urinary and sexual organs the amphioxus is the real typical primitive vertebrate ; it affords the key to the mysteries of the structure of man and the higher vertebrates. The kidneys of the amphioxus—first discovered by Boveri in 1890—are typical "fore kidneys," composed of a double row of short segmental canals (Fig. 252 *x*). The inner aperture of these pronephridia opens into the mesodermic body-cavity (the middle part of the cœloma, *B*) ; the external aperture into the ectodermic mantle or peri-branchial cavity *(C)*. Their position, their structure, and their relation to the branchial vessel make it clear that these segmental pronephridia correspond to the rudimentary fore kidneys of the craniotes. The mantle-cavity into which they open seems to be homologous to the prorenal duct of the latter.

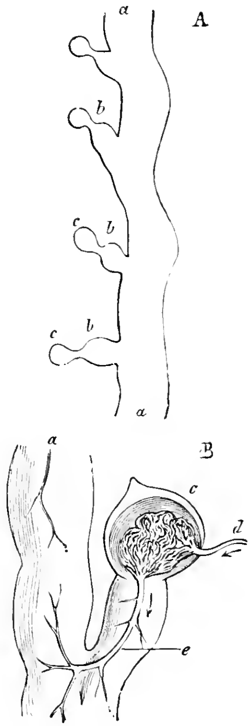


Fig. 478.—*A* **Part of the kidneys of bdellostoma.** *a* prorenal duct *(nephroductus)*, *b* segmental or primitive urinary canals *(pronephridia)*, *c* renal capsules *(capsulæ Malpighianæ)*. *B* **Portion of same,** highly magnified. *c* renal capsules with the *glomerulus*, *d* afferent artery, *e* efferent artery. From *Johannes Müller* (myxinoides).

The next higher vertebrates, the cyclostomes, yield some very interesting data. Both orders of this class, the myxinoides and petromyzontes, have still the fore kidneys inherited from the acrania—the former permanently, the latter in their earlier stages. Behind these the primitive kidneys soon develop, and in a very characteristic form. The remarkable structure of the mesonephros of the cyclostomes, discovered by Johannes Müller, explains the intricate formation of the kidneys in the higher vertebrates. We find in the myxinoides *(bdellostoma)* a long tube, the prorenal duct *(nephroductus*, Fig. 478 *a*). This opens with its anterior end into the cœloma by a ciliated aperture, and externally with its posterior end by an outlet in the skin. Inside it open a large number of small transverse canals ("segmental or primitive urinary canals," *b*). Each of these terminates blindly in a vesicular capsule *(c)*, and this encloses a coil of blood-vessel *(glomerulus*, an arterial network, Fig. 478 *B, c*). Afferent branches of arteries *(vasa afferentia)* conduct arterial blood into the coiled branches of the glomerulus *(d)*, and efferent arterial branches *(vasa efferentia)* conduct it away from the net *(e)*. The primitive renal canals *(mesonephridia)* are distinguished by this net-formation from their predecessors, the simpler fore-lying prorenal canals *(protonephridia)*. At first the prorenal duct receives only the former, but afterwards the latter; it is thus converted into the primitive renal duct *(ductus segmentalis)*.

In the selachii also we find a longitudinal row of segmental canals on each side, which open outwards into the primitive renal ducts *(nephrotomes*, p. 346). The segmental canals (a pair in each segment of the middle part of the body) open internally by a ciliated funnel into the body-cavity. From the posterior group of these organs a compact primitive kidney is formed, the anterior group taking part in the construction of the sexual organs. Transverse sections of the shark embryo (Figs. 416, 417) show that these segmental nephridia of the vertebrates are originally the connecting canals between the dorsal and ventral cœlom-pouches, between the myocœl of the episomites and the gonocœl of the hyposomites (cf. p. 322).

In the same simple form that remains throughout life in the myxinoides and partly in the selachii we find the primitive kidney first developing in the embryo of man and the higher craniotes (Figs. 481, 482). Of the two parts that compose the comb-shaped primitive kidney the longitudinal channel, or nephroduct, is always the first to appear; afterwards the transverse "canals," the excreting nephridia, are formed in the mesoderm; and after this again the Malpighian capsules with their arterial coils are associated with these as cœlous outgrowths. The primitive renal duct, which appears first, is found in all craniote embryos at the early stage in which the differentiation of the medullary tube takes place in the ectoderm, the severance of the chorda from the visceral layer in the entoderm, and the first trace of the cœlom-pouches arises between the limiting layers (Fig. 479). The nephroduct (*ung*) is seen on each side, directly under the horny plate, in the shape of a long, thin, thread-like string of cells. It presently hollows out and becomes a canal, running straight from front to back, and clearly showing in the transverse section of the embryo its original position in the space between horny plate *(h)*, primitive segments *(uw)*, and lateral plates *(hpl)*. The first origin of this nephroduct is still disputed, some embryologists deriving it from the ectoderm, others from the mesoderm; according to a third view the anterior (inner) part of the nephroduct comes originally from the middle, and the posterior (outer) part from the outer germinal layer. The decision as to its embryological origin will affect its phylogenetic significance. Probably the nephroduct of the vertebrates is homologous to the primary nephridia of earlier vermalia, and therefore a "water-vessel" or stem-kidney *(archinephros)*. Its migration in the embryonic shield of the amniotes is very important (Fig. 480). In these it early abandons its superficial position, passes inwards between the provertebral plates and lateral plates, and at last comes to lie on the

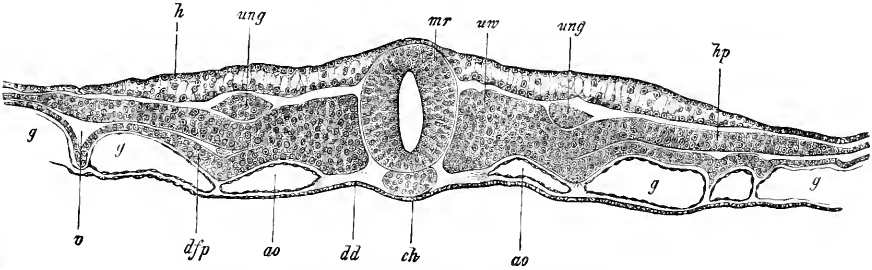


FIG. 479.—**Transverse section of the embryonic shield of a chick,** forty-two hours old. (From *Kölliker.*) *mr* medullary tube, *ch* chorda, *h* horny plate (skin-sense layer), *ung* nephroduct, *uw* episomites (dorsal primitive segments), *hp* skin-fibre layer (parietal layer of the hyposomites), *dfp* gut-fibre layer (visceral layer of hyposomites), *ao* aorta, *g* vessels. (Cf. transverse section of duck-embryo, Fig. 367.)

inner surface of the body-cavity (cf. Figs. 142–150, and Plate VI., Figs. 4–8 *u*). During this migration of the nephroduct a large number of small transverse canals are formed on its inner and lower side (Fig. 481 *a*), corresponding to the segmental pronephridia of the myxinoides (Fig. 478 *b*). At the internal end of each "primitive urinary canal" an arterial network is formed of a branch of the aorta, and this makes a vascular coil *(glomerulus)*. It was formerly supposed that the glomerulus in a sense hollowed out in itself the vesicular internal end of the urinary canal. But Richard Semon shewed in his able work, *On the Morphological Significance of the Primitive Kidney* (1890), that this belief was wrong, and that each renal Malpighian capsule is an outgrowth of the body-cavity, a branch of the cœloma into which the internal end (the ciliated funnel) of a canal opens, and into which a vascular canal penetrates from within. As the originally very short urinary canals lengthen and multiply, each of the two primitive kidneys assumes the form of a half-feathered leaf (Fig. 482). The lines of the leaf are represented by the urinary canals *(u)*, and the rib by the outlying nephroduct *(w)*. At the inner edge of the primitive kidneys the rudiment of the ventral sexual gland *(g)* can now be seen as a body of some size. The hindermost end of the nephroduct opens right behind into the last section of the rectum, thus making a cloaca of it. However, this opening of the nephroducts into the intestine must be regarded phylogenetically as a secondary formation. Originally they

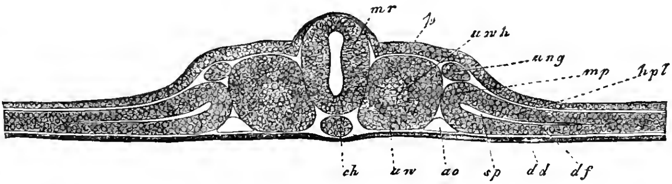


FIG. 480.—**Transverse section of the embryo of a chick,** second day of incubation. *h* horny plate, *mr* medullary tube, *ung* nephroduct, *ch* chorda, *uw* provertebral cord, *hpl* skin-fibre layer, *df* gut-fibre layer, *mp* mesenteric or middle plate (connecting the two fibrous layers), *sp* body-cavity (cœloma), *ao* primitive aorta, *dd* gut-gland layer. (From *Kölliker.*)

open, as the cyclostomes clearly show, quite independently of the gut, in the external skin of the abdomen.

In the myxinoides the primitive kidneys retain this simple comb-shaped structure, and a part of it is preserved in the selachii ; but in all the other craniotes it is only found for a short time in the embryo, as an ontogenetic reproduction of the earlier phylogenetic structure. In these the primitive kidney soon assumes the form (by the rapid growth, lengthening, increase, and serpentining of the urinary canals) of a large compact gland, of a long, oval or spindle-shaped character, which passes through the greater part of the embryonic body-cavity (Figs. 441 *m*, 477 *m*, 483 *n*). It lies near the middle line, directly under the primitive vertebral column, and reaches from the cardiac region to

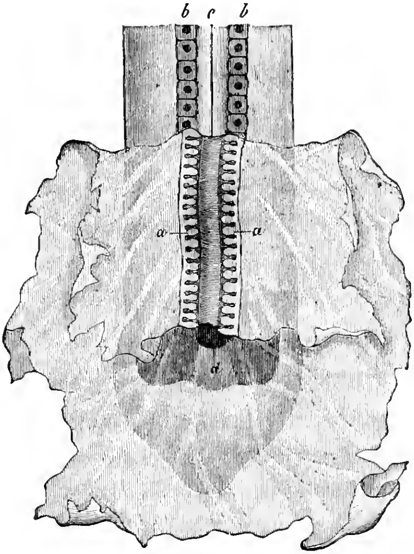


FIG. 481.

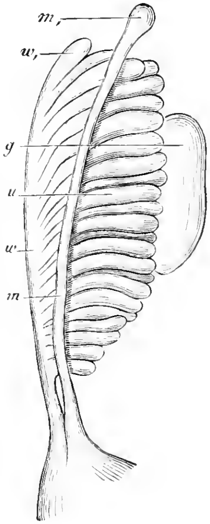


FIG. 482.

FIG. 481.—**Rudimentary primitive kidneys of a dog-embryo.** The hind end of the embryonic body is seen from the ventral side and covered with the visceral layer of the yelk sac, which is torn away and folded down in front in order to show the nephroducts with the primitive urinary canals *(a)*. *b* primitive vertebral column, *c* spinal cord, *d* entrance into the pelvic-gut cavity. (From *Bischoff.*)

FIG. 482.—**Primitive kidneys of a human embryo.** *u* the urinary canals of the primitive kidneys, *w* Wolffian duct, *w'* uppermost end of same (Morgagni's hydatid), *m* Müllerian duct, *m'* uppermost end of same (Fallopian hydatid), *g* gonad (ventral sexual gland). (From *Kobelt.*)

the cloaca. The right and left kidneys are parallel to each other, quite close together, and only separated by the mesentery—the thin narrow layer that attaches the middle gut to the under surface of the vertebral column. The passage of each primitive kidney, the nephroduct, runs towards the back on the lower and outer side of the gland, and opens in the cloaca, close to the starting-point of the allantois; it afterwards opens into the allantois itself (Fig. 211).

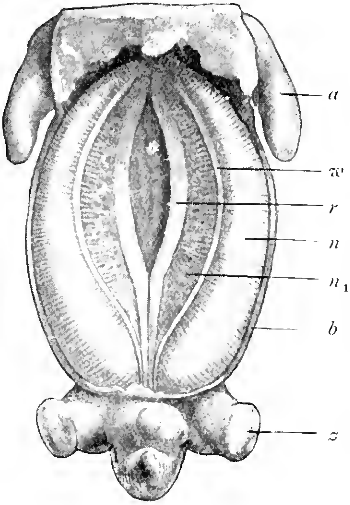


FIG. 483.

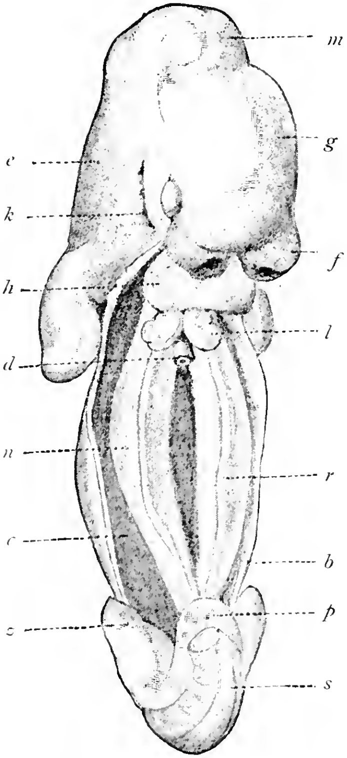


FIG. 484.

FIG. 483.—**Pig-embryo,** fifteen mm. long, magnified six times, seen from the ventral side. *a* fore leg, *z* hind leg, *b* ventral wall, *r* sexual prominence, *w* nephroduct, *n* primitive kidneys, n_1 their inner part. (From *Oscar Schultze.*)

FIG. 484.—**Human embryo** of the fifth week, nine mm. long, magnified ten times, seen from the ventral side (the anterior ventral wall, *b*, is removed, the body-cavity, *c*, opened). *d* gut (cut off), *f* frontal process, *g* cerebrum, *m* middle brain, *e* after brain, *h* heart, *k* first gill-cleft, *l* pulmonary sac, *n* primitive kidneys, *r* sexual region, *p* phallus (sexual prominences), *s* tail. (From *Kollmann.*)

The primitive or primordial kidneys of the amniote embryo were formerly called the "Wolffian bodies," and sometimes the "Oken's bodies." They act for a time as kidneys, absorbing unusable juices from the embryonic body and conducting them to the cloaca—afterwards to the allantois. There the primitive urine accumulates, and thus the allantois acts as bladder or urinary sac in the embryos of man and the other amniotes. It has, however, no genetic connection with the primitive kidneys, but is a pouch-like growth from the anterior wall of the rectum (Fig. 440 *u*). Thus it is a product of the visceral layer, whereas the primitive kidneys are a product of the middle layer. Phylogenetically we must suppose that the allantois originated as a pouch-like growth from the cloaca-wall in consequence of the expansion caused by the urine accumulated in it and excreted by the kidneys. It is originally a blind sac of the rectum (Plate VII., Fig. 15 *hb*). The real bladder of the vertebrate certainly made its first appearance among the dipneusts (in lepidosiren), and has been transmitted from them to the amphibia, and from these to the amniotes. In the embryo of the latter it protrudes far out of the not yet closed ventral wall. It is true that many of the fishes also have a "bladder." But this is merely a local enlargement of the lower section of the nephroducts, and so totally different in origin and composition from the real bladder. The two structures can be compared from the physiological point of view, and so are *analogous*, as they have the same function; but not from the morphological point of view, and are therefore not *homologous*. The false bladder of the fishes is a mesodermic product of the nephroducts; the true bladder of the dipneusts, amphibia, and amniotes is an entodermic blind sac of the rectum.

In all the anamnia (the lower amnion-less craniotes—cyclostomes, fishes, dipneusts, and amphibia) the urinary organs remain at a lower stage of development to this extent, that the primitive kidneys *(protonephri)* act permanently as urinary glands. This is only so as a passing phase of the early embryonic life in the three higher classes of vertebrates, the amniotes. In these the permanent or after or secondary (really *tertiary*) kidneys *(renes* or *metanephri)* that are distinctive of these three classes soon make their appearance. They represent the third and last generation of the vertebrate kidneys. The permanent kidneys do not arise (as was long supposed) as independent glands from the alimentary tube, but from the last section of the primitive kidneys and the nephroduct. Here a simple tube, the secondary renal duct, developes from it, near the point of its entry into the cloaca; and this tube grows considerably forward. With its blind upper or anterior end is connected a glandular renal blastema that owes its origin to a differentiation of the last part of the primitive kidneys. This rudiment of the permanent kidneys consists of coiled urinary canals with Malpighian capsules and vascular coils (without ciliated funnels), of the same structure as the segmental mesonephridia of the primitive kidneys. The further growth of these metanephridia gives rise to the compact permanent kidneys, which have the familiar bean-shape in man and most of the higher mammals, but consist of a number of separate folds in the lower mammals, birds, and reptiles. As the permanent kidneys grow rapidly and advance forward, their passage, the ureter, detaches altogether from its birth-place, the posterior end of the nephroduct; it passes to the posterior surface of the allantois. At first in the oldest amniotes this ureter opens into the cloaca together with the last section of the nephroduct, but afterwards separately from this, and finally into the permanent bladder *(vesica urinaria)* apart from the rectum altogether. The bladder originates from the hindmost and lowest part of the allantoic pedicle *(urachus)*, which enlarges in spindle shape before the entry into the cloaca. The anterior or upper part of the pedicle, which runs to the navel in the ventral wall of the embryo, atrophies subsequently, and only a useless string-like relic of it is left as a rudimentary organ; this is the single vesico-umbilical ligament *(ligamentum vesico-umbilicale medium)*. To the right and left of it in the adult man are a couple of other rudimentary organs, the lateral vesico-umbilical ligaments *(ligamenta vesico-umbilicalia lateralia)*. These are the degenerate string-like relics of the earlier umbilical arteries.

Though in man and all the other amniotes the primitive kidneys are thus early replaced by the permanent kidneys, and these alone then act as urinary organs, all the parts of the former are by no means lost. The nephroducts become very important physiologically by being converted into the passages of the sexual glands. In all the gnathostomes—or all the vertebrates from the fishes up to man—a second similar canal developes beside the nephroduct at an early stage of embryonic evolution. The latter is usually called the Müllerian duct, after its discoverer, Johannes Müller, while the former is called the Wolffian duct. The origin of the Müllerian duct is still obscure; comparative anatomy and ontogeny seem to indicate that it originates by differentiation from the Wolffian duct. Perhaps it would be best to say: "The original, primary nephroduct divides by differentiation (or longitudinal cleavage) into two secondary nephroducts, the Wolffian and the Müllerian ducts." The latter (Fig. 482 *m*) lies just on the inner side of the former (Fig. 482 *w*). Both open behind into the cloaca. (Cf. Tables LVII.–LIX.)

However uncertain the origin of the nephroduct and its two products, the Müllerian and Wolffian ducts, may be, its later development is clear enough. In all the gnathostomes the Wolffian duct is converted into the spermaduct, and the Müllerian duct into the oviduct. Only one of them is retained in each sex; the other either disappears altogether, or only leaves relics in the shape of rudimentary organs. In the male sex, in which the two Wolffian ducts become the spermaducts, we often find traces of the Müllerian ducts, which I have called "Rathke's canals" (Fig. 489 *c*). In the female sex, in which the two Müllerian ducts form the oviducts, there are relics of the Wolffian ducts, which are called "the ducts of Gaertner."

We obtain the most interesting information with regard to this remarkable evolution of the nephroducts and their association with the sexual glands from the amphibia (Figs. 485–491). The first structure of the nephroducts and its differentiation into Müllerian and Wolffian ducts are just the same in both sexes in the amphibia, as in the mammal embryos (Figs. 487, 491). In the female amphibia the Müllerian duct developes on either side into a large oviduct (Fig. 488 *od*), while the Wolffian duct acts permanently as ureter *(u)*.

In the male amphibia the Müllerian duct only remains as a rudimentary organ without any functional significance, as Rathke's canal (Fig. 489 *c*); the Wolffian duct serves also as ureter, but at the same time as spermaduct, the sperm-canals *(ve)* that proceed from the testicles *(t)* entering the fore part of the primitive kidneys and combining there with the urinary canals.

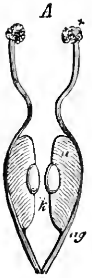


FIG. 485.

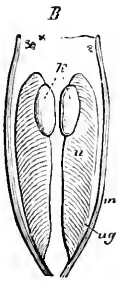


FIG. 486.

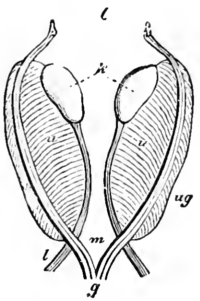


FIG. 487.

FIGS. 485, 486, 487.—**Primitive kidneys and rudimentary sexual organs.** Figs. 485 and 486 of amphibia (frog-larvæ); Fig. 485 earlier, 486 later stage. Fig. 487 of a mammal (ox-embryo). *u* primitive kidney, *k* sexual gland (rudiment of testicle and ovary). The primary nephroduct (*ug* in Fig. 485) divides (in Figs. 486 and 487) into the two secondary nephroducts—the Müllerian *(m)* and Wolffian *(ug')* ducts, joined together behind in the genital cord *(g)*. *l* ligament of the primitive kidneys. (From *Gegenbaur.*)

FIGS. 488, 489.—**Urinary and sexual organs of an amphibian** (water salamander or triton). Fig. 488 of a female, 489 of a male. *r* primitive kidney, *ov* ovary, *od* oviduct and *c* Rathke's duct, both developed from the Müllerian duct, *u* primitive ureter (also acting as spermaduct [*ve*] in the male, opening below into the Wolffian duct [*u'*]), *ms* mesovarium. (From *Gegenbaur.*)

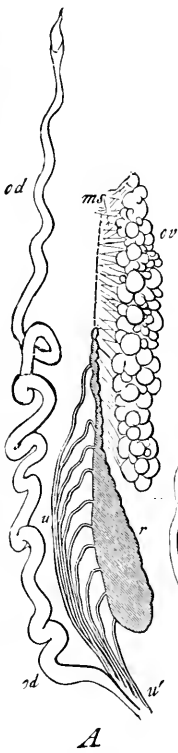


FIG. 488.

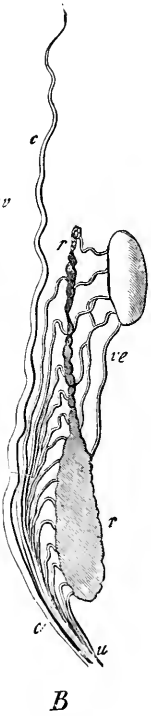


FIG. 489.

In the mammals these permanent amphibian features are only seen as brief phases of the earlier period of embryonic development (Fig. 487). Here the primitive kidneys, which act as excretory organs of urine throughout life in the amnion-less vertebrates, are replaced in the mammals by the permanent kidneys. The real primitive kidneys disappear for the most part at an early stage of development, and only small relics of them remain. In the male mammal the *epididymis* developes from the uppermost part of the primitive kidney; in the female a useless rudimentary organ, the *epovarium*, is formed from the same part. The atrophied relic of the former is known as the *paradidymis*, that of the latter as the *parovarium*.

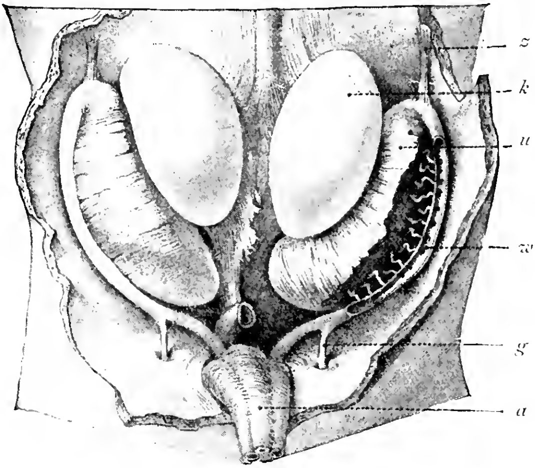


Fig. 490.—**Primitive kidneys and germinal glands of a human embryo,** 77 mm. in length (beginning of the sixth week), magnified fifteen times. *k* germinal gland, *u* primitive kidney, *z* diaphragmatic ligament of same, *w* Wolffian duct (opened on the right), *g* directing ligament (gubernaculum), *a* allantoic duct. (From *Kollmann.*)

The Müllerian ducts undergo very important changes in the female mammal. The oviducts proper are developed only from their upper part; the lower part dilates into a spindle-shaped tube with thick muscular wall, in which the impregnated ovum developes into the embryo. This is the womb (*uterus*). At first the two wombs (Fig. 494 *u*) are completely separate, and open into the cloaca on either side of the bladder (*vu*), as is still the case in the lowest living mammals, the monotremes. But in the marsupials a communication is opened between the two Müllerian ducts, and in the placentals they combine below with the rudimentary Wolffian ducts to form a single "genital cord" (*funiculus genitalis*). The original independence of the two wombs and the vaginal canals formed from their lower ends is retained in many of the lower placentals, but in the higher they gradually blend and form a single organ. The conjunction proceeds from below (or behind) upwards (or forwards). In many of the rodents (such as the hare and squirrel) two separate wombs still open into the simple and single vaginal canal; but in others, and in the carnivora, cetacea, and ungulates, the lower halves of the wombs have already fused into a single piece, though the upper halves (or "horns") are still separate ("two-horned" womb, *uterus bicornis).* In the bats and lemurs the "horns" are very short, and the lower common part is longer. Finally, in the apes and in man the blending of the two halves is complete, and there is only the one simple, pear-shaped uterine pouch,

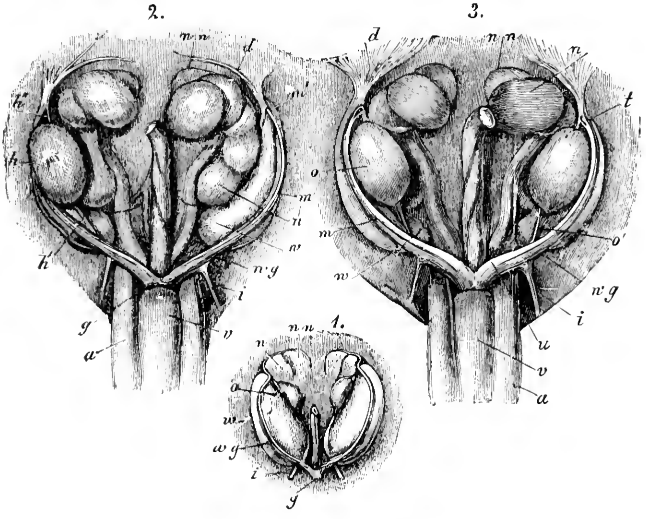


FIG. 492. FIG. 491. FIG. 493.

FIGS. 491-493.—**Urinary and sexual organs of ox-embryos.** Fig. 491, female embryo 1½ inches long; Fig. 492, male embryo 1½ inches long; Fig. 493, female embryo 2½ inches long. *w* primitive kidney, *wg* Wolffian duct, *m* Müllerian duct, *m'* upper end of same (opened at *t*), *i* lower and thicker part of same (rudiment of uterus), *g* genital cord, *h* testicle (*h'* lower and *h''* upper testicular ligament), *o* ovary, *o'* lower ovarium ligament, *i* inguinal ligament of primitive kidney, *d* diaphragmatic ligament of primitive kidney, *nn* accessory kidneys, *n* permanent kidneys, under them the S-shaped ureters, between these the rectum, *v* bladder, *a* umbilical artery. (From *Kölliker.*)

into which the oviducts open on each side. This simple uterus is a late evolutionary product, and is found *only* in the ape and man.

In the male mammals there is the same fusion of the Müllerian and Wolffian ducts at their lower ends. Here again they form a single genital cord (Fig. 492 *g*), and this opens similarly into the original urogenital sinus, which developes from the lowest section of the bladder *(v).* But while in the male mammal the Wolffian ducts develop into the permanent spermaducts, there are only rudimentary relics left of the Müllerian ducts. The most notable of these is the "male womb" *(uterus masculinus)*, which originates from the lowest fused part of the ducts, and is homologous with the female uterus. It is a small, flask-shaped vesicle without any physiological significance, which opens into the ureter between the two spermaducts and the prostate folds *(vesicula prostatica)*.

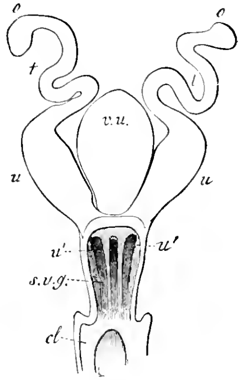


FIG. 494.—**Female sexual organs of the monotreme** *(ornithorhynchus*, Fig. 323). *o* ovaries, *t* oviducts, *u* womb, *sug* urogenital sinus; at *u'* is the outlet of the two wombs, and between them the bladder *(vu)*. *cl* cloaca. (From *Gegenbaur*.)

The internal sexual organs of the mammals undergo very distinctive changes of position. At first the germinal glands of both sexes lie deep inside the ventral cavity, at the inner edge of the primitive kidneys (Figs. 482 *g*, 487 *k*), attached to the vertebral column by a short mesentery *(mesorchium* in the male, *mesovarium* in the female). But this primary arrangement is retained permanently only in the monotremes (and the lower vertebrates). In all other mammals (both marsupials and placentals) they leave their original cradle and travel more or less far down (or behind), following the direction of a ligament that goes from the primitive kidneys to the inguinal region of the ventral wall. This is the inguinal ligament of the primitive kidneys, known in the male as the Hunterian ligament (Fig. 495 *gh*), and in the female as the "round maternal ligament" (Fig. 496 *r*). In woman the ovaries travel more or less towards the small pelvis, or enter into it altogether. In the male the testicles pass out of the ventral cavity, and penetrate by the inguinal canal into a sac-shaped fold of the outer skin. When the right and left folds ("sexual swellings") join together they form the *scrotum*. The various mammals bring before us the successive stages of this displacement. In the elephant

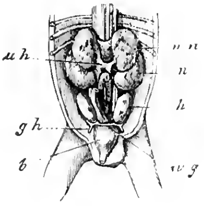


FIG. 495.

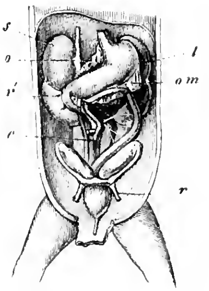


FIG. 496.

FIGS. 495, 496.—**Original position of the sexual glands in the ventral cavity of the human embryo** (three months old). Fig. 495 male (natural size). *h* testicles, *gh* conducting ligament of the testicles, *wg* spermaduct, *h* bladder, *uh* inferior vena cava, *nn* accessory kidneys, *n* kidneys. Fig. 496 female, slightly magnified. *r* round maternal ligament (underneath it the bladder, over it the ovaries), *r'* kidneys, *s* accessory kidneys, *c* cœcum, *o* small reticle, *om* large reticle (stomach between the two), *l* spleen. (From *Kölliker*.)

and the whale the testicles descend very little, and remain underneath the kidneys. In many of the rodents and carnassia they enter the inguinal canal. In most of the higher mammals they pass through this into the scrotum. As a rule, the inguinal canal closes up. When it remains open the testicles may periodically pass into the scrotum, and withdraw into the ventral cavity again in time of rut (as in many of the marsupials, rodents, bats, etc.).

The structure of the external sexual organs, the copulative organs that convey the fecundating sperm from the male to the female organism in the act of copulation, is also peculiar to the mammals. There are no organs of this character in most of the other vertebrates. In those that live in water (such as the acrania, and cyclostomes, and most of the fishes) the ova and sperm-cells are simply ejected into

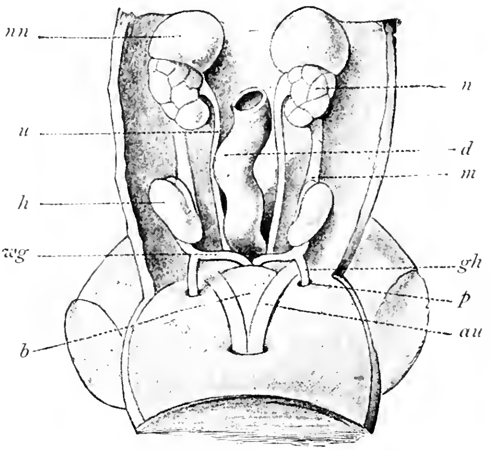


FIG. 497.—**Urogenital system of a human embryo** of seven cm. in length, double natural size. *h* testicles, *wg* spermaducts, *gh* conducting ligament, *p* processus vaginalis, *b* bladder, *au* umbilical arteries, *m* mesorchium, *d* intestine, *u* ureter, *n* kidney, *nn* accessory kidney. (From *Kollmann*.)

the water, where their conjunction and fertilisation are left to chance. But in many of the fishes and amphibia which are viviparous, there is a direct conveyance of the male sperm into the female body; and this is the case with all the amniotes (reptiles, birds, and mammals). In these the urinary and sexual organs always open originally into the last section of the rectum, which thus forms a cloaca (p. 774). Among the mammals this arrangement is permanent only in the monotremes, which take their name from it (Fig. 494 *cl*). In all the other mammals a frontal partition is developed in the cloaca (in the human embryo about the beginning of the third month), and this divides it into two cavities. The anterior cavity receives the urogenital canal *(sinus urogenitalis)*, and is the sole outlet of the urine and the sexual products; the hind or anus-cavity passes the excrements only.

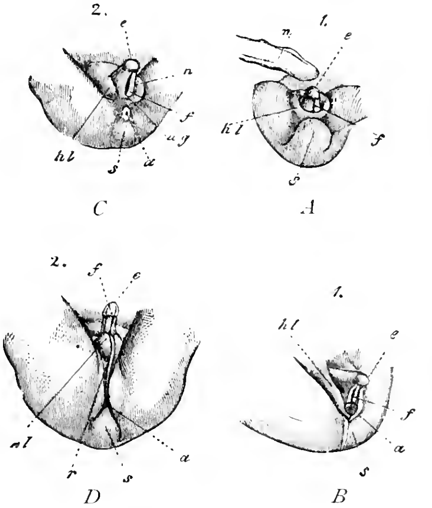


Fig. 498.—**The external sexual organs of the human embryo.** *A* neutral embryo of the eighth week (twice natural size, still with cloaca). *B* neutral embryo of the ninth week (twice natural size; anus separate from the urogenital outlet). *C* female embryo of the eleventh week. *D* male embryo of the fourteenth week. *e* sexual prominence (phallus), *f* sexual groove, *hl* sexual swelling (tori), *r* raphe (seam of the penis and scrotum), *a* anus, *ug* urogenital aperture, *n* umbilical cord, *s* tail. (From *Ecker.*) (Cf. Table LIX.; Figs. 499-504, and Plate XXX.)

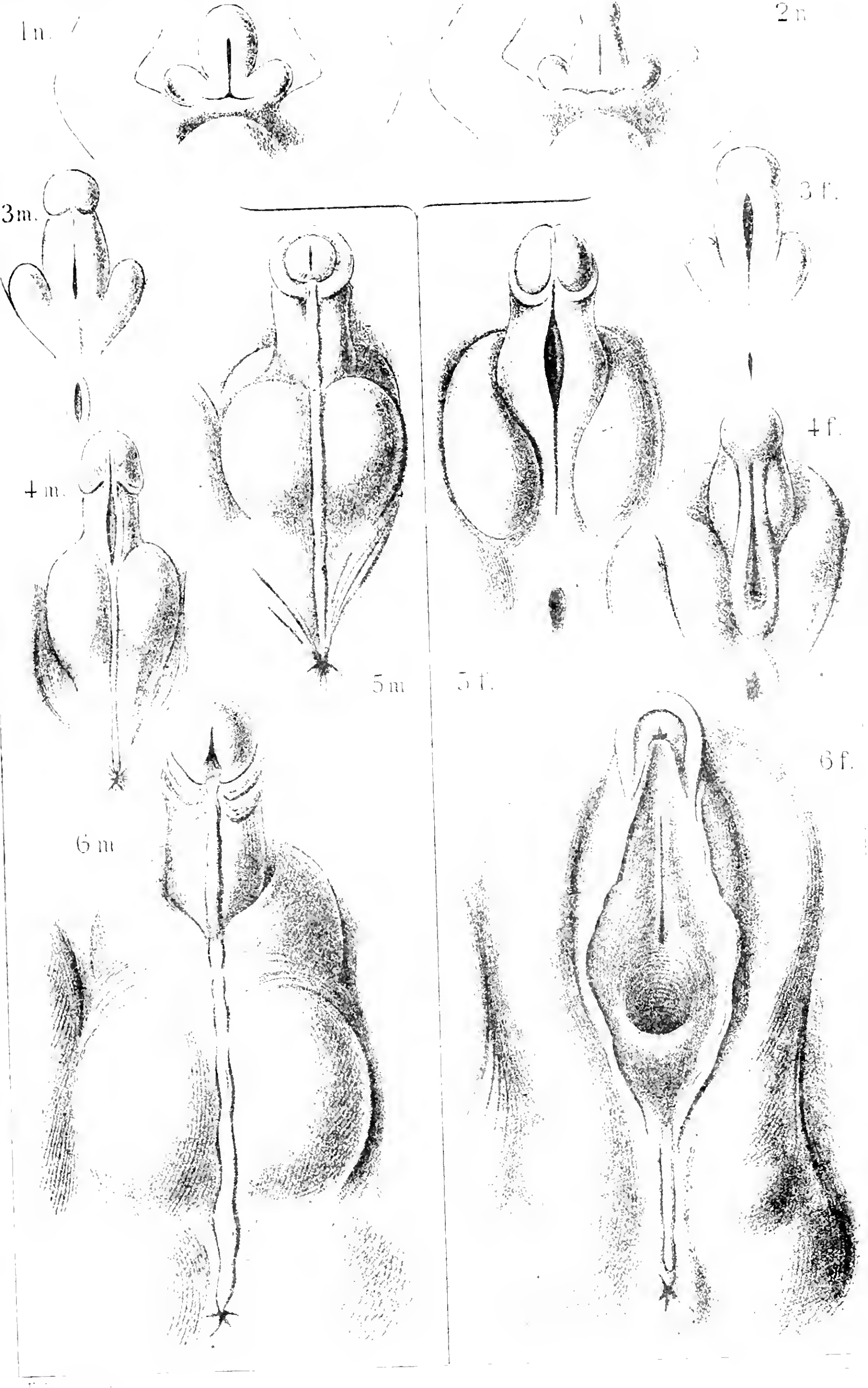
Even before this partition has been formed in the marsupials and placentals, we see the first trace of the external sexual organs *(genitalia*, Plate XXX.). First a conical protuberance rises at the anterior border of the cloaca-outlet—the sexual prominence *(phallus*, Fig. 497 *A*, *e*, *B*, *e*; Figs. 500 *gh*, 501-504 *p*). At the tip it is swollen in the shape of a club ("acorn" *glans)*. On its under side there is a furrow, the sexual groove *(sulcus genitalis, f)*, and on each side of this a fold of skin, the "sexual pad" *(torus genitalis, h l)*. The sexual protuberance or phallus is the chief organ of the sexual sense (p. 682); the sexual nerves spread on it *(nervi pudendi)*, and these are the principal organs of the specific sexual sensation. As erectile bodies *(corpora cavernosa)* are developed in the male phallus by peculiar modifications of the blood-vessels, it becomes capable of erecting periodically on a strong accession of blood, becoming stiff, so as to penetrate into the female vagina and thus effect copulation. In the male the phallus becomes the penis (Fig. 498 *D*, *e*); in the female it becomes the much smaller clitoris (Fig. 498 *C*, *e*); this is only found to be very large in certain apes *(ateles)*. A prepuce ("fore-skin") is developed in both sexes as a protecting fold on the anterior surface of the phallus.

The external sexual member *(phallus)* is found at various stages of development within the mammal class, both in regard to size and shape, and the differentiation and structure of its various parts; this applies especially to the terminal part of the phallus, the glans, both the larger *glans penis* of the male and the smaller *glans clitoridis* of the female. The part of the cloaca from the upper wall of which it forms belongs to the *proctodæum*, the ectodermic invagination of the rectum (p. 754); hence its epithelial covering can develop the same horny growths as the corneous layer of the epidermis. Thus the glans, which is quite smooth in man and the higher apes, is covered with spines in many of the lower apes and in the cat, and in many of the rodents with hairs (marmot) or scales (guinea-pig) or solid horny warts (beaver). Many of the ungulates have a free conical projection on the glans, and in many of the ruminants this "phallus-tentacle" grows into a long cone, bent hook-wise at the base (as in the goat, antelope, gazelle, etc.). The different forms of the phallus are connected with variations in the structure and distribution of the sensory corpuscles—*i.e.*, the real organs of the sexual sense, which develop in certain papillæ of the corium of the phallus, and have been evolved from ordinary tactile corpuscles of the corium by erotic adaptation (p. 682).

The formation of the *corpora cavernosa*, which causes the

EMRYONIC DEVELOPMENT OF THE PHALLUS

The Evolution of Man V Ed Pl XXV



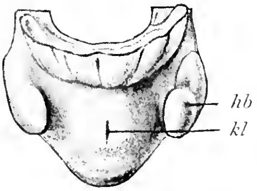


FIG. 499.

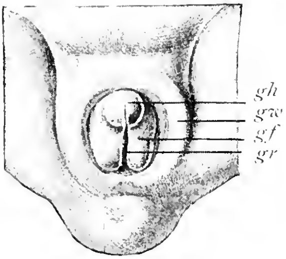


FIG. 500.

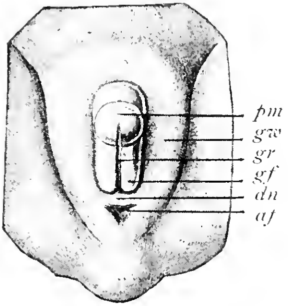


FIG. 501.

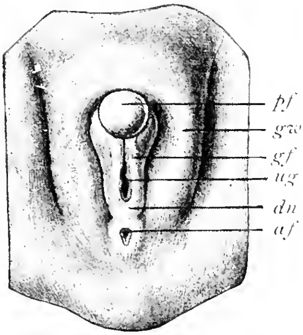


FIG. 502.

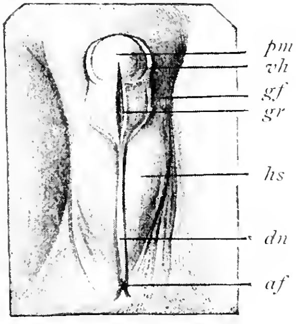


FIG. 503.

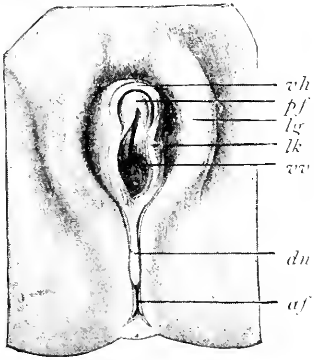


FIG. 504.

FIGS. 499–504.—**Development of the external sexual organs in the male and female human embryo,** at four stages. (From *Ecker*, *Ziegler*, and *Hertwig*.) Fig. 499 (six weeks old) and Fig. 500 (eight weeks old) represent the hind end of two neutral embryos, in which difference of sex cannot yet be detected. Figs. 501 and 503 show the modification of the neutral structure in the male, Figs. 502 and 504 in the female sex (Figs. 501 and 502 are two and a half months old; Figs. 503 and 504 are three months old). The letters have the same meaning throughout: *kl* cloaca, *hb* hind leg, *gh* phallus, *gr* genital groove, *gf* genital fold, *gw* genital pads, *pm* penis, *pf* clitoris, *ug* entrance into the urogenital sinus (vestibule of the vagina, *vv*), *af* anus, *dm* perinæum, *dn* seam (*raphe perinei*), *vh* prepuce, *hs* scrotum, *lg* large labia pudendi, *lk* small labia pudendi. (Cf. Plate XXX.)

stiffness of the phallus and its capability of penetrating the vagina, by certain special structures of their spongy vascular spaces, also shows a good deal of variety within the vertebrate stem. This stiffness is increased in many orders of mammals (especially the carnassia and rodents) by the ossification of a part of the fibrous body *(corpus fibrosum)*. This penis-bone *(os priapi)* is very large in the badger and dog, and bent like a hook in the marten; it is also very large in some of the lower apes, and protrudes far out into the glans. It is wanting in most of the anthropoid apes; it seems to have been lost in their case (and in man) by atrophy.

The sexual groove on the under side of the phallus receives in the male the mouth of the urogenital canal, and is changed into a continuation of this, becoming a closed canal by the juncture of its parallel edges, the male urethra. In the female this only takes place in a few cases (some of the lemurs, rodents, and moles); as a rule, the groove remains open, and the borders of this "vestibule of the vagina" develop into the smaller labia *(nymphæ)*. The large labia of the female develop from the sexual pads *(tori genitales)*, the two parallel folds of the skin that are found on each side of the genital groove. They join together in the male, and form the closed scrotum. These striking differences between the two sexes cannot yet be detected in the human embryo of the ninth week (Fig. 498 *B* and Fig. 500; Plate XXX., Figs. 1 and 2). We begin to trace them in the tenth week of development, and they are accentuated in proportion as the difference of the sexes developes. This is clearly seen in Plate XXX., on which two ventral stages are depicted above (Figs. 1 and 2), and form different later stages in Figs. 3–6, to the left *(m)* of a male, to the right *(w)* of the female genitals. The meaning of the various parts will be seen by comparison with Figs. 499–504 and the explanation of these.

Sometimes the normal juncture of the two sexual pads in the male fails to take place, and the sexual groove may also remain open *(hypospadia*, Fig. 505). In these cases the external male genitals resemble the female, and they are often wrongly regarded as cases of hermaphrodism. Other malformations of various kinds are not infrequently found in the human external sexual organs, and some of them have a great morphological interest. The reverse of hypospadia (Fig. 505), in which the penis is split open below, is seen in *epispadia*, in which the urethra is open above (Fig. 506). In this case the urogenital canal opens above at the dorsal root of the penis; in the former case down below. These and similar obstructions interfere with a man's generative power, and thus prejudicially affect his whole development. They clearly prove that our history is not guided by a "kind Providence," but left to the play of blind chance.

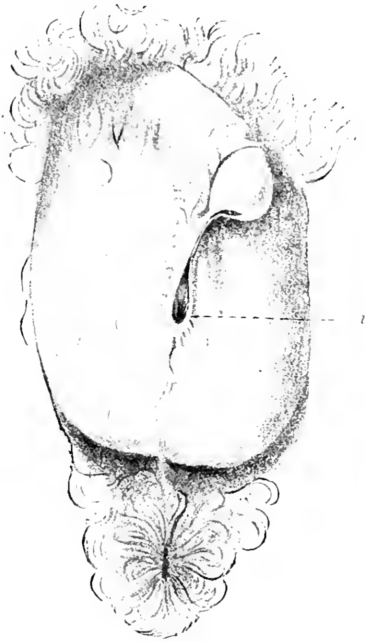


FIG. 505.

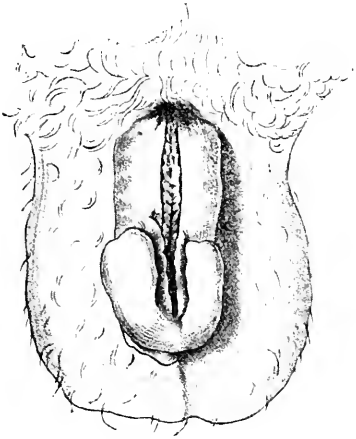


FIG. 506.

FIG. 505.—**Hypospadia of a man** of twenty-two years (*external male hermaphrodism*). The normal closing of the sexual groove is incomplete, also the juncture of the sexual pads; hence the scrotum is cleft in front; the urogenital canal opens at the lower end of the cleft (at *u*). As the penis also is imperfectly developed, and looks like a large clitoris, there is a strong external resemblance to the female genitals ("false hermaphrodism"). (From *W. Gruber*.)

FIG. 506.—**Epispadia of a man,** the opposite of Fig. 505. The penis is cleft at the tip; the urogenital canal issues above at its dorsal root. (From *Bergh*.)

We must carefully distinguish the rarer cases of real hermaphrodism from the preceding. This is only found when the essential organs of reproduction, the genital glands or gonades of both kinds, are united in one individual. In these cases either an ovary is developed on the right and a testicle on the left (or *vice versa)*; or else there are testicles and ovaries on both sides, some more and others less developed. As hermaphrodism was probably the original arrangement in all the vertebrates, and the division of the sexes only followed by later differentiation of this, these curious cases offer no theoretical difficulty. But they are rarely found in man and the higher mammals. On the other hand, we constantly find the original hermaphrodism in some of the lower vertebrates, such as the myxinoides, many fishes of the perch-type *(serranus)*, and some of the amphibia (ringed snake, toad). In these cases the male often has a rudimentary ovary at the fore end of the testicle; and the female sometimes has a rudimentary, inactive testicle. In the carp also and some other fishes this is found occasionally. We have already seen how traces of the earlier hermaphrodism can be traced in the passages of the amphibia.

Man has faithfully preserved the main features of his stem-history in the ontogeny of his urinary and sexual organs. We can follow their development step by step in the human embryo in the same advancing gradation that is presented to us by the comparison of the urogenital organs in the acrania, cyclostomes, fishes, amphibia, reptiles, and then (within the mammal series) in the monotremes, marsupials, and the various placentals (cf. Tables LVII.–LIX.). All the peculiarities of urogenital structure that distinguish the mammals from the rest of the vertebrates are found in man; and in all special structural features he resembles the apes, particularly the anthropoid apes. In proof of the fact that the special features of the mammals have been inherited by man, I will, in conclusion, point out the identical way in which the ova are formed in the ovary. In all the mammals the mature ova are contained in special capsules, which are known as the *Graafian follicles*, after their discoverer, Roger de Graaf (1677). They were

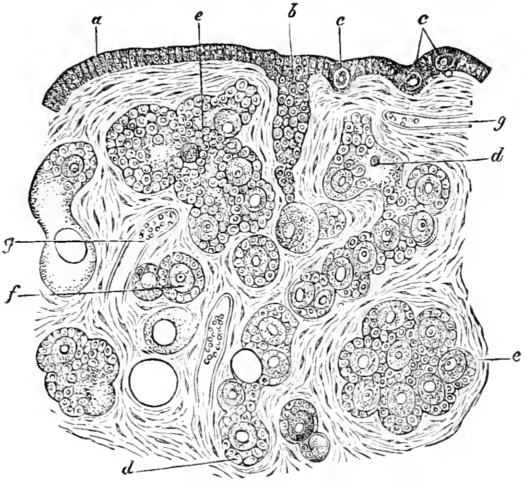


FIG. 507.

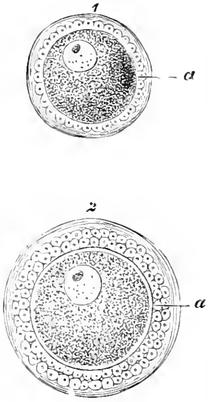


FIG. 508.

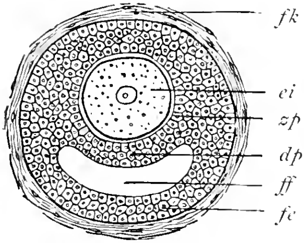


FIG. 509.

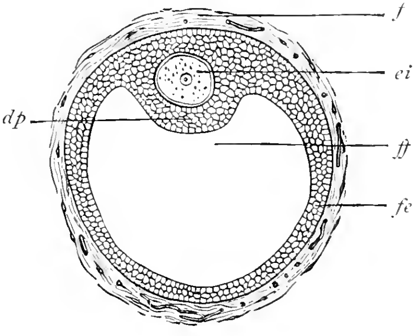


FIG. 510.

FIGS. 507–510.—**Origin of human ova in the female ovary.** Fig. 507. **Vertical section of the ovary** of a new-born female infant. *a* ovarian epithelium, *b* rudimentary string of ova, *c* young ova in the epithelium, *d* long string of ova with follicle-formation (Pflüger's tube), *e* group of young follicles, *f* isolated young follicle, *g* blood-vessels in connective tissue (stroma) of the ovary. In the strings the young ova are distinguished by their considerable size from the surrounding follicle-cells. (From *Waldeyer.*)

FIG. 508.—**Two young Graafian follicles,** isolated. In *1* the follicle-cells still form a simple, and in *2* a double, stratum round the young ovum; in *2* they are beginning to form the ovolemma or the zona pellucida *(a).*

FIGS. 509 and 510.—**Two older Graafian follicles,** in which fluid is beginning to accumulate inside the eccentrically thickened epithelial mass of the follicle-cells (Fig. 509 with little, 510 with much, follicle-water). *ei* the young ovum, with embryonic visicle and spot, *zp* ovolemma or zona pellucida, *dp* discus proligerus, formed of an accumulation of follicle-cells, which surround the ovum, *ff* follicle-liquid *(liquor folliculi)*, gathered inside the stratified follicle-epithelium *(fe)*, *fk* connective-tissue fibrous capsule of the Graafian follicle *(theca folliculi).*

formerly supposed to be the ova themselves; but Baer discovered the ova within the follicles (p. 42). Each follicle (Fig. 511) consists of a round fibrous capsule *(d)*, which contains fluid and is lined with several strata of cells *(c)*. The layer is thickened like a knob at one point *(b)*; this ovum-capsule encloses the ovum proper *(a)*. The mammal ovary is originally a very simple oval body (Fig. 482 *g*), formed only of connective tissue and blood-vessels, covered with a layer of cells, the ovarian epithelium or the female germ epithelium. From this germ epithelium strings of cells grow out into the connective tissue or "stroma" of the ovary (Fig. 507 *b*). Some of the cells of these strings (or Pflüger's tubes) grow larger and become ova (primitive ova, *c*); but the great majority remain small, and form a protective and nutritive stratum of cells round each ovum—the "follicle-epithelium" *(e)*.

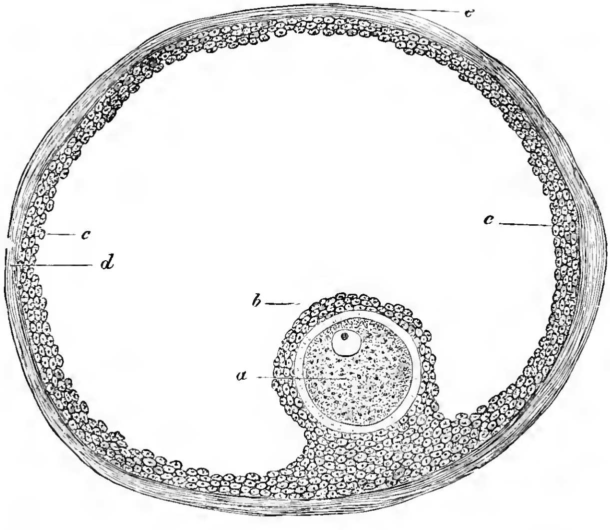


FIG. 511.—**A ripe human Graafian follicle.** *a* the mature ovum, *b* the surrounding follicle-cells, *c* the epithelial cells of the follicle, *d* the fibrous membrane of the follicle, *e* its outer surface.

The follicle-epithelium of the mammal has at first one stratum (Fig. 508 *1*), but afterwards several *(2)*. It is true that in all the other vertebrates the ova are enclosed in a membrane, or "follicle," that consists of smaller cells. But it is only in the mammals that fluid accumulates between the growing follicle-cells, and distends the follicle into a large round capsule, on the inside wall of which the ovum lies, at one side (Figs. 509, 510). There again, as in the whole of his morphology, man proves indubitably his descent from the mammals.

In the lower vertebrates the formation of ova in the germ-epithelium of the ovary continues throughout life; but in the higher it is restricted to the earlier stages, or even to the period of embryonic development. In man it seems to cease in the first year; in the second year we find no new-formed ova or chains of ova (Pflüger's tubes). However, the number of ova in the two ovaries is very large in the young girl; there are calculated to be 72,000 in the sexually-mature maiden. In the production of the ova men resemble most of the anthropoid apes.

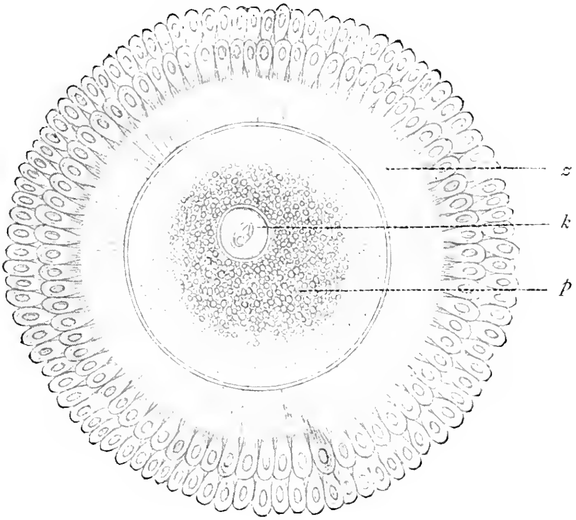


FIG. 512.—**The human ovum** after issuing from the Graafian follicle, surrounded by the clinging cells of the *discus proligerus* (in two radiating crowns). *z* ovolemma (zona pellucida, with radial porous canals), *p* cytosoma (protoplasm of the cell-body, darker within, lighter without), *k* nucleus of the ovum (embryonic vesicle). (From *Nagel*, magnified 250 times.) (Cf. Figs. 1 and 14, pp. 97 and 112.)

Generally speaking, the natural history of the human sexual organs is one of those parts of anthropology that furnish the most convincing proofs of the animal origin of the human race. Any man who is acquainted with the facts and impartially weighs them will conclude from them alone that we have been evolved from the lower vertebrates. The larger and the detailed structure, the action, and the embryological development of the sexual organs are just the same in man as in the apes. This applies equally to the male and the female, the internal and the external, organs. The differences we find in this respect between man and the anthropoid apes are much slighter than the differences between the various species of apes. But all the apes have certainly a common origin, and have been evolved from a long-extinct early-Tertiary stem-form, which we must trace to a branch of the lemurs. If we had this unknown pithecoid stem-form before us, we should certainly put it in the order of the true apes in the primate system; but within this order we cannot, for the anatomic and ontogenetic reasons we have seen, separate man from the group of the anthropoid apes. Here again, therefore, on the ground of the pithecometra-principle, comparative anatomy and ontogeny teach with full confidence the descent of man from the ape.

FIFTY-SEVENTH TABLE

SYNOPSIS OF THE STEM-HISTORY OF THE HUMAN RENAL SYSTEM (STILL VERY UNCERTAIN)

I. First stage: **Stem-kidneys (archinephros).**

The kidney is formed, in the unsegmented ancestors of the vertebrates, of a couple of simple, tubular, glandular canals (probably arising originally from the ectoderm, afterwards found in the mesoderm—or lateral, glandular grooves of the epidermis?).

I. A. **Stem-kidneys of the platodes.**

The kidneys of the platodes are originally a pair of simple glandular tubes of the ectoderm, opening outwards in the epidermis (afterwards longitudinal canals in the mesoderm). As there is no body-cavity in the platodes, the inner ends of their stem-kidneys (excretory tubes or water-vessels) have not yet an outlet; their subsequent branches are also blind-closed ciliated clubs.

I. B. **Stem-kidneys of the vermalia.**

The two tubular cutaneous glands lengthen into coiled glandular canals, the inner end of which opens into the body-cavity by a ciliated funnel (or the two cœlom-pouches pierce outwards?).

I. C. **Stem-kidneys of the prochordonia.**

With the division of the body into head and trunk (branchial and hepatic gut) there is a differentiation of the ducts of the stem-kidneys into two sections: head-kidneys (the later "fore-kidneys") and trunk-kidneys (the later prorenal duct). The former open in front by a ciliated funnel into the head-cavity: the latter outwards and behind by a uroporus (?).

II. Second stage: **Fore kidneys (pronephros).**

With the incipient articulation of the vertebrate body the kidneys also undergo a segmental articulation; the cavity of each primitive segment communicates by a prorenal canal *(pronephridium)* with the trunk renal duct (now the prorenal duct, *nephroductus*, or segmental duct). (?)

II. A. **Fore kidneys of the prospondylia.**

The simple body-cavity of each primitive segment forms a lateral outgrowth, which opens outwards into the ectodermic nephroduct (perhaps also, originally, into a lateral longitudinal groove of the horny plate, from which the nephroduct originated by constriction (?). Cf. Plate VI., Figs. 5-8).

II. B. **Fore kidneys of the acrania (amphioxus).**

Each primitive segment has divided by a lateral constriction (formation of the frontal septum) into an upper or dorsal cœlom-pouch *(myotome*, episomite) and a lower or ventral cœlom-pouch *(gonotome*, hyposomite); from the cavity of the former *(myocœl)* issues the muscular secretion (urine), and from the cavity of the latter *(gonocœl)* the sexual products. Both secretions are conveyed by the segmental prorenal canal, which opens with a ciliated funnel into a diverticulum of the gonotome, with an outer opening in the nephroduct. The latter is in the amphioxus enlarged into a mantle (or peribranchial) cavity. A segmental loop of the intestinal vein pushes into the cœlom-diverticulum, into which the ciliated funnel opens.

II. C. Fore kidneys of the cyclostomes.

The fore kidneys form a pair of small racemose glands in the hindmost part of the head section, which are originally composed of a small number (generally three to four) of segmental tubes; these pronephridia open with their median ciliated funnels into the head-cœlom (or the primary pericardial cavity, *cardiocœl)*, with their lateral openings into the anterior end of the prorenal duct. The pronephros is permanent in the myxinoides, but degenerates at an early period in the petromyzontes. Its function is taken up by the primitive kidneys.

II. D. Fore kidneys of the gnathostomes.

The fore kidneys make an early appearance in the embryos of all the gnathostome craniotes, as a heritage from the cyclostomes, but have generally lost their physiological significance, and soon atrophy. Among the anamnia they remain sometimes in the teleostei, and have a passing function in the larvæ of the amphibia. In the amniotes they are merely rudimentary organs (according to certain recent indications the inner funnel of the Müllerian duct seems to be developed from them?).

III. Third stage: Primitive kidneys (mesonephros).

The segmental fore kidneys (pronephros) of the earliest and lowest vertebrates are gradually replaced by a second generation of nephridia—segmental canals which develop backwards, upwards, and outwards from the former: these dorso-lateral prorenal canals *(mesonephridia)* open originally—like their predecessors, the ventro-median prorenal canals *(protonephridia)*—inwards with ciliated funnels into the body-cavity, and outwards into the nephroduct; thus the fore kidney duct becomes the primitive kidney duct.

III. A. Primitive kidneys of the cyclostomes.

While the small fore kidneys remain as rudimentary "head-kidneys," opening into the head-cœlom, the long primitive kidneys ("trunk kidneys") develop behind them; in very simple and primitive form in *bdellostoma:* numbers of short segmental canals open with the internal ciliated funnels into the cœlom, and with the outer end into the long fore kidney duct, which thus becomes the primitive kidney duct. In the other cyclostomes *(myxine, petromyzon)* the primitive kidneys become larger and more complex.

III. B. Primitive kidneys of the anamnia (ichthyoda).

In all the anamnia (the fishes, dipneusts, and amphibia) the primitive kidneys are the sole urinary organs. The fore kidneys are found in the embryo, but quickly atrophy, except in a few teleostei and amphibian larvæ. There are as yet no permanent kidneys. The ciliated funnels *(nephrostomes)*, with which the prorenal canals originally open into the ventral cavity, remain in many of the selachii and amphibia. In these groups the compact primitive kidney divides into an anterior germinal part (sexual kidney) and a posterior urinary part (pelvic kidney). At the same time, the nephroduct splits into two parallel ducts, an inner (median) Müllerian duct and an outer (lateral) Wolffian duct. The former acts as oviduct, the other as urino-sperm duct.

III. C. Primitive kidneys of the amniotes.

In all the amniotes the permanent or after kidneys alone act as urinary organs; these are wanting in the five lower classes of vertebrates. They originate from the hindmost section of the primitive kidneys and the nephroduct. The anterior genital part of the primitive kidneys becomes the *paradidymis* (in the female the rudimentary *parovarium*).

IV. Fourth stage: **Permanent kidneys (metanephros).**

The segmental primitive kidneys *(mesonephros)* of the anamnia or ichthyoda are gradually replaced by a third generation of segmental canals, which develop in the rear of the former. These after-kidney canals *(metanephridia)* compose the excretory apparatus of the permanent kidneys (the cortical substance with the coiled canals and the Malpighian capsules); they open into the ejection-apparatus, which is formed from the medullary substance (pyramids with straight canals, renal pelvis, and ureter), and which developes from the hindmost section of the nephroduct. The ciliated funnels of the primitive kidneys disappear in the permanent kidneys.

IV. A. **Permanent kidneys of the reptiles.**

The permanent kidneys of the earlier amniotes lie far back in the pelvis, in accord with their phyletic origin from the hind urinary part of the primitive kidneys. Their surface is composed of a number of folds at first.

IV. B. **Permanent kidneys of the mammals.**

The permanent kidneys of the later amniotes move forward. Their original folded surface disappears in most of the mammals, and the bean-shaped organ usually has a smooth surface, as in man. The special features of the human kidneys resemble those of the apes.

FIFTY-EIGHTH TABLE

SYNOPSIS OF THE STEM-HISTORY OF THE HUMAN SEXUAL ORGANS

LVIIIA. First Section : **Sexual and urinary organs are separate, and have no relation to each other.**

I. First period : **Gastræad-gonades.**

The sexual cells or gonidia (ova and sperm cells) develop from one of the two primary germinal layers, at first generally, afterwards from a pair of lateral cells at the edge of the primitive mouth [the "primitive cells of the mesoderm" *(promesoblasts)* or "primary sexual cells" *(progonidia)*].

II. Second period : **Platode-gonades.**

The production of sexual cells is restricted to a pair of lateral strings of cells in the wall of the primitive gut or to two mesodermic streaks, which spread from the primitive mouth between the two primary germinal layers (germinal parts or *primitive gonades)*.

III. Third period : **Vermalian-gonades.**

The solid mesodermic streaks dilate from the primitive gut, and thus become a couple of simple sexual pouches *(primary cœlom-pouches)*; their cavity is the rudiment of the *cœloma* or *enterocœl*; the cœlom-epithelium of their wall yields the sexual products (ova in front, sperm-cells behind).

IV. Fourth period : **Prochordonia-gonades.**

The two hermaphroditic glands divide by a transverse constriction into an ovary (in front) and a testicle (behind). Afterwards hermaphrodism is replaced by gonochorism (separation of the sexes), the ovary being transmitted to one (the female) part of the offspring, and the spermary to the other (male).

V. Fifth period : **Acrania-gonades.**

As the segmentation of the vertebrate body commences, starting from the muscular system of the episomites, the gonades of the hyposomites also divide into a row of sexual glands on each side, like the segmental gonades of the amphioxus.

VI. Sixth period : **Cyclostome-gonades.**

The segmental structures of the sexual glands (still found in the embryos of the selachii) coalesce at an early embryonic stage into a single gonad on each side. The ripe sexual products fall into the body-cavity, and are ejected by a pore in the ventral wall (a *porus genitalis* behind the anus).

LVIIIB. Second Section : **Sexual and urinary organs joined.**

(Genital and urinary systems combined in a urogenital system.)

VII. Seventh period : **Proselachii-urogenitals.**

The nephroduct, which acted merely as ureter in the five preceding stages, now becomes sexual duct also, and in both sexes accomplishes the ejection of the sexual products.

VIII. Eighth period: **Ganoid-urogenitals.**

The anterior part of the nephroduct divides into two canals, of which the inner or middle (Müllerian duct) acts as genital duct in both sexes (as in some of the ganoids), while the outer or lateral (Wolffian duct) only acts as urinary duct. The hind part of the nephroduct, which receives both ducts, is a combined "urogenital" duct.

IX. Ninth period: **Dipneust-urogenitals.**

The cleavage of the nephroduct into two parallel canals is complete. The external canal (Wolffian duct) acts as ureter in both sexes, and also as sperm duct in the male, while the Müllerian duct developes into the oviduct (as in the later selachii and the dipneusts). The single bladder developes from the ventral wall of the rectum (lepidosiren).

X. Tenth period: **Amphibian-urogenitals.**

From the uppermost part of the atrophying primitive kidneys the paradidymis is formed in the male and the parovarium in the female. The Wolffian duct acts still in both sexes as ureter, and in the male as spermaduct also. The Müllerian duct acts as oviduct in the female; in the male it is a rudimentary organ (Rathke's duct).

XI. Eleventh period: **Proreptile-urogenitals.**

The permanent kidneys replace the degenerating primitive kidneys as urinary organs; they develop from the hind end of the latter out of a later-formed piece. Into this "metanephro-blastema" a blind-sac shaped projection of the hind end of the nephroduct makes its way from behind, and developes into the ureter. The bladder protrudes from the ventral opening of the embryo, and forms the allantois. The phallus developes from the anterior wall of the cloaca, and becomes the penis in the male, the clitoris in the female.

XII. Twelfth period: **Monotreme-urogenitals.**

The neck of the bladder (or the base of the allantoic pedicle) receives the mouths of the secondary nephroducts and ureters, and developes into the urogenital sinus. The lower end of the oviduct expands on each side into a muscular womb (uterus). The phallus assumes the distinctive monotreme structure (a pair of erectile bodies in the cloaca-wall).

XIII. Thirteenth period: **Marsupial-urogenitals.**

The cloaca is divided by a partition into a urogenital aperture in front and anus behind. A vaginal canal proceeds from the lower part of the uterus on each side. The two erectile bodies of the monotremes (corpora cavernosa urethræ) unite, and connect with two upper corpora cavernosa penis, which develop from the ischium. The male sinus urogenitalis becomes the urethra. The ovaries and testicles begin to move away from the place of their development.

XIV. Fourteenth period: **Lemur-urogenitals.**

Müllerian and Wolffian ducts fuse into genital cords below. The uterus bicornis is formed by the coalescence at the lower part of the two wombs. Part of the allantois is converted into the placenta. The testicles pass from the ventral cavity through the inguinal canal into a couple of folds of the skin (genital swellings), which unite to form the scrotum.

XV. Fifteenth period: **Ape-urogenitals.**

The two wombs unite in their whole length, and form a single pear-shaped uterus, as in man. The edges of the sexual groove develop into the small labia pudendi. The penis hangs freely from the pubic bone, and assumes the special features that distinguish the anthropoid apes and man.

FIFTY-NINTH TABLE

SYNOPSIS OF THE HOMOLOGIES OF THE SEXUAL ORGANS IN BOTH SEXES OF THE MAMMALS

LIX. A. Homologies of the Internal Sexual Organs (Germinalia).

C. Common Rudiments of the Internal Sexual Organs.	**M. Internal Male Parts.**	**F. Internal Female Parts.**
1. Germinal gland (gonad).	1. Testicle *(spermarium* or *testis).*	1. Ovary *(ovarium* or *oophoron).*
2. Chains of primitive ova (indifferent sex-cells).	2. Sperm-ampullæ, sperm-canals.	2. Graafian follicle.
3. Wolffian duct (lateral nephroduct).	3. Spermaduct *(spermaductus, vas deferens).*	3. Gaertner's duct (rudimentary canal).
4a. Müllerian duct (median nephroduct).	4a. Rathke's duct (rudimentary canal in the amphibia).	4a. Oviduct *(oviductus* or *tuba Fallopia).*
4b. Anterior (upper) part of the Müllerian duct.	4b. Morgagni's hydatid.	4b. Fallopian hydatid.
4c. Posterior (lower) part of the Müllerian duct.	4c. Uterus masculinus *(vesicula prostatica).*	4c. Uterus (womb), vagina.
5. Relics of the primitive kidneys *(pronephros, corpus Wolffii).*	5. Epididymis.	5. Epovarium.
6. Inguinal ligament of the primitive kidneys *(ligamentum protonephro-inguinale).*	6. Hunterian ligament *(gubernaculum Hunteri).*	6. Round ligament of the womb *(ligamentum uteri rotundum).*
7. Genital mesentery *(mesogonium).*	7. Mesentery of testicles *(mesorchium).*	7. Mesentery of ovaries *(mesovarium).*

LIX. B. Homologies of the External Sexual Organs (Genitalia).

C. Common Rudiments of the External Sexual Organs.	**M. External Male Parts.**	**F. External Female Parts.**
8. Phallus.	8. Penis.	8. Clitoris.
9. Glans. Sexual sense-organ.	9. Glans penis.	9. Glans clitoridis.
10. Prepuce *(præputium).*	10. Prepuce of the penis.	10. Prepuce of the clitoris.
11. Genital pads *(tori genitales).*	11. Scrotum.	11. *Labia pudendi majora.*
12. Cleft between the genital pads.	12. Scrotum-seam *(raphe scroti).*	12. *Vulva.*
13. Genital folds (edges of the genital groove, *plicæ genitales).*	13. Ventral wall of the male urethra.	13. *Nymphæ, labia pudendi minora.*
14. Urogenital sinus.	14. Male urethra.	14. *Vestibulum vaginæ.*
15. Accessory glands of the urogenital sinus.	15. Cowper's glands.	15. Bartolini's glands.

EXPLANATION OF PLATES

Plates IV. and V. Sandal-shaped embryos of six amniotes.

(Between pp. 302–303.)

The eighteen figures of these Plates show the highly characteristic sandal-embryo or "sole-shaped embryonic shield" of six amniotes from the dorsal side (from above) at three stages of development.

On Plate IV. are the embryos of three sauropsids: *L* lizard, *T* tortoise, *H* hen; on Plate V., the embryos of three mammals: *P* pig, *H* hare, *M* man. The obvious resemblance of the three corresponding stages would be even greater if it had been possible to place side by side exactly corresponding stages. But illustrations of these delicate objects at such early stages are very difficult to get at just the same age, and the soft bodies soon change their form in consequence of the necessary treatment with preparing fluids; moreover, the same object is often differently depicted by different observers, according to the microscopic illumination, and so on. Apart from this, there is a substantial identity at the corresponding stages, not only in outward appearance, but also in internal structure.

The first row (across, I.) shows the six sandal-embryos at the characteristic stage of development that I have called the "chordula" or chorda-larva (Figs. 86–89). The vertebrate organism is still unsegmented or "invertebrate" at this stage; it consists merely of the six fundamental organs (pp. 243, 244). We see the medullary groove in the fore half of the back, and the primitive groove (primitive mouth) and neurenteric canal in the hind half. (Cf. Figs. 124–136.)

The second row (middle row, II.) shows the commencement of segmentation or vertebration in the sandal-embryo. In the middle of the dorsal shield there are four to six pairs of provertebræ (episomites), the first cervical vertebræ. The fore-lying (upper) third forms the head of the embryo; in this the simple brain makes its appearance as a vesicular bulb of the medullary tube. In the hind third the medullary groove is still wide open, and passes by the neurenteric canal into the primitive gut. (Cf. Figs. 134–138.)

The third row (III.) shows the sandal-embryo at a later stage of vertebration. At each side of the closed medullary tube we already see ten to twelve pairs of provertebræ; the number continually increases with the growth of the hind end of the body. In front we see the articulation of the brain, the simple vesicle dividing by transverse constrictions into three to five cerebral vesicles. The optic vesicles are seen to right and left in the fore brain (above). (Cf. Figs. 156–166.)

Plate I. (frontispiece). Evolution of the human face.

This Plate shows the changes that the human face undergoes in the course of individual life. The face is seen from the front. (Cf. Plate XXIV. and the explanations in Chapter XXV., pp. 685–689, and especially Figs. 373–379, with explanations.)

Plate XXIV. Evolution of the mammal face.

The twelve figures of this Plate show the face of four different mammals at three stages of individual development: Mi–Miii man, Bi–Biii bat, Ci–Ciii cat, and SI–SIII sheep. The three stages have been chosen so as to correspond as closely as possible in the four mammals; they have been reduced to about the same size, and are seen from the front. The letters have the same meaning throughout: *a* eye, *v* fore brain, *m* middle brain, *s* frontal process, *k* roof of nose, *o* upper jaw process (of the first gill-arch), *u* lower jaw process (of the first branchial arch), *h* second gill-arch, *d* third branchial arch, *r* fourth gill-arch, *g* auditory cleft (relic of the first gill-cleft), *z* tongue. (Cf. Plate I. and the explanations in Chapter XXV., pp. 685–690.)

Plates XXVIII. and XXIX.

Fore feet (carpomela) and hind feet (tarsomela) of twelve different mammals. Copied from Huxley's *Elementary Atlas of Comparative Osteology*, 1864 (Plates X. and XII.).

1. **Man** *(homo sapiens).*
2. **Gorilla** *(gorilla gina).*
3. **Chimpanzee** *(anthropithecus niger).*
4. **Orang** *(satyrus orang).*
5. **Climbing ape** *(ateles belzebuth).*
6. **Clawed ape** *(hapale jacchus).*
7. **Lemur** *(lichanotus indri).*
8. **Bear** *(ursus labiatus).*
9. **Pig** *(sus scrofa).*
10. **Rhinoceros** *(rhinoceros indicus).*
11. **Ox** *(bos taurus).*
12. **Horse** *(equus caballus).*

Plate XXVIII. represents the left fore foot (hand) of seven primates (Figs. 1–7), one carnivore (Fig. 8), and four ungulates (Figs. 9–12). Plate XXIX. represents the left foot (foot) of the same twelve genera.

Bones of hand *(carpalia).*		Bones of foot *(tarsalia).*	
a Scaphoideum	= a *Radiale.*	a Astralagus	= a *Tibiale.*
b Lunatum	= b *Intermedium.*	b a + b	= b *Intermedium*
c Triquetrum	= c *Ulnare.*	c Calcaneus	= c *Fibulare.*
d (Centrale)	= *(Centrale regr).*	d Naviculare	= d *Centrale.*
e Trapezium	= *Carpale I.*	e Cuneiform I.	= Tarsale I.
f Trapezoides	= *Carpale II.*	f Cuneiform II.	= Tarsale II.
g Capitatum	= *Carpale III.*	g Cuneiform III.	= Tarsale III.
h Hamatum	= *Carpale IV. & V.*	h Cuboides	= *Tarsalia IV. & V.*

Cf. pp. 713 and 736.

CHAPTER XXX.

RESULTS OF ANTHROPOGENY

Retrospect along the line of embryology. Explanation of it by the biogenetic law. Its causal connection with phylogeny. Inheritance of features acquired by adaptation. Rudimentary organs in man. Dysteleology. Heritages from the apes. Man's place in the classification of the animal world. Man as vertebrate and mammal. Special relationship of man and the apes. Evidence on the ape-question. Divine origin of man. Adam and Eve. Embryology of the soul. Immense psychic differences within a single class of animals. Mammal souls and insect souls. Ant souls and coccus souls. Human souls and ape souls. Organ of psychic action: central nervous system. Ontogeny and phylogeny of the soul. Monistic and dualistic theories of the soul. Psychic inheritance. Significance of the biogenetic law for psychology. Importance of anthropogeny for the victory of the monistic philosophy. Nature and spirit. Natural science and mental science. Monism and dualism. Reform of philosophy by anthropogeny.

Now that we have traversed the wonderful region of human embryology and are familiar with the principal parts of it, it will be well to look back on the way we have come, and forward to the further path to truth to which it has led us. We started from the simplest facts of ontogeny, or the development of the individual—from observations that we can repeat and verify by microscopic and anatomic study at any moment. The first and most important of these facts is that every man, like every other animal, begins his existence as a simple cell. This round ovum has the same characteristic form and origin as the ovum of any other mammal. From it is developed in the same manner in all the placentals, by repeated cleavage, a multicellular blastula. This is converted into a gastrula, and this in turn into a blastocystis (or embryonic vesicle). The two strata of cells that compose its wall are the primary germinal layers, the skin-layer (ectoderm) and gut-layer (entoderm). This two-layered embryonic form is the ontogenetic reproduction of the extremely important phylogenetic stem-form of all the metazoa, which we have called the gastræa. As the human embryo passes through the gastrula-form like that of all the other metazoa, we can trace its phylogenetic origin to the gastræa.

As we continued to follow the embryonic development of the two-layered structure, we saw that first a third or middle layer (mesoderm) appears between the two primary layers; when this divides into two, we have the four secondary germinal layers. These have just the same composition and genetic significance in man as in all the other vertebrates. From the skin-sense layer are developed the epidermis, the central nervous system, and the chief part of the sense-organs. The skin-fibre layer forms the corium and the motor organs—the skeleton and the muscular system. From the gut-fibre layer are developed the vascular system, the muscular wall of the gut, and the sexual glands. Finally, the gut-gland layer only forms the epithelium, or the inner cellular stratum of the mucous membrane of the alimentary canal and glands (lungs, liver, etc.).

The manner in which these different systems of organs arise from the secondary germinal layers is essentially the same from the start in man as in all the other *vertebrates*. We saw, in studying the embryonic development of each organ, that the human embryo follows the special lines of differentiation and construction that are only found otherwise in the vertebrates. Within the limits of this vast stem we have followed, step by step, the development both of the body as a whole and of its various parts. This higher development follows in the human embryo the form that is peculiar to the mammals. Finally, we saw that, even within the limits of this class, the various phylogenetic stages that we distinguish in a natural classification of the mammals correspond to the ontogenetic stages that the human embryo passes through in the course of its evolution. We were thus in a position to determine precisely the position of man in this class, and so to establish his relationship to the different orders of mammals.

The line of argument we followed in this explanation of the ontogenetic facts was simply a consistent application of the biogenetic law. In this we have throughout taken strict account of the distinction between palingenetic and cenogenetic phenomena. Palingenesis (or "synoptic development") alone enables us to draw conclusions from the observed embryonic form to the stem-form preserved by heredity. Such inference becomes more or less precarious when there has been cenogenesis, or disturbance of development, owing to fresh adaptations. We cannot understand embryonic development unless we appreciate this very important distinction. Here we stand at the very limit that separates the older and the new science or philosophy of nature. The whole of the results of recent morphological research compel us irresistibly to recognise the biogenetic law and its far-reaching consequences. These are, it is true, irreconcilable with the legends and doctrines of former days, that have been impressed on us by a more or less religious education. But without the *biogenetic law*, without the distinction between *palingenesis* and *cenogenesis*, and without the theory of *evolution* on which we base it, it is quite impossible to understand the facts of organic development; without them we cannot cast the faintest gleam of explanation over this marvellous field of phenomena. But when we recognise the causal correlation of ontogeny and phylogeny expressed in this law, the wonderful facts of embryology are susceptible of a very simple explanation; they are found to be the necessary mechanical effects of the evolution of the stem, determined by the laws of heredity and adaptation. The correlative action of these laws under the universal influence of the struggle for existence, or—as we may say in a word, with Darwin—"natural selection," is entirely adequate to explain the whole process of embryology in the light of phylogeny. It is the chief merit of Darwin that he explained by his theory of selection the correlation of the laws of heredity and adaptation that Lamarck had recognised, and pointed out the true way to reach a causal interpretation of evolution.

The phenomenon that it is most imperative to recognise in this connection is the inheritance of functional variations. Jean Lamarck was the first to appreciate its fundamental importance in 1809, and we may therefore justly give the name of Lamarckism to the theory of descent he based on it. Hence the radical opponents of the latter have very properly directed their attacks chiefly against the former. One of the most distinguished and most narrow-minded of these opponents, Wilhelm His, affirms very positively that "characteristics acquired in the life of the individual are not inherited." The innumerable proofs that are advanced of it are declared by him to be "a hand-full of anecdotes that remind us vividly of the hallucinations of the pregnant, and have no claim whatever to scientific consideration."

This "exact" anatomist is outstripped by his colleague and friend, the "exact" physiologist, Victor Henson, of Kiel, the leader of the famous Kiel "plancton-expedition" that tries to give an "exact" explanation of the phenomena of marine life by counting how many million individuals of each species can live in a cubic mile of sea-water. Henson admires the pseudo-mechanical theories of His that were described in the third Chapter (p. 49), and thinks any refutation of them is "out of the question," expressing his gratification that His has delivered embryology from the need of explaining its phenomena by "mysterious heredity." In the opinion of these "exact embryologists" the biogenetic law is nonsense, and heredity should be excluded from science altogether. It would be just as reasonable to ask the physicist to abandon the study of gravitation or electricity because we do not know the real character of these forces and of the general law of substance.

However, the inheritance of acquired characters is denied, not only by these thorough opponents of evolution, but even by scientists who admit it and have contributed a good deal to its establishment, especially Weismann, Galton, Ray-Lankester, etc. Since 1884 the chief opponent has been August Weismann, who has rendered the greatest service in the development of Darwin's theory of selection. In his work on *The Continuity of the Germ-plasm*, and in his recent excellent *Lectures on the Theory of Descent* (1902), he has with great success advanced the opinion that "only those characters can be transmitted to subsequent generations that were contained in rudimentary form in the embryo." However, this germ-plasm theory, with its attempt to explain heredity, is merely a "provisional molecular hypothesis"; it is one of those metaphysical speculations that attribute the evolutionary phenomena exclusively to internal causes, and regard the influence of the environment as insignificant. Herbert Spencer, Theodor Eimer, Lester Ward, Hering, and Zehnder have pointed out the untenable consequences of this position. I have given my view of it in the tenth edition of the *History of Creation* (pp. 192, 203). I hold, with Lamarck and Darwin, that the hereditary transmission of acquired characters is one of the most important phenomena in biology, and is proved by thousands of morphological and physiological experiences. It is an indispensable foundation of the theory of evolution.

Of the many and weighty arguments for the truth of this conception of evolution I will for the moment merely point to the invaluable evidence of dysteleology, the science of rudimentary organs. We cannot insist too often or too strongly on the great morphological significance of these remarkable organs, which are completely useless from the physiological point of view. We find some of these useless parts, inherited from our lower vertebrate ancestors, in every system of organs in man and the higher vertebrates. Thus we find at once on the skin a scanty and rudimentary coat of hair, only fully developed on the head, under the shoulders, and at a few other parts of the body. The short hairs on the greater part of the body are quite useless and devoid of physiological value; they are the last relic of the thicker hairy coat of our simian ancestors. The sensory apparatus presents a series of most remarkable rudimentary organs. We have seen that the whole of the shell of the external ear, with its cartilages, muscles, and skin, is in man a useless appendage, and has not the physiological importance that was formerly ascribed to it. It is the degenerate remainder of the pointed, freely moving, and more advanced mammal ear, the muscles of which we still have, but cannot work them. We found at the inner corner of our eye a small, curious, semi-lunar fold that is of no use whatever to us, and is only interesting as the last relic of the nictitating membrane, the third, inner eye-lid that had a distinct physiological purpose in the ancient sharks, and still has in many of the amniotes.

The motor apparatus, both skeleton and muscular system, provides a number of interesting dysteleological arguments. I need only remind the reader of the projecting tail of the human embryo, with its rudimentary caudal vertebræ and muscles; this is totally useless in man, but very interesting as the degenerate relic of the long tail of our simian ancestors. From these we have also inherited various bony processes and muscles, which were very useful to them in climbing trees, but are useless to us. At various points of the skin we have cutaneous muscles which we never use—remnants of a strongly-developed cutaneous muscle in our lower mammal ancestors. This "panniculus carnosus" had the function of contracting and creasing the skin to chase away the flies, as we see every day in the horse. Another relic in us of this large cutaneous muscle is the frontal muscle, by which we knit our forehead and raise our eye-brows; but there is another considerable relic of it, the large cutaneous muscle in the neck *(platysma myoides)*, over which we have no voluntary control.

Not only in the systems of animal organs, but also in the vegetal apparatus, we find a number of rudimentary organs, many of which we have already noticed. In the alimentary apparatus there are the internal breast-gland *(thymus)* and the remarkable thyroid gland *(thyreoi dea)*, the seat of goitre and the relic of a ciliated groove that the tunicates and acrania still have in the gill-pannier; there is also the vermiform appendix to the cœcum. In the vascular system we have a number of useless cords which represent relics of atrophied vessels that were once active as blood-canals—the *ductus Botalli* between the pulmonary artery and the aorta, the *ductus venosus Arantii* between the portal vein and the vena cava, and many others. The many rudimentary organs in the urinary and sexual apparatus are particularly interesting. These are generally developed in one sex and rudimentary in the other. Thus the spermaducts are formed from the Wolffian ducts in the male, whereas in the female we have merely rudimentary traces of them in Gaertner's canals. On the other hand, in the female the oviducts and womb are developed from the Müllerian ducts, while in the male only the lowest ends of them remain as the "male womb" *(vesicula prostatica)*. Again, the male has in his nipples and mammary glands the rudiments of organs that are usually active only in the female.

A careful anatomic study of the human frame would disclose to us numbers of other rudimentary organs, and these can only be explained on the theory of evolution. Robert Wiedersheim has collected a large number of them in his work on *The Human Frame as a Witness to its Past.* They are some of the weightiest proofs of the truth of the mechanical conception and the strongest disproofs of the teleological view. If, as the latter demands, man or any other organism had been designed and fitted for his life-purposes from the start and brought into being by a creative act, the existence of these rudimentary organs would be an insoluble enigma; it would be impossible to understand why the Creator had put this useless burden on his creatures to walk a path that is in itself by no means easy. But the theory of evolution gives the simplest possible explanation of them. It says: The rudimentary organs are parts of the body that have fallen into disuse in the course of centuries; they had definite functions in our animal ancestors, but have lost their physiological significance. On account of fresh adaptations they have become superfluous, but are transmitted from generation to generation by heredity, and gradually atrophy.

We have inherited not only these rudimentary parts, but all the organs of our body, from the mammals—

proximately from the apes. The human body does not contain a single organ that has not been inherited from the apes. In fact, with the aid of our biogenetic law we can trace the origin of our various systems of organs much further down to the lowest stages of our ancestry. We can say, for instance, that we have inherited the oldest organs of the body, the external skin and the internal coat of the alimentary system, from the gastræads; the nervous and muscular systems from the platodes; the vascular system, the body-cavity, and the blood from the vermalia; the chorda and the branchial gut from the prochordonia; the metamerism or articulation of the body from the acrania; the primitive skull and the higher sense-organs from the cyclostomes; the limbs and jaws from the selachii; the five-toed foot from the amphibia; the palate from the reptiles; the hairy coat, the mammary glands, and the external sexual organs from the promammals. When we formulated "the law of the ontogenetic connection of systematically related forms," and determined the relative age of organs, we saw how it was possible to draw phylogenetic conclusions from the ontogenetic succession of systems of organs.

With the aid of this important law and of comparative anatomy, we were also enabled to determine "man's place in nature," or, as we put it, assign to man his position in the classification of the animal kingdom. In recent zoological classification the animal world is divided into the twelve stems or phyla we have seen, and these are broadly subdivided into about sixty classes, and these classes into at least 300 orders. In his whole organisation man is most certainly, in the first place, a member of one of these stems, the vertebrate stem; secondly, a member of one particular class in this stem, the mammals; and thirdly, of one particular order, the order of primates. He has all the characteristics that distinguish the vertebrates from the other eleven animal stems, the mammals from the other sixty classes, and the primates from the 300 other orders of the animal kingdom. We may turn and twist as we like, but we cannot get over this fact of anatomy and classification. Of late years this fact has given rise to a good deal of discussion, and especially of controversy as to the particular anatomic relationship of man to the apes. The most curious opinions have been advanced on this "ape question," or "pithecoid theory." It is as well, therefore, to go into it once more and distinguish the essential from the unessential. (Cf. above, pp. 633–635.)

We start from the undisputed fact that man is in any case—whether we accept or reject his special blood-relationship to the apes—a true mammal; in fact, a placental mammal. This fundamental fact can be proved so easily at any moment from comparative anatomy that it has been universally admitted since the separation of the placentals from the lower mammals (marsupials and monotremes). But for every consistent subscriber to the theory of evolution it must follow at once that man descends from a common stem-form with all the other placentals, the stem-ancestor of the placentals, just as we must admit a common mesozoic ancestor of all the mammals. This is, however, to settle decisively the great and burning question of man's place in nature, whether or no we go on to admit a nearer or more distant relationship to the apes. Whether man is or is not a member of the ape-order (or, if you prefer, the primate-order) in the phylogenetic sense, in any case his direct blood-relationship to the rest of the mammals, and especially the placentals, is established. It is possible that the affinities of the various orders of mammals to each other are different from what we hypothetically assume to-day. But, in any case, the common descent of man and all the other mammals from one stem-form is beyond question. This long-extinct promammal was probably evolved from proreptiles during the Triassic period, and must certainly be regarded as the monotreme and oviparous ancestor of *all* the mammals.

If we hold firmly to this fundamental and most important thesis, we shall see the "ape-question" in a very different light from that in which it is usually regarded. Little reflection is then needed to see that it is not nearly so important as it is said to be. The origin of the human race from a series of mammal ancestors, and the historic evolution of these from an earlier series of lower vertebrate ancestors, together with all the weighty conclusions that every thoughtful man deduces therefrom, remain untouched; as far as these are concerned, it is immaterial whether we regard true "apes" as our nearest ancestors or not. But as it has become the fashion to lay the chief stress in the whole question of man's origin on the "descent from the apes," I am compelled to return to it once more, and recall the facts of comparative anatomy and ontogeny that give a decisive answer to this "ape-question."

The shortest way to attain our purpose is that followed by Huxley in 1863 in his able work, which I have already often quoted, *Man's Place in Nature*—the way of comparative anatomy and ontogeny (cf. Plates XVII.-XXIX.). We have to compare impartially all man's organs with the same organs in the higher apes, and then to examine if the differences between the two are greater than the corresponding differences between the higher and the lower apes. The indubitable and incontestable result of this comparative-anatomical study, conducted with the greatest care and impartiality, was the pithecometra principle, which we have called the Huxleian law in honour of its formulator—namely, that the differences in organisation between man and the most advanced apes we know are much slighter than the corresponding differences in organisation between the higher and lower apes. We may even give a more precise formula to this law, by excluding the platyrrhines or American apes as distant relatives, and restricting the comparison to the narrower family-circle of the catarrhines, the apes of the Old World. Within the limits of this small group of mammals we found the structural differences between the lower and higher catarrhine apes—for instance, the baboon and the gorilla—to be much greater than the differences between the anthropoid apes and man. If we now turn to ontogeny and find, according to our "law of the ontogenetic connection of systematically related forms," that the embryos of the anthropoid apes and man retain their resemblance for a longer time than the embryos of the highest and the lowest apes, we are forced, whether we like it or no, to recognise our descent from the order of apes. From the foregoing facts of comparative anatomy we can assuredly construct an approximate picture in the imagination of the form of our early Tertiary ancestors; however we may frame this in detail, it will be the picture of a true ape, and a distinct catarrhine ape. This has been shown so well by Huxley (1863) that the recent attacks of Klaatsch, Virchow, and other anthropologists, have completely failed (cf. pp. 631–634). All the structural characters that distinguish the catarrhines from the platyrrhines are found in man. Hence in the genealogy of the mammals we must derive man immediately from the catarrhine group, and locate the origin of the human race in the Old World. Only the early root-form from which both descended was common to them.

It is, therefore, established beyond question for all impartial scientific inquiry that the human race comes directly from the apes of the Old World; but, at the same time, I repeat that this is not so important in connection with the main question of the origin of man as is commonly supposed. Even if we entirely ignore it, all that we have learned from the zoological facts of comparative anatomy and ontogeny as to the placental character of man remains untouched. These prove beyond all doubt the common descent of man and all the rest of the mammals. Further, the main question is not in the least affected if it is said: "It is true that man is a mammal; but he has diverged at the very root of the class from all the other mammals, and has no closer relationship to any living group of mammals." The affinity is more or less close in any case, if we examine the relation of the mammal class to the sixty other classes of the animal world. In any case, the whole of the mammals, including man, have had a common origin; and it is equally certain that their common stem-forms were gradually evolved from a long series of lower vertebrates.

The resistance to the theory of a descent from the apes is clearly due in most men to feeling rather than to reason. They shrink from the notion of such an origin just because they see in the ape organism a caricature of man, a distorted and unattractive image of themselves; because it hurts man's æsthetic complacency and self-ennoblement. It is more flattering to think we have descended from some lofty and god-like being; and so, from the earliest times, human vanity has been pleased to believe in our origin from gods or demi-gods. The Church, with that sophistic reversal of ideas of which it is a master, has succeeded in representing this ridiculous piece of vanity as "Christian humility"; and the very men who reject with horror the notion of an animal origin, and count themselves "children of God," love to prate of their "humble sense of servitude." In most of the sermons that have poured out from pulpit and altar against the doctrine of evolution human vanity and conceit have been a conspicuous element; and, although we have inherited this very characteristic weakness from the apes, we must admit that we have developed it to a higher degree, which is entirely repudiated by sound and normal intelligence. We are greatly amused at all the childish follies that the ridiculous pride of ancestry has maintained from the Middle Ages to our own time; yet there is a large amount of this empty feeling in most men. Just as most people much prefer to trace their family back to some degenerate baron or some famous prince rather than to an unknown peasant, so most men would rather have as parent of the race a sinful and fallen Adam than an advancing and vigorous ape. It is a matter of taste, and to that extent we cannot quarrel over these genealogical tendencies. Personally, the notion of ascent is more congenial to me than that of descent. It seems to me a finer thing to be the advanced offspring of a simian ancestor, that has developed progressively from the lower mammals in the struggle for life, than the degenerate descendant of a god-like being, made from a clod, and fallen for his sins, and an Eve created from one of his ribs. Speaking of the rib, I may add to what I have said about the development of the skeleton, that the number of ribs is just the same in man and woman. In both of them the ribs are formed from the middle germinal layer, and are, from the phylogenetic point of view, lower or ventral vertebral arches.

But it is said: "That is all very well, as far as the human body is concerned; on the facts quoted it is impossible to doubt that it has really and gradually been evolved from the long ancestral series of the vertebrates. But it is quite another thing as regards man's mind, or soul; this cannot possibly have been developed from the vertebrate-soul."[1] Let us see if we cannot meet this grave stricture from the well-known facts of comparative anatomy, physiology, and embryology. It will be best to begin with a comparative study of the souls of various groups of vertebrates. Here we find such an enormous variety of vertebrate souls that, at first sight, it seems quite impossible to trace them all to a common "primitive vertebrate." Think of the tiny amphioxus, with no real brain but a simple medullary tube, and its whole psychic life at the very lowest stage among the vertebrates. The following group of the cyclostomes are still very limited, though they have a brain. When we pass on to the fishes, we find their intelligence remaining at a very low level. We do not see any material advance in mental development until we go on to the amphibia and reptiles. There is still greater advance when we come to the mammals, though even here the minds of the monotremes and of the stupid marsupials remain at a low stage. But when we rise from these to the placentals we find within this one vast group such a number of important stages of differentiation and progress that the psychic differences between the least intelligent (such as the sloths and armadillos) and the most intelligent placentals (such as the dogs and apes) are much greater than the psychic differences between the lowest placentals and the marsupials or monotremes. Most certainly the differences are far greater than the differences in mental power between the dog, the ape, and man. Yet all these animals are genetically-related members of a single natural class.

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[1] The English reader will recognise here the curious position of Dr. Wallace and of the late Dr. Mivart.—TRANS.

We see this to a still more astonishing extent in the comparative psychology of another class of animals, that is especially interesting for many reasons—the insect class. It is well known that we find in many insects a degree of intelligence that is found in man alone among the vertebrates. Everybody knows of the famous communities and states of bees and ants, and of the very remarkable social arrangements in them, such as we find among the more advanced races of men, but among no other group of animals. I need only mention the social organisation and government of the monarchic bees and the republican ants, and their division into different conditions—queen, drone-nobles, workers, educators, soldiers, etc. One of the most remarkable phenomena in this very interesting province is the cattle-keeping of the ants, which rear plant-lice as milch-cows and regularly extract their honied juice. Still more remarkable is the slave-holding of the large red ants, which steal the young of the small black ants and bring them up as slaves. It has long been known that these political and social arrangements of the ants are due to the deliberate co-operation of the countless citizens, and that they understand each other. A number of recent observers, especially Fritz Müller, Sir J. Lubbock (Lord Avebury), and August Forel, have put the astonishing degree of intelligence of these tiny articulates beyond question.

Now, compare with these the mental life of many of the lower, especially the parasitic, insects, as Darwin did. There is, for instance, the cochineal insect *(coccus)*, which, in its adult state, has a motionless, shield-shaped body, attached to the leaves of plants. Its feet are atrophied. Its snout is sunk in the tissue of the plants of which it absorbs the sap. The whole psychic life of these inert female parasites consists in the pleasure they experience from sucking the sap of the plant and in sexual intercourse with the males. It is the same with the maggot-like females of the fan-fly *(strepsitera)*, which spend their lives parasitically and immovably, without wings or feet, in the abdomen of wasps. There is no question here of higher psychic action.

If we compare these sluggish parasites with the intelligent and active ants, we must admit that the psychic differences between them are much greater than the psychic differences between the lowest and highest mammals, between the monotremes, marsupials, and armadillos on the one hand, and the dog, ape, or man on the other. Yet all these insects belong to the same class of articulates, just as all the mammals belong to one and the same class. And just as every consistent evolutionist must admit a common stem-form for all these insects, so he must also for all the mammals.

If we now turn from the comparative study of psychic life in different animals to the question of the organs of this function, we receive the answer that in all the higher animals they are always bound up with certain groups of cells, the ganglionic cells or neurona that compose the nervous system. All scientists without exception are agreed that the central nervous system is the organ of psychic life in the animal, and it is possible to prove this experimentally at any moment. When we partially or wholly destroy the central nervous system, we extinguish in the same proportion, partially or wholly, the "soul" or psychic activity of the animal. We have, therefore, to examine the features of the psychic organ in man. The reader already knows the incontestable answer to this question. Man's psychic organ is, in structure and origin, just the same organ as in all the other vertebrates. It originates in the shape of a simple medullary tube from the outer membrane of the embryo—the skin-sense layer. The simple cerebral vesicle that is formed by the expansion of the head-part of this medullary tube divides by transverse constrictions into five, and these pass through more or less the same stages of construction in the human embryo as in the rest of the mammals. As these are undoubtedly of a common origin, their brain and spinal cord must also have a common origin.

Physiology teaches us further, on the ground of observation and experiment, that the relation of the "soul" to its organ, the brain and spinal cord, is just the same in man as in the other mammals. The one cannot act at all without the other; it is just as much bound up with it as muscular movement is with the muscles. It can only develop in connection with it. If we are evolutionists at all and grant the causal connection of ontogenesis and phylogenesis, we are forced to admit this thesis: The human soul or psyche, as a function of the medullary tube, has developed along with it; and just as brain and spinal cord now develop from the simple medullary tube in every human individual, so the human mind or the psychic life of the whole human race has been gradually evolved from the lower vertebrate soul. Just as to-day the intricate structure of the brain proceeds step by step from the same rudiment in every human individual—the same five cerebral vesicles—as in all the other craniotes, so the human soul has been gradually developed in the course of millions of years from a long series of craniote souls. Finally, just as to-day in every human embryo the various parts of the brain differentiate after the special type of the ape-brain, so the human psyche has proceeded historically from the ape-soul.

It is true that this monistic conception is rejected with horror by most men, and the dualistic idea, which denies the inseparable connection of brain and mind, and regards body and soul as two totally different things, is still popular. But how can we reconcile this view with the known facts of evolution? It meets with difficulties equally great and insuperable in embryology and in phylogeny. If we suppose with the majority of men that the soul is an independent entity, which has nothing to do with the body originally, but merely inhabits it for a time, and gives expression to its experiences through the brain just as the pianist does through his instrument, we must assign a point in human embryology at which the soul enters into the brain; and at death again we must assign a moment at which it abandons the body. As, further, each human individual has inherited certain personal features from each parent, we must suppose that in the act of conception pieces were detached from their souls and transferred to the embryo. A piece of the paternal soul goes with the spermatozoon, and a piece of the mother's soul remains in the ovum. At the moment of conception, when portions of the two nuclei of the copulating cells join together to form the nucleus of the stem-cell, the accompanying fragments of the immaterial souls must also be supposed to coalesce.

On this dualistic view the phenomena of psychic development are totally incomprehensible. Everybody knows that the new-born child has no consciousness, no knowledge of itself and the surrounding world. Every parent who has impartially followed the mental development of his children will find it impossible to deny that it is a case of biological evolutionary processes. Just as all other functions of the body develop in connection with their organs, so the soul does in connection with the brain. This gradual unfolding of the soul of the child is, in fact, so wonderful and glorious a phenomenon that every mother or father who has eyes to observe is never tired of contemplating it. It is only our manuals of psychology that know nothing of this development; we are almost tempted to think sometimes that their authors can never have had children themselves. The human soul, as described in most of our psychological works, is merely the soul of a learned philosopher, who has read a good many books, but knows nothing of evolution, and never even reflects that his own soul has had a development.

When these dualistic philosophers are consistent they must assign a moment in the phylogeny of the human soul at which it was first "introduced" into man's vertebrate body. Hence, at the time when the human body was evolved from the anthropoid body of the ape (probably in the earlier Tertiary period), a specific human psychic element —or, as people love to say, "a spark of divinity"—must have been suddenly infused or breathed into the anthropoid brain, and been associated with the ape-soul already present in it. I need not insist on the enormous theoretical difficulties of this idea. I will only point out that this "spark of divinity," which is supposed to distinguish the soul of man from that of the other animals, must be itself capable of development, and has, as a matter of fact, progressively developed in the course of human history. As a rule, reason is taken to be this "spark of divinity," and is supposed to be an exclusive possession of humanity. But comparative psychology shows us that it is quite impossible to set up this barrier between man and the brute. Either we take the word "reason" in the wider sense, and then it is found in the higher mammals (ape, dog, elephant, horse) just as well as in most men; or else in the narrower sense, and then it is lacking in most men just as much as in the majority of animals. On the whole, we may still say of man's reason what Goethe's Mephistopheles said:—

> "Life somewhat better might content him
> But for the gleam of heavenly light that Thou hast lent him.
> He calls it reason; thence his power's increased
> To be still beastlier than any beast."

If, then, we must reject these popular and, in some respects, agreeable dualistic theories as untenable, because inconsistent with the genetic facts, there remains only the opposite or monistic conception, according to which the human soul is, like any other animal soul, a function of the central nervous system, and developes in inseparable connection therewith. We see this *ontogenetically* in every child. The biogenetic law compels us to affirm it *phylogenetically*. Just as in every human embryo the skin-sense layer gives rise to the medullary tube, from the anterior end of which the five cerebral vesicles of the craniotes are developed, and from these the mammal brain (first with the characters of the lower, then with those of the higher, mammals); and as the whole of this ontogenetic process is only a brief, hereditary reproduction of the same process in the phylogenesis of the vertebrates; so the wonderful spiritual life of the human race through many thousands of years has been evolved step by step from the lowly psychic life of the lower vertebrates, and the development of every child-soul is only a brief repetition of that long and complex phylogenetic process. From all these facts sound reason must conclude that the still prevalent belief in the immortality of the soul is an untenable superstition. I have shown its inconsistency with modern science in the eleventh chapter of the *Riddle of the Universe.*

Here it may also be well to point out the great importance of anthropogeny, in the light of the biogenetic law, for the purposes of philosophy. The speculative philosophers who take cognisance of these ontogenetic facts, and explain them (in accordance with the law) phylogenetically, will advance the great questions of philosophy far more than the most distinguished thinkers of all ages have yet succeeded in doing. Most certainly every clear and consistent thinker must derive from the facts of comparative anatomy and ontogeny we have adduced a number of suggestive ideas that cannot fail to have an influence on the progress of philosophy. Nor can it be doubted that the candid statement and impartial appreciation of these facts will lead to the decisive triumph of the philosophic tendency that we call "monistic" or "mechanical," as opposed to the "dualistic" or "teleological," on which most of the ancient, medieval, and modern systems of philosophy are based. The monistic or mechanical philosophy affirms that all the phenomena of human life and of the rest of nature are ruled by fixed and unalterable laws; that there is everywhere a necessary causal connection of phenomena; and that, therefore, the whole knowable universe is a harmonious unity, a *monon.* It says, further, that all phenomena are due solely to mechanical or efficient causes, not to final causes. It does not admit free-will in the ordinary sense of the word. In the light of the monistic philosophy the phenomena that we are wont to regard as the freest and most independent, the expressions of the human will, are subject just as much to rigid laws as any other natural phenomenon. As a matter of fact, impartial and thorough examination of our "free" volitions shows that they are never really free, but always determined by antecedent factors that can be traced to either heredity or adaptation. We cannot, therefore, admit the conventional distinction between nature and spirit. There is spirit everywhere in nature, and we know of no spirit outside of nature. Hence, also, the common antithesis of natural science and mental or moral science is untenable. Every science, as such, is both natural and mental. That is a firm principle of Monism, which, on its religious side, we may also denominate Pantheism. Man is not above, but in, nature.

It is true that the opponents of evolution love to misrepresent the monistic philosophy based on it as "materialism," and confuse the philosophic tendency of this name with a wholly unconnected and despicable moral materialism. Strictly speaking, it would be just as proper to call our system spiritualism as materialism. The real materialistic philosophy affirms that the phenomena of life are, like all other phenomena, effects or products of matter. The opposite extreme, the spiritualistic philosophy, says, on the contrary, that matter is a product of energy, and that all material forms are produced by free and independent forces. Thus, according to one-sided materialism, the matter is antecedent to the living force; according to the equally one-sided view of the spiritist, it is the reverse. Both views are dualistic, and, in my opinion, both are false. For us the antithesis disappears in the monistic philosophy, which knows neither matter without force nor force without matter. It is only necessary to reflect for some time over the question from the strictly scientific point of view to see that it is impossible to form a clear idea of either hypothesis. As Goethe said, "Matter can never exist or act without spirit, nor spirit without matter."

The human "spirit" or "soul" is merely a force or form of energy, inseparably bound up with the material substratum of the body. The thinking force of the mind is just as much connected with the structural elements of the brain as the motor force of the muscles with their structural elements. Our mental powers are functions of the brain as much as any other force is a function of a material body. We know of no matter that is devoid of force, and no forces that are not bound up with matter. When the forces enter into the phenomenon as movements we call them living or active forces; when they are in a state of rest or equilibrium we call them latent or potential. This applies equally to inorganic and organic bodies. The magnet that attracts iron filings, the powder that explodes, the steam that drives the locomotive, are living inorganics; they act by living force as much as the sensitive mimosa does when it contracts its leaves at touch, or the venerable amphioxus that buries itself in the sand of the sea, or man when he thinks. Only in the latter cases the combinations of the different forces that appear as "movement" in the phenomenon are much more intricate and difficult to analyse than in the former.

Our anthropogeny has led us to the conclusion that in the whole evolution of man, in his embryology and in his phylogeny, there are no living forces at work other than those of the rest of organic and inorganic nature. All the forces that are operative in it could be reduced in the ultimate analysis to growth, the fundamental evolutionary function that brings about the forms of both the organic and the inorganic. But growth itself depends on the attraction and repulsion of homogeneous and heterogeneous particles. Seventy-five years ago Carl Ernst von Baer summed up the general result of his classic studies of animal development in the sentence: "The evolution of the individual is the history of the growth of individuality in every respect." And if we go deeper to the root of this law of growth, we find that in the long run it can always be reduced to that attraction and repulsion of animated atoms which Empedocles called the "love and hatred" of the elements.

Thus the evolution of man is directed by the same "eternal, iron laws" as the development of any other body. These laws always lead us back to the same simple principles, the elementary principles of physics and chemistry. The various phenomena of nature only differ in the degree of complexity in which the different forces work together. Each single process of adaptation and heredity in the stem-history of our ancestors is in itself a very complex physiological phenomenon. Far more intricate are the processes of human embryology; in these are condensed and comprised thousands of the phylogenetic processes.

In my *Generelle Morphologie*, which appeared in 1866, I made the first attempt to apply the theory of evolution, as reformed by Darwin, to the whole province of biology, and especially to provide with its assistance a mechanical foundation for the science of organic forms. The intimate relations that exist between all parts of organic science, especially the direct causal nexus between the two sections of evolution—ontogeny and phylogeny—were explained in that work for the first time by transformism, and were interpreted philosophically in the light of the theory of descent. The anthropological part of the *Generelle Morphologie* (book vii.) contains the first attempt to determine the series of man's ancestors (vol. ii., p. 428). However imperfect this *progonotaxis* was, it provided a starting-point for further investigation. In the thirty-seven years that have since elapsed the biological horizon has been enormously widened; our empirical acquisitions in paleontology, comparative anatomy, and ontogeny have grown to an astonishing extent, thanks to the united efforts of a number of able works and the employment of better methods. Many important biological questions that then appeared to be obscure enigmas seem to be entirely settled. Darwinism arose like the dawn of a new day of clear monistic science after the dark night of mystic dogmatism, and we can say now, proudly and gladly, that there is daylight in our field of inquiry.

Philosophers and others who are equally ignorant of the empirical sources of our evidence and the phylogenetic methods of utilising it, have even lately claimed that in the matter of constructing our genealogical tree nothing more has been done than the discovery of a "gallery of ancestors," such as we find in the mansions of the nobility. This would be quite true if the genealogy given in the second part of our anthropogeny were merely the juxtaposition of a series of animal forms, of which we gathered the genetic connection from their external physiognomic resemblances. As we have sufficiently proved already, it is for us a question of a totally different thing—of the morphological and historical proof of the phylogenetic connection of these ancestors on the basis of their identity in internal structure and embryonic development; and I think I have sufficiently shown in the first part of this work how far this is calculated to reveal to us their inner nature and its historical development. I see the essence of its significance precisely in the proof of historical connection. I am one of those scientists who believe in a real "natural history," and who think as much of an historical knowledge of the past as of an exact investigation of the present. The incalculable value of the historical consciousness cannot be sufficiently emphasised at a time when historical research is ignored and neglected, and when an "exact" school, as dogmatic as it is narrow, would substitute for it physical experiments and mathematical formulæ. Historical knowledge cannot be replaced by any other branch of science.

It is clear that the prejudices that stand in the way of a general recognition of this "natural anthropogeny" are still very great; otherwise the long struggle of philosophic systems would have ended in favour of Monism. But we may confidently expect that a more general acquaintance with the genetic facts will gradually destroy these prejudices, and lead to the triumph of the natural conception of "man's place in nature." When we hear it said, in face of this expectation, that this would lead to retrogression in the intellectual and moral development of mankind, I cannot refrain from saying that, in my opinion, it will be just the reverse; that it will promote to an enormous extent the advance of the human mind. All progress in our knowledge of truth means an advance in the higher cultivation of the human intelligence; and all progress in its application to practical life implies a corresponding improvement of morality. The worst enemies of the human race—ignorance and superstition—can only be vanquished by truth and reason. In any case, I hope and desire to have convinced the reader of these chapters that the true scientific comprehension of the human frame can only be attained in the way that we recognise to be the sole sound and effective one in organic science generally—namely, the way of Evolution.

SIXTIETH TABLE

Phylogeny of Functions (=Physiogeny).

SYNOPSIS OF THE CHIEF STAGES IN THE STEM-HISTORY OF MAN'S VITAL ACTIVITIES

I. First chief stage: The vital functions of the protists.

The organism is a simple plastid (at first unnucleated cytode, then nucleated cell), afterwards a simple association of homogeneous cells: no tissue, no gut.

1. First stage: **The life of the chromacea.**

The protophytic organism (without organs), born by spontaneous generation (p. 492), is a homogeneous granule of plasm, or a vegetal moneron (*chroococcus*, p. 502); its whole life consists of the chemical process of plasmodomism (=carbon-assimilation), growth, and multiplication by cleavage.

2. Second stage: **The life of the algaria.**

The protophytic organism is a simple vegetal cell (*eremosphæra*, *palmella*, p. 508), developed from the chromacean cytode by the oldest biological process of differentiation—separation of the internal nucleus (caryoplasm) from the external cytosoma (cytoplasm), p. 506. The caryoplasm effects reproduction and heredity; the cytoplasm, nutrition and adaptation.

3. Third stage: **The life of the protozoa.**

The protozoic organism is a simple animal cell, formed by metasitism (p. 508) from the vegetal algarian cell; the plasmodomous metabolism of the latter has been converted into the plasmophagous nutrition of the other. The movements of the naked cytosoma (with no cell-membrane) are amœboid at first (*amœbina*), afterwards flagellate (*infusoria*), pp. 506–511.

4. Fourth stage: **The life of the cenobia.**

By the permanent conjunction of homogeneous protozoic cells are formed the first animal cell-communities (*cenobia*), round colonies of flagellate cells, like the *catallacta* and *volvocina*. The wall of the hollow sphere is a single stratum of cells, like the blastoderm of the blastula. Cf. the *blastæada*, pp. 513–16.

II. Second chief stage: The vital functions of the cœlenteria.

The organism is a multicellular metazoon without cœloma, composed of at least two strata of cells (tissues, ectoderm and entoderm) with a single gut-tube (primitive gut and primitive mouth), but without anus, cœloma, or blood-vessels.

5. Fifth stage: **The life of the gastræads.**

The hollow sphere of the cenobium (4) has changed into the gastræa (p. 515), the primitive mouth and gut having been formed by invagination, and thus a division of labour having set in in the simple stratum of cells; the blastoderm divides into animal ectoderm and vegetal entoderm (p. 516); the former (skin-layer) assumes the functions of sensation and movement, the latter (gut-layer) the functions of nutrition and reproduction.

6. Sixth stage: **The life of the platodes.**

The floating uni-axial form of the gastræa changes into the creeping bilateral form of the platodaria *(cryptocœla)*. When pronephridia develop from a pair of cutaneous glands, and the epidermic vertical plate is converted into the hypodermic cerebral ganglion, we have the turbellaria *(rhabdocœla*, p. 536). The psyche advances a stage by the development of rudimentary sense-organs.

III. Third chief stage: The vital functions of the vermalia.

The organism is a worm-like animal—*i.e.*, a metazoon with body-cavity and anus, but not yet segmented, and without the typical characters of one of the higher animal stems.

7. Seventh stage: **The life of the rotatoria.**

The primitive vermalia have been evolved from the turbellaria (6) by the formation of the second aperture of the gut (anus) and the perienteric body-cavity *(gastrotricha*, p. 542); the nutritive process differentiates; no blood-vessels.

8. Eighth stage: **The life of the nemertina.**

By the formation of blood vessels in the higher vermalia a special circulatory system differentiates from the visceral system (p. 544). It consists of two median blood-canals, which lie in the wall of the gut, and are connected before and behind by a loop round the gut; the dorsal tube (or vessel) and the ventral tube (or vessel). Cf. the simplest forms of the *nemertina*, Fig. 298.

9. Ninth stage: **The life of the enteropneusta.**

The gut divides into two sections, the head-gut (for respiratory purposes) and the trunk-gut (for digestion). In the head-gut the gill-clefts break outwards (branchial gut); in the trunk-gut hepatic sacs are formed (hepatic gut). Vascular arches develop between the gill-clefts, rising from the ventral to the dorsal vessel. The two chief blood vessels run in the dorsal and ventral mesentery, the permanent central partition between the cœlom pouches. Cf. *balanoglossus*, Fig. 299.

10. Tenth stage: **The life of the prochordonia.**

The vermalian organism reaches the stage of the earliest chordonia *(chordata* or chorda-animals), of which the actual copelata (the lowest tunicates) are a modified relic. The dorsal nervous stem sinks, and becomes the medullary tube. Underneath it the chorda is formed, as internal supporting skeleton, from a median groove of the dorsal wall of the gut. Opposite to this "upper epibranchial groove" the glandular hypobranchial groove differentiates in the middle line of the ventral wall of the branchial gut, and conveys food to the hepatic gut. (Cf. *appendicaria*, Fig. 276.) An ontogenetic silhouette of these important prochordonia-ancestors has been preserved in the chordula of the tunicates and vertebrates. Cf. pp. 229-41.

IV. Fourth chief stage: The vital functions of the Vertebrates.

The vertebrate organism developes from the unsegmented chordonia by internal metamerism of the long body, or vertebration. This segmental articulation first affects the muscular system in the dorsal body *(episoma)* and the sexual system in the ventral body *(hyposoma)*; thus are formed two rows of trunk-muscles above and of gonades below. After this there is segmentation of the renal, nervous, and vascular systems, and finally of the skeletal system. The consequent multiplication of and division of labour among the organs involve a higher and richer development of all the vital powers.

11. Eleventh stage: **The life of the acrania.**

The earliest vertebrate organism attains on the whole the stage of the actual acrania *(amphioxus)*. The six fundamental organs (p. 243) have been inherited by the primitive vertebrates *(prospondylia*, pp. 253, 555) from their prochordonia ancestors; but their functions (and consequently their structures) have been much developed. The brisker swimming movement of the lengthening body leads to segmentation of the muscles of the trunk *(episoma)* and of the gonades. This is followed by a correlative metamerism of the nervous, renal, and vascular systems. Cf. amphioxus, Chapters XVI. and XVII.

12. Twelfth stage: **The life of the cyclostoma.**

The earliest craniote organism partly resembles the actual *myxinoides*, partly the *petromyzontes*, in its general features. The anterior end of the medullary tube expands and forms the brain; the three higher sense-organs are formed. The fore part of the perichorda becomes the skull. The simple, spindle-shaped heart (of the prochordonia) divides into atrium and ventricle. The segmental pronephridia (of the acrania) become a compact head-kidney *(pronephros)*. The metamerous gonades join together and form a single pair of glands.

13. Thirteenth stage: **The life of the fishes.**

The gnathostome-organism attains in the Silurian period the general features of the actual selachii. In the skin (hitherto naked and smooth) placoid scales develop, and bony teeth in the mouth. A pair of nasal pits, and upper and lower jaws, are formed in the head. Eyes, auditory vesicles, and brain advance. The swimming is regulated by two pairs of fins; the air-filled floating bladder, an outgrowth from the gullet, acts as hydrostatic organ. The circulation is improved by the formation of the "conus arteriosus." The sexual products are carried off by the prorenal ducts.

14. Fourteenth stage: **The life of the dipneusts.**

The fish-organism changes during the Devonian period into that of the paladipneusta (like the modern *ceratodus)*. The hydrostatic floating-bladder is converted into the respiratory lung. The single atrium of the heart divides into two; the right receives venous blood from the body, the left arterial blood from the lungs. Cf. the Devonian dipneusts, Figs. 310–313.

15. Fifteenth stage: **The life of the amphibia.**

The dipneust organism abandons aquatic life and takes to terrestrial during the Carboniferous period (possibly just before it). The polydactyl fish-fins change into the pentadactyl legs. Branchial respiration is more and more replaced by pulmonary. Cf. the Carboniferous mailed amphibia *(stegocephala*, Figs. 314–317).

16. Sixteenth stage: **The life of the reptiles.**

The amphibian organism passes into the reptile structure during the Permian period. The gills are lost altogether with the abandonment of aquatic life; breathing is purely pulmonary. The epidermis, hitherto soft and slippery, cornifies; the horny scales of the epidermis *(pholides)* appear above the bony scales of the corium *(lepides)*. Adaptation to reproduction on land leads to the formation of the protective embryonic membranes and organs of the amniotes *(amnion* and *serolemma : allantois)*. Cf. the earliest proreptiles *(tocosauria*, Figs. 318–321).

17. Seventeenth stage : **The life of the monotremes.**

The reptile organism, as seen in the earliest tocosauria of the Permian period, changes during the subsequent Triassic period into the form of the earliest mammals *(promammalia)*, like the actual monotremes. The body is covered with hair and sebaceous glands ; the mammary glands develop on the ventral side, and give milk to the young. The maxillary apparatus undergoes a profound modification ; the quadrate bone becomes the anvil, the lower-jaw process the hammer ; the joint of the quadrate bone is replaced by a temporal joint. The circulation divides into larger and smaller, the partition between the two halves of the heart being now complete. Respiration improves, the lungs advancing in structure, and the diaphragm (as respiratory muscle) completely separating the thoracic and abdominal cavities. The brain and sexual organs assume the specific mammal form. Cf. the monotremes, Figs. 322–325.

18. Eighteenth stage : **The life of the marsupials.**

The monotreme organism is converted during the Jurassic period (?) into the marsupial, the cloaca being divided by a frontal septum *(perineum)* into a urogenital sinus in front and anus behind. Viviparous reproduction takes the place of oviparous ; the food-yelk of the ova atrophies. Teats are developed on the mammary glands, and the live-born young suck the milk through these. Cf. the marsupials, Fig. 326.

19. Nineteenth stage : **The life of the lemurs.**

The marsupial organism is converted during the Cretaceous period into that of the earliest placentals, the placenta being now developed from the allantois. The marsupial bones on the symphysis (which were present in marsupials and monotremes) disappear. Brain and sense-organs attain the higher form that raises the placentals above their marsupial ancestors. A branch of the latter becomes the stem-group of the earliest primates, the lemuravales. The habit of climbing trees brings about the special form of the limbs of the prosimiæ. Cf. the lemurs, Figs. 328 and 329.

20. Twentieth stage : **The life of the apes.**

The prosimian organism is converted during the earlier Tertiary period (Eocene ?) into that of the true ape *(simiæ)*—first the platyrrhine (western apes, with thirty-six teeth, broad nasal septum, and short meatus of ear), afterwards the catarrhine (eastern apes, with thirty-two teeth, narrow nasal septum, and long meatus). A complete bony partition is formed between the eye-orbits and the temporal depressions. The single pear-shaped uterus of the apes is evolved from the double (afterwards bicornous) uterus of the lemur. The placental circulation is completed by the formation of the decidua. Cf. the apes, Figs. 330 and 331.

21. Twenty-first stage : **The life of the anthropoid apes.**

The cynopitheca-organism changes during the later Tertiary period into that of the anthropomorpha (like the living anthropoid apes). The tail atrophies. The sacrum becomes stronger, four to five of the sacral vertebræ fusing together (in most of the apes only two or three). The adoption of the erect posture gives a more human shape to most parts of the skeleton. Cf. the anthropomorpha, Figs. 235–244.

22. Twenty-second stage : **The life of man.**

The anthropoid organism of the man-like apes advances towards the end of the Tertiary period (?) into that of primitive man *(homo primigenius, homo Neander,* similar to *homo Veddalis, homo Australis,* etc.) ; the gradual transition is illustrated by the fossil *pithecanthropus erectus* of Java (Fig. 338).

When the habit of walking erect and of using the hand for grasping became thoroughly established, the crude sound-language of the social anthropoid apes was replaced by the articulate speech of man. The development of civilisation led to the gradual progress of the brain and psychic life, that raises civilised man above barbarians and savages. The latter have inherited not only their organs, but their physiological functions, from the anthropoid apes.

Note to the Genetic Tables.

The sixty Genetic Tables that are appended to the thirty Chapters of this work are intended to give brief and convenient synopses of the chief principles contained in it. Seeing the intricate and extensive character of the scientific matter of the work, it is hoped that they will help the reader. From the nature of the case, they chiefly take the form of phylogenetic hypotheses. The three great groups of empirical evidence—paleontology, comparative anatomy, and embryology—are, as a rule, still incomplete. Hence, undismayed by the fears of the "exact" school, we are compelled to fill up the historical gaps with "provisional hypotheses"; even if these are afterwards replaced by better, they will have had a temporary value. As to the various groups of the phyletic system (classes, orders, families, etc.) which are adduced as stages of our ancestry, it must be borne in mind that they comprise not only living representatives, but also their more numerous extinct relatives, which are only partly known to us. Hence it is important to keep to the essential and characteristic features in defining a group, and disregard the accidental features of different members of it. The first complete attempt to construct a "natural classification of organisms" in this sense on a phylogenetic basis is found in my *Systematic Phylogeny*.

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GLOSSARY

Though some care has been taken to explain unusual terms as they occur in the course of the present work, the reader will probably find it convenient to have an alphabetical list of these for reference. The translation of Professor Haeckel's works into English is beset by a dual difficulty. Not only does the distinguished zoologist frequently coin a new term—generally from the Greek, as is usual in scientific nomenclature—where it seems advisable, but he at the same time frequently gives a vernacular equivalent for a familiar technical phrase. It is necessary to follow his lead in both cases, however much the inexpert reader may be startled by the one and the expert by the other. *The Riddle of the Universe*, *The Wonders of Life*, and *The Evolution of Man* were written for the general reader, not for students of the sciences they embody. In German scientific terminology generally there is a far greater practice of using compound native terms than in English. Thousands of the Greek or Latin names that we use in botany or zoology, in anatomy or physiology, are represented in German by simpler Teutonic words. Professor Haeckel follows this practice very generously when he is writing "popular studies" of his Monistic philosophy. The translator has endeavoured to follow Haeckel's desire and practice as far as it was possible to do so without causing confusion in regard to biological terms that may be assumed to lie within the acquaintance of the general reading public.

As far as the present work is concerned, the reader may be advised to pay particular attention to certain constantly recurring terms. A clear understanding of these at the outset is essential for following the argument with ease. These terms have been explained in the text, but it may be useful to draw up here a list of the chief of these essential phrases before commencing the alphabetical list of incidental terms.

"Ontogeny" is the development of the individual organism (*on*), or, more usually, the science of such development. It is not necessarily identical with "embryology," though in the work it will generally be found to be so. It may, however, refer also to the development of the child during many years after birth.

"Phylogeny" is the development of the species, or group of individuals (*phylon* = the tribe), in historic time, or the science of such development. Human phylogeny means the development of the race as a whole from inferior animal species; human ontogeny the development of the individual human being.

The "biogenetic law," or "fundamental law of biogeny" (the science of the development of life), affirms that ontogeny is a more or less complete recapitulation of phylogeny; that, in other words, in the embryonic development of the individual of any species we can more or less clearly discern stages corresponding to those through which the species as a whole passed in its upward evolution.

"Palingenesis" refers to the embryonic or ontogenetic development in so far as it does faithfully reproduce the evolutionary stages through which the ancestors of the individual passed; wherever the development of the individual does this it is said to be "palingenetic," and the stage or structure of embryonic growth that recalls (*palin* = again, a second time) the past is "palingenetic."

"Cenogenesis" expresses the fact that not all parts or phases of the embryonic growth are reproductions of the past. In the later and higher animals the embryonic growth itself has been modified by adaptation to new conditions. The new features that have been thus introduced, and that interfere with the embryo's recapitulation of ancestral history, are said to be "cenogenetic" (*cenos* = new, *genea* = development).

The reader must thoroughly understand these terms at the outset. They particularly express Professor Haeckel's great part in building up the science of human evolution, and form, as it were, the hinges of his argument. Such terms as "heredity" and "adaptation" may be presumed to be familiar to the least expert reader, and need not be enlarged upon. The other phrases that may present some difficulty will be best arranged in alphabetic order. It will be understood that there is no pretence to explain or analyse the thousands of classification-names of animals that occur throughout the work; nor has it seemed necessary to give the etymology of anatomic or embryological terms (where the application is clear), nor to include terms that are explained in the text whenever they occur.

Aboral: opposite to the mouth

Achromin: the uncolourable matter of the nucleus

Acœlous: animals without body-cavity

Acrania: head-less animals

Acroganglion: vertical ganglion

Amitotic: without mitosis

Amnion: the inner fœtal membrane, the water sac

Amniotes: animals with an amnion (fœtal membrane)

Amœboid: like the amœba in movement

Amphigony: the union of male and female cells

Amphirhina: animals with two nostrils

Anamnia: animals without an amnion

Anastomosis: the opening of blood-vessels into each other (*stoma* = mouth)

Animalculists: the early scientists who thought the human organs lay pre-formed in the spermatozoa

Anthropistic: exaggerating the importance of man

Anthropogeny: the science of the evolution (*genea*) of man (*anthropos*)

Anthropology: the science of man

Antimera: opposed or antithetic parts (*mera*)

Apothelia: "derivative tissues" from the epithelia

Archenteron: primitive gut

Archephyta: the earliest vegetal organisms

Archezoa: the earliest animal organisms

Archeozoic: "primitive life" period in geology

Archiblastic: with primitive or palingenetic cleavage

Archigastrula: primitive type of gastrula

Archigony: the spontaneous generation of life at the beginning of organic history
Area opaca: the dark germinative area
Area pellucida: the light germinative area
Asymmetry: absence of symmetry
Atavism: latent heredity, or inheritance from a more or less remote ancestor (*atavus* = grandfather)
Atrium: literally "hall," vestibule
Axial rod: the first structure of the vertebral column, lying along the axis of the body

Biogeny: the science of the evolution of life (*bios*)
Biomoneron: unit of life
Bionomy: the science of the relations of living things to each other and their environment
Biserial: having a series of radii on each side
Blastema: embryonic cellular growth
Blastocœl: the segmentation-cavity in the embryo
Blastocrene: seat or source (*crene*) of development
Blastoderm: the single cell-layer of the blastula
Blastomeres: cells into which the fertilised stem-cell breaks up
Blastophylls: the germinal layers
Blastoporus: the primitive mouth
Blastula: the stage at which the embryo consists of a hollow sphere with a single layer of cells
Branchial: pertaining to the gills

Capital: of the head (*caput*)
Carcinom-cells: cancrous cells
Cardiac: of the heart
Cardiocœl: the cavity enclosing the heart
Caryokinesis: the movement of the nuclei of the two cells at conception
Caryoplasm: the protoplasm of the cell-nucleus
Catalytic: of the nature of catalysis (change effected in a body by the mere presence of another body)
Centrosoma: "central body" of the stem-cell
Centrolecithal: ova that have the yelk at the centre
Chorda dorsalis: not the spinal cord, but the first cartilaginous structure of the vertebral column
Chordæa: the hypothetical ancestor of all the chordonia
Chordonia: animals with a chorda dorsalis
Chordula: the stage at which the embryo developes a chorda between the neural and alimentary canals
Chorology: the science of geographical distribution
Chromatin: the colourable matter of the nucleus
Ciliated: equipped with cilia (*lashes*) or hair-like processes
Cloaca: literally "sewer," a common outlet for urine, excrements, and sexual products
Coccygeal: of the coccyx (lowest part of the vertebral column)
Cœlenterata: the lower metazoa (sponges, hydropolyps, medusæ, corals, platodes, etc.), without blood or body-cavity (*cœloma*)
Cœloma (cœlom, or cœlum): the body-cavity in its earliest stage
Cœlomaria: animals with body-cavity (*cœloma*)
Cœlomation: embryonic formation of the cœlomula
Cœlom-pouches: the two sacs or vesicles from which the body-cavity is formed
Cœlous: pertaining to the cœloma, or body-cavity
Concrementa: growths, accretions
Cosmogony: the science of the evolution of the world
Craniota: animals with cranium (skull)
Cryptorchism: failure of the testicles to descend

Cutaneous: of the skin (*cutis*)
Cyclostoma: "round-mouthed" animals, sometimes classed as fishes
Cytodes: particles of living matter below the cell stage
Cytoplasm: the protoplasm of the cell-body
Cytosoma: the body of a cell, as distinct from the nucleus
Cytula: the fertilised ovum

DECIDUATES: animals with decidua
Delamination: cleavage into plates or layers
Deutoplasm: "secondary plasm"
Dipleurous: double-breasted
Discoblastic: ova in which the protoplasm forms a disk at one side of the yelk
Dorsal: pertaining to the back (dorsum)
Dualism: the conviction of the ultimate duality of existence—the independent existence of matter and spirit
Dysteleology: the science of rudimentary organs

ECTOBLAST = ectoderm
Ectoderm: the outer germinal layer
Endoblast = entoderm
Endostyle: hypobranchial groove
Enterocœla: animals with true body-cavity
Entoderm: the inner germinal layer
Epiblast = ectoderm
Epigastrula: the mammal gastrula
Epigenesis: the formation of parts or structures in the embryo, in opposition to the older belief that they were inherited ready formed, or "preformed"
Epiphysis: the third eye in our vertebrate ancestors
Episoma: the dorsal half of the body (*soma*)
Episomites: segments of the dorsal half of the body
Epithelium: superficial cell-tissue
Ergonomy: division of labour
Ethology: the science of the habits (*etha*) of animals
Evolution: the term is often used in German to indicate, not development in general, but embryonic development as now conceived

FOLLICLE: capsule
GASTRÆA: a hypothetical animal form in the series of man's ancestors, with two strata of cells and a primitive gut-cavity and mouth
Gastræads: living organisms that resemble the hypothetical gastræa
Gastrula: the stage at which the embryo consists of two strata of cells and a primitive gut-cavity and mouth
Gastrulation: formation of the gastrula in the embryo
Gemmation: budding
Germinal layers: the earliest simple strata of cells out of which all the later tissues and organs are developed
Germinal vesicle: the stem-cell nucleus
Germinative area: the region in the embryo from which development proceeds
Gnathostome: "jaw-mouthed"—animals with jaws
Gonades: the sexual glands
Gonidia: the sexual cells
Gonochorism: separation of the sexes in different individuals
Gonocœl: cavity of ventral segments
Gonoducts: sexual ducts or passages
Gonotomes: ventral or sexual segments
Gynecomast: a male with developed breasts

HEPATIC: of the liver
Hermaphrodism: the quality of having both sexes in one individual
Heterochronism: alteration of the time-order of embryonic development by fresh adaptation

Heterotopism: alteration of the locality (*topos*) of certain structures in embryonic development
Histogeny: the genesis of tissues
Histology: the science of tissues (*hista*)
Histonal: tissue-forming
Holoblastic: cleaving as a whole (*holon*)
Homodynamism: the morphological equivalence of the successive segments of the body
Homology: identity, as distinguished from analogy (likeness)
Hypermastism: the possession of more than the normal number of breasts
Hyperthelism: having more than the normal nipples
Hypoblast = entoderm
Hypobranchial groove: a ciliated channel below (*hypo*) the gills for conveying food
Hypophysis: a urinary appendage in our vertebrate ancestors
Hyposoma: the ventral half of the body
Hyposomites: segments of the ventral half of the body

ICHTHYODA: animals of the fish (*ichthys*) type
Indecidua: animals without a decidua
Invagination: folding or curving in, as when a thin india-rubber ball is pressed inwards so as to form a cup

LAMINA or lamella: a thin plate or stratum
Leucocytes: white blood-cells

MACROSPORES: "large spores," the female cells
Mandibular: pertaining to the jaws
Maxillary: pertaining to the jaws
Mechanicism: the system that explains phenomena by mechanical or unconscious agencies
Medullary tube: the earliest form of the spinal marrow (*medulla*)
Meroblastic: cleaving only in part (*meron*)
Merocytes: "partial cells," or yelk-cells
Mesenchymic: pertaining to the mesenchyma (vascular and connective tissues)
Mesentery: a partition between the viscera
Mesoblasts: the middle germinal layers
Mesoderm: the middle germinal layer
Microspores: "small spores," the male cells
Metabolism: the circulation of matter in the organism
Metacœlom: secondary body-cavity
Metagaster: the "after" or permanent gut
Metagastrula: modified or cenogenetic gastrula
Metamera: segmented parts or successive sections
Metamerism: articulation, division into sections
Metamerous: segmented, articulated
Metamorphosis: transformation, evolution
Metaphyta: tissue-forming, higher plants
Metasitism: the change from inorganic to organic feeding—from plant to animal
Metatrophy: "change of diet," metasitism
Metazoa: tissue-forming animals, with gut
Methoria: the limiting or external layers of the embryo
Metova: mature ova
Microsomata: small particles or granules in protoplasm
Mitosis: indirect cell-cleavage (p. 107)
Monads: the ultimate units in the theory of Leibnitz
Monism: the conviction that all things we know are aspects of one fundamental substance
Monogony: non-sexual reproduction

Monomeric : not broken up into segments
Monophyletic : having one common origin
Monorhina : animals with single nostril
Moræda : organisms of the morula type
Morphology : the science of organic forms or structures, including chiefly (but larger than) anatomy
Morula : the embryo at the mulberry-shape stage
Myocœl : muscle-cavity of dorsal segments
Myotome : muscular plate or layer

Nephridia : renal (kidney) passages
Nephrotome : kidney-plate or layer
Neurenteric canal : an embryonic channel from the dorsal nerve-tube to the gut
Neuroporus : neural pore or channel
Nictitating : winking
Notochord : the chorda dorsalis (*notos* = back)
Nuclein : the matter of which the cell-nucleus is composed

Œcology : the science of the homes (*oikos*) of animals
Omphalo-mesenteric : of the navel and mesentery
Organogenesis : the development of organs
Osseous : bony
Osteology : the science of the bones
Oviparous : animals that lay eggs
Ovolemma : the membrane surrounding the ovum
Ovulists : the early scientists who thought the human organs lay pre-formed in the ovum

Parablast : an accessory embryo in His's theory
Parenchymatose : of parenchyma, a pulpy mass of cells with vacuoles (spaces)
Parthenogenesis : virgin-birth (*parthenos* = virgin) ; birth without fertilisation by the male
Pedicle : stalk-like process
Pentadactyl : "five-toed"
Periblastic : ova in which the protoplasm is distributed round (*peri*) the yelk
Peribranchial : surrounding the gills
Perichorda : sheath surrounding the chorda
Perigastral : surrounding the gut
Periphery : circumference, outer surface
Peristoma : region about the mouth
Petromyzontes : "stone-suckers," the lampreys
Phagocytes : eating cells
Phytoplasm : vegetal plasm
Pithecometra : "ape-measurement" —principle for estimating differences between man and the ape
Planeton : organic matter floating on the sea
Planocytes : travelling cells
Plasmodomous : organisms that "build up" plasm — vegetal organisms
Plasmophagous : organisms that "feed" on plasm—animal organisms
Plasson : plasm
Plastids : the lowest organic elements (cells and cytodes)
Plastidules : molecules of plasm or plasson
Polydactyl : "many-toed"
Polymastism = hypermastism
Polyphyletic : having more than one source or origin
Polyspermism : fertilisation of the ovum by more than one sperm-cell
Primitive-groove : a groove or furrow on the dorsal surface of the gastrula
Primitive gut : the first cavity in the animal body, serving as stomach or gut
Prochordonia : the extinct common ancestors of the chordonia (animals with chorda)
Prochorion : the primitive chorion
Progaster : the primitive stomach or gut (*gaster*)

Progonotaxis: scheme of ancestral development
Promesoblasts: the earliest cells of the mesoderm
Pronephridia: primitive - kidney canals
Properistoma: region of the primitive mouth
Prorenal: of the primitive kidneys
Prospondylus: the hypothetical extinct ancestor of all the vertebrates
Prostoma: the primitive mouth (*stoma*)
Protists: the lowest unicellular forms of life
Protophyta: "primitive plants"
Protova: primitive, immature ova
Protozoa: the most primitive animal forms
Provertebræ: primitive or rudimentary vertebræ
Pseudocœla: animals with false body-cavity
Pseudopodia: "false feet," like the projections of the amœba
Psychic: pertaining to the soul (*psyche*)

RACEMOSE: having the appearance of a bunch of grapes
Renal: pertaining to the kidneys (*renes*)
Rhodocytes: red blood-cells

SAGITTAL: in the direction of an arrow (*sagitta*)
Sauropsids: reptiles and birds
Scatulation: packing, boxing-up
Sclerotome: skeleton-plate or layer
Sebaceous: fatty
Segmentation: cleavage
Septum: partition
Serous: pertaining to serum, watery
Sessile: fixed, stationary
Somites: segments, or successive parts. of the body (*soma*)
Spermacytes: sperm-cells
Splanchnocœl: "intestinal cavity"
Statocyst: organ or vesicle of equilibrium
Stem-cell: the fertilised ovum
Stem-form: ancestral form of a group
Stem-history: phylogeny, the history of the species or larger group
Stem-zone: dorsal body or episoma
Strobilation: formation of strobila, scaley articulation
Symbionta: organisms joined by symbiosis
Symbiosis: the joint or blended life of two organic beings in one

TELEOLOGY: the system that sees final or purposive or intelligent causes at work in the evolution of life
Telolecithal: having the yelk (*lecithus*) at one end (*telos*)
Thoracic: of the chest
Tocosauria: the earliest reptiles

UMBILICAL: pertaining to the navel (*umbilicus*)
Umbilical vesicle: the yelk-sac
Uterus: the womb

VASCULAR: pertaining to the blood vessels (*vascula*)
Vertebræa: the extinct primitive vertebrate
Villi: tufts, projections
Vitelline: pertaining to the yelk (*vitellus*)
Viviparous: bearing young alive (as opposed to egg-laying animals)

YELK-SAC: part of the primitive gut which encloses the yelk

ZONA pellucida: the ovolemma
Zoophytes: literally "animal-plants," but long known to be *animals* of somewhat advanced type, the cœlenteria
Zooplasm: animal plasm