The Evolution of Man, V.2

Ernst Haeckel

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THE EVOLUTION OF MAN
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CHAPTER 2.16. STRUCTURE OF THE LANCELET AND THE SEA−SQUIRT.

In turning from the embryology to the phylogeny of man—from the development of the individual to that of the species—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 were complete in all cases, it would be very easy to construct the whole story of evolution on an embryonic 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 change of the 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. The young of animals (not only detached larvae, 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. Moreover, 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 traces of their ancestors. The higher the individual organism is in the animal kingdom, the less completely does it reproduce in its embryonic development 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 evolutionary 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 development of the individual (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 the original features have been preserved by heredity, and modifications have 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. 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 different kinds of rocks: there are, firstly, the volcanic rocks which were formed directly by the cooling at the surface of the molten mass of the earth; secondly, there are the 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 (sandstone, limestone, 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, which 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 2.18).

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 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 lower vertebrates and their invertebrate ancestors. Especially in the lowest of all the vertebrates, the lancelet or 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 evolution 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 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 ontogeny. We are thus in a position to form a fairly complete idea of the past development of man's ancestors within the vertebrate stem by putting together and comparing the embryological developments of the various groups of vertebrates. And 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 very lowest groups of animals.

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 understood unless we 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 evolutionary 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 the structure 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 sea−squirt (Ascidia). 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 sea−squirt, 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.

It lives on the flat, sandy parts of the Mediterranean coast, partly buried in the sand, and is apparently found in a number of seas.* (* See the ample monograph by Arthur Willey, Amphioxus and the Ancestry of the Vertebrates; Boston, 1894.) 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 in 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 or three genera.

(FIGURE 2.210. The lancelet (Amphioxus lanceolatus), twice natural size, left view. The long axis is vertical; the mouth−end is above, the tail−end below; 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.

FIGURE 2.211. 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 gonads (g). ao aorta (here double), c corium, ec endostyl, f fascie, gl glomerulus of the kidneys, k branchial vessel, ld partition between the coeloma (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 coeloma (subchordal body−cavity), si principal (or subintestinal) vein, sk perichorda (skeletal layer).)

Johannes Muller 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 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 that have no vertebrae 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.

Opposed to the Acrania is the second division of the vertebrates, which comprises all the other members of the stem, from the 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 embryology, 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 vertebrae nor skull nor limbs (Figures 1.83 to 1.86). And even after the formation of the primitive vertebrae has begun, the segmented foetus 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−shaped foetus, 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 (Figure 2.210) 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, and a thin underlying cutis−layer. Along the middle line of the back runs a narrow fin−fringe which expands behind into an oval tail−fin, and is continued below in a short anus−fin. The fin−fringe is supported by a number of square elastic fin−plates.

In the middle of the body we find a thin string of cartilage, which goes the whole length of the body from front to back, and is pointed at both ends (Figure 2.210 i). This straight, cylindrical rod (somewhat compressed for a time) is the axial rod or the chorda dorsalis; in the lancelet this is the only trace of a vertebral column. The chorda develops no further, 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 (Figure 2.211). The perichorda forms a cylindrical tube immediately over the chorda, and the central nervous system, the medullary tube, is enclosed in it. This important psychic organ also remains in 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 bulbous swelling of the canal. This must be regarded as the beginning of 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, Figure 2.210 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 (Figure 2.210 d). 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, Figure 2.210 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 larvae 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.

(FIGURE 2.212. Transverse section of an Amphioxus−larva, with five gill−clefts, through the middle of the body.

FIGURE 2.213. Diagram of the preceding. (From Hatschek.) A epidermis, B medullary tube, C chorda, C1 inner chorda−sheath, D visceral epithelium, E sub−intestinal vein. 1 cutis, 2 muscle−plate (myotome), 3 skeletal plate (sclerotome), 4 coeloseptum (partition between dorsal and ventral coeloma), 5 skin−fibre layer, 6 gut−fibre layer, I myocoel (dorsal body−cavity), II splanchnocoel (ventral body−cavity).)

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, diatoms, 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 (Figure 2.210 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 develops, 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 circulatory system in this animal is not less interesting. All the other vertebrates have a compressed, thick, pouch−shaped heart, which develops from the wall of the 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 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. On the under−side of the gill−crate, 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 (Figure 2.210 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 (Figure 2.214 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 (Figures 1.210 o and 2.212 E). 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 versa. 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 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.

(FIGURE 2.214. Transverse section of a young Amphioxus, immediately after metamorphosis, through the hindermost third (between the atrium−cavity and the anus).

FIGURE 2.215. 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 myocoel, II splanchnocoel, I1 dorsal fin, I2 anus−fin.)

The coeloma 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 1.10), in these the two coelom−pouches are divided at an early stage by transverse constrictions into a double row of primitive segments (Figure 1.124), and each of these subdivides, by a frontal or lateral constriction, into an upper (dorsal) and lower (ventral) pouch.

These important structures are seen very clearly in the trunk of the amphioxus (the latter third, Figures 2.212 to 2.215), but it is otherwise in the head, the foremost third (Figure 2.216). 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. Figure 1.81). The branchial gut lies free in a spacious cavity filled with water, which was wrongly thought formerly to be the body−cavity (Figure 2.216 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 (M1, U). The real body−cavity (Lh) is very narrow and entirely closed, lined with epithelium. The peribranchial cavity (A) is full of water, and its walls are lined with the skin−sense layer; it opens outwards in the rear through the respiratory pore (Figure 2.210 c).

On the inner surface of these mantle−folds (M1), 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 roundish four−cornered sacs, which can clearly be seen from without with the naked eye, as they shine through the thin transparent body−wall. These sacs are the sexual glands they are the same size and shape in both sexes, only differing in contents. In the female they contain a quantity of simple ova (Figure 2.219 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.

(FIGURE 2.216. 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 (M1) and to the chorda−sheath. N medullary tube, Ch chorda, Lh body−cavity, A atrium, L upper wall of same, E1 inner wall, E2 outer wall, Lh1 ventral remnant of same, Kst gill−reds, M ventral muscles, R seam of the joining of the ventral folds (gill−covers), G sexual glands.)

Above the sexual glands, 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 (Figure 2.217 x). They are short segmented canals; corresponding to the primitive kidneys of the other vertebrates (Figure 2.218 B). Their internal aperture (Figure 2.217 B) opens into the body−cavity; their outer aperture into the atrium (C). The prorenal canals lie in the middle of the line 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 primitive kidneys of the Amphioxus show clearly that they are equivalent to the prorenal canals of the Craniotes (Figure 2.218 B). The prorenal duct of the latter (Figure 2.218 C) corresponds to the branchial cavity or atrium of the former (Figure 2.217 C).

(FIGURE 2.217. 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 gonocoel), x pronephridium, B its coelom−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.

FIGURE 2.218. 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.)

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 unmistakably 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 1.11.)

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.

(FIGURE 2.219. 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, co umlaut coeloma (body−cavity), e endostyl (hypobranchial groove), g gonads (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.)

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. The other group are the Petromyzontes, or lampreys, which are a familiar delicacy in their marine form. 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 with the Amphioxus. The chorda is of the same simple character in both; also the medullary tube, that lies above the chorda, and the alimentary canal below it. However, in the lamprey the spinal cord swells in front into a simple pear−shaped cerebral vesicle, and at each side of it there are a very simple eye and a rudimentary auditory vesicle. The nose is a single pit, as in the Amphioxus. The two sections of the gut are also just the same and very rudimentary in the lamprey. 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 and a ventricle. 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 Ascidia, 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 Ascidiae 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 Ascidiae form 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 Ascidiae 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 Ascidiae 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 Ascidia the name of “the microcosm.”

(FIGURE 2.220. Organisation of an Ascidia (left view); the dorsal side is turned to the right and the ventral side to the left, the mouth (o) above; the ascidia 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.)

FIGURE 2.221. Organisation of an Ascidia (as in Figure 2.220, seen from the left). sb branchial sac, v stomach, i small intestine, c heart, t testicle, vd sperm−duct, o ovary, o apostrophe 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.))

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 (Figure 2.220 cl). It is also called the branchial cavity and the cloaca, because it receives 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 Ascidia 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 apostrophe). 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. The food of the Ascidia also consists of tiny organisms, infusoria, diatoms, 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. The adjoining small intestine usually forms a loop, bends forward, and opens by an anus (Figure 2.220 a), not directly outwards, but first into the mantle cavity; from this the excrements are ejected by a common outlet (a apostrophe) 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. In many of the Ascidiae a glandular mass opens into the gut, and this represents the liver. In some there is another gland besides the liver, and this is taken to represent the kidneys. The body−cavity proper, or coeloma, 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.

There is no trace in the fully−developed Ascidia 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, and that there is a rudimentary medullary tube above it. The latter is wholly atrophied in the developed Ascidia, and looks like a small nerve−ganglion in front above the gill−crate. 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. The muscular system is very slightly and irregularly developed. Immediately under the thin corium, and closely connected with it, we find a thin muscle tube, as in the worms. On the other hand, the Ascidia 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. It retains permanently the simple tubular form that we find temporarily as the first structure of the heart in the vertebrates. This simple heart of the Ascidia 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 Ascidia 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 Ascidiae are hermaphrodites. Each individual has a male and a female gland, and so is able to fertilise itself. The ripe ova (Figure 2.221 o apostrophe) 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 duct (vd). Fertilisation is accomplished here, and in many of the Ascidiae developed embryos are found. These are then ejected with the breathing−water through the cloaca (q), and so “born alive.”

If we now glance at the entire structure of the simple Ascidia (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 Ascidia 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 develops from the ovum of the Amphioxus as from that of the Ascidia—a typical chordula.

CHAPTER 2.17. EMBRYOLOGY OF THE LANCELET AND THE SEA−SQUIRT.

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 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, 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 General Morphology (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 Ascidia. 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 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 Ascidiae. We cannot say that the vertebrates are descended from the Ascidiae—and still less the reverse—but we can say that of all the invertebrates it is the Tunicates, and, within this group, the Ascidiae, 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 Ascidia. We begin with the ontogeny of the Amphioxus.

From the concordant observations of Kowalevsky at Naples and Hatschek at Messina, it follows, firstly, that the ovum−segmentation and 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, which we have already described as original or primordial; the development of the Ascidia 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 seawater, 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 gonads, proceed through the gill−clefts into the branchial gut, and are discharged from this through the mouth.

The ova are simply round cells. They are only 1/250 of an inch in diameter, and thus are only half the size of the mammal ova, and have no distinctive features. 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 (Chapter 1.7). The active elements of the male sperm, the cone−shaped spermatozoa, are similar to those of most other animals (cf. Figure 1.20). 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, Figure 1.2). 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 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 foetus attains the familiar blastula shape and forms a hollow ball, the wall of which consists of a single stratum of cells (Figure 1.38 A to C). This layer is the blastoderm, the simple epithelium from the cells of which all the tissues of the body proceed.

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 (Figure 1.38 D). This pit becomes deeper and deeper (Figure 1.38 E and F); at last the invagination (or doubling) 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 (Figure 1.38 E). From hemispherical the body soon becomes almost spherical once more, and then oval, the internal cavity enlarging considerably and its mouth growing narrower (Figure 2.213). 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 (Figures 1.29 to 1.35).

As in all the other animals that form an archigastrula, the whole body is nothing but a simple gastric sac or stomach; its internal cavity is the primitive gut (progaster or archenteron, Figure 1.38 g, 1.35 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, the inner or vegetal germ−layer, from which develop the wall of the alimentary canal and all its appendages, the coelom−pouches, etc. (Figures 1.35 and 1.36 i). The outer stratum of cells, or the non−invaginated part of the blastoderm, is the ectoderm, 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 from the outer 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 (Figure 1.36). As in many other lower animals, the 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).

In the further course of its rapid 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 (Figure 1.39). In the middle of the dorsal surface a shallow longitudinal groove or furrow is formed (Figure 1.79), 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 (Figures 1.83 m and 1.84 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 foetal membranes.

Simultaneously with the construction of the medullary tube we have in the Amphioxus−embryo the formation of the chorda, the coelom−pouches, and the mesoderm proceeding from their wall. These processes also take place with characteristic simplicity and clearness, so that they are very instructive to compare with the vermalia on the one hand and with the higher vertebrates 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 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 (Figure 1.83 p). They indicate the original starting−point of the two coelom−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.

Immediately after their formation the two coelom−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 (Figure 1.82). 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 vertebrae"). They have a different future above and below. The upper or dorsal segments, the episomites, lose their cavity later on, and form with their cells the muscular plates of the trunk. The lower or ventral segments, the hyposomites, corresponding to the lateral plates of the craniote−embryo, fuse together in the upper part owing to the disappearance of their lateral walls, and thus form the later body−cavity (metacoel); in the lower part they remain separate, and afterwards form the segmental gonads.

In the middle, between the two lateral coelom−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 (Figures 1.83 and 1.84 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.

In consequence of these important folding−processes in the primitive gut, the simple entodermic tube divides into four different sections:—

1. underneath, at the ventral side, the permanent alimentary canal or permanent gut;
2. above, at the dorsal side, the axial rod or chorda; and
3. the two coelom−sacs, which immediately sub−divide into two structures:—

3A. above, on the dorsal side, the episomites, the double row of primitive or muscular segments; and

3B. below, on each side of the gut, the hyposomites, the two lateral plates that give rise to the sex−glands, and the cavities of which partly unite to form the 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 earlier stages 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. 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.

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 larvae 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, and a lower or ventral vessel, corresponding to the subintestinal vein, at the lower border of the gut. 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 gill−clefts, supported on a number of stiff branchial rods; these are connected in pairs by transverse rods.

(FIGURES 2.222 TO 2.224. Transverse sections of young Amphioxus−larvae (diagrammatic, from Ralph.) (Cf. also Figure 2.216.) In Figure 2.222 there is free communication from without with the gut−cavity (D) through the gill−clefts (K). In Figure 2.223 the lateral folds of the body−wall, or the gill−covers, which grow downwards, are formed. In Figure 2.224 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, E1 the same as visceral epithelium of the mantle−cavity, E2 as parietal epithelium of the mantle−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” (Figures 1.98 to 1.102). 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 (one−eighth of an inch), it has substantially the same structure as the adult. As regards the remaining organs of the Amphioxus, we need only mention that the gonads or sexual glands are developed very late, immediately out of the inner cell−layer of the body−cavity. Although we can find afterwards no continuation of the body−cavity (Figure 2.216 U) in the lateral walls of the mantle−cavity, in the gill−covers or mantle−folds (Figure 2.224 U), there is one present in the beginning (Figure 2.224 Lh). The sexual cells are formed below, at the bottom of this continuation (Figure 2.224 S). 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 Ascidia, 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 Ascidiae that show most clearly the relationship of the vertebrates to the invertebrates, and the larvae 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 1/250 to 1/125 of an inch in diameter. In the thick fine−grained yelk we find a clear round germinal vesicle of about 1/750 of an inch in diameter, and this encloses a small embryonic spot or nucleolus. Inside the membrane that surrounds the ovum, the stem−cell of the Ascidia, after fecundation, passes through just the same metamorphoses as the stem−cell 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. A real gastrula (a simple bell−gastrula) is formed from the blastula by invagination, in the same way as in the amphioxus.

Up to this there is no definite ground in the embryology of the Ascidiae 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 Ascidiae 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 the organs that are otherwise only found in Vertebrates. The formation of these very important organs takes place in the Ascidia−gastrula in precisely the same way as in that of the Amphioxus. In the Ascidia (as in the other case) the oval 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 skin 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 Ascidia−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.

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 round 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. It is afterwards composed of several rows of cells. In the Ascidia−larva, also, the chorda develops from the dorsal middle part of the primitive gut, while the two coelom−pouches detach themselves from it on both sides. The simple body−cavity is formed by the coalescence of the two.

When the Ascidia−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 oar−like tail. These free−swimming larvae 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 oars, 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 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 Ascidia. 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 Ascidia 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 out−growths, 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 modification of others, gradually assumes the appearance we have already described.

(FIGURE 2.225. An Appendicaria (Copelata), seen from the left. m mouth, k branchial gut, o gullet, 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 living Tunicates there is a very interesting group of small animals that remain throughout life at the stage of development of the tailed, free Ascidia−larva, and swim about briskly in the sea by means of their broad oar−tail. These are the remarkable Copelata (Appendicaria and Vexillaria, Figure 2.225). 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 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 Ascidia−larvae, 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 (Figure 2.225 c), and serves as an attachment for the muscles that work the flat oar−tail.

Among the various modifications which the Ascidia−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 Ascidia 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. 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 which can be found in the adult Ascidia. 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 Ascidia 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 Ascidia as in the Amphioxus. The ejection−opening of this peribranchial cavity corresponds to the branchial pore of the Amphioxus. In the adult Ascidia the branchial gut and the heart on its ventral side are almost the only organs that recall the original affinity with the vertebrates.

The further development of the Ascidia 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 Ascidia degenerates more and more, 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 Ascidia, 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 Ascidia 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.

CHAPTER 2.18. DURATION OF THE HISTORY OF OUR STEM.

Our comparative investigation of the anatomy and ontogeny of the Amphioxus and Ascidia has given us invaluable assistance. We have, in the first place, bridged the wide gulf that has existed up to the present 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 coelomula, the chordula, etc.

Thus the embryology of the Amphioxus and the Ascidia 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 the reader 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 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 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). 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 foetal 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 ontogeny shrinks into insignificance when we compare it with the enormous period that has been necessary for phylogeny, 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 mine 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.

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. The organic history of the earth could not commence until it was possible for water to settle on our planet 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 foetus contains more than ninety per cent of water, and not ten per cent of solids. In the lower marine animals, especially certain medusae, 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 series 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 1000 feet thick must be 500,000 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 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.

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

COLUMN 1 : Groups (V. down to I.).

COLUMN 2 : Systems (XIV. down to I.).

COLUMN 3 : Formations (38 down to 1).

COLUMN 4 : Synonyms of Formations.

V. Anthropolithic group, or anthropozoic (quaternary) group of strata : XIV. Recent (alluvium) : 38. Present : Upper alluvial.

V. Anthropolithic group, or anthropozoic (quaternary) group of strata : XIV. Recent (alluvium) : 37. Recent :

Lower alluvial.

V. Anthropolithic group, or anthropozoic (quaternary) group of strata : XIII. Pleistocene (diluvium) : 36. Post−glacial : Upper diluvial.

V. Anthropolithic group, or anthropozoic (quaternary) group of strata : XIII. Pleistocene (diluvium) : 35. Glacial : Lower diluvial.

IV. Cenolithic group, or cenozoic (tertiary) group of strata : XII. Pliocene (neo−tertiary) : 34. Arverne : Upper pliocene.

IV. Cenolithic group, or cenozoic (tertiary) group of strata : XII. Pliocene (neo−tertiary) : 33. Subapennine : Lower pliocene.

IV. Cenolithic group, or cenozoic (tertiary) group of strata : XI. Miocene (middle tertiary) : 32. Falun : Upper miocene.

IV. Cenolithic group, or cenozoic (tertiary) group of strata : XI. Miocene (middle tertiary) : 31. Limbourg : Lower miocene.

IV. Cenolithic group, or cenozoic (tertiary) group of strata : Xb. Oligocene (old tertiary) : 30. Aquitaine : Upper oligocene.

IV. Cenolithic group, or cenozoic (tertiary) group of strata : Xb. Oligocene (old tertiary) : 29. Ligurium : Lower oligocene.

IV. Cenolithic group, or cenozoic (tertiary) group of strata : Xa. Eocene (primitive tertiary) : 28. Gypsum : Upper eocene.

IV. Cenolithic group, or cenozoic (tertiary) group of strata : Xa. Eocene (primitive tertiary) : 27. Coarse chalk : Middle eocene.

IV. Cenolithic group, or cenozoic (tertiary) group of strata : Xa. Eocene (primitive tertiary) : 26. London clay : Lower eocene.

III. Mesolithic group, or mesozoic (secondary) group of strata : IX. Chalk (cretaceous) : 25. White chalk. : Upper cretaceous.

III. Mesolithic group, or mesozoic (secondary) group of strata : IX. Chalk (cretaceous) : 24. Green Sand : Middle cretaceous.

III. Mesolithic group, or mesozoic (secondary) group of strata : IX. Chalk (cretaceous) : 23. Neocomian : Lower cretaceous.

III. Mesolithic group, or mesozoic (secondary) group of strata : IX. Chalk (cretaceous) : 22. Wealden : Weald−formation.

III. Mesolithic group, or mesozoic (secondary) group of strata : VIII. Jurassic : 21. Portland : Upper oolithic.

III. Mesolithic group, or mesozoic (secondary) group of strata : VIII. Jurassic : 20. Oxford : Middle oolithic.

III. Mesolithic group, or mesozoic (secondary) group of strata : VIII. Jurassic : 19. Bath : Lower oolithic.

III. Mesolithic group, or mesozoic (secondary) group of strata : VIII. Jurassic : 18. Lias : Liassic.

III. Mesolithic group, or mesozoic (secondary) group of strata : VII. Triassic : 17. Keuper : Upper triassic.

III. Mesolithic group, or mesozoic (secondary) group of strata : VII. Triassic : 16. Muschelkalk : Middle triassic.

III. Mesolithic group, or mesozoic (secondary) group of strata : VII. Triassic : 15. Bunter : Lower triassic.

II. Paleolithic group, or paleozoic (primary) group of strata : VIb. Permian : 14. Zechstein : Upper permian.

II. Paleolithic group, or paleozoic (primary) group of strata : VIb. Permian : 13. Neurot sand : Lower permian.

II. Paleolithic group, or paleozoic (primary) group of strata : VIa. Carboniferous (coal−measures) : 12. Carboniferous sandstone : Upper carboniferous.

II. Paleolithic group, or paleozoic (primary) group of strata : VIa. Carboniferous (coal−measures) : 11. Carboniferous limestone : Lower carboniferous.

II. Paleolithic group, or paleozoic (primary) group of strata : V. Devonian : 10. Pilton : Upper devonian.

II. Paleolithic group, or paleozoic (primary) group of strata : V. Devonian : 9. Ilfracombe : Middle devonian.

II. Paleolithic group, or paleozoic (primary) group of strata : V. Devonian : 8. Linton : Lower devonian.

II. Paleolithic group, or paleozoic (primary) group of strata : IV. Silurian : 7. Ludlow : Upper silurian.

II. Paleolithic group, or paleozoic (primary) group of strata : IV. Silurian : 6. Wenlock : Middle silurian.

II. Paleolithic group, or paleozoic (primary) group of strata : IV. Silurian : 5. Llandeilo : Lower silurian.

I. Archeolithic group, or archeozoic (primordial) group of strata : III. Cambrian : 4. Potsdam : Upper cambrian.

I. Archeolithic group, or archeozoic (primordial) group of strata : III. Cambrian : 3. Longmynd : Lower cambrian.

I. Archeolithic group, or archeozoic (primordial) group of strata : II. Huronian : 2. Labrador : Upper laurentian.

I. Archeolithic group, or archeozoic (primordial) group of strata : 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, amoebae, rhizopods, infusoria, and other Protists). During this 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.

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 (Palaeodus) 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 paleozoic 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 paleozoic period as “the age of fishes.” Among the paleozoic plated fishes or Ganoids the Crossopterygii and the Ctenodipterina (dipneusts) 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 animals; 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 (Archeopteryx, Odontornis).

Finally, the most advanced and (for us) the most important class of the vertebrates, the mammals, made their 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 some extinct ape or lemur 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. 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 (quaternary) age : 0 : 5.
Total : 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.

Before we approach our proper 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. Speech 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.

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.

This “comparative anatomy” and evolution of languages 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 view of their origin is now accepted by all the chief philologists who have worked in this branch and are unprejudiced.

But the point to which I desire particularly to draw the reader's attention in this comparison of the Indo−Germanic languages with the branches of the vertebrate stem is, that one 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 lemur, and the lemur from the marsupial, many people imagine that 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 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 Ascidia, 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 Gastraea, that most instructive form that gives the clearest possible picture of an animal with two germinal layers. The Gastraea itself has originated from the simple multicellular vesicle, the Blastaea, 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 Amoeba, 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 amoeboid 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 amoeboid coils.

But the further question now arises: “Whence came these first amoebae 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 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.

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 General Morphology, or to the essay on “The Monera and Spontaneous Generation” in my Studies of the Monera and other Protists.* (* 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.—Translator.) I have given there fully my own view of this important question. The famous botanist Nageli 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, 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−water. Our demand for a knowledge of causes compels us to assume this. If we believe that the whole inorganic history of the earth has proceeded on mechanical principles without any intervention of a Creator, and 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 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 Zollner, 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. 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, and the external, softer cellular substance or the protoplasm of the cell−body. 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 boon formed by spontaneous generation at the commencement of the history of life.

CHAPTER 2.19. OUR PROTIST ANCESTORS.

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. Phylogeny us a whole is an inductive science. 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. All the interesting phenomena that we meet in ontogeny and paleontology, comparative anatomy and dysteleology, the distribution and habits 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.

But 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 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.

I must point out at once, however, 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. 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. But, for the present, 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.

In my first efforts to construct the series of man's ancestors 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.

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 globule of structureless plasm or plasson. 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 regarded 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.

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 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. Chapter 1.6.)

(FIGURE 2.226. Chroococcus minor (Nageli), magnified 1500 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 to d).

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 anatomic 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 imagine the simplest possible organism, we should frame something like the moneron.

The Monera that we find to−day in various forms fall into two groups according to the nature of their nutrition—the Phytomonera and the Zoomonera; 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 (Figure 2.226) 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, from 1/7000 to 1/2500 of an inch in diameter.

(FIGURE 2.227. Aphanocapsa primordialis (Nageli), magnified 1000 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 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 the continuous assimilation of inorganic matter, 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 floating matter in the arctic seas. The tiny plasma−globules of this species are of a greenish−brown colour, and have a diameter of 1/10,000 to 1/5000 of an inch. There is no membrane discoverable in the simplest Chroococcacea, but we find one in other members of the same family; in Aphanocapsa (Figure 2.227) the enveloping membranes of the social plastids combine; in Gloecapsa they are retained through several generations, so that the little plasma−globules are enfolded in many layers of membrane.

Next to the Chromacea come the Bacteria, which have been evolved from them by the remarkable change in nutrition which gives us the simple explanation of the differentiation of plant and animal in the protist kingdom. The Chromacea build up their plasm directly from inorganic matter; the Bacteria feed on organic matter. 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 class them with the true fungi. The Bacteria, like the Chromacea, have no nucleus. As is well−known, they play an important part in modern biology as the causes of fermentation and putrefaction, and of tuberculosis, typhus, cholera, and other infectious diseases, and as parasites, 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 Protamoeba, or unnucleated Amoeba. I have, in the first volume, pointed out the great importance of the ordinary Amoeba in connection with several weighty questions of general biology. The tiny Protamoebae, 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 Amoebae; but they differ from them very materially in having no nucleus in their cell−body. The short, blunt, finger−like processes that are thrust out at the surface of the creeping Protamoeba serve for getting food as well as for locomotion. They multiply by simple cleavage (Figure 2.228).

(FIGURE 2.228. A moneron (Protamoeba) in the act of reproduction. A The whole moneron, moving like an ordinary amoeba 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 Amoeba. The earliest process of inorganic differentiation in the structureless 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. By this important differentiation of the plasson into nucleus and cell−body, 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 science. We have a direct instance of this earliest process of differentiation to−day in the ontogeny of many of the lower Protists (such as the Gregarinae).

The unicellular form that we have in the ovum has already been described as the reproduction of a corresponding unicellular stem−form, and to this we have ascribed the organisation of an Amoeba (cf. Chapter 1.6). The irregular−shaped Amoeba, 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 (Figure 1.16). As the unripe ova (the protova that we find in the ovaries of animals) cannot be distinguished from the common Amoebae, we must regard the Amoeba as the primitive form that is reproduced in the embryonic stage of the amoeboid 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 Amoebae (Figure 1.18). Large unicellular organisms like the Amoebae 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 Amoebae in size, shape, the character of their nucleus, and movement of the pseudopodia, that it is impossible to distinguish them without knowing their subsequent development.

Our phylogenetic interpretation of the ovum, and the reduction of it to some ancient amoeboid 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 amoeboid cell of the simplest character. The egg lived for thousands of years as an independent unicellular organism, the Amoeba. 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 gastraea−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.

The earliest ancestors of our race were simple Protophyta, and from these our protozoic ancestors were developed afterwards. 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 Moraeada, which represent the third stage in our genealogy, are very simple associations of homogeneous, indifferent cells—undifferentiated colonies of social Amoebae or Infusoria. To understand the nature and origin of these protozoa−colonies we need only follow step by step the first embryonic 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 (Figure 2.229). 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 1.8). 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. 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. Figure 1.38). The outcome of this repeated cleavage is the formation of a round cluster of cells, composed of homogeneous, indifferent cells of the simplest character (Figure 2.230). This is called the morula (= mulberry−embryo) on account of its resemblance to a mulberry or blackberry.

(FIGURE 2.229. 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).

FIGURE 2.230. Morula, or mulberry−shaped embryo.)

It is clear that this morula reproduces for us to−day the simple structure of the multicellular animal that succeeded the unicellular amoeboid form in the early Laurentian period. In accordance with the biogenetic law, the morula recalls the ancestral form of the Moraea, 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 amoeboid cells. The oldest Amoebae lived isolated lives, and even the amoeboid 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 Amoebae 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 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 Moraeada, we have only to follow the further embryonic development of the morula. We then see that the social cells of the round cluster secrete a sort of jelly or a watery fluid inside their globular body, and they themselves rise to the surface of it (Figure 1.29 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.

This interesting blastula is very important. The conversion of the morula into a hollow ball 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 foetal 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 processes; the body swims about by the vibratory movement of these lashes or whips (Figure 1.29 F).

We still find, both in the sea and in fresh water, various kinds 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 ciliated homogeneous cells. There are “blastaeads” of this kind even among the Protophyta—the familiar Volvocina, formerly classed with the infusoria. The common Volvox globator is found in the ponds in the spring—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 Halosphaera 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, Magosphaera, etc.) are similar in structure to these vegetal clusters, but differ in their animal nutrition; they form the special group of the 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 (Magosphaera planula), Figures 2.231 and 2.232). The fully−formed body is a gelatinous ball, with its wall composed of thirty−two to sixty−four ciliated 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 amoeba. 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 magosphaera−form with which we started. This completes the life−circle of the remarkable and instructive animal.

If we compare these permanent blastulae with the free−swimming ciliated larvae or blastulae, 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 Blastaea. 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 ciliated cells. There were probably many genera and species of these blastaeads in the Laurentian period, forming a special class of marine protists.

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 2000 yards) 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 Halosphaera viridis in 1879.

The next stage to the Blastaea, and the sixth in our genealogical tree, is the Gastraea 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 (Figure 1.29 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 Gastraea from the Blastaea. A pit−shaped depression appears at one side of the spherical blastula (Figure 1.29 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 (Figure 1.29 J). In explaining the phylogenetic origin of the gastraea in the light of this ontogenetic process, we may assume that the one−layered cell−community of the blastaea 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 the animal functions of locomotion, sensation, and protection. This was the first division of labour among the originally homogeneous cells of the blastaea.

(FIGURE 2.231. The Norwegian Magosphaera planula, swimming about by means of the lashes or cilia at its surface.

FIGURE 2.232. Section of Magosphaera planula, showing how the pear−shaped cells in the centre of the gelatinous ball are connected by a fibrous process. Each cell has a contractile vacuole as well as a nucleus.)

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 1.8 and 1.9) 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 gastraea.

The gastraea probably lived in the sea during the Laurentian period, swimming about in the water by means of its ciliary coat much as free ciliated gastrulae 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 no doubt 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 gastraeads and other lower animals, especially the sponges.

The fact that there are still in existence various kinds of gastraeads, or lower Metazoa with an organisation little higher than that of the hypothetical gastraea, is a strong point in favour of our theory. There are not very many species of these living gastraeads; 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 gastraead stem.

The Gastremaria and Cyemaria, the chief of these living gastraeads, are small Metazoa that live parasitically inside other Metazoa, and are, as a rule, 1/50 to 1/25 of an inch long, often much less (Figure 2.233, 1 to 15). Their soft body, devoid of skeleton, 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, Figure 1.29 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 1/25 to 1/8 inch in diameter, in the fluid contents of which the little parasites were swimming. The cup−shaped body of the Pemmatodiscus (Figure 2.233, 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 skin 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 or gut layer (i), the prismatic 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 gastraeads (Mesogastria).

Probably a near relative of the Pemmatodiscus is the Kunstleria Gruveli (Figure 2.233, 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.

Pemmatodiscus and Kunstleria may be included in the family of the Gastremaria. To these gastraeads with open gut are closely related the Orthonectida (Rhopalura, Figure 2.233, 3 to 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 gastraeads are of both sexes, the male (Figure 1.3) being smaller and of a somewhat different shape from the oval female (Figure 1.4).

The somewhat similar Dicyemida (Figure 1.6) 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 (Figures 1.7 to 1.15) 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. I adhere to the phylogenetically important theory that I advanced in 1876, that we have here real gastraeads, 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.

(FIGURE 2.233. Modern gastraeads. Figure 1. Pemmatodiscus gastrulaceus (Monticelli), in longitudinal section. Figure 2. Kunstleria gruveli (Delage), in longitudinal section. (From Kunstler and Gruvel.) Figures 3 to 5. Rhopalura Giardi (Julin): Figure 3 male, Figure 4 female, Figure 5 planula. Figure 6. Dicyema macrocephala (Van Beneden). Figures 7 to 15. Conocyema polymorpha (Van Beneden): Figure 7 the mature gastraead, Figures 8 to 15 its gastrulation. d primitive gut, o primitive mouth, e ectoderm, i entoderm, f gelatinous plate between e and i (supporting plate, blastocoel).)

The small Coelenteria 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 gastraeads. The genus Haliphysema (Figures 2.234 and 2.235) 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 (Figure 2.235 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 gastraeads chiefly in being attached at one end (the end opposite to the mouth) to the floor of the sea.

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.

The simplest sponges (Olynthus, Figure 2.238) 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 gastraeads that 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 gastraeads 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).

(FIGURES 2.234 AND 2.235. Prophysema primordiale, a living gastraead.

FIGURE 2.234. The whole of the spindle−shaped animal (attached below to the floor of the sea).

FIGURE 2.235. The same in longitudinal section. The primitive gut (d) opens above at the primitive mouth (m). Between the ciliated cells (g) are the amoeboid ova (e). The skin−layer (h) is encrusted with grains of sand below and sponge−spicules above.

FIGURES 2.236 TO 2.237. Ascula of gastrophysema, attached to the floor of the sea. Figure 2.236 external view, 2.237 longitudinal section. g primitive gut, o primitive mouth, i visceral layer, e cutaneous layer. (Diagram.)

FIGURE 2.238. Olynthus, a very rudimentary sponge. A piece cut away in front.)

The lowest form of the Cnidaria is also not far removed from the gastraeads. 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 (Figures 2.236 and 2.237). 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.

In all these rudimentary living coelenteria the sexual cells of both kinds—ova and sperm cells—are formed by the same individual; it is possible that the oldest gastraeads 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 sexual cells originally proceeded from the edge of the primitive mouth of the gastraead.

CHAPTER 2.20. OUR WORM−LIKE ANCESTORS.

The gastraea theory has now convinced us that all the Metazoa or multicellular animals can be traced to a common stem−form, the Gastraea. 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 in the individual from the simple embryonic form of the gastrula, so they have all descended in past time from the common stem−form of the Gastraea. In this fact, and the fact we have already established that the Gastraea has been evolved from the hollow vesicle of the one−layered Blastaea, and this again from the original unicellular stem−form, we have obtained a solid basis for our study of evolution. The clear path from the stem−cell to the gastrula represents the first section of our human stem−history (Chapters 1.8, 1.9, and 2.19).

The second section, that leads from the Gastraea to the Prochordonia, is much more difficult and obscure. By the Prochordonia we mean the ancient and long−extinct animals which the important embryonic form of the chordula proves to have once existed (cf. Figures 1.83 to 1.86). The nearest of living animals to this embryonic structure are the lowest Tunicates, the Copelata (Appendicaria) and the larvae of the Ascidia. As both the Tunicates and the Vertebrates develop from the same chordula, we may infer that there was a corresponding common ancestor of both stems. We may call this the Chordaea, 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 Chordaea from the Gastraea; 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?”

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 Annelids (earth−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 Wurtzburg, 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. 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 unique 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 Haeckelogony: An Academic Protest against Haeckel'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 science 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 Coelenterata and Worms are "lower animals"; he even declared that the unicellular Protozoa were degenerate Coelenterata. In his opinion "degeneration is the great principle 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 embryology 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. Of late years this hypothesis, which raised so much dust and controversy, has been entirely abandoned by most competent zoologists, even those who once supported it. Its chief supporter, Dohrn, admitted in 1890 that it is "dead and buried," and made a blushing retraction 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 Medusae, 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 establishment and its profound significance, it may very well claim to be a THEORY, and so should be described as the chordonia or chordaea 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 Vermalia, 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 very early times 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 a 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, Figure 2.225).

The chordaea−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 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 hypothesis of the descent of the two stems from a common ancestor, an unsegmented 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 research made by 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 our purpose that we must consider it a 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 Vermalia or worm−like animals, 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, and give us clear indications of the way in which the Chordonia were developed from the Vermalia, and these from the Coelenteria.

While we seek the most important of these palingenetic forms among the groups of Coelenteria 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 Gastraea gradually became the more developed Chordaea.

We find our first solid datum in the gastrula of the Amphioxus (Figure 1.38). Its bilateral and tri−axial type indicates that the Gastraeads—the common ancestors of all the Metazoa—divided at an early stage into two divergent groups. The uni−axial Gastraea 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 Gastraea 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 has three axes. 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 Gastraeads, and thus produced the stem−forms of all the bilateral animals.

The Gastraea 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 sexual cells, and effected reproduction. In order to understand the further development of the gastraea, 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 Coelenteria and the Coelomaria. 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.

(FIGURE 2.239. 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 Zurich, was found in September, 1899, at Ajaccio in Corsica (creeping between fucoidea). It is one−twelfth of an inch long, one−twenty−fifth of an inch broad, and violet in colour. a mouth, g auditory vesicle, e ectoderm, i entoderm, o ovaries, a spermaries, f female aperture, m male aperture.)

The primitive worms (Platodaria) are very small flat worms of simple construction, but of great morphological and phylogenetic interest. They have been hitherto, as a rule, regarded as a special order of the Turbellaria, and associated with the Rhabdocoela; but they differ considerably from these and all the other Platodes (flat worms) in the absence of renal canals 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, Amphichoerus, Convoluta, Schizoprora, etc.) are very soft and delicate animals, swimming about in the sea by means of a ciliary coat, and very small (1/10 to 1/20 inch 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, which consists of entodermic cells with vacuoles. The food passes through the 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 Acoela (without gut−cavity or coelom), or, more correctly, Cryptocoela, or Pseudocoela. The sexual organs of these hermaphroditic Platodaria are very simple—two pairs of strings of cells, the inner of which (the ovaries, Figure 2.239 o) produce ova, and the outer (the spermaria, s) sperm−cells. These gonads are not yet independent sexual glands, but sexually differentiated cell−groups in the medullary substance, or, in other words, parts of the 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 bulbous 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 represents the first rudiment of a neural ganglion (vertical brain or acroganglion).

The 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 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 Rhabdocoela on account of the simple construction of their gut; they are, as a rule, less than a quarter of an inch long and of a simple oval or lancet shape (Figure 2.240). The surface is covered with ciliated epithelium, a stratum of ectodermic cells. The digestive gut is still the simple primitive gut of the gastraea (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 Gastraea) 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 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 Coelomaria; 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. 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 gonads or sexual glands—a pair of testicles (Figure 2.241 h) and a pair of ovaries (e). They open externally, sometimes by a common aperture (Monogonopora), sometimes by separate ones, the female behind the male (Digonopora, Figure 2.241). The sexual glands develop originally from the two promesoblasts or primitive mesodermic cells (Figure 1.83 p). As these earliest mesodermic structures extended, and became spacious sexual pouches in the later descendants of the Platodes, probably the two coelom−pouches were formed from them, the first trace of the real body−cavity of the higher Metazoa (Enterocoela).

The gonads are among the oldest organs, the few other organs that we find in the Platodes between the gut−wall and body−wall being later evolutionary products. One of the oldest and most important of these are the kidneys or nephridia, which remove unusable matter from the body (Figure 2.240 nc). These urinary or excretory organs were originally enlarged skin−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 Coelenteria (Gastraeads, Sponges, Cnidaria) or the Cryptocoela. They are first met in the Turbellaria, and have been transmitted direct from these to the Vermalia, and from these to the higher stems.

Finally, there is a very important new organ in the Turbellaria, which we do not find in the Cryptocoela (Figure 2.239) and their gastraead ancestors—the rudimentary nervous system. It consists of a couple of simple cerebral ganglia (Figure 2.241 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 smell pits (na), rudimentary eyes (au), and, less frequently, auditory vesicles.

On these principles I assume that the oldest and simplest Turbellaria arose from Platodaria, and these directly from bilateral Gastraeads. The chief advances were the formation of gonads and nephridia, and of the rudimentary brain. On this hypothesis, which I advanced in 1872 in the first sketch of the gastraea−theory (Monograph on the Sponges), there is no direct affinity between the Platodes and the Cnidaria.

(FIGURE 2.240. A simple turbellarian (Rhabdocoelum). m mouth, sd gullet epithelium, sm gullet muscles, d gastric gut, nc renal canals, nm renal aperture, au eye, na olfactory pit. (Diagram.)

FIGURE 2.241. The same, showing the other organs. g brain, au eye, na olfactory pit, n nerves, h testicles, male symbol male aperture, female symbol female aperture, e ovary, f ciliated epiderm. (Diagram.)

(FIGURES 242 AND 243. Chaetonotus, 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.))

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 difficulty 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. Among these worms we find some important forms that show considerable advance in organisation from the platode to the chordonia stage. Three of these phenomena are particularly instructive: (1) The formation of a true (secondary) body−cavity (coeloma); (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 1/250 to 1/1000 inch long. Zoologists differ as to their position in classification. In my opinion, they approach very close to the Rhabdocoela (Figures 2.240 and 2.241), and differ from them chiefly in the possession of an anus at the posterior end (Figure 2.242 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). 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 gonads (Figure 2.243 e).

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 group 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 Gastraeads; 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. In their more advanced mesoderm we find a few contractile longitudinal canals which force the blood through the body by their contractions; these are the first blood−vessels.

(FIGURE 2.244. 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.)

FIGURE 2.245. A young Enteropneust (Balanaglossus). (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.

Figure 2.246. Transverse section of the branchial gut. A of Balanoglossus, B of Ascidia. r branchial gut, n pharyngeal groove, asterisk 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).)

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 1/5 to 2/5 inch and a length of several yards (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 a good deal of 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 blood is red, and the red colouring−matter is haemoglobin, 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 pieces. The chief of these primitive blood−vessels is the one that lies above the gut in the middle line of the back (Figure 2.244 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 (Figure 2.244 l).

After the Nemertina, I take (as distant relatives) the Enteropneusta; they may be classed together with them as Frontonia or Rhyncocoela (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 (Figure 2.245) 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 segmentation; (2) the ciliary coat of the soft epidermis; (3) the double rows of gastric pouches, alternating with a single or double row of gonads; (4) separation of the sexes (the Platode ancestors were hermaphroditic); (5) the ventral mouth, underneath a protruding snout; (6) the anus terminating 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 (Figure 2.245 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 (gill) 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 (Figure 2.246 A*). This ventral half, the glandular walls of which are clothed with ciliary epithelium and secrete mucus, corresponds to the pharyngeal or hypo−branchial groove of the Chordonia (Bn), the important organ from which the later thyroid gland is developed in the Craniota (cf. Chapter 2.16). The agreement in the 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 system is a long dorsal neural string that runs above the gut and corresponds to the medullary tube of the Chordonia. Bateson believes he has detected a rudimentary chorda between the two.

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 (Figure 2.225) and the tailed larvae of the ascidia 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 importance (Chapters 2.16 and 2.17). 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 Gastraeads 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 Gastraea and the Chordaea. Even in this modified chordaea−theory the six fundamental organs of the chordula would retain their great 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 gonads (lying to right and left of the primitive mouth) would form the coeloma. 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 sketch of man's ancestry 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]:—

A. MAN'S GENEALOGICAL TREE, FIRST HALF: EARLIER SERIES OF ANCESTORS,

WITHOUT FOSSIL EVIDENCE.

COLUMN 1 : CHIEF STAGES. COLUMN 2 : ANCESTRAL STEM−GROUPS. COLUMN 3 : LIVING RELATIVES OF ANCESTORS.

STAGES 1 TO 5. PROTIST ANCESTORS. UNICELLULAR ORGANISMS.

1 to 2. Protophytes. : 1. Monera. Without nucleus. : Chromacea. (Chroococcus.) Phycochromacea.

1 to 2. Protophytes. : 2. Algaria. Unicellular algae. : 2. Paulotomea. Palmellacea. Eremosphaera.

3 to 5. Protozoa. : 3. Lobosa. Unicellular (amoebina) rhizopods. : 3. Amoebina. Amoeba Leucocyta.

3 to 5. Protozoa. : 4. Infusoria. Unicellular. : 4. Flagellata. Euflagellata. Zoomonades.

3 to 5. Protozoa. : 5. Blastaeades. Multicellular hollow spheres. : 5. Catallacta. Magosphaera, Volvocina, Blastula.

STAGES 6 TO 11. INVERTEBRATE METAZOA ANCESTORS.

6 to 8. Coelenteria, without anus and body−cavity. : 6. Gastraeades. With two germ−layers. : 6. Gastrula. Hydra, Olynthus, Gastremaria.

6 to 8. Coelenteria, without anus and body−cavity. : 7. Platodes I. Platodaria (without nephridia). : 7. Cryptocoela. Convoluta, Proporus.

6 to 8. Coelenteria, without anus and body−cavity. : 8. Platodes II. Platodinia (with nephridia). : 8. Rhabdocoela. Vortex, Monotus.

9 to 11. Vermalia, with anus and body−cavity. : 9. Provermalia. (Primitive Worms.) Rotatoria. : 9. Gastrotricha. Trochozoa, Trochophora.

9 to 11. Vermalia, with anus and body−cavity. : 10. Frontonia. (Rhynchelminthes.) Snout−worms. : 10. Enteropneusta. Balanoglossus, Cephalodiscus.

9 to 11. Vermalia, with anus and body−cavity. : 11. Prochordonia. Chorda−worms. : 11. Copelata. Appendicaria. Chordula−larvae.

STAGES 12 TO 15. MONORHINA ANCESTORS.

Oldest vertebrates without jaws or pairs of limbs, single nose. : 12. Acrania I. (Prospondylia.) : 12. Amphioxus larva.

Oldest vertebrates without jaws or pairs of limbs, single nose. : 13. Acrania II. More recent. : 13. Leptocardia. Amphioxus.

Oldest vertebrates without jaws or pairs of limbs, single nose. : 14. Cyclostoma I. (Archicrania.) : 14. Petromyzonta larvae.

Oldest vertebrates without jaws or pairs of limbs, single nose. : 15. Cyclostoma II. More recent. : 15. Marsipobranchia. Petromyzonta.

B. MAN'S GENEALOGICAL TREE, SECOND HALF: LATER ANCESTORS, WITH FOSSIL EVIDENCE.

COLUMN 1 : GEOLOGICAL PERIODS. COLUMN 2 : ANCESTRAL STEM−GROUPS. COLUMN 3 : LIVING RELATIVES OF ANCESTORS.

Silurian. : 16. Selachii. Primitive fishes. Proselachii. : 16. Natidanides. Chlamydoselachius. Heptanchus.

Silurian. 17. Ganoides. Plated−fishes. Proganoides. : 17. Accipenserides. (Sturgeons.) Polypterus.

Devonian. : 18. Dipneusta. Paladipneusta. : 18. Neodipneusta. Ceratodus. Protopterus.

Carboniferous. : 19. Amphibia. Stegocephala. : 19. Phanerobranchia. Salamandrina. (Proteus, triton.)

Permian. : 20. Reptilia. Proreptilia. : 20. Rhynchocephalia. Primitive lizards. Hatteria.

Triassic. : 21. Monotrema. Promammalia. : 21. Ornithodelphia. Echidna. Ornithorhyncus.

Jurassic. : 22. Marsupalia. Prodidelphia. : 22. Didelphia. Didelphys. Perameles.

Cretaceous. : 23. Mallotheria. Prochoriata. : 23. Insectivora. Erinaceida. (Ictopsida +.)

Older Eocene. : 24. Lemuravida. Older lemurs. Dentition. 3. 1. 4. 3. : 24. Pachylemures. (Hyopsodus +), (Adapis +).

Neo−Eocene. : 25. Lemurogona. Later lemurs. Dentition. 2. 1. 4. 3. : 25. Autolemures. Eulemur. Stenops.

Oligocene. : 26. Dysmopitheca. Western apes. Dentition. 2. 1. 3. 3. : 26. Platyrrhinae. (Anthropops +), (Homunculus +).

Older Miocene. : 27. Cynopitheca. Dog−faced apes (tailed). : 27. Papiomorpha. Cynocephalus.

Neo−Miocene. : 28. Anthropoides. Man−like apes (tail−less). : 28. Hylobatida. Hylobates. Satyrus.

Pliocene. : 29. Pithecanthropi. Ape−men (alali, speechless). : 29. Anthropitheca. Chimpanzee. Gorilla.

Pleistocene. : 30. Homines. Men, with speech. : 30. Weddahs. Australian negroes.

CHAPTER 2.21. OUR FISH−LIKE ANCESTORS.

Our 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 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.

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 1.11, Figure 1.98 to 1.102). 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 (gill) and hepatic (liver) gut; and (4) the internal articulation or metamerism. The first three features are shared by the Vertebrates with the ascidia−larvae and the Prochordonia; the fourth is peculiar to them. Thus the chief advantage in organisation by which the earliest Vertebrates took precedence of the unsegmented Chordonia consisted in the development of internal segmentation.

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 2.16 and 2.17.) The Amphioxus, the lowest Vertebrate, and the Ascidia, the nearest related Invertebrate, descend from a common extinct stem−form, the Chordaea; and this must have had, substantially, the organisation of the chordula.

However, the Amphioxus is important not 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. 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, Figures 1.98 to 1.102), 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 (Chapter 2.20). 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 bulbous enlargement of the fore end of the medullary tube. 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 midway 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.

(FIGURE 2.247. 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.)

The few surviving species of the Cyclostoma are divided into two orders—the Myxinoides and the Petromyzontes. The former, the hag−fishes, have a long, cylindrical, worm−like body. They were classed by Linne 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 consists of the Petromyzontes or lampreys; the small river lamprey (Petromyzon fluviatilis) and the large marine lamprey (Petromyzon marinus, Figure 2.247). 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 larvae 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 = double−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. A very rudimentary skull is developed at the foremost end of their chorda. At this point a soft membranous (partly turning into cartilage), small skull−capsule is formed, and encloses the brain.

The brain of the Cyclostoma is merely a very small and comparatively insignificant swelling of the spinal marrow, a simple vesicle at first. 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 lampreys there are only two, and in the hag−fishes 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. 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.

When we consider all these peculiarities in the structure 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, 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.

(FIGURE 2.248. Fossil Permian primitive fish (Pleuracanthus Dechenii), from the red sandstone of Saarbrucken. (From Doderlein.) 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.

FIGURE 2.249. 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.)

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 they 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 palaeontology, 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. 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 frame work 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 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. 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 depressions in the fore part of the skin 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. 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.

(FIGURE 2.250. Fully developed man−eating shark (Carcharias melanopterus), left view. r1 first, r2 second dorsal fin, s tail−fin, a anus−fin, v breast−fins, h belly−fins.)

Finally, the fourth character of the Gnathostomes in their simple embryonic form is the two pairs of extremities or limbs—a pair of fore legs (breast−fins in the fish, Figure 2.250 v) and a pair of hind legs (ventral fins in the fish, Figure 2.250 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 (Figures 2.248 to 2.252). Next to this is the more advanced sub−class of the plated fishes or Ganoids (Figures 2.253 to 2.255). 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 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.

(FIGURE 2.251. Fossil angel−shark (Squatina alifera), from the upper Jurassic at Eichstatt. (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.)

The earliest fossil remains of Vertebrates that we know were found in the Upper Silurian (Chapter 2.18), 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. (Figure 2.248). These ancient cartilaginous fishes agree in most points of structure with the real sharks (Figures 2.249 and 2.250); but in other respects they seem to be so much simpler in organisation that many palaeontologists 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, Figure 2.251). 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 eleven yards long, and has teeth two inches long; but among the fossil species we find teeth six inches long (Figure 2.252).

From the primitive fishes or Selachii, the earliest Gnathostomes, was developed the legion of the Ganoids. 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, Figure 2.255) 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 (Figure 2.253); a single, greatly modified survivor of the group is still found in the large rivers of Africa (Polypterus, Figure 2.255, 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 (Figure 2.254, immediately behind the head).

Part of these Crossopterygii approach very closely in their 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 paleontological 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 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 (the paleozoic age). The number increases considerably in the Carboniferous and Permian deposits. We find many species both of the articulate and the vertebrate stem that lived on land and breathed the atmosphere; their aquatic ancestors of the Silurian period only breathed water. This 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.

(FIGURE 2.252. Tooth of a gigantic shark (Carcharodon megalodon), from the Pliocene at Malta. Half natural size. (From Zittel.))

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.

(FIGURE 2.253. A Devonian Crossopterygius (Holoptychius nobilissimus, from the Scotch old red sandstone. (From Huxley.)

FIGURE 2.254. A Jurassic Crossopterygius (Undina penicillata), from the upper Jurassic at Eichstatt. (From Zittel.) j jugular plates, b three ribbed scales.

FIGURE 2.255. A living Crossopterygius, from the Upper Nile (Polypterus bichir).

FIGURE 2.256. Fossil Dipneust (Dipterus Valenciennesi), from the old red sandstone (Devon). (From Pander.)

FIGURE 2.257. The Australian Dipneust (Ceratodus Forsteri). B view from the right, A lower side of the skull, C lower jaw. (From Gunther.) 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).)

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 (lung) 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. 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 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 “amphibian.” 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.

(FIGURE 2.258. Young ceratodus, shortly after issuing from the egg, magnified ten times. k gill−cover, l liver. (From Richard Semon.)

FIGURE 2.259. Young ceratodus six weeks after issuing from the egg. s spiral fold of gut, b rudimentary belly−fin. (From Richard Semon.))

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.

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 original form of a bi−serial or feathered leaf, and was on that account described by Gegenbaur as a “primitive fin−skeleton.” 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 modern dipneusts, 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.

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.

CHAPTER 2.22. OUR FIVE−TOED ANCESTORS.

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 Linne, 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 (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") (Figure 2.260). It is among these, and 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).

(FIGURE 2.260. Fossil amphibian 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.)

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; on it 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.

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 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.* (* The tree−frog of Martinique (Hylades martinicensis) loses the gills on the seventh, and the tail and yelk−sac on the eighth, day of foetal life. On the ninth or tenth day after fecundation the frog emerges from the egg.) This is also the case with certain small, serpentine Amphibia, the Caecilia (which live in the ground like earth−worms).

(FIGURE 2.261. 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.)

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 breathe by lungs. 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 develops from an egg in our ponds.

(FIGURE 2.262. Larva of the common grass−frog (Rana temporaria), or “tadpole.” m mouth, n a pair of suckers for fastening on to stones, d skin−fold from which the gill−cover develops; behind it the gill−clefts, from which the branching gills (k) protrude, s tail−muscles, f cutaneous fin−fringe of the tail.)

The common frog leaves the egg in the shape of a larva, like the tailed salamander (Figure 2.261), and this is altogether different from the mature frog (Figure 2.262). 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.

We find the larvae 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 gills, 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.

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. In a second order of the salamanders the gills are lost in the metamorphosis, and when fully grown they have only pulmonary respiration. 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 larvae of our salamanders (Figure 2.261) 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.

(FIGURE 2.263. Fossil mailed amphibian, from the Bohemian Carboniferous (Seeleya). (From Fritsch.) The scaly coat is retained on the left.)

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 amphibian 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. 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 ontogenetic loss of the gills and the tail in the frog and toad can only be explained 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.

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.

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 (Figure 2.264) and the extinct Rhyncocephala of the Permian period (Figure 2.265) 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.

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 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 single extinct stem−form that it is difficult to entertain the idea of their 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 (Palaehatteria, Homoeosaurus, Proterosaurus) are found towards the close of the Permian period. Among the important changes of the vertebrate organisation that marked 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 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 Protamniote 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. Chapter 1.15). 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.

The formation of the amnion and the allantois and the complete disappearance of the gills 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 are found in these only. One striking embryonic character of the Amniotes is the great curve of the head and neck in the embryo. 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 reconstruction 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.

(FIGURE 2.264. The lizard (Hatteria punctata = Sphenodon punctatus) of New Zealand. The sole surviving proreptile. (From Brehm.))

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 Protamniote 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 Protamniote, the ancestor of the whole group, belongs in its whole organisation to the reptile class.

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 Protamniote 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. 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 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.

(FIGURE 2.265. Homoeosaurus pulchellus, a Jurassic proreptile from Kehlheim. (From Zittel.))

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 lizard of New Zealand, Hatteria punctata (Figure 2.264). 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 Palaehatteria, that Credner discovered in the Plauen terrain at Dresden in 1888, belongs to the same group (Figure 2.266). The Jurassic genus Homoeosaurus (Figure 2.265), of which well−preserved skeletons are found in the Solenhofen schists, is perhaps still more closely related to them.

Unfortunately, the numerous fossil remains of Permian and Triassic Tocosauria that we have found in the last two decades are, for the most part, very 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 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 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 (Figure 2.267). 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.

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. Linne drew attention to this fact in the first edition of his famous Systema Naturae (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.

(FIGURE 2.266. Skull of a Permian lizard (Palaehatteria longicaudata). (From Credner.) n nasal bone, pf frontal bone, l lachrymal bone, po postorbital bone, sq covering bone, i cheek−bone, vo vomer, im inter−maxillary.)

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. It is only in the mammals that the mother suckles its young, and this rightly gives the name to the whole class (mamma = breast).

(FIGURE 2.267. 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 Parietal eye, Bo joint at back of head, Pt pterygoid−bone, Md lower jaw.)

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 Mammal 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 Kueper. One of the earliest forms is the genus Dromatherium, from the North American Triassic (Figure 2.268). 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. We do not find any positive trace 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.

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, Figures 2.269 and 2.270). 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 1879; 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. 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 (Figure 2.270) the formation of the scapula among other parts is curious; it is quite 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. 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.

(FIGURE 2.268. Lower jaw of a Primitive Mammal or Promammal (Dromatherium silvestre) from the North American Triassic. i incisors, c canine, p premolars, m molars. (From Doderlein.))

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 Australia 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 (Figures 2.269 and 2.270). The other form, the land duck−bill, or spiny ant−eater (Echidna hystrix), is very much like the anteaters 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 hedgehog. A cognate form (Parechidna Bruyni) has lately been found in New Guinea.

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.

The Australian duck−bills are distinguished externally by a toothless bird−like beak or snout. This absence of real bony teeth is a late result of adaptation, as in the toothless Placentals (Edentata, armadillos and ant−eaters). The extinct Monotremes, to which the Promammalia belonged, must have had developed teeth, inherited from the reptiles. 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.

(FIGURE 2.269. The Ornithorhyncus or Duck−mole. (Ornithorhyncus paradoxus).

FIGURE 2.270. Skeleton of the Ornithorhyncus.)

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, and most of the jaws 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 (Figure 2.272) 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, 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.

(FIGURE 2.271. Lower jaw of a Promammal (Dryolestes priscus), from the Jurassic of the Felsen strata. (From Marsh.))

From the comparative anatomy and ontogeny of the existing Marsupials we may draw very interesting conclusions as to their 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 (Figure 2.272). In the giant kangaroo, which is as tall as a man, the embryo only develops 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.

(FIGURE 2.272. The crab−eating Opossum (Philander cancrivorus). The female has three young in the pouch. (From Brehm.)

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 oldest and nearest to the common stem−form of the whole class. To this family belong the crab−eating opossum of Brazil (Figure 2.272) and the opossum of Virginia, on the embryology of which Selenka has given us a valuable work (cf. Figures 1.63

to 1.67 and 1.131 to 1.135). 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.

CHAPTER 2.23. OUR APE ANCESTORS.

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.

(FIGURE 2.273. Foetal membranes of the human embryo (diagrammatic). m the thick muscular wall of the womb. plu placenta [the inner layer (plu apostrophe) 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 Kolliker.))

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 (Chapter 1.15). 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. Figures 1.194 to 1.196). 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 (Chapter 1.15). 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 foetal 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 develops 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 villi between the maternal blood−vessels and those of the foetus 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 into the foetal 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.

Branches of the blood−vessels penetrate into the chorion−villi from within, starting from the gut−fibre layer of the allantois, and bringing the blood of the foetus through the umbilical vessels (Figure 2.273 chz). On the other hand, a thick network of blood−vessels develops 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 network 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 foetal placenta (Figure 2.273 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. Figure 1.196).

(FIGURE 2.274. 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.)

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 Lemurs (Prosimiae), 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 foetal 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 foetal placenta alone comes away; the uterine placenta is not torn away with it.

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, Figure 2.273 chl) and the thickly−tufted chorion (chorion frondosum, Figure 2.273 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 (Figures 1.197 and 1.200)—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.

(FIGURE 2.275. The Slender Lori (Stenops gracilis) of Ceylon, a tail−less lemur.)

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 foetal 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 foetal 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. Figures 1.199 and 1.200.)

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 foetus 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 Lemurs (Tarsius) a discoid placenta with decidua is developed.

While these 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 (Chapter 1.15), 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 (Prosimiae), apes (Simiae), and man (Anthropi). The lemurs or half−apes are the stem−group, descending from the older Mallotheria of the Cretaceous period. From them the apes were evolved in the Tertiary period, and man was formed from these towards its close.

The Lemurs (Prosimiae) 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 (3.1.4.3. over 3.1.4.3.). The Necrolemurs (Adapida, Figure 2.274) have only forty teeth, and have lost an incisor in each jaw (2.1.4.3. over 2.1.4.3.). The dentition is still further reduced in the Lemurogona (Autolemures), which usually have only thirty−six teeth (2.1.3.3. over 2.1.3.3.). 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 by several different species during this long period. Some of these were almost as big as men, such as the diluvial lemurogonon Megaladapis of Madagascar.

(FIGURE 2.276. The white−nosed ape (Cercopithecus petaurista).)

Next to the lemurs come the true apes (Simiae), 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."

(FIGURE 2.277. The drill−baboon (Cynocephalus leucophaeus) (From Brehm.))

In the very first exposition of his profound natural classification (1735) Linne placed the anthropoid mammals at the head of the animal kingdom, with three genera: man, the ape, and the sloth. 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 Gottingen 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 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 tight coverings for thousands 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.

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 ape. 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 Linne's order of the Primates (excluding the bats), and divided it into three sub−orders, the first composed of the half−apes (Lemuridae), the second of the true apes (Simiadae), the third of men (Anthropidae).

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. 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 (Simiae 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 were 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, 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"), 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.

(FIGURES 2.278 TO 2.282. Skeletons of man and the four anthropoid apes. (From Huxley.) Cf. Figures 1.203 to 1.209.

FIGURE 2.278. Gibbon (Hylobates).

FIGURE 2.279. Orang (Satyrus).

FIGURE 2.280. Chimpanzee (Anthropithecus).

FIGURE 2.281. Gorilla (Gorilla).

FIGURE 2.282. Man (Homo).)

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 Hapalidae), 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 premolars, 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. Most of the eastern apes have, it is true, rather flat noses, like, for instance, the white−nosed monkey (Figure 2.276); 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” (Platyrrhinae), and those of the Old World “narrow−nosed” (Catarrhinae). 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 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 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 (Figures 2.278 to 2.282). 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—baboons (Cynopitheca) or tailed apes (Menocerca, Figure 2.276). 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.

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 1.15)—the gibbon (Hylobates, Figure 1.203) and orang (Satyrus, Figures 1.204 and 1.205) in South−Eastern Asia and the Archipelago; and the chimpanzee (Anthropithecus, Figures 1.206 and 1.207) and gorilla (Gorilla, Figure 1.208) 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 works for impartial treatment of the question of affinity is Robert Hartmann's little work on The Anthropoid Apes. Hartmann divides the primate order into two families: (1) Primarii (man and the anthropoid apes); and (2) Simianae (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 (page 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.

(FIGURE 2.283. Skull of the fossil ape−man of Java (Pithecanthropus erectus), restored by Eugen Dubois.)

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 in 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" (Figure 2.283). 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 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 to 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. Bumuller, etc.).

As the Pithecanthropus walked erect, and his brain (judging from the capacity of his skull, Figure 2.283) was midway between the lowest men and the anthropoid apes, 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, (chapter 28) 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.

SYNOPSIS OF THE CHIEF SECTIONS OF OUR STEM−HISTORY.

FIRST 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 Amoeba).

SECOND STAGE: THE BLASTAEADS.

Man's ancestors are round coenobia 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 Magospherae and Volvocina, equivalent to the ontogenetic blastula: hollow globules, the wall of which consists of a single layer of ciliated cells (blastoderm).

THIRD STAGE: THE GASTRAEADS.

Man's ancestors are Gastraeads, 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 STAGE: THE PLATODES.

Man's ancestors have substantially the organisation of simple Platodes (at first like the cryptocoelic Platodaria, later like the rhabdocoelic Turbellaria). The leaf−shaped bilateral−symmetrical body has only one gut−opening, and develops the first trace of a nervous centre from the ectoderm in the middle line of the back (Figures 2.239 and 2.240).

FIFTH 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 (coeloma). The dorsal ectoderm forms the vertical plate, acroganglion (Figure 2.243).

SIXTH STAGE: THE PROCHORDONIA.

Man's ancestors have substantially the organisation of a simple unarticulated Chordonium (Copelata and Ascidia−larvae). The unsegmented chorda develops between the dorsal medullary tube and the ventral gut−tube. The simple coelom−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.

SEVENTH 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 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 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 (the upper and lower jaws). The floating bladder (lung) and pancreas grow out of the gut.

TENTH 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) Lemurs (Prosimiae); (6) Western apes (Platyrrhinae); (7) Eastern apes (Catarrhinae): 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.

CHAPTER 2.24. EVOLUTION OF THE NERVOUS SYSTEM.

The previous chapters have taught us how the human body as a whole develops 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 (kidney) system. The reproductive apparatus comprises the different organs of sex (embryonic glands, sexual ducts, and copulative organs).

As we know from previous chapters (1.11 to 1.13), 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 (skin) 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.

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 Chapter 1.3).

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 Gastraea; 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 Gastraea 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 Gastraeads (Figure 2.233); and it is also the case potentially with the gastrula.

We shall easily see that the gastraea 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, 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 is 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.

(FIGURE 2.284. The human skin in vertical section (from Ecker), highly magnified, a horny layer of the epidermis, b mucous layer of the epidermis, c papillae 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.)

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 Gastraea (Figure 1.30 e). We find this in the lowest Zoophytes—the Gastraeads, Physemaria, and Sponges (Figures 2.233 to 2.238). The lowest Cnidaria (the hydroid polyps) also are little superior to the Gastraeads 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.

(FIGURE 2.285. Epidermic cells of a human embryo of two months. (From Kolliker.))

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 (Figure 2.241 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 earth−worm, the first rudiment of the central nervous system (Figure 1.74 n) is a local thickening of the skin−sense layer (hs), which afterwards separates altogether from the horny plate. In the earliest Platodes (Cryptocoela) 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 develops 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.

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 (Figure 2.284 a, b). It develops 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 (Figure 2.284 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 papillae (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 (Figure 1.145 hpr, and Figures 1.161 and 1.162 cp).

In the same way, all the parts and appendages of the epidermis develop by differentiation from the homogeneous cells of this horny plate (Figure 2.285). At an early stage the simple cellular layer of this horny plate divides into two. The inner and softer stratum (Figure 2.284 b) is known as the 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—sweat, fat, etc. The external appendages are the hairs and nails.

The cutaneous glands are originally merely solid cone−shaped growths of the epidermis, which sink into the underlying corium (Figure 2.286 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 (Figure 2.284 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 (Figure 2.286), 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.

(FIGURE 2.286. Rudimentary lachrymal glands from a human embryo of four months. (From Kolliker.) 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 (Figures 2.287 and 2.288) 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. The milk is formed by the liquefaction of the fatty milk−cells inside the branching mammary−gland tubes (Figure 2.287 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 (Figure 2.288). 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. 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 is usually only one pair 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 (Figure 1.103). This polymastism points back to an older stem−form. We often find these accessory breasts in the male also (Figure 1.103 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 1.11) dealt with this remarkable and interesting instance of atavism.

(FIGURE 2.287. 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.))

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 (Figure 2.264), and the mammals have inherited them from the earliest representatives of this class, the stem−reptiles (Tocosauria). Like the hoofs (ungulae) of the Ungulates, the nails of apes and men have been evolved from the claws of the older mammals. In 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.

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 had a complete scaly coat, inherited from their Carboniferous ancestors, the mailed amphibia (Stegocephala); the bony scales of their corium were covered with horny scales. 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 (page 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 two inches 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 (Figure 2.289). 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 foetal 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 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.

(FIGURE 2.288. Mammary gland of a new−born infant, a original central gland, b small and c large buds of same. (From Langer.))

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.

(FIGURE 2.289. Embryo of a bear (Ursus arctos), twice natural size. A seen from ventral side, B from the left.)

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 (Figures 1.203 and 1.207). 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.

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 (Figure 1.9) 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 develops 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.

(FIGURE 2.290. Human embryo, three months old, natural size, from the dorsal side: brain and spinal cord exposed. (From Kolliker.) h cerebral hemispheres (fore brain), m corpora quadrigemina (middle brain), c cerebellum (hind brain): under the latter is the triangular medulla oblongata (after brain).

FIGURE 2.291. Central marrow of a human embryo, four months old, natural size, from the back. (From Kolliker.) h large hemispheres, v quadrigemina, c cerebellum, mo medulla oblongata: underneath it the spinal cord.)

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. 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 column. 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 (Figure 1.171). 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 the region of the loins (at the first lumbar vertebra) below (Figure 2.291). 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 (Figure 2.291 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.

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 (Figures 2.292 and 2.293). 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 worm−shaped piece, the vermis cerebelli, above, and by the broad pons Varolii below (Figure 2.292 VI).

(FIGURE 2.292. 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 I to XII indicate the roots of the twelve pairs of cerebral nerves in a series towards the rear.)

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 develops 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 (Figures 2.290 m and 2.291 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” (Figure 2.291 c). Finally, we have the fifth and last section, the medulla oblongata (Figure 2.291 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 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 develops in them all from the same rudimentary structure, the five simple cerebral vesicles of the embryonic brain.

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 vertebrate, 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. All that we can discover is a small vesicular bulb at the foremost part of the tube, a degenerate rudiment of a primitive brain. We meet the same simple medullary tube in the first structure of the ascidia larva, 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 and spinal cord. It is probable that this differentiation was more advanced in the extinct Provertebrates, and the brain−bulb more pronounced (Figures 1.98 to 1.102). 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 Ascidiae 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).

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. Chapter 2.20).

(FIGURE 2.293. 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. f1 to f2 frontal convolutions, C central convolutions, S fissure of Sylvius, T temporal furrow, Pa parietal lobes, An angular gyrus, Po parieto−occipital fissure.)

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. 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 (Figures 1.133 to 1.137). 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. Figures 1.143 to 1.146).

(FIGURES 2.294 TO 2.296. Central marrow of the human embryo from the seventh week, 4/5 inch long. (From Kolliker.)

FIGURE 2.294. The brain from above, v fore brain, z intermediate brain, m middle brain, h hind brain, n after brain.

FIGURE 2.295. The brain with the uppermost part of the cord, from the left.

FIGURE 2.296. Back view of the whole embryo: brain and spinal cord exposed.)

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. In this way the central marrow of the Vertebrates divides clearly into its two chief sections, brain and spinal cord. 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 (Figure 1.153 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, Figure 1.154 v, m, h). Then the first and third are sub−divided by fresh constrictions, and thus we get five successive sections (Figure 1.155).

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 (Figure 1.155 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 (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 (m), produces the corpora quadrigemina and the aqueduct of Sylvius. From the fourth vesicle, the hind brain (h), develops the greater part of the cerebellum—namely, the vermis and the two small hemispheres. Finally, the fifth vesicle, the after brain (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 develops 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.

(FIGURE 2.297. 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), vw vitelline veins, us primitive segment, rm spinal cord.)

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 (Figure 2.300) 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) develops in two different directions; one of these is followed 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 (Figures 2.293 and 2.301 to 2.304).

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 curve in the brain along with the bending of the head and neck; the whole of the upper dorsal surface of the brain develops 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.

(FIGURE 2.298. 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.)

FIGURE 2.299. 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.)

FIGURE 2.300. 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 apostrophe roots of the spinal nerves, t terminal fibres of the spinal cord. (From Gegenbaur.)

FIGURE 2.301. Brain of an ox−embryo, two inches 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.)

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) the middle brain and the middle part of the hind brain are well developed. In the mammals these parts do not grow, and the fore−brain develops 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 (Figures 2.301 to 2.303). 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.

(FIGURE 2.302. 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.)

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.

(FIGURE 2.303. 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.

In the lower mammals the surface of the cerebral hemispheres is quite smooth and level, as in the rabbit (Figure 2.304). 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 (Figures 2.292 and 2.293). 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.

(FIGURE 2.304. Brain of the rabbit. 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 oculo−motor nerve, 5 to 8 cerebral nerves. In A the roof of the right hemisphere (I) is removed, so that we can see the corpora striata in the lateral ventricle. (From Gegenbaur.))

The central marrow (brain and spinal cord) develops 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 (Figure 1.171), and are, like it, products of the skin−sense layer.

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, without their organs than the circulation without the heart and blood. And as the central marrow develops 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 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.

CHAPTER 2.25. EVOLUTION OF THE SENSE−ORGANS.

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 and temperature. 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 Gastraea 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 by 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 naivete 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.

(FIGURE 2.305. Head of a shark (Scyllium), from the ventral side. m mouth, o olfactory pits, r nasal groove, n nasal fold in natural position, n apostrophe nasal fold drawn up. (The dots are openings of the mucous canals.) (From Gegenbaur.))

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).

(FIGURES 2.306 AND 2.307. Head of a chick embryo, three days old: 2.306 front view, 2.307 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.

FIGURE 2.308. 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 double apostrophe second gill−arch, sp choroid fissure of eye, s gullet.

FIGURES 2.309 AND 2.310. Heads of chick embryos: 2.309 from the end of the fourth, 2.310 from the beginning of the fifth week. Letters as in Figure 2.308, except: in inner, an outer, nasal process, nf nasal furrow, st frontal process, m mouth. (From Kolliker.) Figures 2.306 to 2.310 are magnified to the same extent.)

There is little to be said of the development of the lower sense−organs. We have already considered (Chapter 2.24) 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 2.29). 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 2.27). 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 (Chapter 1.13). 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). 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 (Figure 2.249).

(FIGURE 2.311. Frontal section of the mouth and throat of a human embryo, neck half−inch 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.)

This first rudimentary structure of the double nose is the same in all the Gnathostomes; 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 (Figure 2.305 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 apostrophe). 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.

(FIGURE 2.312. 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 partition (e) into two halves (n, n). (From Gegenbaur.))

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. 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” (Figures 2.306 n and 2.307 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 (Figure 2.310 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” (Figure 2.309 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 nasal processes (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 (Figure 2.305 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 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 (Figures 2.306 to 2.310 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 develops 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 (Figures 2.306 to 2.310 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, develops from the foremost part of the frontal process.

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 develops into the nasal cavity, the air−passage and the organ of smell. The lower cavity forms the permanent secondary mouth (Figure 2.312 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 the lesser form of the same defect. At the same time as the horizontal partition of the hard palate a vertical partition is formed by which the single nasal cavity is divided into two sections—a right and left half (Figure 2.312 n, n).

(FIGURES 2.313 AND 2.314. Upper part of the body of a human embryo, two−thirds of an inch long, of the sixth week; Figure 2.313 from the left, Figure 2.314 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.))

The double nose has now acquired the characteristic form that man shares with the other mammals. Its further development is easy to follow; it consists of the formation of the inner and outer processes of the walls of the two cavities. 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 (Figures 2.313 to 2.316). As can be seen in any human embryo during the first month, there is at first no trace of the external nose. It only develops afterwards from the foremost nasal part of the primitive skull, growing forwards from behind. The characteristic 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.

(FIGURE 2.315. 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.)

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 develops, without preconceived design, from a simple process of the outer germinal layer. The fully−formed human eye is a round capsule, the eye−ball (Figure 2.317). 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 (Figure 2.317 l). It is a lenticular, bi−convex, 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 aqueus) that is found in front of the lens (at the letter m in Figure 2.317). 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. 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 (winking) membrane,” in the lower Vertebrates (Chapter 1.5). 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—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 (n). 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 (Figures 1.155 a and 2.297 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.

(FIGURE 2.316. Face of a human embryo, eight weeks old (From Ecker.))

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 (Figure 2.318, 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 hollow 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.

As the lens separates from the corneous plate and grows inwards, it necessarily hollows out the contiguous primary optic vesicle (Figure 2.318, 1 to 3). This is done in just the same way as the invagination of the blastula, which gives rise to the gastrula in the amphioxus (Figure 2.38 C to 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. 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 (Figure 2.319 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.

(FIGURE 2.317. The human eye in section. a sclerotic coat, b cornea, c conjunctiva, d circular veins of the iris, e choroid coat, 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), n pigment membrane, o retina, p Petit's canal, q yellow spot of the retina. (From Helmholtz.))

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.

(FIGURE 2.318. 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.))

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, develops from the outer skin. From the skin—the horny plate—also arises the delicate conjunctiva, which afterwards covers the outer surface of the eyeball. The lachrymal glands are ramified growths from the conjunctiva (Figure 2.286). 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. 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 semi−lunar fold, a useless rudimentary organ (Chapter 1.5). 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.

(FIGURE 2.319. Horizontal transverse section of the eye of a human embryo, four weeks old (magnified one hundred times). (From Kolliker.) 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).

FIGURE 2.320. 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 (Figure 2.320 a). 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 (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 (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 (Figure 2.320, 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 auditory 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 (Figure 2.321), 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.

(FIGURE 2.321. 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.)

FIGURE 2.322. Development of the auscultory labyrinth of the chick, in five successive stages (A to E). (Vertical transverse sections of the skull.) fl auscultory pits, lv auscultory vesicles, lr labyrinthic 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 (Figure 2.322 A fl). 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. As it separates from its source, the horny plate, and presses inwards and backwards into the skull, it changes from round to pear−shaped (Figures 2.322 B lv and 2.323 o). The outer part of it is lengthened into a thin stem, which at first still opens outwards by a narrow canal. This is the labyrinthic appendage (Figure 2.322 lr). In the lower Vertebrates it develops 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. But in the mammals the labyrinthic appendage degenerates. In these it has only a phylogenetic interest as a rudimentary organ, with no actual 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.

It is only the inner and lower bulbous part of the separated auscultory vesicle that develops 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 (Figure 2.320 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 hag−fishes only one. The very complex structure of the cochlea, one of the most elaborate and wonderful outcomes of adaptation in the mammal body, develops 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 auditory nerve, 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 develops from the nervous structure that appears at its dorsal limit. On the other hand, all the membranous, cartilaginous, and osseous coverings of the labyrinth are formed from the mesodermic head−plates.

(FIGURE 2.323. 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 Kolliker.))

The apparatus for conducting sound which we find in the external and middle ear of mammals develops 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.

(FIGURE 2.324. 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 (Figures 2.313 and 2.315). 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 (Figure 2.324). 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. 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. 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, 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 it 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.

CHAPTER 2.26. EVOLUTION OF THE ORGANS OF MOVEMENT.

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 contractility 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.

(FIGURE 2.325. The human skeleton. From the right.

FIGURE 2.326. The human skeleton. Front.)

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.

(FIGURE 2.327. The human vertebral column (standing upright, from the right side). (From H. Meyer.))

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 (Figure 2.325, the human skeleton seen from the right; Figure 2.326, front view of the whole skeleton). As in 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 or extremities is composed of two groups of parts—the skeleton of the extremities proper and the zone−skeleton, which connects these with the vertebral column. The zone−skeleton of the arms (or fore legs) is the shoulder−zone; the zone−skeleton of the legs (or hind legs) is the pelvic zone.

(FIGURE 2.328. A piece of the axial rod (chorda dorsalis), from a sheep embryo. a cuticular sheath, b cells. (From Kolliker.))

The vertebral column (Figure 2.327) 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 vertebrae are separated from each other by elastic ligaments, 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 vertebrae 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 vertebrae, twelve dorsal vertebrae, five lumbar vertebrae, five sacral vertebrae, and four to six caudal vertebrae. The uppermost, or those next to the skull, are the cervical vertebrae (Figure 2.327); they have a hole in each of the lateral processes. There are seven of these vertebrae 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 hedgehog. 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 vertebrae. 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 vertebrae. Next to these come the dorsal (or pectoral) vertebrae, which number twelve to thirteen (usually twelve) in man and most of the other mammals. Each dorsal vertebra (Figure 1.165) 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 vertebrae comes a short but stronger section of the column, formed of five large vertebrae. These are the lumbar vertebrae (Figure 1.166); 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 pelvic zone. The sacrum is formed of five vertebrae, 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 or six) of small degenerated vertebrae, 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. It afterwards atrophies; but the relic of the atrophied caudal vertebrae and of the rudimentary muscles that once moved it remains permanently. Sometimes, in fact, the external tail is preserved. 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.

(FIGURE 2.329. Three dorsal vertebrae, from a human embryo, eight weeks old, in lateral longitudinal section. v cartilaginous vertebral body, li inter−vertebral disks, ch chorda. (From Kolliker.)

(FIGURE 2.330. 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 Kolliker.))

In the human vertebral column there are usually thirty−three vertebrae. It is interesting to find, however, that the number often changes, one or two vertebrae 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 vertebrae, besides six cervical and four lumbar. In this way the contiguous vertebrae of the various sections of the column may take each other's places.

In order to understand the embryology of the human vertebral column we must first carefully consider the shape and connection of the vertebrae. Each vertebra has, in general, the shape of a seal−ring (Figures 1.164 to 1.166). The thicker portion, which is turned towards the ventral side, is called the body of the vertebra, and forms a short osseous disk; the thinner part forms a semi−circular arch, the vertebral arch, and is turned towards the back. The arches of the successive vertebrae 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.

(FIGURE 2.331. Intervertebral disk of a new−born infant, transverse section. a rest of the chorda. (From Kolliker.))

While the solid, massive bodies of the vertebrae 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 (costae). In reality the ribs are merely large and independent lower vertebral arches, which have lost their original connection with the vertebral bodies.

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 (Chapter 1.14). 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 (Figure 2.210 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, permanently in the Copelata (Figure 2.225 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 medullary furrow, the simple chorda. (Cf. Figures 1.131 to 1.135 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 (Figure 2.328 b) belong to the entoderm (Figures 2.216 to 2.221). At an early stage the chorda develops a transparent structureless sheath, which is secreted from its cells (Figure 2.328 a). This chordalemma is often called the “inner chorda−sheath,” and must not be confused with the real external sheath, the mesoblastic perichorda.

(FIGURE 2.332. Human skull.

FIGURE 2.333. Skull of a 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.)

But this unsegmented primary axial skeleton is soon replaced by the segmented secondary axial skeleton, which we know as the vertebral column. The provertebral plates (Figure 1.124 s) differentiate from the innermost, median part of the visceral layer of the coelom−pouches at each side of the chorda. As they grow round the chorda and enclose it they form the skeleton 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 (scleroblast). 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 vertebrae. They are not numerous at first, but soon increase as the embryo grows longer (Figures 1.153 to 1.155).

(FIGURE 2.334. 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 to VIII first to sixth branchial arches. (From Gegenbaur.)

FIGURE 2.335. Roofs of the skulls of nine Primates (Cattarrhines), seen from above and reduced to a common size. 1 European, 2 Brazilian, 3 Pithecanthropus, 4 Gorilla, 5 Chimpanzee, 6 Orang, 7 Gibbon, 8 Tailed ape, 9 Baboon.)

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 vertebrae 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 (Figure 1.6). 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 vertebrae. 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 (Figures 1.182 ch and 2.329 ch). In the cartilaginous vertebral bodies themselves, which afterwards ossify, the slender remnant of the chorda presently disappears (Figure 2.330 ch). But in the elastic inter−vertebral disks, which develop from the skeletal plate between each pair of vertebral bodies (Figure 2.329 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 (Figure 2.331 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 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.

(FIGURE 2.336. Skeleton of the breast−fin of Ceratodus (biserial feathered skeleton). A, B, cartilaginous series of the fin−stem. rr cartilaginous fin−radii. (From Gunther.)

FIGURE 2.337. 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.)

FIGURE 2.338. 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.))

The bony skull (cranium), the head−part of the secondary axial skeleton, develops 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 (Figure 2.332), 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 below and the curved dorsal vault 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 encloses the entrance of the alimentary 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 vertebrae, 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 vertebrae. 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 vertebrae (like the three hind−most cranial vertebrae)." And when Oken (without knowing anything of Goethe's discovery) found at Ilenstein, "a fine bleached skull of a hind, the thought flashed across him like lightning: 'It is a vertebral column.'"

(FIGURE 2.339. Skeleton of the fore leg of an amphibian. h upper−arm (humerus), ru lower arm (r radius, u ulna), rcicu apostrophe, wrist−bones of first series (r radiale, i intermedium, c centrale, u apostrophe ulnare). 1, 2, 3, 4, 5 wrist−bones of the second series. (From Gegenbaur.)

FIGURE 2.340. Skeleton of gorilla's hand. (From Huxley.)

FIGURE 2.341. Skeleton of human hand, back. (From Meyer.))

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 (Figure 2.333) they thought they could prove in this way that the fully−formed mammal skull was made of from three to six vertebrae.

The older theory was refuted by simple and obvious facts, which were 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 (Figures 2.249 to 2.251), 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) provertebrae, 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.

(FIGURE 2.342. 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, a 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.))

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 vertebrae,” at each side of the head of the Selachii (Figure 2.334), the following pairs of 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 to X, six branchial arches in the narrower sense (III to 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 provertebrae. 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 provertebrae have been discovered in the anterior (pre−chordal) part of the Selachii−skull; this would bring up the number of cranial somites to twelve or sixteen, or even more.

(FIGURES 2.343 TO 2.345. Arm and hand of three anthropoids.

FIGURE 2.343. Chimpanzee (Anthropithecus niger).

FIGURE 2.344. Veddah of Ceylon (Homo veddalis).

FIGURE 2.345. European (Homo mediterraneus). (From Paul and Fritz Sarasin.))

In the primitive skull of man (Figure 2.323) 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 vertebrae; 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 (Figure 2.333). 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. Figs 1.145 and Chapters 1.13 and 1.14.)

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.

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 these in figures.

Without adducing a single solid reason, or offering any alternative explanation, he rejected evolution 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 (Figure 2.283). 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 (Figure 2.335, 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 Brazilian Indian (Figure 2.335, 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 Figure 2.335, and reduced them to a common size.

(FIGURE 2.346. Transverse section of a fish's tail (from the tunny). (From Johannes Muller.) a upper (dorsal) lateral muscles, a apostrophe, b apostrophe lower (ventral) lateral muscles, d vertebral bodies, b sections of incomplete conical mantle, B attachment lines of the inter−muscular ligaments (from the side).)

We turn now to the branchial arches, which were regarded even by the earlier natural philosophers as “head−ribs.” (Cf. Figures 1.167 to 1.170). 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. Chapter 2.25.) 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 stirrup, 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 the hyoid bone 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. Figures 1.169 and 2.320.)

It was Carl Gegenbaur again who solved the difficult problem of tracing the skeleton of the limbs of the Vertebrates to a common 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. The lowest and earliest Vertebrates, the Acrania and

Cyclostomes, had, like their invertebrate ancestors, no pairs of limbs, as we see in the Amphioxus and the Cyclostomes to−day (Figures 2.210 and 2.247). 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 (Figures 2.248 to 2.259). The third group comprises the four higher classes of Vertebrates—the amphibia, reptiles, birds, and mammals; in these quadrupeds 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 (Figures 2.263 to 2.265).

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 (Figure 2.257). Both the breast−fin and the belly−fin are flat oval paddles, in which we find a biserial cartilaginous skeleton (Figure 2.336). 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, 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.* (* 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.)

We find the same biserial primitive fin more or less preserved in the fossilised remains of the earliest Selachii (Figure 2.248), Ganoids (Figure 2.253), and Dipneusts (Figure 2.256). 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 on the other (Figure 2.337). We thus get the uniserial fin, which has been transmitted from the Selachii to the rest of the fishes (Figure 2.338).

(FIGURE 2.347. Human skeleton. (Cf. Figure 2.326.)

FIGURE 2.348. Skeleton of the giant gorilla. (Cf. Figure 1.209.))

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.* (* The 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 Figure 2.339 shows.) In the dipneust ancestors of the Amphibia the radii gradually atrophy, and are lost, for the most part, on the other side of the fin−rod as well (the lighter cartilages in Figure 2.338). 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 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 (Figure 2.339 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 (Figure 2.260), 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 (Figure 2.341). 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 coracoideum. In the same 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).

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 Figures 2.260, 2.265, 2.270, 2.278 to 2.282, and 2.348.) 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 a complete parallel in all the parts of the fore leg and the hind leg.

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 higher classes of Vertebrates, we may at once infer a common descent of them from a single stem−form. This stem−form was the earliest amphibian 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 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. It is true that the skeleton of the limbs of the various mammals undergoes many distortions and degenerations besides the special adaptations (Figure 2.342). 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, IV) the second and fifth toes are also atrophied, and only the third and fourth are well developed (VI, 3). Nevertheless, all these different fore−feet, as well as the hand of the ape (Figure 2.340) and of man (Figure 2.341), 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 (Figure 2.342 a to p).

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, Figure 2.344) are midway between the chimpanzee (Figure 2.343) and the European (Figure 2.345). More considerable are the differences in structure and the proportions of the various parts between the different genera of anthropoid apes (Figures 2.278 to 2.282); 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 (Chapter 1.15).

The complete unity of structure which is thus revealed by the comparative anatomy of the limbs is fully confirmed by their embryology. However different the extremities of the four−footed Craniotes may be in their adult state, they all develop from the same rudimentary structure. 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. 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 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 (Figure 1.174). 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.

The embryonic development of the muscles, or ACTIVE organs of locomotion, is not less interesting than that of the skeleton, or PASSIVE organs. 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, developing from the mesoderm. This was afterwards replaced by a pair of internal lateral muscles, that developed from the middle wall of the coelom−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. Figures 1.124, 1.158 to 1.160, 2.222 to 2.224 mp). In the unarticulated stem−forms of the Chordonia, which we have called the Prochordonia, the two coelom−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 (Figures 1.124 and 1.158). This segmentation 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 segmentation of the muscular system, and the two entered into very close correlation.

The episomites or dorsal coelom−pouches of the Acrania, Cyclostomes, and Selachii (Figure 1.161 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 wall of the coelom−pouches, and proceeds from the dorsal to the ventral wall. From these segmental muscle−plates, which are chiefly concerned in the segmentation of the Vertebrates, proceed the lateral muscles of the stem, as we find in the simplest form in the Amphioxus (Figure 2.210). By the formation of a horizontal frontal septum they divide on each side into an upper and 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 (Figure 2.346). 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.* (* 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 coelom−pouches. This also applies originally to the primary muscles of the limbs, as these too belong phylogenetically to the hyposoma. (Cf. Chapter 1.14))

CHAPTER 2.27. THE EVOLUTION OF THE ALIMENTARY SYSTEM.

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 the formation of organs—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 Blastaea the homogeneous 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 the whole body. Thus arose the primary germinal layers—the inner, alimentary, or vegetal layer, and the outer, covering, or animal layer. (Cf. Chapter 2.19.)

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. 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 (Figures 1.30 to 1.35). The elaborate alimentary canal of the higher animals develops ontogenetically from the same simple primitive gut of the gastrula.

This gastraea theory is now accepted by nearly all zoologists. 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.

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. 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, the mouth, 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 (Chapter 2.23). 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 (Figure 2.311).

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. Into this opens on either side a narrow canal (the Eustachian tube), through which there is direct communication with the tympanic cavity of the ear (Figure 2.320 e). The pharynx is continued in a long, narrow tube, the oesophagus (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 lungs are found, in man and all the mammals, to the right and left in the pectoral cavity, with the heart between them. 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 develops from a part of the alimentary canal. In front of the larynx is the thyroid gland, which sometimes enlarges and forms goitre.

The oesophagus 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 is a membrano−muscular partition that completely separates the thoracic from the abdominal 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 coeloma or pleuro−peritoneal 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 oesophagus. 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 (Figure 2.349) is a long, somewhat oblique sac, expanding on the left into a blind sac, the fundus of the stomach (b apostrophe), but narrowing on the right, and passing 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.

(FIGURE 2.349. Human stomach and duodenum, longitudinal section. a cardiac (end of oesophagus), 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.)

FIGURE 2.350. Median section of the head of a hare−embryo, one−fourth of an inch 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 develops from the mouth−cleft, vh ventricle of the cerebrum, v3, third ventricle (intermediate brain), v4 fourth ventricle (hind brain), ck spinal canal.)

Next to the stomach comes the longest section of the alimentary canal, the middle gut or small intestine. Its chief function is to absorb the peptonised fluid mass of food, or the chyle, and it is subdivided into several sections, of which the first (next to the stomach) is called the duodenum (Figure 2.349 fgh). It is a short, horseshoe−shaped loop of the gut. The largest glands of the alimentary canal open into it—the liver, 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. The pancreas lies a little further back and more to the left. 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. 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 caecum. The atrophied end of the caecum is the famous rudimentary organ, the vermiform appendix. 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. 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.

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 gastraead−ancestors, and that every gastrula brings before us to−day. We have already pointed out (Chapter 1.9) how the epigastrula of the mammals (Figure 1.67) can be reduced to the original type of the bell−gastrula, which is now preserved by the amphioxus alone (Figure 1.35). 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 Gastraea, in which the whole body is nothing but a double−walled gastric sac.

We already know from embryology the manner in which the gut develops in the embryo of man and the other mammals. From the gastrula is first formed the spherical embryonic vesicle filled with fluid (gastrocystis, Figure 1.106). 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.

As we have seen, this simple cylindrical gut−tube is at first completely closed before and behind in man and in the Vertebrates generally (Figure 1.148); 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 (Figure 2.350 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 develops from the hind gut; this is the important embryonic structure that forms into the placenta in the Placentals (including man). 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 urinary sac (Figure 1.195).

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.

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.

(FIGURE 2.351. 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.))

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 Gastraeads, 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 freshwater Polyps (Hydra), and the ascula−embryos of many other Coelenteria (Figures 2.233 to 2.238). Even in the simplest forms of the Platodes, the Rhabdocoela (Figure 2.240), 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.

(FIGURE 2.352. Gut of a human embryo, one−sixth of an inch long, magnified fifteen times. (From His. Showing: Epiglottis, Tongue, Hypophysis, Hepatic duct, Tail, Allantoic duct, Tail−gut, Umbilical cord, Larynx, Rudimentary lungs, Stomach, Pancreas, Bladder, Wolffian duct, Rudimentary kidneys.))

We have the same simple form in the gut of the lowest Vermalia (Gastrotricha, Figure 2.242, 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 (Figure 2.242 a).

We see a great advance in the structure of the vermalian gut in the remarkable Balanoglossus (Figure 2.245), 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, Figure 2.245 k); the hind half, the trunk−gut (truncogaster), alone acts as digestive organ (hepatic gut, d). The differentiation of these two parts of the gut in the Enteropneust is just the same as in all the Tunicates and Vertebrates.

It is particularly interesting and instructive in this connection to compare the Enteropneusts with the Ascidia and the Amphioxus (Figures 2.220 and 2.210)—the remarkable animals that 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 develops palingenetically from the primitive gut of the gastrula, 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, Figures 1.83 and 1.85 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 Ascidia. 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.

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 (Figure 1.171). These are most interesting embryonic structures. They show us that all the higher Vertebrates reproduce in their earlier 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, and a posterior digestive section, the hepatic gut. As we find this highly characteristic differentiation of the gut into two 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. Chapters 1.12, 1.14 and 2.20, and Figures 2.210, 2.220, 2.245.) It is entirely wanting in all the other Invertebrates.

(FIGURE 2.353. Gut of a dog−embryo (shown in Figure 1.202, 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.

FIGURE 2.354. The same gut seen from the right. a lungs, b stomach, c liver, d yelk−sac, e rectum.)

There is at first only one pair of gill−clefts in the Amphioxus, as in the Ascidia and Enteropneusts; and the Copelata (Figure 2.225) 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 (Figure 2.247); some of the Selachii six or seven pairs, most of the fishes only four or five pairs. In the embryo of man, and the higher Vertebrates generally, where they make an appearance at an early stage, only three or four pairs are developed. In the fishes they remain throughout life, and form an exit for the water taken in at the mouth (Figures 2.249 to 2.251). 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 organ of hearing; 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. Chapter 2.25.)

(FIGURE 2.355. 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.)

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 jaws, 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 (Figures 2.248 to 2.251), 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 teeth are developed from the skin that clothes the jaws. As the whole mouth cavity originates from the outer integument (Figure 2.350), 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 (Figure 2.351), are in the same position as their teeth in this respect (Figure 2.252). The osseous matter of the tooth (dentine) develops 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.

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.

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 Ascidia, 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.

(FIGURE 2.356. 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.)

But, although the anterior section of our alimentary canal thus entirely loses its original character of branchial gut, it retains the physiological character 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 (Figures 2.354 C, 1.147 l). These vesicles are found in all the Vertebrates except the two lowest classes, the Acrania and Cyclostomes. 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 swimming movements up and down, and so is a sort of hydrostatic apparatus—the floating bladder of the fishes (nectocystis, Chapter 2.21). 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 (Figure 2.254).

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 (Figure 2.257).

(FIGURE 2.357. Thoracic and abdominal viscera of a human embryo of twelve weeks, natural size, (From Kolliker.) 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 caecum 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.)

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 (Figure 1.149). 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. 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.

We must refer here to an interesting rudimentary organ of the respiratory gut, the thyroid gland, 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 goitre, a growth that hangs at the front of the neck. But it is much more interesting phylogenetically. As Wilhelm Muller, 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 Ascidia and Amphioxus, and conveys food to the stomach. (Cf. Chapter 2.16, Figure 2.246). We still find it in its original character in the larvae of the Cyclostomes (Figures 2.355 and 2.356).

The second section of the alimentary canal, the trunk or hepatic gut, 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 oesophagus 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, the yelk−sac and allantois, are already known to us. The two large glands that open into the duodenum, the liver and pancreas, are growths from the middle and most important part of the trunk−gut.

Immediately behind the vesicular rudiments of the lungs comes the section of the alimentary canal that forms the stomach (Figures 2.353 d and 2.354 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 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 oesophagus. Underneath this on the left the blind sac (fundus) of the stomach bulges out, and thus the later form gradually develops (Figures 2.349 and 1.184 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, Figure 2.349 d).

Underneath the stomach there now develops 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. 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 (Figure 1.147 g). 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 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 (Figures 2.353 f, and 2.354 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 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 (Figure 2.357). 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 side. 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 develops from the duodenum, the pancreas or sweetbread. It is wanting in most of the lowest classes of Vertebrates, and is first found in the fishes. This organ is also an outgrowth from the gut.

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 caecum (Figure 2.357 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 caecum 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” is very interesting 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. These urinary organs, acting as reservoir and duct for the urine excreted by the kidneys, originate from the innermost part of the allantoic pedicle. In the Dipneusts and Amphibia, in which the allantoic 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 develops in the higher mammals. This is lost at birth. But the long stalk or pedicle of the allantois remains, and forms with its upper part the middle vesico−umbilical ligament, 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 urogenital aperture in front from the anus−opening behind. (Cf. Chapters 2.22 and 2.29.)

CHAPTER 2.28. EVOLUTION OF THE VASCULAR SYSTEM.

The use that we have hitherto made 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, and they must be carefully distinguished.

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. 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 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 cavities of the body, especially the body−cavity, or coeloma. 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 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. 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 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.

(FIGURE 2.358. 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.)

FIGURE 2.359. Vascular tissues or endothelium (vasalium). A capillary from the mesentery. a vascular cells, b their nuclei.)

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 (haemocytes) 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 circulate among them in much smaller quantity. When the colourless cells increase at the expense of the red we get anaemia (or chlorosis).

(FIGURE 2.360. 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 coeloma (secondary body−cavity). So skin−fibre layer, Sp gut−fibre layer, v blood−vessels in latter, ao primitive aortas, containing red blood−cells.)

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 have only colourless lymph−cells in the circulating fluid. There is an exception in the Nemertines (Figure 2.358) and some groups of Annelids. When we examine the colourless blood of a cray−fish or a snail (Figure 2.358) under a high power of the microscope, we find in each drop numbers of mobile leucocytes, which behave just like independent Amoebae (Figure 1.17). 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 Amoebae, they take particles into their cell−body. On account of this feature these amoeboid 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.

The red blood−cells 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 (haemoglobin) 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 (Figure 2.358). The mammals are distinguished from the other Vertebrates by the circular form of their biconcave red cells and by the absence of a nucleus (Figure 1.1); only a few genera still have the elliptic form inherited from the reptiles (Figure 1.2). In the embryos of the mammals the red cells have a nucleus and the power of increasing by cleavage (Figure 1.10).

The origin of the blood−cells and 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 coeloma. 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 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 (Figure 2.360 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 (Figure 2.361 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 Figure 1.152. In this we see clearly how a number of stellate cells proceed from the "vascular layer" and spread in all directions in the "primary body−cavity"—i.e. in the spaces between the germinal layers. 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.

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 Ruckert 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. Their origin is still much disputed.

(FIGURE 2.361. Merocytes of a shark−embryo, rhizopod−like yelk−cells underneath the embryonic cavity (B). (From Ruckert.) 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 apostrophe a deeper nucleus, in the act of cleavage, k asterisk chromatin−filled border−nucleus, freed from the surrounding yelk in order to show the numerous pseudopodia of the protoplasmic cell−body.)

Half of the twelve stems of the animal world have no blood−vessels. 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, or is a subsequent formation. Amoeboid planocytes, which migrate from the entoderm and reach this fluid−filled primary cavity, live and multiply there, and form the first colourless blood−cells. 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.

(FIGURE 2.362. Vascular system of an Annelid (Saenuris), 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.)

The earliest Vermalia in which we first find this independent vascular system are the Nemertina (Figure 2.244). 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 haemoglobin, 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 (Figure 2.362). 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, Figure 2.245). 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.

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 (Figure 2.221). By its original position behind the gill−crate, on ventral side of the Tunicates (sometimes more, sometimes less, forward), the head 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 (Chapter 2.16). 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 Ascidia−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).

(FIGURE 2.363. 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.)

FIGURE 2.364. The five arterial arches of the Craniotes (1 to 5) in their original disposition, a arterial cone or bulb, a double apostrophe aorta−trunk, c carotid artery (foremost continuation of the roots of the aorta). (From Rathke.)

FIGURE 2.365. The five arterial arches of the birds; the lighter parts of the structure disappear; only the shaded parts remain. Letters as in Figure 2.364. s subclavian arteries, p pulmonary artery, p apostrophe branches of same, c apostrophe outer carotid, c double apostrophe inner carotid. (From Rathke.)

FIGURE 2.366. The five arterial arches of mammals; letters as in Figure 2.365. v vertebral artery, b Botall's duct (open in the embryo, closed afterwards). (From Rathke.))

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 (Figure 2.359).

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. Figure 2.210). 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, Figures 1.98 to 1.102).

(FIGURES 2.367 TO 2.370. 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 Figure 2.367 only three, in Figure 2.368 all five, of the aortic arches are given (the dotted ones only are developed). In Figure 2.369 the first two pairs have disappeared again. In Figure 2.370 the permanent trunks of the artery are shown; the dotted parts disappear, s subclavian artery, v vertebral, ax axillary, c carotid (c apostrophe outer, c double apostrophe inner carotid), p pulmonary.)

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 amoeboid cells (leucocytes, Figure 1.12) 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, Figure 2.358). 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. 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.

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. The hind section, the auricle, receives the venous blood from the body and passes it on to the anterior section, the ventricle. 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 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 (Figure 2.363 abr). On each side 5 to 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 (Figure 2.364) the chief parts of the arterial system develop in all the higher Vertebrates.

(FIGURE 2.371. Heart of a rabbit−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.)

FIGURE 2.372. Heart of the same embryo (Figure 2.371), from the front. v vitelline veins, a auricle, ca auricular canal, l left ventricle, r right ventricle, ta arterial bulb. (From Bischoff.))

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 (Figure 2.365 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 (Figure 2.262), 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 (Figure 2.365). In the mammals this has been developed from the LEFT half of the same fourth arch (Figure 2.366).

(FIGURE 2.373. 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.)

FIGURE 2.374. Heart of the same dog−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)

FIGURE 2.375. Heart of a human embryo, four weeks old; 1. front view, 2. back view, 3. opened, and upper half of the atrium removed. a apostrophe left auricle, a double apostrophe right auricle, v apostrophe left ventricle, v double apostrophe right ventricle, ao arterial bulb, c superior vena cava (cd right, cs left), s rudiment of the interventricular wall. (From Kolliker.)

FIGURE 2.376. 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.)

FIGURE 2.377. Heart of a human embryo, eight weeks old, back view. a apostrophe left auricle, a double apostrophe right auricle, v apostrophe left ventricle, v double apostrophe right ventricle, cd apostrophe right superior vena cava, ci inferior vena cava. (From Kolliker.))

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 (Figures 2.367 to 2.370). 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, Figure 2.367). 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 Figures 2.364 and 2.368) the pulmonary arteries.

The human heart also develops in just the same way as that of the other mammals (Figure 2.378). We have already seen the first rudiments of its embryology, which in the main corresponds to its phylogeny (Figures 1.201 and 1.202). 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. The structure is then hollowed out, forms a simple tube, detaches from its place of origin, and henceforth lies freely in the cardiac cavity. 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.

(FIGURE 2.378. 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.))

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 (Figures 2.371 and 2.372). The foremost section, which is turned towards the ventral side, and from which the aortic arches rise, reproduces the arterial bulb of the Selachii. The middle section is a simple ventricle, and the hindmost, the section turned towards the dorsal side, into which the vitelline veins 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 (Figure 2.371 b); and the constriction between the atrium and ventricle is called the auricular canal (Figure 2.372 ca). The heart of the human embryo is now a complete fish−heart.

(FIGURE 2.379. Transverse section of the back of the head of a chick−embryo, forty hours old. (From Kolliker.) m medulla oblongata, ph pharyngeal cavity (head−gut), h horny plate, h apostrophe thicker part of it, from which the auscultory pits afterwards develop, hp skin−fibre plate, hh cervical cavity (head−coelom or cardiocoel), hzp cardiac plate (the outermost mesodermic wall of the heart), connected by the ventral mesocardium (uhg) with the gut−fibre layer or visceral coelom−layer (dfp apostrophe), 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, g vessels.)

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. Figures 2.373 to 2.378). 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, Figures 2.375 c and 2.377 c); the left auricle receives the pulmonary veins. In the same way a superficial interventricular furrow is soon seen in the ventricle (Figure 2.376 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 (Figure 2.376 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.

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. 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.

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, Figure 2.379 uhg). The mesocardium divides two lateral cavities, Remak's “neck−cavities” (Figure 2.379 hh). These cavities afterwards join and form the simple pericardial cavity, and are therefore called by Kolliker the “primitive pericardial cavities.”

(FIGURE 2.380. Frontal section of a human embryo, one−twelfth of an inch 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 double cervical cavity of the Amniotes is very interesting, both from the anatomical and the evolutionary point of view; it corresponds to a part of the hyposomites of the head of the lower Vertebrates—that part of the ventral coelom−pouches which comes next to Van Wijhe's “visceral cavities” below. Each of the cavities still communicates freely behind with the two coelom−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−coeloma,” and by Hertwig the “pericardial breast−cavity.” As it now encloses the heart, it may also be called cardiocoel.

The cardiocoel, or head−coelom, 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. Figure 1.180 h). 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, which is the first structure of the primary diaphragm (Figure 2.380 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. These canals, which belong to the dorsal part of the head−coelom, 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 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, 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 partition. But it was probably in the Permian sauro−mammals 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 and the later dorsal part.

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, 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.

(FIGURE 2.381. 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 coelom, hk top of heart, ks head−sheath, amniotic fold, h horny plate. (From Remak.)

(FIGURE 2.382. 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.))

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 develops from its inner wall. The pleural sacs that enclose the lungs are dorsal parts of the head−coelom, originating from the pleuroducts; the pericardium in which the heart afterwards lies is also double originally, being formed from ventral halves of the head−coelom, 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 out−growth, 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 quadrupeds 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.

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 rabbit, the two embryonic hearts are still far apart at the stage when there are already eight primitive segments (Figure 1.134 h). So also the two coelom−pouches of the head in which they lie are still separated by a broad space. It is not until the permanent body of the embryo develops 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 cardiocoel disappears, the two cervical cavities freely communicate (Figure 2.381), and form, on the ventral side of the amniote head, a horseshoe−shaped arch, the points of which advance backwards into the pleuro−ducts or pleural cavities, and from there into the two peritoneal sacs of the trunk. But even after the conjunction of the cervical cavities (Figure 2.381) 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 (Figures 2.379 s and 2.382 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.

Thorough opponents of the biogenetic law 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.

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 system are still very obscure and controverted. The characters of the embryonic circulation of the Amniotes, which we have previously considered (Chapter 1.15), are late acquisitions and entirely cenogenetic. (Cf. Chapter 1.15 and Figures 1.198 to 1.202.)

In the Selachii also we find a longitudinal row of segmental canals on each side, which open outwards into the primitive renal ducts (nephrotomes, Chapter 1.14). 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.

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 (Figures 2.386 and 2.387). 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 coelous 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 coelom−pouches arises between the limiting layers (Figure 2.385). 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). As the originally very short urinary canals lengthen and multiply, each of the two primitive kidneys assumes the form of a half−feathered leaf (Figure 2.387). 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 as a secondary formation. Originally they open, as the Cyclostomes clearly show, quite independently of the gut, in the external skin of the abdomen.

(FIGURE 2.395. Primitive kidneys and germinal glands of a human embryo, three inches 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.))

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 (Figures 1.183 m, 1.184 m, 2.388 n). It lies near the middle line, directly under the primitive vertebral column, and reaches from the cardiac region to 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.

(FIGURES 2.396 TO 2.398. Urinary and sexual organs of ox−embryos. Figure 2.396, female embryo one and a half inches long; Figure 2.397, male embryo, one and a half inches long. Figure 2.398 female embryo two and a half inches long. w primitive kidney, wg Wolffian duct, m Mullerian duct, m apostrophe upper end of same (opened at t), i lower and thicker part of same (rudiment of uterus), g genital cord, h testicle, (h apostrophe, lower and h double apostrophe, upper testicular ligament), o ovary, o apostrophe lower ovarian 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 Kolliker.))

The primitive or primordial kidneys of the amniote embryo were formerly called the “Wolffian bodies,” and sometimes “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 (Figure 1.147 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. 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 amnionless 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, develops, 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 growth, 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 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; that is the single vesico−umbilical ligament. To the right and left of it in the adult male are a couple of other rudimentary organs, the lateral vesico−umbilical ligaments. 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 develops beside the nephroduct at an early stage of embryonic evolution. The latter is usually called the Mullerian duct, after its discoverer, Johannes Muller, while the former is called the Wolffian duct. The origin of the Mullerian 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 Mullerian ducts.” The latter (Figure 2.387 m) lies just on the inner side of the former (Figure 2.387 w). Both open behind into the cloaca.

However uncertain the origin of the nephroduct and its two products, the Mullerian and the Wolffian ducts, may be, its later development is clear enough. In all the Gnathostomes the Wolffian duct is converted into the spermaduct, and the Mullerian 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 Mullerian ducts, which I have called “Rathke's canals” (Figure 2.394 c). In the female sex, in which the two Mullerian ducts form the oviducts, there are relics of the Wolffian ducts, which are called “the ducts of Gaertner.”

(FIGURE 2.399. Female sexual organs of a Monotreme (Ornithorhynchus, Figure 2.269). o ovaries, t oviducts, u womb, sug urogenital sinus; at u apostrophe is the outlet of the two wombs, and between them the bladder (vu). cl cloaca. (From Gegenbaur.)

FIGURES 2.400 AND 2.401. Original position of the sexual glands in the ventral cavity of the human embryo (three months old).

FIGURE 2.400 male (natural size). h testicles, gh conducting ligament of the testicles, wg spermaduct, h bladder, uh inferior vena cava, nn accessory kidneys, n kidneys.

FIGURE 2.401 female, slightly magnified. r round maternal ligament (underneath it the bladder, over it the ovaries). r apostrophe kidneys, s accessory kidneys, c caecum, o small reticle, om large reticle (stomach between the two), l spleen. (From Kolliker.))

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 (Figures 2.390 to 2.395). The first structure of the nephroduct and its differentiation into Mullerian and Wolffian ducts are just the same in both sexes in the Amphibia, as in the mammal embryos (Figures 2.392 and 2.396). In the female Amphibia the Mullerian duct develops on either side into a large oviduct (Figure 2.393 od), while the Wolffian duct acts permanently as ureter (u). In the male Amphibia the Mullerian duct only remains as a rudimentary organ without any functional significance, as Rathke's canal (Figure 2.394 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.

In the mammals these permanent amphibian features are only seen as brief phases of the earlier period of embryonic development (Figure 2.392). 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 develops 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.

(FIGURE 2.402. Urogenital system of a human embryo of three inches 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 Kollman.))

The Mullerian 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 develops into the embryo. This is the womb (uterus). At first the two wombs (Figure 2.399 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 Mullerian ducts, and in the Placentals they combine below with the rudimentary Wolffian ducts to form a single “genital cord.” The original independence of the two wombs and the vaginal canals formed from their lower ends are 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 rabbit 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, uteris 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, 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.

(FIGURES 2.403 TO 2.406. Origin of human ova in the female ovary.

FIGURE 2.403. 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 (Pfluger'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.)

FIGURE 2.404. 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).

FIGURES 2.405 AND 2.406. Two older Graafian follicles, in which fluid is beginning to accumulate inside the eccentrically thickened epithelial mass of the follicle−cells (Figure 2.405 with little, 2.406 with much, follicle−water). ei the young ovum, with embryonic vesicle 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).)

In the male mammals there is the same fusion of the Mullerian and Wolffian ducts at their lower ends. Here again they form a single genital cord (Figure 2.397 g), and this opens similarly into the original urogenital sinus, which develops 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 Mullerian ducts. The most notable of these is the “male womb” (uterus masculinus), which originates from the lowest fused part of the ducts, and corresponds to 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).

(FIGURE 2.407. 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 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 (Figures 2.386 g and 2.392 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 (Figure 2.400 gh), and in the female as the “round maternal ligament” (Figure 2.401 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 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 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 (Chapter 2.22). Among the mammals this arrangement is permanent only in the Monotremes, which take their name from it (Figure 2.399 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, and is the sole outlet of the urine and the sexual products; the hind or anus−cavity passes the excrements only.

Even before this partition has been formed in the Marsupials and Placentals, we see the first trace of the external sexual organs. First a conical protuberance rises at the anterior border of the cloaca−outlet—the sexual prominence (phallus, Figure 2.402 A, e, B, e). 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 (Chapter 2.25); the sexual nerves spread on it, 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; in the female it becomes the much smaller clitoris; this is only found to be very large in certain apes (Ateles). A prepuce (“foreskin") is developed in both sexes as a protecting fold on the anterior surface of the phallus.

(FIGURE 408. 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. Figures 1.1 and 1.14.)

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 proctodaeum, the ectodermic invagination of the rectum (Chapter 2.27); 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 papillae of the corium of the phallus, and have been evolved from ordinary tactile corpuscles of the corium by erotic adaptation (Chapter 2.25).

The formation of the corpora cavernosa, which cause the 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 (nymphae). 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. We begin to trace them in the tenth week of development, and they are accentuated in proportion as the difference of the sexes develops.

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). 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, in which the penis is split open below, is seen in epispadia, in which the urethra is open above. 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.

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 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 hemaphrodism 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. 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 formerly supposed to be the ova themselves; but Baer discovered the ova within the follicles (Chapter 1.3). Each follicle (Figure 2.407) 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 (Figure 2.387 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 (Figure 2.403 b). Some of the cells of these strings (or Pfluger'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).

The follicle−epithelium of the mammal has at first one stratum (Figure 2.404 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 (Figures 2.405 and 2.406). 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 (Pfluger'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.

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.

CHAPTER 2.30. RESULTS OF 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 Gastraea. As the human embryo passes through the gastrula−form like that of all the other Metazoa, we can trace its phylogenetic origin to the Gastraea.

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 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 inheritance of acquired characters is denied, not only by 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 (pages 192 and 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, in both the skeleton and muscular systems, provides a number of interesting dysteleological arguments. I need only recall the projecting tail of the human embryo, with its rudimentary caudal vertebrae 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 thymus−gland and the thyroid gland, 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 caecum. 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 Mullerian 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 Gastraeads; 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 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 Pro−mammals. 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 twelve stems or phyla, and these are broadly sub−divided 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. Chapter 2.23.)

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; so 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. 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. We can assuredly construct an approximate picture in the imagination of the form of our early Tertiary ancestors from the foregoing facts of comparative anatomy; 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. Chapter 2.23). 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. Quite certainly 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 aesthetic 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.”* (* The English reader will recognise here the curious position of Dr. Wallace and of the late Dr. Mivart.—Translator.) 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.

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 honeyed 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 cooperation of the countless citizens, and that they understand each other. A number of recent observers, especially Fritz Muller, 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 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 given 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 develops 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 cognizance 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 sub−stratum 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 study 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 General Morphology, 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 General Morphology (Book 7) contains the first attempt to determine the series of man's ancestors (volume 2 page 428). However imperfect this attempt 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 workers 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 this work 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 formulae. 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.

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