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CONTRIBUTIONS
TO THE
HISTORY OF DEVELOPMENT
IN ANIMALS.

I. ON FŒTAL CIRCULATION.



BY

WILLIAM MACDONALD, M.D., F.R.S.E.,

PROFESSOR OF CIVIL AND NATURAL HISTORY, ZOOLOGY, AND COMPARATIVE ANATOMY, ST ANDREWS,
FELLOW OF THE ROYAL COLLEGE OF PHYSICIANS, EDINBURGH.

^e EDINBURGH:
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Preparing for Publication.

No. II.—ON THE OSSEOUS SYSTEM.

No. III.—ON THE NERVOUS SYSTEM.

CONTRIBUTIONS
TO THE
HISTORY OF DEVELOPMENT IN ANIMALS.

On the Course of the Blood Circulating in the Embryo.

FROM the very minute size of the human ovule, embryologists were early constrained to examine the changes during incubation of the hen's egg, where its relatively greater bulk and size of the different parts enabled them to determine the various stages of development. The ready facility of procuring, at any period of the year, by the aid of artificial incubation, impregnated eggs at all stages, for the purpose of microscopic observation and dissection, has tended greatly to advance a knowledge of this important subject. The numerous observers in all parts of the world have greatly extended this from their independent observations, though this has sometimes introduced a rather voluminous nomenclature, by having applied names to some parts which, without their knowledge, had been previously otherwise named. On the present occasion I will pass over the more transient tissues that have been described as resulting from development, and only describe the more persistent membranes and fluids of chick in ovo more familiar to us.

All the data adduced in this communication have been drawn from the discoveries of embryologists, detailed and published in the elementary text-books in the hands of the medical student, compiled from the discoveries of Wagner, Van Bæer, Müller, Purkinje, Valentine, Coste, and other continental embryologists; from Barry, Wharton Jones, Allen Thompson, Paterson, Reid, Goodsir, and others in this country. All describe the impregnated ovum during the first day of incuba-

tion as consisting of a germ vesicle and vitellus in their special membranes within the chorion—a thin, structureless, semi-transparent, nonvascular membrane, internally smooth, but covered externally with numerous projecting villi. The egg, when initiated in the ovisac, lies amidst the stroma or thick fibrous substance of the ovary—the theca or chorion, in section, appearing as a ring surrounding the vitellus or yolk, and the germ vesicle containing the germ spots or macula. Immediately around the cell in which the ovule lies there is a net-work of blood-vessels, from the ovary entering the capsule of each individual ovule, and most conspicuous in the riper or more mature ovules. Even the smallest in the bird are found to contain many dark vitelline globules, which is not the case in higher animals.

The usual diagramatic sections may suggest an erroneous idea of the relative position of the different parts, and mislead by exhibiting in cross section the germ spot in the germ vesicle contained within the centre of the yolk, instead of being on its circumference. This has evidently suggested the opinion that the germ vesicle had a globular form, and rose from the centre of the yolk, while common sense might have rationally suggested that the periphery was a likelier situation, regulated by the relative density or specific gravity of the different parts.

Müller, in his "Elements of Physiology," translated by Baly, notices that the ova of ichthya, nantia, and amphibia, are developed in a manner different from the rest of the vertebrata, being destitute of both amnion and allantois. That in reptilia, including serpents, lizards, crocodiles, and turtles, the ova are furnished with both amnion and allantois. These membranes have been long ago observed by Aristotle in birds, which, however, differ from reptiles by their anterior cerebral flexure in the *sella turcica* along the base of the cranium, which in reptiles is quite straight. The difference in the temperature of the blood might also have prevented jumbling birds and reptiles together, in a classification based upon minute anatomical differences in the bones of the palate and nose.

The ovum, when expelled from the ovary in birds passes down the oviduct; greatly increases in the bulk of the yolk and the chorion, having its external surface covered with villi,

which, on entering the cloaca, are compressed and flattened by the deposition of carbonate of lime forming the egg-shell, cutting off all maternal connection when laid, externally perfectly smooth, without visible pores, but still pervious to air; internally, its surface is roughened by shallow depressions, in which the chorion villi are flattened. The internal surface of the chorion is perfectly smooth, thin, structureless, and non-vascular, and contains, as Aristotle long ago described, the vitellus or yolk, in its thin, transparent, structureless, non-vascular, vitellary membrane, supported by an albuminogelatinous substance, denser around the yolk, and so dense on its surface as to form the internal coat of the contents of the egg, but of smaller bulk. A small quantity of air collects principally at the broad end of the egg, allowing the germ vesicle, the lightest of all the contents of the egg, to rise prominently to the chorion in whatever position the egg may lie during the daily turning while incubating. The vitellus consists—1st, Of the albumen, which liquefies and partly escapes through the egg-shell, and partly infiltrates into the yolk, as described by Professor Clark of Harvard University, Massachusetts; Bischoff names it the *tunica media*, or fluid area within the chorion. 2dly, The yolk, a globular body in the thin, transparent, structureless, non-vascular, vitellary membrane, containing a mass of small yellow granules, mixed with some oil globules. In its centre the yellow granules enlarge and float in a yellow fluid, probably thinned by the infiltration of the albumen just noticed, allowing them to rise toward the *proliferous or embryonic germ disc*, forming the layer of large yellow globules over the upper surface of the yolk, which Professor Robin, member of the Institute and the Faculty of Medicine of Paris, describes when thus spread over the upper surface of the yolk, as the inner layer of the umbilical vesicle at a later stage of development.

The germ vesicle, the most important of the egg's contents, resulting from impregnation, is described by Wagner as a globule resting in a depression of the yolk, which constantly bears it up in contact with the chorion lining of the egg-shell. The globular form may be fairly questioned, for shortly after incubation has begun, about the middle of the first day it rises

to the chorion, and extends itself in a lengthened convexo-concave oval lenticular form, lying across the long axis of the egg. Its edges are at first partially covered with the albumen, which decreases as development proceeds.

The Germ vesicle consists of a thin, transparent, structureless, non-vascular germ membrane (the future amnion), firmly continuous with the margin of the concave embryonic germ disc, which splits up, in the course of the first day, into the serous, vascular, and mucous layers.

I. The serous or animal layer, the main seat of germ development, has an oval concave form stretching across the long axis of the egg. Along the centre of its upper surface there is a delicate white streak, *nota primativa*, which is subsequently spread out into the *area pellucida*—a pyriform, transparent membrane, on which the early germ extends, rising slightly above the general level of the germ disc, and at one end a collection of nucleated cell granules, which becomes the head of the embryo, gradually tapering towards the tail, and described as like a flat-bottomed boat upturned. As development proceeds the greatly increased bulk of the head, extending beyond the *area pellucida*, bends it downwards, carrying along with it the *corda centralis*, or centro-cord, still enclosed in the expanding amnion, with the cerebral cells beyond the portion of the spinal canal, narrowed by the four square plates on each side, the lamellar tubercles connected with the basilar centrum, which Agassiz considers the summit of the spinal column, fused into the basilar stem of the *posterior crane*. The number of these lamellar tubercles increases along the vertebral column as it lengthens.

The cerebral cells, at first supported on the same plane by the dura mater, after the cerebral flexure, rest upon the platform of the *anterior crane*, formed by the double meso-cranial and pro-cranial segments. Reichert describes these as connected to the basilar stem by means of the *trabecula*, as stated by Huxley, to the *basi-occipital* and *basi-sphenoid* so firmly connected that Scemmering always described them together. The flexure is principally in the brain, with a slight inclination of the basilar summit.

II. The vascular or intermediate layer, consisting of a series of vascular sinuses, filled with venous blood discs, connected by a continuous vessel, lying along the centre of the ventral aspect of the serous layer from stem to stern, is suddenly arrested in the form of a conical sac by the flexure of the anterior pro-cranial double segments, and their dependent *facio-mandibular costæ*, of the face chest, or *upper mandible*, projected beyond the mucous layer, giving it, in the bird, the form of a very prominent beak, having the amnion closely attached to the edge of the bill (or alveolar margin of the palate, in the human embryo), and along the margin of the whole ventral laminæ, which subsequently close in forming the parietes of the chest and abdomen. The amnion thus incloses those portions of the embryo derived from the serous layer, amidst the amniotic fluid, excluding entirely the vascular and mucous layers and the organs developed from them. These different organs are supported, like the cerebral cells, on a shut serous sac, which though apparently containing them, yet excludes them from its cavity, as a double night-cap does the head. The heart, included in its especial involucrum, is likewise really external to the cavity of the pericardium.

III. *The Mucous or Vegetative Layer.*—The respiratory, digestive, intestinal, and excretory organs are more tardily developed from the mucous or vegetative envelope.

The yolk, in its thin, transparent, structureless, non-vascular membrane, covered by a layer of large yellow globules rising from its centre, which Professor Robin, of the College of France and Member of the Institute, describes as forming the inner layer of the umbilical vesicle, the very vascular envelope to the yolk, by which it is ultimately drawn into the jejunum at the umbilicus, between the egress of the umbilical vein, filled with venous blood, and the entrance of the umbilical arteries, carrying pure oxidised blood from the chorion.

The mucous layer, depending from the external base of the metacranium or postcrane, descends in front of the cervical vertebræ, lining the nasal, oral, and faucial passages. The pharynx, continued into the œsophagus, in birds swells, in part of its course, into the crop or *ingluvies*, where grain may be

stored and fitted for digestion, after which the tube is contracted to its previous size, till near the gizzard it bulges again into the *proventriculus*, a smaller cavity, but studded with an abundance of large glandular follicles, variously disposed, supplying a copious secretion of gastric juice to be mixed with the food.

The intestinal canal in birds, as in other classes, varies with the different natures and habits of this extensive class, and the relative length of their bodies. Its calibre is pretty generally equal throughout; the division into large and small intestines can scarcely be said to exist. The duodenum, from the pylorus, forms a long loop, and, after sundry convolutions, is continued into the cloaca, near which there are generally two cæca, about the end of the third day, communicating with the gut, which may indicate the limit between the large and small intestines, and where the yolk is finally drawn into the intestines.

There is great difficulty in awarding to each day its particular acts of development, as some organs continue longer under the process than others; all that can be attempted is an approximation to the order.

The third day is the most remarkable in the whole history of development, from the great general vigour of the formative evolution of the organs and the peculiar form of the embryo. The dorsal laminae, forming the neuro-vertebral arches covering the cerebro-spinal axis, and the extension of the rudimentary vertebral centres fore and aft, in or upon the centrochord (incorrectly noto-chord from its place in the central axis of the embryo). These are at first cartilaginous, like the lamellar tubercles and the base of the cranium, whose expanded dome is the stout membranous *dura mater* on which superficially the ossification of the upper cranial segments is completed. The examination of the egg at the beginning of this period must be conducted with much care, as the albumen is entirely removed over the germ vesicle, which lies close under the chorion shell lining, alone protected by its amnion. The vitelline membrane is exceedingly thin, easily torn, and resolved by the fluidising power of the albumen among its granules, in the progress of developing the embryo. The air space at the broad end of the egg has greatly

enlarged, and by its elasticity antagonising the denser remains of the albumen collected in the sharp point. The Germ vesicle, with its embryo, is still supported within the full influence of the chorion shell lining. The umbilical vesicle from the mucous layer has grown around nearly two-thirds of the yolk, forming the very vascular vitellicle of Owen; its terminal capillary sinus becomes a mere line around its arterial vascular area, and its veins disappear some days later. According to Rathke and Van Bæer, the lungs are evolved during the fourth day of incubation as two small laterally compressed thin sacculi, tapering from before backwards, ending in a blunt point, springing from the end of the narrow tube of the trachea, which originates from the anterior surface of the œsophagus, with a slight bulging containing the upper larynx, protected by the thyroid (*pomum Adami*), suspended from the hyo-facio-mandibular cleft. By the fifth day the centro-chord becomes involved in the centro-vertebral stem by the sphenoidal trabeculæ, beyond the basilar summit, through the basi-sphenoid, vomer, perpendicular plate of the ethmoid, and cartilage of the nose, the whole length of the chordo-centralis, as seen in the *Amphioxus lanceolatus*.

The upper and lower extremities now bud forth in a rudimentary condition. The cerebro-neural system becomes so greatly developed, that it is necessary to devote a separate communication on so important a subject, which is reserved for a future contribution, along with the osseous system, both preparing for publication.

The mucous layer continues to be developed on a shut serous sac, which, while it covers the whole viscera, and forms the basis of omentum and mesentery with the umbilical vesicle, the mesocolon, and the envelope of the allantois, still excludes them and the other organs of the chest, abdomen, and pelvis, with all the vascular system, and even the heart, in its own pericardium.

About the sixth day the allantois grows with great rapidity, forming at this date a very large flattened bladder, almost twice its former size, as nearly to inclose the embryo in its amnion. The Wolffian bodies and their derivatives, having many remarkable relationships, their shut sacculles, stretching along on

both sides of the spine, elongate into tortuous ducts, evidently secreting. There are certain small points, like the Malpighian bodies of the kidneys, which appear to consist of convoluted tubes, terminating in cloacæ. The kidneys and suprarenal capsules, and the sexual organs, also appear in the same locality, but so rudimentary at that time that it is difficult to determine whether testes or ovaries. The fuller consideration of these important organs will be more appropriately taken up along with the development of the human ovule.

The Heart and Blood-Vessels.

In the base of the heart, as it lies in the *fovea cardiaca*, where the *punctum saliens* instigates the first contraction of the heart by which its cavity, filled with a pale orange or yellowish fluid (the *plasma* or *liquor sanguinis*), is discharged. The heart being the only muscular organ of the vascular system, propels the *plasma* among the venous biconcave blood-discs, by the *ductus venosus*, into the rete venosum; and the terminal sinus or peripheral vein, with its fringe of minute vessels, forming the capillary area under the oxidising influence of the chorion. At first, only a few bright specks appears among the dark capillaries, which afterwards increase in number and size as the rootlets, forming larger and larger vessels, till at length the blastine arteries, coming from each side of the arterial vascular area, enter the embryo near the point of the upturned coccyx, covered by the pedicle of the allantois on its way to be expanded in the tunica media. This gives the relative anatomy previous to the closing of the ventral laminae; as this progresses the *ductus venosus* is carried lower and lower, till the umbilicus is formed, through which the pedicle of the umbilical vesicle is interposed between vein and arteries on its way to be expanded over the yolk in the *tunica media*. These arteries are continued as hypogastric till they enter the iliac arteries, which send a part of the blood to the lower trunk and extremities; but the main portion is sent upwards by the right and left trunks of the aortæ, along the sides of the spinal column as high as the *fovea cardiaca*, where each of them divides into two terminal branches, directed forward to the

base of the heart, where they form the aortic bulb or *truncus arteriosus*, from which the subclavian and carotid arteries are given off to supply the upper trunk and extremities and the head, as in the adult, with pure arterial blood, and continued to those regions till reduced by the capillaries, and returned by the jugular and subclavian veins, forming the *venæ cavæ superiores*, which pour their venous blood into the auricle, where it meets with the reduced blood from the inferior extremities brought by the *vena cava*, along with the venous blood of the portal circulation from the liver,—the whole venous blood collected in the heart completing a course of the circulation, is continued while the embryo is a mere appendage to the heart, under the control of the ganglio-sympathetic nervous system (as in the mollusca and lower classes), before the respiratory, digestive, intestinal, or excretory systems have been developed.

Professor Allen Thompson describes the course of the blood in a downward course, having seen the blood flow in the early development of the *chick in ovo* down the aortæ. It would be no proof, and be discourteous to so accurate and acute a microscopist, to contradict or deny what he saw. Possibly the blastine arteries may enter the aortæ higher before the closure of the abdomen, and descend to the iliacs, which I don't think at all probable. I unhesitatingly deny that the blastine arteries, after the closure of the abdomen and the development of the large broad sternum, reaching to near the pubis, can possibly communicate with the aortæ higher than through the umbilicus, were the *ductus venosus* and umbilical vesicle to pass out over the entering blastine arteries.

The *punctum saliens*, from the lower surface of the base of the heart, or the auriculo-ventricular septum, initiates the separation of the ventricle, by a muscular septum, into right and left ventricles; subsequently, from the upper surface a similar muscular septum is begun in the auricle from both its surfaces, but never completed. In the human fœtus, the *foramen ovale* continues to exist till after birth; and numerous instances have been met with, as shown by dissection, even far into adult life, without inconvenience. The ventricles depending from the lower surface of the base of the heart, as they

become enlarged, the right ventricle shows a tendency to rise over the left, tending to turn the apex of the heart towards the left side, but extending upwards, at the same time, beyond the plane of the auriculo-ventricular septum, covers the upper surface of the *truncus arteriosus*, tending slightly to the left side. A similar extension of the left ventricle, passing towards the right under the right ventricle, carries it obliquely across to the right side; so that when all is prepared, these advanced horns of the ventricles, each having three semilunar valves, are ready to engulf the *truncus arteriosus*—that from the right ventricle on the upper surface forming the pulmonary arteries to the right and left lungs, while the horn of the left ventricle plunges into the lower part of the *truncus arteriosus*, carrying up with it a portion of one of the terminal branches of the aorta, which soon becomes atrophied into a mere tendon, but long fancied, under the title of *ductus arteriosus*, to communicate between the heart and the descending aorta; the left ventricle rising over the right pulmonary artery to form the arch of the aorta, thus replacing its bulb, the subclavian and carotid arteries continue to be sent to the upper trunk extremities and head, as it did previous to the change of the bulb, by the inflation of the lungs from the first whiff of inspiration.

As soon as the circulation is so far established, from the iliac arteries sending the main part of the oxidised blood by the double trunks of the aorta ascending upward, one on each side of the spinal column, the following arteries are given off to the right and left within the abdomen under the pleura :—

1. The mesocolic artery, ramifying at first behind the pleura or serous shut sac lining the abdomino-thoracic visceral cavity of the bird. It supplies liberally the vascular envelope of the allantois, arising from the coccygeal body at the termination of the coccyx, curved greatly towards the umbilicus, before the perinæum exists of any extent, and while the rectum is still a shut sac. The pedicle of the allantois, through the umbilicus, passes into the *tunica media* (Bischoff), and swells into a large balloon or bladder formed of a thin, transparent, structureless, non-vascular membrane, expanding greatly within the very vascular mesocolic envelope in which it is included, thus

affording a wide circulation of the arteries among the capillaries from which the numerous small vessels unite to form the mesocolic vein, the first tributary to the portal system. This extensive temporary circulation, as *diverticulum sanguinis*, seems to be required in the early embryonic life prior to the development of the digestive and intestinal system, and the organs derived from these; for as soon as the colon is developed, the expanded allantois becomes atrophied, its pedicle drawn through the umbilicus, and shrivelled into the urachus along the fundus of the bladder. The commencement of the small tubular colon, found in all mammals below the chiropods, probably becoming shrivelled into the *appendix vermiformis* of the *caput cæcum coli*.

2. The mesenteric artery, distributed on the umbilical vesicle, which forms a very vascular envelope covering the yolk, and the large yellow globules which arise from its centre forming the inner layer of the umbilical vesicle, according to Professor Robin. After completing this primary purpose of the circulation in the umbilical vesicle, the blood is reduced and carried by the mesenteric veins to form the second tributary to the portal circulation, till the development of the small intestines is completed, and from which there is a communication in the pedicle of the umbilical vesicle, through which the yolk at a later stage is dragged into the intestines. The blood-vessels afterwards become restricted within the mesentery, still continuing to send their venous blood as a tributary to the portal circulation.

3. The cœliac axis, from which the splenic, gastric, and hepatic arteries are distributed to the spleen, stomach, and liver. The veins containing their reduced blood unite behind the pancreas to complete the stem of the portal circulation flowing into the *sinus portarum* in the longitudinal fissure of the liver. In the transverse fissure the right and left portal veins circulate in company with branches of the hepatic artery through the different lobes of the liver, from which the blood is conveyed by three hepatic veins entering so obliquely into the inferior vena cava as to act as valves, preventing regurgitation, at a point where it mingles with the whole venous blood collected in the heart, which by its contraction propels down the

ductus venosus to the *rete venosum*, the capillary and vascular area and blastine arteries carrying the purified blood into the aorta, thus completing the course of the circulation, which is repeated during embryonic life. After this the aortæ extend upward to the fovea cardiaca, where they divide each into two terminal branches, which have been long supposed and erroneously described as branchial arches. Reichert long ago showed they had no connection with branchiæ, as there is no such organs in the embryo, their function being executed entirely by the chorion villi, although he still maintains that they are analogous to the vascular arches in the gills of fishes, but without branching like them. Such is the persistence of early prejudice even among our most distinguished observers. The name of visceral arches, which he proposed, is equally inappropriate, as they are merely the terminal branches of the aortæ forming the aortic bulb or *truncus arteriosus*.

The following notes on the development of the heart is equally applicable to the chick in ovo as to the *fœtus in utero*, and may be introduced here, avoiding repetition of the changes in the structure of the heart preparatory to its altered circulation. After the first sacculated form of the heart, with a single cavity, had been so far enlarged by the addition of a ventricle of an elongated form, developed on the opposite surface of the base of the heart through which the auriculo-ventricular orifice is opened, allowing the free flow of blood into the ventricle, instantly stimulating it to contract, and forcing it back through the auricle and down the *ductus venosus*, still the only outlet from the heart onward through the *rete venosum*, terminal sinus, and to the capillary area beneath the influence of the chorion, and then returned through the arterial vascular area, to the blastine arteries, supplied from each side, and still continued double through the hypogastric and iliac arteries, and aortæ, to the fovea cardiaca, as already described.

The progressive changes in the structure of the heart, preparatory to the pulmonic circulation, have led to the very important practical views of Dr Tonge, lately communicated to the Royal Society by Dr Beale, where the extension of the

ventricles has been traced as arising from the arteries. This is the natural result of adhering to the established theory, which I consider both anatomically and physiologically erroneous. By commencing the course of development from the centre of the base of the heart, where the *punctum saliens* may fairly be supposed to institute the first act of the circulation, by contracting the auricle while a single sacculated cone, and the formation of the ventricle, by the commencement and completion of the muscular septum, forming the right and left ventricles, the subsequent auricular septum, incomplete from the *foramen ovale*, permitted the passing and repassing of the venous blood, to and from the ventricles, towards the oxidising organs, whether the chorion villi of the egg-shell lining, or those of the human ovule, before and after they are imbedded in the sinuses of the spongy mass of the uterine placenta; and, at length, towards the latter end of pregnancy from the same point, stimulating the extension of the septum from the right ventricle into the *truncus arteriosus* over which the anterior horn of the right ventricle extended inclining towards the left, beyond the plane of the auriculo-ventricular septum, contracting gradually into a tubular form, towards the superior margin of the bulb from whence the subclavian and carotid arteries are distributed to the upper trunk and extremities of the head. Within this horn the three semilunar valves begin to appear within its upper part, ready to burst into the bulb, still inclining downwards and to the left, preparatory to becoming the pulmonary artery, quickly dividing into two branches, to the right and left lobes of the lungs. The same force from the same point instigates the activity of the left ventricle to extend towards the right, below the anterior horn of the right ventricle, ready to engross the lower portion of the bulb in a similar tubular form with its three semilunar valves, after the lung-cells are inflated, carrying away with it a portion of one of the terminal branches of the aortæ, represented as the imaginary *ductus arteriosus*, playing so important a role in the fanciful established theory of the foetal circulation, fostered by early prejudice during three centuries, and still obstinately maintained in all canonical institutions. As soon as the magic impulse is given, the horn of the left ventricle, as the aorta

rises from below, and bending over the right pulmonary artery, to which it is attached as above described, forms the arch, crowned with the subclavian and carotid arteries, in the same order as they were previously sent from the *truncus arteriosus*. The aorta then bends to the same part of the cervico-vertebral stem of the spinal column, supplying in its descent the same organs, but in a reversed order to that before the inflation of the lung-cells. The principal difference between the position of the heart in the bird and foetus arises from there being only one visceral cavity common to the respiratory and intestinal organs; whereas in the foetus, by the separation of the thorax and abdomen, the heart soon begins to descend towards the diaphragm, on which it rests, enclosed in its pericardium, carrying the terminal aortic branches along with it. This may also be assisted by a partial raising of the upper dorso-cervical vertebræ and cranium, though in a less exaggerated scale than in the long-necked birds. In the foetus this upward extension is continued in a relatively greater rate than in the adult, the infant at birth being short-necked when compared with the bulk of the cranium.

Believing that the germ vesicle in the impregnated egg is entirely the result of conception, I presume to have shown, from the valuable demonstration of the forementioned distinguished embryologists, that the heart is first formed by a projection of the forehead and face segments, arresting and stagnating the vascular layer, so as to form a conical sac with two inferent veins entering at one angle of the base, and one efferent vein at the opposite angle—the only outlet from the single cavity of the primitive heart. The *truncus arteriosus*, or aortic bulb, rising behind the heart, is connected solely with the arterio-vascular circulation; and the heart alone is connected with the veno-vascular circulation; and also, that the only vascular communication between them, during the non-breathing life of the embryo, was by means of the capillaries, under the same anatomical and physiological laws as in adult life, from veins which first communicated in the capillaries with arteries, and from these again with veins only in the capillary area. I hope I may be allowed to assume that the circulation is instituted by the

first contraction of the conical sac, the only muscular organ connected with the blood circulation of the embryo of the *chick in ovo*, discharging the plasma among the venous blood-discs, even before the ramification of the *rete venosum* had extended from the *ductus venosum* to the terminal sinus, which by its capillary fringe lies within the influence of the chorion shell lining, and, therefore, before any communication could exist between the chorion and the embryo. Van Bæer had shown that the vascular system was stored with these blood discs prior to the true blood circulation, and Wagner even describes a slight rhythmic undulation before it fully succeeded to start the circulation of the *plasma* among the venous blood discs, as far as the capillary area, within the oxidising influence of the chorion egg-shell lining, to be returned through the arterial rete or vascular area, where, by the gradually increasing size of the vessels, the trunk of the blastine artery, from each side of the chorion, are at length communicated by the hypogastric arteries along with the iliac arteries, which, having no other arterial communication upward but with the aortæ, the circulation of this oxidised blood can only ascend towards the head of the embryo, and by means of the terminal aortic branches forming the *truncus arteriosus*, or aortic bulb, this pure blood is circulated through the head and upper trunk and extremities, and returned in a reduced venous condition to the auricle of the heart, still a single cavity, thus completing the first course of the embryonic circulation, which it continues to pursue while the development progresses in preparing the embryo for a completely altered course of circulation, from the inflation of the lung-cells by the first whiff of respiration.

I believe it will be found by any independent observer, carefully examining the subject, that the blastine arteries, even before the closure of the abdomen, from the first communicated with their hypogastric extensions into the iliac arteries near the coccyx, having the pedicle of the allantois in its envelope interposed; the caudal curvature of the sacro-coccygeal termination of the vertebral centro-chord occurred at the same time as the anterior cephalic flexure. The exit of the *ductus venosus* may have been slowly lowered by the

gradual closure of the ventral laminæ, and the development of the broad and long sternum of the bird, to nearly the same point, forming the upper margin of the umbilicus, by which it early issued into the *tunica media*. Some time may have elapsed before the lower wall of the abdomen from the pubis and the extension of the perinæum was required, by the development of the urinary bladder and the cloaca, before the upward bending of the sacro-coccygeal curvature was bent backward.

I have adduced sufficient structural and functional evidence against the usual and established doctrine of the circulation, trusting to unsound physiology, and based upon false anatomy, so far as the development of the ovum is concerned ; and when it is considered that the whole animals of the zoological scale, vertebral and invertebral, whether oviparous, ovoviviparous, as well as viviparous, result from the impregnated germ of an ovule. I might claim a decision in favour of this description of the course of the circulation in birds.

The great interest connected with this subject, both in a scientific and professional point of view, requires that the subject should be pursued through the development of the fœtus during pregnancy, with which I will now proceed.

On the Development of the Human Ovule.

Whether the description of Wagner be adopted as to the development of the vascular system, as in the *chick in ovo*, with all those changes so minutely described by him, and supposed to have been passed through by the human ovule, still the Graafian vesicle as its ovisac, enveloped in the chorion, villous externally, but smooth internally, like the egg-shell lining enclosing the vitellus or yolk, and the germ vesicle, with the same appendages as the chick, with the development of the heart and vascular system similarly established in as advanced a stage as it is in the chick by the fourth and fifth days of incubation, when it is ready to be projected from the Graafian vesicle by a *vis a tergo* into the oviduct or fimbriated extremity of the Fallopian tube ; or, prefer the simpler physiological view proposed by Rathke and

Reichert, according to the nucleated-cell theory of Schleiden and Schwann, as more applicable to the human ovule, in either of these views, the human ovule has the same elementary constituents as in birds and mammals, differing only in the minute size of the vitellus and germ vesicle. "The ripest ovule in the human ovary seldom measures more than from one-twentieth to one-fifteenth of a line in diameter, rarely exceeding one-tenth. This may account for the little that has been known of it before comparatively recent times." Van Bæer was the first who described the human ovule in his "Epistola de Ovi Mammalium et Hominis Genesi," (1827.) Probably Dé Graff, Prevost, and Dumas may have seen it previously. Van Bæer at first considered it like the germ vesicle of birds, mistaking the granular layer of the Graafian vesicle for the proliferous embryonic disc, and the stratum of yellow globules on the surface for the bird's yolk.

Purkinje, the discoverer of the germ vesicle, disputed Bæer's opinion, believing it to be analogous to the yolk and its contents, a conjecture equally unsound.

I will now proceed to describe shortly the prominent points in the development of the human ovule, taking the simple example of Aristotle ("Hist. Animal." iv. 3), describing the embryo of birds to consist of the following parts:—

1. The chorion, villous externally, but smooth within.

2. The germ vesicle, consisting of the germ membrane or amnion, firmly connected to the margin of the proligerous embryonic germ disc, the lower portion of the vesicle enclosing the embryo with its fluid.

3. The vitellus, or yolk.

Adopting the simple arrangement of the membranes composing the human ovule, when ejected from the Graafian vesicle by a *vis a tergo* through the walls of the ovary into the oviduct, when not larger than an orange pip, it is not easy to understand how the minute organised automaton moves about in its new situation, unless by the force of the pulsation of its vascular system within the branching villous tufts of the chorion, caused by their alternate protrusion and retraction giving force and motion, as it occurs in the ambulacral sucking feet of the asteriæ.

The smooth internal surface of the chorion, though permeated by the vascular tufts just referred to, encloses within it a gelatino-albuminous substance, "*tunica media*" (Bischoff), known as the white, or albumen. The germ vesicle is of an oval lenticular discoid shape, consisting of the embryonic germ disc and a transparent, thin, structureless, non-vascular germ membrane or amnion enclosing a fluid.

The embryonic germ disc may be supposed to split up, as in birds, into serous, vascular, and mucous layers.

1. Restricting, at present, the consideration to the serous and vascular layers, with their relations to the circulation, there may be noticed on the upper surface of the germ disc, within the amnion, an aggregate of dark nucleated cell granules lying on the *nota primitiva*, the prototype of the central spinal axis, above the *corda centralis* (incorrectly *dorsalis*), at one extremity a few nucleated cells forming the germ spot, the basis of the future embryonic head, from which the embryo gradually tapers to the other extremity.

The "*area pellucida*," as the extension of the *nota primitiva*, becomes more pyriform and bulging around the head of the embryo, at first surrounded by a similar pyriform dark fringe of minute vessels from the vascular layer, as in the chick in ovo, where the four lamellar tubercles contract the rudimentary *medulla oblongata* in the upper basilar region of the vertebral column. The anterior cerebral cells beyond it are enclosed in their special involucre—the arachnoid and *pia mater*—supported on the same plane with the termination of the embryo, upon the dense *dura mater*, previous to the sudden flexure of the procranium and costæ of the face chest. The greatly enlarged anterior crane of the embryo, still within the amnion, firmly attached to the edge of the lower *facio-mandibular* or oral cleft, or hard palate, is continued all round the margin of the vertebral laminæ, which extend outwardly from the spinal column before bending down to close in the parietes of the abdomen, as far as the umbilicus; the lower edge formed by the termination of the sacro-coccygeal curvature produced at the same time as the anterior cephalic flexure.

The cerebral cells consist—First, of the large hemispherical convolutions forming the pros-encephalon, resting upon the

floor of the ethmo-frontal platform. Secondly, the optic ganglia and thalami, with the tractus optici, which may be considered as the pillars of the proboscidean or anterior spinal marrow, with the commissure and optic nerve, abruptly giving off the retina to the eyeball in the orbital cavity beneath the ethmo-frontal platform, forming the roof of the orbital or first facio-mandibular cleft of the face chest, through which surrounding objects communicate impressions by the eye to the mind. The sides of this orbital cavity are furnished internally by the os planum and portions of the ethmoid; its outer wall is formed by the malar bone, which at the same time unites with the lower portion of the lachrymal and upper portion of the Highmor antrum to complete the floor of the orbit, leaving a tunnel beneath it for the infra-orbital nerve to be spread out upon the face.

2. The nasal cleft, the mandible including the Highmor antrum, forms the large mass of the *mandibular costæ* or segment of the face. The floor of the second mandibular or nasal cleft is formed by the hard palate, and enclosed laterally by the outer wall of the mandible, internally by the vomer, and roofed in by the floor of the Highmor antrum; this forms the passage communicating with the air-passages of the lungs, the pharynx, &c. &c.

3. The oral cleft, under the hard palate, forms the roof of the mouth and of the *fovea cardiaca*. The mouth is laterally completed, by the buccal parietes of the cheek, having the floor on the upper surface of the tongue resting upon the hyoid bone, which forms a lower part of the oral cleft.

4. The hyoid cleft is formed below the hyoid bone.

5. The thyroid cleft by the thyroid and cricoid cartilages.

These clefts have been incorrectly described as branchial clefts, and by Reichert as visceral clefts, with which they have no analogy.

The embryo, enclosed within the amnion and the serous layers, excludes the vascular and the mucous layers, and the different organs derived from them.

The heart, as already described in the chick in ovo, is a sacculated cone, even after the addition of the ventricle; it alone regulates the venous circulation, having no connection what-

ever with the arterial, except receiving a small branch for its nutrition. The arterial circulation, on the other hand, arising from the capillary area, oxidised within the villous tufts of the chorion, proceeds, as in fishes, to form the larger arterial circulation distributed through the body, till it again enters the capillary area to be reduced into venous blood, and thus completes the course of the circulation in the embryo from its first place in the Graafian vesicle, during its transit in the Fallopian tube, till it enters the uterus, and at length stranded on the decidual surface, and invested in the placenta prior to the inflation of the lungs. The active development of the heart, however, progresses by the gradual formation of a muscular septum, commencing where the *punctum saliens* acts, in the centre of the *auriculo ventriculo-septum*, growing at the same time from the roof and floor beneath the lining membrane of the ventricle towards the apex. Until the septum is completed, the blood flows freely between the ventricles and also from the auricles, which is instantly forced back into the auricle to be transmitted through the *ductus venosus*, the first part of the umbilical vein, still the only outlet from the heart. Even after the auricular septum has begun to be developed, dividing the auricle into right and left compartments, it is never completed till after birth, leaving the *foramen ovale*, through which the blood passes and repasses into the left ventricle, as freely as if no septum existed.

As development in the heart advances, each of the ventricles enlarge considerably, and, towards the close of pregnancy, begin to encroach over the fleshy base of the heart where the bulb is attached to, as Rathke has described, by extending the ventricles beyond the line of the auriculo-ventricular septum, separated by the ventricular septum. In this manner the anterior point of the right ventricle grows over the upper surface of the *truncus arteriosus*, preparing to form the first part of the root of the pulmonary artery inclining to the left side. On the internal surface of this projection the three semilunar valves project into this tube, carrying along with it the extension of the ventricular septum. A similar extension of the left ventricle, crossing towards the right under the projection of the right ventricle, is ready to burst into the lower

part of the *truncus arteriosus*. As soon as the lung-cells are inflated, the right ventricle bursts through the upper part of the bulb to form the pulmonary artery, which divides into right and left branches—the right dipping beneath the aorta, which had burst through the lower part of the bulb, carrying away the remains of the terminal branches of the primitive aortæ, and, rising over the right pulmonary, forms the arch of the aorta in its way to gain the descending aorta, from which the subclavian and carotid arteries continue to be sent to the head, upper trunk, and extremities as during the embryonic condition. A small part of one of the terminal aortic branches still adheres, called the *ductus arteriosus*, soon shrivelled up into a tendon connecting the arteries below the arch. These changes, however, are not completed till the lung-cells are inflated, after birth permitting the capillaries of the pulmonary artery, readily into the cell walls, no longer in a collapsed condition, allowing the venous blood to circulate and be oxidised through the membrane of the air-cells as it had previously been through the chorion villi, so that the capillary tubes between the pulmonary arterial branches, becoming the rootlets of the pulmonary veins, the blood, without rupture of the tubes or the intervention of any substance, is arterialised by the air-bath in the lung-cells through the membranous cell-walls, as it had previously been in the uterine placental sinuses, filled with pure maternal blood, in which the branching foetal tufts had been bathed and oxidised, fitted to continue the circulation.

From the lung-cells, in like manner, the oxidised or arterial blood is conveyed by four or more pulmonary veins into the left auricle, from whence it passes into the left ventricle, and sent by the aorta, now single, and its branches, throughout the whole system. As soon as these additional outlets from the ventricles allow the flow of blood to escape, the *ductus venosus* from the auricle becomes atrophied into the round ligament of the liver, which would prevent the flow of blood, as it does in mammals, even if proper obstetric caution did not in the case of a human child mechanically tie the umbilical cord, lest in some cases of twins the vascular connection of both were united. This shrivelling of the *ductus venosus* should indicate

the previous course of the blood before the arterial outlets were opened, and may be urged as an additional argument in favour of the views now submitted.

By the gradual enlargement of the uterus and its cavity, the automatic ovule moves about like a radiate animal till the end of the eighth week, when its chorion villi collect together at a particular part, and stretching out its villi like grapplings, is stranded on the decidual surface, giving the first impulse to the formation of the placenta by the close aggregation of most of the chorion villi, leaving the rest of it merely a thin transparent membrane. The branching villous tufts, grappling among the vesicles of the decidua vera, become soon involved with the material produced by the *decidua vera*, forming the bulkiest portion of the placental mass of a spongy vesicular substance having many large sinuses. These are lined by the inner vascular membrane connected with the maternal veins, into which the maternal curling capillary arteries pour their arterial blood. In these sinuses, thus formed and supplied, the branching foetal vascular tufts, enclosed in the villi, are freely bathed in the maternal blood, but without any vascular maternal connection.

The circulation of dark venous blood, brought by the *ductus venosus* from the venous heart of the foetus, enters the lower part of these branching tufts, and turning suddenly upon itself at their blunt terminations, returns down by the capillary rootlets of the arteries extending through the placenta, and at length ramifying in large vessels for some time on its surface beneath the placental membrane derived from the amnion, and covering, at the same time, the two umbilical arteries, which tortuously twining around the umbilical vein form the umbilical chord. These arteries enter the umbilicus as hypogastric, and are continued into the iliac arteries, sending a portion of its arterial blood downwards to nourish the lower trunk and extremities, but driving the main portion upwards by uniting into a single trunk above the promontory of the sacrum, forming the abdominal aorta, from which the following branches are given off, as has already been described in the circulation of the *chick in ovo*, but here repeated for clearness.

1. The mesocolic artery ramifies through the very vascular

envelope of the allantois, arising from the coccygeal body at the end of the coccyx, and not, as usually described, from the termination of the rectum, then a shut sac; the narrow pedicle of the allantois and its envelope, passing through the umbilicus into a large bladder formed of a thin, transparent, structureless, non-vascular membrane, expanding within the *tunica media* so considerably as to cover a large portion of the embryo in its amnion. This vascular envelope may be required in the early stages of development to afford an extended arterial circulation, while the embryo is merely an appendage of the heart, before it is either a breathing, digesting, or excreting animal, and before the development of these organs from the mucous layer. The capillaries of the mesocolic artery carry their blood to the mesocolic veins, forming the first tributary to the portal system.

2. The mesenteric artery ramifies over the umbilical vesicle derived from the mucous layer of the germ disc, and extending a narrow pedicle onward to the *tunica media*, affording a very vascular envelope around the yolk, contained in its own thin, transparent, structureless, non-vascular, vitelline membrane, covered by the layer of large yellow globules derived from its centre, which Professor Robin describes as the inner or intermediate lining of the umbilical vesicle. This vesicle also expands greatly in the *tunica media*, till the digestive tube begins to be developed from the upper part of the mucous layer, depending from the lower external base of the meta-cranium or postcrane, and lining the nasal and oral passages; the pharynx is continued into the œsophagus, and, as it enters the abdomen through the diaphragm, swells out into the cardia of the stomach, in the left hypochondria, close to the spleen. From this the large curvature, crossing the fore part, terminates at the pylorus in the duodenum, completing the anterior part of the gastric convolution, and then dives into the epigastrium, on the right side of the spine, and completes the backward turn of this convolution by crossing the spine behind the pancreas to the commencement of the jejunum in the left iliac fossa. From this place the jejunum rises over the fore part of the abdomen toward the umbilicus, through which, at a later period, the yolk is drawn along with the pedicle

of the umbilical vesicle; thence descending into the right iliac fossa on the right of the spine, which it crosses posteriorly to complete the jejunal convolution in the left iliac fossa. Here the ileum begins the last convolution of the small intestines, by again crossing the fore part of the abdomen to the right iliac fossa, where it enters the colon behind the caput cæcum coli, and its appendix vermiformis, protected by a valve preventing regurgitation into the small intestines. This may be considered like the termination of the digestive tube in the case of the echinidæ, where the central tube of the lantern of Aristotle is continued by the œsophagus into the digestive tube considerably enlarged, and continued twice round the visceral cavity without any demarcation, showing the different divisions of stomach or intestines, ending in the cæcal extremity at the anal orifice in the centre of the upper surface of the echinus.

In the human foetus, however, it is continued into the colon. The *appendix vermiformis* may be considered as the remnant of the pedicle of the vascular envelope of the allantois, and the long tubular cæcum in all mammals below the quadrumana; the colonial convolution from the right iliac fossa, descending behind the lower abdominal wall in its course across to the left iliac fossa, where it terminates by the sigmoid flexure into the rectum opening into the abdomen.

After the intestines have been completed, the mesenteric artery, which had formerly circulated through the very vascular umbilical vesicle, now supplies the mesentery, and terminating in the capillary rootlets of the mesenteric vein, which forms the second tributary to the portal circulation, along with the mesocolic, splenic, and other veins from the cæliac axis completing the sinus portarum.

The abdominal aorta, as it continues its upward course, passing between the pillars of the diaphragm, gives off the phrenic arteries for its nutrition, and then entering the thorax in the mediastinum behind the pleura, divides, as in birds, into double trunks, one on each side of the spine, till they arrive at the *fovea cardiaca*, or faucial den below the very bent procrane and face chest of the foetus. From this point they each divide into two right and left terminal branches, which proceed forwards to form the truncus arteriosus, or aortic

bulb attached to the base of the heart, here projected further than in birds towards the diaphragm. By the formation of the bulb, the distribution of the subclavian and carotid arteries derived from it, together with the course of the venous blood in the superior venæ cavæ, having been already very fully described, scarcely requires to be repeated here. It may be necessary to take a short *resumé* of the form and contents of the fœtal heart, which, previous to the inflation of the lungs by respiration, is entirely connected with the distribution of venous blood from its four sources, whether a single or a fourfold cavity, with only one outlet, the *ductus venosus*, really the first portion of the umbilical vein carrying the whole venous blood, after the placenta is formed, to be purified there, and returned by the umbilical arteries as already fully described. This, though directly contrary to the usually received and established doctrine, is simpler and more rational, being consistent with correct anatomy and the general laws of physiology, in the course emanating from the fœtus to be oxidised in the placenta, and returned by the umbilical arteries to the arterial system, which distributes it to the different organs throughout the fœtus, from capillaries to trunks, as in fishes.

A more detailed account of the objections to the received opinions will be found in a following chapter.

The venous blood, coming from four sources, and collected in the right auricle, is now sent into the right ventricle, its return being prevented by the tricuspid valves around the auriculo-ventricular orifice being loosened, as it were, by the elongation of the columnæ carniæ, allowing the valves to completely check the return of blood to the auricle, while the larger tricuspid valve allows the current to pass behind it, through the semilunar valves by the pulmonary artery, onward through the membranous walls of the long cells by means of the capillaries as just described.

The Four Venous Sources.

1. The azygeal veins, arising from the sinuses of the corda centralis, in or upon which the centres or bodies of the vertebral segments are formed.

2. The subclavian and jugular, returning the venous blood from the head, the upper trunk, and extremities, to form the superior venæ cavæ, which pour their blood into the right auricle.

3. The blood from the lower trunk and extremities, and several of the viscera of the abdomen, and form the vena cava inferior, in its ascent to the heart.

4. The blood returning from the mesocolon, mesentery, and spleen, unite to form the portal system in the longitudinal fissure of the liver, which, after circulating by the portal veins, through the different lobes of the liver, is at length conveyed by the three hepatic veins, entering near the termination of the inferior vena cava before it enters the right auricle.

5. To these may be added the venous circulation in the fœtus through the ductus venosus and placenta.

After this long digression on the changes which occur in the circulation just previous to birth, I think it necessary to return to the early condition of the human ovule.

The heart and embryonic circulation, sufficiently completed in the Graafian vesicle to permit its moving by its own power, as soon as it is ejected from the Graafian vesicle through the walls of the ovary, at the *corpus luteum*, into the expanded Fallopian fimbriæ, moving in its onward journey down the oviduct. If, however, it should elude the grasp of the fimbriæ, and escape into the abdomen, it there also, by its own automatic power, attaches itself to some part of the abdominal surface, and, like a parasitic worm, is developed without any vascular connection with the maternal circulation. In this abnormal position it is occasionally as far developed as a fœtus of the same age in the uterus, as particularly shown in a case of extra uterine gestation, described by Dr Branxton Hicks in the "Lancet," where a fœtus was discovered lying immediately behind the walls of the vagina so distinctly, that after cautious examination it was decided to remove it by an incision through its walls, and thus relieve the mother from her painful and dangerous situation. The operation, however, was unsuccessful, but the advanced condition of the fœtus was fully made out.

Many other cases of extra uterine gestation might here be adduced, to show the automatic power of the ovule with the

circulation established within the chorion, enabling it to move about, and at the same time controvert the idea, that the chorion is only added during its progress down the Fallopian tube. It is curious that, in these cases of extra uterine gestation, the effusion of *decidua vera*, preparing the uterus for the reception of the ovule, is generally spread out over the uterine surface. Dr Robert Lee has recorded one exception.

In the normal course of development the ovule moves down the Fallopian tube, possibly aided by its ciliæ, till it reaches the uterus, generally about the end of the second week after impregnation.

Dr Churchill remarks, "that it is difficult to determine the precise period at which the ovule arrives at the uterus, as several days may elapse from the moment of conception. One of the earliest ovules is recorded by Velpeau, which could not have been more than fourteen days old, given to him by a midwife who was herself the subject of the miscarriage." Dr Allen Thompson and others have given notices of still earlier ovules. Wharton Jones, also, in the "Philosophical Transactions," 1837, has given descriptions of several early ovules. Wagner remarks that little confidence can be safely reposed in the description of the very early embryos.

The size of the human ovule, ready to enter the uterus, is a little less than two-fifths of an inch in diameter, as figured by Velpeau in the case above referred to, with all its villi extended, as it enters the lateral horn of the uterus about the end of the second week after conception, by which time the whole internal surface of the uterus is covered by the *decidua vera*. The ovule is usually described as pushing before it the portion of the *decidua vera* covering the orifice of the Fallopian tube, which continues to be expanded over it as the *decidua reflexa*, growing with its growth as development proceeds; at least such is the representation of Hunter and all the great authorities on the subject.

I am inclined to doubt the whole of this diagrammatic representation of the *decidua reflexa*, and if any such special membrane really exists, it must have been brought with the ovule in its passage down the Fallopian tube, which may have suggested the idea of its being entirely formed there, covering it

as it enters the uterus, and may, in fact, be merely a part of the chorion villi not required to form the placenta.

The difficulty of detailing the different steps of development occurring in the successive stages of the *chick in ovo* is greatly increased in the case of the foetus, and can only be safely attempted in a very general way with these organs, more completely dependent and connected with the heart and the vascular circulation.

After the commencement of the second month the growth of the human embryo becomes extremely rapid and very considerable. The amnion, like a capacious bladder, investing its whole surface from mandibular cleft along the margin of the ventral laminae as far as the umbilicus, entirely excluding from the serous amniotic cavity the vascular and mucous layers and the organs developed from them. Through the umbilicus the different organs pass in the following order from above:—

1. The *ductus venosus*, the first portion of the umbilical vein, passes from the heart to the placenta, conveying only venous blood.

2. The pedicle of the umbilical vesicle extended into the *tunica media* covering the yolk.

3. The two umbilical arteries arising in the placenta enter through the umbilicus, and are continued by the hypogastrics as their termination into the iliacs, thus communicating with the arterial system of the foetus.

4. Lastly, There emerges below the arteries the pedicle of the allantois, with its vascular envelope from the mesocolic artery. The expansion of the allantois, becoming atrophied within the lower anterior wall of the abdomen, behind the urinary bladder, is shrivelled up as the urachus.

During the fifth or sixth week the heart is greatly enlarged, and turned more to the left side of the chest. It is enclosed in its pericardium, but excluded from the cavity; is lying on the surface of the diaphragm, in the anterior mediastinum. The lungs in their pleura lie on either side of the heart, also resting on the diaphragm, but separately contained in their own serous envelope, but really excluded from the cavity of the pleura; in this manner they, as it were, form both the anterior mediastinum containing the heart, and the posterior

mediastinum, allowing the descending aorta and œsophagus to be conducted along the spine. The relation of the heart and the terminal branches of the aorta has been figured by Wagner in a foetus of the fifth week, when laid open from the abdominal aspect, with the aortic bulb rising behind and giving off the subclavian and carotid arteries. He has also given a back view of the heart and blood-vessels from the same foetus, showing their passing upwards quite distinct from the heart, and in this position continuing the course of the subclavian and carotid arteries from below upwards, as it occurs in the adult. The same illustration shows the early condition of the lungs, as two sacculi at the lower end of the trachea without any connection with the circulating system,—mere sacs about a line in length, with traces of vesicular division, and hanging by the rudimentary trachea, a mere thread, showing superiorly a slight enlargement—the future larynx. The liver is very large, consisting of two lobes full of small hollow granules or cæca. Under the left lobe the stomach appears as an elongated tube, crossing transversely in a very curved form to the right side, from which the intestine is continued in a long and somewhat twisted loop towards the umbilicus, as has already been more fully detailed. The Wolffian bodies are situated along the vertebral column. The kidneys and supra-renal capsules only make their appearance in the course of the seventh week, succeeded by the evolution of sexual organs as long slender bodies. The urinary bladder, about the end of the second month, appears as a mesial enlargement continued upward as a hollow canal, connected with the pedicle of the allantois, shrivelled into the urachus from the umbilicus. At this period the embryo is about nine lines in length, its large head now fairly rounded off; the corpora quadrigemina become relatively subordinate both in place and size under the cerebral convolutions; the eyelids may be traced in a circular form over the eyeballs, becoming subsequently more oval. In the ear, considerable advance has been made in the development of the various parts of this important organ. The mouth is a large triangular space cleft upwards, and communicating with the nasal cavity; hence the occurrence of cleft palate, so frequently met with in children, truly

depending on the bilateral type of the human being, each half contributing its share in forming the mouth, which extends laterally nearly the whole breadth of the face. The nostrils are mere depressions or pits, one on each side of the nasal septum formed by the nasal cartilage continuous with the vomer; the external nose is partially indicated by the rudiments of the bridge of the nose.

The abdomen appears distended, having very thin parietes; the upper extremities show the rudiments of five fingers, and the division into arm and fore-arm; the lower extremity, though less developed, still the division between thigh and leg is marked, and even the toes are slightly indicated.

All these particulars now detailed become more distinct after the eighth week; the head larger; the lips begin to be formed; the tongue merely budding at the bottom of the mouth; the fingers and toes more distinctly pinched off from the rest of the hands and feet. The embryo is from ten to twelve lines in length, weighing more than a drachm; the umbilical vesicle enclosing the coil of the intestine and yolk is completely retracted within the cavity of the abdomen, reducing the size of the umbilicus.

These particulars are principally abstracted from Wagner's "Elements of Physiology," who has given several figures of embryos of the fifth, sixth, and seventh weeks.

By the beginning of the third month, the principal changes referred to are increased size. It is generally at this time, about the tenth week, as already noticed, that the placenta begins to be formed, which is not completed till the end of the twelfth week, so that till the ovule was stranded on the decidual surface of the uterus it cannot be in any way connected with the mother, existing solely on its own resources from the heart and vascular system, under the influence of the membranous chorion which entirely envelopes it. Nor should this be considered at all wonderful or inexplicable, when we keep in mind that not less than from ninety to ninety-five per cent. of the animal organic world are oviparous, entirely detached from any possible communication with their parent. After the placenta has been formed, through the membranous villi of the chorion after they have branched out into tufts and

been surrounded with the spongy mass from the uterine portion, the whole oxidation is as completely drawn from the chorion villi as it is in the chick in ovo under the influence of the shell lining. Forty weeks being the general term of pregnancy, the first eight weeks during which the ovule has passed a complete independent roving life being one-fifth of its period of foetal existence, and it is nearly a fourth of the same period before it is in any way connected with the uterus.

The chief organs which now become visible, though probably evolved from a rudimentary condition during the second month, are the thymus and spleen, neither of which is well understood—the internal parts of the ear, and small bones. During the third and fourth months there is a progressive increase of the different organs, exhibiting a nearer approximation to a greater perfection of the forms peculiar to foetal state, as well as those more permanent after birth. The *membrana pupilaris*, the gluing together of the eyelids, and their complete coalescence, occurs at the beginning of the fourth month; the rapid growth of the supra-renal capsules, by the middle of the third month are twice the size of the imperfectly-formed kidneys, a mere aggregation of three or four little lobules, immediately diminish like other temporary foetal organs, particularly the Wolffian bodies, which shrink greatly, and finally disappear entirely by the end of the fourth month, although some traces may continue to exist in the female till after birth. While this tendency to decrease and disappear among the temporary organs, an increased activity of formative energy is exerted among the permanent structures; the extremely small kidneys at the end of the third month consisting of seven or eight lobules—the future pyramids of Malpighii; the ureters still terminate in the common external duct with the sexual organs and Wolffian bodies, and the rectum in the cloaca at first detached, then opening into the anus. The most remarkable of the transformations occur in the genitals.

The heart, by the tenth week, exhibits by sulci externally a division between the auricles. The *septum ventriculorum* is nearly complete, and externally showing a distinct sulcus towards the apex. The Eustachian valve is very large. The elevation of the head, by the elongation of the cervical verte-

bræ, is distinctly marked from the upper trunk. The abdomen is enlarged, and the pelvic region extended, as shown by the increased distance between the umbilicus and the perinæum—the umbilical opening being considerably reduced in width. The embryo, in the course of the third month, is $2\frac{1}{2}$ inches long, and weighs 1 ounce; its head large and globular. In the fourth month the embryo grows very rapidly, measuring at least 4 inches, and weighing about 5 ounces. By the middle or end of the fifth month, when half of its fœtal life is spent, it is nearly 12 inches long; when the epidermis is developed, the nails on the fingers and toes becoming more horny and consistent. The body covered with a sort of down, the hair at the same time sprouting on the head.

The first motions of the fœtus are usually perceived by the beginning of the sixth month, though the mother may have felt slight flutterings earlier. The child born before this is capable of breathing (?). The head becomes very large, forming nearly a quarter of the whole fœtus. The face, with the wrinkled appearance of an old man, is soon modified by an increased deposition of fat, making the body plump. Very considerable changes occur in the sexual organs.

During the seventh month the length of the fœtus becomes 16 inches, weighing about 2 lbs., at which time it is perfectly capable of maintaining an independent existence; and if born, may be reared. The skin is red, and in addition to the hair and down, the body is coated with a thick clumsy matter. The membrana pupillaris disappears, and the eyelids are no longer sealed. During the ninth month the ossification of the cranium increases, closing upon the fontanelles. The hair of the head becomes more abundant, the downy covering of the body falling off. The embryo is 18 inches long, and weighs from 5 to 6 lbs. During the tenth month both size and weight vary greatly in different cases, measuring from 18 to 20 inches, and weighing from 7 to 10 lbs.

The regular period of pregnancy terminates in the human female at the end of the fortieth week, or tenth lunar month after conception, most probably influenced by the progress in the development of the different organs, but especially of the heart and the larger blood-vessels connected with it, as has

been fully detailed when considering the necessary alteration preparatory to the change in the course of the blood, after the lung cells have been expanded by the first whiff of inspiration. The gradual growth during the latter month of pregnancy, especially the last, of the ventricles advancing over the *truncus arteriosus*, and finally enveloping it, by the part of the base of the heart to which it had been attached becoming thinned out, to be merely a valve somewhat prematurely, so that by some sudden check to the maternal system, such as a stumble or a fall, and even sometimes by a panic, the valves of the ventricles are burst, cutting off the terminal branches of the ascending foetal aortæ and their arterial blood. The ventricles can only discharge the venous blood with which they are then filled. The circulation is there checked from the collapsed condition of the lung-cells. In this manner the frequent still-births during the last month may perhaps be accounted for. If, however, the check alluded to has roused the foetus to stimulate uterine action, the premature delivery may secure the necessary inflation of the lungs, by which the new-born infant may be saved in time, though perhaps with some difficulty, by the usual means adopted by accoucheurs.

The usually described course of the Foetal Circulation.

From the days of Galen, and perhaps earlier, when neither anatomy nor experimental physiology were much practised nor well understood,—

1. The course of the circulation was described as starting from the placenta, where the blood had been oxidised and transmitted to the heart of the foetus by the umbilical vein, which immediately after entering the abdomen divides into several branches, two or three going directly to the left lobe of the liver, carrying arterial blood, a single branch communicates with the portal vein in the transverse fissure.

2. It then continues as the ductus venosus, which passes directly backward, and joins the inferior cava, where its pure oxidised blood mingles with the reduced venous blood returning from the lower extremities.

3. The blood thus mingled is carried through the right

auricle guided by the Eustachian valve through the foramen ovale, into the left auricle, onward into the left ventricle, into the arch of the aorta, from which it is distributed through the carotid and subclavian arteries, principally to the head and upper extremities, returning reduced by the jugular and subclavian veins, forming the *venæ cavæ*, which pour their blood into the right auricle.

4. From the right auricle the blood is propelled into the right ventricle, which, by the pulmonary artery, sends only a small portion into the lungs; the greater part rushes through the ductus arteriosus, where it is mingled with that portion of the pure blood not transmitted by the carotid and subclavian arteries.

5. Descending along the aorta, a small quantity of this mixed blood is distributed by the external iliac arteries to the lower extremities.

6. The greater portion being conveyed by the internal hypogastric arteries proceeding upwards by the fundus of the bladder within the anterior abdominal wall to the umbilicus, through which they pass, becoming the umbilical arteries, carrying the venous or reduced blood to be oxidised and returned from the placenta, as already mentioned, by the umbilical vein, thus completing one course of the circulation, which continues to be repeated during the whole course of foetal existence. So fanciful a theory could only have been received in the dark ages of anatomical and physiological research, before the practical examination of the foetus had been adopted, as the whole description seems to have been derived from a vague and confused idea drawn from the structure of the heart in the adult.

It is surprising how the great anatomists of the sixteenth and seventeenth centuries could have adopted so crude a theory, as many of them were well acquainted with the development of the *chick in ovo*. Fabricius ab Aquapendente, published a large folio on the development of the *chick in ovo*, fully illustrated by large wood engravings—coarse, indeed, when compared with those of the Dalzells, but perhaps equally truthful, when it is recollected that not less than 90 per cent., and perhaps more, of all animals living, or which have lived, are oviparous and fully developed, without any possible maternal connection; and that even the

ovoviviparous marsupials, though developed, and so far born within the parent, have no maternal connection, "but sent into this breathing world scarce half made up, and that so imperfectly and unfashionably," that they require to be transferred to the marsupial pouch, and there firmly fixed to the mammal teats by means not well known, before they are fitted for a separate existence.

The following objections may now be taken :—

1. The anatomy describing the course of the blood in the umbilical vein, in going through the umbilicus and giving off branches to the liver, is incorrect, as there is no such distribution, and it would be unnecessary to send the oxidised blood beyond what it requires for its growth and nutrition, which it derives from another source; besides, the function of this organ is to act upon reduced or venous blood as a diverticulum sanguinis for the separation of the bile.

2. There is no single branch sent to the portal vein from the *ductus venosus*.

3. The whole anatomy of the heart is erroneous, there being nothing at first but a single cavity; and even when the ventricle is added, some weeks must elapse before any septum is developed, dividing the ventricles into right and left cavities; and for some weeks later none of these structures exist, while the circulation from the heart and blood-vessels has been fully established. From the first, the *ductus venosus* is the only outlet from the heart, which is the only muscular organ connected with the vascular system, and might reasonably have been supposed to give the first impulse to the circulation of its contents, and in a course directly opposed to the one now objected to, which had no muscular organ to aid its course capable of stemming the current from the heart. At the early stage of development neither the pulmonary artery nor aorta exist connected with the heart till towards the close of pregnancy, during the last month, permitting the current of the blood through them in the usually described course.

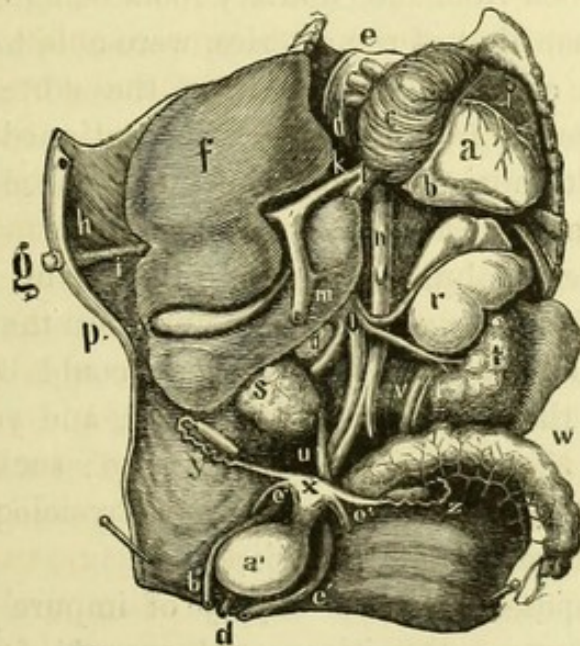
It is subversive of all reasonable physiological inference to fancy that blood oxidised in the placenta should be sent by the umbilical vein and blended with the impure reduced venous blood brought by the inferior cava, and sent through

the cavity of the heart filled with venous blood from the superior cava without mixing with it, in spite of the contraction of the heart (by what force God only knows), through the foramen ovale in the auricular septum before it is developed into the left auricle and ventricle which has no aortic outlet. It is absurd to suppose that the impure, reduced venous blood could be sent only so far along the arch of the aorta as to turn up by the aortic bulb through the carotid and subclavian arteries, to be circulated in the head and upper extremities, and again returned by the jugular and subclavian veins forming the superior venæ cavæ, pouring their blood without jumbling with the blood brought from the placenta and inferior cava, but passing directly into the right pulmonary artery, and by the supposed ductus arteriosus issuing by the pulmonary artery, not yet developed into the descending aorta, at a point where, in the railway language of the day, there are neither switches nor valvular obstruction to direct its downward course, carrying the most reduced venous blood down the aorta, supplying in its descent the visceral organs and its lower extremity with blood of the most impure quality, previous to returning by the umbilical arteries to be oxidised and again circulated. Such a view is physiologically absurd, as the general laws regulating the circulation—the communication between veins and arteries and between arteries and veins—is solely through the capillary area in which the oxidation occurs, while the blood is contained in a bent but continuous tube without any rupture on the interposition of any tissue. How this is accomplished is not well understood; though it was lately proposed by Professor Conheim that there is something like an endosmose and exosmose, by which the blood parts with a portion of its contents, receiving in its turn the oxidising elements. The arteries gradually ramify into smaller and smaller arteries, pouring their blood into the capillary area, from which the minute rootlets and sinuses of the venous system gradually unite into larger and larger veins, much more numerous than the arteries carrying the blood back to the auricle, from which in the fœtus it is again sent by its systole, first into the ventricle, and immediately returned by the ductus venosus and umbilical vein.

Prior to the expansion of the lungs by respiration, there is no

communication between the arteries and the cavities of the heart, whether a single or quadruple cavity. The systole of the auricle forcing the blood into the ventricle, which immediately contracts with its whole force, tilting up the apex, and giving the pulse-beat, when felt in the cord, in cases of prolapsus, or during turning, of from 60° to 70° per minute, while stethoscopically examined through the maternal abdomen it often ranges as high as from 120° to 150° . May not the above explain how the difference occurs, in the frequency and strength of the pulse-beat depending on the tilting on the apex of the heart, as in the adult only felt singly, and the cord in the umbilical vein, in which the whole blood is sent from the heart, prior to respiration, by the contraction of the auricles not being impressed on the cord.

Valentine, in his "Elements of Physiology," describes and figures in the annexed woodcut, drawn from an eighth month foetus, illustrating a special relict of foetal life. After a certain



period of embryonal life, the umbilical vein (*g i*, fig. 400), which returns the renovated blood from the foetal placenta, sends branches to the liver (*f*). Besides this, it unites with the portal vein (*m*), which also ramifies in this gland. And it has also a certain communication with the inferior vena cava (*l*), by means of a vessel—the venous duct of Arantius (*k*)—which passes between the two. Hence part of the purified

blood which is returning from the foetal placenta can avoid the liver, and flow (through *k* and *l*) immediately into the auricle (*c*).

After giving the usual theoretical view now being objected to, he describes also a certain communication with the inferior vena cava by means of the venous duct of Arantius between the umbilical vein and the auricle, showing how the purified blood returning from the placenta can avoid the liver, and flow directly into the auricle. Had this distinguished physiologist and his erudite translator not been blinded by the old obstinate prejudices of three centuries, he might have seen that the current in this lower communication, impelled by the whole active force of the heart, could more easily send its current outwardly through the umbilical vein to the placenta, than receive a current from that organ, which has no mechanical muscular organ connected with it. He would then have seen that the old hypothesis was entirely erroneous, and that the circulation of the pure blood from the capillary roots being of greater collective area than that of the arteries, were able to promote the course of the circulation upwards in the aorta towards the *truncus arteriosus*, from whence it is continued to the head and upper extremities, as more fully described in a former part of the communication.

Professor Cassebohn, in a thesis collected by Haller in the volume, 5 *Disput. Anat.*, clearly points out that, during the collapsed condition of the lungs, there could be no circulation through the walls of the lung-cells, and yet adopts the hypothesis of the old established prejudice; such is the difficulty of even our most distinguished physiologists escaping the incubus of established prejudices.

It was supposed that the supply of impure blood to the viscera and lower extremities could account for their being dwarfed; but the same effect would have been produced upon the whole foetus, retarding its growth. It is more reasonable to suppose that the quantity of oxidised blood, being supplied more largely to the head and upper extremities, where the important cerebral and amniotic neural centres are primarily developed, that these regions grew more rapidly, but in the progress of development a greater share would be accorded to

the viscera and lower extremities as their necessities required. This appears to me a more rational way of accounting for the disparity of the head of the foetus and its lower extremities.

If these reasons are admitted, and the grounds I have described for the views propounded in the former part of the communication are correct, I may be allowed to maintain—

1. That the hypothesis of the course of the foetal circulation, described during the last three centuries, and still obstinately maintained by the most distinguished anatomists, physiologists, and obstetricians, is inconsistent with correct anatomy, sound physiology, and the general laws of hydraulics.

2. That the theory now proposed, supported by the researches of anatomists, physiologists, and embryologists, is more rational and consistent with anatomy and physiology.

3. That it affords the true key to the whole foetal circulation, by the entire separation of the arteries from the cavities of the heart, whether consisting of one or four divisions, which are entirely and solely filled with venous blood.

4. This theory cannot be viewed as at all to be compared with the great Harveian discovery, but in the correction of a long prevalent error, it has the merit of at least capping and culminating it, on the principles of the immortal Harvey, who had overlooked it as completing his own. I feel convinced that till it is adopted there is little chance of any correct view of the foetal circulation being entertained.

Having been challenged by more than one eminent physiologist to adduce evidence experimentally in disproof of this old theory, which never was established on practical experiment or demonstration, nor during the three centuries of its predominance, I hold that it is with the supporters of that theory that the *onus probandi* and *experimentaliter demonstrandi* first lies, and I throw down the gauntlet to any one of the eminent anatomists, physiologists, or embryologists in the numerous medical schools of the vast metropolis or elsewhere, to adduce a single fact resting either on direct observation or experiment, showing the course of the blood from the placenta by the umbilical vein to the heart of the foetus; or that the venous blood returns by the aorta and umbilical arteries in the cord to the placenta for oxidation. Till this is done, I feel no

necessity to adduce any other than theoretical inference on the general physical and organic laws against the foetal circulation, now shown to have been based on false anatomy, and quite inconsistent with the known physiological laws regulating the course of the blood from veins to arteries and from arteries to veins, can only occur in the capillaries, and that it is also inconsistent with the physical laws of hydraulics.

EXPLANATION OF PLATES.

PLATE I.

- Fig. 1. *a.* Area pellucida. *b.* Dorsal laminæ receding to bound the cerebral cells, and the continuation of the spinal marrow and dura mater. *c.* The lamellar tubercles of the vertebral arches. *d.* The cerebral cells—1. the anterior; 2. the optic; 3. medulla. *e.* Anterior fold of the involurum. *cf.* Centro-chord.
- Fig. 2. *a.* Cono-succulate heart. *b.* The dorsal laminæ. *c.* The square plates becoming lamellar tubercles. *d.* Ductus venosus the efferent outlet from the heart. *ef.* The inferent veins leading to the heart.
- Fig. 3. *a.* Involucrum capitis within the amnion. *b.* Involucrum caudæ. *d.* Vault of the cranium, containing the cerebral cells. *e.* The anterior pros-encephalon. *g.* The veins connect with the heart. *h.* The succulate heart—1, 2, 3, 4. The facio-mandibular clefts. *k.* The dorsal laminæ. *l.* The lamellar tubercles.
- Fig. 4. *a.* Head of embryo. *e.* The eyeball. *b.* The spinal column—1, 2, 3. The facio-mandibular clefts. *c.* The curve of the coccyx. *f.* Rete-venosum. *g.* The chorion.
- Fig. 5. *a.* The chorion. *b.* The embryo. *c.* The amnion. *i.* The orbital cleft. *ii.* The nasal cleft. *iii.* The oral cleft. *g.* The eye. *h.* The hemispherical convolutions. *i.* Optic ganglia. *o.* Cerebellum and medulla oblongata. *m.* Mucous layer. *n.* Pedicle. *o.* Umbilical vesicle. *p.* Allantois. *a.* Cerebral cells. 1, 2, 3, 4, 5. The facio-mandibular clefts.
- Fig. 6. *B.* The amnion. *b.* The fluid cavity. *c.* The allantoid. *d.* Its pedicle. *e.* Pedicle; and *f.* Umbilical vesicle. *g.* Anterior; and *h.* Posterior extremities.
- Fig. 7. *a.* The veins connected with—*b.* The heart; *c.* The aortic bulb.

PLATE II.

- Fig. 1. Ideal section of the incubating egg, from Wagner—1. The egg-shell and chorion. 2. The germ vesicle. 3. Chorda centralis. 4. Vitellus or yolk. 5. Vitelline membrane. 6. The air-chamber. 7. Albumen or *tunica media*. 8. Its membrane. 10.
- Fig. 2. The same enlarged. 1. Tunica media within chorion. 2. The amnion. 3. The embryo, on the serous layer. 4. The mucous layer. 5. The yolk. 6. The umbilical vesicle. 7. The rete venosum. 8. The allantois in its vascular envelope. 9. The primitive heart.
- Fig. 3. Ideal section of the placental sinuses and vascular tufts—Reid.

Fig. 4. Ideal section of one of the tufts in a sinus lined with the inner membrane of the maternal vessels, and filled with arterial blood, also from Reid. 1. Maternal curling artery. 2. Returning vein. 3. Wall of the sinus cell. 4 and 5. Villous tufts.

Fig. 5. A single tuft. 1, 3. The arterial branches returning by 4. 2. The venous entering by 5.

Fig. 6. A single branchlet. 1. The entering vein. 3, 4. Returning.

Fig. 7. Anterior views of the relation between the heart and aortic bulb. A. Anterior. 1. The bulb. 2. The terminal arteries. 3, 6. The auricle. 4. The auriculo-ventricular orifice. 5. The commencement of the ventricular septum. 7.

Fig. 8. B. 1. Posterior view. 1. The laryngeal portion of the trachea. 2. The rudimentary lungs. 3. The point of the ventricle. 4. The large auricle. 8, 10. The pneumogastric nerve. 9. The aortic arches. 7. The terminal branches forming the bulb, and the arteries continued from it.

PLATE III.

Fig. 1. 1, 2, 3, 4, 5. The 5 facio-mandibular clefts. 5, 6. The auricle and ventricle. 7. The umbilical vein carrying venous blood to the placenta. 8. The vena cava; receiving 9, the portal system before entering the heart, from which 7, the ductus venosus conveys it to the placenta, in the direction of the arrows. This will be best understood along with Plate IV. on the opposite side of page and view transparent.

PLATE IV.

Fig. 1. 1. The placenta. 2. The tortuous umbilical arteries forming the cord around the umbilical vein. 3. The hypogastric arteries. 4. The iliacs, by their union forming 7, the ascending single abdominal aorta, giving off 5, mesocolic artery. 6. Mesenteric artery. 8. The double thoracic artery. 9. The terminal branches, forming 10, the *truncus arteriosus*. 11. The subclavian. 12. The carotid.

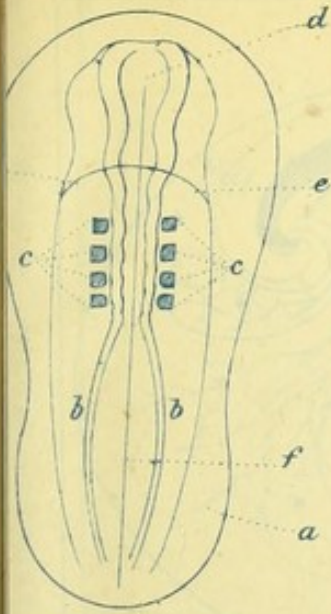


Fig. 1.



Fig. 2.

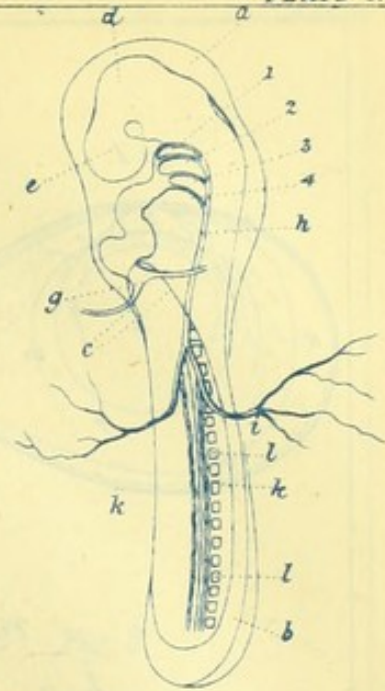


Fig. 3.



Fig. 4.

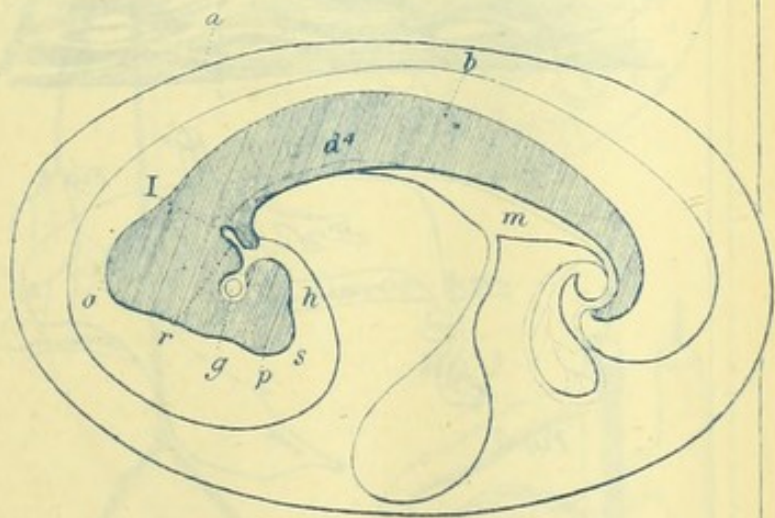


Fig. 5.

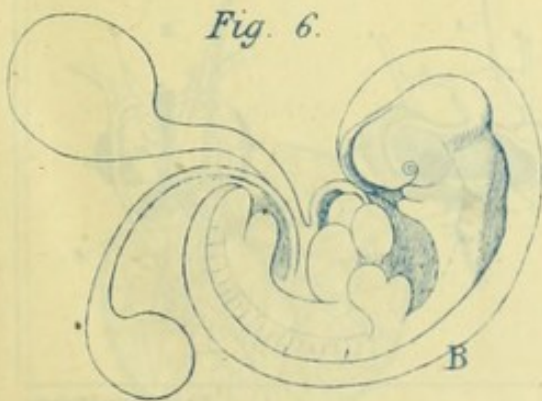


Fig. 6.

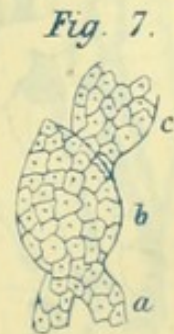


Fig. 7.

Fig. 1.

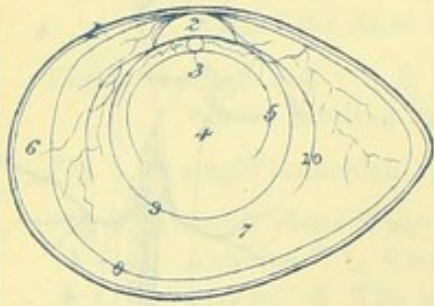


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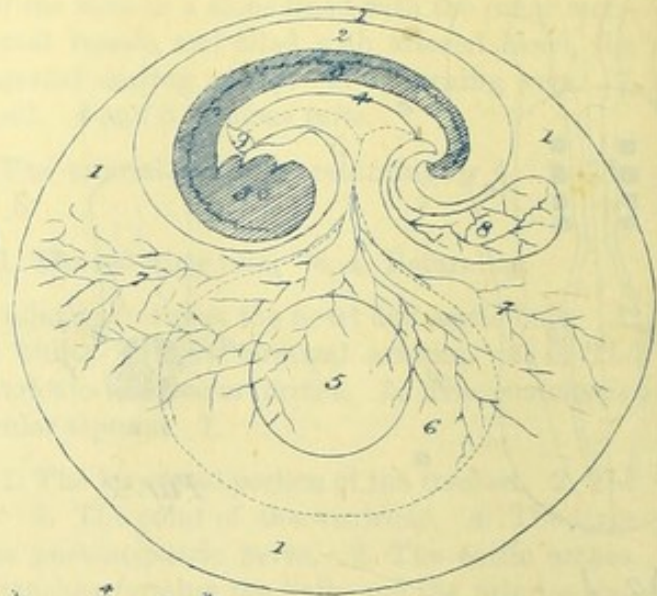


Fig. 3.

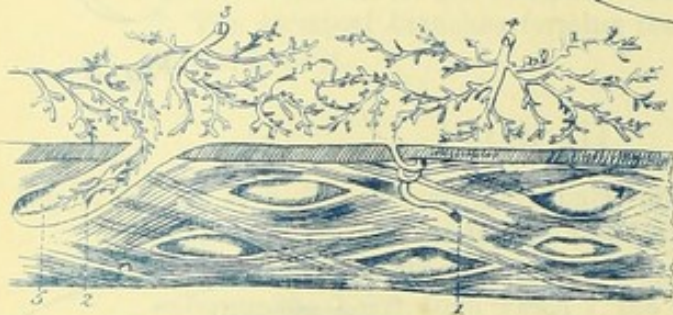


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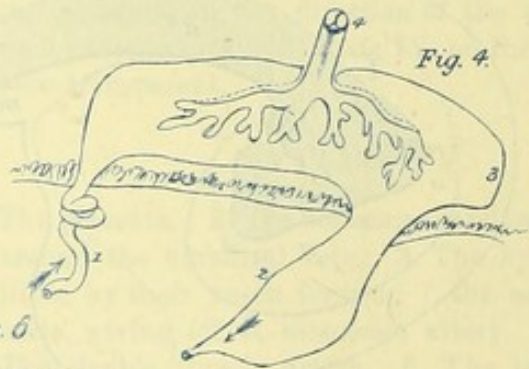


Fig. 5.



Fig. 6.

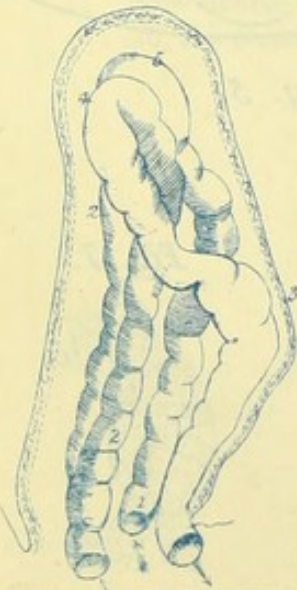


Fig. 7-8.

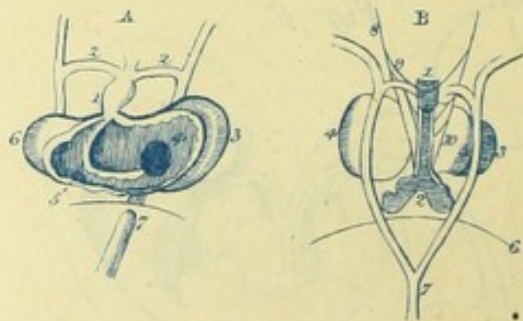


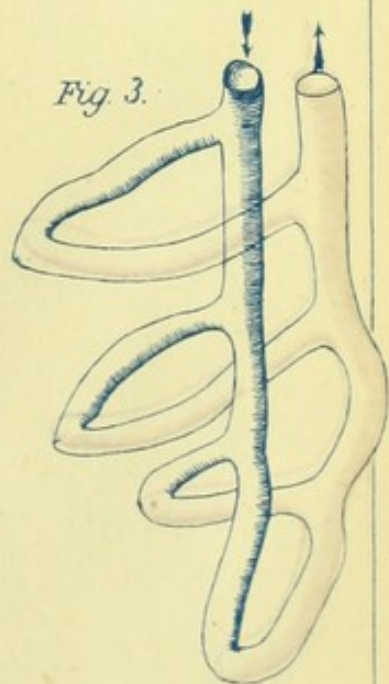
Fig. 1.



Fig. 2.



Fig. 3.



Turn Over

