ON THE

SOURCE AND THE COURSE

OF THE

EMBRYONIC BLOOD CIRCULATION

DURING

DEVELOPMENT IN THE WARM-BLOODED VERTEBRALIA.

BY

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THE main source of knowledge among the ancients of the anatomy of the embryonic blood circulation seems to have been derived from what was then known to exist in the adult. Plato, also from conjectures, represented the blood circulation as consisting of the heart as a knot of blood vessels in which the blood originates, and was then distributed throughout the body. Aristotle, with his vast knowledge of natural science and physical laws, considered the heart as the original source of the blood, and says that the generation of the more perfect animals is made manifest by what may be seen in the bird's egg during incubation, where all parts are not formed at once and together, but in succession to one another, in virtue of a particular primary genital principle,—that all other parts proceed like a child emancipated, as an independent automatic organism, from whence the different organs and members are thrown out subsequently which constitute the perfect animal. He also maintained that no part engenders itself, but, after being engendered by its own automatic force, fashions each part in a pretypified order; hence this primogenate part containing an inherent vital principle, directing sense and motion, and every manifestation of life whence growth and nourishment extend; that as life first begins in the blood, so there it at last fails at death.

To the accounts of the embryonic blood circulation, as given in the most popular anatomical books, showing their false and impossible anatomy and absurd physiology, I now refer, and from the important evidence which the development of the chick *in ovulo-ovi* affords as to the original course of the embryonic blood circulation during the earliest period of development, which cannot be seen in the case of the human embryo from its very minute size and the deep recesses where it first exists.*

From the correspondence of the immortal Harvey, as translated by Dr Willis and published by the Sydenham Society, it appears that Aristotle says, "the generation of the more perfect animals is made manifest by what occurs in the hen's egg, where all parts are not formed at once and together, but in succession to one another; and that it is in virtue of a particular primary genital principle, that all these parts increase and grow by their own automatic force."

Further on, in the same correspondence, he gives Aristotle's view of the order of generation:—"When conception takes place, the germ comports itself like a seed sown in the ground, for seeds likewise contain a first principle *in potentia*, which by-and-by manifests itself by sending forth a root by which aliment is taken up; so in conception, in which all parts of the body inhere *in potentia*, this first vital principle exists in special activity." This shows that, even in the earlier ages of the Greek school, the value of the hen's egg during incubation was fully appreciated; although the ideas of embryonic growth seem rather to have been adopted from conjectures that the embryonic blood circulation was similar to that of the adult, as had been demonstrated by Galen early in the course of the second century of the Christian era, fully established the anatomical knowledge of the human body, he seems to have confirmed

* Professor Valentine, in his Physiology, as quoted by Wagner, describes the bird as the class of animal best adapted for examining the very early embryonic stages, not from any intrinsic quality of their own, but simply from the ease with which, at almost any season, a sufficient supply of fecundated hen's eggs for repeating the experiments of developing the chick *in ovulo-ovi* during incubation, as described by Dr Tonge.

these early conjectures which are still obstinately maintained at the present day.

At the period of Fabricius, *Abaquapendente*, and his illustrious pupil, the immortal Harvey, the value of examination of the hen's egg during incubation did not seem quite sufficient to dispel the prejudice of the then established theory. And quoting from the same correspondence, Harvey declares that the priority of movement at first resides in the blood alone, being that which is first seen in the newly engendered being, not only of the chick *in ovulo-ovi*, but in the embryo of every animal whatsoever. There first appears a red coloured pulsating point or vesicle, with lines or canals extending from it containing blood, and further endowed with vital heat before it is put in motion by the primogenate *punctum saliens*. So that as motion commences in and from the blood, so at the last struggle of mortal agony does motion cease there. Harvey had ascertained by his numerous experiments on the hen's egg, as well as on other embryæ, that the blood is the element of the body, so long as vital heat has not entirely departed, in which the power of returning to life is continued. And since the pulsating vesicle and the blood-vessels extending from it are visible before anything else, he held it as rational to believe that the blood is prior to its receptacles, which are made subservient to it; the vascular ramifications and veins after the pulsating vesicle; and finally the heart itself, as the organ destined to receive and contain the blood, and in all likelihood constructed for the express purpose of impelling and distributing it throughout the body.

This conclusion is favoured by numerous observations, particularly by the fact that some red-blooded animals live for long periods without any pulse being perceptible; some even lie through the whole winter, and yet, after hibernating, escape alive, having lain, in fact, in a half-dead state of asphyxia, syncope, &c. He therefore boldly maintained, against the opinion of Aristotle, that the blood is the prime part first engendered, and that the heart and blood-vessels subsequently formed are merely the organs for its circulation.

It is not a little strange that, with these clear views, Harvey should have supported the established theory of the fœtal circulation, so difficult it is for even the most eminent minds to escape the thraldom of prejudice in favour of long-established theory supported by the majority. Had he thoroughly then wrought out his views of the blood and its fœtal circulution as above expressed, he would then have capped and culminated his immortal discovery, which is still left an open question as regards the early course of the fœtal circulation.

About the middle of the eighteenth century, Caspar Frederic Wolff promulgated in the Petrapolotan Transactions, and afterwards separately published in Berlin, his thesis "*Theoria Generationis*," controverting the evolution theory then prevalent among physiologists.

This distinguished author endeavoured to show, by the numerous observations he had made on the development of the chick, that the fecundated egg, previous to incubation, is very simple in structure, and does not contain, as far as by the greatest attention he could discover, any part to be compared to any organ either of the fœtal or adult animal, but that the several organs of the chick may be seen gradually forming *ab initio* by formation of their parts,—carefully avoiding speculation as to the causes of the phenomena which he had observed, as he considered it was the indulgence in theory, without due attention to facts, that those who had preceded him had been led into error. Being aware of the difficulty of disproving by mere argument the assertion made and supported by an opposing party at that time, that all the organs of an animal really exist, though their minuteness and transparency render them invisible, in the germ of the egg, he at once endeavoured to establish his own opinions, without directly opposing their hypothesis, by recording those observations in the experiments he had made, which seemed to prove the formation of a new part in the egg. Having delayed commencing his experiments beyond the fortieth hour of incubation, the first part he described was the superior mesenteric vascular network lying above the surface of the yolk, but entirely unconnected by tissue, which he believed to be the membrane of the yolk as had been described by others, as the vitelline membrane or vitellicle by Owen, which has no existence in nature. Had he made his examination somewhat earlier, he would have observed that there was a motion in the blood and in the Cuvierian canal and venæ cardinales before the commencement of the heart's action, which in the chick *in ovulo* commences early on the second day of incubation, and was in complete force before the thirtieth hour. According to the calculations of Vierdordt, referred to by Professor Marshall in his valuable "Outlines of Physiology," where it is stated "the whole circulation throughout the body of an adult, with a pulse at 72 per minute, the heart beats are $27\frac{7}{10}$ for each complete course of circulation performed in $23\frac{1}{10}$ seconds, or less than half a minute. Thus, as 72 : 60 :: 27·7 : 23·1."

Supposing that the same rate exists in the embryo of the chick *in ovulo-ovi* or human embryo in this very early stage, allowing the difference of size and force to compensate for the great bulk strength of the adult man, there being at that time no pulmonary circulation in the embryo, the circulation of the chick must have been completed at the rate of half a minute or less; many hundred circulations must have been completed before the time of Wolff's first observation. I will return further on to this part of the subject, in regard to the vascular network in the human embryo.

Wolff followed with great minuteness the changes in this vascular network, extending his observations to the formation of the abdominal viscera and the formation of the intestinal canal, amnion, and other parts of the fœtus, showing very clearly the actual formation of the parts by its own automatic force, and after being first formed, undergoing many important changes before arriving at birth.

These important observations, and the conclusions to which they inevitably lead, Wolff showed that during the development of the fœtus all its organs are actually formed *ab initio*, and not simply evolved from preformed organs invisible from transparent minuteness. This gave a new direction and increased interest to the study of the subject.

He was followed by many other observers, especially Pander, on the incubation of the egg; together with the observations of Meckel, who translated Wolff's observations on the formation of the intestines, &c., by Oken, Blumenbach, Bäer, Rathke, Cuvier, Prevost, and Dumas, and many others, which confirmed and greatly extended the system which Wolff had founded and indeed created,—a new branch of physiology, greatly increasing our knowledge of the structure and function of animals.

I now think it advisable to direct your attention to a sketch of what occurs in the formation of the hen's egg. The internal genitalia of the hen, as in the other warm-blooded vertebral classes, consist of an ovary, with its ovisacs, graafian and other vesicles, with an oviduct having a wide infundibular orifice partially connected to the ovary, and descending downwards towards the cloaca. The ovary of the bird is of a racemose form, where the very numerous ovisacs of various sizes, according to their maturity, are each attached by a short pedicle to a central general stalk, like a bunch of grapes or currants. In birds generally, this racemose ovary is only developed on the left side. In the adult hen, after sexual congress, a mature ovisac bursts and discharges its lining granular membrane along with the graafio-germ ovule, enclosed by the germ vesicle having the cicatricula, a yellowish body projecting and pervious, through which the *sperm zoon* entered and fecundated the different ovisacs as they became mature. This cicatricula may have been a portion of the yellow margin of the ovarian ovisac when it was burst by the graafio-germ ovule, without either yolk or albumen. As soon as the ovisac bursts, the graafio-germ ovule, containing the proligerous embryo germ disc, is precipitated into the infundibular orifice of the oviduct, and in its descent to its lower part, where the oviduct is expanded into what may be called the calcigerous sac, followed by the yolk and albumen, supplied subsequently by the oviduct, and involving the graafio-germ ovule, which from its lightness lies always upon the surface of the yolk uncovered by the albumen, the oval form of the graafio-germ ovule making a slight depression on the upper surface of the yolk in which the cicatricula lies embedded. Neither the yolk nor albumen are enclosed in special membranes, but there is a peculiar molecular arrangement which gives them a membranoid tenacity and distinct form before they are submitted to incubation. I particularly notice this want of a special membrane. While the whole contents of the egg are in this calcigerous cell they are enclosed in the lining membrane of the egg-shell, consisting of a transparent, thin, structureless, and non-vascular membrane, very smooth on the internal surface, enclosing the egg contents, but externally rough and warty by numerous small villous prominences, which, on the deposition of the calcareous matters of the egg-shell, cover them so as to form shallow pits on the roughened inner surface of the egg-shell, which is perfectly smooth externally, without visible pores, but experimentally known to be permeable to air during the daily turning of the egg. As soon as this egg-shell is completed, the egg is at once pressed through the walls of the cloaca, and afterwards deposited in the hen's nest.

I particularly notice what occurs in the descent of the ovule, and also its special source in the ovary while the yolk and albumen are the products of the oviduct, in order to point out the erroneous views of those embryologists who have mistaken the circulation of the mesenteric artery from the ascending abdominal aorta, even so early as the middle of the second day of incubation, as belonging to the vitelline membrane which nowhere exists in nature. After this short notice regarding the egg, you are prepared to examine the course of its development.

Examine an egg during the first stage of incubation, which Wagner has conveniently included within the first two days.

I. Though not very easy to assign accurately or distinctly the operation of each day of incubation during the development of the chick *in ovulo-ovi*, yet a fair approximation in regard to the main points of the vascular system of the embryo, the subject of the present communication, may be arrived at by comparing each day of incubation, nearly the 20th part of the whole period in the domestic hen of incubation, as equivalent to two weeks of the *human utero gestation of 40 weeks.*

After incubation has been continued for ten or twelve hours, if a careful examination be made in removing a small portion of the shell and its lining membrane, the graafio-germ ovule gradually as it increases in size displacing both albumen and yolk, spreading out its globular into a more lenticular form, and from its transparent membranous condition the proligerous embryonic germ disc, with the blastema or germ in the centre of a clear transparent space, the *area pellucida* having along its centre the *nota primitiva*, or primitive streak, supposed to prefigure the *cerebro spinal axis,* or more probably the chorda centralis or axis of the future vertebral column. The nota primitiva rises slightly above the level of the embryonic germ disc, having its anterior point large and blunter, from a group of nucleated cells, from which the head of the embryo is developed. The streak gradually tapering towards the posterior end or tail, both ends bend upwards and inwards, the embryo in this primary condition lying on its back curved in the hollow of the graafio-germ ovule, corresponding to the curve of the egg-shell. Around the area pellucida, at first, the area vasculosa, like a dark ring, encircles the whole; the dark granules of the vascular area shortly become isolated from one another, forming clefts among which a yellow fluid may be seen moving; this is the liquor sanguinis or plasma. By the 16th or 18th hour the circular form of the disc has been greatly elongated and extended the whole length of the chorda centralis, and now appears in a series of azygeal blood sinuses, accompanied by the Wolffian lymph bodies. External to this, the dark four-cornered plates, the future transverse processes or tubers of the dorsal lamellæ, have become greatly increased in number on each side; these are the tubers of the lamellæ meeting to form the spinus processes, which in the first period of development form an inverted arch under the *chorda centralis* and *cerebro-spinal axis;* from these tubers the pedicle, with its rounded head and neck, inclined to the chorda centralis, which, when ossified as the vertebral column, includes them in its spongy osseous substance. These square plates extend the whole length on each side of the chorda centralis, and are covered by the blastoderm or bioplastic serous membrane, the pleura or peritonæum.

I have particularly directed attention to the ovulation of the hen's egg to show that the different sources of the bulky portion of its contents, the white and yolk, are derived from the oviduct, while the graafio-germ ovule is the only portion resulting from *sexual congress* and the intrusion of the *sperm zoon* while still in the *ovary*. This also will tend to correct the mistaken views of those who describe the effect of incubation to develop the ovum into the chick. These bulky constituents of the egg are the natural product of the oviduct, and are completed previous to its being deposited, and are, during incubation, blended together and fluidised, either to be removed through the permeable porous egg-shell, or, as Professor Robin of Paris, a member of the Institute, describes them, as forming the lower film of the *umbilical vesicle,* when it is extended into the *tunica media* of Bischoff, through the unclosed abdomen of the embryo ; or, as Professor Henry Gray of the St George's Hospital Medical School, London, in describing the development of the young pigeon, in a communication to the Royal Society, and afterwards published in the Philosophical Transactions' volume, where he traces the development of the stomach, spleen, liver, and intestines, from the yolk and albumen. This last seems a rational and appropriate conjecture and application of so large a mass of prepared organisable matter toward the development of the embryo.

The *ovarian* or *graafio-germ ovule* is the only portion of the contents of the fecundated hen's egg developed during incubation.

I. The first period of development extends over the first two days, equivalent to the first month of human *utero gestation.* The first period of development includes the changes on the *proligerous embryonic germ disc* enclosed in the ovule, and of the circular form into the oval, having in the centre of the *area pellucida* the primitive streak extending along its middle as it becomes elongated in form : this primitive streak arises from a collection of granules at one end, which form the future head of the embryo, while its extension backwards gradually tapers to a tail ending in the future coccyx ; the embryo thus lying on its back, as is the case of the larval condition of all animals ; and as development proceeds, the embryo bends upwards at each extremity. Along each side of this primitive streak, the whole length of the embryo, the following lines of structure may be seen:—

1. The *azygeal blood sinuses,* divisible into each intervertebral space when developed ; this arises from the separation of the blood granules of the *primary veno cruorine blotch* into isolated clefts, between which a yellow fluid—the *plasma sanguinis*—may be seen in motion. Along with these the *sympatho-ganglionic neuraxis,* extending the whole length of the *central chord,* corresponding to the future intervertebral spaces from the upper part of the *cervical ganglia*, producing the *sympatho-plexic* organs, to supply the *proaxial* region of the head and neck as well as those of the thorax and abdomen, not separated in birds by a complete diaphragm. This *sympatho-ganglionic neuraxis,* according to Bichat, was the source and centre of organic vitality, and by the interganglionic connections of the right and left stem, as well as the filaments extending backwards into what becomes the *cerebro-spinal axis,* though at first consisting merely of expanded fluid vesicles, contained in the membranes covering the future developed *cerebro-spinal axis*, and also forward to the different ganglia and plexuses. There is also along each side the future double aortic tube on birds. Beyond these there is a line of the square ossific blocks, the future tubers or transverse processes of the vertebral column ; these last form, as it were, the trough of the spinal axis enclosing the cerebro-spinal tunnel or canal.

This central stem, as it were, of the future embryo being thus completed, we are now prepared to trace the embryonic blood circulation. This commences in front of the central stem by the projection of the Cuvierian lymph canal, accompanied by the venæ cardinalis forward, to form the conical transparent contractile lymph sac, which Wagner describes as the first form of the sinus venosus, with only one outlet—the ductus venosus—leading to the umbilicus, continued by the umbilical vein, and from thence on the blastoderm membrane to the sinus terminalis of the chorion, to be traced afterwards. This conical union of the lymph sac has two inlets, by which it receives the venæ cavæ after the *venœ-cardinales.*

As soon as the punctum saliens or genital blood particle stimulates the contraction of the conical sac, it discharges its yellow lymph contents down the ductus venosus and onwards to the chorion, when its cavity is at once refilled from the venæ cavæ and cardinalis, which again stimulate the sac to contract. This occurs early in the second day of incubation, and, being continued, the embryonic blood circulation is thus carried on and repeated during incubation till towards its close during the last week, when some preparation is being made for pulmonary respiration and circulation. This change is more rapidly completed in the chick *in ovulo-ovi* than in the human embryo.

The chick, at the beginning of the third week of incubation, having swung from across the long axis of the egg to lie in its long axis, the air space of the broad end now by the removal of the yolk and albumen filling the whole egg-shell not occupied by the chick, the change to the pulmonary respiration and blood circulation is at once effected without any risk of still-birth, as the chick is already lying in atmospheric air, and has been heard to chirp in its *prison cell* a day or two before it escapes the egg-shell. The circulation thus originated continues to be regularly performed in the same manner, till a preparation is required for the pulmonary circulation towards the end of incubation. Previous to the fourth day of incubation, the heart, which at first consisted of a simple conical sac, the sinus venosus, had appended to its base a ventricle still membranous and contractile, thus giving it greater force from its extended contractile membrane to propel the blood through the rapidly growing embryo. This membranous form is subsequently enclosed within muscular walls by the introduction of the muscular tissue among the fibres of the primary membrane. This I will explain more satisfactorily in the description of the human embryo. The first addition of the muscular coat seems to have been more ample in the case of the ventricle enclosing it by forming a septum, dividing it into right and left ventricles, commencing at the apex, and gradually becoming more abundant towards the auriculo-ventricular basis of the heart, and then extending to subdivide the auricle.

The septum thus commenced by the fourth day at the apex of the heart extends upwards, dividing the auriculo-ventricular orifice into two, and still continuing upwards, now subdividing the single auricle, but not so completely, which forms a closed sac, lining the whole cavities of the thorax and abdomen, which in the bird are only partly separated by an incomplete serous diaphragm.

The bioplastic serous membrane in some respects resembles the outer film of a soap-bell, which Mr Plateau, the blind physicist, in a communication to the Academy of Sciences or Institute, explained how, by a suspension of a small quantity of soap in water, films may be obtained in the form of geometric solids from the tension of its outer film and viscosity ; while pure water, and even more viscous fluids, as fatty oils, glycerine, and solutions of gum arabic, possess no such property. He laid down that viscosity must be great, while the tension must be small. In the bioplasm, however, both the viscosity and tension are great, enabling it to be extended to the chorion (or the placenta in the human embryo), enclosing both the umbilical vein from the embryo, and the two umbilical arteries again returning to it. There is another similarity which the bioplasm has to the soap-bell,—the outer layer in both forms a continuous closed cavity, and by its loose primitive form of pavement scales easily continues to expand over the increasing growth of the subjacent intestinal organs, while the viscera and other organs of thorax and abdomen gradually expand and grow, becoming coated with the serous membrane.

The embryo, from the first, within the graafio-germ ovule, is supported from its chorion on the upper part of the blastoderm or germ vesicle, suspended by the bioplastic membrane in the hen, *i.e.*, across the long axis of the egg, thus swinging, as it were, in its greatest transverse diameter during the first two weeks of incubation. In this way, as it expands in size, it gradually presses out the yolk and albumen, now rapidly becoming more fluid, as shown in the diagrams of Professor Allen Thomson. In this way he may concur with the views of Professor Gray, applying the whole fluidised yolk and albumen to the nutrition and growth of the embryo. By the middle of the first day, entirely detached from the yolk and albumen in the area pellucida now elongated, the whole length of the embryo accompanied with the dark veno-cruorine vascular clot. About this period the bioplastic membrane exhibits increasing thickness, still, however, distinctly defined towards the periphery at the limit of the area vasculosa, where it lies, as it were, belonging equally towards the amniotic or external layer of the embryo and the mucous or internal layer. This vascular lamina first becomes distinctly visible between the sixteenth and twentieth hour of incubation. Somewhat earlier than this—about the fourteenth—the first rudiments of the embryo become distinctly visible as a delicate elongated streak, about a line and a half in length, in the middle of the germ area. This is the primitive streak or nota primitiva lying in the long axis of the germ disc, but across the long axis of the egg. Under, the nota primitiva may be seen plainly glistening through. From the twentieth to the twenty-fourth hour the transparent germ area becomes more elongated ; the four-cornered looking plates by this time have been greatly increased in size and number along the whole length of the *chord centralis*, from at least the sella turcica to the coccyx.

II. With the second day of incubation, the embryo, growing more and more disconnected from the germ membrane and yolk, rises more distinctly over the germ area.

By this time the sides, or *laminæ ventralis*, begin to turn inwards also. The embryo, three lines long, broad and more strongly bent at the extremity, with its transverse envelope visible to the naked eye. The four-cornered laminæ gradually rounding, springing up fore and aft, are greatly increased in number; about the thirty-sixth hour as many as from ten to twelve pair may be reckoned; the dorsal laminæ separate still more from one another, so that many spaces or cells become visible between them. The largest and most anterior of these cells point forwards and curved laterally. About this time rudiments of the transverse process of the vertebræ, and further out the laminæ ventralis or ribs begin to appear. The dorsal laminæ extend downward in plates, and converge to close in the cerebro-spinal canal. The ventral laminæ, also, from the margin of the germ disc, spread more in breadth, and inwardly converge to form the lateral parietes of the abdomen, and finally close as far as the umbilicus in that cavity. The vascular and mucous layers follow the turnings of the external muco-muscular coat in the distribution of the blood-vessels from the central stem of the aorta. The area vasculosa has now greatly increased, and the clefts formed by the dark venocruorine granules of blood, in which a yellow lymph or *plasma* may be seen advancing in the centre upon the transparent blastoderm, where the development of the heart has been advancing. At first having the appearance, according to Wagner, of a conical sinuous sac on the blastoderm and muco-muscular laminæ, and as development advances the heart appears as a sac simple and undefined anteriorly (which can scarcely be correct, as by the contraction of the sac its contents would be forced through it). Professor Allen Thomson agrees with him in that opinion, but Pander, Reichert, Prevost, and Dumas take the more rational view of its being closed. This conical sac, pointed above, terminates posteriorly in greater breadth, where two crura connect it towards the spine. These may possibly be the Cuvierian canal and the two cardinal veins which are lost in the venæ cavæ.

The blood now collects in the periphery or chorion of the vascular lamina of the blastoderm, within the circular sinus or *vena terminalis.* The heart soon parts the *ventral laminæ* from one another, intruding like a wedge. The heart now has become more curved or spirally twisted, with greater vigour than heretofore; the blood by degrees acquires a red colour, the whole embryo still more bent on itself; this closes the operations of the second day.

III. The second period in the history of the development of the chick begins with the third day, in the course of which the embryonic blood circulation is established, embracing the further changes that take place during the fourth and fifth days. The first circulation reached its highest development by the end of the fourth day; in the course of this period the embryo is completely detached from the germ membrane.

The *area vasculosa,* from the end of the first to the middle of the second day of incubation, has enlarged greatly into an elongated form, having its outer periphery beset with dark *veno-cruorine granules,* like isolated points; between the clefts channels are formed, in which a yellow fluid in motion may be seen uniting into meshes with one another. In these channels at first a clear fluid of a pale yellow colour, brought on the blastoderm by the Cuvierian canal, accompanied by the *venæ cardinalis* on each side, till they are lost in the venæ cavæ.

The heart now advances as the centre of the vascular system under blastoderm, and appears as a conical sinuous sac, connected with the two venæ cavæ, and a single outlet, the *ductus venosus.* Even at this period certain undulating motions or rhythmical contractions of the heart may be perceived, giving a wavy appearance to the organ, filled with a clear or nearly colourless fluid in motion.

The changes that occur during the second half of the second day are the following:—The first act of the sinus venosus, by the impulse of the punctum saliens, is to discharge the yellow fluid contents of the heart down the ductus venosus behind the peritoneum and liver to the umbilicus, where it enters the blastine or umbilical vein on the blastoderm or germ membrane, to the chorion or sinus semicircularis, in the capillaries of which the blood is arterialised and propelled into the rootlets of the blastine or umbilical arteries, and after circulating from larger to larger branches, circulate on the blastoderm in its return by the blastine or umbilical arteries to the umbilicus, where the two arteries, continued in the hypogastrics, enter the common iliacs in the pelvis, from whence a small portion of the arterial blood is supplied to the lower trunk and extremities, and after circulating through them, it returns as venous blood by the venæ cavæ to the heart, receiving the portal circulation as it proceeds from the liver.

In the bird the arterial blood from the common iliacs is transmitted to the abdominal aortæ, and continued along the spine as high as the fovea cardiaca, from whence it is bent forward to near the sinus venosus without any connection with it, and a little above it and behind, where each of the aortæ terminates in two branches to form the truncus arteriosus or aortic bulb, the left terminal aortæ in the bird is absorbed, the right continuing to give off the right innominata, and the left carotid and subclavian arteries supplying what have been incorrectly called the *branchial arteries*, which even Reichert admits have no connection with branchiæ, though he still names them visceral arches. They are, in truth, the usual arteries given off to the upper trunk and extremities, as well as the neck, head, face, and brain, which are distributed to these extensive and important regions, and after circulating through them, returned as venous by the jugular, facial, and subclavian veins, to form the superior venæ cavæ, which at length pour their whole venous blood into the right auricle, or sinus venosus, thus completing the first course of the embryonic circulation. This is repeated again and again during the first half of the second day.

By the time that Wolff observed what he called the *vitelline circulation*, according to the calculation of Vierdordt, the circulation, occupying less than half a minute, must have been completed more than a hundred times, as already observed. In this way it continues during the most part of incubation. During the second half of the second day, or a little later, the *dorsal laminæ* are closed along the whole line; the head curves itself upward more and more; so also does the tail, which terminates in the coccyx at the umbilicus. The main changes in the cerebral cells proceed to development, but are not on the present occasion to be more particularly described, as it is principally with the blood circulation we are engaged. The blood by degrees acquires a brighter red colour.

The second period of the development of the chick begins with the third day, in the course of which the embryonic circulation is completely established, embracing the further changes that take place during the fourth and fifth days. The third day is the most remarkable in the whole history of the bird development, as from the general vigour of the formative processes all the organs now begin to be evolved, and the characteristic form of the embryo to be distinctly evident. The dorsal laminæ have increased in size, and the vertebral laminæ, growing both anteriorly and posteriorly, surrounding the spinal canal or tunnel laterally and over the *medulla oblongata*. Around the chorda centralis, between it and the vertebral laminæ, arise the first cartilaginous rudiments of the bodies of the vertebræ, which blend superiorly with the lamellæ of the vertebral arches, close in the tunnel of the spinal marrow, surround the cartilaginous column or sheath of the corda centralis, improperly styled notochord or chorda dorsalis.

On the fifth day the rudiments of the future extremities appear, and very important changes occur on the ventral as well as the dorsal laminæ.

Immediately under the head of the embryo three blood-red bounding points are seen exhibiting the alternate contractions of the sinus venosus, which receives the veins, traces the ventricle and the auricle. In this period the heart presents diversities by the addition, first of a ventricle, secondly of a division in the ventricle forming the right and left ventricles. This muscular septum or division is completed during the fourth day, the circulation still continuing as on the second day, but with greater force and energy. The *sinus venosus*, or *auricle*, now clothed with a muscular coat, drives the blood with greater force, but still in the same course. The other two points were the entrance of the blastine arteries into the umbilicus. The ventricle on the fourth day becomes more globular, pointed at its apex, and more of a heart shape. It lies much to the right, while the sinus venosus, which is become more distinct by its muscularity. The muscular mass of the heart, with the *septum ventriculorum*, is produced on the fourth day, but it is not extended through the *auriculo-ventricular orifice* till the fifth day, when the two auricles are formed, into which the heart enlarges by the extension of the ventricular septum, though not complete, from the continuance of the "*foramen ovale*" in its centre, though ultimately covered by a valve. This arrangement is necessary to continue the venous circulation through the heart of the embryo during the *chorionic* or placental circulation, in order to secure the arterialisation of the blood, that the whole tissues of the embryo may be supplied with pure blood, and as there is no other vessel communicating with the placenta and the embryo than the umbilical vein conveying the blood (the venous) impelled by the *punctum saliens* from the *sinus venosus* down the ductus venosus; and from the placenta or chorion of the bird the two blastine or umbilical arteries which enter at the *umbilicus* into the abdomen, and are continued down the hypogastrics till they enter the common iliacs in the pelvis, by which the lower trunk and extremities are partly supplied with arterial blood, the venous circulation returned to the heart by the *inferior vena cava*, along with the portal circulation, after circulating through the liver, and poured into the vena cava just as it is entering the heart.

From the common iliacs the main part of the arterial blood is forced upwards into the abdominal aorta, where it forms a single tube, but virtually two in the human embryo (but in birds double), where it gives from its right side the mesenteric colon arteries, and from its left side the small mesenteric arteries to the small intestines.

Towards the fifth day the chorda centralis begins to disappear, being involved in the solidification of the vertebral bodies. On this day the rudimentary enlargements or processes indicative of their future extremities make their appearance. Very important changes go on during this period in the ventral laminæ, extending from either side of the dorsal laminæ; in this way the amnion, as a complete vesicular envelope, is thrown around the embryo. On the fourth day the muscular mass of the heart and septum ventriculi are produced, but not yet extended through the *auriculo-ventricular* orifice, dividing it into two, till the fifth day, when it extends, subdividing the auricle into right and left, but not so completely as in the case of the ventricle, still leaving the foramen ovale, around the margin of which there is a valve gradually formed. This foramen is absolutely necessary for permitting the continued flux and reflux of the venous blood between the ventricle by the systole of the auricle, when it is immediately returned by the systole of the ventricle with the additional force which the greater muscularity of both ventricles now give it, to send the whole venous blood back into the auricle, to be forced down the *ductus venosus* to the umbilicus and umbilical vein to the chorion or placenta, to be again returned arterialised by the blastine or umbilical arteries returning to the umbilicus, and by the continuation of the hypogastrics into the common iliacs, from which, after distributing a small quantity to the lower trunk and extremities, the whole arterial blood is sent upwards by the abdominal aorta supplying the mesenteric circulation in its ascent, as it does in the adult during its descent, and after giving off the cœliac axis, from which the splenic, hepatic, and gastric arteries are given off, it rises to the fovia cardiaca, about the fifteenth space above the sacrum, from whence it bends upwards to form the bronchus arteriosus, or aortic bulb arch, closed in by the horizontal position of the semi-lunar valves, which cause the whole arterial blood to rebound upwards by the innominata, carotid, and subclavian arteries to the principal arteries of the upper trunk and extremities, the neck, face, head, and brain. After circulating through this important and extensive region, the whole venous blood is returned by the facial, jugular, and subclavian veins, forming the superior venæ cavæ, which pours its blood into the right auricle, thus completing the course of the blood circulation. This course of the circulation continues till towards the end of the last week of incubation, at the beginning of which the embryo, which had from the first been suspended across the long axis of the egg, in the largest cross section, confined, possibly, by its greater size and bulk, now swings round, as it were, like a vessel at anchor or a buoy on the turn of the tide. The embryo now lies in the long axis of the egg, its upper extremity in the broad end in the air space, *folliculis aeris*, having its neck bent, allowing its head to appear below its arm or wing. By this time the whole yolk and albumen have been dissolved, and almost entirely removed, except a small portion to prevent the friction of the shell stopping the regular turning of the egg. At the same time, the great growth of the embryo, and the continued addition of air through the porosity of the shell shortly after the middle of the third week of incubation, is lying in the midst of atmospheric air without any dread of still birth, so that the transition from the chorion to the pulmonic respiration is at once effected, and thus we can account for what has been again and again repeated, that the chick has been heard to chirp a day or two before it broke the shell.

This seems to be sufficient application of what has been observed in the development of the bird, as applicable to the development of the human embryo, to show that the circulation of the embryonic blood commencing in the graafio-germ ovule in the veno-vascular clot of the human ovary, from which the blastoderm or germ membrane issuing by the Cuvierian canal with the yellow lymph of the Wolffian bodies, accompanied by the venæ cardinales of the azygeal sinuses meeting in the primary conical sac of the heart, according to Wagner, which, by the impulse of the punctum saliens, discharges its first yellow lymph contents down the ductus venosus, the only outlet during the gestation period of embryonic life, till the period of placental circulation by the opening of the pulmonic at birth, probably within the last two weeks of utero-gestation, whether at the full time of forty weeks, or at those occasional earlier premature births of weakly human beings permitted to linger through seldom more than a year or two of breathing existence.

The order of development in the human embryo may now be described as if seen in the development of the chick in ovulo as regards the subsequent formation of the heart, which consists of a single transparent sac; when contracted it is at once filled by the dark blood of the venæ cavæ, at once stimulating the next contraction of the sinus to propel its contents down the ductus venosus to the umbilical vein and placenta, where in the capillary area its minute veins enter the rootlets of the umbilical arteries, and thus the arterialised blood of the capillary area is continued by larger and larger branches, till at length considerable trunks circulate upon the surface of the placenta under its membrane, and finally unite to form from each end of the placenta the umbilical artery, and which return the arterialised blood to the fœtus, their tubes uniting with the umbilical vein to form the umbilical cord; and as the umbilical vein had conveyed the whole venous blood of the embryo to the placenta, the umbilical arteries now return the purified blood by the umbilical arteries, which enter the umbilicus, and are at once continued by the hypogastric arteries into the common iliacs in the pelvis, where a portion of this pure blood is distributed to the lower trunk and extremities, and returned by the venæ cavæ as venous, which in its ascent to the sinus venosus receives the venous blood of the organs of the abdomen—the partial circulation—just before it enters the sinus venosus.

To return to the common iliacs, which convey the main portion of the arterialised blood upwards to form the abdominal aorta, which in the human female is a single trunk arising opposite the second lumbar vertebra from the sacrum (where in the adult it divides to form the common aortal), from the right side of which the upper mesenteric artery gives off the ilio colic adextra and colica pancreata oduodenalis, the colica sinistra combining with the colica sinistra, and from the left side giving off the numerous branches to the small intestines derived from the inferior mesenteric supplying the sacrum, and meeting with the ilio-cæcal portion separated by the valve. From this point the whole blood in birds is at once sent down the cloaca to be discharged, as there is no colon in birds; but from the ilio-cæcal valve in man the colon ascends upwards to the lower surface.

The abdominal aorta, though a single tube, may represent the double tube in the bird, and after giving off the inferior and superior mesenteric arteries before entering the thorax, gives off the splenic, gastric, and hepatic arteries to supply these important organs which mingle their venous blood with the portal, and thus combine to supply, along with the blood of the venæ cavæ, the sinus venosus. To return to the abdominal aorta—in passing through the diaphragm and giving off the phrenic arteries, it is again subdivided into two aortæ, passing up on each side of the spine as high as the fovea cardiaca, where they bend forward towards the sinus venosus, but a little behind and above, and so form two terminal branches meeting in the truncus arteriosus. Shortly after this union the right terminal aorta, as far as the thorax, is dwarfed off or absorbed, unless it is separated for the purpose of forming the pulmonary artery, which seems to be indicated, with the singular exception discovered in the dissecting theatre of Dr Handyside, which will be noticed in the Appendix.

By this change the whole purified blood is conveyed to the truncus arteriosus by the left terminal branch of the aorta. The aortic terminal branches, from a subsequent examination of the subject, seem to have been provided with what become the semilunar valve of the heart. The left terminal aorta seems to have exorcised or thrown off the lower branch, leaving it in the mesial plane of the thorax; and the small remains depending from the under curve of the aortic arch, led to the whole delusion of the ductus arteriosus, of which there is no existence in nature—the existence of what become the semilunar valves in all the terminal aortæ, as well as the bulbus arteriosus, forming a horizontal three-starred valve, having prevented the escape of the blood into the cavity, and as it were forced the current to bound upwards into the arch of the aorta, with the arteries that supply the blood to the trunk and upper extremities, and thus to continue the blood circulation during almost the whole period of embryonic life, till the requisite preparation for a change from a placental to a pulmonic circulation and respiration at a near birth, whenever that may occur.

As the main object of this contribution is the history of the development of the human embryonic blood circulation, I now proceed to apply the information afforded in the development of the chick *in ovulo* to enable me to explain those very early stages in the development in the human embryo during the first month of utero-gestation, and I may here explain, when I describe the changes in the human embryo, I freely use the expressions given of the chick *in ovulo,* as if at that time under my own observation.

The internal genitalia in woman after puberty consist, as in the *Marsupialia* and *Ovipara,* of the *ovaries,* with numerous *ovisacs* distributed among the interstices of the fibrous stroma forming the substance of the ovary, and containing within each a graafian follicle more or less advanced, enclosing the graafio-germ ovule, and also the oviducts or Fallopian tubes, in this case communicating with the cornua uteri on each side, thus distinguishing the human genitalia from the form in the other warm-blooded *Ovipara* and *Marsupialia.* In woman after puberty there is menstrually discharged from the graafian follicle in the ovisac the *dark veno-cruorine clot* as the earliest form of the human blood. This clot is discharged from the graafian follicle, unclosed by the germ vesicle, into the infundibular cavity of the Fallopian tube, by which it is conveyed directly into the cornua uteri, augmented by the fluids afforded by the tube and cavity of the uterus, liable to be changed in its quality by the healthy or unhealthy condition of these organs. This is the catamenial fluid menstrually discharged along with the membranous lining of the *ovisac*, which forms the *corpus luteum,* though less perfectly than after impregnation. After sexual congress, when the graafian follicle, with its contained blastema or germ fecundated by the entrance of the *spermzoon* while still in the *ovisac* and enclosed by the *germ vesicle* in the *graafio-germ ovule,* which by bursting is discharged down the Fallopian tube, at length arrives in the cavity of the uterus, soon after the middle of the first month of gestation, enclosed in its own envelope, having the amnion extending dorsally from the whole margin of the *proligerous embryonic germ disc,* at first circular, with the *blastema* in the middle of the *area pellucida* encircled by the *area vasculosa.* The circular germ disc is quickly changed into an elongated oval, which is gradually extended to the whole length of what becomes the future embryo; this is early traced in the midst of the *area pellucida* by the primitive streak or *nota primitiva,* at one end of which there may be seen a few nucleated cells or globules, which afterwards form the head of the embryo; from this point the streak gradually tapers towards the opposite extremity or tail. As the embryo from its earliest appearance may be supposed to be at the lower part of the graafio-germ ovule, it early assumes a curved form, lying upon what ultimately becomes its back, both extremities bent upward, the head of greater size than the opposite termination; and thus it may be more intelligibly figured in a diagram than the form adopted by Wagner. The dorsal expansion of the amnion is completed before the ventral laminæ are commenced, the abdomen being still open.

A rapid change takes place by the change of the circular into the oval form, which is thus extended to the whole length of the embryo. This is also connected with the separation of the granules of the *vascular area* into separate sinuses, which ultimately appear opposite each inter-vertebral space as the azygeal blood sinuses, consisting of the primary *veno-blood cruorine,* accompanied also by the Wolffian lymph bodies, both these forming a line on each side of the centra-chord. Within these lines the *sympatho-ganglionic neuraxis* form a line also the whole length from the cervical region to the coccyx, where the two lines of ganglia unite to form the terminal or *ganglion impar.* External to these there is on each side a row of the primary square blocks which form the tubers or transverse processes of the perineural arches; from these tubers the lamellæ of the vertebra extend dorsally to meet under with that from the opposite side, thus forming, as it were, an inverted arch to support the embryo during development, from the centre of which the spinous processes are derived. From the same tubers the pedicle on each side extends towards the centrachord subsequently enclosed in the cancellated osseous matter, forming the *centrum* of the vertebra. All this occurs within the graafio-germ ovule contained within the chorion membrane as originally discharged from the ovisac; the granulary membrane around the *proligerous embryonic germ disc*, and the fluid which has been incorrectly named vitelline, not to be mistaken for the vitellus of the hen's egg, with which it has no homology, being derived from a different source.

After the dorsal lamellæ proceeding from the tubers have completed the inverted arch, the ventral laminæ or *fasciæ abdominalis* of Wolff begin to project upwards and inwards in order to close in the abdomen. On these, also, there is an extension of the muco-muscular formed envelope of the amnion of the embryo, which I consider incorrectly stated as containing fluid. The muco-muscular envelope of the little embryo is subsequently closed in so far as the umbilicus. In these ventral laminæ we find the ribs early developed upon the same type as the perineural arches. The round head is formed in the inter-vertebral space, articulated partially to the body of the vertebra above and below it; the exceptional case of the first human rib having been adopted injudiciously by Cuvier, who fixes seven instead of six as the number of ribs in mammals, as the characteristic of the vertebral column in mammalia, whereas in man it was a mere exception. From the head of the rib, which thus has normally two half articulating surfaces, there extends the neck to the tuber, from which the body or rib, ending in the cartilage, is continued to the sternum, or to that of the opposite side. Within these ventral laminæ the inner *muco-muscular* layer extends, from which the viscera of the abdomen and thorax are developed, enclosing the vascular branches of the area vasculosa. In addition to the lines marked in the diagram of the central stem, there is superadded the aortic tube, which is at first single through the abdomen; but double through the thorax, to be more particularly described after giving a description of the heart and its vascular connection.

On the Formation of the Heart and Blood Circulation.

Starting from the central column, the blastoderm or germ-membrane advances, the Cuvierian lymph canal and two venæ cardinales upwards, according to Professor Marshall, to form the primary conical lymph-sac, the first form of the heart or *sinus venosus* of the future auricle. Wagner describes this sac as a transparent sinuous conical sac filled with yellow lymph (the colour indicating its transparency), having two inlets for receiving the superior and inferior *venæ cavæ*, and only one outlet for discharging its contents down the *ductus venosus*. He describes this primary sac as arising posteriorly in the Cuvierian canal and vena cardinalis as described by Professor Marshall, which are lost in the trunks of the *venæ cavæ*, and their contents forced into the *sinus venosus* as soon as its first lymph is discharged. He describes the sac as incomplete above, in which he is supported by Professor Allen Thomson, though I think more correctly contradicted by Pander, Prevost, Dumas, and others; if it were open, the contents would there escape.

We may now take a view of the course of the embryonic blood circulation thus originated. As soon as the contents of the ductus venosus is discharged at the *umbilicus*, it is propelled by the umbilical vein into the placenta, where it is circulated through the capillary area, and arterialised in the rootlets of the small branches, which, becoming larger and larger, gradually form considerable trunks, which circulate on the surface of the placenta under the membrane from the chord. Filled with the arterialised blood from each end of the placenta, they unite to form the umbilical arteries, which return to the umbilicus, and there entering the abdomen, as from each side, are continued by the hypogastris into the common iliacs in the pelvis. This anatomical arrangement is agreed to by all who have described the subject, but reversing the current of the circulation and the nature of the blood which they carry.

The arterialised blood thus conveyed to the common iliacs is partly distributed to the lower trunk and extremities, and afterwards returned to the sinus venosus by the inferior vena cava. The main portion of the arterialised blood, however, in the human embryo, is sent up to the abdomen and opposite the second *lumbar vertebra* above the *sacrum;* the two common iliacs unite to form as a single trunk in the embryo the ascending abdominal aorta, which in its ascent gives off the inferior mesenteric artery to supply the mesocolon and mesocæcum, terminating in the allantois, if it really exists in the human embryo.

Secondly, the superior mesenteric artery, to form the mesenteric circulation, supplying from one side the mesocolon to the ascending and transverse colon, and from its other side the small intestines, jejunum and ilium; thus in a manner performing the function of the two abdominal aortæ in the bird. The circulation of the mesentery, so early observed in the bird as the fortieth hour of incubation, was mistaken for the circulation of the vitelline membrane, which nowhere exists in nature, as neither the yolk nor albumen are enclosed in special membranes, their molecules being so arranged as to give them such a membranoid force, keeping them in their primary form till incubation dissolve and remove them in the bird. In the human embryo the ovum is not formed; the graafic-germ ovarian ovule containing the proligerous embryo germ disc lies in a fluid, and not in the vitellus.

This extensive mesenteric circulation, supplied by a current from the ascending aorta, extends downwards to the pelvis, from whence it is returned by the veins forming the basis of the portal circulation. The next branch of the arteries given off from the aorta is the *cœliac axis,* which divides into the *splenic*, *gastric,* and *hepatic* arteries, supplying the spleen, pancreas, and stomach, returning the venous blood to complete the portal circulation in the transverse fissure of the liver, in conjunction with the hepatic artery. After circulating through the whole lobes of the liver, and excreting the bile, its whole venous blood is poured into the vena cava by the three hepatic veins just as it pierces the diaphragm in order to enter the sinus venosus or auricle.

The phrenic arteries are the last branches given off as it passes through the arches of the diaphragm for its supply.

In the human embryo, the aorta, as it enters the thorax, again divides into a right and left trunk, which proceed upwards, one on each side of the vertebral column, as high as the *fovea cardiaca*, opposite the fifteenth dorsal vertebra, *above the sacrum.* From this point they each advance forward towards the primary *sinus venosus*, but behind and a little higher, and completely unconnected with it, still within the thorax. They each terminate in two branches, in order to form the *truncus arteriosus, or aortic bulb and arch*,* from which the innominata divide into the right subclavian and carotic arteries and the left carotic and left subclavian arteries; from these the principal main arteries supply the upper trunk and extremities, the neck, face, head, and brain. The blood, after circulating through these extensive regions, is returned by the jugular, facial, and subclavian veins, forming the superior venæ cavæ, which pour the whole venous blood of the upper region into the *sinus venosus;* and thus also is kept up the blood circulation, once established, before the development of the heart.

I think it is necessary at this stage to describe the order of the formation of the auricles and ventricles of the human heart from the single cavity of the membranous transparent conical sinus venosus, which initiates the first blood circulation entirely detached from the arterial circulation, as the embryonic blood circulating through the heart is entirely venous after it is filled by the inferior and superior venæ cavæ. The first addition was the ventricle, added to the base of the sinus venosus after several courses of circula-

* When Professor Sharpey pointed out the aortic bulb and arch as supplied with arterialised blood from the placenta, and that the heart was beginning to be developed as a long sac or dilated tube, while he figured the aortic arch and bulb (fig. 135, 5th ed.), terminated below by the horizontality of the semilunar valves, as described by Kölliker, he does not seem to have been aware that the heart was at the time in full action, but that the pure arterial blood could only have been supplied to the embryo by the mode first fully pointed out by me in describing the fœtal circulation a few years ago, and now repeated.

tion—also membranous, but connected by the auriculo-ventricular orifice, to allow the flux and reflux from the sinus or auricle to force the venous blood into the ventricular lobe immediately back and then down the ductus tube into the umbilicus current to the placenta, as already described, to be arterialised by the umbilical arterialising capillaries, and returned by umbilical arteries to the umbilicus, and down the hypogastrus into the common iliacs, and by the ascending abdominal aorta, circulating through the body without any connection with the heart, even after it consists of two auricles and two ventricles having muscular parietes.

Although it is necessary to describe the cavities of the heart as having discharged their blood, still there is no vacuum formed, as it is immediately filled up and supplied by the *venæ cavæ* in the same way as the skilful glass-blower keeps up a constant flame. This it is important to keep in view when the number of cavities of the heart becomes increased by the division of the auricles and ventricles. The circulation thus established from the *sinus venosus* down the *ductus venosus, umbilical vein,* to the *placenta,* by the contractile force of the heart, is continued upwards by the same force, as assumed by the older observers, who misstated the fact of the course of the blood up the *umbilical vein,* which is impossible, as the whole then contractile force of the heart drives the current of venous blood down, so that the arterial blood, without any distinct organic force, could not rise against the established current; while the correct course of the circulation now offered, besides the increased muscularity of the two umbilical arteries, formed from the greater area of the capillaries and small branches, can better assist the progress of the blood upwards.

After the embryonic blood circulation has been established as now stated, there depends from the primary *sinus venosus* at its base a ventricle through which the auriculo-ventricular orifice is pierced. By thus giving a greater superficial extent to the cavities of the heart, though still membranous, it is able to force the circulation through the whole substance of the rapidly increasing embryo. In the course of the second week this ventricle becomes divided by a septum, which, with the membranous coats of the primary heart, begins to be clothed in muscular parietes, thus acquiring much greater power to propel the circulation; still there is no change in the course of the embryonic blood circulation above described. The heart, entirely supplied with venous blood, without any connection with the arteries, is able to forward the blood to the placenta. The arterial blood, returning from the *placenta,* is conveyed entirely, as already stated, by the umbilical arteries, the hypogastric and iliac arteries, to the abdominal aorta, and upwards to form its two thoracic trunks, the aortic bulb and arch, from which the arterial blood is distributed through the upper part of the body, without having any connection whatever with the cavities of the heart. Soon after the truncus arteriosus is formed, the right thoracic aorta and its terminal branches are absorbed, so that the whole embryonic arterial blood circulation is then continued by the left aorta. A very interesting exception to this has lately occurred in Dr Handyside's dissecting-room of the Royal College of Surgeons, Edinburgh, where the left aortic terminal branch continued the supply of the arterial blood to the *truncus arteriosus,* or aortic bulb and arch, giving off the usual branches; but the right terminal branch, when removed from the aortic arch, passed behind the aortic bulb towards the left ventricle, and, as the pulmonary artery became connected at the close of utero-gestation with the lungs, carried the venous blood to be aerated and returned to the left auricle and ventricle under the pulmonic respiration.

Dr Morris Tonge, in the abstract of his paper on the semilunar valves of the aorta and pulmonary artery of the heart of a chick, as it appears in the "Proceedings of the Royal Society of London," quotes the evidence of Kölliker as the only embryologist from whom he got any information as to the development of the semilunar valves of the aorta and pulmonary arteries, and states that he had been unable to discover any later than his.

After the formation of the aorta and pulmonary artery by the division of the truncus arteriosus into two vessels, the large single arterial trunk forming the arch of the aorta gives off the main arteries distributed to the upper trunk and extremities, the neck, head, face, and brain, which continue to be distributed after birth. These have in the embryo been incorrectly described as branchial arteries, but even Reichert admits that they have no connection whatever with branchia, though he still describes them as visceral arches. The division here described is not of the truncus arteriosus itself, but merely the cutting-off of the lower terminal branch of the left aorta, excised, as it were, by the aorta itself; and a small tag of its coat, dependent from the concave arch of the aorta, seems to have originated the idea of the *ductus arteriosus*, which occurs nowhere in nature, but is distinctly stereotyped in all the anatomical text-books in the hands of the medical student, even in their latest editions, up to the important anatomy of Professor Gray of the St George's Hospital Medical School, which lately appeared in its voluminous and very fully illustrated edition. This will be fully noticed in the Appendix.

To return to the abstract of Dr Tonge, where he states that simultaneously with the development of the semi-lunar valves (which Kölliker describes as at first horizontally placed, and, thus obstructing the current of the blood from flowing into the thorax of the embryo, causes it as it were to rebound upwards to the main and primary branches from the arch of the aorta), Kölliker is quoted to have discovered, in the embryo of the seventh week, the semi-lunar valves already present in both arteries, but as crescentic growths projecting horizontally from the middle and epitherial coats of the arterial tubes like a three-rayed star. When they first become visible as distinct pockets he had not yet investigated.

The division of the *truncus arteriosus* is described by Rathke as occurring in birds and mammals by the formation on its interior of two oppositely situated longitudinal ridges, which then grow together throughout their whole extent, and completely divide the vessel into two lateral halves—the one representing the aorta, and the other the pulmonary artery. Dr Tonge remarks, though the semi-lunar valves are correctly stated by Kölliker to develop simultaneously with the division, he gives no information in which they are connected with it or the part of the vessel in which they originate, nor gives any drawings of them in their rudimentary state. Hence he was led to conclude that very little was known about them, but they seemed valuable as throwing some light on the congenital malformations of the heart. He accordingly, during 1865-7, investigated the embryo of the common fowl, as he had no opportunity of investigating either the human or other mammalian embryos on this point; but from the great likeness between the hearts of birds, mammals, and man, at different periods of their development, it seemed pretty certain that the arterial semi-lunar valves in all these warm-blooded classes would pass through the same stages of development, and when fully developed would be quite similar.

He then proceeds to describe his well-contrived experiments on the development of the chick in embryo, in the fecundated hen's egg incubated by artificial heat, and the "heart of more than fifty such embryos at various stages of development were examined." The embryos were prepared by immersing them in strong alcohol immediately after they were carefully removed from the egg. By this means the large vessels distended with blood were obtained in a hardened condition; they were afterwards rendered transparent by soaking them in strong glycerine, in which they were dissected and examined by strong transmitted light, and afterwards mounted in glycerine jelly.

The new facts observed demonstrate—1. The manner in which the *truncus arteriosus* divides into two vessels different from those commonly supposed to occur. 2. The close connection between this process of division and the formation of the semi-lunar valves of the aorta and pulmonary artery, and their place of origin and mode of development.

Dr Tonge then gives a brief account of the manner in which he thinks the division of *truncus arteriosus* takes place. It should be said that about the third day of incubation, just before the division begins, the somewhat spirally twisted (?) *truncus arteriosus* is everywhere smooth and free from ridges on its interior, ending abruptly in three pairs of branchial arches which then exist—these are the third, fourth, and fifth pair. There is no valvular apparatus at its branchial end, but next the ventricle the deficiency of valves seems to be supplied by a considerable development of the elastic wall of the truncus arteriosus, so that the original circular form becomes slit-shaped, whose two lips seem to prevent in a great measure the reflux of blood into the ventricle before the semi-lunar valves are sufficiently developed to do so.

The division of the vessel commences about the 106th hour of incubation, rather less than a fifth of the whole period of twenty-one days—equal to four days and ten hours of incubation.

It begins at the branchial end or upper part of the *truncus arteriosus* by extension into it of a plain septum growing horizontally downwards from the terminal arterial wall between the openings of the fourth and fifth pair of branchial arches ; its lower margin is forked, so that it extends further along the sides, inclined a little obliquely across the vessel, sloping downwards from left to right ; the little channel in front of this septum leads to the third and fourth pair of branchial arches, and is the rudimentary aorta ; the channel behind it leads to the fifth pair, forming the rudimentary pulmonary artery. At the same time, or slightly before it, the canal of the vessel just below the septum becomes constricted by the formation,—1. On its interior and left surface of two flattened prominences, separated by a groove, which are the rudiments of the anterior semi-lunar valve of each artery ; 2. On its anterior and right surface of a flattened ridge, extending obliquely across the vessel, nearly opposite the rudimentary anterior valve, afterwards becoming prominent and pyramidal in the centre, and extending gradually down the surface of the vessel ; the right and left ends of this ridge are the rudimentary inner semi-lunar valves of each artery. As these growths enlarge, the forked septum grows downwards in the artery, twisting gradually from left to right, its left leg passing between and separating the rudimentary anterior semi-lunar valve, and its right leg growing into the central portion of the oblique ridge on the posterior surface, now becoming prominent and pyramidal, separating from each other the rudimentary inner valves. Between the outer and inner semi-lunar valves of each artery there exists a vacant space on the walls of the vessels, from which the outer semi-lunar valve in each artery, which appears later than the others, afterwards grows out. The division of the truncus arteriosus proceeds by the gradual growth downwards of the forked septum along the course of the ridge, on the posterior surface becoming gradually more prominent, the right leg of the fork being always a little in advance of the other. The anterior or left leg of the fork corresponds with the right margin of the anterior aortic valve, and terminates almost immediately on the anterior surface without forming a ridge, as there is along the posterior. As the forked system between the aorta and pulmonary artery grows down the vessels, the semi-lunar valves gradually become more and more developed ; the rudiments of the outer valve appear about the 117th hour of incubation, by which time the aorta and pulmonary artery are closed in by the horizontally placed semi-lunar valves, but entirely unconnected with the heart till near the close of incubation, though a preparation is being made for the pulmonary circulation. The 117th hour of incubation is nearly the fifth day.

Beyond this point it is at present unnecessary to quote from Dr Tonge.

I consider a much simpler mode of accounting for the division of the pulmonary artery from the aorta, is the arrangement of the thoracic aortæ already described, each dividing into two terminal branches connected with the bulbus arteriosus, conveying the arterialised blood from the placenta upwards, each branch being supplied with the horizontally placed semi-lunar valves, as well as the truncus arteriosus itself, as shown by Kölliker, and also in Quain's Anatomy, 5th edit., fig. 135.

The right aortic trunk and its terminal branches, as already noticed, having been absorbed, the whole circulation is now continued by the left aorta, instead of the complex arrangement given of the division of the truncus arteriosus about the third day of incubation, just before the division begins, ending in the three pairs of branchial arches. The whole circulation is continued by the left aorta till its lower terminal branch is simply cut off by the action of the tube itself, and left lying in the upper-middle cavity of the thorax, to be afterwards connected with branches to the lungs on both right and left sides. While this lower branch continued in connection with the aorta there did not exist any connection with the heart, which lay at some distance below it; any appearance of tissue depending from the lower arch of the aorta could only be left by the lower branch thus cut off. I suppose that this led to the fanciful idea of the ductus arteriosus crossing through both auricles of the heart onward to the descending aorta. Judging from the diagrams usually promulgated through the anatomical text-books, it is entirely gratuitous, and repeated from one to another without any authority from nature.

Referring again to the formation of the semi-lunar valves and their connection with the division of the truncus arteriosus, Dr Tonge notices the following as the new facts arrived at with respect to their origin and development:—

1. It is a remarkable fact that the rudiments of the semi-lunar valves first appear in the interior of the bulbous arteriosus at a *considerable distance from the heart* (at this time entirely disconnected with the heart), — near the origin of the branchial arteries, and not near the heart, as one might have been led to expect.

2. It is also very remarkable that the anterior and inner semi-lunar valves of each artery appear before the partition which has already begun to separate the aorta from the pulmonary artery, and has quite descended to that part of the truncus arteriosus in which these valves originate.

3. That the rudiment of the outer valve in each artery arises from the inside of the wall of the truncus arteriosus left vacant by the anterior and inner valves about the fifth day of incubation.

4. About the 144th hour of incubation they are still solid, and distant from the heart, and sufficiently deve-

loped to close completely the vessels, preventing the escape of the blood into the thorax.

5. The pocketing of each valve commences as it appears, and at the 147th hour, about the end of the seventh day or first week of incubation, the whole arterial branches are still entirely disconnected with the heart; and this course of the embryonic blood-circulation continues unchanged till preparation is being made for the alteration of the pulmonic respiration, towards the close of utero-gestation in woman, about the thirty-sixth week or later, though somewhat earlier where premature birth occurs, along with the expansion of the lung cells by admission of air on the first inspiration. Should the pulmonary circulation be admitted previous to the expansion of the lung cells, still-birth will be the consequence, which cannot occur in the case of the chick *in ovulo,* as by the time that the preparation is being made for the pulmonic circulation the chick lies in the cavity of the egg-shell, nearly entirely relieved of the yolk and albumen, except what is left necessary for the rotation of the chick in the altered position of the egg; the size of the primary air-vessel being increased, through the perosity of the egg-shell, from the external atmosphere, which now entirely fills the space not occupied by the chick, whose position had changed, at the beginning of the third week, from lying across the long diameter of the egg to the long axis, during which process the pulmonary circulation had been completed.

Having thus traced the course of the human embryonic blood circulation during the first three months of utero-gestation, it will be found that it continues in the same course as just stated till about the thirty-sixth week, or a little later.

During the last month of utero-gestation, in a fœtus born at the full time (a considerable change takes place in preparation for the pulmonary circulation somewhat earlier in those weakly seven-month children, who continue to struggle through existence for a few years), there is considerable activity in extending the development of the heart, which is described by Quain and others as existing, at first appearing as an elongated sac or dilated tube lying on the fore part of the embryo (evidently the superior vena cava), and having two veins connected with it from behind (evidently the Cuvierian canal and venæ cardinalis). Very soon this tube, acquiring contractile walls, becomes curved and bent on itself, projecting on the neutral aspect of the body. From the form of the arch of the aorta, as given in the 135th fig. of Quain's Anatomy, it represents, entirely isolated from the heart, as in the embryonic condition, the aortic bulb and arch closed in by the horizontally placed semi-lunar valves; and this part of the circulation in the embryo can only be supplied with placental blood in the manner stated in this communication, and ineffectually submitted to anatomists and physiologists for reconsideration for the last thirty years.

Referring to the description already given of the formation of the heart, first, as a single cavity connected with the placenta by the ductus venosus and umbilical vein, and continued by the return to the embryo by the umbilical arteries connected with the arterial circulation upwards in the embryo, as already described, this course of the blood continues after the number of the cavities of the heart have been increased by the addition of a ventricle, and its subsequent subdivision by a muscular septum into right and left, the whole being enclosed in muscular walls, and also the auricula with its muscular wall subdivided in the course of the second month by the extension of the septum ventriculi, separating the auriculo-ventricular orifice into two, and then extending upwards, dividing it into right and left auricle, but not so completely as in the case of the ventricles, and leaving the foramen ovale in the centre to allow of the flux and reflux of the venous blood, to pass and repass through the whole cavities of the heart in order to be sent to the placenta. About the time now specified there is a considerable activity in the development of the heart and its cavities; the first mesial septum begins to be altered by the increased growth of the heart, the apex gradually turning towards the left, while the base of the heart inclines to the right side; still, the embryonic blood circulation continues in the same course as at first.

The next altered direction occurs at the time specified, preparing for the pulmonic circulation; the right ventricle gradually rises upward over a portion of the left ventricle and auricle, dipping into the mesial portion of the thorax, and forming the infundible of the right ventricle. The same activity takes place in the left ventricle to form its infundibular extremity under the right auricle, and rising upwards towards the *truncus arteriosus* or *aortic bulb.* Concurrently with the active development of the infundibular portion of the ventricles, the terminal branches also extend to unite with them; thus the right ventricle at once communicates with the terminal branch of the aorta separated to form the pulmonary artery, and sends its whole blood by two branches, right and left, into the lungs, which if the lung cells have been expanded by the first inspiration, is at once returned from each lung by two pulmonary veins, which, from carrying arterialised blood, perhaps ought to have been described as arteries. It is not a little interesting that there should be a marked coincidence in regard to the vascular state of the placental circulation by a single venous trunk, carrying the whole venous blood into the placenta, and its return arterialised by two umbilical arteries; and that in the pulmonic circulation the whole venous blood from the right ventricle by the single pulmonic artery should be sent to the lungs by a single vessel, and return from each lung by the two pulmonary veins, carrying arterialised blood first into the left auricle and left ventricle onward through the aorta into the arch, distributing its contents to the upper trunk and extremities and head, and onward, now turning down its current through the single aortic trunk in its descent, the various arteries of the thorax, and continuing through the arches of the diaphragm into the abdomen, supplying the same arteries in its descent as in its embryonic ascent, and at length dividing into the common iliacs at the same point of the vertebral columns where it united to form the single ascending abdominal aorta, the circulation through the system being conducted by the arteries, while the placental circulation is cut off at birth. This change completely alters the course of the adult from the embryonic circulation, without the jumble required to support the established theory of fœtal circulation.

On the Sources of the Venous Circulation.

Van Baer has no doubt whatever that the blood circulation commencing in the area vasculosa is distributed through all the tissues and vessels of the embryo from its earliest appearance in the veno-vascular circulation of the graafio-germ blotch. The first circular area vasculosa, consisting of dark venous blood molecules, gradually divided by deep clefts, as described by Wagner, isolated from one another, in which a yellow lymph may be perceived in motion, advancing on the blastoderm or germ membrane from the centrachord in the Cuvierian canal, on each side of which the venæ cardinales, filled with venous blood from the azygeal sinuses, projected forwards to the primary sinus venosus a transparent contractile conical sac, at first filled with yellow fluid from the Cuvierian canal, being the *plasma sanguinus*, filling the first *sinus venosus*, which receives the two venæ cavæ, and whose only outlet is for the discharge of its yellow lymph contents down the *ductus venosus* behind the peritoneum, the liver, and intestines, towards the *umbilicus*, where it enters the *umbilical vein*, which continues the venous fluid towards the *placenta*. Here the venous contents are distributed through the capillary area of the *placenta*, and in the minute rootlets of the *umbilical arteries*, and, entering larger and larger branches, at length form principal trunks, which, ramifying under the membrane connected with the umbilical cord, at length unite to form an umbilical artery from each end of the *placenta*, which return by the cord to the embryo accompanying the umbilical vein. On entering the umbilicus, each artery is continued separately by a hypogastric artery into the common iliac arteries in the fœtus, conveying the whole arterialised blood from the placenta.

As there is no other vascular connection between the placenta and the embryo, there can be no other means of transmitting the arterialised blood to the embryo; and as the whole contractile force of the *sinus venosus,* on the impulse of the *punctum saliens,* forces its venous contents down the *ductus venosus,* it is not likely that the established opinion, that the arterialised blood from the placenta to the embryo could force its way upwards against the current of the stream, impelling the whole current downwards; and as the whole connection is formed by the umbilical vein and two arteries, there is no means of connecting the placenta with the *omphalo-mesenteric arteries* assumed by the supporters of the established theory, though all their descriptions have no foundation, anatomically or physiologically, in nature. Although mistaking the nature of the blood circulating through the umbilical vein and arteries, they are anatomically correct in their connection with the embryo.

Returning to the pelvis, where the arterialised blood had been received by the common iliacs, a small part of which distributed to the lower trunk and extremities, and after circulating through these regions returns by the *inferior vena cava* to the heart, the main portion of the arterialised blood ascends upwards to the abdomen, and opposite the second lumbar vertebra (from the sacrum) the two streams of the aortal blood unite, are there contained and carried upwards by the abdominal aorta in a single tube, but in some degree acting as a double vessel, distributing from its right side the inferior mesenteric artery to supply *mesocæcum rectum,* and afterwards the superior mesenteric artery to supply the mesocolon as it ascends upwards to the right hypochondrion under the liver, and the transverse colon as it is festooned across to the left hypochondrion in a curve similar to the great curve of the stomach, and then downwards by the descending colon into the sigmoid flexure and rectum.

From the left side of the abdominal aorta the numerous aortic branches supply the small intestines, thus in a manner functionally acting as two vessels. The whole arterial circulation, through the extensive region of the intestines, returns the venous blood through the portal system along with that returned from the arterial circulation of the cœliac axis, embracing the gastric, splenic, and hepatic arteries. The venous blood from these, meeting the intestinal blood in the porta of the liver, and, after circulating through that important organ with the hepatic artery, separating the bile from the blood, is returned by the three hepatic veins into the vena cava, just before entering the right auricle of the heart.

To return to the *abdominal aorta:* just as it enters between the pillars of the *diaphragm* it gives off the *phrenic arteries* to supply that important muscle, and as it enters the thorax it is again subdivided into two aortic trunks, each passing upwards upon its own side of the *centrachord* as high as what becomes the *fovea cardiaca* of fifteenth dorsal vertebra from the sacrum, when the vertebral column is ossified. From this point the two aortæ suddenly bend forward to a point below which the *sinus venosus* had been previously formed, as already described. A little above and behind, and entirely unconnected with it, the two aortæ terminate in two branches, which unite to form the *truncus arteriosus*, or *aortic bulb* and *aortic arch*, from which the *innominata* afterwards divide into the right carotid and subclavian arteries and the left carotid and *subclavian arteries*, from which the *branchial arches* have been described, but incorrectly—as even Reichert admits they have no connection with *branchiæ;* they are in truth the arteries distributed to the upper trunk and extremities, the neck, face, head, and brain, and returned, after circulating through these important regions, by the jugular, facial, subclavian veins, to form the *superior venæ cavæ*, which pour the whole embryonic venous blood of the upper trunk, &c., into the sinus venosus of the right auricle of the heart, there blending the whole embryonic blood of the body to be forwarded down the *ductus venosus* to the *placenta*, thus completing one course of the *embryonic blood circulation*, early in the second week of *utero-gestation* supplying the whole body with pure unmixed arterialised blood, and avoiding the incongruous jumble of the established system.

Referring again to the veno-cruorine graafio-germ clot, there seem to exist the following venous systems :—

1. The azygeal veins, arising from the *sinuses* of the *chorda centralis,* in or upon the bodies or centres of the vertebral segments.

2. The subclavian and jugular, returning the venous blood from the head, upper trunk, and extremities, forming the superior vena cava, pouring their blood into the right auricle.

3. The blood from the lower trunk and extremities by the vena cava.

4. The portal system, from the venous blood arising from the mesocolon, mesentery, gastric, and spleen, meeting in the longitudinal fissure of the liver to form the portal system, which is at length, after circulating through the liver, conveyed by the three hepatic veins into the inferior termination of the vena cava just before it enters the right auricle.

5. To these may be added the venous circulation of the embryo.

In the early condition of the embryo the circulation seems to have been sufficiently completed in the *graafio-germ ovule* to permit its moving by its own automatic power as soon as it is ejected from the graafian follicle through the walls of the ovary into the expanded Fallopian fimbriæ in its onward journey down the oviduct. Should it, however, elude the grasp of the fimbriæ, and escape into the abdomen, it there, by its own automatic vascular power, grows like a parasite, and is developed without any previous preparation of uterine *dissidua veræ.* In this abnormal position it is occasionally so far developed as an embryo of the same age in the uterus, as particularly shown in an extra-uterine case described by Dr B. Hicks in the *Lancet,* where a fœtus was discovered lying immediately behind the walls of the vagina, so distinctly that, after cautious examination and consideration of the case, it was decided to remove it 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 embryo, with the circulation established, with the chorion within the ovule, enabling it to move about freely, and at the same time controvert the idea that the chorion is only added during its progress down the Fallopian tube. It is curious to observe that in these cases of extra-uterine gestation, the effusion of the *dissidua vera,* as it were preparing the *uterus* for the reception of the *ovule,* is generally spread out over the uterine surface. Dr Robert Lee has recorded one exception.

Several cases of a cardiac and other abnormal embryos might be here recorded to show the vague ideas widely entertained as to these interesting cases.

It must also be recollected the blood of the embryo circulation, in relation to the maternal vascular circulation, is a closed blood circulation, whether uterine or extra-uterine, especially before it adheres to the placenta in the third month of gestation, a period of frequent abortion, compactly clothed in its muco-muscular envelope with the first course of the embryonic blood repeated from the venous heart, whether as a single auricle or with the addition of the ventricle developed from its auriculo-ventricular basis, and even after the addition of the ventricular septum, which extends through the auricle, having the foramen ovale in its centre, to allow the whole venous blood to be circulating with the full heart force through placental circulation, returning to the umbilicus of the embryo by the umbilical arteries. These are continued by the hypogastrics into the common ilias, a small portion circulating through the pelvis, lower trunk, and extremities ; but the main part of the arterial circulation is carried on by the abdominal aorta, which in the human embryo is a single trunk from the second lumbar vertebra above the sacrum, where, in the adult, the single abdominal aorta divides into the two common iliac arteries.

The embryonic arterial circulation is continued up to the truncus arteriosus by aortic bulb and arch, there checked by the horizontal position of the semicircular valves at the terminal branches of the aorta, causing the current of arterial blood, as it were, to rebound upward to what have been called branchial arteries. The arterial embryonic blood is thus circulated quite unconnected with the heart during the placental circulation, till preparation is being made for opening the pulmonary circulation.

This in the bird is during the third week of incubation, when the transition is completed more quickly without any risk of still-birth, as the chick in ovulo is already breathing pure air previous to chipping the egg-shell, and has been heard to chirp ; while the embryo in utero cannot break till born at the full time, or forty weeks, except in those premature cases when puny fœtuses of the sixth, seventh, or eighth month live only a few months.