X. *Observations on the Development of the Semilunar Valves of the Aorta and Pulmonary Artery of the Heart of the Chick. By* Morris Tonge, *M.A., M.D. Communicated by Dr.* Beale, *F.R.S.*

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In the accounts of the development of the heart of vertebrate animals given by various embryological writers, we find an apparently clear description of the mode in which the permanent aorta and pulmonary artery are formed by the longitudinal division of a single large vessel, the truncus arteriosus, into two vessels. The truncus arteriosus is, as is well known, the large arterial trunk that commences in the originally single ventricle of the heart, and terminates by splitting up into the branchial arteries. It conveys the whole of the blood from the ventricle to the system of the embryo, and is also known by the name of *bulbus aortæ* (see Plate XXXI. fig. 1). In studying the descriptions given by different authors of its division into two vessels, it appeared to me very strange that with such a clear description of the mode of division nothing at all, or only very little, should be said about the mode of development of the semilunar valves attached to the commencement of these vessels. Kölliker is the only author I have been able to find who makes any mention of their mode of development, and his account, which I shall presently quote, is very brief and unsatisfactory. Nowhere have I found any drawings of these parts in their rudimentary state. I was therefore obliged to conclude that very little was known about this point, probably in consequence of the difficulty of accurately examining such minute parts at an early period of development, and I was hence led to attempt the observations recorded in the present paper. They were made during the years 1865, 1866, and 1867, on the embryo of the common domestic fowl, artificially incubated. Though not nearly as complete as I could have wished them to be, they nevertheless demonstrate certain new and interesting facts connected with the development of the semilunar valves, and the formation of the aorta and pulmonary artery in the bird's heart. These appear to me to be valuable, as possibly throwing light on some of the congenital malformations of this part of the heart. In working at the development of the semilunar valves, I was also obliged to examine very closely into the mode of division of the truncus arteriosus into two vessels, and found that the manner in which it becomes divided differs from that usually described to occur in some very important particulars. The development of the semilunar valves is so closely connected with the process of division of the truncus arteriosus that I have found it best to unite the description of each stage of the one with that of the corresponding stage of the other.

As the satisfactory examination of these minute parts is difficult, and requires a peculiar mode of preparation of the embryo, I will first give a brief account of the method I followed successfully. It was obvious that these tissues being from the first highly elastic, and also contractile, would collapse immediately the circulation stopped, and in this collapsed condition it would be impossible to examine the anatomy of the interior of the vessel with any degree of certainty, the difficulty being enhanced by the softness of the tissues in their natural state. It seemed to me that this was the point where former investigators must have failed. The desideratum was to obtain the large vessels in a distended and hardened state, and at the same time transparent and fit for examination by transmitted light. To effect this the embryo immediately on its removal from the egg was immersed in strong spirit of wine, the sac of the amnion being first slit open, where this had closed up, in order that the spirit might come freely into contact with every part of the surface of the embryo. As the spirit permeates the tissues of the embryo, which it does rapidly, the capillaries and smaller vessels are soonest contracted by it, and the blood being thus prevented from escaping from the larger arteries before the heart's action is stopped, they become greatly distended. When this distension with blood reaches its maximum in the arteries, the blood accumulates in the cavities of the heart and in the large veins, the impediment caused by the closure of the systemic capillaries and small arteries acting backwards throughout the circulation. By this treatment it was found that the cavities of the heart, and the large vessels nearest to the heart, became fully distended with blood, and becoming coagulated and hardened by the spirit retained the distended condition. The embryos were allowed to remain in the alcohol for a few hours or days, according to their size, in order that they might become completely hardened. By careful management of the position of the embryo in the corked glass tube, I was frequently able to obtain a colourless clot in the large vessels, owing to the sinking of the corpuscles before the blood had coagulated or the spirit had penetrated the walls of the artery. The best position for obtaining this result was to keep the head of the embryo downwards, and the body a little inclined towards its dorsal surface. The embryos after being hardened in spirit were of course perfectly opaque, and could only be examined by reflected light till they had been rendered transparent. This was effected by soaking them in strong PRICE's glycerine for several days. After this the portions required for examination were removed, and dissected and examined in glycerine by strong transmitted light under a compound microscope fitted with an erector and a low power (1 inch). The hardness of the tissues permitted sections to be made readily in various planes, and their transparency under strong light enabled the course of the vessels distended with coagulated blood to be readily followed. Where it was required to examine the structure of the interior of the cavities of the heart and great vessels the coagula, if opaque, were first carefully picked out by needles: if a colourless coagulum had been obtained this troublesome process was often unnecessary. After dissection in strong glycerine the specimens were mounted for drawing and description. They were preserved in glycerine jelly, this medium retaining the specimen in any position in which it was required to be drawn or described, and allowing of its being readily altered to a fresh position where it was necessary that the same object should be seen from different points of view. The observations were made on more than fifty embryos in various stages of development, and the most satisfactory dissections were converted into permanent preparations. The preliminary experiments on artificial incubation, as well as on the best method of preparing the embryos, consumed much time. Much time and pains were also spent in conducting the incubating-process, and before I had gained experience the incubation of a number of eggs for several days often led to no result.

The account of my own observations will be best prefaced by quoting the statements of RATHKE and KÖLLIKER with reference to the development of this part of the heart; KÖLLIKER'S observations are the latest I have been able to discover.

RATHKE* says, "The anterior chamber of the heart remains single in fishes, and in them developes itself into the so-called bulbus aortæ (Herz-Zwiebel). In the Batrachia it lengthens itself, and forms the trunk for all the arteries of the body. This, however, does not remain so smooth and simple internally as on the exterior; but the wall of the anterior chamber of the heart while it lengthens sends inwards two longitudinal ridges situated opposite to one another, so that the cavity of the arterial trunk which arises from it becomes very incompletely divided into two lateral halves. The same developmental process is also remarked in Birds and Mammalia; in them, however, the two ridges become higher, then grow together throughout their whole length, and completely divide the hollow of the chamber into two lateral halves. When this has taken place, a division results by a resorption through the middle of the wall and newly formed septum of the anterior chamber of the heart; and this now becomes divided into two canals, of which one represents the commencement of the aorta, the other the commencement of the pulmonary artery. In the Snake, and probably also in other reptiles, three partitions arise on the inside of the anterior chamber of the heart, the free borders of which ultimately grow together, and so the chamber gets divided into three canals lying beside one another, of which one represents the commencement of the pulmonary artery, the two others the commencement of the two roots of the aorta." RATHKE'S description therefore relates solely to the division of the truncus arteriosus. With reference to the development of the semilunar valves he is silent.

KÖLLIKER'S† account of the division of the truncus arteriosus is as follows:—"Simultaneously with the formation of the septum of the ventricles proceeds also the division of the truncus arteriosus into the *pulmonary artery* and *permanent aorta*, which, though apparently only a continuation of the process which takes place in the separation of the ventricles, is yet to be distinguished from it. Thus while in the ventricles it is the muscular structure of the heart which grows out and ultimately developes itself into a complete septum, in the primitive aorta it is the vascular wall, having more the structure of connective tissue, that effects the separation. Therefore the division of the truncus arte-

* Entwickelung der Wirbelthiere, S. 82, pp. 187–188 (1861).

† Entwickelungsgeschichte des Menschen, pp. 404, 405 (1861).

riosus cannot be described as if it were formed by an inward growth of the ventricular septum, as also comes out in the clearest manner from the fact that in certain creatures the aorta divides at a time when the ventricle is still single. This is the case in the Viper, according to RATHKE, in which, at the time when the truncus arteriosus divides into three vessels, the ventricle still possesses no trace of a septum. Therefore, as RATHKE correctly observes, the cause of the division of the primitive aorta into two canals cannot with Von BAER be sought in certain peculiarities of the circulation, in a particular direction of the current of blood, but it depends solely and alone on particular developmental phenomena of the arterial wall. Now, concerning the peculiarities in man, I have in the fourth week found the truncus arteriosus still completely single, and with round *lumen* *. Transverse sections examined under the microscope already show clearly three tunics,—a thin tough *adventitia*, a strong clear *media*, and an inner cellular layer as *intima*. In the fifth week likewise the artery was still single, but its *lumen* was now flattened out transversely and slit-shaped. In the seventh and eighth week I found the vessel already completely doubled, and I was not here able to make out the intermediate stages, and to follow the gradual formation of the septum. I was more fortunate with calf embryos of 7‴–8‴ long; and I here first found an aorta with a *lumen* like a figure of 8, or, in other words, with two slight ridges in the interior, which resulted from growths of the tunica media, and, secondly, others which contained two *lumina* within a common *adventitia*, each of which possessed its own separate *tunica intima*, but connected *tunicæ mediæ*. In consequence of this it cannot well be doubted that the division of the truncus arteriosus essentially comes to pass by a growth of its middle coat, followed at a later period by that of the *adventitia*, which is, however, in Man effected very early, since even at the eighth week both the large arteries possess all their proper coats."

With respect to the development of the semilunar valves, he says, "Simultaneously with the division the semilunar valves also become developed, and I saw them already present in both arteries in an embryo of the seventh week. They are, however, at first nothing but horizontally projecting crescentic growths of the middle and of the epithelial coats by which the *lumen* at this spot receives the form of a three-rayed star. At what time they first become visible as distinct pockets I have not yet investigated."

I now pass on to my own observations. They were made only on the embryo of the fowl, as I have had no opportunity of investigating that of Man or any other mammalian animal. But from the great likeness between the hearts of Birds, Mammalia, and Man at different stages of their development, it seems pretty certain that the arterial semilunar valves in Man and Mammalia generally must pass through the same stages of devolopment as those of the Bird, which in the fully developed state quite resemble them.

As is well known, the heart of Birds and Mammalia in its earliest condition is a simple

* I have left this word untranslated because no single English word exactly expresses its meaning. It is obviously the bright area of the interior of a transverse section of the vessel held up to the light. This bright area being bounded by the inner edge of the transverse section, shows the form of the vascular canal at this point.

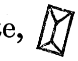
tube, into the hinder or caudal end of which the omphalo-mesenteric veins open, while the branchial arteries emerge from the anterior or cephalic end. This tube soon increases in length and capacity, and becomes doubly bent upon itself, so that its general direction is at first from the entrance of the veins towards the head and ventral surface of the embryo, then bending backwards towards the caudal end, and from left to right, and then again bending towards the head and ending in the branchial arteries. As the contractile muscular tissue augments about the bends, the cephalic or left bend gradually becomes developed into a rudimentary auricle, the caudal or right bend, and the portion of tube between it and the cephalic bend, into the ventricle, while the considerable portion of the tube situated between the caudal bend and the branchial vessels remains free, or almost entirely so, from muscular tissue, and forms the bulbus aortæ or truncus arteriosus (Plate XXXI. fig. 1). About the third day of incubation this large arterial trunk, into which the still single ventricle pours its blood, does not appear to be separated by any valvular apparatus whatever from the cavity of the ventricle. The vessel is twisted somewhat spirally after its exit from the ventricle, and the aperture of its transverse section is not everywhere circular, being oval or squarish at the bends. It is quite single and undivided throughout, and no ridges can be seen on its interior. It becomes gradually narrower as it approaches the point of division into the branchial arteries, in which it terminates abruptly. There is no valvular apparatus of any kind at the point of division into the branchial arteries, which are three on each side at this period. The first and second pair of branchial arteries have now disappeared; the third, fourth, and fifth pair remain, and unite posteriorly to form the descending aorta. The deficiency of valves seems to be supplied by a considerable development of the elastic wall of the truncus arteriosus next the ventricle. This does not take place equally round the opening into the ventricle, but occurs principally on two opposite sides of the interior of the vessel, so that the circular aperture of communication between the ventricle and truncus arteriosus gradually becomes slit-shaped.

The period at which the division of the truncus arteriosus into two vessels commences is, in the common fowl, about the 106th hour of incubation (four days and ten hours), or rather more than one-fifth ($4\frac{2}{5}$) of the whole period of incubation, which is twenty-one days. There are three branchial arteries on each side, but they do not now come off abruptly from the end of the truncus arteriosus. Looked at sideways, the two anterior or upper pair of arches are seen to be separated from the posterior or fifth pair by a partition just extending a little way into the branchial end of the truncus arteriosus (Plate XXXI. fig. 2). This partition does not pass quite horizontally across the vessel, but is slightly inclined upwards from right to left, and extends a little further along the right side of the truncus arteriosus than it does along the left side; it is in fact a prolongation into the truncus arteriosus of the arterial wall between the fourth and fifth pair of vascular arches, and separates the rudimentary aorta from the rudimentary pulmonary artery, the little channel leading to the third and fourth pair being the first trace of a separate aorta, and that leading to the fifth pair the first trace of a separate pulmonary artery. On looking from front to back (Plate XXXI. fig. 3) or from back to front through the septum between them, its cardiac edge is seen to be forked, so that it extends further along the sides than the centre of the vessel. Thus, as is well seen in the preparation from which the drawing was taken, the rudimentary aortic and pulmonary vessels are incompletely separated below, where they first leave the truncus arteriosus. That there now exist two channels distinctly separated from one another just above the forked septum is shown by a transverse section of the vessel at this point. Plate XXXI. fig. 5 is a drawing of such a section, looking from the distal side towards the heart. The section made a little lower through the forked part of the septum (Plate XXXI. fig. 6) gives the idea of two prominent ridges forming on the interior of the vessel, and being about to adhere. They are not, however, continued throughout the truncus arteriosus, a section through its central portion being nearly quadrangular and free from ridges (Plate XXXI. fig. 7), but at this period almost directly subside into the wall of the vessel (Plate XXXI. fig. 8). It is very remarkable that even at this early period, when the rudimentary aorta and pulmonary artery have only just appeared, the rudiments of some of the semilunar valves are already to be seen a little below the forked septum and at a considerable distance from the heart. The situation at which they first appear, and their position with reference to the rudimentary vessels, is roughly indicated in Plate XXXII. fig. 37. They are pretty accurately represented in the drawing (Plate XXXI. fig. 9) of this part of the interior of the truncus arteriosus. On looking into the lower end of the section, which has been made just below the rudimentary valves, they appear as somewhat flattened pyramidal projections, passing obliquely upwards on the wall of the vessel and separated by a triangular groove. These are the anterior aortic and pulmonary semilunar valve-rudiments, which are the first to appear. On examination by transmitted light their situation is indicated by a slight opacity of the vessel, which is constricted at this part. Their upper edges are situated just below the termination of the left leg of the fork of the septum, which can be seen above them (Plate XXXI. figs. 8 & 9), and which, as the septum passes down the vessel, gradually grows between these valve-rudiments, passing from the left side rather towards the front of the truncus arteriosus, and separating the anterior aortic from the anterior pulmonary semilunar valve. By the time that the partition has descended as far as these valves, they have become larger and more developed, and the rudiments of the inner semilunar valves have begun to appear. About the time that the anterior valve-rudiments appear, the right side and posterior surface of the interior of the vessel nearly opposite to them becomes thickened and rather prominent in the centre. This is the commencement of a thick pyramidal and somewhat rounded ridge that forms gradually along the posterior surface of the vessel. As the septum grows down the truncus arteriosus, the right leg of the fork becomes continuous with the central portion of this ridge, and follows its line obliquely down the posterior surface of the vessel from right to left, the left leg of the fork, as we have seen, passing down on the front of the vessel obliquely from left to right. The rudiments of the inner semilunar valves of the aorta and pulmonary artery grow out on each side of this pyramidal ridge. Its position and relations to the anterior valve-rudiments are shown in Plate XXXI. figs. 9 & 10, and also a little later, at the 115th hour of incubation in Plate XXXI. fig. 12. In consequence of these formations in the interior of the truncus arteriosus, its canal at the level of the upper margin of the rudimentary valves becomes irregularly slit-shaped, as in Plate XXXI. fig. 12, the long axis of the slit being inclined from the right downwards and to the left across the vessel. As the development of this portion of the truncus arteriosus proceeds, the part situated between it and the heart, and which is at this time free from ridges on the interior, seems to become somewhat shorter and wider.

About the same time, at the middle of the fifth day, or 108th hour of incubation, the opening into the ventricle is a somewhat rectangular slit having a direction nearly horizontally backwards (Plate XXXI. fig. 11) and a little from left to right. The left-hand lip of the slit is more prominent than the right-hand lip, the latter rather nearer the ventricle. A small triangular projection fills up each end of the slit. The lips of the slit are not quite parallel to each other, as the left-hand lip has an upward slope from before backwards. Thus the aortic and pulmonary streams of blood are already in process of separation.

At the next stage of development that I have been able to observe, at the 117th hour of incubation (four days twenty-one hours), the ventricle exhibits a very slight division by the still quite rudimentary septum of the ventricles. The ventricular end of the truncus arteriosus is still slit-shaped, the left lip of the slit running obliquely upwards and backwards, while the right is more horizontally situated and less prominent. Above this the canal of the truncus arteriosus is rather oval, the anterior surface of its interior being smooth and concave, without any appearance of ridges, while its posterior surface is already becoming convex by the formation of the lower part of the rounded ridge, which terminates by passing obliquely into the left lip of the arterio-ventricular slit, and which forms in the lower part of the vessel when scarcely any trace of it is to be seen in the central portion. The extension of the partition between the fourth and fifth pair of branchial arches has advanced still further down the vessel, so that the trunks of the rudimentary aorta and pulmonary artery, when filled with clot, are now distinctly seen by transmitted light (Plate XXXI. fig. 13), though there is not at present any indication of the division on the external surface of the vessel; owing to the advance of the outer semilunar valves of the rudimentary trunks, and the still slight development of the rudiments of the anterior and inner valves, the blood can still pass freely backwards from the aorta and pulmonary artery into the still undivided part of the truncus arteriosus, so that, as is seen in the drawing (Plate XXXI. fig. 13), the clot in the latter vessel is continuous with those in the former. As soon as the outer (lateral) valve-rudiments appear, by which time the anterior and inner rudiments have become still more developed, the clots in the aorta and pulmonary artery become cut off from the clot in the lower part of the truncus arteriosus, which clot is then small, though above the valves the vessels are quite distended. This is shown in Plate XXXI. figs. 14 & 15; the outer valve-rudiments are there just beginning to appear.

At the 130th hour of incubation (five days ten hours) we find that the pyramidal ridge on the posterior surface of the truncus arteriosus has become more developed at every part of it, being very strongly marked near the valves, only slightly so in the middle portion of the vessel, but again becoming prominent below, where it terminates by suddenly narrowing, and being slightly twisted on itself slants into the edge of the left lip of the opening into the ventricle, passing downwards and forwards. The channel for the pulmonary blood is represented by the deep groove that passes down the left side of the ridge, and terminates in the wide and sloping surface of the left lip of the slit. The groove on the right side of the ridge forms the channel for the aortic blood, and passes almost directly downwards to the posterior end of the slit. Thus the aortic groove passing directly downwards, the pulmonary groove, which is at first situated to its left, gradually twists round the lower end of the ridge separating the two, and expanding out below opens obliquely into it. The figures 16, 17 & 18 are drawings of a section of the truncus arteriosus at this period, which includes the valves and the descending septum, and shows pretty clearly the mode in which the vessel is dividing and the stage of development attained by the valves. In Plate XXXI. figs. 17 & 18, the shape of the rounded pyramidal ridge is well seen. A prominent convex ridge separates the two free convex and sloping sides of the pyramid. Below it is almost lost on the wall of the vessel, whose canal is almost circular a short distance below the valves. Above it projects forwards into the vessel for about two-thirds of the diameter of the vessel at the apex of the fork of the descending septum, and it represents what was originally the right leg of the fork. The other leg of the forked septum is represented by a slighter ridge, which bounds the rudiment of the anterior aortic valve on the left, and is very soon lost on the wall of the vessel. The fork of the septum grows down the vessel along the course of the prominent posterior ridge, and on the anterior aspect of the vessel along the slighter ridge to the left of the anterior aortic valve and the adjacent part of the groove separating the anterior aortic from the anterior pulmonary valve. This anterior portion of the fork is, as we have seen, very slightly marked, and is very soon lost on the wall of the vessel. The posterior ridge is, on the contrary, already distinct along the whole of the truncus arteriosus, though most so above and below. At no time during the division of the vessel does the anterior portion of the fork of the septum extend for more than a very short distance along the anterior surface of the artery; so that the division cannot be correctly described as occurring by the formation of *two* longitudinal ridges situated opposite to one another, and their subsequent growth together throughout their whole length, as RATHKE states to be the case, but must be described as taking place by the growth down the vessel of a forked septum which extends into the vessel nearly horizontally from between the fourth and fifth pair of branchial arteries, and which has already separated the rudimentary aorta and pulmonary artery before any *ridges*, properly so called, have appeared in the vessel, and which subsequently follows the course of a single prominent pyramidal ridge which forms gradually along the whole of the posterior surface of the vessel, being at first a little on its right side, and afterwards a little on its left. The septum, therefore, grows down the truncus arteriosus in a *spiral* twisting from left to right.

The position and shape of the cardiac surfaces of the rudimentary semilunar valves at the 130th hour is also shown in Plate XXXI. figs. 16, 17, 18. The anterior valves are the most developed, and the outer and inner valves are formed on the same type. They are best described as solid pyramidal growths of the vascular tissue, and have very much the shape of a short crystal of triple phosphate, , the flat base being attached to the wall of the artery, while the sloping ends look upwards and downwards, and the edge projects into the centre of the vessel. This edge is sometimes a little flattened or notched. The upper ends slope upwards and are not at first horizontal, though sometimes slightly concave. The inner semilunar valve of each artery is seen to have a similar form to that of the anterior valve, and to grow out from the corresponding convex side of the posterior pyramidal ridge, into which their sloping lower ends are continued. The main purpose of this very prominent portion of the posterior ridge seems to be to afford a sufficiently large surface on each side for their attachment and continuous development, as well as a firm basis of support for them against the pressure of the blood-column in the rudimentary trunks. The anterior valves have a sufficiently large and firm basis of attachment in the anterior wall of the vessel, and the presence of a very prominent ridge between them would interfere with their development and narrow the artery unnecessarily. We find, therefore, that they are separated only by a very slight edge and a groove. The lateral or outer valves of the aorta and pulmonary artery have just appeared. That of the aorta is well seen in Plate XXXI. fig. 18. It originates nearly opposite to the other valves at the outer portion of the vessel. It has the same pyramidal shape, but is more notched on the inner edge; and if this notch deepens much, the single valve may develope into two valves. The outer valve of the pulmonary artery appears about the same time as the outer aortic valve; it is similar to it in shape, and similarly situated with respect to its fellow valves.

From the foregoing observations it will be seen that KÖLLIKER's statement, that the semilunar valves are at first nothing but horizontally projecting *crescentic* growths, cannot be accepted as quite applicable to them in this early period of their development.

Ten hours later, at the 140th hour of incubation, we find that the division between the aorta and pulmonary artery has extended much nearer the heart, and that the rudiments of the outer valve in each artery having become more developed, the reflux of blood into the still undivided portion of the truncus arteriosus is very inconsiderable. Plate XXXI. fig. 19 shows the appearance of this part viewed from behind by transmitted light. The clots above the semilunar valves have been removed. The channel followed by the pulmonary blood is indicated by the direction of the clot in the undivided portion of the vessel, and passes obliquely upwards across the anterior part of the truncus arteriosus. The aortic blood passes directly upwards from the ventricular opening towards the aorta, at the posterior part of the vessel. The upper surfaces of the valves are shown in Plate XXXI. figs. 20 & 23, and the upper surface of the anterior valve in each artery is also seen in Plate XXXI. fig. 19, in which figure the profile of the inner and outer valves is also seen. The valves are still quite solid. Their upper surfaces slope upwards from the centre towards the periphery of the vessel, and are slightly concave, especially in the case of the anterior valves. The inner valve of the pulmonary artery and the outer valves of both vessels are seen to be distinctly notched; they do not yet accurately close the canal of the vessel when it is fully distended, so that an irregular aperture is seen in the centre. It does not receive exactly the form of a three-rayed star till some hours later.

The present form and position of the lower forked margin of the descending septum is seen in Plate XXXI. fig. 21. The plane of the septum passes across the vessel from before directly backwards, and the lower forked margin is now very distinctly seen to be formed by the union of the prominent posterior pyramidal ridge with the slighter anterior ridge bounding the anterior aortic valve on the left, and being almost immediately lost on the anterior wall of the vessel. On either side of the fork are seen the apertures of the aorta and pulmonary artery, and the pyramidal prominences of the anterior and inner valves. The under surfaces of the valves are a little more rounded off; the outer valves are still not very conspicuous from below. In Plate XXXI. fig. 22 the shape of the opening into the ventricle is shown. It is no longer a slit, as its two lips have been gradually undergoing the changes by which its anterior portion ultimately becomes the upper part of the infundibulum leading into the pulmonary artery, while the posterior portion becomes the upper part of the aortic infundibulum. This is effected by a widening of the fissure, principally at its ends, by an absorption or arrest of development of the ends of each lip of the fissure, while the development of the central portion proceeds uninterruptedly, and by the hollowing out of the upper surface of the front of the posterior lip. A prominence is thus left about its centre, in which the posterior pyramidal ridge terminates below. The anterior portion of the forked septum ultimately grows into the remains of the central part of the right-hand lip of the fissure. During the time that these changes have been going on the septum of the ventricles has been gradually growing up between the left and right ventricle, and has now attained a considerable development. An oval aperture exists in its upper part, and leads from the left into the right ventricle. This aperture has a right border opening into the right ventricle, and a left border opening from the left ventricle. The anterior part of the right border becomes continuous with the central part of the posterior or left-hand lip of the arterio-ventricular opening, and therefore with the lower end of the pyramidal ridge on the posterior surface of the vessel. At a later period the posterior part of the lower half of the right border of the septal aperture bends round so as to become continuous with the central portion of the anterior or right-hand lip of the arterio-ventricular opening. The bearing this has on the union of the septum between the aorta and pulmonary artery with the upper part of the ventricular septum will be presently described. Where this union fails to occur, a permanent aperture of communication remains between the right and left ventricle.

Later still, at the 144th hour of incubation, or the end of the sixth day, the semilunar valves are sufficiently developed to prevent the reflux of blood through them, though they are still quite solid. Accordingly we find the aorta and pulmonary artery distended by large clots, while the portion of the truncus arteriosus below them is empty and collapsed, or only has a small clot extending into it from the ventricle. The trunks, however, still exhibit no separation externally, though, as is seen in Plate XXXI. fig. 24, their right and left branches are separating. This drawing (the auricles and sides of the ventricles having been removed) shows remarkably well the considerable distance still separating the arterial aspect of the semilunar valves from the bases of the ventricles, owing to the great distance from the heart at which their rudiments first appear. A small channel between the edges of the valves is seen leading downwards from either vessel, that from the pulmonary artery taking a sweep forwards towards the anterior part of the base of the right ventricle, while that from the aorta passes directly downwards towards the oval opening in the interventricular septum. The appearance of the semilunar valves, as viewed from above, is seen in Plate XXXI. fig. 25. They are three in each artery, are still solid; their upper surfaces, very slightly concave, are now nearly horizontal, and the *lumen* of the vessel at this point, owing to their close approximation, now possesses the form of a three-rayed star. This seems to me to be the stage of their development described by KÖLLIKER, though the valves can still scarcely be called crescentic. The edge of each pyramid that projects into the central canal of the vessel is prolonged for some way down the wall of the undivided portion of the truncus arteriosus towards the ventricles. On looking upwards through the lower end of the section, therefore, as shown in Plate XXXI. fig. 26, we see little angular projections of the vascular wall into the collapsed canals of the aorta and pulmonary artery, which are the lower portions of the rudimentary valves cut across. One of these (inner valve) is seen on each side of the section of the posterior ridge. The enormous development of this ridge, compared with that of the very slightly marked edge forming the left border of the anterior aortic valve, is well seen. The aortic and pulmonary channels are seen to communicate below the valves in front of the posterior ridge.

At the earliest period of the development of the heart the two lips of the opening between the ventricle and truncus arteriosus appear to exercise a valvular function, preventing in a measure the reflux of blood from the truncus arteriosus into the ventricle. As the slit widens, the valvular function gradually becomes less and less, and at the period of development just described is completely abolished.

The next stage in the development which it is important to notice is soon after the end of the sixth day, at the 147th hour of incubation. The development of the heart is now advancing with great rapidity; its appearance at this time, as seen by transmitted light, is shown in Plate XXXI. fig. 27, and Plate XXXII. fig. 28. The breadth of the aorta and pulmonary artery and of the valves has increased very much, and the division between the vessels has descended so very close to the base of the heart that the undivided portion of the truncus arteriosus has disappeared externally, the bases of the semilunar valves being now on a level with the bases of the ventricles. The root of the pulmonary artery now has a position in front and a little to the left of the root of the aorta, which is becoming hidden behind it. There is still, however, no division externally between the large trunks. The semilunar valves, both aortic and pulmonary, are still more developed in the direction of their depth than transversely; they are still solid. Their upper surfaces are horizontal or slightly concave, and hollowed near the arterial wall, as is well seen from the shape of the base of the large coloured clot which fills the pulmonary artery: this shows that the hollowing-out process, by which they become membranous, is just commencing. The development of the valves proceeds by the gradual hollowing out of the solid pyramidal mass of tissue above and next the arterial wall, while it grows at the sides and below and towards the middle of the artery. The oval aperture of communication between the ventricles is still open; but its channel is becoming more and more directed towards the aorta, and less towards the right ventricle (Plate XXXI. fig. 27). The septum of the ventricles has become much thicker. The margin of the left opening of the channel through the septum is becoming rounded off, so that the canal is funnel-shaped towards the left ventricle. The lower part of the orifice into the right ventricle afterwards closes up, while the upper part leading to the aorta, as well as the funnel-shaped canal leading from the left ventricle, remain permanently open, and become the infundibulum or sinus of the aorta. At the sixth day, and earlier, the orifice in the interventricular septum is seen to be formed of a connective tissue-like structure, similar to that of the adjacent portion of the truncus arteriosus, and quite distinct from the muscular substance of the lower portion of the septum.

At the 165th hour of incubation the union of the upper part of the ventricular septum with the forked lower border of the division between the aorta and pulmonary artery, which has now quite reached the base of the ventricles, is approaching completion: in other words, the separation of the infundibulum or conus arteriosus of the aorta from that of the pulmonary artery is now nearly effected. The drawings (Plate XXXII. figs. 29, 30, 31) from hearts that had been incubated for this space of time (six days twenty-one hours) show the appearance of the right ventricular border of the orifice in the interventricular septum, and of the under aspect of the semilunar valves, and of the division between the vessels. Figs. 30 & 31 were taken from a heart whose development was further advanced than in fig. 29, and show the mode in which the separation between the aortic and pulmonary blood becomes completed.

The lower border of the partition between the aorta and pulmonary artery now appears as a thick round ridge on the left side of the termination of the truncus arteriosus, arching over above and becoming lost on the interior of the right side of the junction of the truncus arteriosus with the right ventricle; its vertical plane is nearly at right angles to that of the septum of the ventricles. The pyramidal inner semilunar valves are seen projecting from either side of this rounded ridge into the orifices of the aorta and pulmonary artery respectively. The other semilunar valves are seen growing from the wall of the vessel. Viewed from below, they still have a pyramidal shape. The left ventricular border of the channel through the septum of the ventricles has become more sloped off. The right ventricular border is seen in Plate XXXII. fig. 29. It forms an oval orifice whose upper half is sloped and rounded off towards the aortic orifice just above it, to which the channel through the septum is directed. Its lower half is sharp and well defined, and the anterior part of this, near its junction with the upper half, passes off obliquely into the rounded ridge on the left side, which forms the greater portion of the division between the aorta and pulmonary artery; this is well seen in Plate XXXII. figs. 29, 30, 31. As the completion of the partition proceeds, the posterior part of the sharp and well-defined lower margin of the orifice grows off at its junction with the upper half sharply upwards and outwards to the right, bending round the upper part of the inside of the base of the right ventricle, and then passing forwards to join the right side of the division between the vessels, where this loses itself on the wall of the pulmonary infundibulum a little below the remains of the central part of the right leg of the arterio-ventricular fissure. This process is just commencing in Plate XXXII. fig. 29. In Plate XXXII. figs. 30 & 31, it has proceeded to a considerable extent, and the aortic and pulmonary infundibula now communicate by an hourglass-shaped aperture whose plane is twisted on itself, so that the portion on one side of the constriction of the hourglass is nearly at right angles to that on the other. The closure of this aperture by the growth of its margin all round completes the separation between the aortic and pulmonary infundibula. If we consider it closed by an imaginary plane surface, the course of the plane will be at first vertically downwards, then gradually *twisting* from left to right, and at the same time *bending* towards the left. Plate XXXII. fig. 38 further illustrates the mode of completion of the division between the two infundibula, which are already beginning to assume their ultimate positions with respect to each other.

The anterior and inner semilunar valves of the aorta and pulmonary artery are just beginning to form pockets, the part corresponding to the corpus arantii, and the margin of the valve generally, being very thick and solid. The outer valves as yet do not form pockets, and their development is less advanced than that of the other valves, as it has been throughout. In the preparation from which figs. 30 & 31 were taken, there are four valves in the pulmonary artery, the outer valve-rudiment having split into two valves. The valves do not appear to descend any more towards the ventricles in their further development, but remain nearly stationary in position, the further descent of the partition merely completing the arterial infundibula below them.

The trunks of the aorta and pulmonary artery are now beginning to separate externally, and about the middle of the eighth day, at the 180th hour of incubation, the large vascular trunks have become quite separate down to the semilunar valves, and have attained almost their final relative positions. The aperture of communication between the arterial infundibula has closed up till it is now only a semilunar slit, and the thick rounded ridge on the left side of the termination of the truncus arteriosus forms the principal part of the septum between them. The semilunar valves of each artery are larger and more developed, and the sinuses of Valsalva are beginning to appear; but there is still no pocketing of the outer valves. They are shown in Plate XXXII. fig. 32.

About the end of the eighth day, at the 189th hour of incubation, the aperture in the infundibular septum is a very minute slit, and very soon afterwards is quite closed up. The anterior and inner valves of each vessel are more membranous, with a solid pyramidal corpus arantii; the lateral valves are just beginning to pocket. The valves have gradually become semilunar in shape when viewed from below.

The latest period at which I have been able to observe the development of the valves is the thirteenth day of incubation. They are then miniatures of those of the heart at full term, though rather thicker in comparison with their area. This is still more the case a few days earlier. Hence the principal changes in them after the closure of the infundibular aperture seems to be an increase in area and gradual diminution in thickness, so that, concurrently with the increase in size and strength of the other parts of the heart, they gradually assume the membranous form characteristic of the perfect valves. The great vessels are now quite separated down to their roots, and the heart itself presents externally very much the appearance of the adult heart.

Recapitulation.

I will now recapitulate briefly the principal steps in the formation of the aorta and pulmonary artery.

At first, just before the division commences, the truncus arteriosus, round and smooth on the inside, ends abruptly in the three pairs of branchial arteries, third, fourth, and fifth, which then exist. It is slightly thickened round its ventricular aperture.

Then, at the 106th hour of incubation, the division between the fourth and fifth pair of branchial arteries extends nearly horizontally into the vessel, as a plane septum with forked margin. At the same time the canal of the vessel just below this becomes constricted by the formation almost simultaneously,

1°, on its anterior and left surface, of two flattened pyramidal promimences separated by a groove—the rudiments of the anterior semilunar valve of each artery;

2°, on its posterior and right surface of a flattened ridge, afterwards becoming prominent and pyramidal, and extending gradually down the posterior surface of the vessel.

As these growths enlarge, the forked septum grows downwards into the artery, twisting from left to right, its left leg passing between and separating the anterior prominences, and its right leg passing along the central portion of the posterior ridge.

By the time the forked septum has reached the part where the anterior valve-rudiments first appeared, these are more distinctly developed, and the rudiments of the inner semilunar valves of each artery have begun to grow out from the posterior ridge on each side of the septum, an unoccupied space being left on the wall of the vessel on each side for the development of the outer valve in each artery.

During these changes the aperture into the ventricle has become a slit with two lips, a left-hand and a right-hand lip, the left-hand lip sloping from before backwards and upwards into the artery. The central portion of the vessel remains smooth and free from ridges on its inside, but along the posterior surface, above and near the ventricle, the pyramidal ridge forms, which ultimately joins the left-hand lip of the ventricular slit.

As the forked septum grows down the vessel, the semilunar valves gradually become more developed, and the outer semilunar valve in each artery appears. The leg of the fork which proceeds along the posterior ridge is always prominently developed, while that on the anterior aspect of the vessel is but slightly marked.

By the time the division has reached the ventricular aperture, the original right-hand leg of the fork has wound round to the centre of the left-hand lip of the slit, the left leg to the centre of the right-hand lip, so that the aortic channel has passed from front to back, the pulmonary channel from back to front. The way the septum twists down the vessel is shown in the diagram of imaginary cross sections of the vessel just above the lower margin of the division at different periods (Plate XXXII. fig 39).

During the division of the vessel the ends of each lip of its ventricular orifice have gradually disappeared so as to leave the central portions prominent, and a channel in front and to the left, and behind and to the right. These channels become the roots of the aorta and pulmonary artery, by the growth of the forked septum into the prominent central portions that remain.

The arterial infundibula are finally separated from each other by the union of the lower border of the forked arterial septum with the portion of the right ventricular border of the orifice in the septum of the ventricles, viz. the lower half of this border. Its anterior portion is continued upwards and forwards into the termination of the original right leg of the fork, in the central part of the left-hand lip of the ventricular slit, while its posterior portion passes off slantingly upwards into the termination of the original left leg of the fork in the central part of the right-hand lip of the slit. Thus a twisted hourglass-shaped aperture connects the two arterial infundibula, which become separated by its gradual closure.

The left ventricular opening of the orifice in the septum, with the upper part of the right ventricular opening, and the channel between them, remain permanently open, and develope into the aortic infundibulum.

Conclusions.

The following are the most important new facts at which I have arrived :—

1. That in the heart of the common fowl the division of the truncus arteriosus into the aorta and pulmonary artery does not take place by the formation of *two* longitudinal oppositely situated ridges along the whole length of the vessel and their subsequent growth together, as RATHKE states to occur in Reptiles, Birds, and Mammalia.

2. That this process of division of the truncus arteriosus is accurately described as occurring by the gradual extension into it of the septum between the fourth and fifth

pair of branchial arteries, from the branchial arteries towards the heart, the septum being at first situated nearly horizontally, and then twisting from left to right as it grows down the vessel, and following the line of a single thick rounded and somewhat pyramidal ridge that forms gradually along the posterior surface of the vessel.

3. The opening from the ventricle into the truncus arteriosus is at first circular, but soon becomes a slit with two lips, from a greater development of the vascular tissue in this situation. These lips at first exercise a valvular function, in preventing the reflux of blood from the truncus arteriosus into the ventricle. As the semilunar valves become developed, this valvular function gradually becomes abolished, that of the semilunar valves being substituted for it.

4. The valvular function of the lips of the slit becomes abolished by the widening of its ends and the greater development of the central portion of each lip, especially of the left-hand one. The widened ends of the slit ultimately form the roots of the aorta and pulmonary artery, which have then become separated by the growth of the septum down the vessel into the central portion of each lip.

5. It is a remarkable fact that the rudiments of the semilunar valves first appear on the interior of the truncus arteriosus *at a considerable distance from the heart*, near the termination of the truncus arteriosus in the branchial arteries, and not near the heart, as one might have been led to expect.

6. It is also very remarkable that the rudiments of the anterior and inner semilunar valves of each artery make their appearance before the partition, which has already begun to separate the aorta from the pulmonary artery, has quite descended to that part of the truncus arteriosus in which these valves originate.

7. The rudiments of the anterior semilunar valves of the aorta and pulmonary artery are the first to appear, those of the inner valve of each artery the next, and those of the outer valves the last. The development of the last valve to appear remains behind that of the others throughout.

8. The anterior valve-rudiments appear close together, rather on the right side of the anterior surface of the inside of the truncus arteriosus, about the 106th hour of incubation, simultaneously with the commencement of the division and a short distance below it, and opposite the commencement of the ridge which forms on the posterior surface of the vessel and which appears about the same time.

9. The rudiment of the inner valve of each artery grows from the corresponding side of the ridge which forms gradually on the posterior surface of the vessel a little later than the anterior valves.

10. The rudiment of the outer valve in each artery arises from that part of the inside of the wall of the truncus arteriosus left vacant, between the outer margins of the rudiments of the anterior and inner valves, soon after the 117th hour of incubation. It arises level with the other valves, when the aorta and pulmonary artery are already separated from each other for some little distance, and therefore a little nearer to the heart than the other valves, though still at a considerable distance from it.

11. The anterior valve-rudiments commence as transverse thickenings of the interior of the vessel, sloping off above and below into the general surface of the vessel, and are separated by a slight groove.

12. The inner and outer valves first appear as simple pyramidal thickenings of the vascular wall.

13. All the semilunar valves are solid at first.

14. The anterior and inner valves consist of one single segment for each valve.

15. The outer valve is at first a single pyramidal eminence. It may remain single, or become deeply notched and develope into two valves or more.

16. By the time the third valve in each vessel has appeared, the form of the valves has become more defined. They then have the shape of a short crystal of triple phosphate , its flat surface being attached, its edge projecting into the vessel, and its ends sloping off upwards and outwards above and below. The valves are more developed in the direction of their length than transversely, and their course down the wall of the vessel is parallel to that which the axis of its canal afterwards assumes.

17. About the 144th hour of incubation they are, though still solid, sufficiently developed to close the canal of the vessel pretty completely, and to prevent much reflux of blood into its undivided portion.

18. By this time the valvular function of the two lips of the opening into the ventricle has become quite abolished.

19. The valves are further developed by the hollowing out of the solid pyramid above and near the wall of the vessel, while they grow in other directions.

20. The pocketing of each valve commences in each in the order of its appearance, and begins in the anterior and inner valves of each artery about the time that their bases have descended to the level of the bases of the ventricles, *i. e.* at the 147th hour of incubation, and is distinct in these valves at the 165th hour. The pocketing of the outer valve is not distinct till much later. About the time that it commences, the valves have assumed nearly their final positions with respect to the base of the heart, and the aperture of communication between the arterial infundibula is nearly closed up.

21. After the complete separation of the aortic and pulmonary infundibula from each other, the further changes in the semilunar valves consist principally in increase in size and diminution in thickness, so that they become more and more membranous, *pari passu*, with the growth of the other parts of the heart.

22. The aperture in the septum of the ventricles does not close up entirely, in the manner commonly supposed, but finally developes into the aortic infundibulum. After its closure has proceeded to a certain extent, the lower half of the right ventricular border of the aperture unites with the lower border of the septum between the aorta and pulmonary artery in a peculiar manner, described more at length above. This separates the pulmonary infundibulum and the root of the pulmonary artery from the root of the aorta and the canal of the aperture in the septum, which then forms the aortic infundibulum.

23. The complete closure of the infundibular aperture takes place about the end of the eighth day of incubation.

24. The fifth vascular arch on each side gives off the branch to the lung of that side, and becomes ultimately the corresponding branch of the pulmonary artery, according to the view long ago propounded by Von BAER.

I cannot conclude without thanking several kind friends for assistance received from them during the preparation of this paper, which I here beg leave to acknowledge. In particular Dr. BEALE, who suggested the best mode of heating the incubating-apparatus, and has given me much valuable advice; the Rev. GEORGE KEMPSON and my cousin Mr. CHARLES PADDISON, who sent me abundant supplies of fresh eggs; and Dr. CAYLEY, who has kindly revised the translations from the German authors referred to.

EXPLANATION OF THE PLATES.

PLATE XXXI.

The drawings (with the exception of figs. 37, 38, 39) are all copies of preparations. They were made with the aid of the camera lucida, the preparations being all viewed by *transmitted* light, and variously magnified from 24 to 59 diameters.

Fig. 1. Heart and branchial arches *in situ*, from the Chick at the middle of the fourth day of incubation, showing the convoluted tubular form then possessed by the heart.

a. Auricle. *b*. Ventricle. *c*. Truncus arteriosus. *d*. Branchial arches. *e*. Pericardium.

Fig. 2. Heart and a portion of the branchial arches of Chick at the 106th hour of incubation. The left side of the heart and truncus arteriosus is seen in the drawing.

a. Truncus arteriosus. *b*. Ventricle. *c*. Rudimentary aorta. *d*. Rudimentary pulmonary artery. *e*. Septum forming between rudimentary aorta and pulmonary artery. *f*. Opening into ventricle. 3, 4, 5. Third, fourth, and fifth branchial arteries respectively.

Fig. 3. The same preparation viewed on its anterior surface.

g. Forked lower margin of arterial septum. *h*. Edges of groove between anterior valve-rudiments.

Other letters the same as in fig. 2.

Fig. 4. Diagram of branchial end of truncus arteriosus at the 106th hour of incubation, to show the part at which the sections drawn in figs. 5, 6, and 7 are made.

Fig. 5. Cross section of truncus arteriosus of Chick at 106th hour of incubation, made in the line 1, 1, fig. 4, showing the shape of the channels of the rudimentary aorta and pulmonary artery, separated by the nearly horizontal septum.

a. Aorta. *b*. Pulmonary artery.

Fig. 6 Cross section of same truncus arteriosus made in line 2, 2, fig. 4, through lower forked margin of the septum between the rudimentary aorta and pulmonary artery.

a. Aortic channel. *b.* Pulmonary channel.

Fig. 7. Section of the same truncus arteriosus near its central portion. The slight convexity of the posterior surface indicates the position of the prominent pyramidal ridge afterwards formed here.

Fig. 8. Portion of truncus arteriosus at 106th hour of incubation. The section has been made between the line 2, 2 in fig. 4, and one a little above the centre of the vessel. Figs. 9 and 10 are from the same preparation viewed in different positions.

v. Ventricular end of truncus arteriosus. *e.* Aorta. *f.* Pulmonary artery. *g.* Lower ends of forked margin of septum.

Fig. 9. The lower end of the preparation is looked into obliquely so as to show the left side and corresponding part of the anterior and posterior surfaces of the inside of the vessel. At the upper end the cut end of the left leg of the forked septum is seen terminating on the wall of the vessel, and just below and in a line with it the rudiment of the anterior aortic valve is seen as a flattened ridge, separated from the anterior pulmonary valve-rudiment by a groove expanding out below. The under surface of the rudiment of the anterior pulmonary valve is seen to the left of this in the preparation. The left leg of the forked septum afterwards grows down along the left edge of the rudiment of the anterior aortic valve and the adjacent part of the groove between the anterior valve-rudiments.

a. Anterior aortic valve-rudiment. *b.* Anterior pulmonary valve-rudiment. *c.* Edge of anterior aortic valve along which the septum grows. *d.* Left lower end of forked arterial septum. *e.* Cut edge of cardiac end of section.

Fig. 10. Same preparation more highly magnified and turned into a different position. The lower end is looked into obliquely, so that the right side and posterior part of the inside of the vessel are seen. At the upper aperture of the vessel the termination of the right leg of the forked septum is seen. Below this is the commencement of the ridge on the posterior surface. It is at this time merely a thickened ridge passing obliquely across and down the vessel, from the right side towards the posterior surface. Its ends are the rudiments of the inner semilunar valves of each artery, while its central portion afterwards becomes prominent and pyramidal. The lower face of the ridge slopes off rapidly into the wall of the vessel. Between the right end and the rudiment of the anterior aortic valve (its corner just seen) a light space is seen in the drawing, where the outer aortic valve afterwards becomes developed.

a. Part of anterior aortic valve. *b.* Rudimentary ridge on posterior surface. *c.* Space where lateral valve subsequently developes. *d.* Right lower end of forked arterial septum losing itself on wall of artery. *e.* Aorta. *f.* Pulmonary artery.

Fig. 11. From Chick at the 108th hour of incubation, to show the form of the opening from the ventricle into the truncus arteriosus. The ventricle has been cut across just below the opening and the truncus arteriosus near the centre of the vessel.

a. Slit-shaped opening into truncus arteriosus. *b.* Thickened lips of slit. *c.* Base of ventricular cavity just below arterial opening. *d.* Cut edge of ventricle.

Fig. 12. Portion of truncus arteriosus from Chick at the 115th hour of incubation; the section made through forked margin of septum above and central part of vessel below.

a. Anterior aortic valve-rudiment. *b.* Anterior pulmonary valve-rudiment. *c.* Commencement of ridge on posterior surface. *d.* Aortic channel. *e.* Pulmonary channel. *f.* Line (left edge of anterior aortic valve) followed anteriorly by arterial septum.

Fig. 13. Left side of heart, branchial arches, and part of descending aorta of Chick at the 117th hour of incubation. The auricles have been removed. Although there is no trace of any division externally, the clots in the vessels show that the division between the rudimentary aorta and pulmonary artery has already advanced some distance. The absence of the rudiment of the outer semilunar valve of the pulmonary artery is shown by the continuity of the clot in that vessel with the clot in the undivided portion of the truncus arteriosus.

a. Ventricle. *b.* Truncus arteriosus. *c.* Carotid. *d.* Aorta. *e.* Pulmonary artery. *f.* Descending aorta. 3, 4, 5. Third, fourth, and fifth branchial arteries respectively.

Fig. 14. Heart, branchial arches, and part of descending aorta of Chick at the 117th hour of incubation. The auricles removed. The division in the clot marks the situation of the upper margins of the semilunar valves at this time. The rudimentary trunks are separate up to this point.

g. Rudimentary semilunar valves.

Other letters the same as in fig. 13.

Fig. 15. Same preparation turned round so as to show the aorta. The clot in the rudimentary aorta is seen, like that in the pulmonary artery, and for the same reason, to be cut off from that in the undivided part of the truncus arteriosus.

Lettering the same as in fig. 14.

Fig. 16. Portion of truncus arteriosus of Chick at the 130th hour of incubation, included between sections made just above the valves and a short distance below them, showing the interior of the vessel below the valves.

a. Anterior aortic valve. *b.* Anterior pulmonary valve. *c.* Pyramidal ridge on posterior aspect of vessel. *d.* Left edge of anterior aortic valve-rudiment, along which the division proceeds anteriorly. *e.* Pulmonary artery. *f.* Aorta. *g.* Cut edge of vessel.

Fig. 17. The same preparation turned, so as to give a better view of the aortic orifice, and to show the pyramidal shape of the rudimentary semilunar valves.

h. Lateral aortic valve. *i.* Inner aortic valve.

Other letters the same as in fig. 16.

Fig. 18. The same preparation turned, so as to give a better view of the outer aortic valve. The rounded form of the ridge on the posterior surface and the pyramidal shape of the anterior aortic valve are well seen.

Letters the same as in fig. 17.

Fig. 19. Portion of truncus arteriosus of Chick at the 140th hour of incubation, included between a section just above the valves and one at the base of the ventricles.

a. Aorta. *b.* Pulmonary artery. *c, c.* Anterior semilunar valves. *d, d.* Other semilunar valves. *e.* Septum between aorta and pulmonary artery. *f.* Opening from ventricle into lower part of truncus arteriosus. *g.* Clot in truncus arteriosus below valves.

Fig. 20. View of upper surfaces of the semilunar valves of the aorta and pulmonary artery at the 140th hour of incubation. The inner valve of each artery is seen to grow entirely from the side of the thick septum corresponding to the rounded pyramidal ridge on the posterior surface; the outer and anterior valves grow from the corresponding parts of the wall of the artery. The outer valve in the aorta is seen to be deeply notched. The anterior pulmonary valve is also slightly notched, and the outer valve very much so, the notches in the last fitting corresponding projections of the rudimentary inner valve.

a. Aorta. *b.* Pulmonary artery. *c, c.* Inner valves. *d, d.* Anterior valves. *e, e.* Lateral valves.

Fig. 21. The same preparation turned over to show the under aspect of the descending septum and valves.

a. Aorta. *b.* Pulmonary artery. *c.* Anterior aortic valve. *d.* Anterior pulmonary valve. *e.* Inner aortic valve. *f.* Ridge on posterior aspect of vessel.

Fig. 22. Portion of truncus arteriosus remaining between the last section and the ventricle, showing the arterial aspect of the opening into the ventricle. The channel for the pulmonary blood is seen to groove the anterior part of the left-hand lip. The slight prominences on the front of the vessel show the future position of the bases of the anterior and outer pulmonary valves. These are rather exaggerated in the drawing.

a. Left-hand lip of ventricular opening; its prominent central portion becomes continuous with the ridge on the posterior part of the truncus arteriosus. *b*. Future base of outer pulmonary valve. *c*. Future base of anterior pulmonary valve. *d*. Future base of anterior aortic valve. *e*. Future base of outer aortic valve.

Fig. 23 shows the upper surfaces of the valves of the aorta and pulmonary artery at the 140th hour of incubation. The outer valve of the pulmonary artery is here developing into two valves.

a. Aorta. *b*. Pulmonary artery. *c*, *c*. Anterior valves. *d*, *d*. Lateral valves. *e*, *e*. Inner valves.

Fig. 24. Heart and truncus arteriosus of Chick at the 144th hour of incubation. The auricles and part of the ventricles removed. Right side of the preparation. A small coloured clot is seen in the aorta. The upper surfaces of the aortic valves are seen to be nearly horizontal, and still at a considerable distance from the bases of the ventricles. The aortic portion of the channel of the undivided part of the truncus arteriosus is seen leading down to the opening in the ventricular septum, between the edges of the anterior and inner aortic valves.

a. Aortic valves. *b*. Channel between edges of aortic valves. *c*. Clot in aorta. *d*. Cavity of right ventricle. *e*. Muscular substance of right ventricle.

Fig. 25. Portion of truncus arteriosus of Chick at the 144th hour of incubation included between sections just above the semilunar valves and about the same distance from the base of the ventricles, turned so as to show the upper surfaces of the valves. These are seen to be three in each artery, and close the canal of each vessel pretty accurately.

a. Aorta. *b*. Pulmonary artery.

Fig. 26. The same preparation turned so as to show its under surface.

a. Aorta. *b*. Pulmonary artery. *c*. Rounded ridge on posterior aspect. *d*. Edge along which arterial septum grows anteriorly.

Fig. 27. Heart and great vessels of Chick at the 147th hour of incubation. The auricles have been removed, as well as the posterior part of each ventricle. The valves completely close the canal of the vessel, a thread-like channel remaining between their edges.

a. Aorta. *b*. Pulmonary artery. *c*. Right branch of pulmonary artery. *d*. Left branch of pulmonary artery. *e*. Aortic valves. *f*. Pulmonary valves. *g*. Septum of ventricles. *h*. Right ventricle. *i*. Left ventricle. *j*. Aperture in septum of ventricle leading from left to right ventricle.

PLATE XXXII.

Fig. 28. The same preparation turned so as to show the anterior surface of the heart instead of the posterior. The branches of the aorta are seen passing in front

of the pulmonary artery. The anterior and outer pulmonary valves are seen extending down the wall of the vessel towards the heart.

k. Branches from arch of aorta. The other letters the same as in fig. 27.

Fig. 29. From the heart of the Chick at the 165th hour of incubation. To show the mode of union of the lower border of the forked division between the aorta and pulmonary artery with the lower portion of the right ventricular border of the aperture in the septum of the ventricles. A horizontal section has been made through both ventricles close to the base of the heart, and just below the orifice of communication between the ventricles. The truncus arteriosus has been cut across just above the rudimentary semilunar valves. The eye looks through the base of the right ventricle into the aortic portion of the truncus arteriosus and the aperture of the aorta, into which the semilunar valves are seen to project.

a. Orifice of aorta; the triangular projections are the aortic valves. *b*. Opening of pulmonary artery. *c*. Rounded ridge with which anterior part of lower margin of septal orifice (*d*) becomes continuous. *h–e*. Muscular substance of ventricle. *f*. Entrance of orifice in septum leading from left to right ventricle. *g*. Base of cavity of left ventricle. *i*. Cut edge of septum ventriculorum. *j*. Right ventricular orifice of channel in septum ventriculorum, leading into truncus arteriosus.

Fig. 30. From the heart of the Chick at the 165th hour, much magnified. Its development was further advanced than in the preceding specimen. Preparation and position similar to that of fig. 29.

The growth of the inner valves from the thick rounded ridge is well shown in this and the following figure.

a. Under surface of anterior pulmonary semilunar valve. *b*. Lower border of fork of arterial septum. *c*. Entrance of pulmonary artery. *d*. Rounded ridge with which anterior part of lower margin of septal opening (*e*) becomes continuous. *f*. Muscular substance of ventricle. *g*. Cavity of left ventricle. *h*. Entrance of canal in septum leading from left to right ventricle. *i*. Cut edge of septum between ventricles. *j*. Aperture of canal in septum opening into right ventricle. *k*. Aortic entrance and valves. *l*. Base of cavity of right ventricle. *m*. Upper part of margin of septal opening continued into right side of forked arterial septum.

Fig. 31. The same preparation turned over a little so as to show all the pulmonary semilunar valves.

a. Inner pulmonary valve. *l*. Inner aortic valve.

The other letters the same as in fig. 30.

Fig. 32. From the heart of the Chick at the middle of the 8th day of incubation, showing the upper surfaces of the semilunar valves. The aorta and pulmonary

artery have been cut across just above the semilunar valves, and the ventricles cut off just below them.

A. Aorta. P. Pulmonary artery. *a, a.* Lateral valves. *b, b.* Inner valves. *c, c.* Anterior valves. *d, d.* Cut edge of arterial wall. *e, e.* Muscular substance of ventricle.

Fig. 33. Heart and great vessels of Chick at the end of the 13th day of incubation. The muscular substance of the front of the ventricles has been removed. The septum and apex are left.

a. Aorta. *p.* Pulmonary artery. *l. v.* Left ventricle. *r. v.* Right ventricle. *m. v.* Mitral valve.

Fig. 34. shows the distal portion of the truncus arteriosus and its principal branches at the 140th hour of incubation. The truncus arteriosus has been cut across just above the rudimentary semilunar valves. The shaded portions are the clots in the vessels. The right side of the preparation is here seen.

a. Truncus arteriosus. *b.* Aorta. *c.* Pulmonary artery. *d.* Origin of branch to right lung. *e.* Descending aorta. *f.* Ductus arteriosus. *g.* Portion of third branchial artery between carotid and fourth branchial artery (descending aorta) nearly obliterated. 3, 4, 5. Third, fourth, and fifth branchial arteries (right side).

Fig. 35. Front view of same preparation. Part of its left side is also seen. Owing to the absence of colour in the clots in the fourth vascular arch and left branch of the pulmonary artery, the latter vessel is not traceable to its termination, and the fourth arch seems to be obliterated.

i. Left carotid. *l.* Arch of aorta. Other letters the same as in fig. 34.

Fig. 36. Left side of same preparation. Outline of left branch of pulmonary artery only just traceable to its termination in descending aorta. Fourth vascular arch apparently obliterated.

Letters the same as in figs. 34 & 35.

Fig. 37. Diagram of magnified truncus arteriosus about 106th day of incubation. The forked septum between the fourth and fifth pairs of branchial arteries is seen just extending into the truncus arteriosus. The dotted lines indicate the directions taken by the right and left legs of the fork in their growth down the vessel.

a. Rudimentary anterior valves. *b.* Commencement of ridge on posterior surface of vessel. *c.* Forked septum growing into vessel between fourth and fifth pair of branchial arteries. *d.* Thickening of truncus arteriosus at ventricular opening. 3, 4, 5. Third, fourth, and fifth pair of branchial arteries respectively.

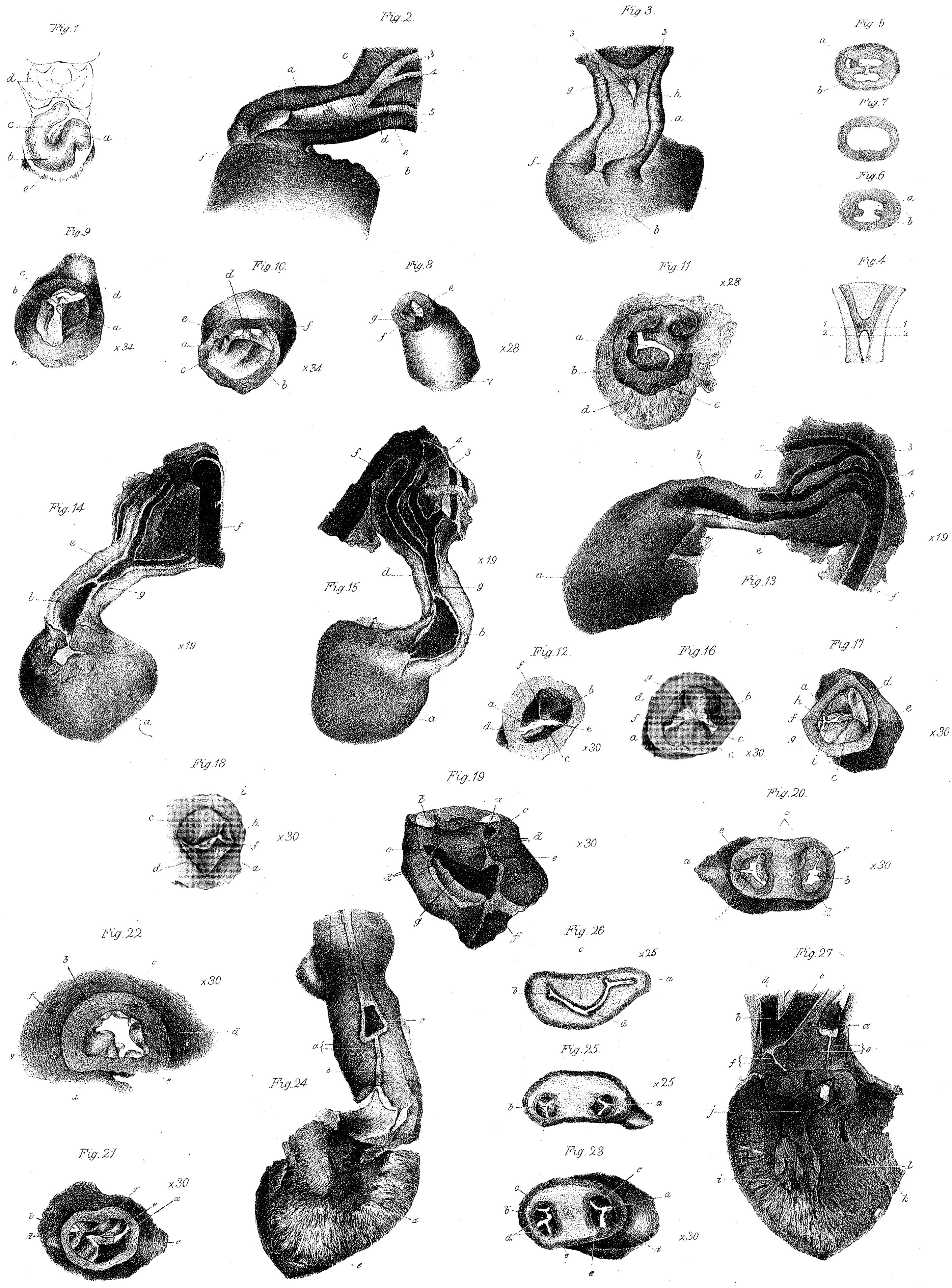
Fig. 38. Diagram of upper portion of septum of ventricles and base of the truncus arteriosus, to illustrate the way in which the lower border of the forked

septum between the aorta and pulmonary artery becomes united with the lower half of the right ventricular border of the aperture in the septum of the ventricles, and thus completes the separation of the aortic from the pulmonary infundibulum. The semilunar valves are omitted for the sake of clearness. The dotted line shows the part which afterwards becomes closed up.

a. Cut surface of truncus arteriosus. *b.* Cut edge of ventricle. *c.* Interventricular septum. *d.* Left ventricle. *e.* Right ventricle. *f.* Aorta. *g.* Pulmonary artery. *h.* Orifice in septum becoming the opening of the aorta into the left ventricle. *i.* Opening of right ventricle into pulmonary artery. *j.* Dotted line showing position of hourglass-shaped aperture. *k.* Forked lower border of arterial septum.

Fig. 39. Imaginary sections of the truncus arteriosus made just above the semilunar valves at different periods of development, showing the gradual changes in the position of the roots of the aorta and pulmonary artery during the process of the division of the truncus arteriosus, and their position at its termination.

1. At commencement of process of division of the truncus arteriosus. 5. At termination of same. 2, 3, 4. At intermediate stages. *a.* Aorta. *b.* Pulmonary artery.



W. H. Wesley lith.

Fig. 28

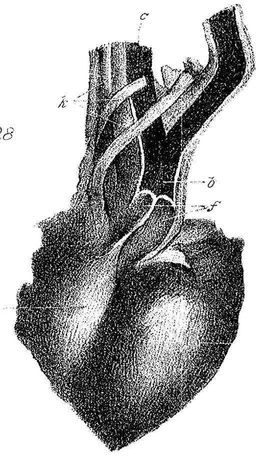


Fig. 29

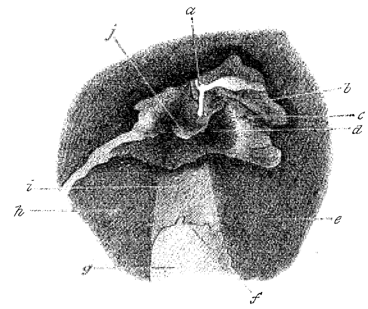


Fig. 30

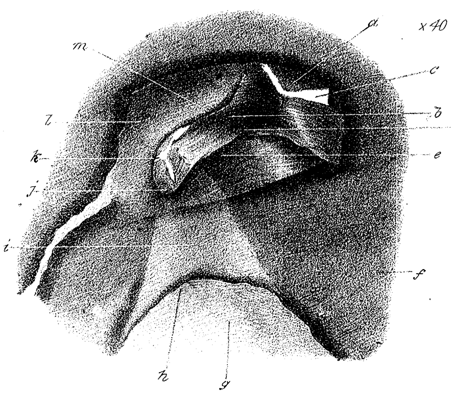


Fig. 31

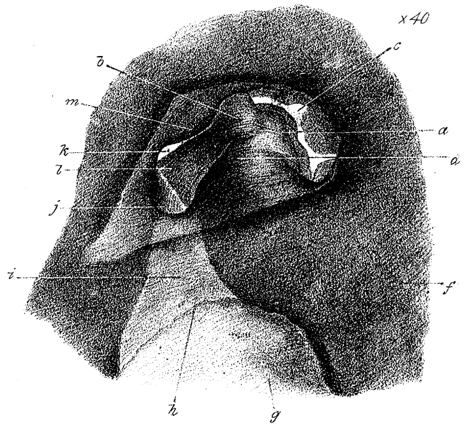


Fig. 32

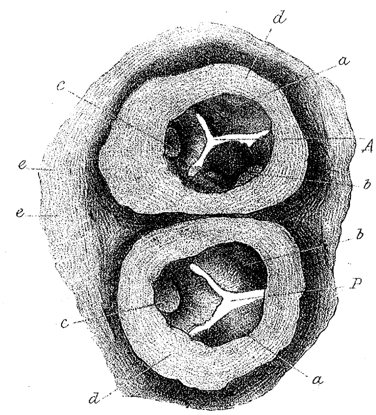


Fig. 33

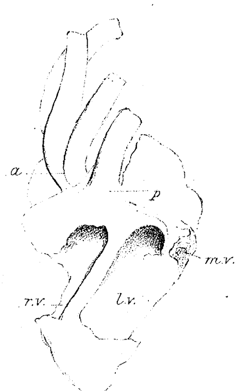


Fig. 34

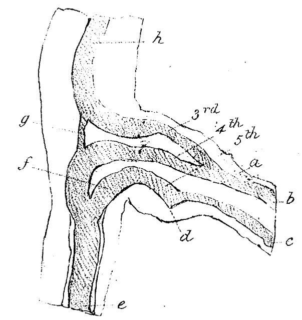


Fig. 35

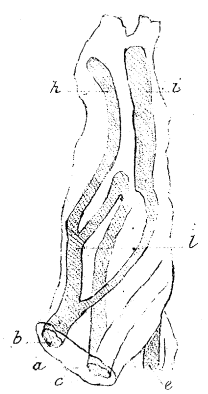


Fig. 36

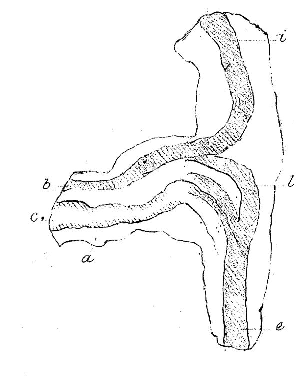


Fig. 37

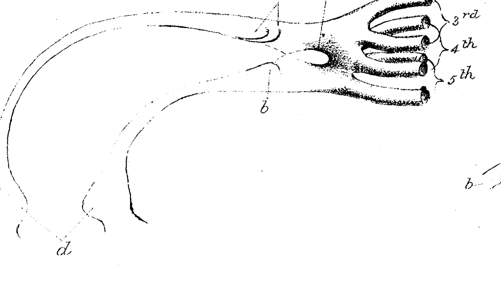


Fig. 38

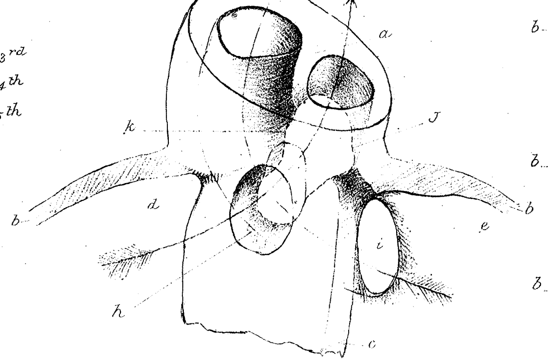


Fig. 39