

## **On the development of the vascular system in the foetus of vertebrated animals. Part 2 / by Allen Thomson.**

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### **Publication/Creation**

[Edinburgh?] : [publisher not identified], [1831]

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*On the Development of the Vascular System in the Fœtus of Vertebrated Animals.* Part II. By ALLEN THOMSON, M. D late President of the Royal Medical Society.—*Continued.*

*From the Edinburgh New Philosophical Journal for January 1831.*

HAVING in the former part of this essay considered the mode of formation of the Heart in the different orders of vertebrated animals, I shall now give some account of that of the other parts of the vascular system ; viz. of the Bloodvessels of the body.

There seem to be two modes principally in which bloodvessels are developed ; the one, by isolated points and vessels, has been already alluded to, in the account given of the commencement of the circulation, as it occurs on the vascular area of the yolk ; the other, taking place after the commencement of the circulation, by the prolongation of loops or folds from vessels already formed, is most easily seen on the transparent parts of the Batrachian reptiles.

The sac of the yolk, or covering which the yolk receives from the layers of the germinal membrane, is the part on which, in all vertebrated animals, the blood and vessels appear to originate, and it is the only part in which, in healthy animals, the formation of bloodvessels has been observed to take place independently of the heart or general circulation. During the development of the vascular area (to the detail of which it is now unnecessary to recur), no difference has as yet been observed between the mode of the formation of arteries and veins. The blood appears to circulate sooner in the veins than in the arteries of the area, but, in the early stages of development, these vessels are to be distinguished from one another only by their distribution, and the direction of the currents of blood in them. About the fourth or fifth day of incubation, the coats of the arteries begin to appear thicker than those of the veins, and very soon the external appearance of these vessels affords a character sufficiently distinctive. As far as has been ascertained, there does not appear to be any immediate connexion between the formation of vessels in the area, and that of the heart itself : these processes seem, for a time at first, to go on simultaneously, but independently of one another ; and, in-



deed, the origin of the heart may not inaptly be compared to that of some of the larger bloodvessels. Even when that organ begins to move, no blood enters it from the area: according to Baer, its motion is undulating for a few hours, until it sucks, from the veins immediately adjacent, a portion of their contents, and soon, by a regular contraction of its parietes, propels the blood through its anterior part and the arteries connected with it.

At the same time that the vascular area is formed, some vessels are likewise developed in the body of the embryo, in which also the blood and vessels containing it appear to be simultaneously produced. But after the circulation has commenced, the second process to which I have alluded, viz. the prolongation of loops from vessels already existing, seems to be more frequently resorted to for the development of new vessels in the fœtus.

This process has been described by Spallanzani \*, Fontana †, and Döllinger ‡, as it occurs in the finny tail and external gills of the common frog and water newt. In these animals, the course of the blood is at first very simple. In the early stages of development, there is no capillary network on the tail; but an arterial vessel, continued from the descending aorta, runs below the caudal vertebræ to the end of the tail, where it joins at an acute angle with a returning vein, which, in the abdomen, becomes the vena cava inferior. At a later period, it is well known that the tail of these animals is covered by a network of minute vessels, which communicate with the primary artery and vein. Through this network the blood is spread over the whole surface of the tail. The development of these vessels has been shewn to be owing, not to their formation separately in the parenchyma of the tail, but to the prolongation of communicating vessels formed between the primary trunks. The communicating branches at first pass directly from the artery to the vein, but in the progress of development I have observed them to become gradually longer, and extend themselves from the middle to the lateral expanded parts of the tail: other loops are formed in succession from the newly generated vessels, and new ones again from them, till, in the course of ten or more

\* Experiments on the Circulation of the Blood, &c.

† Reil's Archiv für die Physiologie, B. ii. S 480.

‡ Denkschriften der Königl. Akad. München. B. vii.



days, the whole of the finny part of the tail is covered by beautiful and minute arteries and veins. The loop of vessel when short and newly formed, has at first more the appearance of artery than vein, as the blood passes through it in jerks: as the loop elongates, however, and new branches proceed from it, the blood moves in jerks only in that part of the loop which communicates with the arterial trunk, while in the part connected with the returning vein, the motion of the stream of blood becomes uniform.

Rusconi\* has shewn very beautifully, that vessels are thus looped out during the development of the gills of the aquatic salamander. I find that nearly the same appearances present themselves in the gills of the frog, as well as in the extremities of the salamander. The anterior extremities of the salamander, when they first begin to sprout, form two small tubercles situated behind the head, altogether destitute of circulating blood. Shortly after the appearance of these tubercles, a single vessel is seen winding round their extremities, which returns to the body without giving off any branches. The parenchyma of each of the toes, as it buds out from the end of the limb, receives a small loop from the original vessel. Communicating branches are likewise thrown across at the joints, and, as the limb becomes larger, numerous capillary vessels are formed in the same way as the primitive trunks.

Spallanzani, and some other observers, have noticed similar appearances in the extremities of the chick, when they begin to be formed; and the same may be seen in those of the rabbit, and of some other mammiferous animals; from which there appears every reason to believe that, after the circulation of the blood has commenced, the development of new vessels from those already formed, takes place principally by means of loops in Warm as well as in Cold blooded animals.

I ought now, in conformity with the plan previously laid down, to proceed to treat of the development of the individual parts of the vascular system in vertebrated animals; but it must appear obvious, that a detailed account of the development of

\* *Amours des Salamandres Aquatiques, et développement, &c.* See Plate II. Figs. 8, 9, 10, 13, H h.



all, or even of the more important bloodvessels of the body, besides being too extensive a subject for our present limits, would prove uninteresting from the want of connexion existing between the facts already ascertained. I shall therefore confine myself for the present to one branch of the subject only, viz. the Development of the Bloodvessels more immediately connected with Respiration in the foetal or adult animal. This branch of the subject, besides being the most nearly allied to that treated of in the first part of the essay, is rendered one of the most interesting to comparative anatomists, not only by the diversity of the form and by the number of the organs which appear to carry on the respiratory function in the foetus of vertebrated animals, but also by the singular analogies in the structure of these animals which the study of the development of their respiratory organs points out both in their transitory and permanent condition.

The principal organs which appear to perform a respiratory function in the foetus, or which, being formed before birth, are destined for the respiration of the adult animal, may be enumerated in the following order, being that in which they succeed one another, either in individual animals, or in the different orders of the class Vertebrata. 1. The sac of the Yolk; 2. The External Gills; 3. The Internal Gills; 4. The Allantois; 5. The Placenta; 6. The Lungs\*.

\* Some of these, as well as other parts of the ovum, have received so many different names, from the various authors who have described them, that it appears necessary to anticipate a little, and to give a few of the synonymes by which they are generally known in the different orders of vertebrated animals.

1. The sac of the yolk is generally known by this name in Fishes, Reptiles, and Birds. We have only in these animals to guard against confounding the *sac of the yolk* or covering given to this part by the layers of the germinal membrane, with the *proper envelope of the yolk* which exists before development commences, and encloses it while in the ovarium. In Mammalia, this part is most frequently called the Umbilical Vesicle, and sometimes the *tunica erythroides*. The distinctive character of the sac of the yolk is, that it remains connected or communicating with the intestine during some period of foetal life, and has mesenteric arteries or veins, or both, ramified on its surface.

2. The Allantois, (a name derived originally from the vesicular membrane of mammalia) does not exist in the foetus of aquatic animals, such as that of fishes and batrachia. In adult batrachia it forms the urinary bladder,



In proceeding to describe these organs, I shall endeavour to shew the manner in which they contribute to perform the function of respiration in each of the four orders of vertebrated animals, beginning with fishes, in which they appear to be simplest; and I shall confine myself principally to the relation of those facts which have been most lately ascertained, and which appear to establish most clearly the analogy existing between the organs under consideration.

It is from the study of the structure of the respiratory organs, and of the arteries distributed upon them, that the chief part of our knowledge regarding the mode in which the function of respiration is performed by them has been obtained, as little or no direct or strictly physiological evidence has hitherto been procured from the observation of their mode of action. The description of these organs indeed might be considered as a subject merely anatomical, were it not that in observing their development during fœtal life, their variation in size, and alteration in form at different periods, and the changes in the distribution of the vessels supplying them with blood, we are enabled to perceive certain ends to which these changes of structure are directed, and thus acquire some insight into the mode of operation of each of them.

It is now well known that the constant presence of oxygen in some form or other is absolutely necessary for the development of the embryo of all animals. The evolution of those rudimentary parts even, the formation of which precedes that of the

as well as in the tortoise. It is called Chorion by Emmert in the lizard, and by Pander in the bird; Umbilical vesicle by Haller in the bird, in which he was the first to shew its connection with the funis of the urachus. In Mammalia it has been called Endochorion, from its lining the chorion. This part is always formed by the expansion of the cloacal part of the intestine, and carries upon it the ramifications of the umbilical arteries and veins.

3. The internal gills are those formed in the course of the branchial plates or hoops which surround the pharynx.

4. The external gills are appendages of the foregoing, connected generally with the *outer* part of the branchial plates, and receiving a covering from the integuments.

5. The Amnios, a covering proper to the fœtus, connected with its integuments, and formed by a reflection of the serous layers of the germinal membrane.

6. The Chorion, the external envelope of the whole ovum.



blood, is almost immediately put a stop to by the removal of oxygen from the medium in which they are placed, before any particular part of the embryo is formed upon which the changes of respiration are afterwards more immediately produced. In the early stages of development, then, there appears to be what may be called a General or Interstitial Respiration\*, or a change essential to life, produced by oxygen in all the substance of the embryo, or of its accessory parts, which, as the foetus is more perfectly formed, takes place in particular organs only. As soon as a peculiar nutritive fluid, and a central propelling organ, are produced, this fluid is exposed on the expanded surface of the yolk, to the influence of the respiratory medium, either directly, or through the coverings of the ovum.

*Development of the Respiratory Organs in the Foetus of Fishes.*

The sac of the yolk, the principal respiratory organ of the foetus of fishes, differs considerably in its relations in the Osseous and Cartilaginous tribes.

In the foetus of osseous fishes, as in that of the *Blennius viviparus*, described by Rathke† and Forchhammer‡, the yolk, after it has received a covering from the expanded layers of the germinal membrane, hangs like a loose bag from the abdomen, and is connected by a narrow opening with the anterior part of the intestine. The vascular network spread over this covering of the yolk at a later period, as has previously been remarked, is formed entirely of veins in osseous fishes. A branch of the mesenteric veins (Pl. III. Fig. 1, *y'*) running along the back part of the abdomen, dips down to join the yolk at the place where this sac is connected with the intestine; this vein is divided into numerous minute ramifications on the back part of the yolk, and its capillary vessels unite below with those of another vein occupying the anterior side (*yy*), and conveying the blood

\* See Geoff. St Hilaire on this subject, in the *Memoires du Museum*, tom. x.

† Geschichte des Embryo der Fische, in Burdach's *Physiol.* B. 2. S. 201.

‡ De *Blennii Vivipari* formatlone et evolutione. Kiliae, 1819.



which traverses the surface of the yolk to the vena cava, and thence to the auricle of the heart (*a'*).

The liver, which in the early stages of development of all vertebrated animals appears to be intimately connected with the veins of the yolk, is formed in osseous fishes from a mass of granular substance (*c*) deposited in the hollow between the yolk and back part of the intestine. This mass, as it increases in size, is collected round the trunk of the vein distributed on the posterior surface of the yolk, and is gradually supplied with vessels formed by the subdivision of the main trunk of the vein. As the liver becomes larger, and receives arterial vessels from the cœliac trunk, the sac of the yolk is diminished in bulk, and the blood is not so uniformly distributed over its surface as before; the general capillary network being less supplied with blood, two or three of its vessels become dilated, and convey the greater part of the blood, which previously was spread over the surface of the yolk, directly from the liver to the heart. At last, when the yolk is much diminished in size, only one of these vessels remains, becoming the hepatic vein.

The envelope of the ovum of osseous fishes is generally so thin, that, from the first formation of the blood, the changes induced by the surrounding water are not materially impeded. When the fœtus, or little fish, bursts its covering, and escapes from the ovum, it swims about in the water, with the yolk, proportionally very large, hanging from its abdomen, and the blood is then more directly exposed to the current of water\*. Towards the latter end of fœtal life, the yolk, while still of a considerable size, is in some fishes enclosed in the abdomen, and probably serves for some time to nourish the animal, while in others its substance is almost entirely absorbed before its enclosure.

In some of the larger cartilaginous fishes, on the other hand, as the Rays and Sharks, the sac of the yolk is connected with the *posterior* part of the intestine, and arterial as well as venous bloodvessels are distributed on the vascular area covering its surface (Fig. 6. of the Skate). The vessel ramified on the yolk appears to be a branch of the cœliac artery. The vein formed

\* See account of the Spawning of Salmon, &c. by Daniel Ellis, Esq. in vol. iv. of this Journal.



by the union of the capillary vessels of this artery, conveys the blood which passes over the yolk to the liver; so that the distribution of the omphalo-mesenteric vessels in the fœtus of these fishes resembles that in lizards, birds, and mammalia.

As most of the fishes of this tribe are more or less ovo-viviparous, or retain their ova in the body during a longer or shorter period after development begins, the blood of the fœtus must be made to undergo respiratory changes through the medium of the fluids and membranes with which it is surrounded in the oviduct. The very vascular membrane lining the oviducts in some species of sharks which retain their ova during the whole of development, is destined, without doubt, for the aëration of the fluid surrounding the fœtus; and, according to Sir E. Home\*, it would appear that the effect of this vascular membrane is increased by the entrance of sea-water into the oviduct. The apertures into the cavity of the peritoneum of these animals may also allow the water to come into contact with the oviduct; and, in some of them, which retain their ova for a short time only after development begins, apertures are found in the angles of the horny covering of the egg, through which a current of water is permitted to pass.

The yolk sac, so far as has yet been ascertained, is the only fœtal respiratory organ in osseous fishes; while the blood continues to be exposed to the influence of the water on its surface, the Gills or respiratory organs of the adult become developed. According to Rathke, the rudiments of the gills may be perceived in the embryo of the Blennius some little time after the circulation of the blood has commenced. These organs appear at first to be formed of five pairs of narrow plates, situated transversely on the lower side of the pharynx behind the mouth. These plates, of which the four posterior only become developed to form the perfect branchial hoops of this and other osseous fishes, are at first composed of the same dense gelatinous substance as the rest of the embryo, and do not exhibit any traces of vascularity. The same author has shewn, that the branchial arteries begin to be formed soon after the appearance of the rudimentary hoops, by the subdivision of the arterial vessel rising from the bulb of the aorta (Fig. 1, *b'*), on the lower part of the

\* See an interesting paper in *Phil. Trans.* 1810.



pharynx. At first, this vessel divides itself only into two branches situated immediately behind the mouth, which, passing round the pharynx, reunite with one another on its upper part, below the vertebral column, to form the descending aorta. Shortly afterwards, a farther subdivision of the aorta takes place, by which four new vascular branches (*m*) are formed on each side of the pharynx, behind the one which appeared first, and leading from the ascending to the descending trunks of the aorta. These vessels, the primitive branchial arteries, are at first nearly of a uniform diameter, and do not divide into any branches in their course round the pharynx. Each artery runs along one of the branchial plates or hoops, (Fig. 2, I).

As development proceeds, four transverse clefts, the commencing branchial apertures, appear between the branchial hoops on the lower and lateral parts of the pharynx (Figs. 2 and 3, *o*). The four posterior hoops become stronger, more cartilaginous, and project farther from the side of the œsophagus, and, at the same time, little leaflets or tubercles, the rudiments of those which afterwards form the comb-like fringe of the gill, begin to be formed on their external sides. Each of these leaflets, soon after its first appearance, is furnished by the large vessel of the hoop with a little artery and vein, probably formed in the same manner as the vessels of the tail and gills of the salamander already alluded to. The number and size of the leaflets gradually augment, and, at the same time, each of the vascular arches is farther subdivided, till at last, when the structure of the gill is perfected, instead of the single arterial vessel, which at first winds round each hoop, there are formed a branchial artery and vein, the capillary vessels of which join by a multitude of minute ramifications on the surface of each of the leaflets. It has thus been shown by Rathke, that the branchial vein is originally a continuation of the trunk of the branchial artery. While those changes are taking place, the anterior vascular arch on each side, not contributing, like the posterior, to form the vessels of the gills, gives off an arterial branch (Fig. 1, *t*) at its anterior and convex part, which rises to the head, and corresponds with the carotid artery of higher animals. This vessel now no longer communicates with the ascending aorta, but is supplied with blood by the posterior



part of the arch which joins the first pair of branchial veins at the place where the root of the aorta begins.

The anterior branchial plate, or that situated between the mouth and the foremost branchial apertures (Figs. 2, 3,  $\lambda$ ) instead of being covered by the fringe of leaflets proper to the gills, projects farther backwards in the neck, and begins to overlap the branchial plates posterior to it (Fig. 4, 5  $\lambda$ ). According to Rathke, the anterior part of this plate forms the lower jaw; the posterior part, continuing to extend itself backwards, forms the opercular covering of the gills.

The branchiæ of the Rays and Sharks, again, consist of five pairs of double branchial plates, from the edges of which rows of leaflets are suspended; but, so far as I know, the mode in which they become developed has not been observed. It would be interesting to know in what manner the opercular fold and openings of the gills are formed in these animals, as the smallness of the lower jaw and the absence of the lateral processes of the lingual bone, seem to indicate that only five branchial plates originally exist in the fœtus, and that all of them become developed in the formation of the branchiæ of the adult animal.

The fœtus of cartilaginous fishes besides possessing a yolk-sac, in the vessels of which a large quantity of blood is spread out, are provided, during a considerable period of their fœtal life, with other organs, by means of which the aëration of their blood is promoted. The External Gills or branchial appendages were known to the late Dr Monroe\*, and are described as such by him in the skate, (see Fig. 6, A. H). The connection of these appendages with the hoops of the internal gills, was, however, first shewn by Dr Macartney of Dublin in the fœtus of the shark. They consist, according to this anatomist, of five bundles of tender filaments hanging from each side of the neck. These bundles appear to arise from the external integuments, but are really attached to the internal gills on the inner side of the branchial apertures †.

In some beautiful specimens of the external gills of the *Squalus Catulus* and *S. maximus*, which I had lately an opportunity of seeing in the Museum of the College of Surgeons, Lon-

\* Monroe on Fishes, plate XIV. † Journal de Physique, Fevrier 1818.



don, collected by Sir E. Home and Mr Clift (see sketch, Fig. 7)., I could easily perceive that each of the filaments of which the five bundles were composed consisted of a single fold or loop of vessel, covered by a thin membranous layer prolonged from the integuments. (Fig. 7, A.)

*Development of the Respiratory Organs in the Fœtus of Reptiles.*

1. **BATRACHIA.**—The development of the respiratory organs in the fœtus of these animals is peculiarly interesting on account of the transition which they undergo from an aquatic to an aërial condition; and the observation of the changes of structure which take place during their transformation, appears to have illustrated, more clearly perhaps than that of any other class of animals, the relations of the respiratory and vascular organs to one another.

*Aquatic Salamander.*—Shortly after the fœtus or larva of the Aquatic Salamander leaves the egg, its blood is exposed to the influence of the surrounding water on the surface of the rudimentary intestine, or part corresponding with the sac of the yolk in other animals. The vena cava returning from the tail, on arriving at the posterior part of the intestine, gives off a large branch (Fig. 8, *y*), which is joined by numerous small vessels spread over the lower surface of the abdomen. The small vessels are again united into one venous trunk (*y*), situated near the auricle of the heart, on the left side of the body, where they pour into the heart (*a*) a large quantity of blood which passes over the abdomen, along with that from other parts of the body.

The liver (*c*) is formed in the batrachia, as in cartilaginous fishes and the higher orders of animals, by the subdivision of the venous trunk conveying the blood from the yolk to the heart.

As the development of the fœtus proceeds, its finny tail, as well as the greater part of the integuments of the body, are covered by minute ramifications of vessels, which must contribute materially to aërate more perfectly the blood. As these ramifications become more numerous, the quantity of blood sent over the abdomen becomes less, the liver (Fig. 8. *c*) increases in size, the proper mesenteric vessels are formed, and the trunk of the proper vena cava augments, and carries proportionally a greater quantity of blood directly from the tail to the heart. At the



same time, the formation of the external gills, or more special respiratory organ of the foetus of these animals, commences.

The rudiments of the external gills, very similar in their commencement to the branchiæ of the foetal fish, are to be found at a very early period. Some days before the foetus of the Salamander quits the egg, they are indicated by four transverse opaque bands on the fore part of the body, or pharyngeal portion of the intestine. These transverse bands by their farther development form branchial hoops on each side of the neck. The integuments then begin to bud out at the upper and lateral parts of these hoops, so as to form three small projections or folds of the skin, placed severally opposite the interstices between the hoops. According to Rusconi\*, before these parts, which are the commencing external gills, receive any vessels, the distribution of arteries in the neck is very simple, and analogous to that noticed by Rathke in the foetus of the osseous fish. The arterial vessel prolonged from the bulb of the aorta advancing forwards below the neck, is divided into four pairs of smaller vessels, four of which passing round each side of the pharynx, unite with those from the other side below the vertebral column, to form the descending aorta; each pair of vessels, as it is given off by the aorta, passes along one of the branchial hoops. Rusconi has ascertained, and I have repeated his observations with the same result, that these vessels are at first quite simple in their course round the pharynx, and do not give off any branches.

At the time when the embryo comes out of the egg, the little processes which constitute the commencing external gills, are considerably elongated, and are each supplied with a loop of vessel from the outermost part of one of the branchial vascular arches (Fig. 8, *n*). As the stalk of the gill sprouts out farther from the side of the neck, it acquires considerable length, and the loop of the branchial vessel, consisting simply of an outgoing and returning branch, is prolonged into it. When the primitive stalks of the gills have acquired greater length, new buds of the parenchyma begin to appear on their lower sides, forming the commencing leaflets of the gill (Figs. 8 & 10, *h*),

\* *Amours des Salamandres Aquatiques, et Développement du Têtard, &c.*; and in his *Descrizione Anatomica degli organi della circolazione delle larve, &c.*



and opposite to each of these secondary buds a new branch of vessel is formed by the passage of the blood, directly across the primary stalk, from the outgoing to the returning vessel. As the new buds of the gills become longer, these communicating branches between the primary vessels are produced along with them; new communicating branches are thrown out in their course, while, at the same time, new buds are formed on the primary stalk of the gill. There are generally about thirty of these leaflets on the gills of the larva, at the time that they have attained their full development, which, according to Rusconi, is about the 40th or 45th day; the vessels are then still more minutely ramified on the surface of the leaflets, and as they are almost quite transparent, the circulation of the blood through them forms a truly beautiful spectacle. In this animal, therefore, as in the fish, by tracing the development of these vessels, it is easy to perceive that the branchial arteries and veins are only subdivisions in the course of the aorta itself.

At the period when the gills are fully developed, the distribution of the vessels rising from the heart is the following (Fig. 9): The three foremost pairs only of the branchial vascular arches convey blood to the gills (*m*). At the root of each gill the arterial or outgoing vessel communicates directly, by a short branch, with the vein or returning vessel, so that a considerable portion of the blood propelled into the branchial arteries, along with the whole of that in the fourth or posterior pair of arches, which gives no branches to the gill, is carried directly into the descending aorta (*r s*). From the communicating branch at the root of the foremost gill there arises a small artery (*t*), which is distributed on the parts surrounding the hyoid bone. The parts near the temporal bone receive an artery from the root of the second gill (*t*), and the vertebral artery is given off near the place where the whole of the branchial arches unite to form the roots of the descending aorta (*r*). The anterior extremity, like the pectoral fin of the fish, receives its vessels from the mammary artery (*u*), which arises along with the cœliac, mesenteric, &c. from the descending aorta.

While the external branchiæ are developed, the internal arches upon which they are supported become firmer and more cartilaginous. They are attached anteriorly to the hyoid bone,



and appear to be processes of this bone, which are developed only during foetal life. At the same time, three clefts are formed between these arches on each side of the neck, and below the attachment of the external gills, through which the water taken into the pharynx is driven out by a muscular effort, so as to produce a current near the leaflets of the gills. It is only in the latter stages of foetal development, however, that the aid of these currents through the branchial apertures is required, owing to the existence in the earlier periods of a very singular provision, lately discovered by my friend Dr Sharpey \*, by which, in the batrachian reptiles, as well as in all the mollusca which he has examined, a constant renewal of water is produced, in contact with their respiratory surfaces. Dr Sharpey has shown that, in the batrachia during the early stage of foetal life, the integuments, and especially those parts on which bloodvessels are minutely distributed, possess an inherent power of producing currents in the water near them, without any perceptible muscular action, of impelling, as it were, the water along the surface, and thus forcing it to be constantly in motion. This power of producing currents is strongest in the covering of the gills themselves, but it also exists to a considerable extent in other parts of the body, especially on the tail and lower part of the abdomen †.

A considerable time before the gills of the salamander arrive at their full size, the rudiments of the lungs, the principal respiratory organs of the adult animal, begin to be formed. The lungs may be perceived, according to Rusconi, about the 23d day of the development of the embryo, and they have attained a considerable size by the time that the gills are perfected. About the 40th day they consist of two long shaped sacs situated behind the stomach, close to the vertebral column. They do not contain any air for some time after their formation. According to Rusconi, the larva of the salamander begins to expel air from its mouth about the 30th day; but it is difficult to conceive how air can at this time be introduced into the lungs

\* On the Currents produced by the Respiration, &c. Edinburgh Medical and Surgical Journal, 1830.

† It would be interesting to know if any analogous power exists in the body or gills of the foetus of those cartilaginous fishes in which external gills are found.



from without, as the deglutition of air, according to the observations of the same author, is not seen to commence before the branchial apertures are closed at the period of transformation. In the progress of development, the lungs become more perfectly formed, they are divided into compartments by the intersection of septa arising from their sides, and the air passages to the pharynx become more distinct.

When the period of transformation approaches, a period varying much according to climate, season, situation, &c. the gills begin to shrink, and their vessels to carry less blood. The vessels ramified on the extremities of the leaflets become obliterated, and the parenchyma of the gill is forthwith absorbed or removed. In about a week after this, so much of the gills has been removed that these organs are now reduced to mere tubercles projecting from the side of the neck. At the same time, the clefts, or branchial apertures into the pharynx, are gradually closed by the adhesion of an opercular fold of the integuments projecting from their anterior side, and the cartilaginous hoops which supported the gills become gradually softer and are removed. The respiration of the salamander [is now truly aërial, and this animal rises frequently to the surface of the water to expire and inspire air.

While the transformation in the respiratory organs takes place, the bloodvessels distributed on them also undergo several important changes. The three anterior vascular branchial arches, which previously gave branches to the gills, are now relatively smaller than before (Fig. 11, *m*). The vessels which proceeded to and from the external gills are now wholly obliterated; their communicating branches at the root of the gill-stalks become dilated, and now form part of the continued trunks which wind round the pharynx, and join above it to form the descending aorta (*r s*); so that the branchial arches of the pharynx seem to have resumed the simple form in which they first appeared before the external gills were developed. The arteries going to different parts of the head and neck, and arising from the outer parts of these vascular arches, are now proportionally larger than before. The fourth or posterior pair of arches (*p*) from which the lungs derive their arteries, and which was previously much smaller than the three anterior, now becomes the most consider-



able. The fourth arch communicates with the third arch, and sends a returning vessel contributing to the formation of the aorta; the principal part of the trunk (*p*), however, descends on each side of the vertebral column to the sac of the lungs, upon the cells or compartments of which it is ramified with great minuteness.

*Frog.*—During the first part of foetal development, the respiration of the larva of the common Frog is carried on by nearly the same means as that of the aquatic salamander. The rudimentary intestine, or part corresponding to the yolk sac, seems to be covered by a network of venous vessels, to which the liver holds the same relative position as in the salamander. Branchial appendages, analogous in their structure and relations to those of the salamander, are formed, and the tail, as well as the general integuments of the body, appears to assist the more special respiratory organs in changing the blood. The external branchial appendages exist for a much shorter time in the frog than in the salamander: they never become highly developed, or capable of exposing a large quantity of blood to the influence of the water; but their place is supplied at an early period by internal gills, corresponding in some respects with those of osseous fishes (Figs. 13, and 14, H I).

According to the observations of Baer\*, before the external gills become developed, the distribution of vessels in the neck of the tadpole of the frog resembles in its simplicity that in the foetal fish and salamander. The aorta, rising from the bulb and advancing forwards to the region of the pharynx, is divided into two branches, one of which proceeds to each side of the neck, and gives successively in its course four branchial vascular arches, which, winding round the branchial hoops, reunite with one another on the upper side of the intestine to form the descending aorta.

The external gills generally attain their full size about the 18th day of development (Fig. 13, H.) Soon after this period, they appear to shrink and lessen: their free motion is now impeded by the growth of an opercular fold of the integuments anterior to them (Fig. 13.  $\lambda$ ), which, increasing more and more from before backwards, gradually forms a cover which encloses them entire-

\* In his *Geschichte des Fröschembryo*, in Burdach's *Physiol.* B. ii. S. 222.



ly. On cutting out this opercular fold, the remains of the external gills may be seen for some time after they have been enclosed, but they seem ultimately to be removed by absorption. The internal gills which are in the mean time developed, are by no means, as some have supposed, the enclosed external appendages, but are formed separately on the branchial hoops encompassing the pharynx, like the gills of the adult fish. The outer margin of these branchial hoops is gradually covered with small processes of a soft substance that form the leaflets or comb-like structure of the gills, upon which the minute capillary vessels are afterwards ramified (Fig. 14, A), and these leaflets are not unlike those of the external gills. The branchial hoops are separated from one another by clefts, through which the water introduced into the pharynx passes freely; but after the opercular fold has covered over the external and internal gills, it unites with the integuments on the left side; and only one aperture, situated on the right side, is left, by which the whole of the respired fluid makes its exit from the cavity of the gills\*.

As the vessels of the external gills are formed by the subdivision of the simple branchial arches, and no branch is given off from them before they arrive at the gills, the whole of the blood which passes through the heart must necessarily be exposed in these organs to the influence of the water, before it is sent to nourish any other part of the body.

The mode in which the subdivision of the branchial arteries in the larva of the frog takes place has been observed by Rusconi, and is described by him in his anatomical description of the larva of the aquatic salamander.

Each branchial vascular arch, on entering its respective hoop, gives off a lateral branch, considerably larger than the continuation of its own trunk: this lateral branch accompanies the parent vessel along the hoop, and reunites with it before leaving the gill. As these two vessels proceed along the gill, side by side, and at a short distance from one another, the lateral vessel gives off ten or more cross branches, which pass through the buds of the leaflets, and fall again into the parent vessel. The lateral branch, at its first separation very large, thus becomes gradually

\* In some species of frog, there is an opening on each side of the neck, as in osseous fishes. See Cuvier's *Recherches sur les Reptiles douteux*.



smaller as it proceeds onwards ; and the parent trunk, very small at the place where it gives off the lateral branch, gradually increases in size by the accession of the cross branches, till it is joined again by the lateral trunk itself. As the leaflets of the gills become larger, they are covered by very numerous capillary vessels, formed by the looping out or subdivision of the cross branches, in a manner somewhat analogous to the extension of vessels in the external gills\*. The three anterior pairs of branchial vessels, on coming out of the gills, before uniting with one another and with the posterior pair, to form the descending aorta, give arterial branches to the head, neck, and anterior extremities.

The rudiments of the lungs are to be found adhering to the lower side of the oesophagus, at the time when the external gills are fully formed (Fig. 16, A, *ll*). As development proceeds, the little dense masses constituting the lungs become hollow (Figs. 13, *l*, and 16, B); they gradually expand, their parietes becoming membranous ; they are filled with air, and their cavity is divided into cells by transverse septa rising from their sides (Fig. 14, *ll*). The lungs of the frog, like those of the salamander, receive their vessels from the posterior or fourth branchial arch (Fig. 14, *p*), or that nearest the heart ; but in the frog, this artery traverses the gill before arriving at the lung ; it becomes gradually larger as the lungs become developed and the period of transformation approaches, till the foetal life is at an end, when it carries a proportion of blood considerably greater than the three anterior arches.

As the gills shrink and become smaller, the minute vessels of their leaflets first disappear, and then the cross branches from which they arose are obliterated. The apertures or clefts between the branchial hoops are closed up, the leaflets are partly absorbed, and the branchial hoops themselves are gradually softened down and removed. The large lateral branches of the branchial arteries also begin to carry less blood, and are at last

\* These two parallel vessels, it is obvious, represent the rudimentary state of the branchial vessels of fishes ; the large lateral tributary branch corresponding with the artery, and the main trunk with the vein. It appears not improbable, that the vessels of the gills in fishes are subdivided in a similar manner to that alluded to above ; though, at the same time, it must be acknowledged that the double vessel has not as yet been remarked in the foetal fish.



obliterated when the gills have disappeared, so that the main trunks only of the branchial arteries remain. These (the main trunks) continue to carry blood to the arteries of the head, neck, and anterior extremities (Fig. 15, *t u*). According to Rusconi, the returning branches of the first, third, and fourth arches are obliterated, those of the second only remaining to form the roots of the aorta (*r r'*). The anterior extremities (Fig. 14, *g'*) in the mean time increase in size, and break through the skin which covers them. The finny tail shrinks, and is gradually absorbed, and the little frog now leaves the water to return only in search of food or protection.

Funk \* and Siebold † have shewn, that as the batrachian reptiles approach to maturity, another organ connected with the respiratory function is developed, which seems calculated for exposing a part of the blood at least to the influence of the oxygenizing medium. A vesicle formed by the extension of the cloacal part of the intestine ‡ becomes expanded so as to occupy a considerable space at the posterior part of the abdomen; the umbilical arteries (Fig. 12, *z*) form a minute vascular network by their subdivision on the surface of this vesicle, and the umbilical vein (*z'*) returning from it conveys the blood which has passed over its surface to the vena portæ and liver, as in the higher animals. This vesicle can only be considered as a rudimentary and imperfect respiratory organ in the batrachian reptiles; but we shall afterwards find that it corresponds with a part which becomes highly developed in the fœtus of lizards, birds, and mammalia, and forms in them a most powerful means of effecting the respiratory changes in the blood.

In speaking of the respiration of the fœtus of batrachian reptiles, it may be interesting to advert shortly to the structure of the adult respiratory organs in some other animals, which appear to be nearly allied to this class, and are now very generally included by naturalists under the same general division. The *Proteus anguinus*, the *Siren lacertina*, and the *Amphiuma didactylus*, and *A. tridactylus*, the species of those animals

\* De Salamandri Terrestri Formatione Vita et Evolutione. Berolini, 1827.

† Quædam de Salamandris et Tritonibus. Berol. 1829.

‡ Seen commencing in the tadpole of the frog in Fig. 14, *v*, and in the adult salamander, Fig. 12.



alluded to best known, appear to be all truly aquatic in their habits, or to live chiefly in water and moist mud; but all of them are provided with organs analogous to the lungs of the adult batrachia, and appear to respire more or less air as well as water.

The principal respiratory organ of the Proteus and Siren is the external gills, into which a large quantity of the blood of these animals is propelled; while the Amphiumas (at least the adult animals) appear to be altogether destitute of gills, and to respire, like the batrachia after they have undergone the transformation, by lungs alone, into which air is from time to time introduced.

Rusconi, in his beautiful memoir on the *Proteus anguinus*, states, that this animal dies as soon as or sooner than most fishes, when taken out of the water. Mr Neill has observed, that the siren which he possesses lived, upon one occasion, for twelve or fourteen hours out of water, and Cuvier informs us, that the Amphiumas or Abranchi are known frequently to lie in dry places for several days, without sustaining any injury; on the other hand, the whole of these animals, even the abbranchous amphiuma, appear capable of remaining below water for a considerable period, without inhaling air, which the existence of lungs in them would lead us to believe is necessary for their respiration.

The external gills of the proteus and siren are fimbriated and branched like those of the salamander; and the principal stalks are suspended, in the same manner, from branchial plates or hoops, which appear to be processes of the hyoid bone. There are also three apertures between these branchial hoops, through which these animals are enabled to expel either air or water, and thus produce currents near the gills.

Though the amphiumas are destitute of any kind of gills, it is a very curious and interesting fact which has been established by Cuvier, that the hyoid bone in these animals bears a considerable resemblance to that of the siren, and other animals in which external gills exist, either permanently or for some period of their life. The hyoid bone consists, in the amphiumas, of a lingual part and two long cornua, which encompass the pharynx. Near the two posterior extremities of these cornua, there



are attached three small cartilaginous arches analogous to branchial plates or hoops. Of the spaces between these arches, in which, had there been gills, one would naturally have expected to find branchial apertures, the two anterior are closed up by the membrane lining the pharynx and by integuments, and the posterior only remains open, forming a permanent aperture in the neck in every respect analogous to the branchial apertures of the proteus, siren, and salamanders. Cuvier states, that the examination of the soft parts, as well as of the skeleton, leads him to believe, that at some previous period of its existence, this animal possesses external gills, similar to those of the larva of the aquatic salamander. The observation of the development of the amphiumas in the foetal state alone, however, will probably enable us to solve this question, as very small specimens (three inches long) have been seen in which no vestige of gills was to be found.

The lungs of the proteus consist of two oval membranous sacs, situated in the posterior part of the abdomen, which are generally only about a twelfth of the length of the body, and are each connected with the pharynx by a long and narrow tube. These sacs are quite smooth in their interior, and are not separated into compartments by membranous septa.

The lungs of the siren and amphiuma, on the other hand, are proportionally much larger than those of the proteus. Those of the siren, according to John Hunter, consist of "two long bags on each side, which begin just behind the heart, and pass back through the whole length of the abdomen, nearly as far as the anus. They are largest in the middle, and honey-combed on the internal surface through their whole length." According to Cuvier, the lungs of the amphiumas are formed by two long cylindrical and very vascular sacs, slightly dilated at the posterior extremity. In neither siren nor amphiumas are there any proper trachea or bronchi.

The heart of these animals seems to hold an intermediate place between that of fishes and batrachia. It consists of a strong fleshy ventricle, a large membranous auricle situated somewhat anterior to and above the ventricle, and a strong muscular bulb, from which the rising aorta springs.

In the proteus and siren, so far as has as yet been ascertained,



there are only three branchial arteries formed on each side of the neck by the subdivision of the aorta; each of these vessels gives a branch to one of the gills. The arteries of the head and neck are derived from the branchial veins or vessels which carry back the blood which has passed through the gills, and from communicating vessels passing between the arteries and veins at the roots of the gill stalks. The pulmonary artery is given off at the place where the posterior branchial artery and vein meet and join with the anterior ones to form the roots of the descending aorta.

From the drawing of the *Amphiuma Didactylus* by Dr Pockels, published by Rusconi (which Cuvier has shewn was erroneously taken by these anatomists for the siren), it appears that the distribution of the branchial arches in this animal resembles more that of the larva of the salamander, there being four branchial arteries, the three anterior of which supply the gills, while the posterior, a fourth, alone is ramified on the sac of the lungs.\*

*Development of the Respiratory Organs in the Ophidia,  
Chelonia and Sauria.*

In proceeding to consider the development of the respiratory organs of the higher orders of reptiles, we pass from those animals which are aquatic, either during the whole or some period of their existence, to those which are entirely aërial during foetal and adult life.

The ova of the serpents, turtles, and lizards, are deposited and become developed in the same medium in which the adult animal respire; but in these animals, as well as in birds and mammalia, a proper envelope for the foetus or annios is formed by the reflection of the serous layer of the germinal membrane †,

\* For a farther account of these animals, see Configliachi and Rusconi *Del Proteo Anguino di Laurenti Monografia*. Pavia, 1819, of which an account is given by D. Ellis, Esq., in Vols. iv. and v. of this Journal.—Cuvier, *Recherches sur les Reptiles douteux*, in Humboldt's and Bonpland's *Recueil d'Observations, &c.*—*Mémoires du Museum d'Hist. Nat.*, tome xiv. 1827. *Sur le Genre de Batraciens nommé Amphiume.*—*Philosoph. Trans.* by Shreibers and John Hunter.—*Wilson's Illustrations of Zoology.*

† See Fig. 21 of annios in birds. ».



and the fœtus is thus kept constantly immersed in a fluid till the period when it begins to inspire air into the lungs.

It is well known that the respiration of the fœtal lizard, like that of other animals, is first carried on by the distribution of the blood over the surface of the sac of the yolk. In the former part of this essay, it was stated that the observations of Dutrochet, Emmert, Hochstetter and Baer, had shown that the embryo of the lizard becomes developed on the surface of the yolk, and that the blood and vessels are first produced in the form of a network, on the surface of the area surrounding the fœtus. This network, like that in the ova of cartilaginous fishes, birds, and mammalia, is composed of the minute ramifications of the omphalo-mesenteric arteries, and of corresponding veins, which carry to the vena portæ the blood that has passed through the network. The sac of the yolk, over which the vascular network spreads itself more and more widely as development proceeds, is at first situated near the internal surface of the shell, or other covering of the ovum, and the blood contained in its vessels is arterialized by the transmission of oxygen from the air without. After the first half of fœtal life has passed, the yolk sac is removed from the inside of the chorion, and its place is supplied by another vesicular membrane coming from the fœtus, which gradually expanding, entirely encompasses the fœtus, and on which the blood is now exposed, in order that it may undergo the necessary respiratory changes. The sac of the yolk still remains, however, covered by its network of vessels, which probably serve to absorb the substance of the yolk for the nourishment of the fœtus, or being now less exposed to the air, perform some subordinate part in respiration (Fig. 17, *x y*).

The vesicular membrane which supplies the place of the yolk sac as a respiratory organ, is the same part in a more expanded condition, which becomes developed in the batrachian tribes at the commencement of their aërial existence. According to the observations of the authors already quoted, the allantois of the *Lacerta agilis* appears, at the earliest period at which it has been seen, in the form of a small vesicle hanging from the lower part of the abdomen, projecting like a process from the cloacal part of the intestine, and resembling in its form and position the urinary bladder (See Fig. 19, Part I.). At this



time the allantois is covered by a network of minute vessels, which become more obvious as the vesicle expands. Continuing to enlarge, it insinuates itself between the foetus and the covering of the ovum (See Diagram, Fig. 18), and its farther progress outwards being impeded, it expands laterally till it envelopes the foetus in its amnios, and the yolk, with a double layer of a vascular membrane (Fig. 17, *z v'*). The vessels distributed on this membrane are the umbilical arteries and veins; the outermost layer is the most vascular, and is applied close to the inner side of the envelope of the egg, where it receives the full influence of the air transmitted to it from without. The allantois continues to act as a respiratory organ till the foetus breaks the shell, or tears the covering of the egg, and comes out fitted for receiving air into its lungs, and respiring solely by these organs. The greater part of the allantois remains in the egg, in the *Lacerta agilis*, and the urinary bladder of the adult is formed by a part at its root separated from it by the urachus, on each side of which the umbilical vessels previously proceeded to gain the expanded part of the vesicle.

The respiration, therefore, of the foetus of the lizard, as well as that of all oviparous animals higher in the scale, is entirely performed by the two membranes to which we have just alluded, viz. the sac of the yolk and the prolongation of the urinary bladder or allantois\*.

Many lizards and serpents, however, are not truly oviparous, but retain their ova till the development of the foetus has proceeded some way, in general till the allantois becomes sufficiently expanded to be fitted to carry on respiration; and some serpents, such as the *Coluber berus*, are almost entirely ovo-viviparous. In this last it is curious to observe that the arterialization of the foetal blood is effected, though by a simpler apparatus, in nearly the same manner as that of mammalia, or truly viviparous animals. The allantois of the viper, after expanding so as to

\* The connexion of the sac of the yolk with the intestine has been demonstrated also in the *Coluber natrix* by Bojanus, *Journal de Physique*, 1829; and Dutrochet has shown very clearly the mode of development of the allantois in the viper, in the *Memoires de la Societ e Medicale d'Emulation*, tom. viii. Several preparations in the College of Surgeons' Museum, London, illustrate these facts extremely well, and some the sac of the yolk of the turtle.



enclose the fœtus and yolk, comes into contact with a vascular lining of the oviduct, and is closely united with it, so that the venous blood of the fœtus is exposed to the influence of the oxygenized arterial blood of the parent.

It is an interesting fact also, that in some of the Testudines, the allantois, or at least a part of it, remains permanently in the adult, and that the umbilical vein continues as in the batrachia to carry off its blood to the liver. In the *Testudo orbicularis*, according to Townson, water is introduced into this sac, and it appears not improbable that the large urinary bladder, or permanent allantois of the turtles and of some serpents, serves as an auxiliary in the function of respiration during the whole of life.\*

Although respiration by means of gills is rendered unnecessary, by the perfect state of the allantois in these reptiles, yet it appears, from some late observations, that at a period of the development of these, as well as of all the more perfect animals which have been examined, corresponding with that at which the branchiæ of fishes and batrachia begin to be formed, the existence of gills in a rudimentary state, is indicated by the structure of the pharynx and surrounding parts. In the early periods of development, the distribution of the arteries especially, which take their origin from the bulb of the aorta, bears a striking resemblance to the primitive simple state in which these vessels have been observed to exist in fishes and batrachia before their gills are formed. In the embryo of the *Lacerta agilis*, while the cavities of the heart are yet single, Baer has observed that the aorta is divided into five pairs of vascular arches, which, after winding round the sides of the pharynx, reunite with one another above it to form the descending aorta. Baer and Rathke have also observed, that while these subdivisions of the aorta—which may very properly be called branchial arteries—exist, the sides of the pharynx are penetrated by transverse fissures, on each side of which runs one of the vessels rising from the bulb of the aorta. The same appearances have been observed by Baer in the fœtus of the *Coluber natrix*, at a corresponding period of its development.

In these animals, however, the transverse plates of the neck,

\* See Carus' *Compar. Anat.*, vol. ii. p. 249.



and the branchial arteries passing along them, do not undergo farther subdivision, or become more fully developed, like the gills of fishes or batrachia; on the contrary, the plates are gradually incorporated with the parietes of the pharynx, the apertures are entirely closed, and the vascular arches are converted, by the obliteration of some parts and the enlargement of others, into the arteries, which, in the adult animal, take their origin from the right and left ventricles or cells of the heart.

Unfortunately, the manner in which the farther development of these parts takes place has not been observed, owing to the difficulty of procuring the ova of the saurian and ophidian reptiles at many different stages of foetal life. From the many varieties in the distribution of the arteries rising from the heart in these reptiles, it appears probable that this would prove a very interesting subject for investigation; and it may be remarked, that no animals are better suited for observation, from the length of time that the blood continues to circulate in the foetus after it has been taken from the ovum.

Two of the branchial arches appear to remain permanent, in order to form the right and left roots of the aorta in the adult lizard and tortoise. The anterior parts only of three other pairs of branchial arches also remain to convey blood into the carotid, subclavian and pulmonary arteries (See Fig. 19).

The development of the lungs has been little attended to in the higher reptiles. In lizards and tortoises the lungs are double, and the pulmonary arteries are derived from the pulmonary arch on each side (See Fig. 19). In serpents, on the other hand, the lungs, as well as the pulmonary artery, are generally single; but in the *Anguis fragilis*, in the adult of which the lungs are double, Rathke has observed, that in the foetus they are at first single; they consist of a mass of dense gelatinous substance, in which a cavity is gradually formed; in this animal the left is gradually separated from the right lung in the progress of development, and the cavities of the two lungs continue to communicate freely with one another for some time.

#### *Development of the Respiratory Organs in Birds.*

For the development of the ova of birds, the application of external heat, as well as the direct agency of air, is required,



and a respiratory change of the blood of the fœtus, comparatively as extensive as that in the adult bird, seems to be necessary. This change is produced by means of the same membranes, viz. the sac of the yolk and allantois, as those on which the blood of the fœtal lizard is exposed, and though these parts are considerably more developed in birds, their relations, as well as the mode in which they are supplied with vessels, are nearly the same as in the higher reptiles. But the facts relative to the structure of these membranes appear to be so well known, as to render it unnecessary for me to enter into any detailed account of them.

While the respiration of the fœtal bird is almost entirely carried on by the membranes of the yolk and allantois, the structure of the parietes of the neck and pharynx, as well as of the adjoining arteries, exhibits certain traces of branchiæ similar to those already alluded to in the embryo of the lizard. These appearances were first discovered by Rathke, and an account of them was published by him in the *Isis*, in 1825; it is since this time that the observations of this author have been extended, and the same appearances discovered in the lizards, serpents, and mammalia by himself, and by Huschke, Baer and others; by which a series of analogies of the most interesting nature has been established between air-breathing animals, and those which are aquatic during the whole or some part of their existence.\*

From the manner in which the rudimentary intestinal canal is formed, it has been shewn that the anterior and posterior parts of the intestine constitute at first two shut sacs, into which the only entrance is by a large opening in the middle between them, by which they communicate with the sac of the yolk. Neither mouth nor anus, therefore, at first exist; but both these apertures are afterwards formed by a wasting away or absorption of the substance of the germinal membrane, at the two extremities of the rudimentary intestine. The opening of the mouth (Fig. 21, *e*) appears towards the end of the second day of incubation, some days before that of the anus is perforated.

\* See the Memoirs of Rathke in the *Répert. Génér. d'Anat. et de Physiol.*, tom. vii., in the *Edinburgh Medical and Surgical Journal*, 1830; and in the *Isis*, 1825, No. 6, and 1828, No. 1; those of Huschke in the *Isis*, 1827, No. 1, and 1828, No. 2; and those of Baer in *Meckel's Archiv.* vol. ii., No. 4; and in *Breschet's Repertoire*, 1829; also Baer, *de ovi mammalium et hominis genesi Epistola*.



The mouth, or anterior opening into the intestinal canal\*, has at first the appearance of a transverse slit, or cleft, on the lower part of the head. On the third day, the part of the intestine into which this opening leads becomes wider anteriorly, and assumes the form of a cone, the apex of which is directed towards the tail of the embryo. The walls of this cavity, which corresponds in many respects with the branchial cavity of cartilaginous fishes, and with part of what is afterwards converted into the pharynx of the bird, become thicker and of a firmer consistence at the same period. Towards the end of the third day six clefts, or transverse slits, make their appearance behind the mouth, three on each side of the intestine. The foremost pair of these clefts appears first, and the second and third after it gradually. The wall of the pharyngeal cavity projects slightly at the parts between the clefts on each side; it is here of a firmer consistence than elsewhere, and has the appearance of being formed of transverse bands, united anteriorly on the mesial line, like the branchial hoops of the fœtus of the batrachia or of fishes, before the leaflets of the gills are formed.

The aorta, in the mean time, begins to divide itself into vessels which correspond with branchial vascular arches. At the end of the second day, the aorta rising from the bulb behind the pharyngeal portion of the intestine, runs forward along the middle and lower part of this cavity, till it approaches the opening of the mouth; here it divides into two branches, which separating from one another, proceed round the sides of the intestine close to the angle of the opening of the mouth, and join again near the vertebral column to form the descending aorta. During the first half of the third day, a second pair of vascular arches is formed behind the first, which encompasses the pharynx in a similar manner, and towards the end of the third day, two other pairs of vascular arches being formed, the anterior part of the intestine is surrounded by four pairs of vascular arches, rising successively from the aorta on the lower side, and joining into the two roots of the aorta on the upper side of the intestine. On the third day, according to Baer, the foremost of these pairs

\* The opening alluded to can scarcely with correctness be called the mouth at this period, this cavity being afterwards formed before it, by the growth of the superior and inferior maxillæ.



of vessels which may be called branchial, the one first produced is the largest, and makes the widest sweep; the fourth, or posterior, is very small and scarcely perceptible.

Each of these vascular arches, in winding round the side of the pharynx, passes along one of the parts which correspond to the branchial hoops; so that each of the three clefts or apertures on each side of the pharynx is situated between two of the vascular arches. At the end of the third and beginning of the fourth day, all the arches, and more especially the fourth, become larger and fuller of blood, and, at the same time, the branchial hoops become thicker, and the apertures between them wider; but in the course of this day the first vascular arch, having attained its full size, soon begins to be less visible, both on account of its own diminution or partial obliteration, and of the enlargement and increased opacity of the branchial hoop along which it passes. Towards the end of the fourth day, this arch is wholly obliterated, and no longer allows of the passage of blood into the root of the descending aorta. A vessel proceeding to the head and neighbouring parts, which afterwards becomes the carotid, has, however, taken its origin from its most anterior part, into which the blood is still propelled from the bulb of the aorta through the communicating vessel of the second arch (Fig. 30).

While the first pair of vascular arches is obliterated, a fifth pair is formed behind the four which previously existed, proceeding in the same manner from the ascending to the descending aorta. At the same time, the first branchial aperture, situated between the first and second vascular arches, is gradually closed, and a fourth appears between the fourth and fifth arches. Thus there exist in the neck of the embryo of the chick five vascular arches and four branchial clefts, corresponding with the appearances in the neck of the salamander and fish, and the analogy between these animals and the fœtal chick before referred to becomes apparent (Fig. 20, *m. o*). Rathke has observed, that the distribution of the arteries, as well as the structure of the branchial hoops, in the fœtus of the *Blennius vivip.*, resemble almost exactly those in the chick on the fourth and fifth days. Baer remarks, that he has never seen more than four vascular arches co-existent in the embryo of the chick. In the embryo of the duck of four days and a half, I have observed four aper-



tures co-existing, and four vascular arches very apparent; from which it appears probable that a fifth also existed, though not easily seen from the small quantity of blood it contained.

On the fourth day, the second arch also becomes less, and on the fifth day is wholly obliterated, while the third and fourth now become stronger. Towards the end of the fifth day (See Fig. 22, *o*), the three remaining clefts on each side of the pharynx become gradually less perceptible, and are soon closed by the union of the integuments on each side of the cleft. The anterior clefts remain open longer than the posterior, and while they are closed on the outside, they are still visible on the inside of the pharynx, in the form of small cavities opening into it (Fig. 23). The third arch, now the most anterior of those remaining, forms the brachial arteries. The vessels of the anterior extremities spring from the place where the third vascular arch joins the root of the aorta (Fig. 30, *w*). They may be perceived with ease on the eighth day, and after this period, the branch (*w*) by which the third arch joins the fourth in the root of the aorta shrinks and gradually becomes smaller, till it entirely disappears before the 13th or 14th day; at which time the whole of the blood sent through the anterior branches from the bulb of the aorta, is carried to the carotid and brachial arteries exclusively, and no longer reaches the root of the aorta. There now remain, therefore, only four vascular arches, viz. the fourth and fifth pairs (*p r*), from which the proper trunks of the aorta and pulmonary arteries are formed.

It has already been shewn, that, on the fifth day, the septum of the ventricles is completed, and separates entirely the right from the left arterial cavity of the heart. These cavities during their contraction propel their contents into the bulb of the aorta, which remains a single cavity for some time after the ventricles are distinct. Towards the end of the fifth or beginning of the sixth day, according to Baer, the bulb of the aorta becomes flattened, and the opposite sides of the tube adhere together along the central part, so as to separate it into two vessels, situated side by side, and enclosed within the same sheath. The vessel situated on the left side, becoming considerably shorter, afterwards forms the root of the pulmonary arteries; that on the right side forms the commencement of the aorta. As these ves-



sels join their respective ventricles, they appear to cross, or to be twisted round one another.

As development proceeds, the root of the aorta is more completely separated from that of the pulmonary artery, and a remarkable change, at the same time, takes place in the direction of the blood through the vessels into which they lead. The blood, propelled by the contraction of the left ventricle through the aortic root (R), instead of going as before into all the vascular branches rising on the fore part of the neck, now passes only into the fourth vascular arch on the right side, and the two arteriæ innominatæ which arise from it (*t, u, r, s*); while the blood from the right ventricle is sent through the pulmonary root (P) exclusively into the fourth arch on the left side, and the two fifth or posterior arches (*p. p*)\*. The fourth arch now becomes gradually larger, and becomes the freest mode of communication between the ascending and descending aortæ; it forms, in fact, the proper arch of the aorta. In the mean time, the fifth arch on the left side becomes less, gradually carries a smaller quantity of blood, and soon after the separation of the aortic and pulmonary roots is entirely obliterated. Three arches only, therefore, now remain, viz. the fourth on the right side or the trunk of the aorta itself, its corresponding arch on the left side, and the fifth on the right, the two last of which soon after give rise to the pulmonary arteries.

On the fifth and sixth days, the parietes of the pharyngeal or branchial cavity of the chick also undergo a transformation. According to Rathke, the part intervening between the mouth and the first pair of branchial apertures becomes thicker and firmer, and is divided by a transverse groove into two portions (Figs. 24 and 25.) The anterior of these (*ε*), bulging out at the sides, forms by its farther development the inferior maxilla; the posterior (*λ*), smooth and projecting less, gives rise to a pendulous fold which overlaps the first branchial slit, and which this author compares to the operculum of fishes †. When the branchi-

\* Baer explains this change by supposing that, when the roots of the pulmonary artery and aorta are separated, the blood acquires a new direction, and is thus driven into their respective vessels.

† From the drawings which Rathke has given of the fœtal fish, there can be no doubt of the correctness of this comparison; but he seems to have omitted to observe, that, before the formation of the opercular body in the fœtus of the chick, the most anterior branchial aperture is closed.



al apertures have closed, the neck begins to become much longer and narrower in proportion to the head and body of the chick. The part immediately before the opercular covering, or between it and the maxilla infer., seems especially to be expanded in producing this elongation; while the opercular covering itself, and the part in which the posterior branchial apertures were situated, remain adhering to the fore part of the thorax. At the same time, the carotid arteries are lengthened out, and the other vascular arches in the fore part of the thorax become straighter, and assume more nearly the position they afterwards have in the adult bird (Fig. 31, *t, u, r, s, p*).

While these changes take place in the branchial hoops and vascular arches, the Lungs begin to be formed. The rudiments of these organs may be perceived as early as on the fourth day. The researches of Rathke\* have shown that the lungs and air passages are developed on the anterior side of the œsophagus, but they render it improbable that these organs are produced, as some have supposed, like a process or diverticulum of the intestinal canal. According to Rathke, the lungs are formed a short time before the trachea or bronchi; they consist, on the fourth and fifth days, of two small mucus-like masses (Fig. 26, A. B.) situated above the pericardium, and before the stomach. The trachea and bronchi (*l'*) appear at first like a thickening of the lower side of the œsophagus; the trachea is at first so short, proportionally to the bronchi, as to be scarcely perceptible. On the fifth day these parts are increased in size (Fig. 27), and have become more distinct, but they are as yet quite solid, and without any internal cavity. On the sixth day, the trachea is elongated proportionally to the bronchi, and a cavity is evident in the interior of the lungs. This cavity, however, is confined to the posterior and lower part of the lungs only, and Rathke has shown that this part (Fig. 28, *l*) afterwards becomes the cellular part of the respiratory organs of the birds. The anterior part (*L*), corresponding to the bronchial part of the lung, still remains quite solid. On the seventh day, the cavity in the

\* Sur le Developpement des Organes Respiratoires, in Breschet's Repertoire d'Anat. et de Physiol.; and translated in Edinburgh Medical and Surgical Journal, Jan. 1830.



cellular part of the lung is increased, and the trachea and bronchi are become quite hollow; minute air-tubes radiating from the extremities of the bronchi, at the same time, appear in the anterior solid part. After this period the whole lung grows rapidly, and approaching the vertebral column and ribs, becomes firmly united to these parts. The bronchial part of the lung remains closely united with the air-sacs till the 12th day (Fig. 29), when the vesicular part begins to increase with great rapidity, and envelopes all the viscera of the chest and abdomen a few days before the chick comes out of the egg.

The communication of these air-sacs with the bones is not established till some days after the end of incubation.

Each of the lungs, shortly after its formation, receives an arterial branch from the pulmonary arches (the fourth left and the fifth right branchial arches), (Fig. 30, *p*). These branches gradually become larger as the lungs are developed; but as the blood which they carry to the lungs is returned to the left auricle by proper veins, the parts of the arches leading into the aorta behind the pulmonary arteries gradually become less. These communicating vessels (Figs. 29, 30 and 31, *p p' d*), forming the ductûs botalli of the bird, still retain a considerable size, till the period when the inspiration of air into the lungs takes place, when the whole of the blood entering the pulmonary arches from the right ventricle, is carried into the pulmonary arteries, and the branches communicating with the aorta are entirely obliterated.\*

#### *Development of the Respiratory Organs in the Fœtus of Mammalia.*

As the ova of mammiferous animals are entirely developed in the uterus, the blood of the fœtus is supplied with air entirely through the medium of the parent, and the respiratory change which it undergoes is comparatively much less perfect in these animals than in birds. During the earlier periods of fœtal development in the mammalia, vascular membranes exist, analogous to those which act as respiratory organs during the whole of fœtal life in birds; but these membranes seem to be capable

\* See Baer's *Entwicklungsgeschichte der Thiere*, and the *Repertoire Générale*, tom. viii.



of producing the changes of respiration during a short time only, and their place is soon supplied by another structure, by means of which the bloodvessels of the foetus are brought into intimate contact with those in the uterus of the mother.

It has already been shown that the foetus of mammalia, like that of other vertebrated animals, becomes developed on the surface of the yolk, and that, while the rudiments of the foetal organs are forming, the yolk is gradually surrounded by the layers of the germinal membrane, upon which a vascular area similar to that in birds is produced. The foetus of mammalia, like the chick in ovo, lies with its left side towards the yolk. The intestine of the foetus necessarily communicates with the yolk-sac, as both these parts are formed by folds of the same layers; and the vascular network of the yolk is formed as in the chick, by the omphalo-mesenteric arteries and veins.

The yolk-sac differs very much in its relations in the different families of the order Mammalia\*. In the common ruminating animals, such as the sheep or cow, and also in the pig and horse, the yolk ceases to increase at a very early period; the part by which it communicates with the intestine is lengthened out, and the sac of the yolk, collapsed and empty, remains hanging for some time from the funis of the umbilicus, attached by a long and narrow cord to a projecting fold of intestine (Fig. 32, *xy*). The yolk at this period has generally received the name of Umbilical Vesicle; it still retains a yellowish colour, a spongy granular consistence, and the ramifications of vessels are visible on it till it at length disappears.

In carnivorous animals the umbilical vesicle, or sac of the yolk, resembles, more than in any others that have been examined, the sac of the yolk in birds. In the cat it is filled with a substance of a dark yellow colour. In the progress of development, however, it comes to have the shape of a long narrow vesicle lying parallel to the long diameter of the foetus, and fastened by its two pointed extremities to the chorion, or outer membrane of the ovum (Fig. 33).

\* See Introduction to this Essay.—See Baer de Ovi Mammalium et Hominis genesi.—Cuvier and Dutrochet in *Mémoires du Museum*, vol. iii.; and Emmert in *Reil's Archiv.*, B. x. h. i.—Blumenbach and Carus' *Comp. Anat.*—Dutrochet in vol. viii. of the *Mémoires de la Soc. Méd. d'Emulation*; and Bojanus in *Meckel's Archiv.* B. iv., and in *Nov. Act. Phys. Med.* tom. x.



In the ovum of the human species,\* the yolk-sac, or umbilical vesicle, is very small and globular, and disappears shortly after the end of the second month. But in the rodentia, as in the rabbit or hare, the umbilical vesicle is highly developed, and the blood-vessels distributed on it comparatively numerous and large. At first this vesicle resembles much the yolk-sac of birds (Fig. 34), but in the later stages of development, it is expanded so as to form a vascular covering over nearly all the parts of the ovum.

The Allantoid Membrane, or expanded portion of the urinary bladder, becomes developed in the fœtus of mammalia, in the same manner as in that of lizards, serpents, and birds. The umbilical vessels are ramified on it, and for some time after its first appearance it preserves the same relations as in these animals.

In ruminating and pachydermatous animals in which the umbilical vesicle is small, the allantois is very highly developed. In the horse, pig, cow and sheep, its growth is very rapid immediately after its first appearance; it fills the whole of the cornua of the uterus, or of the compartment which each ovum occupies (Fig. 32, *z z*). It consists of two layers, the external being most vascular, and is filled with a transparent and sometimes gelatinous substance.

In the cat and dog, again, the allantois envelopes the fœtus in its amnios, and the yolk, much in the same way as in the eggs of birds (Fig. 33), leaving the yolk free on one side, however, during a considerable part of fœtal life.

In the Rodentia, the umbilical vesicle is so much developed, that it appears to have taken the place of the allantois; this latter membrane is proportionally much less extended; it retains its vesicular form for a considerable time, and is enclosed between the folds of the umbilical vesicle (Fig. 34).

The outer layer of the allantois, from its forming a lining to the envelope of the ovum, has been called Endochorion. The umbilical vessels are ramified principally on this part of the allantois, and being brought near into contact with the arterial vessels distributed on the lining of the uterus, the respi-

\* See the description of the membranes in the human embryo, in the *Traité d'Accouchemens* by Velpeau. Paris, 1829. Vol. ii. p. 230.



ratory change of the blood in the umbilical arteries is thus for some time performed.

Very soon, however, after the allantois has expanded, so as to fill the cavity of the uterus, or of the different compartments occupied by the ova, and comes into contact with its parietes, the Placenta, or principal respiratory organ of the fœtal mammiferous animal begins to be formed. The structure of this part may be most easily examined in the ova of ruminating animals, as in the cow. In this animal, when the vascular or external layer of the allantois lines the chorion, the extremities of the umbilical vessels ramified on the allantois, leave that membrane at particular parts, and join the chorion. This latter membrane then becomes uneven at the places where these vessels join it; and as development proceeds, numerous little processes (Fig. 32, A) project from its external surface, upon which the capillary vessels of the umbilical arteries are minutely ramified. These processes gradually prolong themselves outwards, and carry along with them the umbilical vessels, which gradually become larger and more numerous\*. At the same time, the projections situated on the inner membrane of the uterus, corresponding in position and form with those on the chorion of the ovum, become enlarged; into these processes of the uterus the projecting parts of the chorion are gradually inserted. These placental processes of the mother are also very vascular, so that the umbilical arteries of the fœtus carrying venous blood, are brought into contact with those carrying the arterial blood of the uterus, by the influence of which the necessary change or arterialization seems to be effected †.

After a little more than a sixth of the time of uterine gestation has elapsed, at which period the fœtus of the mammiferous animal corresponds in its structure to the chick in ovo on the third and fourth days, rudiments of a branchial apparatus, analogous to those already alluded to in the higher reptiles

\* See a paper by Sir E. Home, *Phil. Trans.* vol. cxii.; and Burdach's *Physiol.*, B. ii. S. 534.

† For an account of the varieties of the form and nature of the placenta in different classes of animals; see another paper by Sir E. Home in the *Phil. Trans.*—Carus' *Comparative Anatomy*, 2d vol.—Jeffray de Placenta, &c.



and in birds, are to be found. We are indebted chiefly to Rathke, Baer, and Burdach for the discovery and elucidation of these interesting facts. The observations of these authors have principally been made on the embryoes of the cow, pig, sheep, dog, rabbit, and of the human species, and the appearances they have observed in all of these animals have been so similar, as to warrant the conclusion, that they are common to all or most of the mammiferous families. The general features in the structure of the neck and pharynx, which assimilate the embryo of the mammiferous animal to that of the aquatic animal in the early stages of their development, are the same as those already mentioned in birds. They consist in the shortness and thickness of the neck, the width of the pharyngeal portion of the intestine, the penetration of its sides by clefts, and the subdivision of the aorta into vessels corresponding in number and distribution with the primitive branchial arteries.

Four openings on each side of the œsophagus have been observed in the embryo of the dog, between three and four weeks old\* ; in that of the sheep of three weeks ; of the pig at three weeks (Fig. 9. part I. and Fig. 37.), and of the rabbit on the twelfth day ; and in the human embryo of six weeks (Fig. 36.) : in the embryo of the dog, some little time before that mentioned above, only three apertures are found. The buccal opening situated anteriorly to the branchial clefts, the inferior maxilla, the hyoid bone, and the opercular fold of integuments, which closes the anterior clefts, are developed in the same manner as in the bird. While three pairs of clefts exist in the sides of the pharynx, there are in the dog (Fig. 35. *m*), as in the chick, only four pairs of vascular arches ; but before the first of these becomes obliterated, a posterior or fifth pair is produced, while, at the same time, the fourth branchial cleft is formed ; so that in the mammiferous animal five pairs of vascular arches, and four pairs of clefts, exist for some time simultaneously in the sides of the neck †.

\* See Fig. 35. the head of the fœtal dog represented by Baer, and given in the first part of the Essay, which I have again inserted, in order that this interesting point of structure may be brought more immediately before the eyes of the reader.

† The vascular arches of mammalia are described by Rathke and Baer in



A few days after the appearance of the fifth arch, the neck begins to elongate, the apertures are closed gradually on the outside, and the lower jaw becomes more developed; while the vascular arches undergo those changes by which the permanent arterial branches, arising from the heart, are formed.

The first and third pair of vascular arches form the carotid and subclavian arteries in Mammalia (Fig. 39. *t, u*), as in birds, and the second pair seems to be wholly obliterated, or at least gives only a small branch; in mammalia, however, the arch of the aorta, or permanent communicating vessel between the ascending and descending aorta, is formed from the fourth branchial arch on the left side (*r*) of the œsophagus; so that the order in which the vessels of the head and superior extremities arise is reversed; the right innominata taking its origin before the vessels of the left side\*.

The pulmonary vessels appear to be given off by the fourth arch on the right and the fifth on the left side (*p' p*), the fifth on the right being wholly obliterated. While, however, the carotid and branchial arteries become developed from the anterior arches, the pulmonary arches do not continue to carry blood to the root of the aorta, as takes place in those of the bird. The parts by which these arches communicate with the root of the descending aorta (forming in birds the ductus botalli) become gradually obliterated, so that of all the five pairs of vascular arches in the embryo of the mammiferous animal, only one, the fourth of the left side, remains prominent.

While these changes take place in the pulmonary arches, the bulb of the aorta, from the single cavity of which the pulmonary and systemic vessels arise for some time in common, is divided, so as to form the roots of the aorta proper and pulmonary arteries. According to Meckel†, the septum which has separated the left ventricle entirely from the right, appears to be

the greater number of embryos in which they have been seen, as simple tubes; but, in one instance, the latter author observed, on the internal and concave border of each vascular arch another small vessel, of which, he says, "je n'ai pas pu saisir les rapports." Could this have been the lateral vessel which, in the frog, gives off the smaller branches to the leaflets of the gill?

\* In birds, the left innominata comes off from the aorta first.

† Meckel's Archiv. B. ii. h. 3; and Journal Complémentaire, tom. i.



continued onwards into the bulb of the aorta, and thus separates this cavity longitudinally into two compartments. The division of the bulb is, however, imperfect for a time; it advances gradually from the part next the ventricle to that from which the vascular arches rise; so that, while the posterior part is divided, the anterior yet remains single, a communication being left at this part between the aortic and pulmonary roots, which admits of the passage of the blood from the right ventricle into the aorta, when the pulmonary arches are obliterated (Fig. 39. A). When the division of the aortic bulb has just taken place, the arch and descending part of the aorta appear to be a continuation of the pulmonary rather than of the aortic root, the latter appearing to lead only into the vessels of the head and anterior extremities. The ductus arteriosus remains for some time, as at first, short and wide, and has the appearance of being an opening of communication between, or a deficiency in, the parietes of the juxtaposed tubes; it afterwards becomes lengthened out and narrowed, and appears during a short period to pass from the aorta to the pulmonary root and aorta continuous with it; but about the tenth week in the human embryo, this part is dilated, and forms a more direct communication between the ascending and the descending aorta, and the ductus botalli is now formed by another part, viz. the end of the pulmonary root leading into the arch of the aorta (Fig. 43).

The lungs of mammiferous animals are developed much in the same manner as those of birds, at least in the earlier stages of their growth. They do not appear to be visible before the period when the branchial apertures begin to close. According to Rathke both lungs are simultaneously produced; they form at first one mass, which is soon divided into the rudiments of the right and left lung by a longitudinal groove (Figs. 40, 41, 42, L). The apertures or tubes of the bronchi and trachea seem to begin in the same way as in birds; but the cellular part of the lung does not become so highly developed as in them, and is intimately united with the bronchial tubes throughout the whole lung. (See the figures taken from Rathke). As the lungs become larger, they receive vessels from the pulmonary arches, which gradually enlarging as the fœtus becomes developed, divert the stream of blood from the arterial duct of the



aorta. This latter opening now diminishes in size, and, at birth, when the efflux of blood to the lungs is suddenly increased, it is closed up.

Having now given a short sketch of the general phenomena which manifest themselves during the development of the rudimentary organs in the embryo of vertebrated animals, and having traced in detail the progress of the heart, bloodvessels, and respiratory organs, during their formation and early growth, it may be proper, in conclusion, to recapitulate the more remarkable facts, or general principles, relating to these subjects, which the observations that have just passed under review appear to establish.

I. From the short account which was given, in the commencement of the Essay, of the formation or origin of parts in the earliest stages of foetal development, it cannot but be apparent that, whatever opinion is formed respecting the nature of the germ, or speck round which the commencing parts of the embryo appear to arrange themselves, there is nothing in the appearance or structure of the germinating spot, so far at least as has been ascertained by the accurate investigations of the most eminent physiologists, which assimilates any of its parts to those of the foetus or perfect animal, the formation of which it precedes. We seem entitled, therefore, in the present state of our knowledge, to regard these germs as wholly invisible—perhaps entirely imaginary, since their existence is only inferred from phenomena which occur during the development of the embryo.

II. We have had an opportunity also of observing how very different the parts of the embryo are on their first appearance in the ovum, from those parts which they represent, and into which they are transformed at a later stage of foetal life, or after birth; and we have seen how gradual the change is by which this transition is effected.

III. From the important place which the cerebral and circulating organs occupy in the perfectly formed animal, many have believed that the formation of the brain and heart precedes that of all other parts; but it has been shown that, though these are among the organs which appear to be most highly developed



or perfected soonest, yet before the commencement of their formation, and certainly before any parts, which may with justice be compared, in function or structure, to these organs, are produced, the substance is deposited from which the head, trunk, and extremities are formed.

The heart has also been supposed to take its origin in consequence of some influence derived from the brain and spinal cord; and many have imagined that the development of the greater number of organs in the body, follows necessarily the presence of the heart, or of certain bloodvessels; but the phenomena of the development of these parts appear to prove such ideas to be erroneous, and to show that we are as yet ignorant of any particular influence which the pre-existence of one part in the early stages of its advancement exerts on the formation of another. Many observations, indeed, show that the brain and heart are nearly simultaneously produced, and that in all those parts which may be examined with ease, a certain quantity of their parenchyma is formed, before they receive the bloodvessels which, at a later period, serve for their nutrition.

IV. The general resemblance which the changes of development in the ova or fœtuses of vertebrated animals bear to one another, is very striking; it illustrates the analogy of structure in the different animals of this class when arrived at their state of maturity, and seems to indicate very clearly, that the general plan upon which their systems and organs are constructed and arranged is the same. This correspondence, indeed, in the relations of organs to one another, and similarity in their construction, to which the name of Type of Organization has been given, appears to be comparatively much more clearly understood, from the knowledge, confined as it yet is, of the development and transformation of the fœtus, than from the immense number of facts which have been established by the examination of the structure of animals in their perfect state.

In examining the embryoes of the vertebrated animals, at a corresponding period in the early stages of their development, it is truly surprising to remark how very much they resemble one another. In some of the higher orders especially, it would be difficult for those unaccustomed to such investigations, to distinguish between the embryoes of the lizard, bird, or mammi-



ferous animal, when they are removed from their ova and divested of the accessory membranes; and impossible for the experienced eye even, to perceive the differences between the embryos of the different families of the same order, as of birds or mammalia.

The following may be regarded as some of the more important particulars in which the phenomena of development correspond in the different orders of vertebrated animals:—1. The ovum being essentially composed of a yolk, or collection of granular substance, enclosed in a membrane, along with some accessory parts, all enveloped by a general covering, to which the name of chorion may be most properly applied. 2. The existence of some part of the yolk, generally of a firmer consistence than the rest, situated towards the upper surface, and of a membranous form, called the germinal membrane, in which the changes connected with the formation of the *fœtus* more immediately take place. 3. The commencement of the formation of the embryo being indicated by the appearance of a streak and small groove, in the centre of the germinal membrane, and this groove afterwards forming the rudiment of, or being converted into, the spinal canal. 4. The separation of the substance of the germinal membrane into three layers, in which different systems of the animal appear to originate. 5. The expansion of these layers of the germinal membrane over the surface of the yolk, so as to form a new covering for this part, situated within its proper membrane; and the development of blood, and of a vascular network on the surface of this covering or yolk-sac. 6. The development of the head, trunk, and extremities, from the outermost or serous layer, as it has been called; the formation of the anterior and posterior extremities taking place sooner or later, according to the circumstances in which development is effected, and according to the mode of life of the perfect animal. 7. The formation of the cavities destined to contain the brain and spinal cord from folds and thickenings of the same layer. 8. The development of the organs of the senses from these cavities, and their contained parts; the early appearance of the eye and ear especially. 9. The formation of the principal circulating organs, such as the heart and larger bloodvessels, from the middle, or, as it has been named, vascular layer. And, 10. The



development of the intestinal, respiratory, and some of the principal secretory organs, by means of folds and other changes of the two interior, or vascular and mucous layers of the germinal membrane. These phenomena, occurring during the development of the fœtuses of vertebrated animals, are so nearly alike, that they may be considered as a strong corroboration of the opinion, that the general plan of construction and arrangement of the organs of all these animals is the same.

V. The same extent of knowledge of the development of the fœtus of Avertebrated animals has not as yet been obtained ; but it appears probable that, notwithstanding the great dissimilarity between the adult members of this class of animals, the observation of the manner in which their organs originate and become developed, may tend also to elucidate their connexions, and point out analogies where they were not before suspected to exist.

Such a knowledge would, I doubt not, instruct us also on the important question which has lately engaged the attention of two of the most distinguished comparative anatomists in France, viz. whether there exists any analogy between the general plan of arrangement in the organs of vertebrated, and those of avertebrated animals ; or inform us whether, among the latter, there is any order or family, resembling more than the others the vertebrata, which forms the connecting link between the simpler and more complicated class of animals. The few observations which have as yet been made on this subject, by those who possessed a general acquaintance with the phenomena of development, have already laid the foundation of this knowledge, and have pointed out some curious and interesting points of resemblance between vertebral and avertebral animals, in regard to which the greatest dissimilarity was previously believed to exist\*.

VI. During the development of any of the vertebrated animals, as the germinating speck passes from the form of a granular mass, in which it first makes its appearance, to the state of embryo in which we perceive the rude sketches of its principal organs, and gradually assumes the more perfect form of fœtus differing little from the adult, the animal makes a gradual transition from a simpler to a more complicated organization. Hence

\* See Burdach's *Physiol.* B. ii. Rathke's and Forchhammer's observations on the development of the craw-fish, lobster, &c.



has arisen the opinion, not uncommon among physiologists, that the foetus, at every successive period of its development, assumes the form of some animal inferior to it in the perfection of its structure. From the analogy which we have already stated to exist between the mode of development of different orders of vertebrated animals, and from the gradual manner in which the complication of their structure is increased, as well as from the resemblance well known to exist in the general plan of their construction, it will immediately be apparent that the foetus of the higher orders of these animals must resemble, at different successive periods, to a certain extent, the adult members of the lower orders; but as the periods at which all the organs correspond are not the same, the resemblance must be considered as imperfect, and is more apparent in respect to particular organs than to general structure. Many differences exist between the organization of vertebrated and avertebrated animals, of so important a nature as to render any comparison such as that just noticed vague and unsatisfactory at any period of the foetal development.

VII. In regard to the formation of the heart, it seems to be established by the observations previously related, that, 1st, this organ consists at first, in all vertebrated animals, of a simple membranous tube, forming a continuation, and connected with the venous and arterial vessels. 2d, This tube of the heart is invariably situated on the lower and anterior side of the œsophagus. 3d, The blood at first enters this tube towards its posterior extremity, and on the left side of the body, and issues at the anterior extremity, and towards the right side. 4th, The changes which the tube undergoes in its gradual conversion into the heart of the adult, are, to a certain extent, the same, or at least analogous, in all the orders of vertebrata. 5th, The auricle and bulb of the aorta are separated from the ventricle by a constriction in the paries of the tube. 6th, A curvature takes place in the tube, so as to bring together its two extremities, or to make the auricle and bulb of the aorta approach one another; this curvature being such, that the auricle is always situated behind, or rather above the ventricles. 7th, In fishes and batrachia, the form of the heart is perfected, the ventricle becomes very thick and muscular, the auricle is dilated, and valves are formed near the apertures, while this organ remains simple and undivided, or while the blood



which enters it is propelled through a single vessel. 8th, In lizards, serpents, and turtles, while the same or analogous changes take place in the general structure of the heart, in the strength and thickness of its parietes, or in the relative position of its parts, the cavities of this organ are more or less completely divided, so as to separate the blood which passes through it into more than one stream; the auricle being divided by the formation of a septum advancing from above downwards, the ventricle, by a partition which rises from the apex towards the base. 9th, The heart of birds and mammalia is seen to undergo the same subdivision, and the right and left cavities communicate for some period of foetal life with one another; but, in these animals, the partitions by which the auricles and ventricles are separated become complete, and no longer leave any opening from the cavities on one side of the heart into those of the other. 10th, In mammalia, the growth of the septum, in the interior of the ventricle, is accompanied by the formation of a notch or constriction on the outside, by which the apex of the heart is rendered double for a time. 11th, At the same time, in the higher reptiles, birds, and mammalia, the bulb of the aorta is also divided, so as to enable each of the ventricles to communicate with those vessels only into which they propel the blood during the whole of life.

VIII. We have seen, that in the early stages of development, there is a uniform disposition of the greater arterial trunks in all the orders of vertebrated animals, though the distribution of these vessels is by no means the same as that which exists permanently. The arteries arising from the bulb of the aorta, and connected with the respiratory organs of the neck, have been chiefly referred to, as affording one of the most remarkable examples of this uniformity of disposition in the vessels of the fœtus, and of the variety of transformation which they undergo during their conversion into the permanent structure.

IX. We have seen that, in all vertebrated animals, the anterior part of the intestinal tube is encompassed by four or five\* pairs of arterial vessels, formed by the subdivision of the as-

\* It appears probable that there are five in all vertebrated animals, excepting the lamprey, myxine, and some others. Baer has endeavoured to demonstrate this in his essay on this subject in the 7th vol. of the *Répert. Génér.*



ending aorta, and that these vessels, after passing round the œsophagus, unite again with one another above this tube, and below the vertebral column, to form the dorsal aorta.

X. It has been seen, that, in the lower aquatic animals, gills become developed along the course of parts of these vessels, while in the higher or air-breathing animals, after being so disposed as to indicate slightly the appearance of gills, these vessels are gradually converted into the systemic and pulmonic arteries by the processes of enlargement, partial obliteration, separation, &c. Though the general phenomena occurring during this transformation of the arteries in the neck, are analogous in all vertebrated animals, there are certain remarkable differences respecting the obliteration of some, and the permanence of others of these vessels, in various species of animals.

1. In cartilaginous fishes, all the branchial divisions of the aorta remain permanent to form gills, undergoing very minute subdivision in these organs, so as to be converted into branchial arteries and veins.
2. In osseous fishes, five pairs of branchial arches are also observed in the fœtus, but only four of these remain to form the gills, the anterior being partly obliterated, gives rise to the roots of the carotid or head artery.
3. In batrachia, we have seen, there is a gradual transition from the structure of fishes to that of the higher reptiles. The gills in the batrachia are, during some period of their existence, developed along the course, or from particular parts of the branchial arches, in which, as in fishes, minutely subdivided branchial arteries and veins are formed; but these last gradually disappear, and more or fewer of the primitive branchial vessels remain.
  - a.* In the batrachia with permanent tails, the aorta is formed, as in the fœtus, by the union of the whole four branchial arches on each side, the pulmonary artery arising from the posterior arch;
  - b.* while in the batrachia without tails, as in the frog, only one branchial vessel remains on each side, so as to form the right and left roots of the aorta; and the pulmonary artery, which in the fœtus was given off from the posterior branchial arch, appears to spring from the aortic root itself, in consequence of the obliteration of the posterior part of the arch communicating with the descending aorta.
4. We have seen that two branchial arches also remain entire in the saurian and



chelonian reptiles; but in these, as well as in all the other animals in which the ventricular part of the heart is more or less divided in the progress of development, the pulmonary arteries—formed, as in batrachia, by the posterior branchial arch—are separated from the aorta and its branches; each of these sets of vessels communicating directly with its proper ventricular cavity.

5. In birds, the second pair of arches, and the fifth arch of the right side, are wholly obliterated without giving rise to any branches. The first and third form the arteriæ innominatæ or carotid and subclavian arteries on both sides, the communicating branches between these arches and the roots of the aorta, being obliterated at an early period. The fourth arch on the right side alone remains entirely pervious during the whole of life, and forms the proper trunk of the aorta from which the innominatæ spring. The fourth arch on the left, and the fifth on the right side, united in a common root, give rise to the pulmonary arteries. These arches remain pervious till birth, forming the ductus botalli or arterial ducts leading from the right ventricle into the aorta.

6. In mammalia, nearly the same changes take place in the transformation of the anterior arches; but the aorta is formed in them by the fourth arch on the *left* side, this vessel descending on the left side of the œsophagus. The fourth arch on the right, and fifth on the left side, appear to give rise to the pulmonary arteries. In the mammalia, the ductus botalli is formed, not as in birds or lizards, by the permanence of the posterior part of the pulmonary arches, but by a communication which remains in the bulb of the aorta between the roots of the pulmonic and systemic trunks\*. Thus it is explained how the aorta of birds corresponds with the right root of this vessel in lizards, and that of mammalia with the left; the arteria innominata of the left side being first given off in birds, while, in mammalia, that on the right springs first from the aorta.

XI. From these observations, it appears that it is erroneous to compare the single heart of fishes or batrachia with the right side or pulmonary cavities of the heart of higher animals. They are similar, it is true, in this respect, that they both pro-

\* There is an approach to this form in the structure of the vessels rising from the heart in some of the saurian reptiles.



pel the blood into a respiratory organ; but the relation of the gills differs widely from that of the lungs to the heart; and it would be more correct to compare the single heart of fishes with the whole heart of the higher animals though divided, or with this organ in the early stages of their foetal development.

XII. We have had an opportunity of observing, that as we ascend in the series of vertebrated animals, the processes by which respiration is carried on in the foetus, become gradually more and more complicated. 1. The ova of fishes are deposited and developed in the same medium in which the adult animal continues to live: *a.* in osseous fishes, the blood is exposed to the influence of the respiratory medium on the sac of the yolk; *b.* and in cartilaginous fishes both on the yolk sac, and in external gills. 2. The ova of batrachian reptiles are deposited, and become developed in water; while the animal, in its adult state, breathes air. The blood in the larva or foetus of these animals is arterialized by means of a yolk little developed, and on external and internal gills: and in the animal arrived at maturity, by means of lungs, and a large urinary bladder or allantois. 3. In the saurian, ophidian, and chelonian reptiles, the ovum being generally deposited in the medium which the animal permanently breathes\*, an amnios or covering for the foetus is formed, by means of which it is kept immersed in a fluid, till the time when it is enabled to respire air; respiration being carried on, during the foetal life of these reptiles, by the sac of the yolk and allantoïd vesicle highly developed. Some of these reptiles, however, seem to be allied in some respects with the batrachia, as in them part or whole of the allantois remains permanent in the adult state. 4. In birds, the application of a considerable external heat is necessary to induce the proper respiratory alteration of the blood, which is exposed, as in the previous class, on the yolk and allantois,—membranes very highly developed in birds. In these animals, a very small pedicle only of the allantois, the urachus, remains in the foetus after birth. 5. In mammalia, again, the ovum being retained in the body of the mother, the respiratory changes are effected by the intervention of

\* Making exception in these, as well as other animals, of such as become developed in the body of the parent.



the maternal blood; and another organ, formed by an extension of the umbilical vessels, is superadded in mammalia to the yolk and allantoid, which exist as in birds. This is the placenta, by means of which vessels, containing the venous blood of the fœtus, are brought closely into contact with the vessels lining the uterus, and containing blood more highly aërated, by which contact their respiration is effected.

XIII. It has also been shewn in the preceding relation, that the gills are invariably formed on processes of the hyoid bone, which are either permanent, as in fishes, or exist only during the larval state, as in batrachia. The operculum is developed from the posterior part of the lower jaw, and this part, as well as the branchiostegous membrane, appears to be intimately connected with the lingual bone or the lateral branches of the hyoid.

XIV. The observations related above, seem to shew that the lungs, though they receive their vessels from branchial arches, which, during some period of fœtal life, are distributed on gills or analogous parts, cannot with accuracy be compared to these latter organs, as has been attempted. The lungs, it has been shewn, are developed on the lower side of the œsophagus, but they do not appear to be formed by a process or diverticulum from the intestinal tube, as observation shews that they are not hollow when first formed, and that a cavity exists for some time in their interior, without its communicating with the hollow of the intestine.

In conclusion, I may state, that, in the preceding pages, I have endeavoured to give as short, and at the same time as accurate, an account of the subjects treated of as their difficulty, and the obscurity which still hangs over many facts connected with them, have enabled me to do.

In many parts I have stated only those of the facts which appear to be most probable, judging of them either from the relations of others to which I have had access, or by observations which I have myself made in confirmation of them. In selecting the drawings which have been given, I have always chosen to copy the delineation of others, when I found that they represented sufficiently accurately the appearances related.



*Explanation of the Plates.*

In all the figures, the following letters indicate the different parts:—

- a*, The ventricle. *a'*, The auricle of the heart. *b*, The bulb of the aorta. *b'*, The ascending aorta. *c*, The liver. *d*, The stomach. *d'*, The œsophagus. *e*, The mouth. *e'*, The anus. *f*, The eye. *g*, The anterior. *g'*, The posterior extremities. *H*, The external gills, the stalks. *h*, The leaflets. *I*, The internal gills or branchial plates. *i*, The leaflets or fringe. *λ*, The operculum. *k*, The rectum and cloaca. *L*, The lungs. *l*, The cellular part. *l'*, The trachea. *m*, The branchial vascular arches. *n*, The returning vessels or branchial veins. *o*, The branchial apertures. *p*, The pulmonary arches or arteries. *r*, The left; *r'*, The right root of the descending aorta. *s*, The descending aorta. *t*, The carotid artery. *u*, The brachial, and in Figs. 9 and 11 the mammary. *w*, Communicating vessels of the branchial arches which are obliterated. *v*, The urinary bladder and allantois. *x*, The artery of the yolk. *y*, The vein carrying blood to the yolk. *y'*, The returning vein of the yolk. *z*, The umbilical artery. *z'*, The umbilical vein. *δ*, Ductus arteriosus. *ι*, Inferior maxilla. *π*, The amnios. *ε*, The chorion. *χ*, The ductus vitello intestinalis.

## FISHES.

- Fig. 1. (From Rathke) Supposed section of the fœtus of the *Blennius Viviparus*, at the middle of fœtal life.
2. (From do.) The anterior part of the body of a very young embryo of the same fish magnified seven times, the sac of the yolk and integuments covering it removed.
3. (From do.) The same seen from below; the heart removed; the abdomen opened to shew the intestinal tube.
4. (From do.) Another embryo farther advanced. The operculum covering the first and second branchial plates.
5. (From do.) The same seen from below.
6. (From Monro) The fœtus of the skate with the yolk sac, half the size of the original. *A*, Anterior part of the body of the natural size, shewing the external gills suspended from the branchial apertures on the lower side of the body.
7. Anterior part of the fœtus of the *Squalus Max.*; half the natural size, seen from above, shewing the external gills. *A*, The extremity of one of the gill filaments magnified.

## REPTILES.

1. *Batrachia.*

8. Fœtus of the Aquatic Salamander one day after its exit from the egg, seen from below. *A*, Natural size.
9. (From Rusconi) Head, &c. of the larva of the same animal at the time when the gills are nearly perfected, opened, and seen from above. Magnified.



10. (From the same) Shews the leaflets of the gills forming.
  11. (From do.) The vessels in the neck of the adult Salamander.
  12. (From Carus) The adult Salamander opened, to shew the urinary bladder or allantois, with the umbilical vein going from it to the liver.
  13. The larva of the frog about 24 days old; shews the connexion of the external with the internal gills, and the left lungs beginning to be formed. A, The natural size.
  14. The larva of the frog at the time of the commencement of its transformation, twice the natural size. A, Exhibits the double row of leaflets on the internal gill.
  15. (From Swammerdam) The principal arteries of the adult frog.
  16. The commencing lungs of the frog; A, in the tadpole on the 18th day, seen from below; B, in the tadpole represented in Fig. 13. seen from the side.
2. *Lizards, &c.*
17. (From Emmert and Hochstetter) Ovum of the *Lacerta agilis*, shewing the fœtus in its amnios, the yolk and allantois with their vessels.
  18. (From Dutrochet) Supposed section of the ovum of the Serpent, shewing the allantois expanding.
  19. (From Bojanus) The heart and arterial vessels of the *Testudo Europæa* from behind.

#### BIRDS.

20. Anterior part of the fœtus of the Duck four days and a-half old, seen on the right side. Magnified about seven diameters.
21. (From Baer) Section of the chick in ovo on the fourth day.
22. (From Rathke) Embryo of the chick on the fifth day. Magnified one diameter.
23. (From do.) Longitudinal and vertical section of the head and neck of the chick on the fifth day, shewing the interior of the pharynx and the remains of the branchial apertures.
24. (From do.) Heart and anterior part of the neck of the same embryo, shewing the infer. maxilla and operculum.
25. Posterior view of the heart and interior of pharynx, at a corresponding period, shewing the branchial arches given off by the bulb of the aorta. A, Section of the extremity of the bulb.
26. (From Rathke) A, The lower, and B, The lateral view of the lungs and trachea of the chick on the fifth day, with the œsophagus.
27. (From do.) The same on the sixth day.
28. (From do.) The same on the seventh day.  
(From do.) The lungs, &c. on the eleventh day, shewing the trachea, aorta, pulmonary arteries, communicating vessels, and the union of the cellular, with the bronchial parts of the lungs.
30. (From Burdach, but reversed.) Diagram shewing the branchial divisions of the aorta of the chick on the lower side of the pharynx,



and the mode of their transformation into the aortic and pulmonary vessels.

31. The position of the ductus arteriosus relatively to the œsophagus in the chick about the 12th day.

#### MAMMALIA.

32. (From Bojanus) Sketch shewing the relative position, size, &c. of the allantois and yolk-sac, &c. in the fœtus of the sheep about three weeks old. A, The fœtus and umbilical vesicle magnified. B, A small part of the fœtal placenta or cotyledon of the calf, shewing the processes of the chorion on which the umbilical vessels are ramified.
33. (From Bojanus) The same in the dog of 24 days.
34. The same in the rabbit of about fourteen days, with the placenta. A, The entire ovum. B, The chorion and umbilical vesicle opened, so as to shew the allantois and placenta.
35. The head and neck of the embryo of the dog of three weeks, represented by Baer, and copied from Fig. 8. of former Essay.
36. The human embryo of about six weeks, in which I found two branchial apertures at least on each side of the neck, the heart exposed. A, The natural size.
37. (From Rathke) Anterior view of the neck of the fœtus of the pig, represented in Fig. 9. of former Essay, shewing the branchial apertures and operculum.
38. Heart and branchial arches in the rabbit, Fig. 34.
39. Diagram of the branchial arches of mammalia, and their transformations, corresponding with that of birds by Burdach. A, Ductus arteriosus of mammalia when just formed.
40. Posterior view of the heart and commencing lungs and trachea of the rabbit, Fig. 34. Magnified three diameters.
41. (From Rathke) The tongue, trachea, and lungs of the fœtal horse seen from above, twice the natural size. A, The same seen from below. B, Section.
42. (From do.) Lungs of the pig farther advanced, twice the natural size, seen from below. A, The same, seen from above. B, Section.
43. The heart, lungs, pulmonary and aortic vessels, and ductus arteriosus of the human embryo of ten weeks, twice the natural size.



Since writing the above, I have had an opportunity of seeing, in the Number of the *Annales des Sciences Naturelles* for September last, the fourth memoir by M. Serres on Transcendental Anatomy, in which this author treats of the Law of Symmetry and Conjunction in the Vascular system of vertebrated animals.

In that memoir, M. Serres relates some minute observations which he has made on the development of several parts of the vascular system, from which he has been led to describe the origin of some of the principal arteries of the body, in a manner different from that generally received by those who have written on this subject, and to form the conclusion, that all single arteries, situated in the median plane of the body, are at first double; that they are formed by the union of two vessels, and that the "Duality of arteries tends to Unity from without inwards, by the laws of formation from the circumference to the centre, or of symmetry and conjunction.

The principal arteries which M. Serres describes as formed and united in the manner alluded to are the Aorta, the Arteria basilaris and Arteria callosa cerebri, and the Umbilical arteries in the funis of the allantois; and he adduces in support of his conclusion observations on the structure of these arteries in the foetus of birds and mammalia at an early stage of its advancement, in cases of malformation, and in the different orders of vertebrated animals in their adult state.

In speaking of the formation of the aorta, M. Serres refers to the observation made by the greater number of those who have attended minutely to the development of the chick (more especially by Pander, *Beiträge zur Entwicklungsgeschichte*, &c. § 13. pl. viii.), that, towards the 60th hour of incubation, the aorta of the chick consists of two vessels quite separate from one another, in the abdominal part of the vessel where it gives off the arteries of the vascular area.

At this period, the abdominal part of the embryo consists simply of the rudimentary vertebral column inclosing the spinal



cord, of the lateral thickened parts of the serous layer of the germinal membrane which form the plates of the abdomen, and of the commencing intestinal folds on the lower surface,—which parts are situated nearly in the same plane with the horizontal part of the germinal membrane. About the middle of this part of the embryo, the two arteries of the vascular area are seen proceeding from it to the transparent and vascular areas; while the aortic branches, with which they communicate, form two parallel vessels, situated one on each side of the rudiments of the vertebræ, and extending from the part of the back opposite to the ventricle of the heart, where they are joined into one trunk, to the end of the tail.

Both Pander and M. Serres have given the name of Umbilical to the arteries of the vascular area, a circumstance which has in some measure tended to obscure their description of them. Pander, indeed, forgetting that the proper umbilical arteries, distributed on the allantois, are produced from the pelvic portions of the aorta, at a period considerably later than the vessels of the area, supposes that the only difference between the structure of the aorta in the foetus, and that in the adult animal, consists in the greater height at which the division of this vessel into the iliac arteries takes place; but this, it is obvious, affords no explanation of the circumstance, that the arteries of the vascular area of the yolk, (forming as their more recent and appropriate name of Omphalo-mesenteric implies), continuations of the intestinal arteries, are each of them given off by a separate branch of the aorta.

M. Serres has also observed, that, between the 40th and 50th hours, or immediately after the circulation of the blood has commenced, the trunk of the aorta is double in its whole extent, from the place at which its branches spring from the bulb of the heart to the end of the tail; and he affirms that it is by the gradual union of these two vessels on the median line that the single aorta of the adult is formed.

Baer, the accuracy of whose researches on development we have so often had occasion to admire, had also directed his attention to the state of the aorta in the early stages of incubation, but apparently without the same success. In his history of the development of the chick (*Répert. Génér. d'Anat. et de Physiol.* tom. 8.



p. 72.), he informs us, that the two vessels into which the ventricle of the heart propels its contents, towards the 40th hour, having passed round the anterior part of the intestinal tube, and proceeded some way along the inferior surface of the vertebral column, *probably* reunite after having been separated for a certain space. He says, that this union cannot, however, be easily shown at this period, because these vessels, on arriving below the vertebral column, appear to lose their parietes, and their contents are too transparent to enable us to trace their course. He adds, that their union can, however, be easily demonstrated before the end of the second day.

These remarks of Baer, and the circumstance that M. Serres makes no allusion in his description of the primitive double state of the aorta, to the existence of the ten branchial subdivisions of this vessel discovered by Huschke, Rathke and Baer, and described at p. 64. of this essay, and that he has given us no information on the means he employed in making this very difficult investigation, have made me think the repetition of the observations of M. Serres necessary, in order not only to inquire into their accuracy, but to endeavour to point out the relations of the two aortic branches described by M. Serres, to the dorsal roots of the aorta formed by the union of the branchial arches on each side of the intestine.

From the very cold state of the weather at the time I made these observations, I found it very difficult to keep the chick alive on the field of the microscope, and to observe the circulation of the blood going on, at the early stage of advancement necessary in this investigation, and I was obliged to have recourse to the plan of making transverse sections of the fœtus in the whole length of its body, in order to ascertain the structure of its vessels,—a mode of observation by no means easy, but one which affords most certain and satisfactory results. In this manner, I have been enabled to confirm the general results stated by M. Serres in regard to the double state of the aorta, in the early stages of the development of the fœtal bird.

In the chick, at the 36th and at the 40th hours of incubation \*, or a little before and immediately after the circulation of

\* In mentioning the hours of incubation, I state the period, not according to the time occupied in the incubation of the individual fœtuses em-



the blood commences, I have seen two vessels rising from the bulb of the heart, winding round the anterior portion of the intestine, and continuing to descend along the body of the fœtus, parallel to but separate from one another in their whole length. These vessels are situated below the spinal marrow, and on each side of the chorda dorsalis\*, or part afterwards occupied by the bodies of the vertebræ. The omphalo-mesenteric arteries are given off from these vessels considerably higher at this than at a later period, and at first sight appear to be the only branches continued from the aortic vessels; but on minute examination, two other smaller vessels may be seen, situated between the omphalo-mesenterics, and descending some little way below the place where these latter arteries pass off into the vascular area: towards the tail of the embryo, these two continuations of the aortic vessels seem to lose themselves in a large vacant space left between the vascular layer of the germinal membrane and the chorda dorsalis.

In the chick at the 48th or 50th hours, or at the period when the circulation of the blood is now completely established on the vascular area, but before the second set of veins have appeared, I have found the two aortic vessels united for a considerable space in the dorsal region. This union seems to commence in the back, nearly opposite to the auricle, but I have not been able to ascertain the precise period at which this process begins: it gradually extends backwards towards the tail, so that, at the 60th or 65th hour, the whole of the dorsal and part of the abdominal aorta is one tube, as far as the place where the omphalo-mesenteric arteries are given off. The omphalo-mesenteric arteries, being shortly after this partially united, appear to arise from one stem.

On the fourth day, the whole of the two abdominal portions of the aorta becomes united, as far as the region where the permanent division of this vessel takes place: here the vessels remain separate, and furnish the umbilical arteries or vessels of ployed, but according to the state of their advancement, and the general periods adopted by Baer, Prevost and Dumas, &c.

\* The Chorda dorsalis, so called by Baer, corresponds in its position to the primitive streak of the cicatricula: it is a small dense cord, situated immediately below the spinal marrow.



the allantoid membrane, which now begins to be developed,—these being the first considerable branches of the iliac arteries which are formed.

While this union of the dorsal and abdominal portions of the double aorta takes place, the two vessels arising from the bulb of the heart, of which the aortæ formed at first the continuation, do not, like these, become united into one trunk, as the observations of M. Serres would lead us to believe. I have already described these two vessels \* as the first pair of branchial arches, the posterior parts of which form the separate roots of the aorta to be found in the chick on the third and fourth days of incubation; these roots being also joined at this period by the four other branchial arches which appear successively on each side of the pharynx. These roots of the aorta and branchial arches, we have already remarked, do not become united to one another, but undergo other very remarkable changes, by their partial enlargement or obliteration. Parts of the first branchial arches give rise to the carotid arteries in all vertebrated animals: while the proper trunk of the aorta, or at least its ascending portion and arch, is produced from other branchial vessels, and the roots into which they are joined; one or more of these serving to form the aorta, according to the class of animals in which the transformation occurs. In Mammalia, the aorta is formed by the permanence of the fourth branchial arch and the aortic root of the left side; in Birds by that on the right; in the greater number of Reptiles by one on each side; in the tailed Batrachia by three or four arches on each side and by both roots; in Osseous Fishes by four; and in the Sharks, Skates, &c. by all the five pairs of branchial vessels and the two roots which are to be found in the early stages of development in the fœtus †.

The discovery of the double state of the dorsal and abdominal aorta in the very young fœtus, made by M. Serres, must, however, be regarded as very interesting, not only as it points out a very singular change, little attended to before it was investigated by this author, taking place in the median arteries, but also as it seems to afford an explanation of some varieties in the

\* See page 64, &c. and figs. 20, 21, and 30. in the last Plate.

† See Figs. 1. 9. 11. 14. 15. 19. 20. 30. 35. 39. in the two last plates.



place of junction of the roots of the aorta, and in the origin of the cœliac, mesenteric and other arteries, which occur in several tribes of reptiles.

The observations of this author in regard to the union of the double arteriæ Basilares and Callosæ, will be read with equal interest, as well as several curious facts mentioned by him respecting the union of the principal venous trunks, and the varieties of distribution of the vessels in the umbilical cord in some mammiferous animals.

A. T.

Dec. 30. 1830.

## ERRATA.

- Page 11. line 34. *after* yolk *insert* which is  
 ..... 12. ... 35. *for* takes *read* take  
 ..... 15. ... 9. ... fig. 17. .... fig. 16.  
 ..... 28. ... 9. ... 20. *dc* ..... 20. *c*.  
 ..... 34. ... 17. *after* 8. and 9. *add* (from Baer)  
 ..... 45. ... *dele* (figs. 2. & 3. *o*.)  
 ..... 70. at bottom, *after* (fig. 33. *insert* of the dog)  
 ..... 72. ... 15. *for* A *read* B  
 ..... 84. ... 16. ... on ..... by















