IV. *The Development of the Branchial Arterial Arches in Birds, with special reference to the Origin of the Subclavians and Carotids.*

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[Plates 22—25.]

The manner in which the large arteries springing from the aorta in the higher Vertebrates have been developed from a set of arches comparable to the branchial vessels of Fishes has been clearly explained by Rathke,* and since his time the views which he first set forward in the year 1857 have been almost universally accepted and taught. I have been led to believe, however, from the observation of certain facts in the anatomy and development of Birds, that the deductions which Rathke made, drawn chiefly from his studies in Mammalian and Reptilian embryology, are not applicable to this class in so far as concerns the origin of the carotid and subclavian arteries. I am inclined to think also that the theories now generally held will be found inadequate to explain the origin of these vessels in the case of Chelonian and Crocodilian Reptiles, and to a less extent probably in Mammals.

Anatomy of the Larger Arteries in Birds.

The aorta, arising from the left ventricle of the heart, passes at first forwards, upwards, and to the right side; then, changing its direction, it arches over the right auricle, and, sweeping backwards dorsal to the root of the right lung, gains the middle line. In the first part of its course two large vessels, the brachio-cephalic or innominate trunks, are given off.

The innominate arteries arise in close proximity to one another. They usually give no lateral branches, but terminate by dividing into carotid and subclavian vessels. Occasionally, however, a small branch is supplied to the front of the trachea, but this is more frequently an offset from the subclavian or carotid.

The common carotid arteries, passing forwards from their origin, bend round the œsophagus to reach its dorsal aspect, and, there approaching one another, gain the middle line, and are continued forwards towards the head in the canal formed by the

* H. Rathke, "Untersuchungen über die Aortenwurzeln und die von ihnen ausgehenden Arterien der Saurier." 'Wien, Akad. Denkschr.,' vol. 13, 1857 (*Abth.* 2), pp. 51—142.

inferior spinous processes. Emerging from this canal opposite the third or fourth cervical vertebra, the vessels separate from one another, and, passing still further onwards, break up into numerous branches. The vessels of the right and left sides are often symmetrical in size and position, but one or other is sometimes of less diameter than its neighbour. In many cases one vessel is wanting altogether (all Passeres, GARROD*).

Fig. 1.

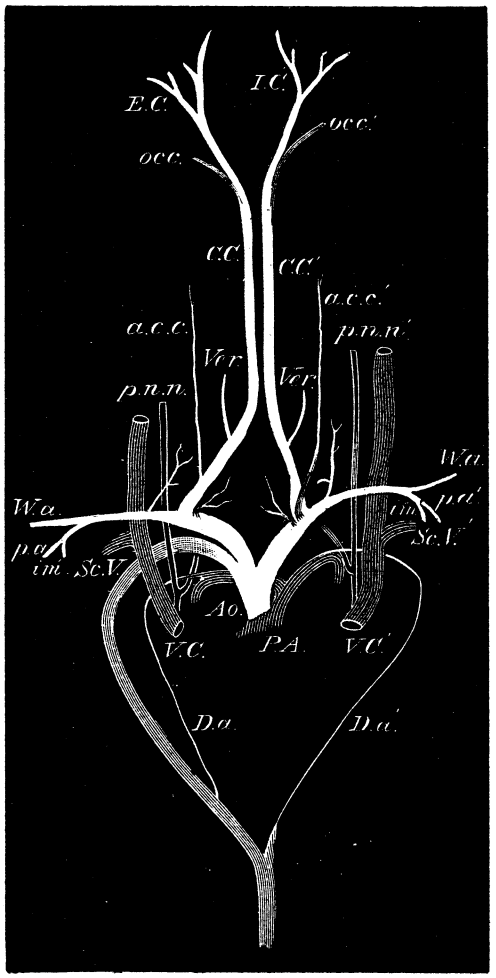


Diagram of the Arterial System of the Bird.

Ao., aorta; *I.*, innominate; *C.C.*, common carotid; *E.C.*, external carotid branches; *I.C.*, internal carotid branches; *occ.*, occipital; *Ver.*, vertebral; *a.c.c.*, arteria collateralis colli; *W.a.*, wing artery; *p.a.*, pectoral artery; *i.m.*, internal mammary; *Sc.V.*, subclavian vein; *V.C.*, vena cava; *p.n.*, pneumogastric nerve; *P.A.*, pulmonary artery; *D.a.*, ductus arteriosus.

In the Ground Hornbill (*Bucorvus abyssinicus*) the arteries, passing forwards to supply the head, run in the lateral parts of the neck, and are not to be compared to

* GARROD, "On the Carotid Arteries of Birds," 'Zool. Soc. Proc.,' 1873, pp. 437–472; also 'Collected Papers,' London, 1881.

the carotids of other Birds; but OTTLEY* has pointed out that two obliterated cords, representing the right and left carotids respectively, are to be found in the usual situation. In some Parrots the carotid artery of the right side runs forward in the usual manner, while the left vessel passes along the lateral aspect of the neck, as in the Ground Hornbill (GARROD).

The branches of the common carotid are numerous: (1) a small branch running upon the front of the trachea, often, however, derived from the subclavian or innominate; (2) branches rising along with No. 1, supplying the lateral parts of the neck, and anastomosing in front with maxillary branches; (3) the vertebral, which after giving a branch to the muscles around the scapula enters the foramen in the transverse process of the second lowest cervical vertebra, and there splits into two divisions, the anterior and larger passing onwards towards the head to anastomose with the occipital artery, the posterior running backwards to the thorax, supplying one or two intercostal spaces; (4) a number of very slender branches are given off to the muscles upon the front of the vertebral column—these correspond in position to the interspaces between the cervical vertebræ; (5) the occipital artery, running in a dorsal direction to anastomose behind the skull with the vertebral artery; (6) a vessel called internal carotid, which, however, distributes a number of branches to the external aspect of the cranium, and to the anastomosis at the back of the orbit, before entering the cavity to supply the brain; (7) the external carotid, so-called, the main artery of the external aspect of the head, dividing into branches named by OWEN† "external maxillary," "laryngeal," "lingual," "hyoid," and "internal maxillary"; from one of the branches or from the main trunk twigs pass backwards in the neck to anastomose with set No. 2. It is important to notice that there is no clear subdivision into branches corresponding to external and internal carotids as in Mammals, but that vessels belonging to the right and left sides, whose destination is the anterior end of the trunk, run forwards underneath the vertebral bodies in the same manner as the aorta passes backwards.

The subclavian arteries, from the extremities of the innominate stems, cross outwards to the anterior limbs. The largest branch is distributed to the pectoral muscles, but, in addition, the internal mammary artery is given backwards, and in many cases a vessel is directed forwards to the ventral aspect of the trachea, and to the skin upon the under-surface of the neck. No intercostal arteries are supplied. The subclavian arteries are distinguished by this important fact, that in their course outwards they pass ventral to the pneumogastric nerves and to the superior venæ cavæ. In this they differ very markedly from the vessels which in Mammals and Lacertilian Reptiles supply the upper limbs, for these, after the manner of intercostal trunks, stretch outwards in a position dorsal to both vein and pneumogastric nerve. In Crocodilian and Chelonian Reptiles the relation of parts is similar to that found in Birds.

* OTTLEY, "The Vessels of the Neck and Head in the Ground Hornbill," 'Zool. Soc. Proc.,' 1879, pp. 461–467.

† OWEN, 'Anatomy of Vertebrates,' London, 1866.

These facts, although probably widely known, do not seem to have been appreciated in their relation to the question of the development of the vessels, inasmuch as it is improbable that an artery running ventral to the vein and nerve, as does the subclavian in Birds, can correspond in origin with a trunk which, as in Mammals, crosses dorsal to these two structures. Only two observers, so far as I have been able to ascertain, have taken notice of the different positions of the vessels. One of these, SABATIER,* has been led to propose a scheme of development differing in some respects from that of RATHKE, while the other, BRENNER,† in a paper on vascular abnormalities, merely notices the facts, and expresses a doubt as to the correctness of the accepted beliefs.

The intercostal arteries are directed chiefly from the aorta, but the first two or three spring from the vertebral.

Vestigial structures.—The right and left pulmonary arteries are each connected to the descending aorta by a ductus arteriosus round which the pneumogastric nerve sends it recurrent branch. These may be looked upon as completing the pulmonary arches. The left ductus arteriosus, passing dorsal to the root of the lung, is a long ligamentous cord which unites with the aorta usually opposite the sixth dorsal vertebra. The right one is described as a short structure passing into the posterior border of the arched portion of the aorta, but I have always found it, in my dissections, of considerable length, terminating in the descending aorta about half the breadth of a vertebra nearer the head than the place of termination of its neighbour of the left side.

Fig. 1, Plate 22, shows the ductus arteriosi of the Nandu (*Rhea americana*).

A vestige of the fourth left arch is present in a few Birds. I have not been fortunate enough to obtain for dissection any of the species in which this structure is found, but Professor A. MACALISTER, of Cambridge, has kindly furnished me with particulars from his own dissections. He has found it as a well-marked cord in the Osprey (*Pandion haliaëtus*) and White-tailed Eagle (*Haliaëtus albicilla*), and some other Raptores. He has also noticed it, but less distinctly, in some of the larger Gulls, especially in *Lestris pomarinus* and *Larus marinus*. When present it stretches from the innominate artery to the aorta as a ligamentous cord. This fact agrees very closely with what I have observed to be the method of its disappearance, described later.

SCHEME OF DEVELOPMENT ACCORDING TO RATHKE.

General accounts of the development of the arterial system in Birds will be found in all works upon Embryology, but the best and most detailed is probably that of FOSTER and BALFOUR.‡ Fig. 2, copied from RATHKE,§ explains the general system.

* SABATIER, 'Études de Circulation Générale,' Montpellier, 1873; and 'Annales des Sciences Naturelles,' 1874.

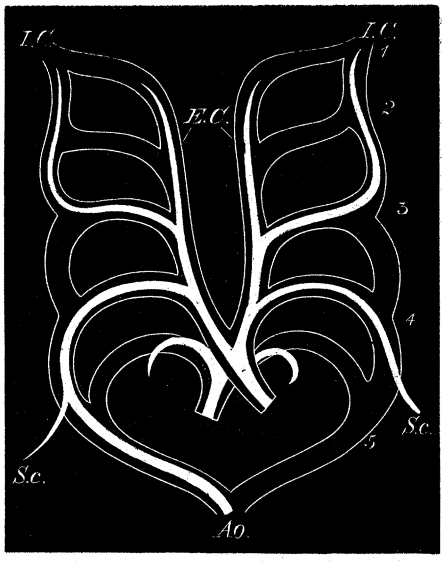
† BRENNER, "Ueber die Verhältnisse des Nervus laryngeus inferior Vagi zu einigen Aortenvarietäten des Menschen, &c.," 'Archiv Anat. Physiol. (*Anat. Abth.*),' 1883.

‡ FOSTER and BALFOUR, 'The Elements of Embryology,' 2nd edit., London, 1883.

§ *Loc. cit.*, Plate 6, fig. 9.

The fifth fœtal arches become the pulmonary arteries of the adult Bird, and each is completed by its ductus arteriosus.

Fig. 2.



Arches of the Bird (RATHKE).

1, 2, 3, 4, 5, branchial arterial arches; *Ao.*, aorta; *S.c.*, subclavian; *E.C.*, external carotid; *I.C.*, internal carotid.

The fourth right arch becomes the aorta, while the dorsal portion of the fourth left disappears, except in those Birds in which it still persists as a solid cord. The subclavian arteries are regarded as lateral branches from the dorsal ends of the fourth or aortic arches, their adult position being reached subsequently by a supposed shortening of the arches from which they spring, by which their bases become fused with the carotid vessels to form the innominate arteries. The base of the left subclavian consequently represents the more ventral portion of the fourth left arch. The common carotids are regarded as the representatives of the vessels which in fœtal life connected, upon the ventral aspect of the alimentary canal, the fourth with the third arches. The external carotids are supposed to be the continuations of these vessels still further onwards in the direction of the second arch. The internal carotids are looked upon as the third arches, the posterior dorsal trunks, by which these should have been connected with the aortic arches, becoming obliterated and disappearing.

Fig. 3, "Diagram of the condition of the arches of the aorta towards the close of incubation," is copied from FOSTER and BALFOUR.* It represents a stage in the development in which the right subclavian artery is supposed to be found arising from the aortic arch, not yet having assumed its adult position. The left subclavian is pictured as being connected by a cord to the left ductus arteriosus, and

* *Loc. cit.*, fig. 93.

dotted lines in front of the fourth arches stand for the already obliterated dorsal connections between the carotid and the aortic arches.

Fig. 3.

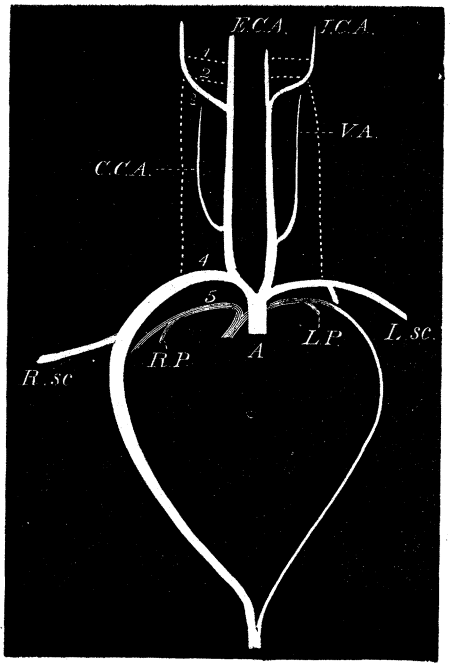


Diagram of the Condition of the Arches of the Aorta towards the close of Incubation. (FOSTER and BALFOUR).

1, 2, 3, 4, 5, the several aortic arches; *E.C.A.*, external carotid; *I.C.A.*, internal carotid; *C.C.A.*, common carotid; *V.A.*, vertebral; *R.sc.*, right subclavian; *L.sc.*, left subclavian; *R.P.*, *L.P.*, right and left pulmonary arteries. The dotted lines show the portions of the arches which have been obliterated.

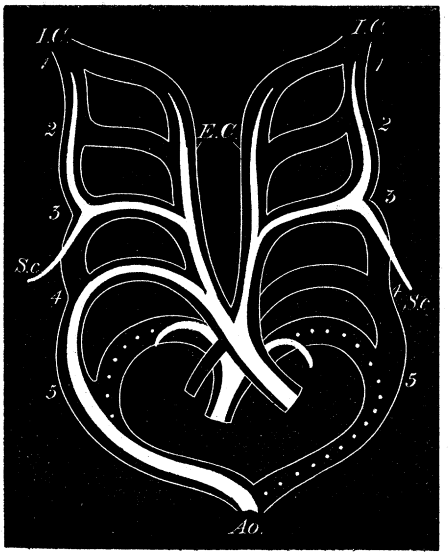
I have examined embryo Chicks in nearly all the stages of their development, but have never seen the subclavian vessel arising from the arch of the aorta as depicted in fig. 3; indeed, it is impossible to conceive that if found in that position it could ever assume its adult relations to the pneumogastric nerve and superior vena cava. Even before the anterior limb has first made its appearance, the large vein of the neck may be seen crossing the ventral aspect of all the arches, and the identity of this vessel with the jugular vein of adult life is indisputable. The pneumogastric nerve is formed at a very early period, as is evidenced by the recurrent course, behind the fifth arch, of its laryngeal branch, which has been carried back by the descent of the arches from the neck into the thorax. If the subclavian artery passed to its adult position along the aortic arch, it would occupy a position dorsal to vein and nerve, instead of one ventral to both.

The scheme which SABATIER* has set forward to explain the origin of the subclavian vessels is shown in fig. 4. It will be noticed that the subclavians are

* SABATIER, *loc. cit.*

represented as arising from the dorsal extremities of the third arches, the vessels which, according to RATHKE, become the internal carotids. To this, however, the same objections hold good, as the relations of the third arch to vein and nerve are similar to those of the fourth.

Fig. 4.



Arches of the Bird (SABATIER).

1, 2, 3, 4, 5, branchial arterial arches; *S.c.*, subclavian; *E.C.*, external carotid; *I.C.*, internal carotid; *Ao.*, Aorta.

Moreover, the common carotid arteries occupy a position dorsal to the œsophagus, and do so from a very early date; this is not what one would expect if they had originally occupied a ventral situation. From the observations detailed in the following pages I have been led to assign the origin of the subclavians to the ventral extremities of the third or carotid arches, and that of the common carotid stems to the third arches and the dorsal vessel above each, as is represented in fig. 2, Plate 22. Under this scheme the numerous branches of the common carotid are to be regarded in the same light as visceral and parietal branches of the aorta.

DEVELOPMENT OF THE SUBCLAVIAN AND CAROTID ARTERIES.

From the examination of a large number of Chick and Duck embryos I have become convinced that the theories now universally held are not in accordance with the facts of development. In relation to the subclavian arteries, the origin of which, as has been explained, RATHKE* assigns to the aortic roots, it ought to be possible to trace their gradual

* RATHKE, "Untersuchungen über die Aortenwurzeln, &c.," pp. 79–81. In this passage, while RATHKE assigns the origin of the subclavian arteries of Birds to the dorsal ends of the fourth arches, he admits

change of position, and to see the steps of the process by which they are supposed to pass from the dorsal to the ventral end of the arch, and finally to observe their gradual fusion with the bases of the carotid arteries to form the innominate trunks. It should be possible to describe in the history of their development distinct stages, in each successive one of which the subclavian arteries should be found springing from the aorta nearer and nearer to its ventral end, until the change is completed by their fusion with the common carotids. And, in addition, the method by which the arteries, arising at first dorsal to the pneumogastric nerves and jugular veins, become afterwards ventral to both should be capable of explanation. But this is not the case. The subclavian artery is to be observed first about the close of the third day of incubation, at a time when the pectoral limb has just begun to be discernible, and at its earliest appearance the artery is found arising from the third arch, not from the fourth. Moreover it springs from the ventral end of the arch, and stretches outwards in a plane superficial to, or ventral to, the pneumogastric nerve and jugular vein. It appears, therefore, first in what is practically its adult position, so that the innominate artery is not formed by the gradual fusion of the bases of subclavian and carotid, but is to be accounted for by the breaking up of the originally simple truncus arteriosus into canals continuous with each of the arches.

According to RATHKE,* the common carotid with its branches representing the external carotid branches of the Mammal is the persistent ventral communicating vessel running from the fourth arch towards the head, while the internal carotid is the third arch, the dorsal communication between it and the fourth having disappeared. If this were true, then the subclavian, arising in the manner described above, should spring from the common carotid at the place of origin of its internal and external branches. But, in addition to this, it may be established by direct observation that at a period when the third arch is still dorsally connected with the fourth (during the sixth day) it is the common carotid artery, not the internal carotid alone, which is continued from the dorsal end of the arch to the head. The external carotid branches are not therefore the product of the ventral trunk, but are to be regarded simply as visceral and parietal branches of a dorsal vessel. The ventral trunk remains as a small branch from the subclavian or innominate arteries to the front of the trachea.

Description of Observations.

The earlier stages in the development of the arteries may be studied by the direct observation of the circulation in Duck or Chick embryos of from three to five or six

that his direct observations upon their development do not satisfactorily prove this. His theory is founded upon the analogies between the development of Birds and Mammals, and he had already found in Sheep and Pig embryos that the subclavian arteries in these forms first appeared as branches from the original aortic roots. ("Ueber die Entwickelung der Arterien, welche bei den Säugethieren von dem Bogen des Aorta ausgehen," 'MÜLLER, Archiv Anat. Physiol.,' 1843, pp. 276–302.)

* RATHKE, *loc. cit.*, pp. 75–78.

days. In opening the shell, the vascular area of the yolk-sac is to be preserved intact. The whole of the contents of the egg may be floated in water, and the embryo, together with the vascular area, after having been clipped from its connections, may be transferred to a slide and examined under the microscope. In Duck embryos of from three to five days the circulation may be easily observed under a low power with transmitted light, but in later stages a strong simple lens with reflected light will be found more convenient.

In Duck embryos, in the course of the fourth day, three arches may be seen: the first or mandibular, the second or hyoidean, and the third or carotid. In the earlier stages of this day the first is usually the largest, and is placed almost directly in a line with the truncus arteriosus, but in the later stages the second arch has increased in size relatively to the mandibular, and receives the direct flow of blood from the vessel springing out of the ventricle. The blood from the arches flows towards the anterior and posterior extremities of the embryo in a dorsal vessel, and there is no trace of a branch from the ventral extremity of the first arch. At the close of the fourth day I have been able to observe distinctly only two arches, the second and third, but it is to be noted that the tissue of the mandibular bar has by this time increased in density, and may possibly obscure a slender vessel. The pectoral limb forms but an indistinct projection on the lateral wall of the embryo, and no vessel can be seen running into it.

At the close of the fifth day three arches are distinctly to be seen: the third or carotid, the fourth or aortic, and the fifth or pulmonary. The first and second of these are nearly of equal size, while the third is much smaller. The ventral ends of the arches are all in close contact with one another, each division of the truncus arteriosus breaking up into the three vessels simultaneously. As they pass round the throat, however, the arches separate, and finally terminate at some little distance from one another in a continuous longitudinal vessel, the posterior portion of which, carrying blood towards the tail, is the aorta, while the anterior portion, in which the current is directed forwards towards the head, may be termed carotid. The vessel which passes forwards from the ventral extremity of the arches towards the head is small, and cannot be traced for any distance. On the other hand, I have seen in all my specimens a hitherto undescribed branch taking its origin from the anterior border of each division of the truncus arteriosus where it is passing into the carotid arch. This vessel, which afterwards becomes the subclavian artery, S in fig. 4 (Plate 22), runs backwards and dorsalwards for some distance along the ventral ends of the arches, and is lost upon the side of the neck near the spot where the superior cardinal vein passes into the ductus Cuvieri. The heart is still considerably in front of the limb, which at this date forms a distinct projection on the side of the embryo. No arterial vessel can be traced into the limb, nor are any of the intercostal branches of the aorta in the vicinity larger than the others. The aorta gives off a number of lateral branches (intervertebral) in front of the anterior limbs, and, as these are not found in the adult, it is probable that they have disappeared during the descent of the heart and arches from the neck into the thorax; but, on the other hand, during the

process the ventral vessel which I have described would be placed, on account of its posterior direction, in circumstances exceptionally favourable to development.

In the Chick during the fourth day a vessel similar to that which has been described in the Duck may be seen (Plate 22, fig. 4). About the beginning of the fifth day I have been able to trace it to the limb. At this date it is not apparent at first sight, as it is hidden to a great extent by the projecting portion of the auricle, but it may be demonstrated in the following manner. After the embryo has been rapidly and carefully removed from the egg in the manner already described, the amnion is to be ruptured and pulled aside. If, then, the neck be straightened by pushing the head forwards, the artery may be seen arising from the anterior border of the right or left division of the truncus arteriosus, at the spot where the arches are being given off. By depressing the prominent part of the auricle the vessel may be followed by the eye as it passes backwards. It passes first the ventral ends of the arches, and at the lower border of the fifth or pulmonary a lateral branch coursing in a direction dorsal and slightly towards the head is given off to the superficial parts of the neck. Behind this the vessel may be seen to cross the ductus Cuvieri, and still further backwards it may be traced to the base of the limb, getting deeper as it approaches its destination. If, now, the projecting portion of the hyoidean bar be pushed aside, a slender branch will be seen to be directed forwards upon the ventral aspect of the throat, arising from the base of the vessel just described. This small vessel can be followed but for a short distance. It is the only ventral prolongation forwards from the carotid arch. On the other hand, the vessel reaching towards the head from the dorsal end of the arch is large and prominent.

It is to be noted, therefore, from the direct observation of the growth of the blood-vessels in the living Chick, that no branch from the aortic root, the place of origin which RATHKE assigns to the subclavian, can be traced into the limb; but, on the other hand, an artery can be seen springing from the ventral end of the third arch, and may be traced on the fourth or fifth day to the limb. Further, the vessel on the ventral aspect of the throat, which RATHKE supposed became the external carotid branches of the common carotid stem, is seen to be of small size compared with the dorsal vessel, and to be connected at its base with the subclavian artery.

The presence of an artery running towards the limb from the ventral end of the third arch, and the relations of the dorsal carotid to the supply of the head, may be confirmed by sections of hardened embryos. But it is to be noticed that, owing to the oblique course of the subclavian artery, it is impossible to trace its entire length in one series of sections. Plates 22 and 23, figs. 5–10, represent a series of transverse sections through the anterior portion of the body of a Chick embryo about the close of the third day. The first of the series, fig. 5, is carried across the head slightly obliquely at the anterior end of the alimentary canal. Beneath the base of the brain the extremity of the notochord is seen, and immediately beneath that the carotid arteries, which here, for the first time in this stage of development, come into contact with one another. The anterior cardinal veins lie in the lateral aspects of the section. The

succeeding figures represent sections taken at intervals from the series passing backwards towards the heart. The carotid arteries may be traced backwards to the right and left aortic roots, their direct continuity with these being clearly demonstrated.

No other arterial vessel is to be seen ventral to the throat or in any other part of the section until the heart is reached. The first indication of any other artery in the neck is seen in fig. 7, the fourteenth of the series immediately above the level of the truncus arteriosus, where the ventral carotid is seen of exceedingly minute size. The sections posterior to this show vessels running backwards, behind and external to the pericardium, in the position of the ventral subclavian already described in the living specimen.

Plate 23, figs. 11 to 14, represents longitudinal antero-posterior sections through a Chick embryo at the close of the fourth day. The first two, figs. 11 and 12, are carried through the right side of the body, the second two, figs. 13 and 14, through the left side. They show the carotid and subclavian arteries in their relations to other parts. In the first section, fig. 11, the arterial arches are cut across close to their origin from the truncus arteriosus. The section is a little deeper in front than behind, and the alimentary canal and the superior cardinal vein are both to be seen in the anterior portion, while behind they are lost, to become visible, however, in the succeeding sections. Ventral to the extremities of the arches a vessel is seen running backwards and outwards, breaking up into two at the level of the most posterior arch. By comparing this section with the one immediately following it this vessel is seen to be on a plane superficial to the anterior cardinal vein. Of the sections through the left side, fig. 13 is the more superficial, and by comparing it with fig. 14, the deeper one, the same relations are established. The dorsal branch of the artery is more distinctly evident, and is seen to break up into secondary branches in the superficial parts of the neck.*

In the two deeper of the four sections the carotid arteries are represented passing forwards dorsal to the alimentary canal, and they are evidently continuous with the dorsal ends of the arches. In these sections I was not able to find any ventral carotid vessel, so that it is probable that if such is present its size must be small compared to that of the other arteries figured. Figs. 15, 16, show the arches of a Chick embryo at

* His, in his work, 'Die erste Entwickelung des Hühnchens im Ei,' Leipzig, 1868, figures on Plate XI., figs. 6 and 8, blood-vessels running in the body wall, in the position of the artery marked *s* in figs. 5–14 described above. In the description of his plates His does not take notice of these vessels, but they have the appearance of being continuous with the vessels which, in the succeeding fig. 9, he represents in the fore-limb.

In another work, 'Anatomie menschlicher Embryonen' (Heft I.: Embryonen des ersten Monats), His describes and figures an artery arising from the ventral end of the fourth arch. Of this vessel he says, at page 79, "Von dem Anfangsstücke des vierten Bogens geht ein Aestchen in die Rumpfwand. Der Gedanke, dass es der Anfang einer Arteria subclavia sein möchte, lässt sich deshalb nicht festhalten, weil dies Gefäss nach Rathke's Beobachtungen aus dem Endstücke des vierten Aortenbogens entsteht." —[September 21, 1887.]

the close of the fourth day, and demonstrate the continuity of the great carotid artery at this date with the dorsal end of the arches. Fig. 15 shows the aorta, the dorsal ends of the three arches in close proximity, and the carotid arteries; fig. 16, the section immediately following, represents the terminations of the three arches in the aortic roots.

The carotid arteries, prolonged through the neck from the dorsal ends of the arches, do not at first occupy the middle line, like the aorta in its backward course, but run forwards, separated from one another by some distance, being nearer to one another in front and behind than in the middle portion of their course. This may be seen by an examination of figs. 5–10. RATHKE* has described the course of the carotid arteries in the neck of the Chick, and pointed out that they are at first placed at some distance from the middle line, and that it is not until the eleventh or twelfth day that they assume their median position. I have found in my dissections, however, the two arteries in close proximity on either side of the middle line during the seventh, and even at the close of the sixth, day. It is important to notice, however, that even when they are at some distance from one another they are the continuation of dorsal vessels, and are not ventral arteries which are passing upwards to assume a dorsal position, as RATHKE believed.

Figs. 17 to 26 are chosen at intervals from a series of vertical transverse sections of a Chick embryo at the close of the fifth day. They demonstrate the relations of the carotid arteries to the vascular arches at a later stage of development than the preceding series. They also show, along with the next series, the first stages in the disappearance of the fourth left arch. Fig. 17 shows a section through the cardiac end of the truncus arteriosus, and five canals are found, three lying to the right side and two to the left; but the more anterior of the two is large, and bears evidence of being made up of two canals, which are fusing with one another. This becomes more apparent in the next section, which follows in the actual series immediately upon its predecessor, the two portions of the anterior large canal being partially constricted off from one another. Fig. 19, which still shows the undivided truncus arteriosus, presents a section of six passages, the two portions of the originally large one being now distinctly separate. The next section, which is a little more dorsal than the last, shows the two divisions of the truncus arteriosus immediately ventral to the ends of the arches. This and the next figure show traces of lateral branches passing from the most anterior arch. Fig. 22, at a short interval from the last, shows the arches as

* RATHKE, "Ueber die Carotiden der Krokodile und der Vögel." 'MÜLLER, Archiv Anat. Physiol.,' 1850, pp. 184-192.

RATHKE, "Ueber das Verhalten der Carotidenstämme des Huhnes während ihrer Entwickelung." 'MÜLLER, Archiv Anat. Physiol.,' 1852, pp. 372-374.

RATHKE, "Bemerkungen über die Entstehung der bei manchen Vögeln und den Krokodilen vorkommenden unpaarigen gemeinschaftlichen Carotis." 'MÜLLER, Archiv Anat. Physiol.,' 1858, pp. 315–322.

RATHKE, "Bemerkungen über die Entstehung der Carotis subvertebralis bei der Krähe." 'MÜLLER, Archiv Anat. Physiol.,' 1859, pp. 382–384.

they are passing dorsalwards by the sides of the alimentary canal, and the superior cardinal veins on each side external to the arteries. In the anterior portion of the section the carotid arteries are shown cut across as they run forwards. The next four figures, which complete the series, represent the extremities of the arches, and they demonstrate the continuity of the carotids with the dorsal ends of the most anterior arches, and show that they occupy the same plane as the aortic roots. The three arches present on the fifth day are the third, fourth, and fifth; and it is important to notice at this date the proximity of their dorsal ends to one another, and the continuation forwards from the third of the great artery to the head.

On the fifth day the canal leading to the fourth left arch becomes fused with that leading to the third, but the arch is still of undiminished size in its course dorsalwards. The next series, figs. 27 to 30, show the arches of an embryo Chick about the beginning of the sixth day. The fourth left arch is now reduced to a cord lying between the carotid and pulmonary vessels, and it may be traced dorsalwards to the extremity of the arches, where it probably joins the aortic root.

These facts account for the presence in some of the Raptores of a solid cord stretching from the innominate artery to the aorta. In most Birds this cannot be found, and the fourth left arch has probably disappeared altogether. I am inclined to think, however, that in some cases the cord above described fuses with the coats of the pulmonary arch immediately behind it, as I have found in certain instances —notably in the Heron (*Ardea cinerea*), Solan Goose (*Sula alba*), and Swan (*Cygnus olor*)—a ligamentous band stretching from the base of the left innominate artery to the ventral surface of the left pulmonary vessel. In the series of sections the connection of the carotid artery with the dorsal end of the arches is still apparent.

In embryos at the close of the sixth day, and in older forms, the arrangement of the vessels may be investigated by dissection under water with the aid of a simple lens. If such a dissection be made at the close of the sixth day, there will be found three arches upon the right side, but only two upon the left. The subclavian arteries arise upon each side from the anterior border of each division of the truncus arteriosus, just beyond the pericardium. They pass outwards and backwards ventral to the pneumogastric nerve and the accompanying vein, and reach the limbs, in which they may be traced for some distance. Indistinct indications of branches may be noticed, but not so clearly as to admit of accurate description. The carotid artery is continued upwards from the dorsal end of the third arch upon each side, and is the only vessel which carries the blood supply to the head. The carotid arch upon each is connected dorsally to the arch behind it, namely, the fourth upon the right side and the fifth upon the left, the fourth left having disappeared. The dorsal connecting vessel is at this date slender, but it may always be demonstrated by careful dissection. In one instance, in which the injection of the blood-vessels was exceedingly successful, I noticed upon the right side a slender lateral branch given off from the connecting cord apparently to the muscles of the neck. This vessel, if its presence be

constant, probably is the suprascapular artery, which, in adult life, arises either from the base of the carotid or from the vertebral. It is important to notice at the close of the sixth day that, while the third arch is still complete, the common carotid artery, the *only vessel which passes to the supply of the head*, is prolonged from the *dorsal extremity* of the arch, and occupies a position on the front of the ventral bodies close to the middle line and to its fellow of the opposite side. The subclavian artery is also found in what is practically its adult position. Fig. 31 represents diagrammatically the arteries upon the right side at the close of the sixth day.*

The changes which take place in the later stages of incubation are easily followed. The heart passes still further back into the thorax, so that the subclavian arteries, which, upon the sixth day, were directed backwards a little, pass, upon the ninth day, almost directly outwards, and, at a period still later, will be found to stretch forwards a little. On the ninth day most of the adult branches may be dissected out; one small one from the base of the parent trunk, passing forwards and inwards to the front of the œsophagus and trachea, can be traced for a short distance, and seems to represent the ventral prolongation of the truncus arteriosus. The connecting cord between the dorsal end of the third or carotid and the arch immediately succeeding it is lost about the close of the seventh day, and the space between the carotid artery and the aorta is slightly enlarged; but otherwise these two arches maintain their relative positions to one another. At this time, too, the common carotids may easily be followed forwards upon the dorsal aspect of the alimentary canal, and most of their branches may be made out.

Summary of the Embryology of the Carotid and Subclavian Arteries in the Bird.

After the disappearance of the first two arterial arches (mandibular and hyoidean), which takes place in the Chick on the third day, the three permanent arches become established. From the most anterior of these, the carotid arch, two vessels are prolonged forwards. One of these, from the ventral extremity of the arch, runs upon the under-surface of the alimentary canal, and is of small size. It can be traced only for a short distance towards the head. It survives in the adult as a slender set of branches from the subclavian or from the base of the common carotid, directed to the ventral surface of the trachea and œsophagus and neighbouring parts. This is the vessel which RATHKE regarded as the common and external carotid. The other forward

* In a paper, "Entwickelung der Branchialbogen und Spalten des Hühnchens," in 'Archiv Anat. Physiol. (*Anat. Abth.*),' 1887, Dr. MALL, in the course of a research into the development of the thyroid and thymus glands, figures, in a Chick of the seventh day, the right subclavian artery as arising from the ventral end of the third arch, and passing in its course superficial to the jugular vein. Dr. MALL does not, however, in his paper consider the question of the development of the blood-vessels. [Sept. 21, 1887.]

prolongation is from the dorsal end of the arch. It is large and always easily followed. It is at first in direct continuity, upon each side, with the aortic root, but afterwards this continuity is interfered with by the dwindling of that portion of the stem which lies between the extremities of the third and fourth arches. The connection is finally completely broken through by the end of the seventh day. RATHKE regarded this as the internal carotid, but it constitutes the sole blood-supply of the head, and becomes the common carotid of the adult Bird, which is thus the persistent third arch (see fig. 2, Plate 22) and its dorsal continuation forwards.

Confirmation of the fact just stated with regard to the common carotid artery is found in a remarkable abnormality which I met with in the dissection of a Guillemot (*Uria troile*), and which is represented in Plate 25, fig. 32. The remains of the dorsal connection between the third and fourth arches upon the right side are present as a distinct cord passing between *the common carotid artery* and the descending portion of the aortic arch. The cord is connected with the carotid artery immediately behind the origin of the vertebral branch. The other arteries were quite normal. The only interference with the usual arrangement which the presence of this cord entailed was that the carotid artery of the right side reached the dorsal aspect of the œsophagus a little earlier than its fellow of the left side.

If RATHKE'S theory be accepted, the presence of this cord remains unexplained. According to him, if the dorsal connection between the third and fourth arches were found persisting, it would stretch the whole length of the neck from the internal carotid artery at the base of the skull to the aorta in the thorax. I have found in the Crocodile (fig. 33), upon both sides of the neck, cords similar to that described in the Guillemot, from the lower ends of the common carotids to the aortæ.

The subclavian artery at its earliest appearance is a branch derived from the ventral end of the third arch, and not from the aortic root as RATHKE has it. It is appreciable, at the end of the third day, as a vessel passing backwards in the ventro-lateral parts of the neck, and may be traced into the limb at the end of the fourth or in the earlier hours of the fifth day. Its most important branch, upon the fourth and fifth days, is one to the superficial parts of the neck, and passes from the parent trunk in a dorsal direction. Its adult arrangement of branches is discernible on the ninth day.

The arches arise at first in close contact with one another on each side from the extremity of each division of the truncus arteriosus, and it is only when the parent vessel splits up into its component parts that the ventral ends of the arches are separated from one another. The innominate arteries, while theoretically expressing the ventral vessels uniting the third and fourth arches, are really portions of the truncus arteriosus. In the same way the first portion of the aorta and the first portions of both pulmonary arteries, as far outwards as the spots where the obliterated ducti arteriosi spring, are developments from the truncus arteriosus. The aortic arch

was supposed by RATHKE* to have shortened considerably, in order to bring the subclavian from a position upon the root to the innominate stem. The improbability of this is shown by a comparison of Plate 22, fig. 1, and Plate 25, fig. 32, which represent the various obliterated cords attached to the aorta. Each of these maintains the relative position which in early fœtal life it occupies, and which a subsequent shortening of the large trunk would have altered.

COMPARATIVE ANATOMY OF THE CAROTID AND SUBCLAVIAN ARTERIES.

General Statement.

The examination of the comparative relations of the carotid and subclavian arteries in the different groups of Vertebrates throws additional light on the manner in which these vessels are developed in the Bird. The chief difficulty is to be met with in connection with the nomenclature, and is to be accounted for by the fact that accurate comparisons between the arteries of different groups have not been made, observers having often named vessels from their position in one form without reference to their relations in others. This is particularly the case with reference to the carotid system.

The carotid system consists of the following parts:—(1) The third arch; (2) its dorsal prolongation towards the head; (3) its ventral prolongation towards the head. The last-named portion, the ventral prolongation towards the head, is, in the Amphibia, an artery supplying the ventral aspect of the neck, extending as far as the tongue, to which it distributes branches. It has been named variously "lingual artery" and "external carotid artery," but, if the name carotid be applied to it at all, it were better called "ventral carotid." Passing from the Amphibia to the higher forms, RATHKE† believed that this vessel increased in importance, and from supplying the tongue only, as in Amphibia, it became, in Reptiles, Birds, and Mammals, the artery which was distributed to all the external parts of the head; hence its name of "external carotid." But upon close comparison of the arteries in these different groups it becomes evident that this vessel, instead of increasing, diminishes in importance as the higher forms are reached. In Crocodiles it supplies only the trachea and lateral parts of the neck, and is called "arteria collateralis colli." In Chelonian Reptiles its distribution is very similar, and it goes by the name of "common cervical." In Birds it is still smaller, and is recognised simply as a branch of the subclavian or innominate artery distributed to the front of the trachea. In Mammals I am inclined to believe that it is usually absent, but that, when present, it is represented by the artery "thyroidea ima."

The first and second portions of the carotid system, the third arch, and its dorsal

* RATHKE, "Untersuchungen über die Aortenwurzeln, &c.," p. 80.

† *Loc. cit.*, p. 76.

continuation forwards, must be considered together, as in most forms it is impossible to draw an exact line of separation between them, owing to the disappearance of the vessel connecting, on the dorsal aspect of the alimentary canal, the third arch with the arch immediately behind it. The names applied to this continuous trunk, formed from the two portions already noticed, are very confusing. RATHKE called it "internal carotid," and believed that it supplied only the brain; but it is obvious, from what has been pointed out with regard to the so-called "external carotid," that this vessel constitutes the whole supply of the head, both internally and externally, and may with propriety be called "common carotid." In the description which follows of the individual vessels in the different groups I have named this vessel "dorsal carotid," pointing out, where it is possible, the line of separation between the portion of it formed from the third arch and that derived from the dorsal prolongation to the head. In Amphibia the dorsal carotid supplies the brain and external parts of the head, but is not distributed to the tongue. In all the higher forms it supplies the tongue also, owing to the diminished size of the ventral carotid.

These views as to the supply of the external parts of the head by a dorsal and not, as RATHKE believed, a ventral vessel, may easily be proved by reference to Comparative Anatomy. In some Amphibia the third arches are connected dorsally with the aortæ, and in these forms it is easy to follow the continuous dorsal longitudinal vessels running the whole length of the body. The portions of these in front of the heart form the common carotids, and distribute branches to both internal and external parts of the head. In other Amphibia the dorsal connections between the third and fourth arches are obliterated, but, the other vessels remaining unaltered, it is at once evident by comparison that the common carotid artery represents a dorsal trunk. In some Reptiles the dorsal connections between the third and fourth arches persist either as open vessels or as solid cords, and in others they have completely disappeared; indeed, in different species of the same genera, in which all the other arterial vessels present precisely similar relations, the dorsal connecting cords are present constantly in some and absent constantly in others. In these cases, as in the Amphibia, the continuation of the dorsal longitudinal trunk from the aorta into the common carotid is followed without difficulty. The anatomy of the arteries of Birds is almost an exact counterpart of that of the Crocodile; and, apart altogether from the actual observation of the development, it is evident that the relations of parts are to be explained in a similar manner.

The relations of the subclavian artery are much more simple than those of the carotids. RATHKE* believed that there was but one vessel which in the Vertebrate series gave branches to the limb, but in reality there are two such vessels. One of these arises from the aortic root or dorsal portion of the fourth arch, and stretches outwards in a plane dorsal to the pneumogastric nerve and jugular vein. It is found in Amphibians, Lacertilians, and most Mammals. The other arises from the ventral

* RATHKE, *loc. cit.*, pp. 80, 81.

end of the third arch, and stretches outwards in a plane superficial to or ventral to the nerve and vein. It occurs in Chelonian and Crocodilian Reptiles and Birds. Both are sometimes present in one form, and when found together they anastomose with one another in the lateral body-wall near the base of the limb.

Detailed Description of the Carotid and Subclavian Arteries in different Vertebrata.

Amphibia.—In the Amphibia two vessels pass towards the head, the dorsal and ventral carotids. In some of the forms the third or carotid arch is connected dorsally with the aortic (*Menopoma*), but in others, especially in those where the structure known as the carotid gland is largely developed (*Salamandra*, Boas),* the dorsal connection between the carotid and aortic arches disappears when the adult stage is reached; but in either case the anatomy of the dorsal and ventral carotid arteries is practically the same. The dorsal carotid, continued forwards from the dorsal end of the arch, distributes branches to the head, which are named by Ecker† in the Frog ascending pharyngeal, ophthalmic palatine, and internal carotid, the last being the portion of the trunk which supplies the brain. The ventral carotid or lingual artery gives branches to the front of the trachea and to the muscles upon the ventral aspect of the neck, and ends in the tongue. Fig. 5, from Ecker, represents the relative positions of these vessels. The lingual, external, or ventral carotid artery is interesting on account of its limited distribution on the under-surface of the neck, extending forwards only to the posterior edge of the oral aperture, in marked contrast to the so-called external carotid of Mammals, which supplies the whole of the outer aspect of the head.

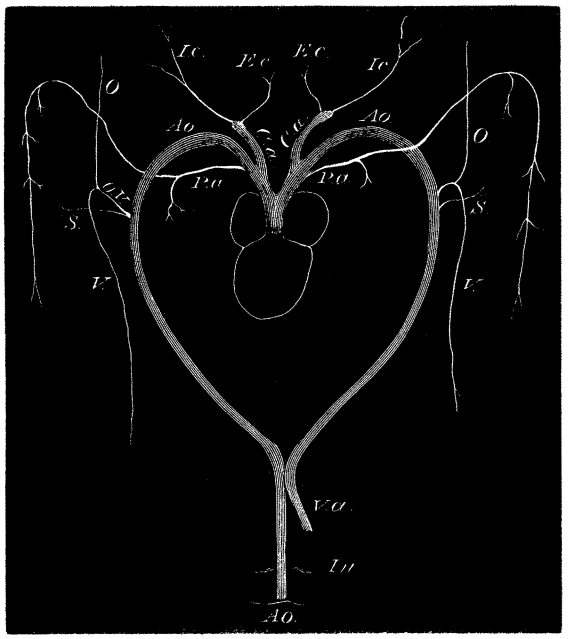
The subclavian artery arises from the aortic root, and in close contact with its base a branch, the occipito-vertebral (*o.v.*), springs, and may be described along with it, as in many of the higher forms they arise by a common stem. The artery is dorsal to the pneumogastric nerve. The occipito-vertebral branch is the most interesting. It divides into two. Its anterior branch, passing forwards, distributes a number of twigs to the back of the head, while the posterior portion, with a direction backwards, gives off several intercostal arteries. The subclavian of the Frog corresponds in origin and position to the artery which in Mammals bears the same name. In Mammals, however, the occipital artery is not commonly found to spring from the subclavian, but in the Porpoise such an arrangement is present. The deep cervical artery of Man, a branch of the subclavian, anastomoses among the muscles of the neck with the occipital artery, and this connection between the two vessels may be looked upon as representing the occipital artery of the Frog. Macalister‡ looks upon the occipital

* Boas, "Beiträge zur Angiologie der Amphibien," 'Morphol. Jahrb.,' vol. 8, 1883, pp. 169–187.

† Ecker, 'Die Anatomie des Frosches,' vol. 2, p. 68, fig. 29. Braunschweig, 1882.

‡ Macalister, "Morphology of the Arterial System in Man," 'Journal of Anatomy and Physiology,' January, 1886.

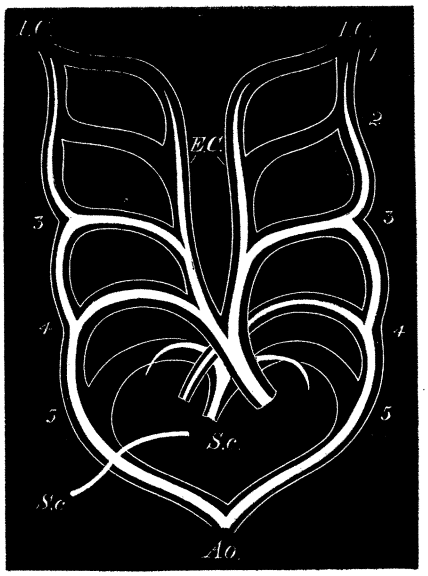
Fig. 5.



Arterial system of Frog (ECKER).

Ao., aorta; *C.a.*, carotid arch; *E.c.*, external carotid or lingual artery; *I.c.*, branches to internal and external aspects of head; *S.*, subclavian; *O.*, occipital; *V.*, posterior vertebral or common intercostal; *P.a.*, pulmonary artery with branch to cutaneous surface; *V.a.*, visceral artery; *In.*, intercostal.

Fig. 6.



Arches of the Lizard (RATHKE).

1, 2, 3, 4, 5, branchial arterial arches; *S.c.*, subclavian; *E.C.*, external carotid; *I.C.*, internal carotid; *Ao.*, aorta.

artery as part of a vascular arch passing from the vessel upon the ventral aspect of the throat towards the dorsal vessel, in the same manner as the carotid, aortic, and pulmonary arches stretch from one to the other. But its connection with the subclavian leads me to believe that it is to be regarded as belonging to the same series as the vessel to the fore-limb in Mammals and some other forms, namely, to that of the vessels running in the somatic wall after the manner of intercostal trunks.

Reptilia. (*a*) *Lacertilia*.—The arterial system of the Lizards resembles in many respects that of the Frog. The aortic and pulmonary arches are present on both sides in all, and in many the carotid arches are connected dorsally with the aortic.

Fig. 6, from Rathke,* represents the scheme of the Lacertilian arrangements. There are many variations in connection with the dorsal communications between the carotid and aortic arches. Plate 25, fig. 34, is a diagrammatic representation of the arches in *Ameiva vulgaris* (Rathke), and shows the dorsal vessel from the carotid arch continued back to the aorta in almost undiminished size. Plate 25, fig. 35,† *Lyriocephalus margaritaceus* (Rathke), presents the connection still patent, but reduced in size very considerably. Fig. 36, *Chamæleo planiceps* (Rathke),‡ represents the connection reduced to a slender cord, and in *Chamæleo vulgaris* (Plate 25, fig. 37), while the arches still retain their relative positions, the connecting link has disappeared altogether. In all the varieties, however, the carotid arteries present exactly similar relations. The dorsal carotid artery is continued forwards from the dorsal end of the arch in direct continuity with the connecting cord when that is present, and, even when the connecting cord has disappeared, is still obviously in the same position, and supplies not only the brain, but the whole of the outer aspect of the head. The branches which it divides into may be named "sub-mental," "inferior maxillary," "transverse facial," "occipital," "temporo-facial," and "internal carotid."

A vessel springs from the ventral end of the third arch and extends forwards upon the under-surface of the neck only as far as the posterior margin of the oral aperture, to end in the tongue. On the way it supplies several branches, one of which, marked *s.c.* in Plate 25, fig. 37, is important, as it is that which represents the subclavian in Chelonians, Crocodiles, and Birds. This vessel has been carefully dissected by me in *Chamæleo vulgaris*.§ It passes outwards and backwards to reach the muscles of the shoulder, among which it ramifies, anastomosing there with branches of the subclavian artery. By an enlargement of this anastomotic vessel, if the original root of the subclavian failed, the blood would reach the limb by a vessel ventral to the pneumogastric nerve. This anastomosis probably explains the difference in position of the subclavian in Lizards and Birds. Another vessel, springing from the carotid arch, is worthy of notice. In those forms in which the

* Rathke, "Untersuchungen über die Aortenwurzeln, &c.," Taf. vi., fig. 8.

† *Loc. cit.*, Taf. ii., fig. 3.

‡ *Loc. cit.*, Taf. ii., fig. 9.

§ "Arterial System of the Chamæleon," 'Glasgow Phil. Soc. Proc.,' 1886.

dorsal connecting trunk between the carotid and aortic arches is still patent there arises from it a small branch which passes into the muscles of the wall of the neck. When the connecting trunk is absent this vessel arises from the base of the dorsal carotid artery. In these circumstances it occupies a position similar to that of the supra-scapular artery in Birds, and marks the position of the posterior extremity of the vessel continued forwards from the dorsal end of the carotid arch.

The subclavian arteries in the Lacertilia correspond in origin to intercostal vessels. They spring in close proximity to one another from the right aortic root in a position dorsal to the pneumogastric nerve. The branches given off before entering the arm are "ascending cervical," "internal mammary," and "internal thoracic."

(*b*) *Crocodilia.*—The chief difficulty in comparing the arteries of the Crocodile with those of the Lizard is occasioned by the difference of nomenclature. In all, the aortic and pulmonary arches are present on both sides, and the carotid arches have always been figured as not connected dorsally with the aortic. In a dissection, however, of the vessels of a young Crocodile (*Crocodilus niloticus*), which measured 29 inches, I found the carotid arches completed on both sides by solid cords. The arrangement met with is represented on Plate 25, fig. 33, and presents an exact counterpart of the relations of the arches in *Chamæleo planiceps* (fig. 36). From the carotid arch upon each side two vessels are prolonged forwards; one, passing from the dorsal end of the arch, corresponds with the dorsal carotid of Lacertilia and Amphibia, and is usually called "common carotid" or "carotis subvertebralis"; the other, from the ventral end of the arch, representing the ventral vessel of Lacertilia and Amphibia, is called "arteria collateralis colli," and has associated with it at its base the subclavian artery.

The subvertebral carotid passes dorsalwards round the œsophagus in the same manner as the carotid artery of Birds. The artery of the right side, although present in the embryo, disappears in the adult. In my specimen I found it reduced to a cord arising from the innominate, and passing round the œsophagus to join the vessel of the opposite side in the middle line underneath the vertebral bodies. It was connected dorsally with the aortic arch in the same way as the artery of the left side. The carotis subvertebralis, as it passes forwards underneath the vertebræ of the neck, is thus formed by the junction of the vessels of the right and left sides, which are continued forwards from the dorsal extremities of the carotid arches, and is therefore to be compared to the median aorta, which is similarly formed and passes backwards in a similar position. Near the head the common vessel splits into its two component portions, and these rapidly break up into branches which supply the external and internal parts. RATHKE has named the branches "internal maxillary," "infra-maxillary," "temporal," and "internal carotid" proper supplying the brain.

The arteriæ collaterales colli of RATHKE pass forwards in the ventro-lateral aspects of the neck. They give branches which ramify upon the under-surface of the trachea and in the muscles of the neck, and terminate at the tongue in anastomosis with the infra-maxillary branches of the carotid stems. They correspond accurately with the

ventral (external) carotid of Lacertilia (see fig. 37, *Chamæleo vulgaris*), but the branch which in the Chamæleon passed to the muscles of the shoulder has now become subclavian.

The subclavian arteries, arising from the innominate stems, or, in other words, from the ventral ends of the carotid arches, in actual proximity to the bases of the last-described vessels, pass forwards and outwards, crossing on their way, ventral to the carotid arteries, the veins from the neck, and the pneumogastric nerves. Before reaching the arm the internal mammary artery is given off, and also a vessel to join in anastomosis with intercostal arteries. From this anastomosis the vertebral springs. There is thus evidence of the anastomotic connection between the arteries arising on the ventral side of the throat and the intercostal arteries dorsally, which has already been noticed in the Chamæleon.

The arrangement of the large arteries in the Crocodile resembles very closely that found in Birds, the main difference lying in the presence of the fourth or aortic arch upon the left side in the former, while in the latter class it is absent altogether. Plate 22, fig. 3, represents my view of the metamorphosis of the arterial arches in the Crocodile.

(*c*) *Chelonians.*—The anatomy of the great arteries in the Chelonian group is similar in most respects to that of the Crocodile. The aortic and pulmonary arches are present on both sides, but in my dissections in this Order I have never found the carotid arch completed by a dorsal connection with the aortic. The common carotid (dorsal carotid) artery is similar in its origin and distribution to the vessel which bears the same name in Birds and Crocodiles, but differs in its course, inasmuch as it does not pass completely round the œsophagus to reach the middle line, but passes forwards in the dorso-lateral parts of the neck. This is the position which the common carotid occupies in the Mammalian class. The Chelonian group, in the arrangement of the vessels, thus forms an important link between Birds and Crocodiles, upon the one hand, and Mammals upon the other; the distribution corresponding exactly with that of the former classes, the course through the neck with that of the latter. The position which the carotid artery holds in the neck is that which, as has already been shown, it occupies during the earlier stages in the embryo Chick. It is possible that the comparative shortness of the neck may be related to the incomplete development of this trunk in Chelonians and Mammals.

The artery which, running upon the ventral aspect of the throat, corresponds to the ventral carotid of the Frog and Lizard, and to the arteria collateralis colli of the Crocodile, has been named in the Chelonian by Rymer Jones* the "common cervical." This vessel springs from the base of the subclavian trunk, and, coursing forwards underneath the trachea towards the oral aperture, gives many branches to the air-

* Rymer Jones. Article "Reptilia," 'Cyclopædia of Anatomy and Physiology,' by Todd, London, 1852.

tube and to the ventral aspect of the neck, and ends in anastomosis with branches from the dorsal carotid.

The subclavian artery arises on each side by an innominate trunk along with the carotid. It passes forwards and outwards, crossing ventral to the pneumogastric nerve and the jugular vein, as in Birds and Crocodiles. Before it reaches the limb two important branches are given off. The first is the internal mammary. The second is a vessel which supplies some intercostal branches and represents the anastomosis between the dorsal and ventral branches in the somatic wall, already described in the Lizard and Crocodile. From this vessel springs a large dorso-cervical or deep cervical artery, which enters into free communication with the occipital from the dorsal carotid, the anastomotic connection between occipital and intercostal being particularly well marked in this group.

Birds.—The arterial system has already been sufficiently described, but a comparison between the individual vessels of this and other groups may be briefly drawn. The pulmonary arches are present on both sides, but the left aortic is absent. The carotid arch is not connected dorsally with the arch behind it, but I have pointed out the occasional presence of a dorsal connection between the two arches (Plate 25, fig. 32). The common carotid (dorsal carotid) is similar in origin, course, and distribution to the subvertebral carotid of the Crocodile. The ventral carotid (arteria collateralis colli of the Crocodile, and common cervical of the Chelonian) is represented by a small vessel springing variably from the innominate, subclavian or base of the carotid stem, ramifying for a short distance upon the ventro-lateral aspects of the neck, and giving branches to the trachea. The subclavian is ventral in position.

Mammals.—The anatomy of the carotid system in this class differs in a marked degree from the arrangements found in the classes already described. A common carotid artery, running in the lateral parts of the neck, divides into two stems—an internal and an external carotid, the former being in many cases entirely devoted to the supply of the brain, the latter to the whole of the external aspect of the head. Rathke* has described the development of these vessels, and holds the common carotid artery to represent the ventral trunk between the carotid and aortic arches, the external carotid being the continuation of this ventral trunk still further forwards, and the internal carotid the third arch and the dorsal continuation towards the head, fig. 7.†

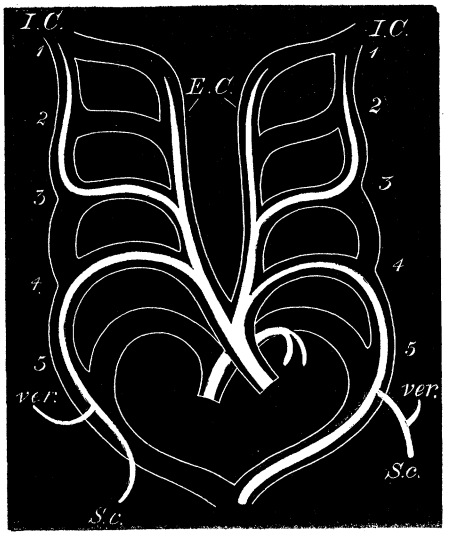
In addition to the embryological evidence with which Rathke supports his scheme, it seems probable that the special development of the brain for which this class is peculiar may have determined the whole of the blood-supply of the dorsal carotid to that organ. The ventral carotid, which in all the other groups examined was represented by a vessel of small size running forwards, never beyond the oral aperture, has been shown in the previous descriptions to maintain an anastomosis

* "Ueber die Entwickelung der Arterien, welche bei den Säugethieren von dem Bogen der Aorta ausgehen." 'Müller, Archiv Anat. Physiol.,' 1843, pp. 276–302.

† Rathke, "Untersuchungen über die Aortenwurzeln, &c.," Taf. vi., fig. 10.

with branches of the dorsal carotid, and it is possible that, by virtue of this connection, the whole of the external branches of the dorsal vessel may have been transferred to the ventral. In the Ground Hornbill (*Bucorvus abyssinicus*), where the dorsal carotids are represented in the whole of their subvertebral course by solid cords, the passage of blood to the head is maintained by an anastomotic vessel occupying the position of the arteria collateralis colli of the Crocodile, which joins in front one of the maxillary branches of the dorsal artery. In this case, therefore, by a secondary change, shown to be so by the fact that the dorsal carotids are still present as solid cords, the whole of the blood-supply of the head passes through the neck by way of the ventral vessels—an arrangement similar to that which is expressed in the explanation which RATHKE has put forward of the Mammalian development.

Fig. 7.



Arches of the Mammal (RATHKE).

1, 2, 3, 4, 5, branchial arterial arches; *S.c.*, subclavian; *ver.*, vertebral; *E.C.*, external carotid; *I.C.*, internal carotid.

On the other hand, it seems more probable, judging from Comparative Anatomy, that the common carotids of Mammals represent the dorsal carotids of other forms, the branch which supplies the brain being specially enlarged so as to seem the continuation of the parent trunk. The ventral carotid artery, which in the passage from Amphibians to Reptiles and Birds has been shown to diminish in size and importance, would be in this scheme absent altogether in most forms, but constant in some (Porpoise, fig. 38) and occasional in others as the thyroidea ima artery. It is also interesting to note that when, as sometimes happens, the common carotid artery in Man is absent, and the external and internal carotids arise separately from the arch of the aorta, it is the internal carotid which occupies at its origin the more anterior or ventral position. I have not had an opportunity of examining the development of

the carotid arteries in Mammals, but I believe that a further investigation is necessary.*

The Mammalian subclavian artery usually springs from the aortic arch, as in the Lacertilian, and its further development has been described by RATHKE. This is not always the case, however. In a paper upon the arterial system of the Porpoise† I have pointed out that the artery which in that animal represents the subclavian of other Mammals does not supply branches to the fore-limb, but is distributed entirely as an intercostal vessel (Plate 25, fig. 38). The artery which supplies the limb occupies a position ventral to the pneumogastric nerve, and expresses the subclavian artery of Birds, so that in this form the two representatives of the subclavian artery found in the Vertebrate series are present. From a description of the arteries of the Narwhal by SEASON WILSON‡ it is evident that the arrangements in that form are similar to those in the Porpoise, so that it is probably true of the Cetacean division generally.

Summary of Comparative Anatomy.

In all forms lower than Mammals and above Fishes a dorsal and a ventral carotid artery are recognisable. The former represents the third arch and its dorsal continuation forwards; it supplies branches to the brain and to the whole of the external parts of the head, except, in the lower forms, the tongue. In certain instances (Birds and Crocodiles) it passes forwards in the middle line immediately underneath the bodies of the cervical vertebræ, the vessels of opposite sides being either in contact with one another (Birds) or fused into a median trunk (Crocodiles). In other cases (Amphibia, Lacertilia, Chelonia) the dorsal carotids are separated from one another, and lie underneath the transverse processes of the vertebræ. In spite of the difference, of course, in the cases above mentioned, the arteries are identical in origin and distribution.

The ventral carotid supplies the tongue in Amphibian and Lacertilian forms, but is reduced in Chelonia and Crocodilia, and does not extend so far forwards as the oral aperture. In Birds it is a slender vessel supplied to the ventral surface of the trachea.

There are two vessels which in different cases may give origin to the subclavian artery. One of these is ventral in origin, and passes out in front of the pneumogastric nerve; the other is dorsal, and crosses behind the nerve. They anastomose with one another in the body-wall. The ventral artery is found in Chelonian and Crocodilian Reptiles, in Birds, and among Mammals in the Cetacean group. The dorsal vessel is

* From the researches of HIS ('Anatomie menschlicher Embryonen,' Leipzig, 1880) it is evident that in early human embryos the ventral carotid reaches as far forwards as the tongue and lower jaw, but it is possible that in subsequent development the origin of the vessels for these parts may be transferred, as in Birds, to the dorsal root.—[September 21, 1887.]

† "Arteries of the Head and Neck of the Porpoise, &c.," 'Glasgow, Phil. Soc. Proc.,' 1886.

‡ WILSON, 'Journal of Anatomy and Physiology,' 1880.

enlarged and prolonged into the limb in Amphibians, Lacertilian Reptiles, and in all Mammals, with the exceptions already noted.

In concluding, I have to offer my thanks to Professor CLELAND for much valuable assistance, and for placing a large number of specimens at my disposal for examination or dissection; to Dr. BRUCE YOUNG for help in the preparation of the plates; and to Mr. CAMPBELL, of the Glasgow Museum, for a large number of Birds for dissection.

DESCRIPTION OF PLATES 22–25.

Fig. 1 (Plate 22). View from behind of Heart and Vessels of Nandu (*Rhea americana*).

Ht. Heart.
Ao. Aorta.
pa. Pulmonary artery.
l.d.a. Left ductus arteriosus.
r.d.a. Right ductus arteriosus.
l.c. Left carotid.
l.s. Left subclavian.
r.c. Right carotid.
r.s. Right subclavian.
p.v. Pulmonary vein.

Figs. 2 and 3 (Plate 22). Scheme of the metamorphosis of the Arches in Birds (2) and Crocodiles (3).

I., II., III., IV., V. The arches.
C.C. Common carotid.
S. Subclavian.
Ao. Aorta.
P. Pulmonary artery.
A.c.c. Arteria collateralis colli.

Fig. 4 (Plate 22). Arches of Embryo at close of fourth day.

Ht. Heart.
Ao. Aorta.
C. Carotid.
S. Subclavian.
V.C. Cardinal vein.
m. Mandibular bar.
h. Hyoidean bar.

Figs. 5–30 (Plates 22–25). Sections of Chick embryos.

Figs. 5–10. Transverse sections through anterior portion of body, at the close of the third day (the sections are slightly oblique). They succeed one another in order, and are taken from a series, of which No. 5 is the

7th, 6 the 10th, 7 the 14th, 8 the 17th, 9 the 18th, and 10 the 19th.

br. Brain.
n. Nerve.
v. Vein.
d.a. Dorsal artery.
ret. Retina.
n.c. Notochord.
v.a. Ventral artery
ph. Pharynx.
per. Pericardium.
tr.a. Truncus arteriosus.
ht. Heart.
s. Subclavian artery.
a. Arch.
av. Ear.

Figs. 11–14. Longitudinal antero-posterior (sagittal) sections, at the close of the fourth day.

Figs. 11 and 12 are carried through the right side, fig. 11 being the more superficial.

Figs. 13 and 14 are carried through the left side, fig. 13 being the more superficial.

a. 3. Third arterial (carotid) arch
a. 4. Fourth arterial (aortic) arch
a. 5. Fifth arterial (pulmonary) arch
} right side.

a′. 3. Third arterial arch
a′. 4. Fourth arterial arch
a′. 5. Fifth arterial arch
} left side.

au. Ear.
v. Vein.
al. Alimentary canal.
ht. Heart.
s. Subclavian.
d.c. Dorsal carotid.

Figs. 15–16. Vertical transverse (frontal) sections, at the close of the fourth day; fig. 15 is the anterior.

a. 3. Third arch.
a. 4. Fourth arch.
a. 5. Fifth arch.
ao. Aorta.
d.c. Dorsal carotid.

Figs. 17–26. Vertical transverse (frontal) sections, at the close of the fifth day; fig. 17 is the 2nd of the series, 18 the 3rd, 19 the 4th, 20 the 7th, 21 the 8th, 22 the 10th, 23 the 14th, 24 the 15th, 25 the 16th, and 26 the 17th.

Figs. 17–19. Sections across the truncus arteriosus, which, while undivided on the surface, shows on section at this stage a set of canals continuous with the arches.

a. 3.
a. 4. } Arches of the right side.
a. 5.

a'. 3.
a'. 4. } Arches of the left side.
a'. 5.

In figs. 17 and 18 *a'*. 3 and *a'*. 4 are fused into one canal.

Figs. 20–26. Arches as in figs. 17–19.

br. Branch from the third arch.
v. Vein.
al. Alimentary canal.
d.c. Dorsal carotid.
ver. Vertebra.
ao. Aorta.

Figs. 27–30. Vertical transverse sections in the earlier stages of the sixth day.

Fig. 27 is carried through the truncus arteriosus, which is still undivided externally.

Figs. 28–30 show the arches as they pass in a dorsal direction.

The references are the same as in the series 17–26.

Fig. 31 (Plate 25). Arches on left side of Chick, at the close of the sixth day.

III., V. Third and fifth arches; the fourth has disappeared.
T.A. Truncus arteriosus.
P. Pulmonary artery.
S. Subclavian.
C.c. Common carotid.
D.B. Ductus Botalli.

Fig. 32 (Plate 25). Adult Guillemot (*Uria troile*); persistence of ductus Botalli between common carotid and aorta, upon the right side.

l.d.a. Left ductus arteriosus.
Ao. Aorta.
D.B. Ductus Botalli between right carotid and aortic arches.
c.a. Common carotid artery.
al. Alimentary canal; *r.l*. Right lung; *l.l*. Left lung.

Fig. 33 (Plate 25). Heart and arches of *Crocodilus niloticus*.

S. Subclavian arteries.
C. Carotid arch.
A. Aortic arch.
P. Pulmonary arch.
Ductus Botalli connect *C.* and *A.*, and *A.* and *P.*

Fig. 34 (Plate 25). Carotid and aortic arches of left side of *Ameiva vulgaris* (RATHKE).

Ao.A. Aortic arch.
C.A. Carotid arch.
c.l. Cervico-lingual artery.
C. Branches to internal and external aspects of Head.

Fig. 35 (Plate 25). Carotid and aortic arches of *Lyriocephalus margaritaceus* (RATHKE), right side. Lettering as in fig. 34.

Fig. 36 (Plate 25). Carotid and aortic arches of *Chamæleo planiceps*, right side (RATHKE). Lettering as in fig. 34.

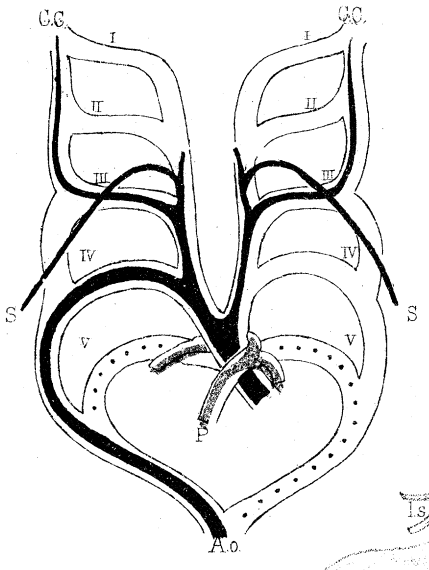
Fig. 37 (Plate 25). Carotid and aortic arches of *Chamæleo vulgaris*, right side.

T.a. Truncus arteriosus.
R.a.r. Right aortic root.
L.a.r. Left aortic root.
C.a. Carotid arch.
L.c.a. Left carotid arch.
C. Carotid artery; *C.e.* External carotid; *C.i.* Internal carotid.
C.l. Cervico-lingual artery; *Sc.* Scapular branch; *l.* lingual; *h.* hyoid.
S.r. Right subclavian artery; *S.l.* Left subclavian.
In. Intercostal arteries.
Ao. Aorta.

Fig. 38 (Plate 25). Arteries of the Neck and Thorax of the Porpoise.

In. Innominate artery.
B.c. Brachio-carotid.
C. Carotid; *C.e.* External carotid; *C.i.* Internal carotid.
h. Hyoid; *l.* Lingual; *oc.* Occipital.
S. Subclavian artery; *th.* Superficial thyroid branch; *as c* Ascending cervical; *sc.* Scapular; *oc.* Occipital; *e.t.* External thoracic; *i.m.* Phrenic and internal mammary.
Br. Brachial.
d.th. Deep thyroid artery.
P.t. Posterior thoracic; *d.* Its dorsal branch.
i.i. Intercostal arteries.
On the right side a portion of the thoracic rete is shown.
pn. Pneumogastric nerve.

Fig. 2.



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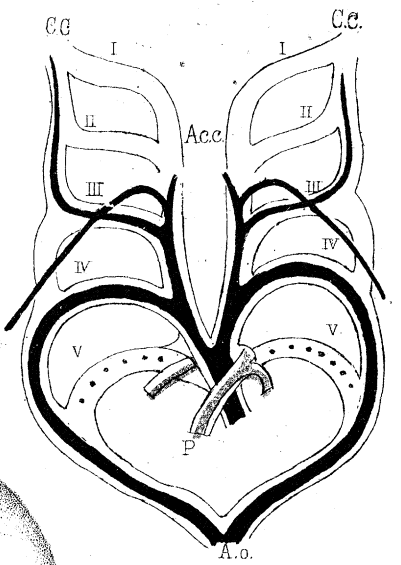

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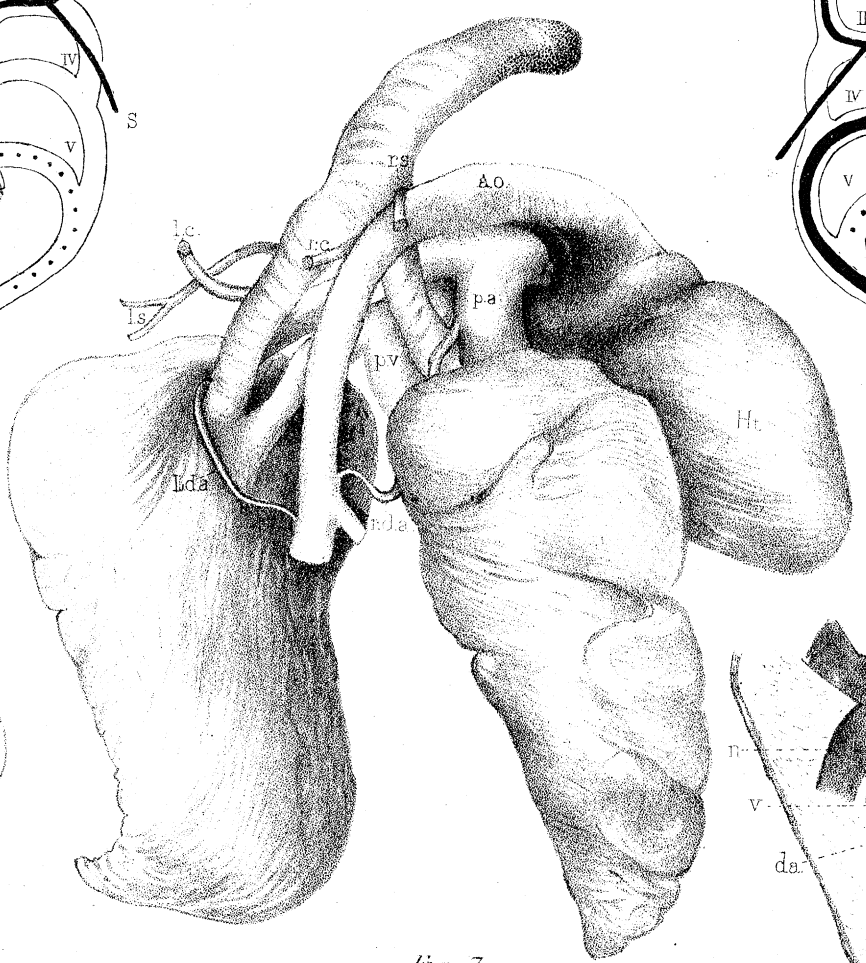

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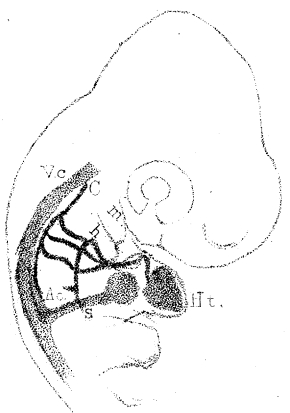

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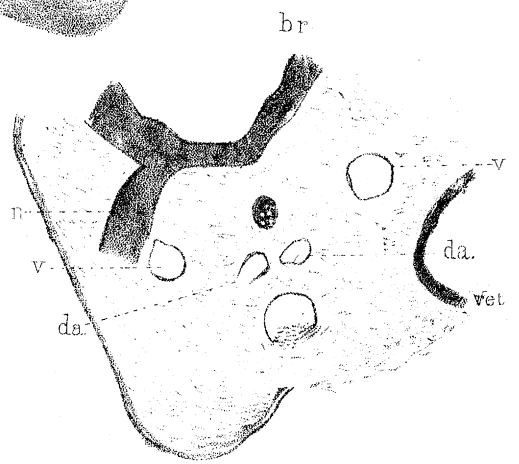

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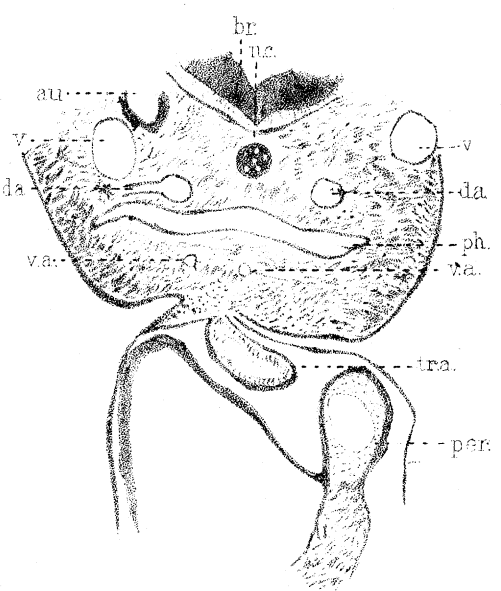

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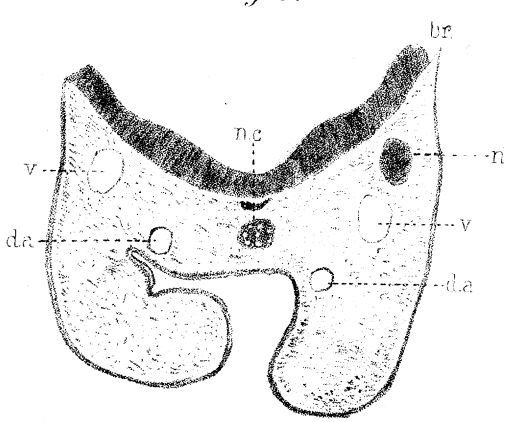

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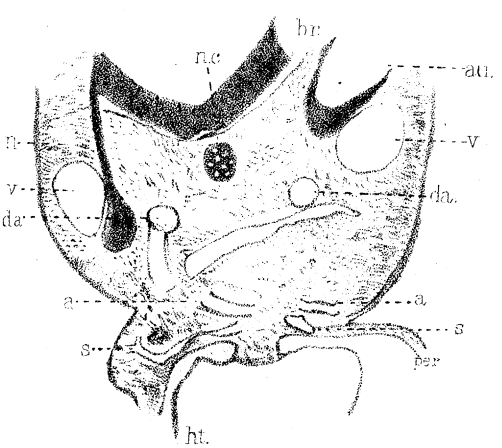

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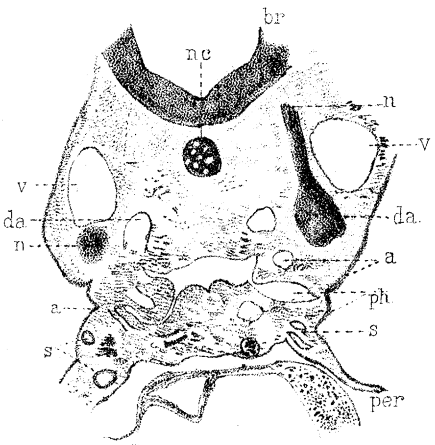
Fig. 9.



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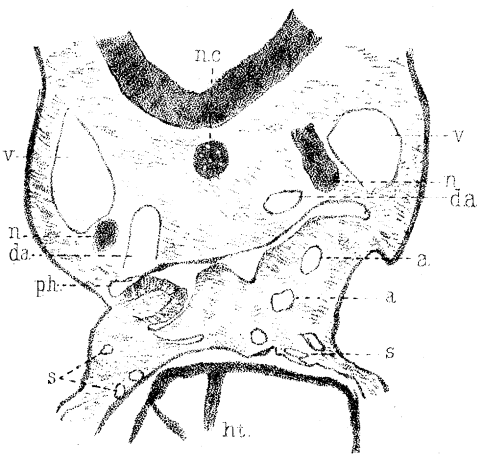

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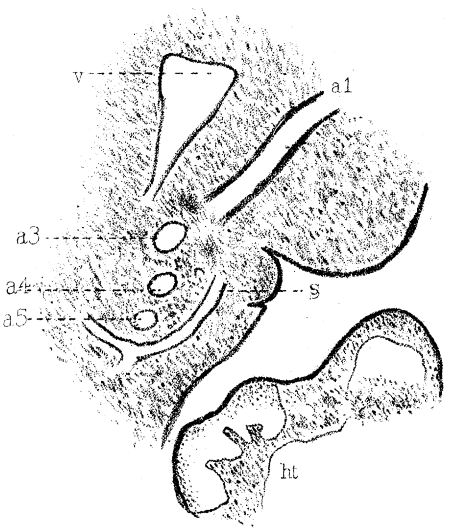

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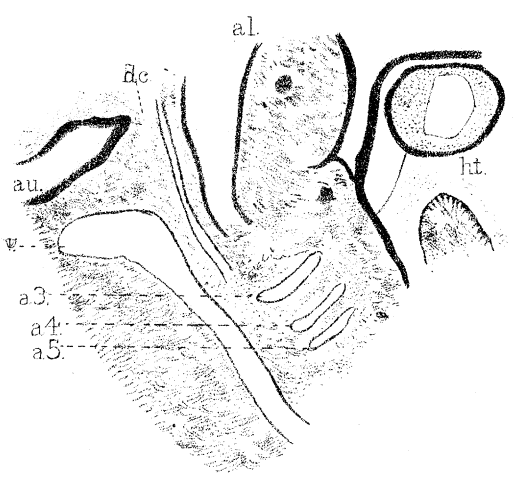

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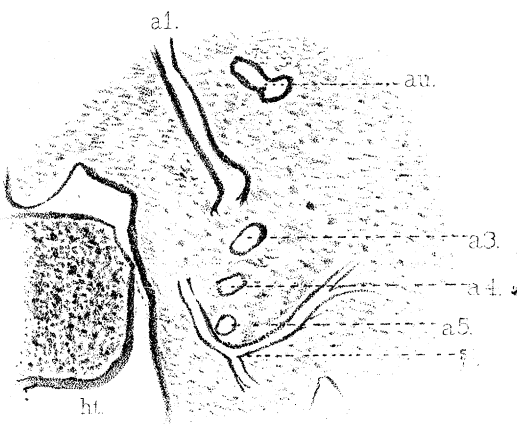


Fig. 14

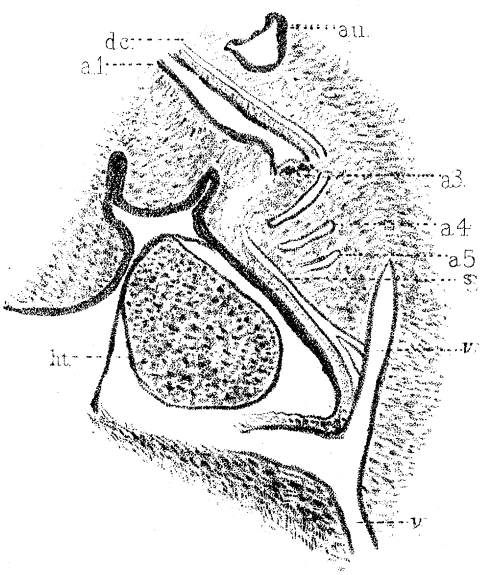
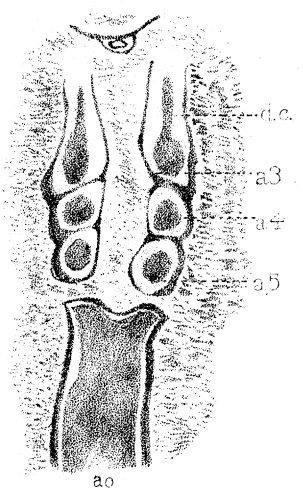
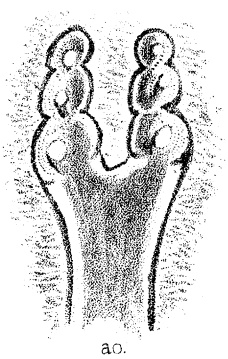


Fig. 16.

Fig. 15.





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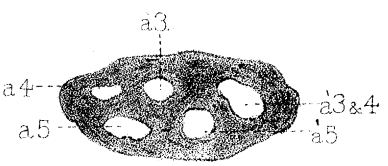

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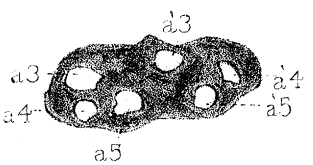

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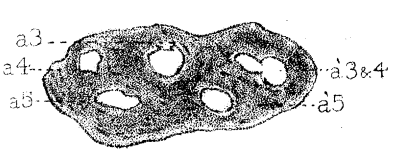

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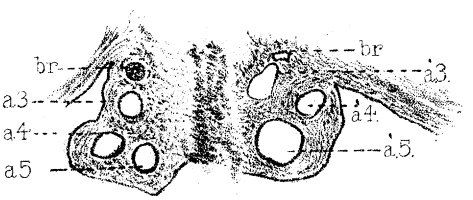

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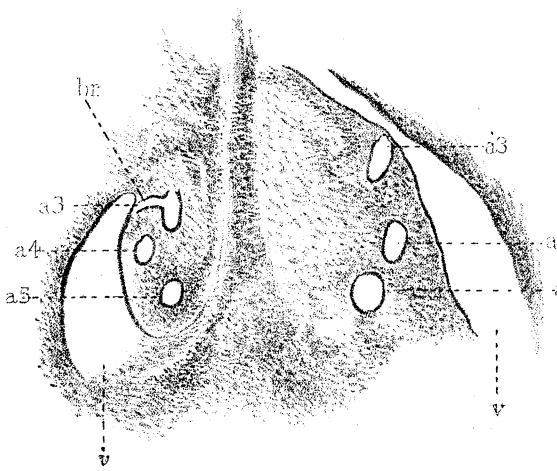
Fig. 21.



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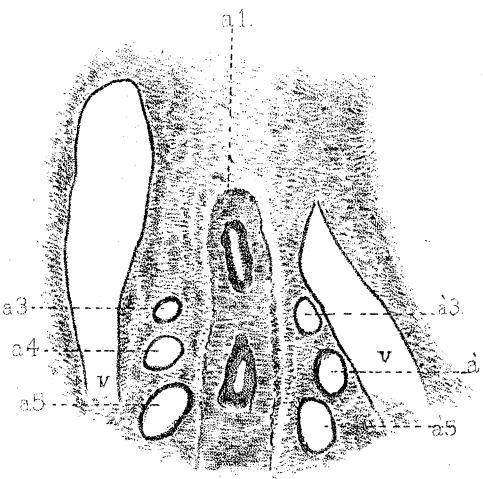

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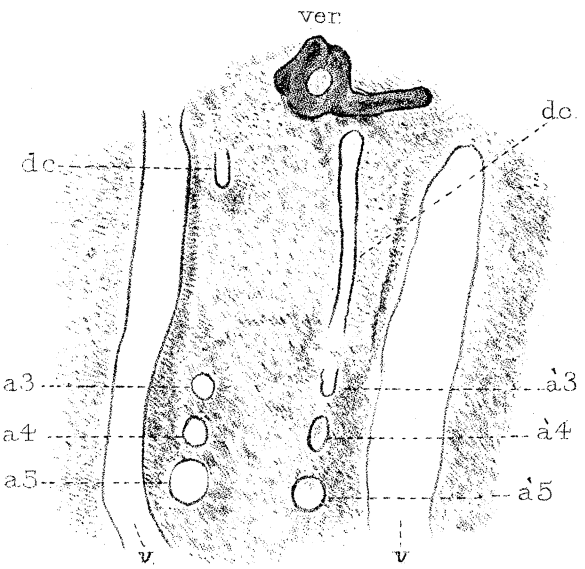

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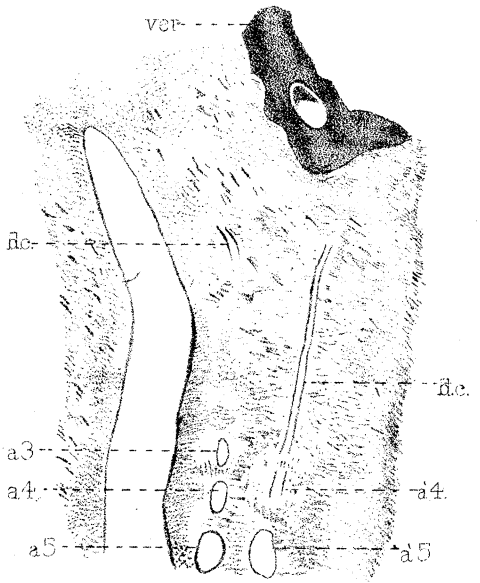

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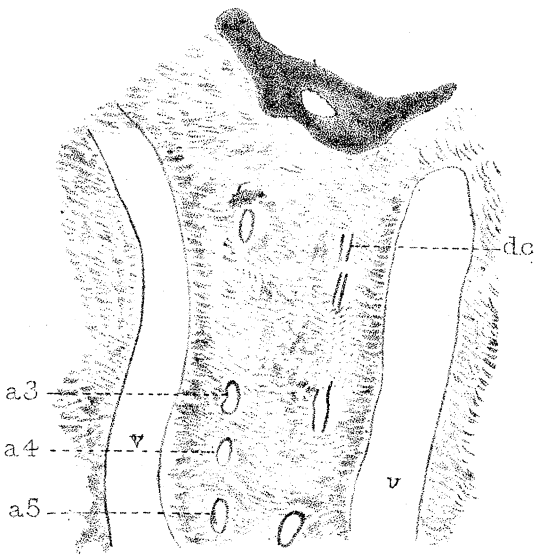

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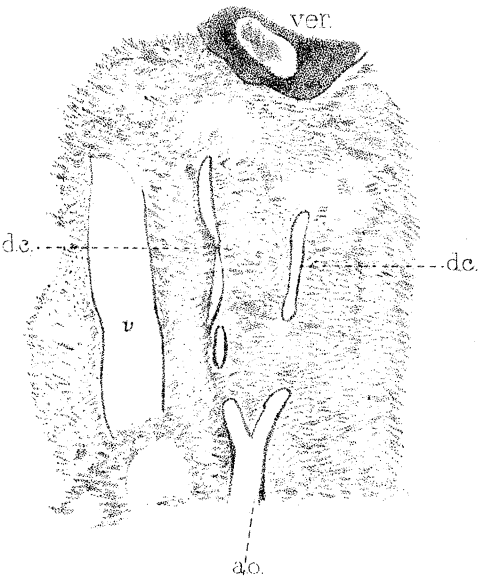

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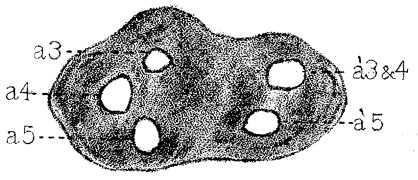

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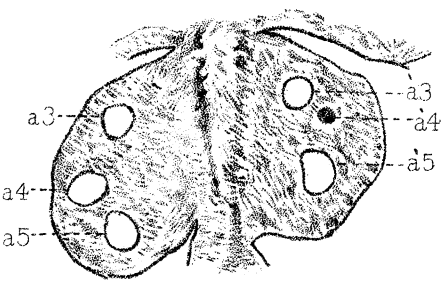

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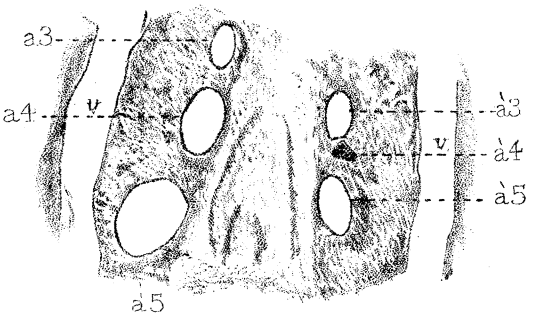

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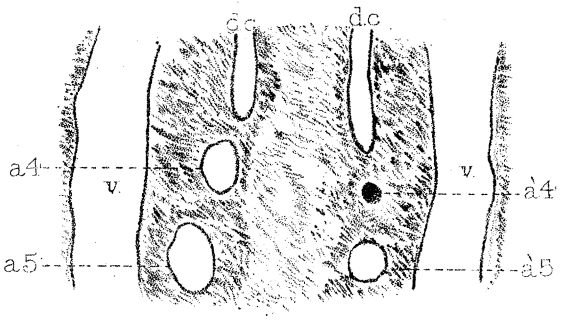
Fig. 30.



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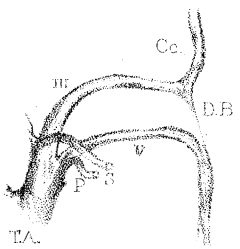

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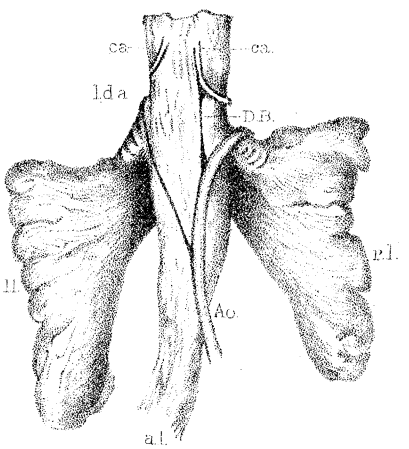

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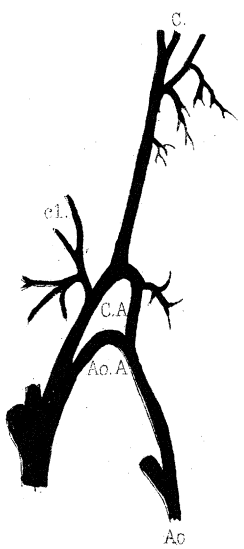
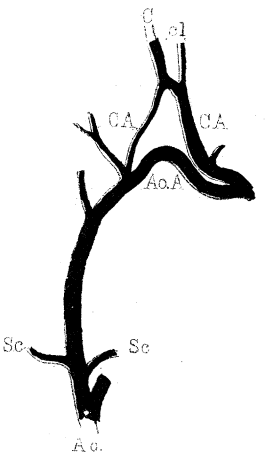


Fig. 33

Fig. 35.



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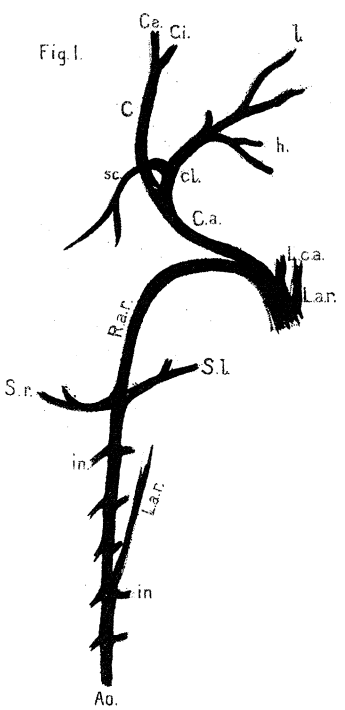

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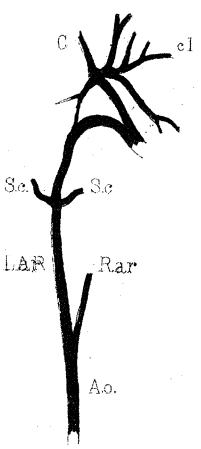

Fig. 38.

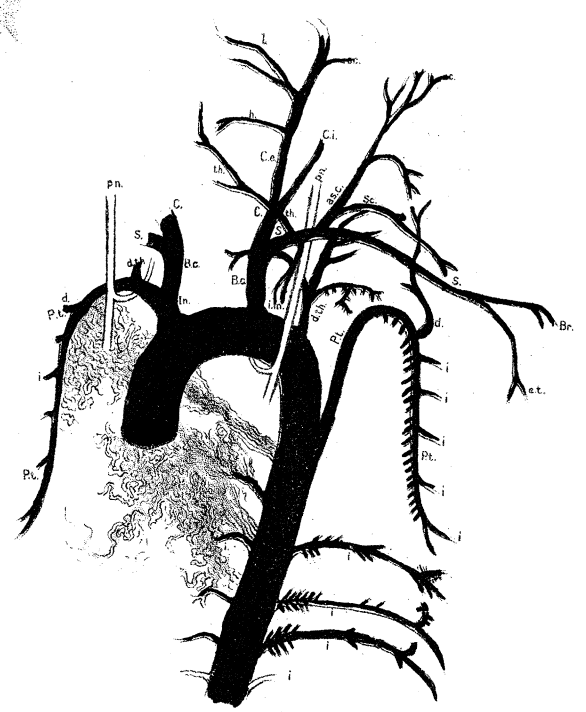

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Fig. 2.

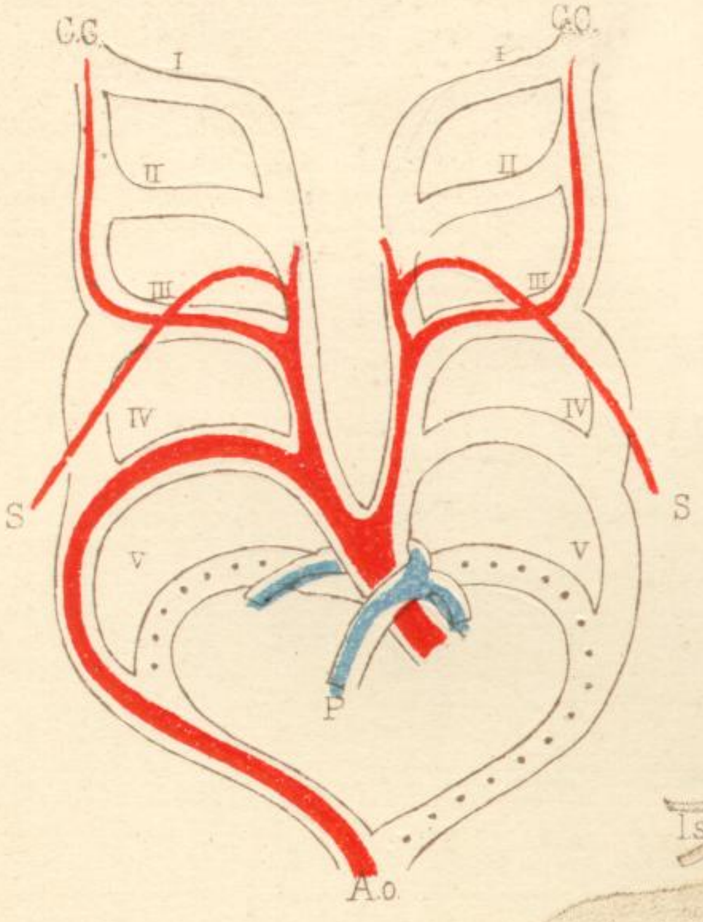
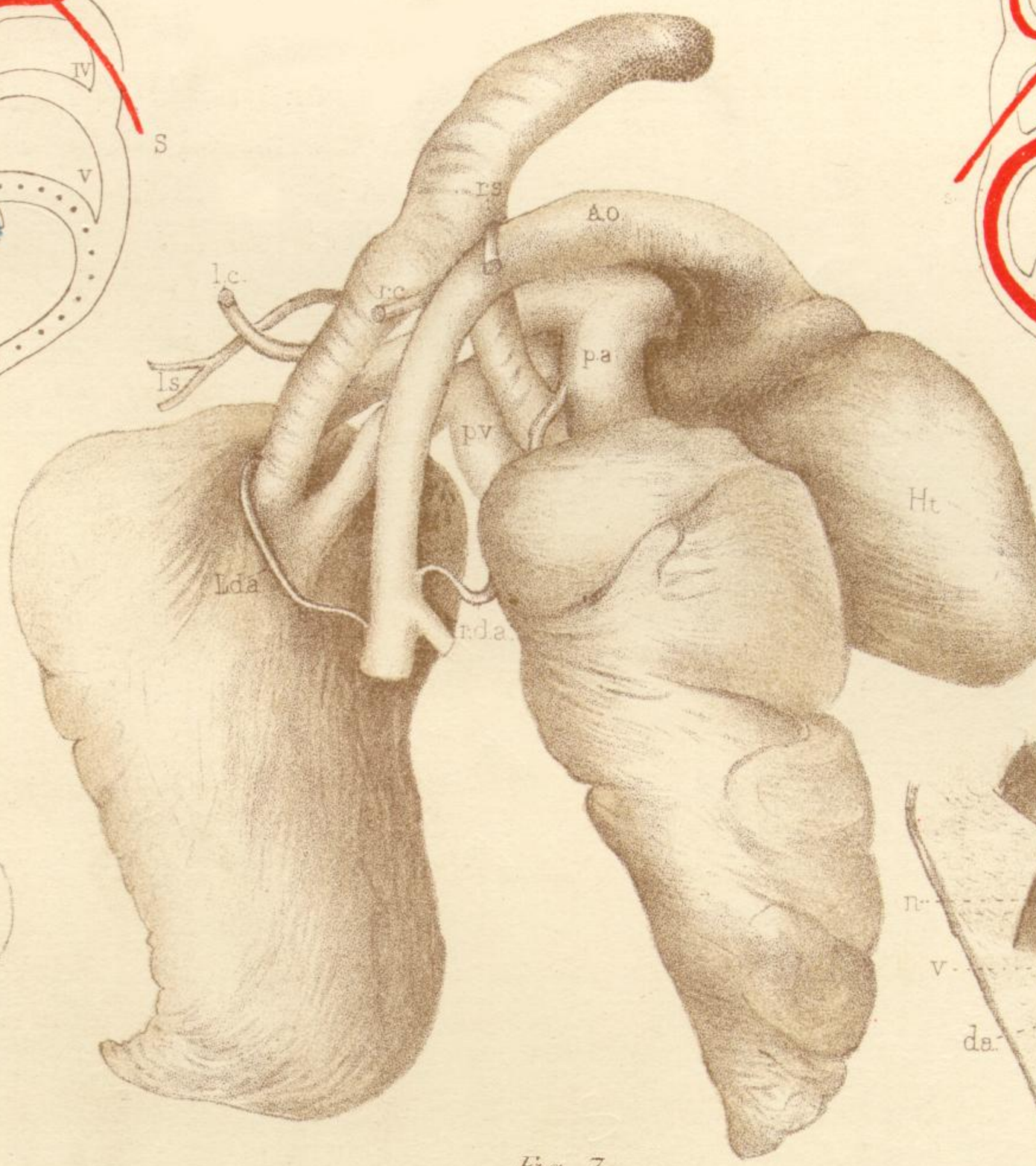


Fig. 1.



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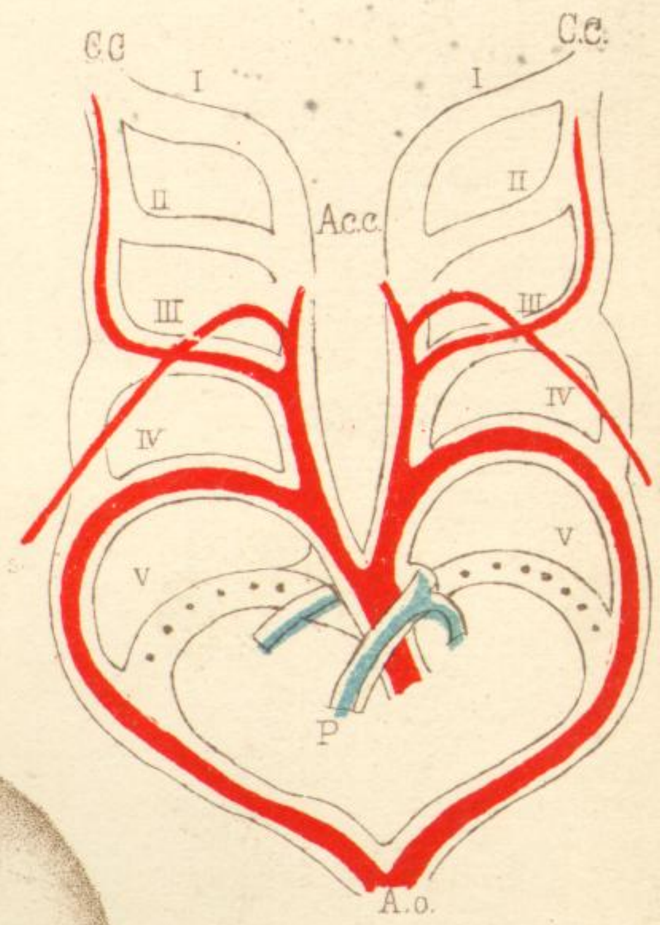
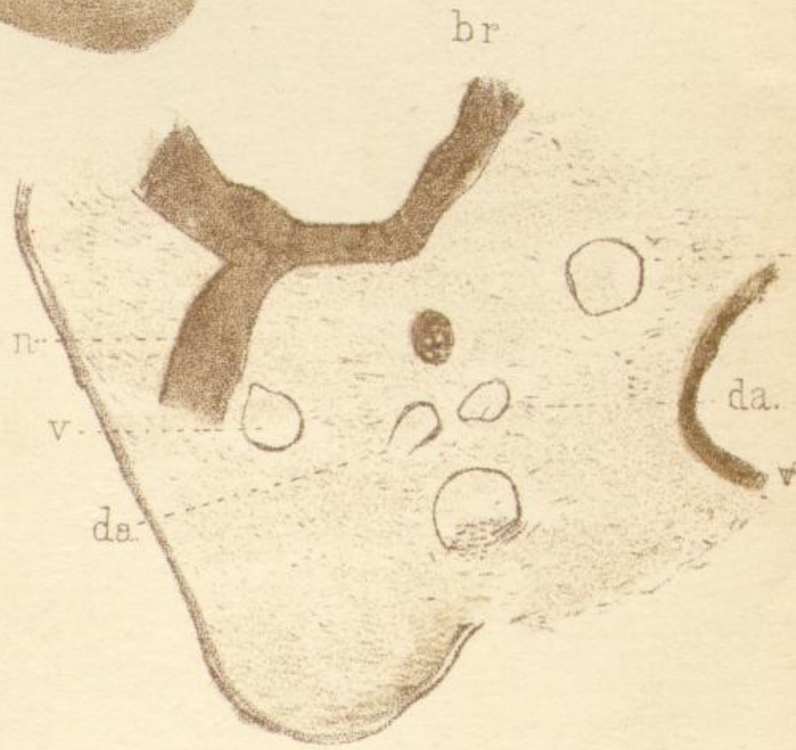


Fig. 4.

Fig. 5.



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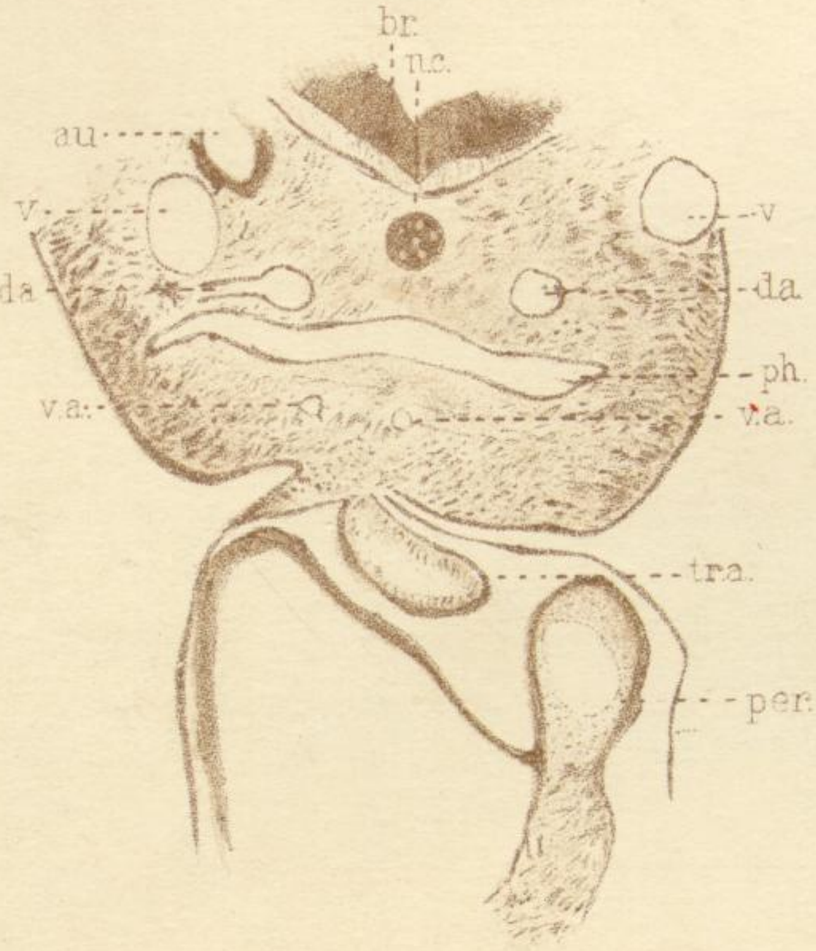

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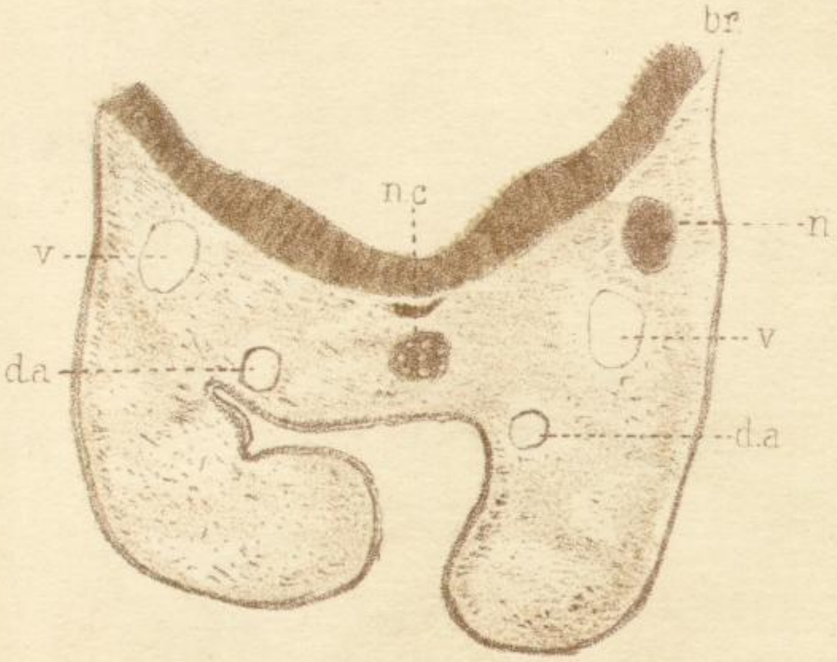

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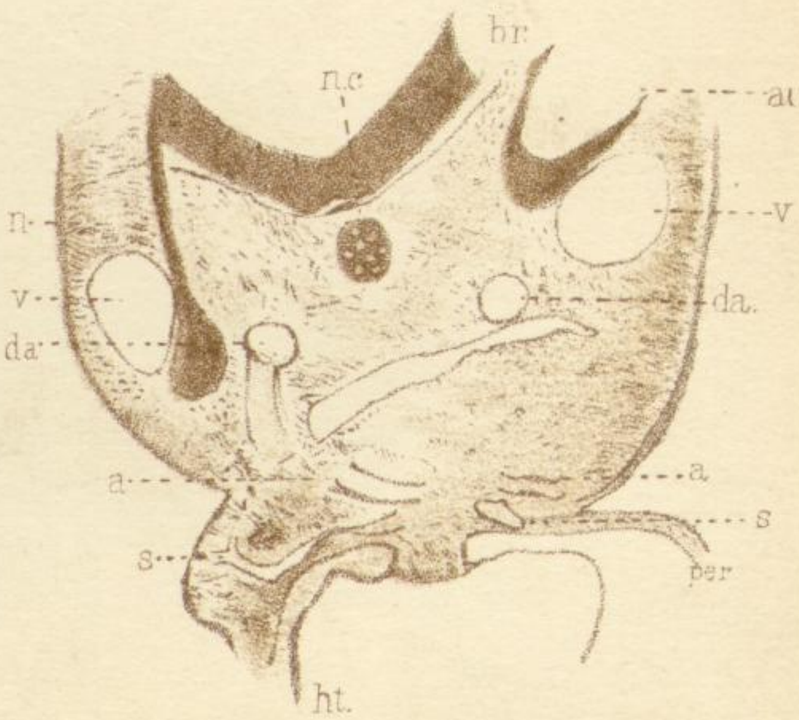

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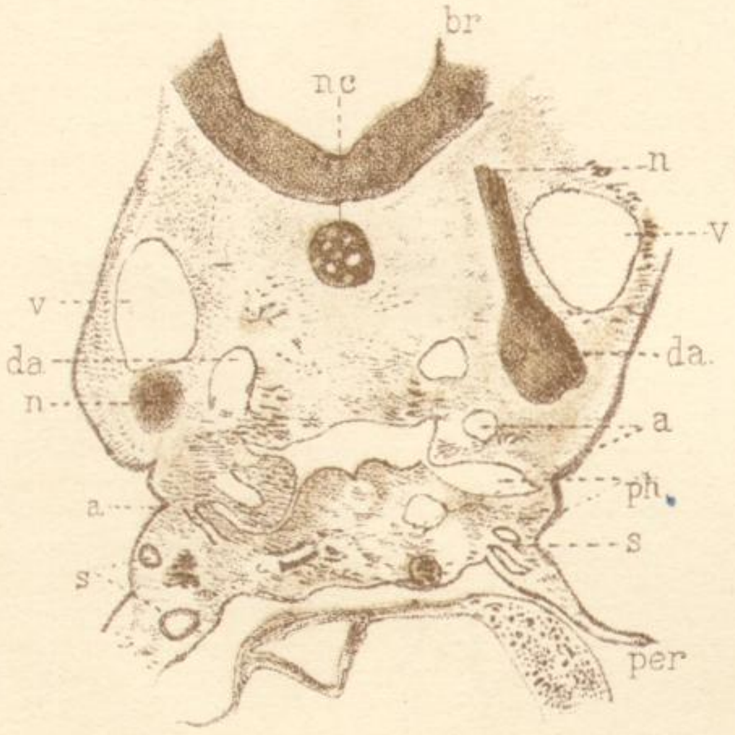

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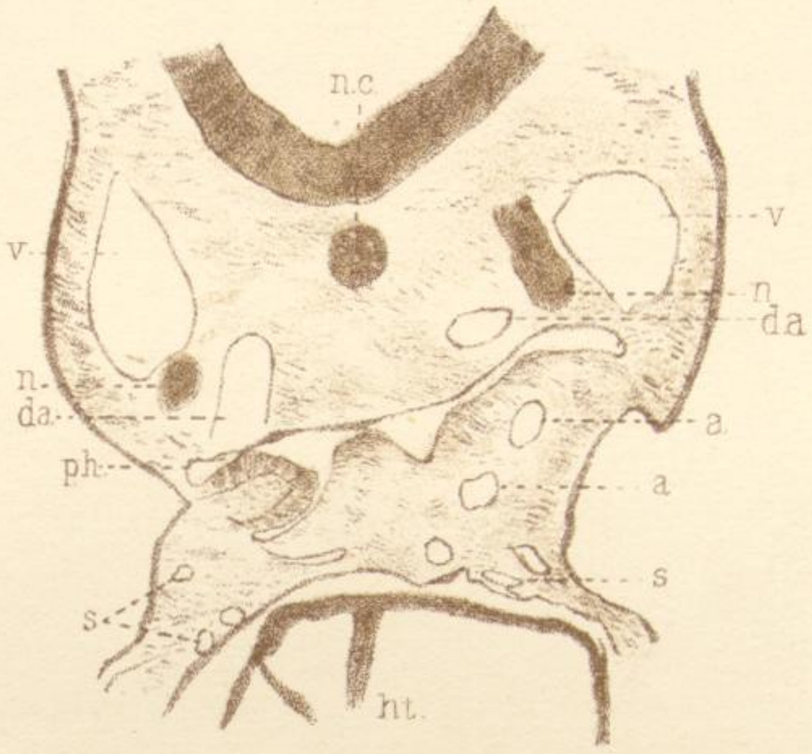

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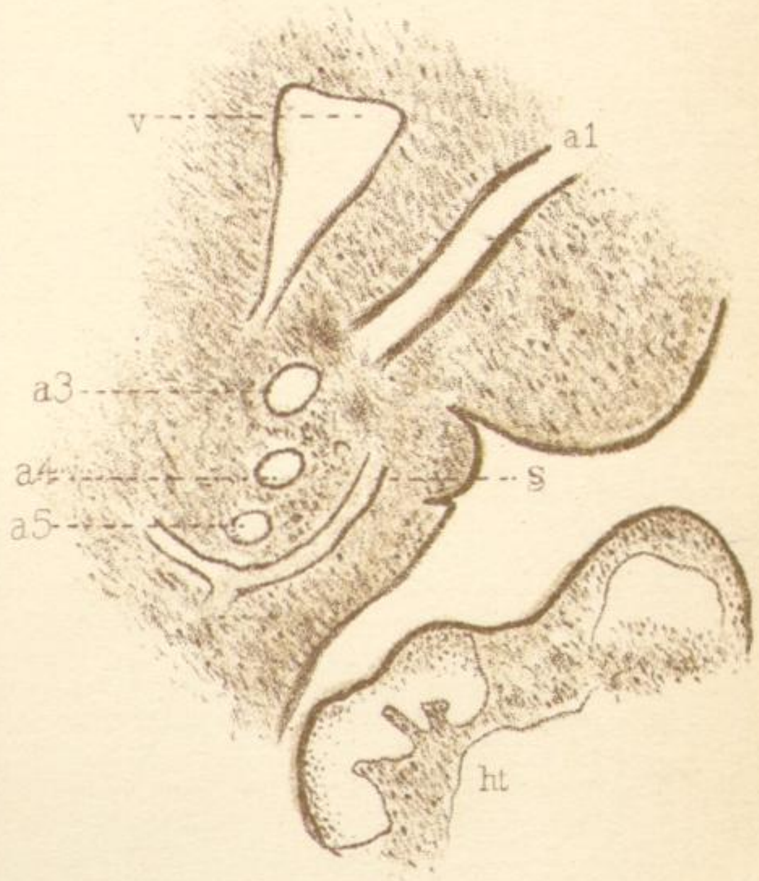

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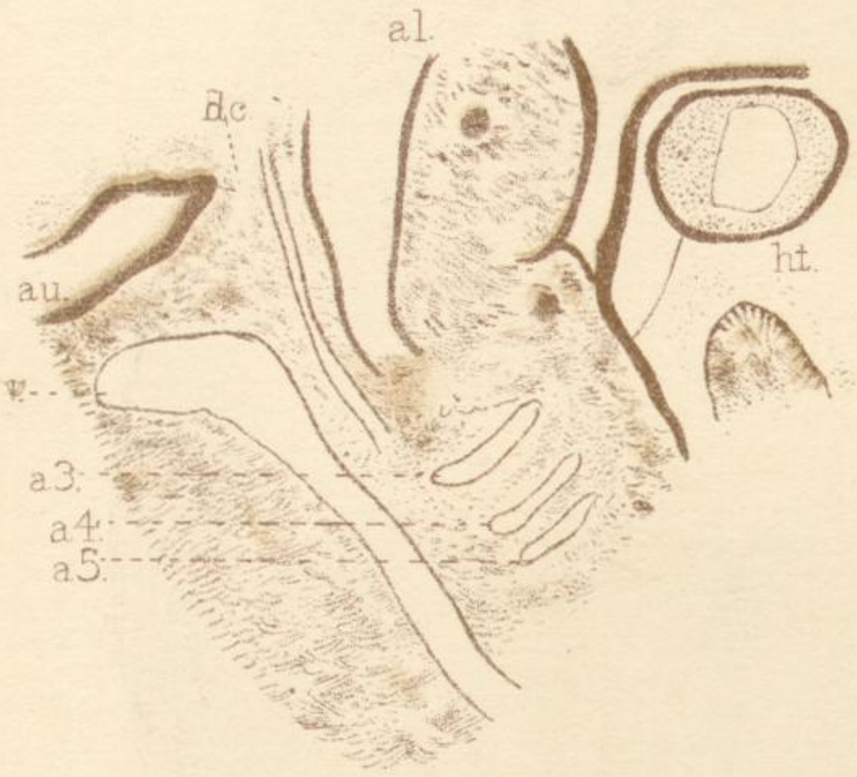

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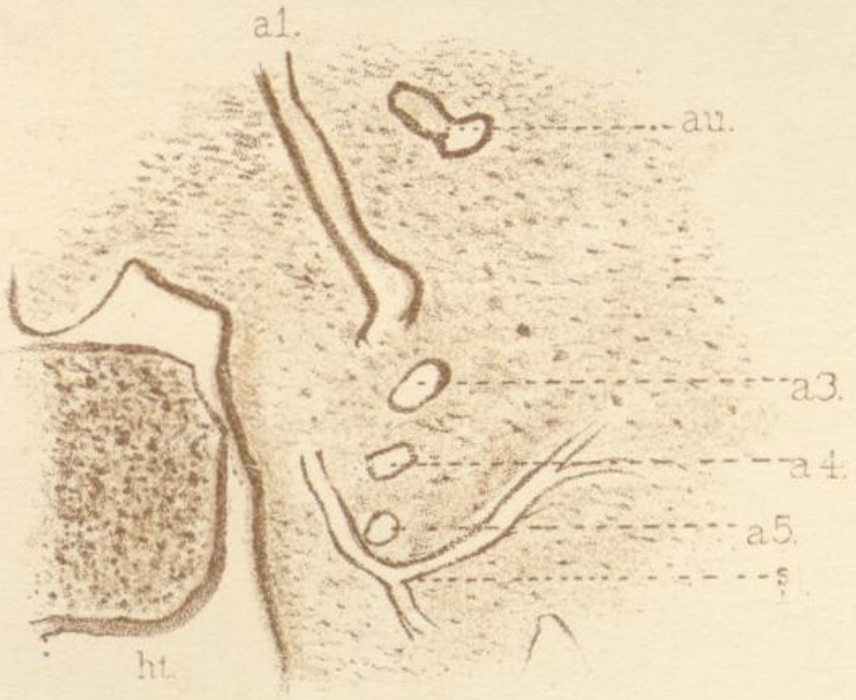


Fig. 14

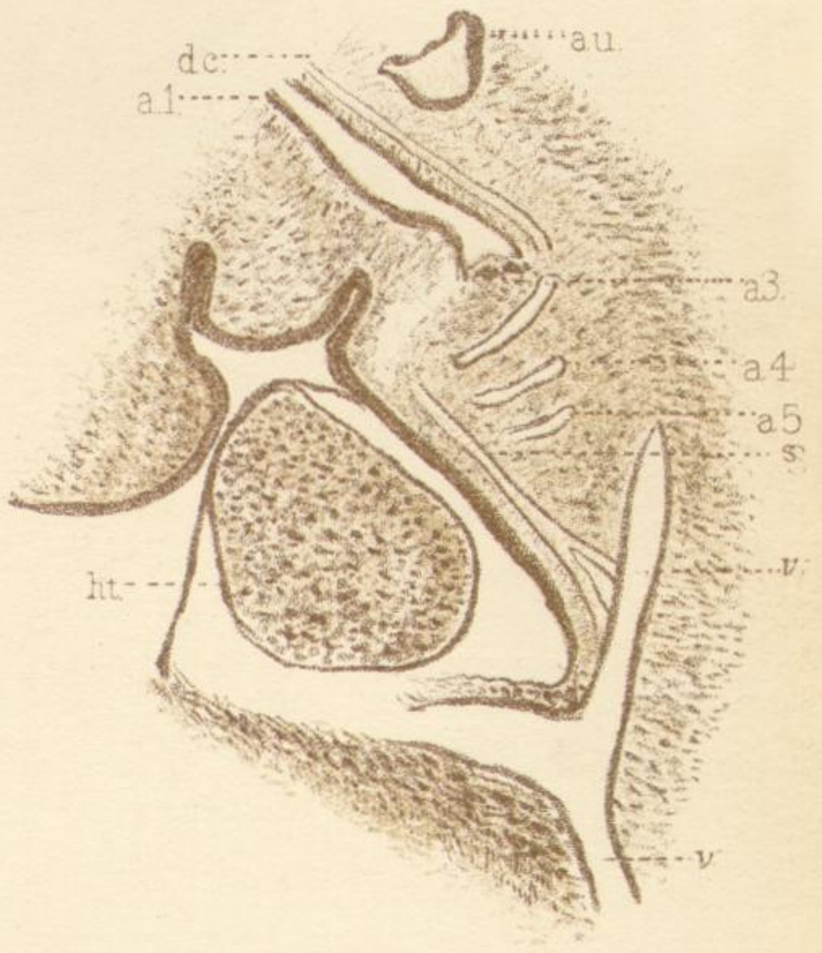
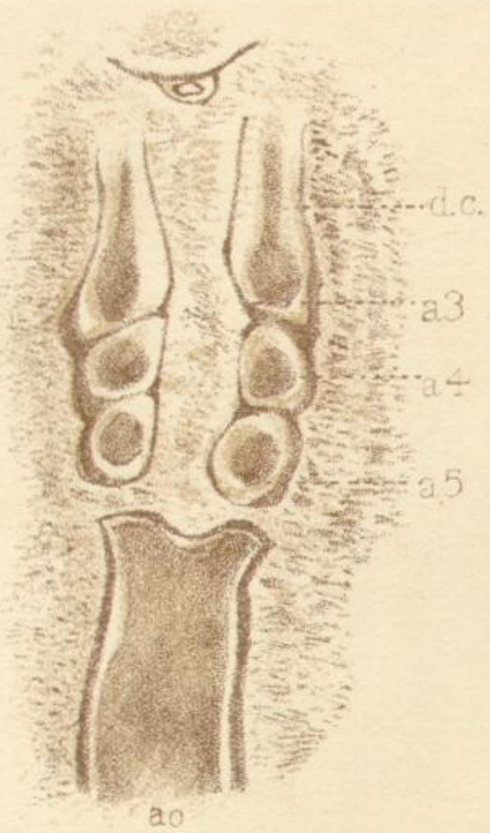


Fig. 16.

Fig. 15.



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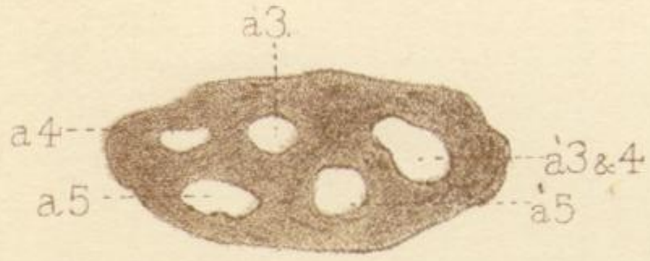

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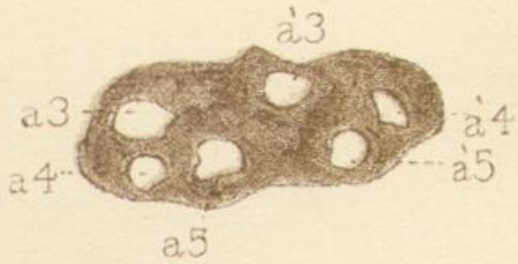
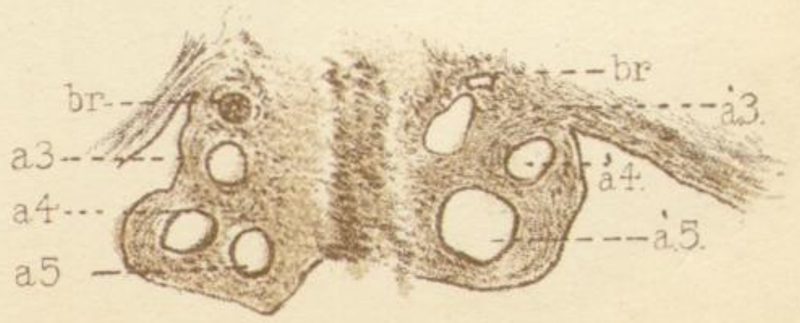


Fig. 18.

Fig. 20.



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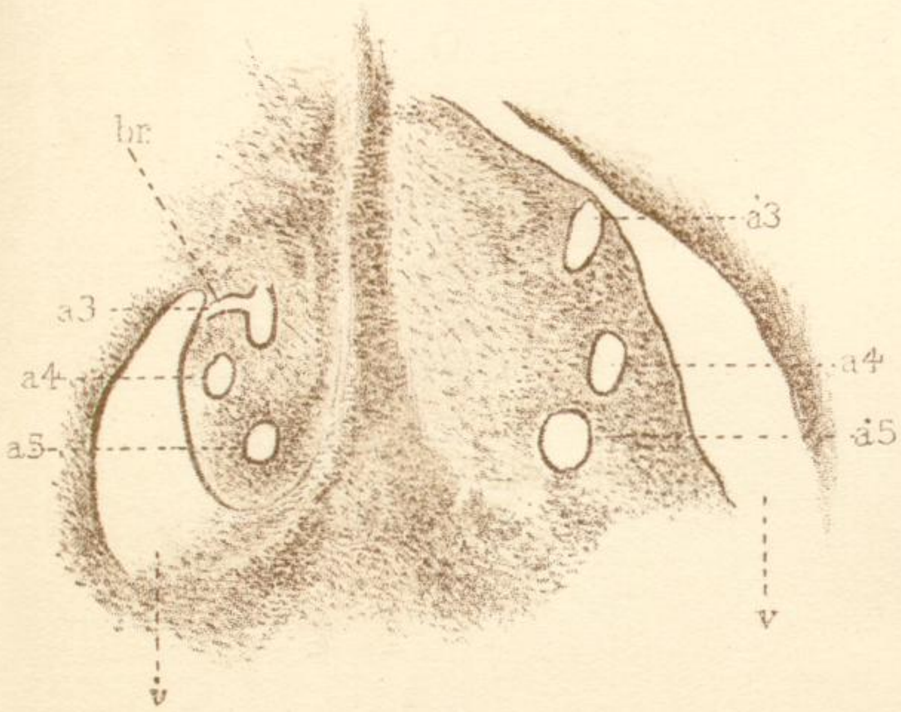

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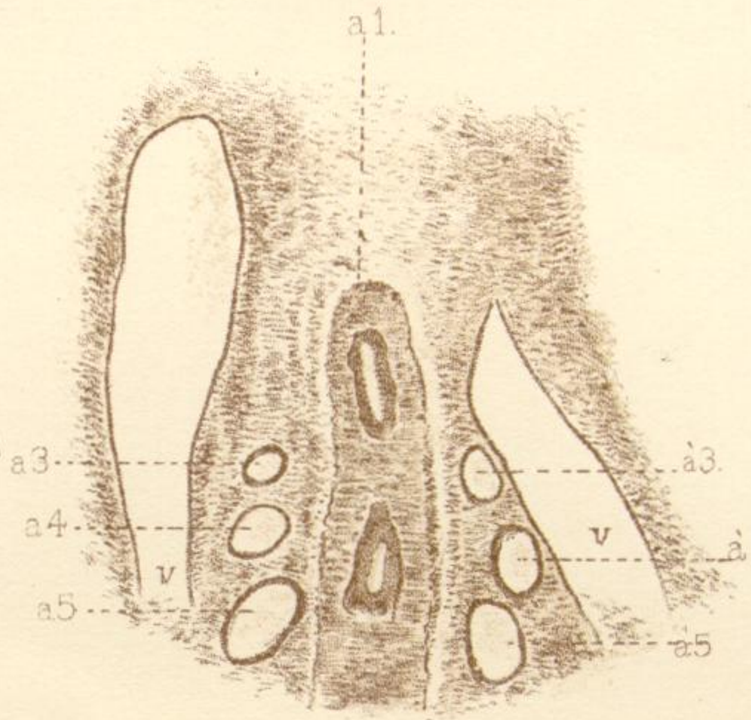

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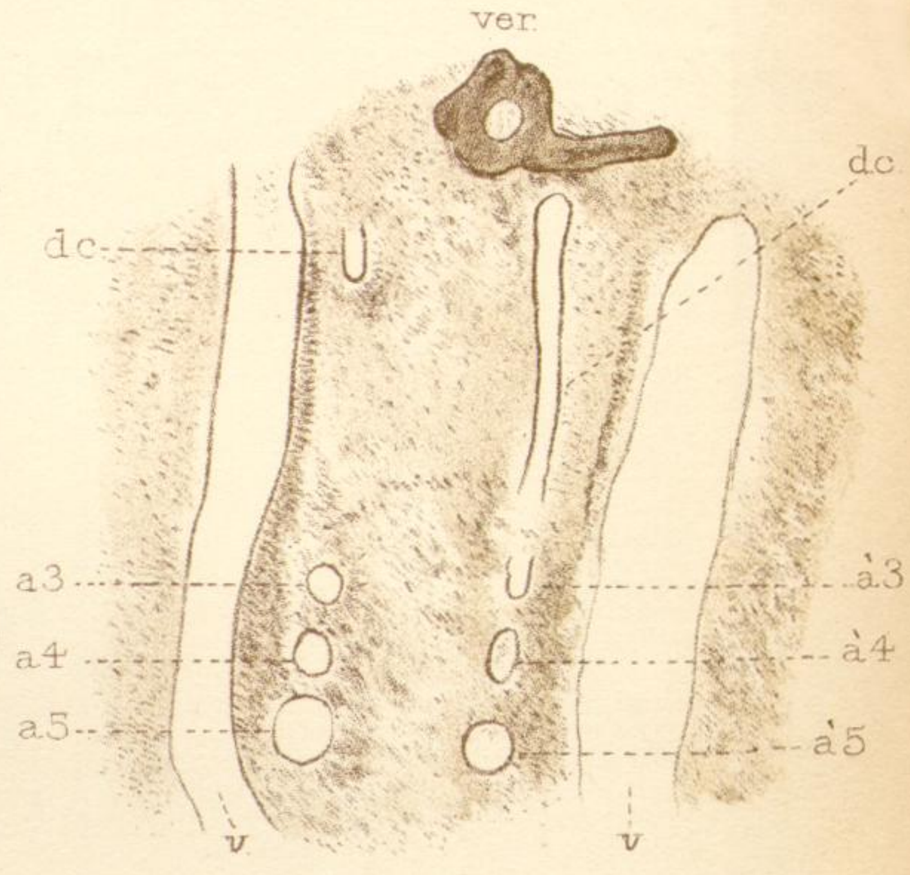

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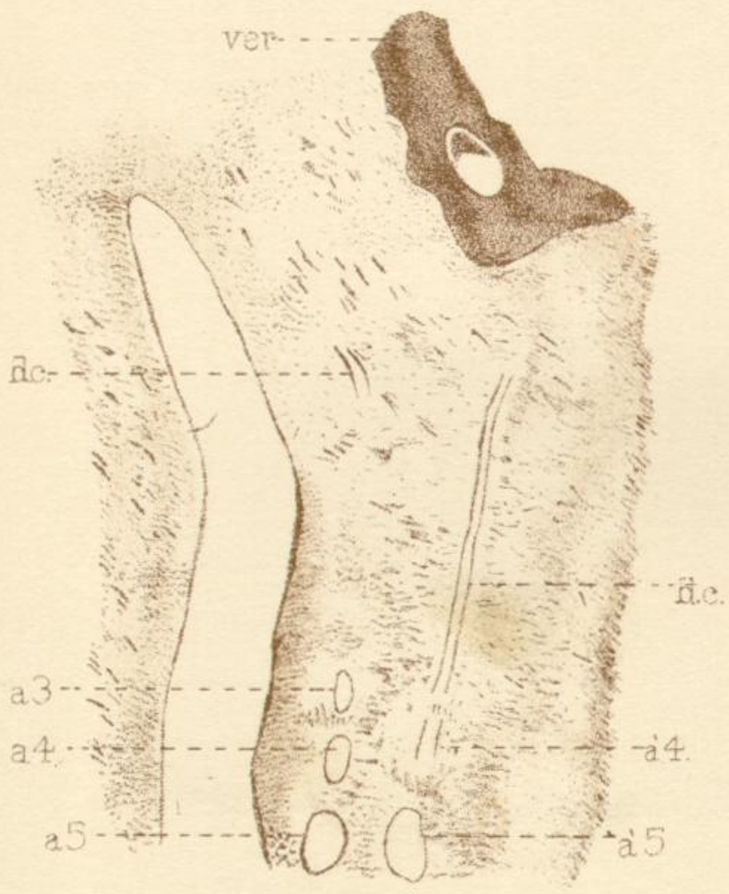

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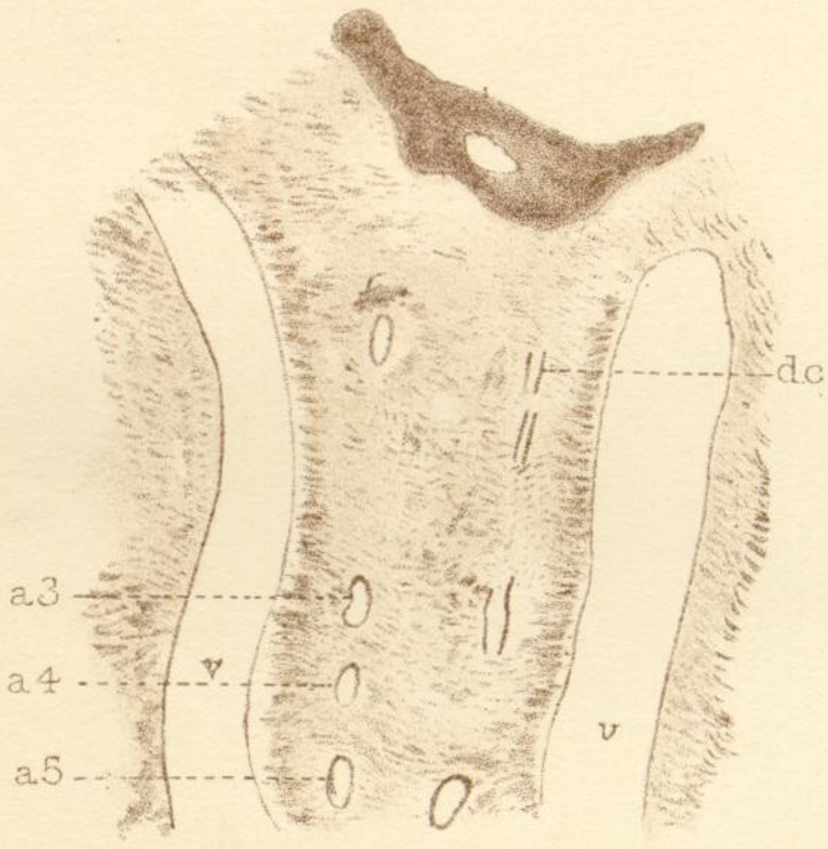

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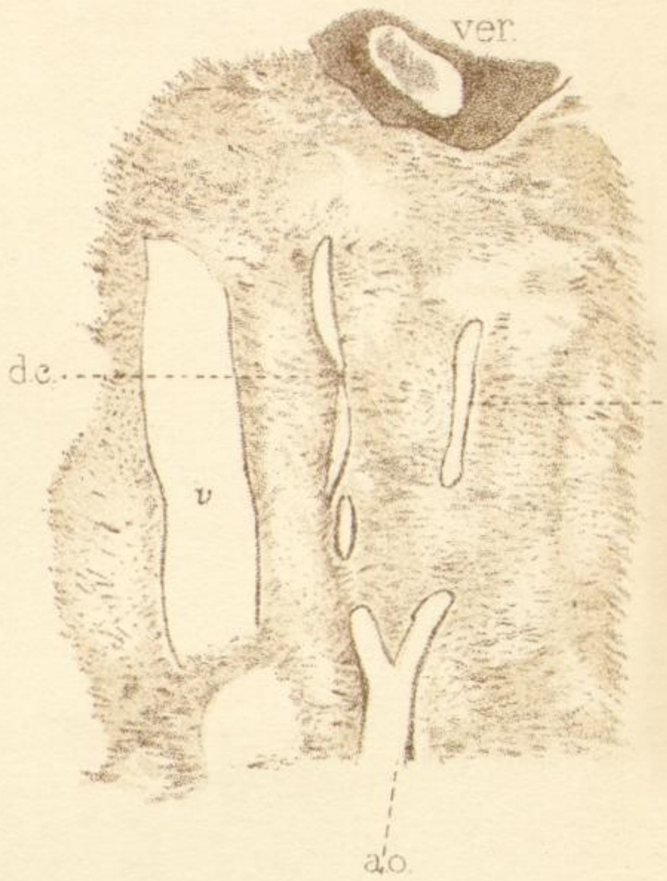

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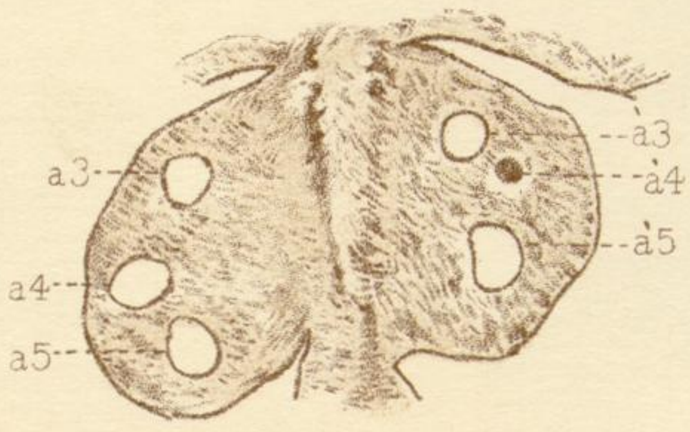

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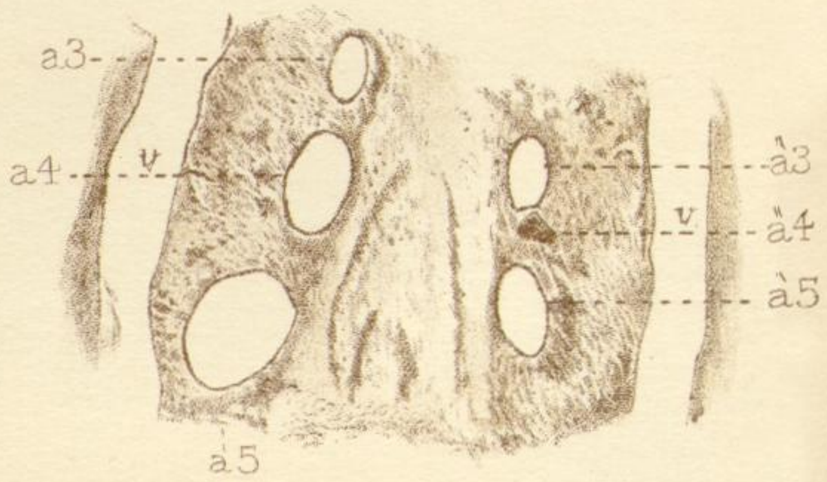

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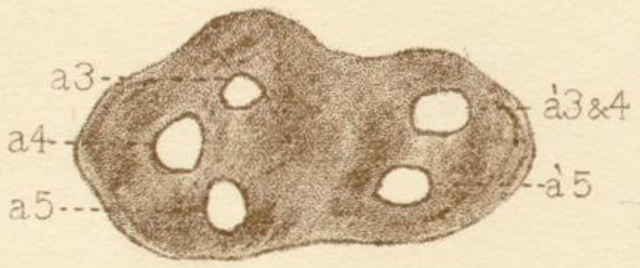

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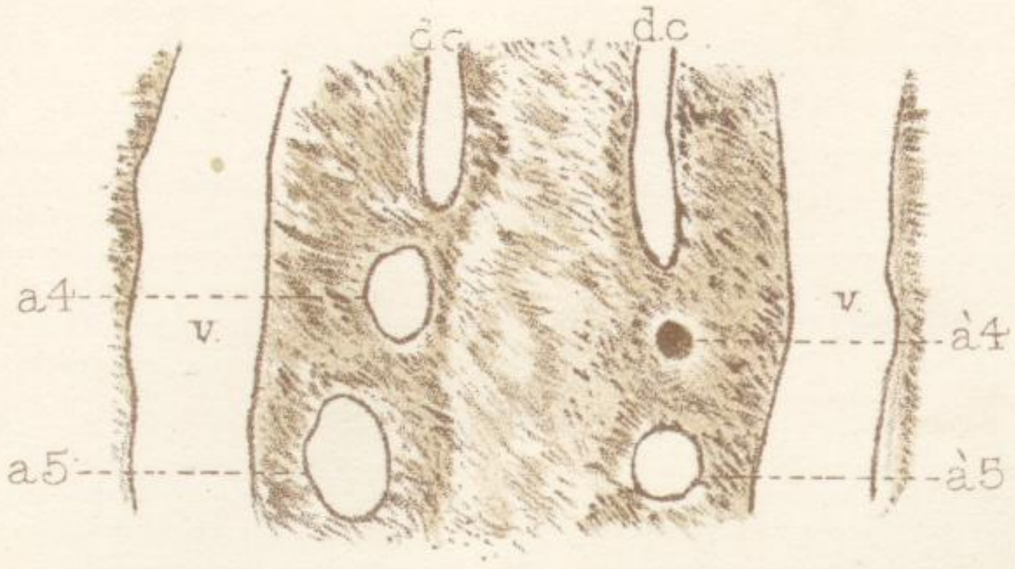

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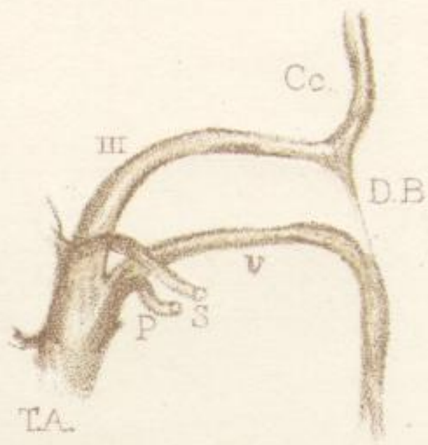

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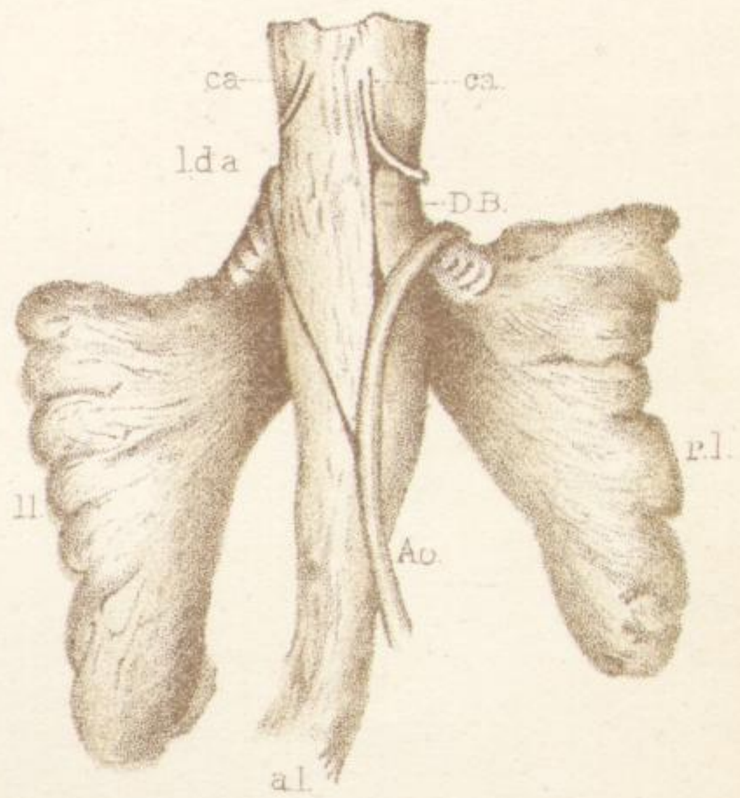

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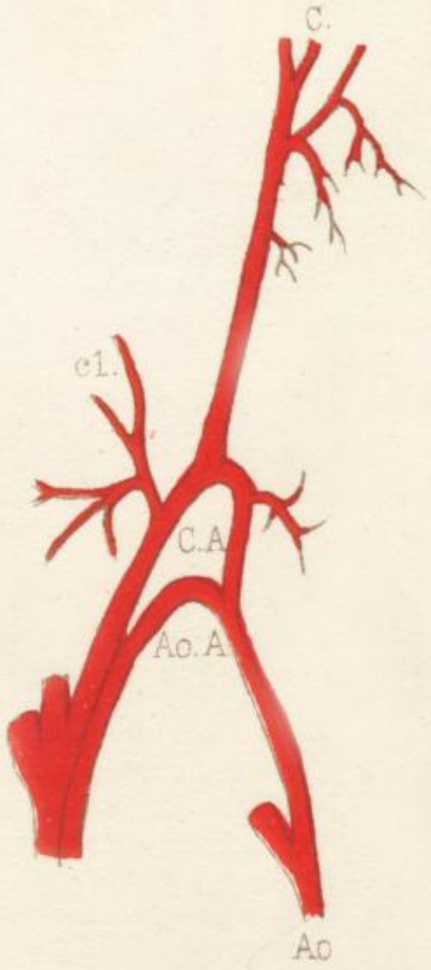

Fig. 33

Fig. 35.

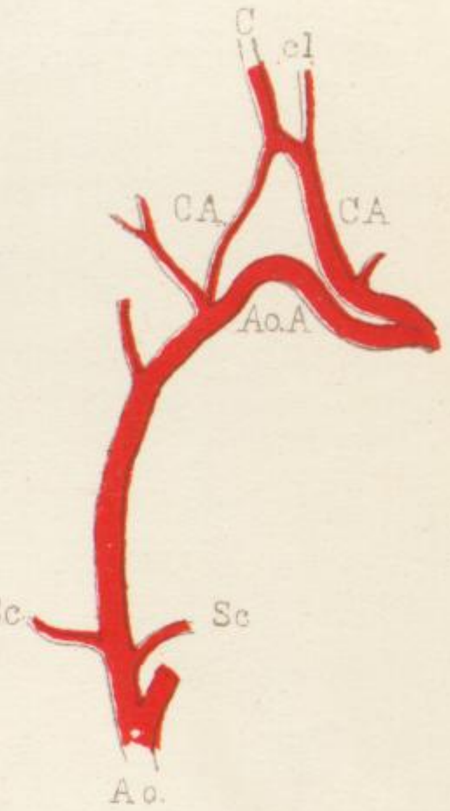

Fig. 37.

Fig. 38.

Fig. 1.

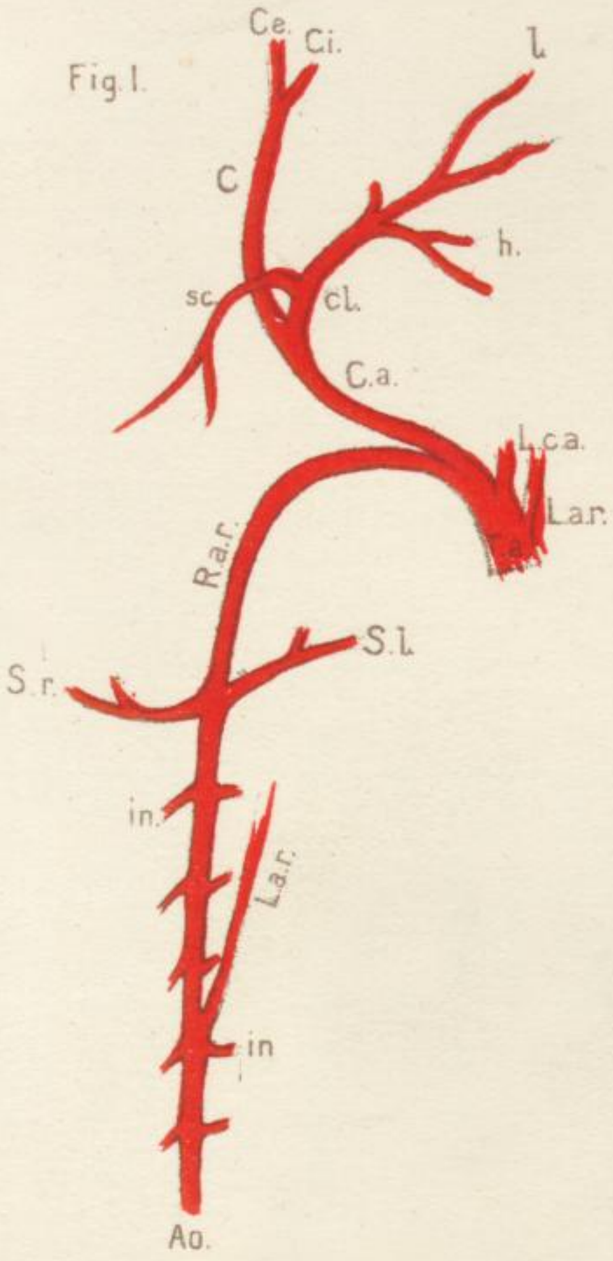

Fig. 36.