

No. 5. — *The Morphology of the Carotids, based on a Study of the Blood-vessels of Chlamydoselachus anguineus, Garman.* By H. AYERS.

CHLAMYDOSELACHUS\* holds undisputed claim to being the most lowly organized Elasmobranch yet discovered, and it was to have been expected that primitive conditions of organization would be retained to a greater extent than in any other known member of the group, the vascular system not excepted.

Almost nothing is known of the vascular system of the Notidanidæ, but it may be inferred from a comparison of their other structures with the corresponding organs in *Chlamydoselachus* that their vascular system will not be found to retain all the primitive characters present in *Chlamydoselachus*. This primitiveness of structure is expressed, 1st, in the retention of a large number of aortic arches; 2dly, in the presence of the complete dorsal aorta, of which the precardiac portion among the remaining vertebrates is almost without exception either extensively or completely atrophied; 3dly, in the extensive venous spaces, always simple in character, developed in the course of the large venous trunks.

While at the Banyuls-sur-Mer zoölogical station in the spring of 1885 I reached the conclusions, (a) that the vascular system of existing sharks had been extensively abbreviated in the course of descent in connection with the development of the head; (b) that formerly there must have been a much larger number of aortic arches than we now find in any member of the Elasmobranch group; and (c) that with the loss of the aortic arches the dorsal aorta of the branchial region had disappeared either entirely or in part. As examples of the latter condition

\* The two papers containing the original descriptions of the systematic position and anatomical characters of *Chlamydoselachus anguineus* from the type in the Museum of Comparative Zoölogy at Cambridge, Mass., include all that is known of the creature:—

<sup>1</sup> Garman, Samuel. New Sharks, *Chlamydoselachus anguineus*, etc. Bull. Essex Institute, Vol. XVI. p. 1.

<sup>2</sup> The same, 1884. *Chlamydoselachus anguineus*, Garman. A Living Species of Cladodont Shark. Bull. Mus. Comp. Zoöl., Vol. XII. No. 1. Cambridge, Mass., 1885.



we have several species of sharks whose anatomy has been described by Hyrtl,<sup>3</sup> Parker,<sup>4</sup> and others, such as *Scyllium*, *Mustelus*, *Zygæna*, etc. Furthermore, it seemed to me that the accumulation of blood-vessels about the hypophysis cerebri could be reasonably accounted for on the assumption that the vessel which Hyrtl<sup>3</sup> describes is in truth a remnant of a much larger vessel of functional activity during embryonic life only, which sustained such relations to the vascular structures about the pituitary space as would lead us to search for the remains of preoral aortic arches. His words are as follows (*loc. cit.*, p. 5): "Bei feinen Injectionen lässt sich leicht erkennen, dass diese Aorta, welche Kopfaorta genannt zu werden verdient, durch eine in die Mittellinie des Schädel-basalknorpels nach vorn gehende Fortsetzung bis zur Eintrittsstelle der Carotis interna in die Schädelkapsel sich erstreckt. Tab. I. Fig. 1, lit. i." Again the vessels called carotids by Hyrtl,<sup>3,5</sup> Müller,<sup>6</sup> and Parker,<sup>4,7</sup> seemed to complete the aortic circulation in front by bringing blood from the ventral to the dorsal side of the digestive tract, and were in a special sense the homologues of the carotids of the Mammalia, of which more will be said further on.

These conclusions were the outgrowth of my verification of Hyrtl's<sup>3</sup> descriptions and figures of the arterial blood-vessels of the head in *Scyllium*, *Acanthias*, and *Mustelus*. I did not at that time expect to be able to verify my conclusions by the dissection of any living animal, and consequently considered the views which form the essence of this paper to be of little value because not demonstrable. The vascular system of *Chlamydoselachus* proves the contrary, however, and under the circumstances it is now a matter of no inconsiderable interest to find out how the Notidanid sharks comport themselves with respect to the cephalic arteries.

I am not certain that Hyrtl has ever seen the "Kopfaorta" as it exists in *Chlamydoselachus*, (i. e. imbedded in the cartilage of the basis cranii,) for from his description of it quoted above it is not clear whether the injected vessel figured in his plate runs in, i. e. through, the basis cranii, or only in the middle line and ventrad of that structure.

<sup>3</sup> Hyrtl, Joseph. Die Kopfarterie der Haifische. Denkschrift. d. Wiener Akad., XXXII., 1872.

<sup>4</sup> Parker, T. J. On the Blood-vessels of *Mustelus antarcticus*. Phil. Trans., Vol. CLXXVII., 1886.

<sup>5</sup> Das Arterielle Gefasssystem der Rochen. Wiener Sitzungsberichte, 1857.

<sup>6</sup> Müller, Johannes. Vergleichende Anatomie der Myxinoiden. Berlin, 1839-41.

<sup>7</sup> Parker, T. J. Zoötomie, 1884.



At present I doubt not that Hyrtl found in every case only an extra-cranial vessel *so far as he traced it*, and that perhaps he did not follow it quite to its end on account of the non-penetration of the injection mass beyond the point of entrance into the cartilage.\* While studying the same species at the Laboratoire Arago it did not occur to me to seek for the vessel within the substance of the cartilaginous brain case, and I always found the vessel very much as Hyrtl figures it, though usually I was not able to trace it so far anteriorly as it is drawn in his plate. Since my attention has been called to the matter I have dissected only one specimen of *Scyllium stellare* from the Museum alcohol collections, but the histological condition of the tissues did not permit a satisfactory determination of the relations of the vessel. Further study of this form is very desirable. So far as the homology of the two vessels is concerned, there can be no question that they have strictly the same morphological value.

To aid in understanding the relations of the carotids, and to serve in the comparison of other forms, as well as to give an idea of the fundamental simplicity of organization of the vascular system, I shall first describe the aortic system of blood-vessels in *Chlamydoselachus* passing thence to a consideration of the homologies in other vertebrates in so far as lies within the scope of this paper.

The sinu-auricular (see Figure 2) valve is placed in the middle of the transverse axis of the sinus venosus with its long axis at right angles to the axis of the latter. It is slit-like and guarded on either side by two broad semilunar tendinous folds, — the sinu-auricular valves. The remaining auricular wall of the sinus is smooth, muscular in some degree, but thin.

The aperture of the auriculo-ventricular valve is placed to the left, below and in front of the sinu-auricular valve, and pierces the thick ventricular wall. Its ventricular end is provided with two cup-shaped folds, the auriculo-ventricular valves. Its auricular end presents a radiate figure formed by the tendinous cords of the muscular plate, which centre here. The dorsal wall of the auricle is smooth without, but rugose within. It is scarcely thicker than the wall of the sinus venosus. The ventral wall of this division of the heart is thick and muscular, and forms a triangular plate which projects beyond the edges of the ventricle,

\* Müller certainly did not see the vessel in any species studied by him, for he says (*loc. cit.*: "Bei den Haien u. Rochen fehlt die vordere umpaare Fortsetzung der Aorta schon ganz, wie bei den Knochenfischen aber die Haien besitzen noch einen circulus cephalicus im Sinne Hyrtl's," etc.



from which at about the middle it may be separated. This plate reaches cephalad to the middle of the conus arteriosus, but is not bound to it in any way.

The *conus arteriosus* (see Figure 2) forms a thick spindle-shaped trunk about an inch long and one fourth of an inch in diameter. It is provided with six rows of valves, all of which are quite small, except the anterior set of three, which are large, tridentate, and formed of a white tough tissue of a cartilaginous consistency. In *Odontaspis* the conus is bounded anteriorly by three large valves, each of which consists of two thin membranes united by a thick median bar which ends in a pointed projection beyond the anterior border of the valve.

The *pylangium* terminates anteriorly in a synangium or bulbus arteriosus, from which spring three vessels, one median and two lateral, the ventral aorta, and the sixth pair of afferent branchial arteries, respectively. The synangium is not so well developed in *Chlamydoselachus* as in *Raja* or most Elasmobranchs, for, while in the former a single pair of afferent branchial arteries arise from it, in the latter the common trunk known as the posterior innominate artery of the skate represents at least three primitive afferent branchial vessels, and in consequence the synangium represents a very much greater portion of the primitive ventral aorta in *Raja* than it does in *Chlamydoselachus*.

The synangium of *Chlamydoselachus* includes the enlarged end of the ventral aorta lying between the last pair of pylangial valves and the point of origin of the ventral aorta (in the restricted sense), and the sixth pair of afferent branchial arteries. It forms a truncated cone-shaped body, the homologue of the bulbus arteriosus of bony fishes. The ventral aorta continues the synangium forwards along the median line, and lies in a distinct sheath formed by the connective tissue separating the basibranchial cartilages from the muscles of the floor of the branchial basket. This sheath forms the outer wall of a lymph space.

The ventral aorta (see Figure 2) ends blindly in front in an anchor-shaped enlargement formed by the bifurcation of the median trunk and the separation of the two resulting vessels, — the anterior innominate arteries, — which curve outwards, upwards, and backwards, quickly splitting into two pairs of vessels the first and second afferent branchial arteries. From the anterior edges of the anterior innominate arteries, equidistant from the median line, arise two small vessels, which, passing forwards, supply the muscles in the ventral wall of the throat. Other small vascular twigs arise from the ventral aorta as well as the afferent branchial arteries to carry blood to the muscles of the ventral portion of



the branchial apparatus and to the heart. In the saurian *Varanus*, according to Wiedersheim,<sup>8</sup> (p. 704, Fig. 540, B,) it appears that a portion of the ventral aorta (or ventral commissures?) remains as a single median trunk, from which both the common carotids are given off just ventrad of the hyoidean apparatus, to rise on either side of the throat. The common carotid trunks thus occupy the position of the hyoidean efferent branchial vessels of the Elasmobranch. This common trunk divides above the level of the pharyngeal roof into an external and an internal branch. We thus see that in different animals the carotids have not the same value *in so far as their proximal ends are concerned*. The afferent branchial arteries (see Figure 2) number six pairs, and are arranged in sets of two pairs each. While the first two pairs of arteries arise from a common trunk, the arteries of the other pairs arise independently, with the members of each pair placed opposite each other.

The anterior innominate artery does not divide into first and second afferent branchial arteries until after it has curved upwards about a quarter of an inch, when the first afferent branchial springs from the anterior edge of the innominate and continues its trunk dorsad, curving gracefully forwards, outwards, and upwards, then considerably backwards to where it enters and supplies the anterior half of the first gill cleft, or the hyoidean demibranch. The second afferent branchial passes backwards at an acute angle from its origin at the posterior border of the root of the first, and in its outward and upward course nears the third afferent branchial where the latter enters its arch.

The sets composed of the afferent branchials three and four, and five and six, respectively, are so disposed that while five and six leave the synangial end of the ventral aorta, three and four arise from the middle of this trunk. There are slight variations in the size of the vessels forming the pairs two, four, and five, the arteries of the left side being larger than those of the right. The afferent branchials three, four, and five run very nearly parallel with one another, and while the efferent branchials of the pairs three and four continue this relation above the intestine, efferent branchial five bends suddenly backward and fuses with the sixth before entering the dorsal aorta.

There are six pairs of efferent branchial arteries (see Figs. 1 and 2), corresponding pair for pair with the afferent branchials just described. Only four pairs reach the median dorsal line to form the dorsal aorta; these are the second, third, fourth, and fifth. The first efferent branchial

<sup>8</sup> Wiedersheim, Robert. *Lehrbuch der vergleichenden Anatomie der Wirbelthiere*. Jena, 1886.



is connected by an anastomosing branch with the second, just as the latter emerges from its arch to enter the roof of the mouth, and thus at least a portion of the blood from the hyoidean demibranch reaches the dorsal aorta; but as the trunk of the first efferent branchial artery passes out of the hyoid arch it curves forwards along the outer edge of the basis cranii, and runs as far forwards as the middle of the orbital region, where it suddenly curves inwards to a point at one side of the median line, just below the pituitary space, the floor of which it perforates to enter the cranial cavity. This is the first impression produced on laying bare the vessels in *Chlamydoselachus*, but, as we shall see later on, all of this trunk lying beyond the upper end of the hyoid is foreign to the first efferent artery, whose continuation we are to seek in the branch uniting it with the second, and is simply the trunk of the common carotid artery.

The commissural branch uniting the hyoidean or first efferent branchial artery to the second is fully as large as the arteries themselves, and from its manner of union with the second and of its separation from the first efferent branchial makes the conclusion unavoidable that it is in truth the continuation of the trunk of the first efferent branchial, which however fails of an independent union with the dorsal aorta, but in a manner similar to that in which the homologous arteries in *Scylium*, *Acanthias*, and *Zygæna* (Hyrtl, *loc. cit.*, Plates I.-III.) are united, i. e. by the fusion of the latter with the next succeeding branchial artery (see Figs. 10 and 11). This method of fusion is carried to an extreme in the bony fishes, where all the efferent branchials of each side unite to form the single pair of aortic roots (Müller, *loc. cit.*, Plate III. Fig. 13), and is also represented in *Chlamydoselachus* in the posterior section of the efferent branchial system by the fusion of the sixth and fifth efferent branchials to form a single aortic root. Under primitive conditions of the hyoidean gill this anastomotic vessel would take blood from the anterior demibranch of the hyoidean gill sac and the posterior demibranch of the mandibular gill sac, — holobranch of Parker. On account of the reduction which has taken place in the spiracular gill among existing Elasmobranchs, this vessel serves simply to convey the blood from the anterior demibranch of the first gill sac into the efferent artery of the first holobranch.

As in the afferent branchial system, so in the efferent branchial system, the component arteries are arranged in pairs, and the pairs correspond, though the paired condition is less marked in the efferent than in the afferent system.



The first and second efferent branchials unite to form a trunk that reaches the aorta as the second aortic root. The third and fourth pairs find independent outlets as the third and fourth aortic roots, while the fifth and sixth pairs fuse directly to produce short common trunks, the last or fifth pair of functional aortic roots.

The distance between the points at which the first and second and the second and third efferent branchials enter the aorta is nearly the same, while the common trunks of the fifth and sixth enter the aorta at a distance behind the fourth twice as great as that between the other pairs.

Unlike all other gnathostomous vertebrates, *Chlamydoselachus* has a dorsal aorta (dorsal vessel) running the entire length of the notochord, to which it is intimately attached through the greater part of its course. There is, however, no trace of a chondrification of its walls, such as frequently occurs in cartilaginous fishes (e. g. *Sturio*). For convenience in describing as well as on morphological grounds, it is desirable to designate two sections of the dorsal aorta by the terms *precardiac* and *postcardiac*. The former receives the aortic roots and supplies the head with arteries, the latter gives off the arteries to the trunk and tail.

The head and all the precardiac portion (see Figs. 1 and 2) of the trunk are supplied with blood by means of the very primitive musculo-spinal arteries and branches of functional or rudimentary aortic arches. This fact is of the greatest importance in any discussion of the homologies of the head arteries, or more exactly precardiac arteries, of the higher Vertebrata. These vessels where more or less rudimentary as regards their main trunks have undergone secondary changes, during which the course of the blood currents through them may have been reversed, and they have usually acquired new outlets, or inlets, as the case may be.

It is convenient to make a further division of the precardiac section into cranial, vertebral, and branchial portions. The precardiac section is marked off posteriorly by the junction of the fifth pair of aortic roots with the sub-chordal vessel. It terminates anteriorly in the pituitary plexus. The postcardiac section extends from the junction of the fifth pair of aortic roots to the tip of the tail. (See Figs. 1 and 2.) With the exception of a slight enlargement in the occipital region, the diameter of the aorta is constant between the occiput and the origin of the celiac artery; from this point backwards the aorta gradually tapers into the small caudal artery. From the occiput forwards the cranial section of the precardiac aorta lies imbedded in the cartilage of the basis



cranii; sinking into the cartilage just in front of the posterior border of the basi-occipital cartilage, it runs forwards, gradually rising to the inner surface of the cranial floor, remaining equidistant from the chorda until near the anterior end of the latter, when the aorta dips slightly to make a bold curve upwards into the pituitary prominence within which it gives off two lateral branches which separate from the median vessel only gradually. (See Figure 3.) These three vessels make their way through the cartilage, and by freely anastomosing with one another form a small but sharply defined plexus, crowning the pituitary prominence, but separated from the cartilage by several well defined layers of connective tissue, one of which bridges over the pituitary depression, and thus excludes the internal carotids from the cerebral cavity. The plexus lies external to the dura mater.

As we have seen, the aorta is made up by the confluence of six pairs of efferent branchial arteries, which pour their blood into the aorta through only *four* aortic roots, and in this condition we recognize the process of reduction, transposition, or utter obliteration at work in getting the creature out of a lower into a higher stage of organization. But the four aortic roots which bring blood from the gills are not the only trunks which from their relations to the aorta and the body make good their claim as aortic arches or roots. As Hyrtl has pointed out, the pair of vessels running from the internal carotid trunk to the aorta in all sharks is most surely an aortic arch, and although it has lost its direct connection with a gill, which we have every reason to believe it formerly had, it still retains its connections with a trunk which has resulted from the obliteration of *a series* of efferent branchial vessels, and through this trunk an indirect connection with the first two functional gills of *Chlamydoselachus*. Besides this pair, there is another whose relations to the dorsal aorta are such as to entitle them to rank as aortic arches. I refer to the two side branches which the dorsal aorta gives off as it approaches the pituitary plexus. To these six aortic arches I would add a pair represented by the anterior portion of the internal carotid arteries, and another pair represented by the efferent vessels of the spiracular pseudobranch, which pour their blood into the dorsal aorta through the ophthalmic artery, internal carotids, carotid plexus, and pituitary plexus, all of which vascular structures anastomose among themselves from without inwards, in the order given. To these still another pair may be added, recognizable in the last pair of efferent branchial arteries (the sixth functional pair), which by means of their fusion with the fifth pair have not been counted. *Chlamydoselachus*



has then, in all, nine aortic arches and remnants of arches, persisting from an earlier and more primitive condition of organization. This count is based on the demonstrations and suppositions, (*a*) that the anastomotic branch between the hyoidean demibranch and first efferent branchial is the continuation of the hyoidean efferent artery; (*b*) that the internal carotids after turning inwards and entering the pituitary space unite with the dorsal aorta; (*c*) that the anterior end of the cranial aorta divides, and that the lateral vessels curve outward each side of the anterior end of the notochord; (*d*) that the efferent artery of the spiracular pseudobranch is connected with the aorta; and (*e*) that the sixth efferent branchial artery formed at one time (probably during embryonic life) an independent aortic root. The fact should not be overlooked that we thus find remnants of two, and perhaps three, aortic arches *in the pituitary space!* (See table on page 218, and Figs. 1 and 2.) That the above method of counting the aortic arches in *Chlamydoselachus* is a correct one, within very narrow limits of error, no one will question who recognizes the vast changes that have been brought about in the vascular system of a higher vertebrate — mammal, for instance — during its phylogenetic course from the fish type upwards, and who recognizes the general law that an organism makes use of rudimentary or disused structures to build up other structures, of different function perhaps, for use under changed conditions of environment, provided the rudiment or disused structure be *suitably placed*. The only portions of the vascular apparatus of the branchial region that are suitably placed for use in case the aorta is reduced, are evidently the dorsal and ventral commissural systems. That the dorsal vessel should be chosen of the two is further evidence of the law, for the dorsal commissure is both more directly connected with the territory to be supplied, and lies deeper in the tissues in a direct line toward the brain; besides, it normally carries the purified blood from the gills, which the ventral commissures do not to so great an extent, lying as they do on the side of the gills where the currents are forming and setting towards the dorsal vessel. As a further illustration, we find in some species of *Myxine* the remnant of a ductus Botalli. This remnant was in early adult life hollow, and connected the gills of its half of the segment with the dorsal aorta. Müller found in some cases that each end of the thread-like remnant was still hollow. These threads arise from the afferent branchial artery of the anterior gill sac, passing thence upwards and forwards, and fuse with the carotid trunks where the latter anastomose with the first efferent branchial arteries. In



this instance the vessel is atrophied during the process of the reduction of the anterior gill, and the blood which formerly passed through it direct to the collecting vessel above its gill now passes backward, and its segment of the collecting vessel is now either carotid or carotid root.

Since the number of efferent branchial arteries uniting to form the dorsal aorta varies in different species, the dorsal aorta cannot be an equivalent structure throughout the vertebrate series.

We know that the cranium itself is not an equivalent structure within the limits of the Elasmobranchii. Abundant proof of this has been collected by Gegenbaur,<sup>12</sup> Froriep,<sup>13</sup> Van Wijhe,<sup>14</sup> Dohrn,<sup>15</sup> and others. Evidence based on the relation of blood-vessels to the cranial floor is worthy of note in this connection. In some Elasmobranchs the anterior pair of musculo-spinal arteries pierces the cranial floor, in other forms this pair is intimately related to the atlas. Where the former condition is present, we can say definitely that at least one vertebra has been added to the cranium, but in the latter case we may have to deal with a suppression of one or more pairs of musculo-spinal arteries, in which case we cannot draw conclusions as to the constitution of the cranium.\*

Since there can be little doubt, if any, that the *primordial cranium* is the same in all cases, it follows that, during the early stages of ontogeny, segments (cranial vertebræ) must have been added to the occipital region in a large number of cases, and we are at once confronted with the difficulty of determining the number of such added segments, and

<sup>12</sup> Gegenbaur, C. Die Metamerie des Kopfes u. die Wirbeltheorie des Kopfskeletes. Morph. Jahrbuch, XIII., 1887.

<sup>13</sup> Froriep, A. Ueber ein Ganglion d. Hypoglossus u. Wirbelanlagen in d. Occipitalregion. Arch. f. Anat. u. Physiol., 1862.

<sup>14</sup> Van Wijhe, J. W. Ueber die Mesodermsegmente u. d. Entwickl. d. Nerven des Selachierkopfes. Konigl. Acad. d. Wissensch., 1882.

<sup>15</sup> Van Bemmelen, J. F. Ueber vermüthliche rudimentäre Kiemenspalten bei Elasmobranchiern. Mitt. d. zoolog. Stat. zu Neapel, VI., 1885.

<sup>16</sup> Dohrn, Alex. Studien zur Urgeschichte der Wirbelthierkörper. Mitt. d. zoolog. Stat. zu Neapel, VII., 1887.

\* Transsections of the basis cranii of *Chlamydoselachus* taken from the vertebral junction forward show at intervals calcified tracts leaving the central perichordal crust, and extending on either side out into the hyaline cartilage. They correspond in position to the neural arches, transverse processes, and hypapophyses of the vertebræ. (See Figure 8.) It may be possible to determine the number of vertebræ entering into the basis cranii of *Chlamydoselachus* by making a perfect series of such sections and counting the number of these vertebral remains.



thereby the limits of the primordial cranium. It is apparent from Müller's studies, that the Myxinoids possess a typical and well developed system of aortic vessels, and that *Petromyzon* differs more in degree than in kind from the Myxinoid type, for the structural plan is undoubtedly the same in both. The views which have hitherto been held by morphologists of the nature of the aorta in Craniates do not permit us to establish a homology of parts between this group and *Amphioxus*, the only living representative of the Acraniates.

Examining first of all the vascular system of *Amphioxus* as the type from which we may expect the simplest exposition of the fundamental vertebrate plan of structure, we find that it resembles in many respects the annelid type. For our purpose now, it will be sufficient to describe its precardial and postcardial sections. We find that, while they are not distinctly separated, the former corresponds to the branchial and prebranchial systems of vessels, the latter to the dorsal aorta, its branches, and its complement, the ventral (subintestinal) vein. Of importance is the fact that there are at first *two* aortic arches, forming the anterior termination of the aortic vessels and in this case of the vascular system, one of which disappears later in life quite completely as an arch, but persists in part as an artery supplying the naso-facial region, and that these arches do not project to the anterior end of the notochord, — a condition that may or may not be a secondary one.

Langerhans<sup>9</sup> (*loc. cit.*, p. 337) describes the arches and dorsal aorta as follows: "Von der Arteria branchialis gehen zwar Gefässe unter dem Constrictor veli zum Mund. Dann aber setzt sich das Herz fort in einem sehr weiten rechts verlaufenden Aortenbogen, während es links keinen ähnlichen entsendet, sondern geschlossen ist. Dieser rechte Aortenbogen zieht hinter dem M. constrictor veli nach oben, liegt in seinem oberen Theil mit dem Muskel, zum Theil in derselben Querebene und verbindet sich mit der rechten Aorta, während die linke anscheinend in keine Beziehung zu ihm tritt. Der Theil der Aorta unmittelbar hinter der Einmündung des Aortenbogens in die rechte Aorta ist bei beiden gleich weit. Nach vorn aber setzt sich die linke Aorta bis zur Mundhöhle als schmales Gefäss fort. Rechts dagegen biegt der grosse sinuöse Aortenbogen, nachdem er sich mit der rechten Aorta verbunden, nach vorn um und erstreckt sich etwas unterhalb und seitlich von der Chorda gleichfalls bis zur Mitte der Mundhöhle nach vorn, um hier abgerundet zu enden."

<sup>9</sup> Langerhans, P. Zur Anatomie der *Amphioxus lanceolatus*. Arch. f. mikr. Anat., Bd. XII., 1876.



Hatschek's studies of the development of the organs of *Amphioxus* do not seem to have been extended to the vascular system, for he does not mention the blood-vessels in his paper.

Schneider<sup>10</sup> quotes Langerhans, and adds the following observations of interest. He says (*loc. cit.*, p. 26): "Am oberen Ende entspringt von jedem Kiemenstabe eine (Taf. XIV. Fig. 2 v. b.) Kiemenvene welche bogenförmig ein wenig nach rückwärts verläuft und sich mit der Aorta verbindet welche jederseits unter der Chorda liegt. Die Kiemenvenen sind sehr dünnhäutig, man kann sie nur sehen, wenn sie mit Blut erfüllt sind. Die Aorten der Kiemengegend zerfallen in zwei Theilen. Der untere Theil liegt in der Falte welche die obere Branchialrinne seitlich begränzt, ihr Querschnitt ist spitzwinkelig, der obere Theil liegt in dem Bindegewebe welches der Chordascheide nach unten aufliegt und welche zu dem Gallertgewebe gehört. Die Aorta ist in der Kiemengegend doppelt, hinter derselben wird sie einfach bis in das Schwanzende. . . . Von der Aorta gehen dreierlei Zweige ab. 1. Arterien nach oben für die Muskeln der Leibeswand; 2. Arterien an der Innenfläche der Bauchhöhle. 3. Capillaren für den Darm. Obgleich die Zweige der ersten und zweiten Gruppe in ihren Verlauf den Arterien höherer Thiere gleichen, lassen sich doch Muskeln an ihnen nicht wahrnehmen. Von der ersten Gruppe entspringt je ein Zweig in einem Myocomma ungefähr in der Mitte desselben. Man kann ihn nach oben verfolgen bis über die Mitte der Chorda am weitesten in Kopftheile (Taf. XIV. Fig. 1, Ao. rechts). Die zweite Gruppe, die Arterien der Bauchhöhlenwand, entspringen an jedem Ligament und laufen auf der Innenkante des Ligaments nach unten. . . . Die der Mitte sich immer näherende Fortsetzung der rechten Aorta sich bis in die Spitze des Kopfes verfolgen lässt. Die linke Aorta verhält sich unregelmässig, sie geht in verschiedenen Exemplaren verschieden weit. . . . Auch Queräste sind vorhanden, welche beide Aorten verbinden. Wenn die linke Aorta früh verschwindet, liefern diese Queräste der rechten Aorta alle die Zweige, welche sonst der linken ausgehen würden."

According to Johannes Müller, the aorta in *Petromyzon* bifurcates a short distance in front of the anterior pair of gill sacs, anterior to the point of origin of the common carotid trunks, the two diverging limbs communicating on either side with the right and left common carotid trunks respectively. But in *Myxine* the aorta is continued to the anterior end of the notochord, and in fact extends by means of short

<sup>10</sup> Schneider, A. Beiträge zur Vergl. Anatomie u. Entwick. d. Wirbelthiere. Breslau, 1879.



terminal branches (e. g. palato-nasal) to the anterior end of the body, and there is no distinct bifurcation, the vessel, on the other hand, being gradually reduced by the numerous lateral branches given off after its passage through the circulus cephalicus. The aorta in *Myxine* is a relatively large vessel until it unites with, or, better, receives the two converging branches of the circulus, when it suddenly contracts, and from this point on is clearly much reduced. This portion of the canal still serves to keep open a direct passageway from the heart to the head, inasmuch as the arterial blood collected from the gills is not only forced upwards and backwards, but also forwards, into the continuation of the aorta, or *A. vertebralis impar*, and into the carotid arteries.

I think, from the evidence gathered in the foregoing paragraphs, that we are now in position to say definitely that between *Amphioxus* and the *Myxinoids* on the one hand, and *Chlamydoselachus* as a representative of the *Elasmobranchii* on the other, it is easy to establish a homology of parts surprising in its completeness. The entire dorsal aorta exists in *Chlamydoselachus*, imbedded in part, it is true, in the basis cranii, while in *Myxine* it lies in the connective tissue underneath the latter. The long ventral aorta in these two forms has been much shortened, but still *in showing traces* of its reduction claims a descent from an *Amphioxus*-like type. Of course we should not expect to find the ventral aorta persisting after the gills in front of it had ceased to be functional, and it might easily shorten before such reduction of the branchial apparatus had taken place, provided means were at hand to enable it to perform its function of pouring blood into the gills. The dorsal aorta, on the other hand, being a distributing trunk in a large sense, would be looked for so long as its territory existed and was not entirely supplied by new vessels; and as we know that its territory persists in all vertebrates, and greatly increases in extent among the higher forms, the latter alternative is the only one we need consider further. We find, on examination, that the recession of the heart is accompanied by the usurpation of the precardiac aortic territory by some of its lateral branches or their smaller offspring. While it is true in general that a reduction of the ventral aorta is followed by a reduction of the dorsal vessel, it is also true that the latter process takes place much more slowly, and for the reasons given above. The only indication of a persistence of the dorsal aorta in groups above the fishes, of which I have been able to find reliable account, is given by Goette.<sup>11</sup>

<sup>11</sup> Goette, Alex. *Entwicklungsgeschichte der Unke*. Leipzig, 1875.



His figures on Taf. XVII. Figs. 306, 317, and 316 *a*, *c*, of frontal sections from embryos of *Bombinator igneus* show that the aortic roots anastomose by means of transverse vessels, and that at an early stage of development there is an anterior (median) prolongation of the dorsal aorta between and beyond the aortic roots! How long this remnant persists is not stated by the author.

A series of transsections (see Figs. 5 *a* to 5 *g*) through the basis cranii of *Chlamydoselachus* in the regions designated below as **1**, **2**, and **3** (see Figure 1) gave the relations of the chorda and aorta to each other shown in the following table. The distances refer to measurements in the perpendicular to the long axis of the animal. The sections were taken from three portions of the basis cranii containing the structures cut from the vertebral junction, middle distance, and the pituitary region respectively, the last piece containing the whole of the "Sattellehne" and the pituitary space, with the foramina of entrance of the carotid arteries and the transverse canal.

#### TABLE OF RELATIONS OF CHORDA AND AORTA.

(*c* = chorda. *a* = aorta.)

**(1)** From the vertebral junction.

Section No. 1	{	<i>c</i> in middle of section.
		<i>a</i> below and entirely outside basis cranii.
" " 2	{	<i>c</i> , the same as No. 1.
		<i>a</i> , " " "
" " 3	{	<i>c</i> in middle of section.
		<i>a</i> inside cartilage, but on lower boundary.
" " 4	{	<i>c</i> in upper half.
		<i>a</i> in middle of lower quarter.
" " 5	{	<i>c</i> in upper half.
		<i>a</i> in middle of lower half.
" " 6	{	<i>c</i> in upper half.
		<i>a</i> in upper quarter of lower half.

**(2)** From this point on, the rise of the aorta is very gradual until the section from middle distance between occipital region and pituitary space is reached, when in

Section No. 1'	{	<i>c</i> in upper third of section.
		<i>a</i> in the middle of section.
" " 2'	{	<i>c</i> in upper quarter of upper half.
		<i>a</i> in middle of section.
" " 3'	{	<i>c</i> , the same as No. 2'.
		<i>a</i> , " " "
" " 4'	{	<i>c</i> , " " "
		<i>a</i> , " " "



Section No. 5'  $\left\{ \begin{array}{l} c \text{ in upper quarter.} \\ a \text{ in the middle third but above the middle.} \end{array} \right.$

From the middle region the chorda and aorta both rise until each breaks through the surface of the cartilage, the chorda to end in the calcareous incrustation of the cartilage, and the aorta to enter the pituitary space from the summit of the saddleback. Two sections from region

(3) gave in

Section No. 1''  $\left\{ \begin{array}{l} c \text{ on the upper surface of cartilage.} \\ a \text{ in upper quarter of upper half.} \end{array} \right.$   
 " " 2''  $\left\{ \begin{array}{l} c \text{ section in front of chorda end.} \\ a \text{ emerges from top of saddleback.} \end{array} \right.$

It will be seen from this table that the chorda occupies in the occipital region the middle of the cartilaginous plate of the cranial floor, and that from the end of the cone-shaped body, which was in the individual dissected about 1 cm. long, the thread remnant rises gradually but continuously until it reaches the inner surface of the floor of the cranium. This point, as the sections show, was *behind* the apex of the pituitary eminence (Sattellehne). Further, we find that the course of the aorta remnant is very nearly parallel with that of the chorda, and that it issues from the apex of the pituitary eminence in exactly the manner described by Gegenbaur for the chorda of other Elasmobranchs.

Gegenbaur<sup>17</sup> has investigated the subject of the chorda termination very thoroughly, and judging from the text and plates mostly by means of longitudinal section. There are several figures of cross sections of the basis cranii, showing the structure which he calls "Chorda," but which resembles the more ventrally placed aorta as I find it in *Chlamydoselachus*. As the author says, it is almost always a very difficult matter to determine the exact position and manner of the chorda termination in adult animals; much easier with young animals or older embryos. The author studied, among others, the genera *Acanthias*, *Heptanchus*, and *Centrophorus*. He says (*loc. cit.*, p. 121): "Die Chorda tritt mit ihrer Aufwärtskrümmung immer näher an die innenfläche der Schädelbasis und steigt dabei in der Sattellehne empor, welche sie dicht unter deren hinterer Fläche durchsetzt, um nahe an der Kante dieses Vorsprunges unter das Perichondrium zu treten. Wo die Sattellehne starke corticale Verkalkungen zeigt ist das zugespitzte Ende der Chorda noch in diese eingebettet. Fig. 7, Taf. XIV. gibt eine Darstellung dieses Verhaltens in einem 22 cm. langen *Acanthias* Embryo auf dem Medianschnitte. Beim ausgewachsenen

<sup>17</sup> Gegenbaur, C. Das Kopfskelet der Selachier. Leipzig, 1872.



Thiere ist derselbe Zustand vorhanden, doch ist die Chorda im Ver-  
 gleiche zum Basalknorpel bedeutend schwächer und die erweiterte Stelle  
 ist nur angedeutet. Das hervortreten des Chorda-Endes aus dem Ba-  
 salknorpel und die Lagerung unter dem bezüglichen Perichondrium hat  
 Köl liker bereits gesehen, jedoch nicht der sehr auffälligen Beziehung  
 zur Sattellehne sondern nur der Gegend der vor der Sattellehne gelager-  
 ten Hypophysis Erwähnung gethan: *In einigen Fällen sah ich das aus  
 dem Knorpel der Sattellehne hervortretende freie Ende der Chorda über  
 die Kante der Sattellehne nach vorn umgebogenen aber immer noch  
 unter dem Perichondrium verlaufend. So einmal bei einem 24 cm.  
 langen Embryo von Acanthias, aber auch bei einem grossen Exemplare  
 von Centrophorus granulosus. Obgleich ich noch vier Acanthias-Embryo-  
 nen darauf untersuchte, gelang es mir nicht, ein jenem ähnliches Verhalten  
 verbreitert zu finden.*"

In the genera Heptanchus, Hexanchus, Centrophorus, Acanthias,  
 Squatina, and Cestracion, the author traced the chorda dorsalis through  
 the basis cranii to the saddleback (Sattellehne) of the pituitary depression,  
 and found that the chorda remnant as regards shape, size, and position  
 was very much alike in Hexanchus and Heptanchus. This remnant was  
 in the form of an elongated conical body projecting into the occipital  
 region of the basis cranii, forming of course the anterior continuation of  
 the chorda in the vertebral column. From the apex of the cone was  
 given off a pale thread of considerable size, which ran forwards usually  
 parallel to the outer surface of the floor of the cranium. The arch  
 formed in approaching the pituitary space is much weaker in Heptan-  
 chus than in Hexanchus. In Cestracion behind the pituitary saddle-  
 back the chorda swells out into a spindle-shaped body, whose fibrous  
 sheath is filled with a cartilaginous tissue, containing numerous round  
 hyaline cells. The structure of this spindle-shaped body, so far as  
 Gegenbaur's description goes, agrees with that of the ventrally placed  
 aorta in Chlamydoselachus, and not with the chorda, though it does  
 agree with the chorda and its tubular enclosure in a very large (10 ft.)  
 individual of Heptabanchias.

With reference to the persistence of the chorda in the cranial floor,  
 Gegenbaur says (*loc. cit.*, p. 122): "Mit dem Nachweise der Fortdauer  
 eines Theiles der Chorda dorsalis im Cranium mancher Selachier ist für  
 diese ein niederstehendes Verhältniss aufgedeckt, nämlich die For-  
 setzung eines bei den meisten Abtheilungen der übrigen Vertebraten  
 bekannten embryonalen und damit vergänglichen Zustandes, der von den  
 ihn daurend besitzenden Formen her sich ableiten lässt. Aus jenen Ver-



halten ergibt sich jedoch noch ein anderes bedeutungsvolleres Moment, jenes, nämlich, welche den von der Chorda durchsetzten Abschnitt des Craniums in gleichen oder doch zunächst ähnlichen Beziehungen zeigt, wie sie die Wirbelsäule zur Chorda besitzt, so das darauf eine Vergleichung jenes Abschnittes des Craniums mit einem Abschnitte der Wirbelsäule sich stützen kann." And further, "Aus der vollen Würdigung dieser Beziehung von Gehirn und Nerven des hinteren Abschnittes ergibt sich der offene Gegensatz zum Vorderen Schädelraum, der von dem hinteren sehr verschiedene Gehirnthteile umschliesst und ebenso in den ihn verlassenden Nerven keinerlei Gemeinsamkeit mit den von Spinalnerven ableitbaren hinteren Nerven wahrnehmen lässt. Die Resultate der Vergleichung der einzelnen Abschnitte des Binnenraumes am ausgebildeten Cranium sind somit mit der Prüfung der Sonderungsvorgänge bei der Entstehung des Knorpelcraniums im Einklange."

To which if we add the weight of evidence afforded by the study of the vascular arrangements described in a previous paragraph, we have increased reason for the separation of the prechordal from the chordal section of the cranium. *For with this addition there is not a single important structure entering into the composition of the head which does not show traces of the originally distinct separation of these regions, now so closely united among all the higher vertebrates.*

Important in this connection is the relation of the chorda in *Bombinator igneus* figured by Goette, *loc. cit.*, Taf. IX. Figs. 164, 165, and 166, Taf. XV. Figs. 283 and 284, in which the author found the chorda dorsalis lying *below* the cartilaginuous cranium, although in intimate contact with it. After its degradation, which takes place in an early stage of development, this portion of the chorda is converted into a (keel-shaped?) calcareous crust, projecting from the ventral surface of the cranium. It is evident that in such a case the dorsal aorta could not become enclosed in the cartilaginous cranium, and in this fact we may have an explanation why a remnant of the aorta is not more uniformly found among the Elasmobranchs in general. It is important to bear in mind the condition of the head region before the cartilaginous cranium has been formed. In such a primitive animal, or at a corresponding stage in a more advanced form, the notochord, dorsal (and possibly ventral) aorta, digestive tract, and nervous cord extend through the head region, all parallel to the long axis of the body, and held in place by the connective tissue lying between them and whatever muscular and skeletal structures may be present. Branches from the nervous axis or the aorta easily find their way through the yielding tissue



to their destination.\* So long as the intervening spaces remain filled with loose connective tissue, all these spaces are eminently vascular and lymphatic. The need of greater strength and power of resistance in the skeletal axis calls for a solidification in and about the notochord, and upon the extent of the hardened area depends the nature of the enclosures. Usually, of course, the notochord forms the centre of the solidified tract, but we have just seen that it may lie on the ventral border of this tract. The structures transverse to the axis are partly enclosed in the solidified tissue, — the proximal portions in the case of the nerves, the proximal or distal in that of the blood and lymph vessels.†

The question of the homology of the carotid arteries has been touched upon by many morphologists, and although the subject has never attracted any very great attention, several explanations have been proposed at various times. The usual one found in our text-books on comparative anatomy and embryology was the result of determinations made by the earlier embryologists, Bischoff, Rathke, and others, of the ontogeny of the vascular system in mammalian and other embryos.

Kolliker's<sup>18</sup> account contains the whole matter in clear and concise form, and I shall quote his words as a statement of the generally accepted views. He says (*loc. cit.*, p. 915): "Die erste Form derselben (i. e. die Arterien) die gleich nach der Entstehung des Herzens und während der Dauer des Kreislaufes im Fruchthofe getroffen wird, ist die (Fig. 560. 1) dass das Herz vorn einen Truncus arteriosus entsendet der nach kurzen verlaufe in zwei Arcus Aortæ sich spaltet, die in der Wand des Kopfdarmhöhle bogenförmig nach der Gegend der späteren Schädelbasis und dann längs dieser convergirend nach hinten laufen, um anfänglich getrennt von einander als doppelte Aorta descendentes zu enden und später unter einander zu unpaaren Aorta zu verschmelzen. Sowie die Kiemenbogen . . . hervortreten, zeigt sich, dass der Anfang der Aortenbogen in den ersten Kiemenbogen liegt, sowie dass auch für die folgenden Kiemen-

\* These are the cranial and spinal nerves, the afferent and efferent branchials, and musculo-spinal arteries for the most part, all of which do not run parallel to the long axis.

† The blood-vessels are affected most by this process, and all except the important trunks rapidly atrophy, leaving as a last trace a fibrous cord imbedded in the solid cartilage.

<sup>18</sup> Kolliker, A. *Entwick. des Menschen*, etc. Leipzig, 1879.

<sup>19</sup> Rathke, H. *Entwicklungsgeschichte der Natter*. Königsberg, 1839.

<sup>20</sup> Rathke. Ueber die Entwicklung der Arterien welche bei Saugethieren von den Bogen der Aorta ausgehen. *Arch. für Anat. und Physiol.*, 1843.

<sup>21</sup> Rathke. *Entwicklungsgeschichte der Wirbelthiere*. Leipzig, 1861.



bogen neue Aortenbogen hervortreten. . . . Die bleibenden grosse Arterien gehen im wesentlichen aus den drei letzten Aortenbogen hervor, *doch erhält sich auch ein Theil des ersten und zweiten Bogens in der Carotis interna und externa.*

“Von den drei letzten bogen wird der vorderste (der dritte der ganzen Reihe) zum Anfang der Carotis interna, während der Carotis communis aus dem Anfange des ursprünglichen ersten Arcus Aortæ sich entwickelt. Von der Aorta thoracica und abdominalis hat Remak zuerst gezeigt das dieselbe beim Hühnerembryo anfänglich doppelt sind, indem die ersten Aortenbogen nicht vereinen sondern als sogenannte ‘primitive Aorten’ von der Wirbelsäule einander parallel bis zum hinteren Leibesende förtgehen. . . . Erst am dritten Tage verschmelzen diese ‘primitiven Aorten’ in ihren vordersten an der Wirbelsäule gelegenen Theile. . . . Hier sind die längstbekannten Arteriae vertebrales posteriores nichts anders als die ‘primitiven Aorten’ und stellen zahlreiche Figuren dieses werkes dieselben als paarige Gefasse am Kopfe und am Rumpfe dar. Die Verschmelzung dieser Gefasse . . . schreitet nach hinten fort.”

Important points in this consideration are (a) the double condition of the aorta in the developing mammal; and (b) the persistence of portions of the first and second aortic arches in the carotid arches.

More recently Macalister<sup>22</sup> has offered an explanation of the carotid arteries which does not harmonize with the facts as I find them, and I shall first quote his remarks, and then show wherein it appears that his conclusions are not tenable in the light of the comparative anatomy of the lower fish forms. He says (*loc. cit.*, p. 193): “The arrangement of the blood-vessels in the adult forms of the lowest, and in the embryos of the higher vertebrates, indicates that the history of the complicated vascular system of the higher forms has been one of a development from a simple and regular ancestral condition of metameric and intermetameric vessels, through easily defined stages, to the more confused and irregular condition of the arterial system in the adults of the higher forms. . . . In the whole organism the vessels would thus form a double series, two longitudinal ventral trunks, two corresponding dorsal trunks, and the lateral uniting trunks in each segment. There are two primitive dorsal vessels in vertebrate embryos, and their fusion can be traced in the chick beginning at the forty-second hour of incubation. This union commences behind the head, and travels backwards rapidly,

<sup>22</sup> Macalister. The Morphology of the Arterial System in Man. Journ. Anat. and Physiol., XX., 1886.



so that after the fifth day there is but a single dorsal vessel for the middle and the hinder part of the body, — the dorsal aorta. In the region of the head and neck of mammals, *the foremost ends of the two vessels remain permanently separate as the internal carotid arteries.* [Italics mine.] . . . There were also originally two ventral longitudinal vessels, but their union probably occurred even earlier than that of the dorsal. . . . The setting apart of one portion of the single ventral vessel to form the heart differentiates the pre- from the post-cardiac portions of the ventral vessel. As a consequence of the cardiac differentiation, the only places where complete metameric arcades remain are the precardiac segments. . . . Behind the heart in higher vertebrates a series of vessels extend from the dorsal aorta through the mesogastric fold, and end in the splanchnopleure; these correspond to the dorsal extremities of the postcardiac lateral metameric arcades. With the condensation of the anterior segments which takes place in the formation of the skull, all distinct vascular metamerism is lost, and the anterior segmental arches become displaced backward or lost. The common and external carotids are continuations of the ventral aorta, while the root of the internal carotid is the altered relic of the third arch, and the ascending continuation of that vessel is the upper part of the dorsal aorta. . . . The only carotid branches which in any way represent rudimental arcades are the occipital and posterior auricular arteries. . . . The cervical dorsal aorta (internal carotid) has only rudimental branches in the neck, represented by the intercarotid ramuli. Its intracranial continuation gives off three lateral neural branches, the posterior, middle, and anterior cerebrals (the first originally being a carotid branch, its root being the so called posterior communicating, but its anastomotic internal branch, which joins the median anastomosis, dilates so as to form its functional root). The ventro-lateral branches are reduced and modified as tympanic, vidian, receptacular, and ophthalmic branches.”

As the foregoing quotations show, Macalister tacitly assumes that the double nature of the dorsal vessel in mammalian embryos is comparable with that of some vermian type. He claims that the anterior ends of the double dorsal vessel are transformed into the internal carotid arteries of the adult, which is certainly true, but not in the sense our author intends it, as appears from the context, for he says further on, that the root of the internal carotid is the altered relic of the third arch. These views were, I believe, first expressed by Allen Thompson<sup>26, 27</sup> in 1831,

<sup>26</sup> Thompson, Allen. The Development of the Vascular System. New Phil. Journ., Edinburgh, 1831.

<sup>27</sup> The same. Quain's Anat., 9th ed., II., 1882.



who also claims to have discovered the facts on which they were based. Surprising is the statement that the external carotids are the continuations of the ends of the anterior bifurcation of the ventral aorta.

It is not possible at the present time to prove beyond doubt that the ancestor of vertebrates possessed only a single dorsal vessel; but the best evidence at the present time (the anatomy and development of the higher worms, and of those vertebrates retaining most of the ancestral features) points to an ancestral form having a single median dorsal vessel.

The embryological evidence cited by Macalister in support of his views, is interpreted by Balfour, Gegenbaur, Kolliker, Hertwig, and others, to be the effect of the shortening of the period of development, the suppression of some of the stages and the adaptation to peculiar embryonic environment.

In passing over the intermediate stages between the fish and mammal, our author has lost sight of the homologies of the vessels he deals with, and, so far as his account runs, has not seen the precardiac aorta in any vertebrate, but considers the two common carotid trunks to represent the pair of aortæ which his theory calls for.

The evidence which I have presented in the preceding pages shows beyond question that the carotid arteries, instead of being derived from the aorta or any of its branches, are derived from the commissures which serve to connect the efferent branchial arteries with one another. The bifurcated end of the aorta in the bird and mammal is only a remnant of a previous complicated vascular apparatus. It is likewise obvious that the carotid vessels cannot strictly be said to arise from, or constitute the remains of, any particular pair of aortic arches, but represent all that is left of the commissural trunk from the most anterior arch of the ancestral form to the most anterior arch of any given existing form.

About the time Macalister's paper on the homology of the blood-vessels of man appeared in England, T. J. Parker, working in New Zealand, published a paper in the Philosophical Transactions on the vascular system of *Mustelus antarcticus*, in which he advances decidedly interesting views as to the homology of the carotids of this southern shark. In the first place, Parker proposes to establish the terminology of these vessels on a scientific basis, and as the result of his studies objects to the use of the terms "internal" and "external" to designate the anatomical relations of the carotids as really misleading. He would substitute and use exclusively throughout vertebrates the terms "anterior" and "pos-



terior,"\* as correctly describing the morphological relations of the vessels. Now, in as far as the terms are applied to the carotid arteries of the higher vertebrates as *names simply*, it matters little which set is used; but when it is proposed to select terms that shall harmonize with the development of the vessels † under consideration, *superior* and *inferior* are undoubtedly the correct ones, or dorsal and ventral.

In the light of Chlamydoselachus we may reasonably choose to retain the terms internal and external as describing at the same time the primitive condition of the vessels in the lowest vertebrates, and, when we consider the relations of the vessels to their territory of distribution (their only *constant* relation), and not alone their origin (in the anatomical sense) and source of supply (their constantly *varying* relation), also their anatomical relations up to and including man. The vessels are really never anterior and posterior so far as their points of origin are concerned, and this, as I understand it, is the basis of Parker's determination. As shown above, in primitive forms (e. g. Amphioxus and Myxine), the region supplied by the internal carotids in Acraniates and Craniates is provided for by branches from the superior portion of the curve of the first pair of aortic arches. The carotids arise from the dorsal prolongations of the aortic roots; i. e. from the tract homologous with the superior commissures of Elasmobranchs, and not, as Macalister and others suppose, the anterior ends of the two lateral aortæ on the one hand, or the corresponding parts of the ventral aortæ on the other. The carotid arteries are, in a strict sense, separated from the aorta by the vessel crossing the space between the dorsal end of the gill and the aorta which lies in the middle line. This vessel is equal to the dorsal portions of the efferent branchial arteries (or the entire epi-branchials of Parker). It is because the inferior commissures are merely passageways for the transmission of blood to the distributing vessels in the dorsal region of demand, that they do not persist, since their function is early assumed by other vessels. As the aorta is gradually reduced by the backward journeying of the heart consequent on the reduction of the branchial vessels and organs, the brain and the enclosing head are removed farther and farther from the aortic arches from which they originally received their blood supply direct, by means of

\* Parker's A. carot. post. = Art. carot. int.

" " ant. = eff. br. art. of mandibular gill, and *both* these vessels supply the region of the external carotid in sharks.

† Cf. Rathke (20) or Balfour (24). Comp. Embryol., II., 1881. I refer here to the development in the higher vertebrates.



numerous small twigs, and the aortic roots plus the superior commissures increase in importance with the retreat of the heart. In the Mammalia, where the aortic roots are reduced to the greatest extent, there is a very great variety in the manner of origin of the carotids from the aorta, or, in other words, the primitive relation of the carotid trunks to the median aorta has undergone a variety of transformations that for the most part are characteristic of the groups in which they are found. They remain as a pair of lateral longitudinal vessels, each of which almost universally divides into two branches, a dorsal and a ventral. The dorsal supplies the structures contained in the cranium, and gives off vessels into the orbital space; it is the internal carotid. The ventral branch supplies the visceral portion of the head and the cranial parietes, at least in part; it is the external carotid artery. The external carotid is then only a ventral branch of the dorsal commissural trunk, while the internal carotid continues the main stem of the common carotid. Of course, the relative sizes of the vessels undergo ceaseless variations as we ascend the series; but the rule is, that the higher the position of the animal in the series, the more important relatively the territory supplied by the external carotid becomes. For example, in man the two vessels, internal and external, are of about the same size; in the cat, the internal is small and the external correspondingly large. The two vessels may be united into a common trunk, and always are when the aortic arch from which they arise is much reduced, or they may arise independently of one another, as in *Myxine*. So long as the dorsal aorta persists entire, the carotids have no existence; but just in proportion as the precardiac section of the aorta is reduced, the carotid arteries become more and more important, until they ultimately entirely replace it, as in the vertebrates above the lower fishes. In *Myxine*, "Aus dem Zusammenflus der Kiemenvenenstämmen entstehen vier Hauptarterienstämmen für den Körper, ein vorderer und hinterer unpaarer mittlerer, welche unter der Wirbelsäule hingehen, und zwei seitliche vordere. Die vorderen Theile des Körpers besitzen also zwei Carotiden und eine unpaare Wirbelarterie [i. e. precardiac Aorta] die hintern Theile des Körpers einen einzigen Arterienstamm, die Aorta descendens. Die Kiemenvenen der zwei oder drei letzten Kiemen gehen direct in die nach vorn und unten gleich sich verlängernde Aorta. Die Kiemenvenen der ersten oder zwei ersten Kiemen gehen nicht mehr in die Aorta über, sondern vereinigen sich jederseits in eine der Aorta parallele vena branchialis communis, welche sich nach vorn als Carotide fortsetzt. Die directe Fortsetzung der Aorta nach vorn, verläuft als arteria vertebralis



impar dicht unter der Chorda und versieht die Seitenmuskeln, das Rückgrath und Rückenmark mit zweigen. Die Carotiden begleiten die Speiseröhre und geben, ihren Seiten angewachsen, Zweige an sie ab. Hinter dem Kopf theilen sich die Carotiden in zwei Aeste welche eine Carotis externa und interna auf jeder Seite entsprechen. Die äusseren Carotiden vertheilen sich in dem Kopfmuskeln und in der Lunge. Die beiden inneren Carotiden verbinden sich bogenförmig unter dem Anfang des Rückgraths. Aus diesem bogen; der auch von hinten das ganz dünn gewordene Ende der unpaaren Wirbelarterie aufnimmt, entsteht nach vorn ein unpaarer starker Stamm. Dieser stellt gleichsam eine unpaare Wirbelarterie des Kopfes dar, er verläuft unter der Wirbelsäule über dem Schlund nach vorn, dann unter der Basis des Hintersehädels und senkt sich, da wo der Basis häutig wird, in der Mitte in die Tiefe, wahrscheinlich die Hirnarterien abgebend, indem er zugleich an dieser Stelle gabelig zwei dünnere Aeste ausschickt, welche divergirend zur Seite des Nasengaumenganges neben den Knorpeligen seitlichen Gaumenleisten nach vorn weitergehen und dadurch in den Stand gesetzt werden wahrscheinlich den Nasensack mit Zweigen zu versehen."

The cephalic circle is complete in only a few forms (Myxinoids, Petromyzon, and the lowest Elasmobranchs). Among the Rays, Sturgeon (and all cartilaginous Ganoids?), and Chimæra, it is incomplete in front. But in *every* vertebrate except Amphioxus the internal carotids have their ends united by anastomosis within the *pituitary space* (Figures 14 and 4 b) usually, but always in this cranial region.

Referring to the anastomotic branch between the hyoidean efferent artery and that from the first branchial arch, Parker suggests that the union thus brought about is entirely a secondary condition, and that the true efferent trunk of the hyoidean gill is to be sought in the posterior (internal) carotid artery. He says (p. 690): "From the above considerations, one is led to look upon the connection of the first (hyoidean) efferent artery with the first epibranchial artery as a secondary one, and it then becomes a matter of considerable interest to find in *Mustelus antarcticus* distinct remains of the dorsal portion of the hyoidean aortic arch, and of its connection with the dorsal aorta. From the dorsal end of the first efferent branchial artery arises a large vessel, the posterior carotid artery. This trunk passes forwards and inwards ventrad of the proximal end of the hyomandibular, to the ventral surface of the auditory capsule, and through a foramen in the skull floor to the orbit. Its further course will be described hereafter; the point of interest for the present purpose is, that shortly before entering



the foramen just mentioned [see Fig. 12] at the point  $x$  in Fig. 12, it gives off a very slender vessel,  $y$ , which passes backwards and inwards along the ventral aspect of the skull and vertebral column, and joins with its fellow of the opposite side to form a delicate longitudinal median trunk,  $z$ , which is continued backwards to the junction of the first pair of epibranchial arteries. I think that there can be no doubt that the posterior carotid artery, from its origin to the point  $x$ , together with its backward continuation,  $y$ , represents the dorsal portion of the hyoidean aortic arch, or hyoidean epibranchial artery, the altered direction of the vessel being accounted for by the changed position of the hyoid arch. The middle trunk,  $z$ , is as obviously the actual anterior portion of what may be called the interhyoidean section of the dorsal aorta. It has clearly nothing to do with the *arteria vertebralis impar* of Myxinoids, which it resembles at first sight, since the latter is a secondary forward prolongation of the aorta altogether cephalad of the gills. As this anterior portion of the dorsal aorta undergoes complete atrophy — if indeed it ever exists — in the Rays as well as in the Holocephali, it is a matter of some interest to find it persisting in a typical Selachian, and one is led to inquire whether it is actually absent in those two forms the arteries of which have been described, or whether it has hitherto been overlooked. I can only say that I have failed to find any mention of it." Parker does not give the title of Hyrtl's <sup>3</sup> important paper in his list of literature, and makes no reference to it anywhere in his text. Presumably, then, he had at least no knowledge of its contents, or he would certainly have greatly modified the paragraph just quoted. In *Chlamydoselachus*, the arteries described by Parker for *Mustelus* are present as a strong pair of vessels diverging from the anterior end of the vertebral portion of the precardiac aorta, curving outward until they reach the internal carotid trunk, into which they open, some distance behind the internal carotid foramina. The fusion takes place even before the internal carotids begin to curve inwards toward the median line. Parker's conclusion, that the posterior carotid to the point  $x$  and the small vessel  $y$  form the hyoidean epibranchial artery is clearly untenable when applied to the more primitive *Chlamydoselachus*.

Parker's argument, that the unpaired aorta formed by the confluence of the vessels  $y$  is not comparable with the *arteria vertebralis impar* of Myxinoids as described by Müller, is I think insufficient, since we know nothing of its developmental history to enlighten us as to its origin and manner of growth, and the adult condition of the vessel cer-



tainly allows the inference that it is a reduced primitive dorsal aorta, — the exact homologue of the dorsal aorta of any vertebrate possessing the precardiac section.

In studying the course of the blood in the vessels of *Chlamydoselachus*, we find that the complete ellipse formed by each efferent branchial artery in the majority of Elasmobranch\* species is wanting, and a single trunk collects the blood from all the gill leaflets borne by an arch, and consequently from one side only of any given gill sack. This is the primitive condition, and from Dohrn's researches we know that it is entirely in agreement with the embryonic structure of most of the Teleost and Elasmobranch embryos studied. It also agrees with the adult condition of *Amphioxus*. Parker very justly takes exceptions to the current use of the term "branchial vein," as applied to an efferent branchial vessel, and I quite agree with him when he says respecting the nature of these arteries (*loc. cit.*, p. 688): "These vessels are usually, but very incorrectly, called *branchial veins*. It would be quite as justifiable to speak of the *portal artery* as to call these obviously arterial vessels veins; a capillary system may be interposed in the course of an artery or of a vein, but this does not make the efferent trunk in the one case a vein, nor in the other the afferent trunk an artery." The collecting trunk is continued uninterruptedly to the dorsal aorta, so that an epibranchial artery in Parker's sense is not present in *Chlamydoselachus*. He says (*loc. cit.*, p. 689): "From the dorsal end of each arterial loop an epibranchial artery is continued backwards and inwards (Fig. 11); by uniting with one another successively in pairs these four trunks form the dorsal aorta. . . . In the embryo the aortic arches are continued directly from the ventral to the dorsal aorta. In the Holocephali and Teleostei there is only one efferent artery to each gill, corresponding to the anterior of the two efferent arteries in the Plagiostome holobranch. This is very evident in *Callorhynchus*, in which the single efferent artery of each gill is always cephalad of the corresponding afferent trunk. These facts tend to confirm the opinion to which one is led by the simple inspection of the parts in the adult *Mustelus* (compare *loc. cit.*, Figs. 6 and 17); namely, that the anterior efferent artery of each holobranch is to be looked upon as its primary revehent trunk and as strictly continuous with the corresponding epibranchial artery, the posterior efferent artery being a secondary vessel which debouches not into the primary trunk of its own, but into that of the next following gill." Such are Parker's conclusions from the study

\* Cf. Hyrtl, *loc. cit.*, p. 4, and Parker (4) and (7).



of the anatomy of an adult *Mustelus*. As a result of his studies of the embryological history of the efferent arteries in *Pristiurus*, Dohrn<sup>24</sup> (page 3) establishes Parker's conclusions in a very complete and interesting manner.

Goette's account of the relations of the developing carotids in the embryos of *Bombinator* is as follows: "Bevor jedoch die Aorta vollständig angelegt ist, entwickelt sich eine neue besondere Verbindungsbahn zwischen den ersten Aortenbogen und der Aortenwurzel. Die Carotis hat sich nämlich schon während der Entwicklung des zweiten Aortenbogens bis an das Wurzelstück des ersten Wirbelbogens verlängert, unter welchem sie in die Sattelgrube eintritt, um von dort aus sich in zwei Aeste fortzusetzen. Der vorderen verläuft als ihre gerade Fortsetzung jederseits an der anatomischen Hirnbasis nach vorn wobei er durch das Austrittsloch des Sehnerven eine A. ophthalmica abgibt; der andere Ast (*R. communicans carotidis posterior*) steigt aus der Sattelgrube gerade auf und umgreift dem Vorderhirn dicht anliegend, dessen Basaltheil oder den Hirntrichter bis an seine Oberseite, wo er in dem sogenannten mittleren Schädelbalken Rathke's eingebettet ist. Von dort aus geht unser *R. communicans* in die Basalarterie seine Seite über, welche alsdann auch eine hintere Fortsetzung im Rückenmarkskanal besitzt sowie diese ihre Fortsetzungen unter dem Hirn und Rückenmark allmählich zusammenrücken, und sich endlich zum unpaaren medianer Stämme vereinigen, erscheint dieser als Zusammenfluss jener nach hinten konvergirendere Karotidenzweige. Die beiden primitiven Wirbelarterien und ihre noch getrennten vorderen Fortsetzungen, die Basalarterien, bilden also jederseits die hintere Hälfte, die inneren Karotiden mit ihren hinteren Verbindungszweigen die vordere Hälfte eines cerebralen Gefässbogens welche dem extracraniellen Herz-Aortenbogen gleichsam von oben aufgesetzt ist . . . so hört es bald noch zu ende der ersten Larvenperiode ganz auf, indem die primitiven Wirbelarterien verschwinden und ihrer Gebiet ganz den Carotiden überlassen (Taf. XXI. Fig. 377)."

The mandibular gill remains in a rudimentary condition, called in the Elasmobranch group spiracular gill or pseudobranch; in the Teleosts, on the other hand, the choroid gland (Balfour,<sup>25</sup> Müller<sup>6</sup>). It is not always present in Teleosts, according to the latter authority, but where it is developed its branches supply the choroid plexus of the eye. The artery of

<sup>24</sup> Dohrn, A. Die Entwicklung und Differenzirung der Kiemenbogen der Sela-chier. Mitt. Zool. Stat. in Neapel., V., 1884.

<sup>25</sup> Balfour, F. M. Comparative Embryology, II. p. 261.



1. bryo of existing Elasmobranch.	Ancestral Form.	(Notidanidae?) Chlamydoselachus.	Mustelus (after Parker).
1st aortic arch.	A. branchialis $x + 1$ .	Two lateral branches from the aorta into pituitary space.	Commissure $w$ (?) anterior carotid artery + pseudobranchial artery = mandibular efferent branchial arteries.
2d aortic arch.	A. branchialis $x + 2$ .	The continuations of the internal carotid into pituitary space.	
3d aortic arch.	A. branchialis $x + 3$ .	The anastomotic branch from the common carotid to the dorsal aorta = <i>mandibular</i> eff. br.	
4th aortic arch.    Hyoidean.	A. branchialis $x + 4$ .	The <i>hyoidean</i> efferent branchial artery.	Vessel $y$ ; posterior carotid artery from origin to $x + 1$ st afferent and 1st efferent branchial arteries.
5th aortic arch.    1st branchial.	A. branchialis $x + 5$ .	1st branchial (efferent) artery.	1st epibranchial artery + 2d afferent, and 2d and 3d efferent arteries.
6th aortic arch.    2d branchial.	A. branchialis $x + 6$ .	2d efferent branchial artery.	2d epibranchial artery + 3d afferent, and 4th and 5th efferent branchial arteries.
7th aortic arch.    3d branchial.	A. branchialis $x + 7$ .	3d efferent branchial artery.	3d epibranchial artery + 4th afferent, and 6th and 7th efferent branchial arteries.
8th aortic arch.    4th branchial.	A. branchialis $x + 8$ .	4th efferent branchial artery.	4th epibranchial artery + 5th afferent, and 8th and 9th efferent branchial arteries.
9th aortic arch.    5th branchial.	A. branchialis $x + 9$ .	5th efferent branchial artery.	



the choroid gland comes from the hyoidean demibranch (Nebenkieme). The gland usually lies within the bony orbit, and with very few exceptions it is present in those species possessing a pseudobranch (i. e. in this case of course the hyoidean demibranch or its rudiment). The mandibular pseudobranch of Elasmobranchs and Ganoids lies behind the orbital territory, but there are cases in which an evident approach to the orbit is recognizable. The vessels of the mandibular pseudobranch consist of an afferent and an efferent artery, as in the perfect branchiæ, but usually they are shifted in position, so as to run more or less parallel to the long axis of the body, instead of transverse, as in the normal condition. The afferent trunk leaves the hyoidean efferent branchial just before the latter leaves the arch and passes forwards to end in the rete mirabile of the spiracular gill, while the efferent trunk arising from the rete passes forwards and inwards across the hind portion of the orbit into the cranial cavity, where it unites with the dorsal aorta by an anastomosis with the internal carotid, near the origin of the ophthalmic artery. The homology of the mandibular artery of *Callorhynchus*, as given by Parker, involves a mistaken identity, as we readily perceive by referring to the author's own works on the Skate and *Mustelus antarcticus*, as well as by reference to figures by Hyrtl (3) and Müller (6). It seems to me clear that the vessel designated *posterior carotid* by Parker is the *arteria vertebralis*.

It is of course possible that the *arteriæ vertebrales* of the Skate are a pair of musculo-spinal branches of a now vanished dorsal aorta, but from their prominent connection with the first efferent branchials of the Skate it is more probable that they are reduced efferent branchials — of the mandibular gill? The relations of the afferent and efferent vessels to the spiracular gill in *Chlamydoselachus* — a few leaflets of which still persist — I have not worked out satisfactorily as yet.

There are traces of other lateral branches to be found in the cartilage at either side of the aorta, between the occiput and pituitary prominence. In two sections I saw lateral unpaired vessels passing out from the median line to fade out in the cartilaginous tissue which appeared to be the cause of their suppression. Heptabranchias shows similar vessels. (See Figure 9.) They are so short and indistinct that it is with difficulty they can be traced without entirely destroying the cartilaginous floor of the skull in shaving it down thin enough to see them. The microscopic sections prepared from one of these transsections showed only a fibrous cord entirely destitute of a cavity. Presumably then the vessels were functional only during embryonic life. There is



a bare possibility that these vessels may have been the musculo-spinal branches of the segments taken into the cranium.

To the characters which Garman has selected as of value in properly placing *Chlamydoselachus* in the zoölogical system may be added : —

1. The dorsal aorta persistent throughout the entire length of the chorda, its precardiac portion of large size to the occipito-atlantal line, where it is suddenly much reduced to enter the cartilaginous basis cranii, through which it runs below and nearly parallel with the chorda, until it reaches the pituitary region, when it rises abruptly and becomes in part suprachordal, ending in a vascular plexus.

2. The absence of a complete vascular loop surrounding each gill slit, ending above in two efferent branchial arteries. *Chlamydoselachus* has but a single efferent branchial, placed in each instance cephalad of the corresponding afferent vessel, agreeing in this with the usual type of structure found in embryos of other Elasmobranchs.

There are several other characters belonging to other portions of the vascular system, of equal importance with the foregoing, indicative of simple organization, which we may take up at some subsequent date.

The character supposed by Müller to be diagnostic of the Cyclostomes, namely, that the dorsal aorta was continued beyond the union of the first pair of persisting efferent branchial arteries, and that it was still further connected with the anterior portion of the cephalic circle (in *Myxine*), is not alone peculiar to this group of fishes, but is also found among several Elasmobranchs. It still remains to be seen whether it is absent in all the bony fishes (including the Ganoids). If so, it would serve to show that the Cyclostomes and lower Elasmobranchs have retained their vascular apparatus in a much more primitive condition than the remaining groups. Müller did not find any trace of the precardiac aorta in *Sturio*, and from his description of the efferent branchial system it is extremely improbable that it exists in any form.

P. S. — The substance of this paper was written out in nearly its present form in the fall and winter of 1887, at which time the dissections were made, but circumstances have delayed the publication till this date.

AUGUST 1, 1889.



## EXPLANATION OF FIGURES.

## REFERENCE LETTERS.

- a.* artery (in Fig. 2, also auricle).  
*a. c.* arcus cephalicus.  
*a. i.* anterior innominate artery.  
*an.* anastomotic branch of first efferent branchial artery.  
*a. pl.* artery connecting pituitary plexus with hypophysis plexus.  
*b. a.* bulbus arteriosus.  
*br.* brachial vein.  
*c.* cranial aorta (in Fig. 7, the cavity of this vessel).  
*c. a.* conus arteriosus.  
*c. c.* anterior carotid commissure (art. com. ant. D. S.).  
*cent.* vertebral centrum.  
*ch.* chorda dorsalis.  
*cæ. mes.* cœliaco-mesenteric artery.  
*cor.* coronary artery (+ hypobranchial trunk).  
*c. p.* art. profunda cerebri.  
*c. p. a.* posterior carotid commissure (art. com. post. D. S.)  
*c. c.* cardinal sinus.  
*c. sh.* chorda sheath.  
*ct.* cartilage of the basis cranii, *c'*, *c''*, *c'''*, three layers of basis cranii.  
*ct. sh.* cartilaginous sheath of chorda and cranial artery.  
*c. v.* cardinal vein.  
*d.* dorsal aorta (posterior to *k*).  
*d. m.* dura mater.  
*e. c.* external carotid artery.  
*e. ex.* elastica externa of notochord.  
*g.* median groove in ventral surface of basis cranii.  
*H.* Hyoid arch.  
*h. v.* hepatic vein.  
*hy.* hypophysis.  
*i. c.* internal carotid artery.  
*i. c. f.* internal carotid foramen.  
*i. j. v.* inferior jugular vein.  
*k.* cephalic aorta. Kopfaorta, arteria spinalis impar Hyrtl, arteria vertebralis impar Müller.  
*kl.* calcareous incrustation.



<i>m.</i>	muscle.
<i>me.</i>	membraneous wall overarching <i>c</i> near its anterior end.
<i>m. s.</i>	arteriæ musculo-spinales.
<i>ms.</i>	arteriæ musculo-spinales of the head.
<i>n.</i>	nasal artery.
<i>n. p.</i>	neural process.
<i>o.</i>	ophthalmic artery.
<i>p.</i>	palatine artery (= maxillary of Parker).
<i>p. c. e.</i>	art. post. cerebri ext. D. S.
<i>p. c. i.</i>	art. post. cerebri int. D. S.
<i>p. c. s.</i>	precaval sinus.
<i>p. pl.</i>	pituitary plexus.
<i>pt.</i>	pituitary space.
<i>r. c.</i>	subdural rete mirabile.
<i>r. c. v.</i>	right cardinal vein.
<i>r. p.</i>	rete mirabile profunda cereori D. S.
<i>s. cl.</i>	subclavian artery.
<i>s. j. v.</i>	superior jugular vein.
<i>sp.</i>	anastomosing branch to spiracle.
<i>s. v.</i>	sinus venosus.
<i>tr.</i>	tropeic vein = lateral abdominal vein.
<i>tr. b.</i>	fibrous trabeculæ crossing the channel of <i>c''</i> .
<i>tr. c.</i>	transverse canal of pituitary region.
<i>tr. p.</i>	transverse process.
<i>v.</i>	ventricle.
<i>v. a.</i>	ventral aorta.
<i>vasc.</i>	vascular layer.

I.-IX. First to ninth pairs of aortic roots (arches).

1-6. First to sixth pairs efferent branchial vessels.

1'-6'. First to sixth pairs afferent branchial vessels.

1''-5''. First to fifth visceral arches.

Fig. 1. A sketch of a dissection of the efferent branchial vessels and the resulting aorta of *Chlamydoselachus anguineus*, natural size. On the right of the figure the vessels are sketched in the outline of the roof of the mouth, to the point of emergence from the tissue surrounding the proximal ends of the gill arches indicated on the left oval outlines. The left internal carotid artery is not shaded, and is sketched for a short distance only to show its course in the chiasm, at which point the cephalic aorta is broken for the sake of clearness. The end of the cranial aorta, and its branches connecting it with the pituitary plexus, are drawn somewhat enlarged.

Fig. 2. A semidiagrammatic figure of a portion of the vascular system of the same fish, showing the relations of the arterial and venous vessels, as seen from the left side. Approximately natural size. At \* the coronary artery is cut off, nor are many of its branches shown. The venous vessels, heart, and ventral aorta are left unshaded. The common and internal carotids have been displaced upwards, and the anastomotic branch broken for sake of clearness.



Fig. 3. A sketch of the left half of the hemisected cranium of *Chlamydoselachus* to show the relations of the notochord and cranial aorta to the basis cranii and to the pituitary prominence and space. Natural size.

Fig. 4. (a) A view of the inner surface of floor of the cerebral cavity in the pituitary region before the removal of the dura mater and tissue which separates the brain cavity from the pituitary excavation and its contents (pituitary plexus, transverse canal, and carotid chiasm). Natural size. (b) A dissection of the ventral surface of the same, to show the chiasm of the internal carotids.

Fig. 5. A series of seven transsections of the basis cranii to show the relations of the notochord, cranial aorta, and the median ventral groove to each other and to the cranial floor.

Figs. 5a and 5b from **1** shown in Fig. 1. Figs. 5c and 5d from **2**; Fig. 5e from **3**; Figs. 5f and 5g from the pituitary prominence. All the figures enlarged. The series progresses cephalad, and the geometrical outlines refer to portions of the median line of Fig. 1.

Fig. 6. Part of the section of the notochord figured in 5a more highly magnified to show the sheaths and external calcified layer.  $\times$  circa 180 diameters.

Fig. 7. A section of the cranial aorta from Fig. 5d, more highly magnified. The fibrous trabeculae cross the cavity of the vessel in all directions.  $\times$  180 diameters.

Fig. 8. A transsection of the basis cranii of *Chlamydoselachus*, near the vertebral articulation, to show the figure made by the calcareous sheath (and its processes) of the notochord, resembling a vertebra of the trunk region.

Fig. 9. A transversely cut piece from the basis cranii of *Heptabranhias* sp. near the anterior third of the distance between the pituitary prominence and the occipital region, to show the chorda (and aorta?) and the blood-vessels enclosed in the cartilage.

Fig. 10. The efferent branchial system and aorta of *Zygæna malleus*, after Hyrtl.

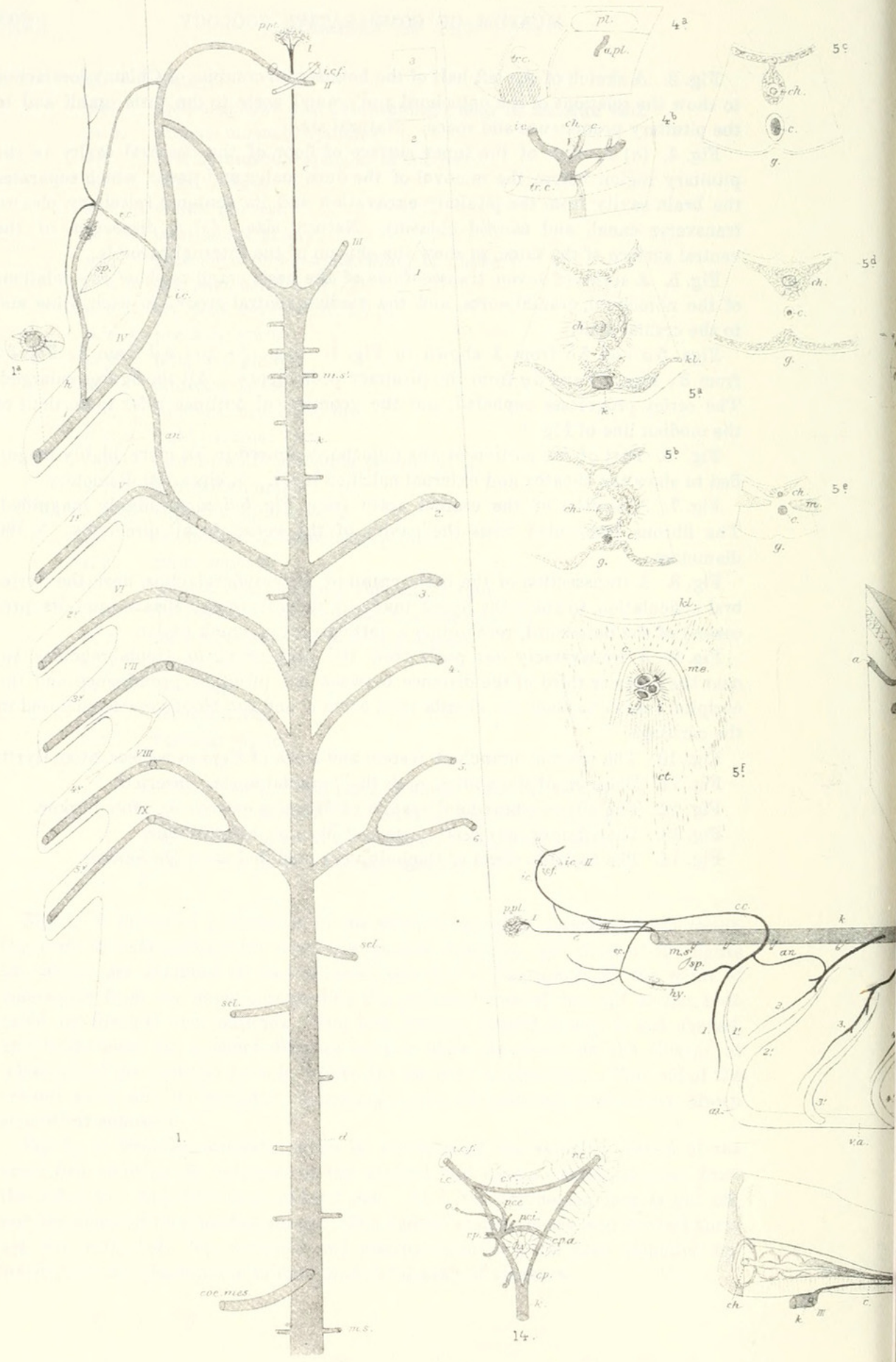
Fig. 11. Diagram of the above, with the "cranial aorta" inserted.

Fig. 12. The efferent branchial system of *Mustelus antarcticus*, after Parker.

Fig. 13. The efferent branchial system of *Myxine*, after Müller.

Fig. 14. The cephalic circle of *Cephaloptera* modified after De Sanctis.









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