ARE THE POLAR AND TRABECULAR CARTILAGES OF VERTEBRATE EMBRYOS THE PHARYNGEAL ELEMENTS OF THE MANDIBULAR AND PREMANDIBULAR ARCHES?

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It is, I believe, now generally accepted that the visceral clefts of the gnathostome vertebrates are intersegmental in position, and that the most anterior somite is the premandibular. Each somite of the region where these clefts occurred must accordingly have lain, primarily, directly dorsal to the related arch, and that part of the axial skeleton developed in relation to that somite must have lain directly dorsal to the skeletal bar developed in the arch. The presence of a premandibular somite strongly suggests a premandibular arch related to it, and there must inevitably have been such an arch if the present mouth has been developed from a pair of mandibular clefts.

The skeletal bars of all these arches, with the possible exception of the premandibular, must have lain, primarily, transverse to the axis of the body, and each of them must have lain directly internal to the artery of the related arch. They probably did not extend upwards as far as the longitudinal aortic vessel into which the efferent arteries fell, but had they extended to it, lying as they did internal to the efferent arteries, they would have passed internal (ventral) to it, as the second pharyngobranchials actually do in both Amia and Hyodon (Allis, 1897, fig. 55, Pl. 35 and 1919, fig. 7, Pl. 21).

In later stages of phylogenetic development, the arches became inclined to the axis of the body, and in the branchial region of the gnathostome fishes two distinctly different forms of arch arose, a sigma-shaped one, in which the pharyngobranchials project postero-mesially, and a V-shaped one, in which those elements of the arches project antero-mesially, the former form of arch being found in all of the recent Elasmobranchii, and the latter form in the Teleostomi and Dipnoi.

In the adults of the recent Selachii, where the sigma-shaped arch is found, the dorsal end of the epibranchial in each of the more anterior arches is somewhat expanded, the posterior corner of this end giving articulation to the pharyngobranchial, and the anterior corner projecting anteriorly beyond it, as is well shown in certain of Gegenbaur's (1872) figures. The efferent artery of each arch, coming upwards along the external surface of the epibranchial, accordingly either passes wholly anterior to the pharyngobranchial, or crosses its anterior edge, and beyond that point lies wholly anterior to it, as shown in my figure of Chlamydoselachus (Allis, 1915, p. 568). Thus the dorsal ends of the pharyngobranchials of these fishes do not now lie directly internal to the efferent arteries of their respective arches, and if that part of the axial skeleton to which any one of them is related were to undergo marked lateral expansion, the skeletal bar of that arch would acquire contact with it dorsal to the dorsal aortic vessel, and would lie posterior to the efferent artery of the arch if the contact was by the pharyngeal element of the arch, but anterior to that artery if the contact was by the epal element. And this is exactly what does occur in the hyal arch of these fishes, for the hyomandibula, which is the epal element of the arch, articulates with the cranial wall dorsal to the lateral dorsal aorta and anterior to the efferent hyal artery (Allis, 1915). In the Batoidei, where the hyomandibula is the pharyngeal element of the hyal arch, it also articulates with the cranial wall dorsal to the lateral aorta, but its primary relations to the efferent hyal artery are obscured by its loss of contact with the dorsal end of the epal element.

In the Teleostomi, where the V-shaped arch occurs, the dorsal ends of the epibranchials are expanded, as they are in the Selachii, but it is the anterior, instead of the posterior, corner of this end that gives articulation to the pharyngobranchial; as shown in my figures of Amia and Scomber (Allis, 1897 and 1903). The dorsal end of the efferent artery of each arch of these fishes accordingly lies either wholly posterior to the pharyngobranchial, or crosses its posterior edge, the reverse of the relations that it has to that cartilage in the Selachii. If one of the branchial bars of these fishes were to acquire contact with a laterally expanded part of the axial skeleton, the point of contact would therefore lie anterior to the efferent artery of the arch and dorsal to the dorsal aortic vessel, and such contact is actually acquired by the first pharyngobranchials in Amia, Scomber and Hyodon (Allis, 1897, 1903 and 1919).

The relations of the arteries, here under consideration, to the cartilages of the hyal and branchial arches thus seem to depend definitely upon whether the skeletal bars of these arches acquire the sigma- or the V-shaped form, and whether their dorsal ends lie opposite an enlarged portion of the axial skeleton, or not, and this must have applied with equal force to the relations of these structures to each other in the mandibular and premandibular arches. In these two latter arches, the dorsal ends of the skeletal bars must inevitably, in all the gnathostome fishes, have assumed the sigma form, for, in all of them, as the present mouth developed, the pharyngeal elements must have been subjected to pressure, or pull, tending to swing them upwards and forwards into a position parallel to the axis of the body, while the articulating ends of the epal and ceratal elements were pushed backwards. It seems reasonable to assume that there was, primarily, an aortic vessel in the premandibular arch, as there actually is in the mandibular arch. The efferent artery of each of these arches would therefore, normally, have passed anterior to the pharyngeal element of the arch in order to reach and fall into the lateral dorsal aorta, and this latter vessel would have extended forwards to the dorsal end of the premandibular artery. From this end of the aorta, the arteria cerebralis of current descriptions must have had its origin, for this is in accord with the conditions that I find in the adults of all of these fishes that I have examined, and with Raffaele's (1892) descriptions of embryos of the Plagiostomi.

Assuming the views above set forth to be correct, it is evident that, in recent fishes, the relations of the arteries here under consideration to the cartilages of the region, should give some indication as to whether the latter are of visceral (branchial), or axial origin, and the conditions in early embryos of Acanthias, as recently described by van Wijhe, are particularly suggestive in this respect.

In a 28 mm. embryo of this fish (Acanthias), the polar cartilage of either side is said by van Wijhe (1922) to be a little rectangular plate lying ventral to the parachordal of its side, slightly posterior to its anterior end and directed vertically toward it. The hind end of the corresponding trabecula is shown lying directly ventral to the polar cartilage, and it is said (*l.c.* p. 283) there to be in contact with the dorso-anterior end of the palatoquadrate. In the figures given, this contact of the trabecula and palatoquadrate is not shown, but as it is said to exist, the adjoining ends of these two cartilages must both lie directly ventral to the ventral end of the polar cartilage, and but slightly separated from it. The dorso-anterior end of the palatoquadrate is said to represent the palatobasal process of Gegenbaur's (1872) descriptions of the adult, but, following Garman (1885), van Wijhe calls it the processus palatotrabecularis. It is evidently considered by him to represent the dorsal end of the entire bar of the mandibular arch, but this I think is incorrect, as will later appear.

The polar cartilages enclose between them a space which van Wijhe calls the "Polfenster," and in this 28 mm. embryo it is said to be traversed by the stalk of the hypophysis and the internal carotid arteries. The latter arteries, running forwards through this fenestra polaris, unite with each other immediately beyond it and then soon separate again, the artery of either side turning laterally and being joined by the efferent pseudobranchial artery (arteria spiracularis, van Wijhe) shortly after the latter artery has given off the arteria ophthalmica magna. The internal carotid is said then to continue onwards, along the lateral surface of the hypophysis, and after giving off the arteria centralis retinae, to first turn upwards across the anterior edge of a median mass of tissue that van Wijhe calls the "Mittelhirnpolster," and then postero-mesially along the dorsal surface of that polster to join and fuse with the artery of the opposite side to form the median arteria basilaris.

The "Mittelhirnpolster" lies partly within and partly anterior to the ventro-posteriorly bent and beak-like tip of the notochord, and corresponds to the cartilago acrochordalis of certain other vertebrates. In Acanthias it does not undergo chondrification, but lateral outgrowths of it chondrify as the pleurosphenoid (van Wijhe), or alisphenoid (Sewertzoff) cartilages, and as these latter cartilages and the acrochordalis tissue are said to be derived from somite I, they form the most anterior portion of the chordal axial skeleton. The internal carotid of these descriptions accordingly does not enter the chordal portion of the cranial cavity until after it has received the efferent pseudobranchial artery and has given off the arteria centralis retinae, and as the internal carotid, up to the point where it receives the efferent pseudobranchial artery, is simply a section of the lateral dorsal aorta, it is evident that it must there have lain, primarily, external to the cranial cavity; and this is in accord with the conditions that I have described in the adult Acanthias blainvillii, in the adults of several others of the Selachii, and in Raia (Allis, 1914, 1912 a, 1912 b), the internal carotid there, after traversing the foramen caroticum and until it has received the efferent pseudobranchial artery, lying either in a canal in the cranial cartilage or between that cartilage and its lining membrane.

In embryos of Acanthias from 29·5 to 32·5 in length, the ventral end of each polar cartilage has fused with the hind end of the corresponding trabecula, but the dorsal end of the cartilage is still free.

In a 39·5 mm. embryo, the polar cartilages of opposite sides have fused with each other both dorsal and ventral to the median artery formed by the fusion of the internal carotids, a posterior portion of the fenestra polaris thus being cut out of the entire fenestra to form a foramen caroticum, and this foramen persists as such in the skull of the adult. That part of the fused polar cartilages that forms the dorsal boundary of this foramen has fused with the ventral surface of the parachordal plate; the parachordal, polar cartilage, and trabecula of either side thus forming a single continuous piece. The palatoquadrate has grown forwards beyond the point where the polar cartilage fuses with the trabecula, and a processus palatobasalis (palato-trabecularis, van Wijhe) has developed on its dorsal edge, this process being directed upwards along the lateral surface of the trabecula definitely anterior to the polar cartilage. A short palatine process of the palatoquadrate projects anteriorly beyond the processus palatobasalis. The internal carotids of opposite sides now fuse with each other before they enter the median foramen caroticum, and the ectodermal stalk of the hypophysis has vanished.

The efferent pseudobranchial artery of these descriptions is the efferent artery of the mandibular arch, and the internal carotid, into which it falls, is simply an anterior prolongation of the lateral dorsal aorta. This latter artery thus lies ventro-mesial to the polar cartilage, and the efferent mandibular artery, in order to reach it, crosses the anterior edge of the latter cartilage, these relations of the arteries to the cartilage being exactly those that the corresponding arteries in the branchial region would have to the pharyngeal elements of those arches if the latter elements were to acquire contact with the axial skeleton. This evidently suggests that the polar cartilage is a pharyngomandibular, and the further facts that this cartilage lies ventral to the jugular vein, lies ventral or posterior to all branches of the nervus trigeminus, and at a marked angle to the palatoquadrate, are all in favour of this view. The fact that the polar cartilage develops independently of the palatoquadrate is in accord with van Wijhe's statement that the several cartilages in the more posterior arches of this fish develop independently of each other, instead of arising by the segmentation of a primarily continuous bar.

In embryos of Scyllium canicula, somewhat different but strictly comparable conditions occur. In the descriptions of embryos of this fish the polar cartilages are not described as independent cartilages, but it seems beyond all question that the so-called trabeculae of these descriptions are, in reality, trabeculo-polar cartilages. Goodrich (1918, p. 21) says of these so-called trabeculae: "At no stage of development do I find the trabeculae bent down at right angles to the parachordal plate, as figured by Sewertzoff, but always from the first more nearly in the same plane"; and van Wijhe (1922) confirms this observation. Goodrich, in making this statement, refers to his figure of a 33 mm. embryo, and the trabeculae, as there shown, do lie nearly in the plane of the parachordals, but they nevertheless lie nearly at right angles to that part of the notochord toward which they are directed, for the anterior end of the notochord turns upwards to such an extent that its tip lies nearly at right angles to its otic and occipital portions. The conditions in this fish are thus strictly comparable to those in Acanthias; and as I find similar relations of the cartilages of this region to the nerves, arteries and jugular vein in the adults of all of the Selachii that I have examined, and also in Raia (Allis, 1912b, p. 58) and Chimaera (Allis, 1917), it is probable that they exist in all the Elasmobranchii.

The polar cartilage of these fishes thus apparently being the pharyngeal element of the mandibular arch, its relations to the trabecula strongly suggest that that cartilage is the corresponding element of the premandibular arch. The dorsal end of the skeletal bar of the latter arch must have lain, primarily, directly ventral to the acrochordalis tissue, and it should there normally have acquired contact or connection with the axial skeleton. This has, however, been prevented partly by the failure of the acrochordalis tissue to chondrify, but mainly because of changes in the region associated with the development of the mouth and the hypophysis. Some fixed support was, however, needed, because of the supporting relations of the cartilage to the roof of the mouth, and it was acquired by fusion with the distal end of the polar cartilage, fusions of the cartilages of one arch with those of an adjoining one being of frequent occurrence in fishes. Furthermore, this assumption offers an explanation of the otherwise apparently inexplicable course of the efferent mandibular artery of these fishes dorsal, instead of ventral to the trabecula.

In Acanthias, as above stated, the polar cartilage fuses with its fellow of the opposite side both dorsal and ventral to the lateral dorsal aorta (internal carotid), as well as fusing with the ventral surface of the parachordal dorsal to the latter vessel. What has been the cause of this fusion with its fellow of the opposite side is not apparent, but, as a result, the lateral dorsal aortae are forced together in the median line and there fuse with each other, the point of fusion lying between the points where the aortae are joined by the efferent arteries of the hyal and mandibular arches. The fusion of these arteries completes the well-known circulus cephalicus, and the efferent mandibular artery of either side is pulled slightly postero-mesially, and hence, in its course upward and inward to reach and fall into the aorta, it crosses the anterior edge of the pharyngomandibular (polar cartilage) definitely dorsal to its ventral end. The efferent artery accordingly lay dorso-posterior to the point of contact of the pharyngomandibular with the pharyngopremandibular when these two elements fused with each other, and hence lies, actually, dorsal to the latter element, this being the reverse of its normal relations. The lateral dorsal aorta lies, on the contrary, actually mesial, but morphologically ventral, to the pharyngopremandibular, and this relation to that cartilage would necessarily result from the fusion of the cartilage with the pharyngomandibular whether the pharyngopremandibular were, before the fusion, directed towards the cranium ventral or dorsal to the aorta, provided only that, in the latter case, the arteria cerebralis ran upwards anterior to the pharyngopremandibular. If the artery ran upwards posterior to the pharyngopremandibular (which seems improbable), and the latter element had acquired contact or connection with the cranium dorsal to the aorta, it might, in fusing with the pharyngomandibular, have pushed the base of the arteria cerebralis outwards, thus forcing it to run upwards lateral and then dorsal to the pharyngopremandibular, as it actually does both in the adult Polypterus and in the youngest larvae of that fish that have as yet been examined and described.

In Scyllium the conditions differ from those in Acanthias in that the pressure, or pull, tending to force the pharyngeal elements of the mandibular and premandibular arches into a position parallel to the axis of the body, has caused a bending upwards and backwards of the anterior end of the notochord, instead of a bending upward and forward of the trabeculo-polar bar; and in both these fishes the impulse did not become effective, so far as the pharyngomandibular is concerned, until after that element had become firmly fused with the parachordal.

If the polar cartilage is the pharyngomandibular, the palatoquadrate must be the epimandibular. The processus basalis and processus palatobasalis are then, respectively, the posterior and anterior corners of the greatly expanded dorsal (proximal) end of this element of the arch, and the processus muscularis (metapterygoideus) is part of a ridge which, as in the branchial arches, formed, primarily, the anterior edge of a groove on the external edge of the element to lodge the arteries and nerves of the arch.

In the Holostei and Teleostei the conditions differ from those above described in certain important details, but not in principle.

In a 10 mm. embryo of Lepidosteus, Veit (1911) shows the trabecular and polar cartilages of either side lying one anterior to the other in the horizontal plane of the related parachordal. In 11 to 12 mm. embryos these primarily independent cartilages have fused with each other and with the parachordal, and the efferent mandibular artery joins the internal carotid ventral to, instead of dorsal to, the so-formed trabeculo-polar bar (Allis, 1909, p. 186). After receiving this artery, the carotid turns upwards between the hind ends of the trabeculae and not, as in the Elasmobranchii, between the polar cartilages.

In an embryo of Amia 8 to 8·8 mm. in length, Pehrson (1922) finds the polar cartilage of either side already fused with both the parachordal and trabecula, but still readily recognizable. It is said to be triangular in shape, the base of the triangle directed forwards, and it is with the lateral one of the two corners of the base that the trabecula has fused. The mesial corner projects slightly forward, and the internal carotid runs upward in the space between this projecting corner and the trabecula. In later stages the projecting mesial corner also fuses with the trabecula, thus enclosing the carotid in a foramen, and this foramen evidently becomes the carotid canal of the adult, which traverses the presphenoid bolster (Allis, 1897). The dorsal end of the efferent mandibular artery, which primarily joined the internal carotid ventral to the trabecula (Allis, 1919, p. 266), also becomes enclosed in the cartilage, and hence, in the adult, has the appearance of traversing the trabecula.

The efferent mandibular (pseudobranchial) artery thus has, in these two ganoids, distinctly different relations to the trabecula from those that it has in the Elasmobranchii, but this is evidently due to the fact that the internal carotid (lateral dorsal aorta) has not here been crowded inwards to the median line by the fusion of the pharyngomandibulars (polar cartilages) of opposite sides, and that the latter cartilages have not fused with the axial skeleton until after they and the pharyngopremandibulars (trabeculae) have both acquired a position in the horizontal plane of the parachordals. Because of this, the ventral end of the pharyngomandibular, in swinging upward, has passed postero-dorsal to the efferent artery of its arch, that artery being held in position distal to the pharyngeal element, between the two process-like corners of the expanded dorsal end of the epimandibular, by its attachment to the carotid. The carotid (lateral dorsal aorta) of either side accordingly runs forwards ventral and mesial to the trabeculo-polar bar until it has received the efferent mandibular artery, when it turns upwards along the actually mesial but morphologically anterior edge of the hind end of the trabecula and enters the cranial cavity, this point corresponding to the point where, in the Selachii (and hence probably in others also of the Elasmobranchii), the artery, after receiving the efferent mandibular artery, pierces the lining membrane of the cranial cartilage and enters the central cavity. The ventral edges of the polar cartilages later grow towards each other, dorsal to the internal carotids, and certainly form the anterior portions of the lateral bounding walls of the pituitary fossa, but whether it is outgrowths of these cartilages, or of the parachordals, that form the posterior portions of those walls cannot be told from the descriptions and figures. It would however seem quite certain that the posterior portions of the walls are of parachordal origin, and correspond to the ventral processes of the median basisphenoid of Stensiö's (1921) descriptions of Wimania and Axelia. But however this may be, the internal carotid of either side lies along the external surface of the wall.

In embryos of the non-siluroid Teleostei the conditions are probably similar to those in the Holostei, for Stöhr (1882) describes, in early embryos of Salmo salar, an independent cartilage which must be a polar cartilage, lying between the trabecula and parachordal. This cartilage is said by him to fuse first with the parachordal and then with the trabecula, and it is evidently represented, in the descriptions of these fishes by other authors, in the so-called anterior prolongation of the parachordal. In an 11 mm. embryo of Salmo trutta, Dohrn (1886) shows these three cartilages already fused to form a continuous bar, and the internal carotid artery runs forward beneath that part of this bar apparently formed by the polar cartilage, there receives the efferent mandibular (pseudobranchial) artery, and then turns upwards through the space enclosed between the trabecular portions of the bars of opposite sides. Up to this point, the carotid is not at any point connected with its fellow of the opposite side either by anastomosis or commissure, the conditions in these embryos thus being similar to those in the Holostei.

In the adults of all of the non-siluroid Teleostei that I have examined, the conditions are markedly different from those above described in trout embryos, for, in later stages of development of all these fishes a certain portion of the trabeculo-parachordal bar undergoes resorption, this resorption apparently involving either the polar cartilages alone, or portions of the adjoining ends of those cartilages and the trabeculae. Associated with this, and with the development of a ventral myodomic compartment, the internal carotids are pressed together in the median line there to fuse with each other as they run upwards in the median vertical myodomic membrane, and the efferent mandibular arteries lose their primitive connections with the internal carotids and become connected with each other by cross-commissure. These connections of these arteries are shown by Dohrn (1886) in an 18 mm. embryo of Salmo trutta, the anastomosis of the internal carotids lying anterior to the hypophysis, and apparently anterior also to the point where the carotids were primarily joined by the efferent mandibular arteries. The anastomosis between the carotids of these fishes is thus quite certainly not the homologue of the anastomosis in the Plagiostomi. The further course of the internal carotid is not given in advanced stages of Salmo, but in such stages of several others of the non-siluroid Teleostei that I have examined (Allis, 1919), the internal carotid, distal to its anastomosis with its fellow of the opposite side, separates into anterior and posterior divisions, and the anterior division runs forwards in the dense fibrous tissue which forms both the dorsal edge of the interorbital septum and the floor of the corresponding part of the cranial cavity, and only enters the latter cavity after it reaches the region of the optic chiasma, that being the region in which the main artery enters the cranial cavity both in the Plagiostomi and the Holostei.

In the Siluridae somewhat different conditions exist. In a 10 mm. embryo of Amiurus, Kindred (1919) shows the trabecula and parachordal of his descriptions already fused to form a single continuous piece, and a polar cartilage must be included in it. The internal carotid runs upwards through a notch in the mesial edge of this continuous bar, this notch being said to lie in or about the middle region of the orbit, and hence certainly anterior to that part of the trabeculo-parachordal bar that corresponds to the polar cartilage. In a 32 mm. larva the condition of these arteries is apparently similar to that which I have described in the adult (Allis, 1908 b), for Kindred says (*l.c.* p. 35): "In the younger stage the internal carotid artery enters the cranium internal to the trabecula, but now it has a different relation. This blood vessel enters a rete mirabile, lateral and posterior to the optic foramen, and a branch to the internal part of the cranium enters through the posterior part of the optic foramen. The external carotid enters the cranium as before, between the branches of the trigeminal nerve."

The conditions in embryos of Amiurus between the two stages above referred to, are not given by Kindred, but it is evident that, during this interval, the internal carotid has cut through the trabeculo-parachordal bar in the region of the fusion of the trabecula with the polar cartilage. How this has taken place is not indicated, but it is said (*l.c.* p. 37) that the trabeculae of the 32 mm. larva "are no longer continuous bars from the ethmoid plate to the parachordal plate, but half-way between those regions a part of each has been resorbed and parasphenoid and suprasphenoid ossifications have replaced it by growth dorsally into this region, forming the posterior margin of the optic foramen and part of the margin of the trigemino-facial foramen."

During this process of resorption of the cartilage, and its replacement by bone, the internal carotid must have slipped outwards to the external surface of the cranium, the artery thus cutting through the cartilage in a manner strictly comparable to that described by Gaupp (1893, p. 403) for the corresponding artery in Rana. The same result would evidently have been attained if, in a fish where the conditions were as in the 8 mm. embryo of Amia described by Pehrson, the secondary fusion of the trabecula with the mesial corner of the polar cartilage were to persist, and the primary fusion, with the lateral corner of that cartilage, be resorbed. The point where the artery of Amiurus finally enters the cranial cavity is, it is to be noted, approximately the same as in the other fishes above referred to. That the external carotid of this fish should enter the cranium with the branches of the nervus trigeminus, as stated by Kindred, seems unusual.

In a 75 mm. specimen of Polypterus, I found the carotid artery running forwards along the external surface of the cranium until it reached the optic foramen, and there entering the cranial cavity immediately posterior to the optic nerve (Allis, 1908 a); and Budgett (1902) shows the artery in a similar position in a 30 mm. embryo of this fish. The artery in this case passes dorsal to the trabecula to enter the cranial cavity, as it does in advanced stages of Amiurus, but there is nothing in the two stages of Polypterus to indicate that the artery has cut through the trabeculo-parachordal bar, as it has in Amiurus. Earlier stages in the development of this fish must be known before this course of the artery can be properly accounted for.

In an embryo of Ceratodus of stage 48, Greil (1913) shows the internal carotid, after receiving the efferent mandibular artery, crossing the ventral surface of a part of the trabeculo-parachordal cartilage that corresponds strictly in position to the polar cartilage of the fishes above referred to. The artery then turns upwards along the mesial edge of the trabecular part of the bar and is connected with its fellow of the opposite side by a cross-commissural vessel which lies posterior to the hypophysis and apparently dorsal to the anterior end of the parachordal plate, the conditions thus being strictly similar to those in the 11 mm. embryo of Salmo trutta described by Dohrn excepting in the position of the cross-commissural vessel between the carotids of opposite sides.

In higher vertebrates, the polar cartilages have been described in certain Aves and Mammalia. In the chick and duck the conditions, as described by Sonies (1907), are strictly comparable to those in certain fishes, excepting in the presence of a so-called processus infrapolaris which projects posteriorly from the dorsal end of each polar cartilage, ventral to the internal carotid (lateral dorsal aorta), and in certain Aves fuses, posterior to that artery, with the parachordal plate. This process and the dorsal end of the polar cartilage of these vertebrates thus have to the internal carotid (lateral dorsal aorta) exactly the same relations which the two fusions of the polar cartilage of Acanthias, with its fellow of the opposite side, have to the same artery, the only difference being that in the one case processes of the polar cartilages fuse with the parachordal, while in the other they fuse with their fellows of the opposite side; and this is evidently related to the absence of a circulus cephalicus in the one and its presence in the other. The ventral of these two fusions represents the primitive relation of the cartilage to the internal carotid (lateral dorsal aorta), and if it alone were to persist, the artery would pass lateral and then dorsal to, instead of ventral and then mesial to the trabecula, as already suggested in one of my earlier works (Allis, 1919).

In Talpa, as described by Noordenbos (1905), there is, in early stages of development, a Y-shaped cartilage between the polar cartilages and the parachordal plate, this cartilage representing that fusion of the polar cartilages of Acanthias lying dorsal to the internal carotids.

The relations of the internal carotid and efferent mandibular arteries of the gnathostome vertebrates to the polar and trabecular cartilages thus strongly suggest that those cartilages are, respectively, the pharyngeal elements of the mandibular and premandibular arches, and if this be so it would seem to follow that the epal element of the premandibular arch, or at least its proximal portion, is represented in the palatine process of the palatoquadrate, that is, in that part of the latter cartilage that lies anterior to its orbital (palato-basal) process. The antorbital wall would then probably have been developed from tissues that are serially homologous with those that give origin to the hyomandibula in the hyal arch of the Teleostomi, and, in the mandibular arch, to the lateral wall of the trigemino-facialis chamber; and the fact that the dorsal end of the antorbital wall fuses with the dorsal end of the dorso-anteriorly directed alisphenoid cartilage, derived from the premandibular somite, is suggestive of such an origin. The prechordal portion of the chondrocranium, exclusive of the sense-organ capsules, would then be wholly of visceral-arch origin, and the enclosure within it of any portion of the brain would be a secondary adaptation.

The chiasma-ridge is generally considered to mark the anterior end of the floor of the brain of the adult vertebrate, but Kingsbury (1920) contends that this ridge simply marks the anterior end of the embryonic neural plate, the actual floor-plate of the brain ending, considerably posterior to it, at the fovea isthmi, which lies, in the adult, slightly posterior to the central point of the summit of the plica encephali ventralis. The floor-plate of the brain and the notochordal plate are said by him to have been primarily coextensive.

All that part of the ventral surface of the adult brain that lies between the fovea isthmi and the chiasma-ridge must therefore have formed, primarily, some part of the anterior surface of the brain, and quite probably the whole of it, and the conditions in recent vertebrates show conclusively that this anterior surface of the brain swung downward and forward over the tip of the notochord until it came in contact with the pharyngopremandibulars (trabeculae). This gave rise to the plica encephali ventralis, and when the pharyngopremandibulars later swung upward into the plane of the parachordals, the brain was bent upward and backward and so gave rise to the marked curvature (Brückenbeuge) found in many vertebrates at the base of the posterior limb of the plica.

The anterior surfaces of the brain and pharyngopremandibulars were certainly, at this early period, covered externally by a layer of ectoderm but slightly separated from them. The middle point of the transverse line separating these two ectodermal surfaces lay in close proximity to the infundibular region of the brain and to the dorsal surface of the anterior end of the archenteric cavity, and it must have already acquired relations to the infundibular tissues, thus forming the beginnings of the hypophysis. As the anterior surface of the brain then swung downward and forward to acquire contact with the pharyngopremandibulars, the related cerebral and visceral-arch ectodermal surfaces must either have been pushed bodily away from the underlying structures, or have been folded, hinge-like, one upon the other, and in either case the hypophyseal tissue would have been held in place by its acquired relations to the infundibulum and hence have given rise either to a short hypophyseal pit, or to a solid cord of ectodermal tissue. That the hypophyseal pit or cord could have been developed after the chiasma-ridge had acquired contact with the pharyngopremandibulars, seems wholly improbable, for in that case an undifferentiated portion of the ectoderm would have had to start out from a relatively distant point—in Amia close to the neuropore (Reighard and Mast, 1908)—either by invagination or solid ingrowth, to seek and find certain nervous tissues with which it had to become associated in order to establish its own special and particular function.

The hypophyseal pit would have lain, at this period, wholly antero-dorsal to the pharyngopremandibulars (trabeculae), with its external opening in the region of the chiasma-ridge, and there lying between ectodermal surfaces that cover, the one that part of the external surface of the brain that lies between the chiasma-ridge and the neuropore, and the other that part of the external surface of the anterior end of the branchial chamber that lies ventral to the outer ends of the pharyngeal elements. The snout had not as yet been developed; and, as the nasal epithelium develops in relation to it, and it encloses the anterior portions of the trabeculae, it is evident that it contains tissues derived both from the cerebral surface just above referred to—which may be called the frontal surface—and from the visceral-arch surface. The dorsal edge of the latter surface lies postero-ventral to the opening of the hypophyseal pit. In order that the pharyngopremandibulars and the tissues related to them could take part in the formation of the snout, they would accordingly have to grow forward either ventral or lateral to the pit. In the former case the pit would be gradually deepened by the progressive coalescence of its edges, and might readily be prolonged until its external opening reached the ventral edge of the neuropore, this giving rise to the conditions actually found in the Cyclostomata and Ganoidei; and that the pit was here quite certainly formed by the gradual coalescence of its edges, and not by invagination, would seem to be shown by its development in Petromyzon, for the slight indentation in the ectoderm that there marks its first appearance lies in the region of the optic recess, and not near the neuropore (von Kupffer, 1894). When the visceral-arch tissues passed lateral to the hypophyseal pit, they would have fused again immediately beyond it, the opening of the pit then lying ventral to the plane of the trabeculae, and ultimately in the stomodaeum, as it does, so far as I can find described, in all vertebrates excepting only the Cyclostomata and Ganoidei.

When, under this assumption, the pharyngopremandibulars grew forward lateral to the hypophyseal pit, they would either be carried, by this growth, bodily forward beyond the pit, or be pushed there by a correlated growth of the pharyngomandibulars (polar cartilages), the pharyngopremandibulars then fusing with each other beyond the pit and so forming the anterior wall of the pituitary fossa; and, whether they passed lateral or ventral to the pit, they would drag after them the epipremandibulars (palatine processes). The epimandibulars (palatoquadrates) would undergo a correlated anterior prolongation and fuse with the distal (hind) ends of the epipremandibulars to form the palato-pterygoquadrates, this giving rise to the well-known maxillary processes of vertebrate embryos. Whenever, in this process, the palato-pterygoquadrates did not retain fixed articular relations with the pharyngopremandibulars (trabeculae), the maxillary processes of opposite sides would meet and fuse in the median line anterior to the hypophyseal pit, and so form the entire primary upper edge of the mouth, as occurs in the embryos of certain vertebrates; but whenever this articular relation was retained, the maxillary processes would not so meet in the median line, fusing, instead, with either the frontal or nasal processes, derived from the frontal ectodermal surface. In the latter case, the median portion of the upper edge of the mouth would nevertheless quite certainly be formed by tissues related to the epipremandibulars, for that part of the palato-pterygoquadrate of the Teleostomi that corresponds to the palatine processes of the Selachii lies anterior to the ridge that forms the hind edge of the surface of articulation with the ectethmoidal (antorbital) process, and a certain median portion of it, which primarily formed the median portion of the upper edge of the mouth, was quite certainly later detached and finally resorbed (Allis, 1914). The frontal and nasal processes are derived from the frontal ectodermal surface and take no part in the formation of the primary upper edge of the mouth.

In the Ganoidei there is an adhesive organ on the anterior end of the snout, formed of two organs, one on either side. The fundament of this organ first appears, in Amia (Rieghard and Phelps, 1908), as a crescent-shaped and elevated area which lies directly in front of the optic vesicles and forebrain, and directly external to a dorsally directed diverticulum of the archenteric cavity. The crescent-shaped area later separates into three hemispherical protuberances, a median one called the button, and two lateral ones which form the fundaments of the two adhesive organs. The hypophysis lies between the button and the anterior surface of the brain, and the stomodaeum anterior to the button and the two lateral protuberances. From the dorsal wall of the short foregut three diverticula arise, the median one related to the button and the lateral ones to the two adhesive organs. The button later disappears by a process of transformation into mesoblast, but the diverticula related to the adhesive organs ultimately break through to the external surface: and Reighard and Phelps express their belief that these diverticula are homologous with the so-called anterior head cavities of selachian embryos.

In Acipenser, a part of the fundament of the adhesive organs is shown by von Kupffer (1893) lying in the median line antero-ventral to the hypophysis, the primitive conditions in this fish thus apparently being similar to those in Amia. In embryos of Polypterus, two adhesive organs are shown by Kerr (1903), but they lie one on either side of the stomodaeum, instead of on the anterior end of the snout, and nothing is said as to their having been primarily connected by a median button. Kerr however says that in occasional embryos the two organs are found fused with each other in the median line, but it is not said on which side of the hypophysis the organs then lie. When the organs are not fused the hypophysis lies between them, in the stomodaeum.

It thus seems probable that it is the fusion, in the median line, of the fundaments of the adhesive organs of opposite sides that causes the displacement of the hypophysis in the Ganoidei, and this is exactly what might be expected under the theory here proposed, for, as the hypophysis lies between the fundament of the organ and the anterior end of the brain, the fundament must have been developed in what I have called the visceral-arch tissues, and if the central point of the fundament, the button of Reighard and Phelps' descriptions of Amia, persisted until after the snout had begun to be developed, the visceral-arch tissues could not readily have separated in the median line in order to pass on either side of the hypophyseal pit, while if the button had been dispersed at an earlier stage they could have so separated.

In Petromyzon no adhesive organs have been described, so far as I know, but the upper lip of this fish has been compared to that part of the snout of the Ganoidei that bears these organs, and the external opening of the hypophysis lies close to the neuropore.

The arteria cerebralis was probably sent upward, primarily, along the anterior edge of the premandibular somite, and it is apparently a serial homologue of the cerebral branches of the intervertebral arteries related to more posterior somites, but as that part of the brain to which it is related projects forward beyond the anterior opening of the chordal portion of the cranium, the artery has followed it, and accordingly, in all the fishes above considered, first enters the central cerebral cavity in the region of the optic chiasma.

If the epipremandibulars are the palatine processes of the palatoquadrates, as here suggested, the dorsal portions, at least, of the mandibular clefts could not have been utilized to form part of the buccal opening, and if these portions of the clefts persisted as evaginations of the foregut, they would probably be represented in the diverticula related to the adhesive organs.

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