CONCERNING THE HOMOLOGIES OF THE HYPOPHYSIAL PIT AND THE POLAR AND TRABECULAR CARTILAGES OF FISHES

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THE hypophysial pit has generally been considered to be a simple invagination of the external ectoderm, but in October 1923 I expressed my conviction that it was in no part such an invagination, being, on the contrary, the result of the folding or rolling together of two ectodermal surfaces and their fusion with each other excepting along the median line. The two surfaces here concerned were said to cover, the one the anterior surface of the brain and the other the corresponding surface of the visceral arches, and they were accordingly called, respectively, the cranial (cerebral) and visceral surfaces. Whenever these two surfaces fused with each other in the median line as well as laterally, the hypophysial pit was said to be reduced to a solid strand of ectodermal tissue. Other authors had previously concluded that the prehypophysial, but not the hypophysial, portion of the naso-hypophysial canal of *Petromyzon* was, in part (Dohrn, 1881) or in whole (de Beer, 1923), developed in what is in principle this manner; and in December 1923 G. Haller showed conclusively that the hypophysial pit of the Plagiostomi, commonly called Rathke's pocket, is so developed, although he makes no definite statement to this effect. The latter fishes will therefore here be first considered.

PLAGIOSTOMI

In a 1·8 mm. embryo of *Acanthias* the anterior end of the head is shown by Scammon (1911) projecting upward somewhat above the surface of the egg, and the neural plate, which lies directly upon the dorsal surface of the alimentary canal, does not extend to its anterior end.

In a 2 mm. embryo the head is lifted somewhat more above the dorsal surface of the egg, and the neural plate extends to the anterior end of the alimentary canal. The anterior end of the head is completely filled by the anterior end of the alimentary canal.

In a 2·5 mm. embryo the optic vesicles appear as depressions in the anterior portion of the cephalic plate, lying one on either side of the median line. In a 2·7 mm. embryo these two depressions have fused with each other in the median line, this either causing or being the result of a depression of that part of the neural plate that extends from its anterior end to the hind end of the infundibulum. Associated with this, that part of the neural plate that lies between the infundibulum and the medulla oblongata has been somewhat lengthened and bent downward, through about 90°, in an evenly curved line the convexity of which is directed dorso-anteriorly. The depression of the infundibulum has pressed downward the dorsal wall of the underlying portion of the alimentary canal to such an extent that this part of the canal has the appearance of being a diverticulum of the more posterior portion, directed anteriorly in the level of its floor. This diverticulum lies immediately anterior to that part of the floor of the alimentary canal that will later form the endodermal lining of the bucco-pharyngeal (oral) plate, and it is accordingly called the preoral gut. The part of the canal that lies immediately posterior to this preoral gut is then called the fore-gut, but this term is misleading, for the preoral gut forms the actual anterior end of the alimentary canal.

The anterior end of the roof of the fore-gut is bent downward in an evenly curved line by the pressure of that part of the neural plate that lies between the infundibulum and the medulla oblongata. This part of the plate later increases in length more rapidly than the underlying portion of the wall of the fore-gut, and even in the 2·7 mm. embryo this has caused the neural plate to bulge dorso-anteriorly away from the wall of the gut, thus forming the beginning of the plica encephali ventralis. This plica is generally considered to be developed as a result of unequal growth of the floor and roof of the brain, but in this 2·7 mm. embryo the neural groove is still widely open without a vestige of a roof.

In the 2·7 mm. embryo the lateral edges of the neural groove have already begun to grow upward to form the lateral walls and roof of the brain, and in older specimens the anterior ends of these lateral upgrowths are prolonged mesially around the anterior end of the cephalic plate and meet and fuse with each other in the median line to form the lamina terminalis. This lamina and the infundibular region of the neural plate then have the appearance of forming the anterior wall of the embryonic brain and will hereafter be so referred to. The lamina, when fully developed, is directed dorso-anteriorly and never comes into contact either with the dorsal surface of the alimentary canal or the outer surface of the egg. The angle between the lamina and the dorsal surface of the egg forms what is commonly called the beginning of the head fold, but it seems better for purposes of description and comparison to consider this part of the fold to be formed of two folds here completely fused with each other, a naso-hypophysial fold which lies immediately beneath the brain and a head fold which always lies beneath the alimentary canal.

In early ancestors of all fishes there were quite certainly visceral arches related to the premandibular section of the alimentary canal, and it is here assumed that there was but one pair of such arches. As the roof of this part of the canal was gradually pressed downward by the descent of the infundibulum, the dorsal ends of the related visceral arches were similarly pressed downward, the dorsal and ventral ends of the arches ultimately lying not far from each other and the arches straddling, U-shaped, the lateral edges of the canal. The bending downward of the anterior end of the roof of the fore-gut similarly carries downward and forward with it the dorsal ends of the mandibular mesodermal arches, and these arches extend from there ventro-posteriorly along the dorso-lateral edges of that part of the floor of the gut that will later become the endodermal lining of the bucco-pharyngeal plate. This shifting downward and forward of the dorsal ends of the mandibular arches must necessarily carry with it the mandibular visceral pouches, and it would seem as if the walls of these pouches must form the lateral portions of the bucco-pharyngeal plate, that plate lying in the floor of the alimentary canal between the ventral ends of the mandibular and premandibular arches.

In later stages the posterior end of the bucco-pharyngeal plate is carried downward by the increase in depth of the alimentary canal, and the plate then has the appearance of forming the anterior wall of the canal, the preoral gut becoming what appears to be a diverticulum that arises from the dorsal surface of the anterior end of the fore-gut, and it has long been known as Seesel's pocket.

In a 6 mm. embryo of this fish described by de Beer (1926) the enclosure of the brain has been completed. The infundibulum has shifted relatively forward and its hind edge now lies at the anterior end of what remains of the preoral gut. The fused naso-hypophysial and head folds extend posteriorly to the hind end of the infundibulum. There the naso-hypophysial fold ends, but the head fold continues onward ventral to the preoral gut and abuts against and fuses with the ventral surface of the fore-gut to form the bucco-pharyngeal plate. There is nothing to indicate definitely in median sagittal sections the limit between cranial and visceral ectoderm, but there is a mass of cells immediately internal to what is certainly the dorsal end of the visceral ectoderm and it is said to be derived from the breaking down of the preoral gut. The mass is directly continuous with the internal surface of the visceral ectoderm and also with the anterior end of the fore-gut, and the notochord runs into it and is there lost. The plica encephali ventralis has been somewhat deepened and projects dorso-anteriorly into the cranial cavity. The brain has thus the appearance of bending downward and backward around the summit of the plica, but there has been no actual further bending downward of the anterior end of the head. The anterior wall of the brain has, however, begun to swing downward and backward around the hind edge of the infundibulum as a transverse axis.

In a 7 mm. embryo also described by de Beer, the plica encephali ventralis has become still more deepened and the anterior surface of the brain has swung further downward and backward. At the hind end of the infundibulum there is, in median sagittal section, a small sharply pointed depression which marks the limit between cranial and visceral ectoderm and indicates the beginning of that swinging together of these two surfaces that gives origin to Rathke's pocket, as explained immediately below. This indentation in the ectoderm thus forms the tip of Rathke's pocket instead of forming, as de Beer concluded, the beginning of its invagination. The mass of cells that in the 6 mm. embryo lay immediately internal to the dorsal end of the visceral ectoderm has been completely dispersed, excepting only that part of it that forms the central portion of the cord of tissue that connects the premandibular somites of opposite sides.

In a 4·5 mm. embryo of one of the Batoidei, species not mentioned, G. Haller (1923) shows the anterior end of the head bent downward and backward to about the same extent that it is in the 7 mm. embryo of *Acanthias* above referred to, but there is only slight indication of a plica encephali ventralis. The anterior end of the notochord is bent downward in the same curved line as the ventral surface of the brain, as is also the anterior portion of the roof of the fore-gut. The cranial ectoderm extends to the hind end of the infundibulum and there meets at an angle of about 45° the morphologically dorsal end of the visceral ectoderm, the latter ectoderm extending from there in a posterior and slightly dorsal direction to the dorso-anterior end of the bucco-pharyngeal plate. The space between these two ectodermal surfaces is called by Haller the "Kieferaugenspalte," but as it forms the deeper, hypophysial portion of the naso-hypophysial fold, it will hereafter be so referred to.

The tip of the hypophysial fold is, at this stage, directed almost directly anteriorly toward the tip of the bent-down anterior end of the notochord, the latter tip being directed posteriorly and slightly ventrally. Dorsal to the visceral and actually dorsal wall of the hypophysial fold there is a mass of cells similar to that described by de Beer in the 6 mm. embryo of *Acanthias,* and it is said by Haller to have been proliferated from the anterior end of the fore-gut. What persists of the preoral gut is said to lie in this mass of tissue, as does also the central portion of the communicating cord that extends between the premandibular somites of opposite sides, the latter apparently lying morphologically dorsal to the former, but the descriptions are not definite as to this.

In later stages of development, the cranial wall of the hypophysial fold continues its swinging motion backward and upward against the visceral wall of the fold and fuses completely with it excepting along the median line, Rathke's pocket thus being cut out of the fold. This swinging together of the two ectodermal surfaces can only extend to the dorso-anterior end of the bucco-pharyngeal plate, for the visceral wall of the fold ends there. The corresponding point in the cranial wall of the fold lies about midway between the hind end of the infundibulum and the optic chiasma, and this determines the position of the external opening of the pocket.

In an 8 mm. embryo of *Raia,* Haller shows Rathke's pocket completely cut out of the hypophysial fold, in the manner above explained, and directed anteriorly and slightly dorsally. The median portion of the communicating strand between the premandibular somites of opposite sides lies dorso-anterior to the tip of the pocket, between it and the tip of the notochord, but the tip of the pocket is directed morphologically dorsal to both of these structures and hence lies between cranial and visceral tissues. The roof of the fore-gut bends downward at its anterior end and is continuous with the hind end of the visceral wall of the pocket in a well-rounded angle, the two walls of which lie nearly at right angles to each other. This angle forms the dorso-anterior edge of the bucco-pharyngeal opening, which has already completely broken through. From there the opening extends postero-ventrally along the anterior edges of the mandibular mesodermal arches, those arches being directed postero-ventrally and lying inclined at an angle of about 30° to the horizontal plane. The bucco-pharyngeal opening has the appearance of leading directly into the anterior end of the fore-gut, and the preoral gut, if present, would lie immediately dorsal to the visceral wall of Rathke's pocket and hence appear to be a diverticulum arising from the anterior end of the dorsal wall of the fore-gut and projecting forward in the same direction as Rathke's pocket.

The maxillary processes have not yet been developed in this embryo. The mandibular mesodermal arch extends from above postero-ventrally and is said to present four regions which are called by Haller, from above downward, the Kieferaugenspaltstueck, Oberkieferstueck, Zwischenstueck and Unterkieferstueck. The Kieferaugenspaltstueck is later said to be the pharyngeal element of the arch and it will be hereafter so referred to. It is said to form no part of the upper jaw. The upper and lower jaw segments are said to be the serial homologues, respectively, of the ceratobranchials and hypobranchials of the more posterior arches, this seeming to indicate that Haller considered the angle of the gape to lie at the dorsal end of the Oberkieferstueck, between it and the maxillary process when the latter develops. This is, however, certainly incorrect, for the upper jaw segment of Haller's descriptions is certainly the epimandibula and the lower jaw segment the cerato + hypomandibula. The pharyngeal segments of the arches of opposite sides are directed anteriorly and slightly dorsally and form the lateral walls of Rathke's pocket, and their presence at this stage of development has apparently prevented the cranial and visceral walls of the hypophysial fold from meeting and fusing with each other along the median line. The distal ends of the pharyngeal segments are connected by a transverse bar of tissue which is called by Haller the hypophysial bolster, but as it forms the dorsal border of the bucco-pharyngeal opening it will hereafter be referred to as the bucco-pharyngeal upper lip. It forms at this stage the actually dorsal wall of the external opening of Rathke's pocket, but after the cranial flexure has been reduced and the pocket reversed in direction, it lies postero-ventral to the opening of the pocket. A large transverse vein lies immediately dorso-posterior to it and is evidently the pituitary, and hence the canalis transversus of Gegenbaur's (1872) descriptions of the adult.

A group of procartilaginous cells has appeared in the pharyngeal segment of each mandibular arch and is called by Haller the posterior portion of the trabecula. It is unquestionably the polar cartilage of current descriptions of the adult, and the manner of its development, in the pharyngeal segment of the mandibular mesodermal arch, seems definite confirmation of my conclusion (Allis, 1923) that this cartilage is the pharyngeal element of the inner cartilaginous bar of the mandibular arch.

In a 20 mm. embryo of *Acanthias* described by Haller, the cranial flexure has been somewhat more reduced than in the 8 mm. embryo above referred to, and in connection with it the infundibulum has shifted somewhat dorso-posteriorly relatively to the underlying visceral tissues. As a result of this, Rathke's pocket has been swung upward and backward around its point of attachment to the bucco-pharyngeal upper lip and it is directed dorso-anteriorly at an angle of about 70° to the horizontal plane, its tip still being directed toward the tip of the bent-down crook-like anterior end of the notochord and separated from it by the median portion of the connecting cord between the premandibular somites. The pharyngeal segment of the mandibular arch has been swung upward and backward to the same extent as Rathke's pocket, and its proximal end is directed toward the ventral surface of the notochord, somewhat posterior to its crook-like anterior end. It lies at a considerable angle to the epal segment of the arch, the sigma-shape thus being already established in the dorsal half of this arch.

A mesodermal fold (Leiste), called by Haller the upper-jaw process, is said to have grown forward (actually ventrally) from the anterior edge of the dorsal end of the epal segment of each mandibular mesodermal arch, and to extend forward beneath the eye to the region between the orbit and the nasal capsule. There it turns mesially and ultimately meets and fuses in the median line with its fellow of the opposite side. A large depression is thus formed on the morphologically ventral but actually posterior surface of this part of the brain, bounded laterally and anteriorly by the upper-jaw processes, morphologically dorsally by cranial ectoderm and posteriorly (actually dorsally) by the anterior edge of the bucco-pharyngeal upper lip which has become considerably thickened. In later stages the fusion of the anterior ends of the upper-jaw processes of opposite sides is prolonged progressively posteriorly (actually dorsally) until the optic chiasma is passed. Beyond this point it is only the morphologically ventral edges of the processes that meet and fuse with each other in the median line and this continues until the hind ends of these ventral edges of the processes meet and fuse, excepting in the median line, with the anterior edge of the bucco-pharyngeal upper lip which has grown forward somewhat to meet them. A primarily external space is thus enclosed and forms the anterior portion of the hypophysial cavity, Rathke's pocket opening directly into its hind end and the cavity opening to the exterior through a short median, so-called hypophysial canal.

Two groups of procartilaginous cells have appeared in each upper-jaw process. In the deeper one of the two the anterior portion of the trabecula is said by Haller to develop, this being the trabecula of current descriptions of the adult. The other group lies ventral to the anterior portion of the trabecula and the cartilage that develops in it is called by Haller the upper-jaw cartilage. It is said to be primarily a wholly independent cartilage but to later fuse with the epimandibula, thus unquestionably being the palatine process of the palatoquadrate of the adult. These two cartilages lie definitely anterior to the mandibular arch and their topographical relations to the infundibular region of the brain and to the dorso-anterior end of the bucco-pharyngeal opening are those that the premandibular mesodermal tissues would normally have if, after being pressed downward by the descent of the infundibulum, the preoral gut had been withdrawn or dispersed. It therefore seems quite certain that these cartilages are of premandibular origin and it is probable that they represent, respectively, the dorsal and ventral halves of the entire arch, instead of being simply the pharyngeal and epal elements of that arch, as I have heretofore considered them to be.

In later stages of development the walls of the hypophysial canal coalesce and so form a solid strand of tissue which extends from the internal surface of the external ectoderm to the wall of the anterior division of the hypophysis. In still later stages this strand breaks down and is wholly dispersed. Its point of attachment to the ectoderm varies somewhat, and may be shifted quite far forward, this evidently being due to a greater forward growth of the bucco-pharyngeal upper lip (hypophysial bolster). When this takes place the strand extends dorso-posteriorly, passing in its course between the polar and trabecular cartilages, and if this were the earliest stage of development known, the preceding ones having been omitted or confused in ontogeny, the hypophysis would probably have been considered to have been developed in relation to a strand of tissue that grew inward from the deeper layer of the external ectoderm.

In these embryos, before the development of the maxillary processes, the mouth opening is pentangular in shape, its ventro-posterior borders being formed by the ventral halves of the mandibular mesodermal arches, its lateral borders by the dorsal halves of the same arches and its anterior border by the frontal surface of the head. The angle between the postero-ventral and lateral borders of either side of the opening lies at about the middle of the height of the alimentary canal and forms the angle of the gape, the angle between the lateral and anterior borders forming the lateral opening of the hypophysial fold and corresponding in position to the lachrymal groove of the mammalian embryo. When the maxillary processes develop, each process projects ventro-mesially from the anterior edges of the adjoining ends of the epal and pharyngeal segments of the mandibular arch, the morphologically anterior edge of the process fusing with the frontal surface of the head and completely closing the lateral opening of the hypophysial fold. This maxillary process of either side is formed by the premandibular mesodermal arch, but the dorsal and ventral ends of that arch have been brought close together by the compression of the related portion of the alimentary canal, as above explained, and it is the angle between the dorsal and ventral halves of the arch, and not the ventral end of the arch, that projects ventro-mesially toward its fellow of the opposite side. There is no mandibular cleft, unless it be that it forms part of the bucco-pharyngeal opening, as it probably does. The premandibular cleft, if it ever existed, must have lain in the median line between the premandibular arches of opposite sides, and have led from the anterior end of the preoral gut into the hypophysial fold somewhat ventral to its dorsal end. There is, in the Plagiostomi, no such opening between the fold and the canal, but there is in *Bdellostoma* and *Acipenser*, as will be later described.

CROSSOPTERYGII

The early development of these fishes is not known (Kerr, 1919).

In later, larval stages of *Polypterus* the hypophysial canal is said to extend from the roof of the buccal cavity to the cavity of the pars anterior of the hypophysis, thus corresponding to the hypophysial canal of embryos of the Plagiostomi. This canal is said to be present even in the adult *Polypterus*, but I found it completely closed in a 75 mm. embryo of *Polypterus senegalus* and also in several adult *Polypterus* that I examined in this respect (Allis, 1922).

The dermo-palatine of the adult turns mesially at its anterior end and meets its fellow of the opposite side in the median line, thus forming a transverse bar across the ventral surface of the chondrocranium that resembles topographically that formed by the palatine processes of the palatoquadrates of the Plagiostomi; and it will be later seen that it is probably this that has determined the opening of the hypophysial canal in the roof of the buccal cavity instead of on the dorsal surface of the snout.

CYCLOSTOMATA

Bdellostoma

Several early stages in the development of *Bdellostoma stouti* are described by v. Kuppfer (1900), but as he did not have a full series of embryos suitable for sectioning, the development of the hypophysial region is not completely and definitely given either in the figures or the descriptions. Certain features of its development, as given by him, are however important and must be briefly considered.

In the earliest embryo described the anterior portion of the brain is deeply embedded in the dorsal surface of the egg, but separated from it by a scoop-shaped fold of the external ectoderm which extends posteriorly, as a fold open laterally on either side, from the lobus olfactorius impar to the region of the recessus preopticus, the alimentary canal extending forward to the latter point. This fold of this fish thus corresponds to the fold that in early embryos of *Acanthias* I have considered to be formed by the complete fusion of the anterior portions of the naso-hypophysial and head folds. The head fold does not in this embryo extend posteriorly beyond this point. The naso-hypophysial fold is, however, prolonged posteriorly by a median pocket-like extension which forces its way between the anterior end of the alimentary canal and the overlying portion of the brain, and extends as far as the anterior end of the infundibular depression. This pocket-like extension of the fold is called by

v. Kuppfer the primary mouth. It presses against the dorso-anterior corner of the anterior end of the alimentary canal and forces it downward and backward, the apposed surfaces forming a transverse membrane which extends from the floor to the roof of the alimentary canal and is called by v. Kuppfer the primary Rachenhaut

There is said to be no cranial flexure in this embryo, but the infundibulum nevertheless lies below the level of the more posterior portion of the floor of the brain and its ventral surface is presented ventro-posteriorly. The anterior corner of this surface projects ventrally and has pressed against the underlying portion of the alimentary canal, there forming on its dorsal surface an angular depression which lies slightly posterior to the anterior end of the canal. This part of the alimentary canal of this fish is thus strictly homologous with the preoral gut of the 2·7 mm. embryo of *Acanthias*.

In the oldest embryo described by v. Kuppfer, the prehypophysial portion of the naso-hypophysial fold has been completely separated from the corresponding portion of the head fold by the development of longitudinal laminar processes, one on either side, which project mesially and meet and fuse with each other in the median line, thus converting the primarily open naso-hypophysial fold into a closed canal. The head fold has been prolonged posteriorly and abuts against the anterior portion of the ventral surface of the fore-gut, the two apposed surfaces forming a membrane which is the homologue of the bucco-pharyngeal plate of the Plagiostomi but is called by v. Kuppfer the secondary Rachenhaut. The hypophysial portion of the naso-hypophysial fold has been prolonged posteriorly from the anterior to the posterior end of the infundibulum, and has to the latter the topographical relations of Rathke's pocket. A perforation in the floor of the naso-hypophysial canal leads directly into the fore-gut and is the pharyngeal opening of the canal of the adult.

Comparing the conditions in this embryo with those in the earlier embryo above described, the conditions in the former would seem to have been directly derived from those in the latter by the simple posterior prolongation of the pocket-like extension of the naso-hypophysial fold from the anterior to the posterior edge of the infundibular depression and the breaking through of the primary Rachenhaut. The conditions in early embryos of *Acipenser*, to be described below, strongly suggest that this is what has actually taken place, but the conditions described by v. Kuppfer in embryonic stages of *Bdellostoma* intermediate between the two above referred to are unfavourable to this view. The descriptions of the latter embryos are, however, not complete and definite and are therefore here left out of consideration, the important feature in the present discussion being that the naso-hypophysial canal is always hollow throughout its entire length and at no time represented in any part by a solid strand of tissue.

In the oldest embryos described the anterior end of the naso-hypophysial canal is shown completely closed in median sagittal section. This section must therefore have passed through the septum that in the adult separates the nasal apertures of opposite sides, these apertures lying on the ventral surface of the anterior end of the snout.

Petromyzontidae

In a 5-day old embryo of *Petromyzon planeri* the anterior end of the head is somewhat lifted above the surface of the egg and the brain is solid (v. Kuppfer, 1894, fig. 1; Plate I). The anterior end of the chordal portion of the floor of the brain is bent downward and the prechordal portion is bent relatively upward, as in the Plagiostomi. The anterior end of the roof of the fore-gut is bent downward in an evenly curved line and the preoral gut compressed, the anterior end of the latter gut extending forward to the region of the recessus preopticus. There is no indication of a plica encephali ventralis in this embryo, and when it later develops it is narrow and slit-like instead of being, as in the Plagiostomi, broad and widely open.

The anterior portion of the naso-hypophysial and head folds are completely fused with each other, as they are in early embryos of *Bdellostoma* and the Plagiostomi, and the so-formed fold extends posteriorly to the region of the recessus preopticus. There the head fold separates from the naso-hypophysial one and is prolonged posteriorly beneath the preoral gut and ends in a broad and shallow buccal depression, the bottom of which later becomes apposed to the ventral surface of the fore-gut to form the bucco-pharyngeal plate. The naso-hypophysial fold is not prolonged, as a fold, beyond the point where the head fold separates from it; but, exactly in the place of the pocket-like posterior extension of the fold in embryos of *Bdellostoma*, there is a solid conical thickening of the deeper layer of the ectoderm, the point of which projects posteriorly between the anterior end of the preoral gut and the overlying portion of the brain. This thickening is generally considered to represent the beginning of a strand-like and wholly independent ingrowth of the cells of the deeper layer of the ectoderm, but its even and unbroken outlines are characteristic of a fold and not of an independent ingrowth of individual cells. Furthermore, comparison with the conditions in *Bdellostoma* and the Plagiostomi, and more particularly with those in early embryos of *Acipenser*, would seem to establish definitely that this thickening was primarily, in ancestors of this fish, a fold, the walls of which have been pressed together and have so completely fused with each other that all indication of the pre-existing cavity has been obliterated. This thickening is later either prolonged posteriorly beneath the infundibulum, or the infundibulum shifts forward above it, and the hypophysis develops in the deeper portion of the strand. It will, therefore, hereafter be referred to as the hypophysial strand.

In later stages, the bucco-pharyngeal upper lip grows forward to the anterior end of the snout, as shown in v. Kuppfer's figures and as fully described by de Beer (1923). It grows forward between the head fold and the prehypophysial portion of the naso-hypophysial fold, completely separating them. It fuses laterally, on either side, with the overlying cranial ectoderm, a deep pit thus being cut out of the median portion of the primarily open naso-hypophysial fold. This pit is called by de Beer the hypophysial depression, and is considered by him and also by Woerdemann (1915) and G. Haller (1923) to be the homologue of Rathke's pocket, but the development in this fish, when compared with that in *Bdellostoma* and the Plagiostomi, would seem to definitely establish that Rathke's pocket is contained in some part of the hypophysial portion of the naso-hypophysial fold and hence in some part of the hypophysial strand of *Petromyzon*. The pit of *Petromyzon* may therefore be called the prehypophysial pit.

In older embryos the deeper end of the hypophysial strand becomes enlarged, a central cavity appears in it and the hypophysis develops in relation to its dorsal wall, the ventral wall remaining membranous (de Beer, 1926). During metamorphosis this hypophysial cavity becomes prolonged posteriorly beneath the anterior end of the notochord and prolonged anteriorly in the hypophysial strand until it reaches and opens into the bottom of the prehypophysial pit. The naso-hypophysial canal of the adult is thus formed, and it is evidently the homologue of the similarly named canal of *Bdellostoma*, notwithstanding that it is developed in a somewhat different manner and does not open at any time into the underlying alimentary canal.

The development of the mandibular and premandibular mesodermal arches is not particularly described, but it seems evident that the posterior portion of the so-called trabeculo-palatine bar of this fish is developed in the pharyngeal segment of the mandibular arch and is hence the polar cartilage. The premandibular arch is said by Haller to have been carried bodily forward by the marked development of the upper lip of the fish. The anterior portion of the trabeculo-palatine bar evidently develops in this arch and quite probably corresponds to the trabecula of the Plagiostomi together with the palatine process of the palatoquadrate. The premandibular arches primarily encircled the preoral gut, just as the more posterior arches encircle the related portions of the alimentary canal. It would therefore be wholly natural and normal that the premandibular cartilaginous bars of this fish should meet and fuse with each other beneath the naso-hypophysial canal, as the trabeculo-palatine bars actually do both in this fish and in *Bdellostoma*.

CHONDROSTEI

In a figure of a median sagittal section through the head of a 45-hour old embryo of *Acipenser sturio* given by v. Kuppfer (1893) the naso-hypophysial and head folds are shown widely separated from each other by the bucco-pharyngeal upper lip, that lip extending forward to the anterior end of the snout and its anterior end being greatly enlarged to form what v. Kuppfer calls the Haftscheibe. The head fold is simply a broad and shallow buccal depression which v. Kuppfer calls the mouth (Mund). Because of the already completed growth forward of the bucco-pharyngeal upper lip the naso-hypophysial fold has been reduced to a median canal called by v. Kuppfer a pocket (Schlauch).

The cells of the walls of this canal (pocket) still retain their radial arrangement and have not fused with each other, but they have been pressed so closely together that the cavity of the canal is completely obliterated except at its outer and inner ends. The walls of the canal arise from the deeper layer, only, of the external ectoderm, the external layer of the ectoderm passing unbroken across the mouth of the canal but there being pressed inward to form a small median conical pit. The deeper end of the canal abuts against and has completely fused with the dorsal wall of the alimentary canal, and the membrane that must primarily have separated the two canals has completely broken down. A small sharply pointed diverticulum of the alimentary canal extends outward a short distance between the walls of the naso-hypophysial canal and apparently represents the preoral gut. What v. Kuppfer considers to represent this latter gut lies ventral to the bucco-pharyngeal upper lip (Haftscheibe) and hence cannot be the primitive anterior prolongation of the alimentary canal.

The anterior end of the brain curves downward through about 45°, and that part of it that lies anterior to the notochord has been somewhat prolonged. The anterior end of the brain, as seen in median sagittal section, extends from the lobus olfactorius impar to what is apparently the hind end of the infundibulum, is of the same length as the naso-hypophysial canal and abuts against or closely approaches it throughout its entire length. The anterior end of the brain of this fish thus has the appearance of being deeply embedded in the dorsal surface of the egg, as it is in the earliest embryo of *Bdellostoma* above considered, and if in the latter embryo the bucco-pharyngeal upper lip had already grown forward to the anterior end of the snout and the so-called primary Rachenhaut of v. Kuppfer's description had already broken through, the conditions would strikingly resemble those in the embryo of *Acipenser*.

In later stages of development the deeper end of the naso-hypophysial canal becomes separated from the dorsal wall of the alimentary canal and is somewhat prolonged dorso-posteriorly beneath the infundibulum, there becoming enlarged to form the hypophysis, the remainder of the canal breaking down and being dispersed. In these embryos the so-called Haftscheibe shifts somewhat ventro-posteriorly and lies on the ventral surface of the snout and the barbels are said to develop in relation to it, these barbels being considered to be the homologues of the adhesive organs of *Amia* and *Lepidosteus.* It however seems probable that they are the homologues of the maxillary breathing valves of the latter fishes.

The anterior end of the head of this fish not having been lifted above the dorsal surface of the egg, and not being prolonged anteriorly beyond it, it is probable that the pharyngeal segment of each mandibular mesodermal arch is directed dorsally or dorso-posteriorly. The polar cartilage, which develops in this segment, would therefore fuse with the anterior end of the parachordal plate instead of with its ventral surface, and it is so shown by de Beer (1925) in a figure of the chondrocranium of a 5-day old embryo of this fish. Sewertzoff

(1928) however says that this cartilage fuses with the ventral surface of the parachordal plate.

The bucco-pharyngeal upper lip, in growing forward, must necessarily either push apart or disperse the premandibular tissues in which, in the Plagiostomi, the palatine processes of the palatoquadrates are developed, and in *Acipenser* these tissues have apparently been dispersed, for the palatoquadrates of this fish are without definite palatine processes. The cartilage called by Parker (1882) the metapterygoideus, is probably developed in relation to the mandibular arch (Allis, 1930), and hence lies posterior to the bucco-pharyngeal upper lip. It would therefore not be displaced by the forward growth of that lip, and there would be nothing to interfere with its meeting and fusing in the median line with its fellow of the opposite side, as it actually does.

HOLOSTEI

In an early embryo of *Amia* described by Reighart and Phelps (1908) and also by Reighart and Mast (1908) the neural canal still lies flat on the dorsal surface of the egg, the neuropore (lobus olfactorius impar) at its anterior end. As the brain develops, its so-called anterior surface accordingly becomes embedded in the dorsal surface of the egg throughout its entire extent, as it does in *Acipenser* and the Cyclostomata. The ectoderm is thickened at the neuropore, and this thickening extends antero-ventrally to form what Reighart and Mast call the fundament of the hypophysis, but which is more properly the fundament of the naso-hypophysial canal. Immediately antero-ventral to this fundament there is a slight crescentic elevation which forms the fundament of the adhesive organ. Immediately beyond this the buccal depression (stomodaeum) later develops. The alimentary canal extends forward to the region of the crescentic elevation and there presents three evaginations, one median and a lateral one on either side, their outer ends coming into contact with the ectoderm immediately beneath the crescentic elevation.

In later stages the crescentic elevation above described separates into three parts, a median button and a U-shaped elevation on either side, each of the latter of which represents one half of the adhesive organ. The button and the related evagination of the alimentary canal later break down and become dispersed. Each of the lateral evaginations becomes constricted off from the alimentary canal and separates into several parts, each of which acquires an opening to the exterior by the breaking through of the ectoderm with which it is in contact. The buccal depression (stomodaeum) comes into contact with the ventral surface of the alimentary canal posterior to these evaginations, and the bucco-pharyngeal plate so formed breaks through to form the bucco-pharyngeal opening. That part of the alimentary canal that lies anterior to this opening is therefore the preoral gut, and it later breaks down and is dispersed. The fundament of the naso-hypophysial canal has in the meantime grown inward as a solid strand until it reaches the ventral surface of the infundibulum. Close to its outer end it is in contact with the dorso-posterior surface of the button and the related evagination of the preoral gut, but it does not elsewhere come into contact with the alimentary canal.

Comparing the conditions in these embryos with those in *Petromyzon*, it is evident that the naso-hypophysial strand of *Amia* corresponds in its relations to the brain and to the bucco-pharyngeal upper lip to the prehypophysial pit of *Petromyzon* together with the hypophysial strand of that fish. The enlarged anterior end of the upper lip, which bears the adhesive organ, is generally considered to be the homologue of the anterior end of the upper lip of *Petromyzon*, which would imply that the stage of development represented in the 5-day old embryo of *Petromyzon* had been omitted in the ontogenetic development of *Amia*.

The growth forward of the bucco-pharyngeal upper lip has apparently pushed to either side the anterior ends of the premandibular tissues in which the palatine processes of the palatoquadrates develop, and these processes are directed anteriorly instead of, as in the Plagiostomi, transversely beneath the trabeculae. In connection with this a maxillary breathing valve has been developed, and it has the topographical relations to the enlarged anterior end of the bucco-pharyngeal upper lip that the tentacles of *Acipenser* have, and also the same relations to that lip that the reflexed antero-ventral edge of the upper lip of *Petromyzon* has; this suggesting that these several structures are homologous. The tentacles of *Acipenser* would then not be the homologues of the adhesive organs of the Holostei, this being as Sawadsky (1912) has, for other reasons, concluded. A maxillary breathing valve could accordingly only be present in fishes in which the bucco-pharyngeal upper lip extends forward to the end of the snout, and it has in fact not been described, so far as I can find, in any of the Plagiostomi. I formerly concluded (Allis, 1900) that it was present in rudimentary form in *Polypterus*, but this is evidently incorrect, for the naso-hypophysial canal of this fish opens in the roof of the buccal cavity, as it does in the Plagiostomi.

TELEOSTEI

In an early embryo of *Hippocampus* described by Dohrn (1881) the alimentary canal is shown extending forward slightly beyond the tip of the notochord. Beyond that point the line of the canal is continued by a band of tissue which extends forward to the anterior end of the head and is there in contact with the deeper layer of the ectoderm at the bottom of a slight depression which represents the beginning of the development of a head fold. Dohrn says that it was impossible to determine whether the cells of this line of tissue were of ectodermal, endodermal or even mesodermal origin. The hypophysis is said to develop in that part of this line that lies directly beneath the infundibulum and to be double at its origin, one part lying on either side of the median line. It is said to lie anterior to the mandibular cleft (mandibulare Spalte), the latter cleft extending upward behind the eyeball to the level of the dorsal ends of the more posterior visceral clefts.

Comparing the conditions in this embryo of *Hippocampus* with those in early embryos of *Bdellostoma*, it is evident that that part of the band-like line of tissue above described that lies anterior to the hypophysis must correspond to the prehypophysial portion of the naso-hypophysial fold of *Bdellostoma* together with that pocket-like prolongation of the fold that reaches and fuses with the anterior end of the preoral gut. The hypophysis of *Hippocampus* would then correspond to that prolongation of the pocket of *Bdellostoma* in which the hypophysis develops, and in the latter fish, as in *Hippocampus*, it is primarily double. That part of the line of tissue that lies posterior to the hypophysis would then be the preoral gut. The buccal depression and the bucco-pharyngeal plate are not yet indicated, for the head fold has not yet been sufficiently developed to bring the external ectoderm in contact with the ventral wall of the fore-gut. When the latter plate develops, it must lie immediately anterior to the ventral ends of the mandibular mesodermal arches, between them and the hind end of the preoral gut.

In a slightly older embryo of *Hippocampus* the ventral ends of the visceral arches are said to have shifted forward relatively to the overlying portion of the brain, the ventral ends of the mandibular arches lying near the anterior end of the embryo and considerably anterior to the hypophysis. The head fold has been somewhat deepened and extends posteriorly beyond the mandibular arches to about the middle of the ventral ends of the hyal arches. The alimentary canal is shown extending forward as a thin band-like structure to the anterior edge of the mandibular mesodermal arches. There it curves ventrally, expands somewhat, and its walls become continuous with the deeper layer of the ectoderm, that layer breaking through at this point but the external layer of the ectoderm passing over it unbroken. The hypophysis remains directly beneath the infundibulum and is there connected by a stalk with the dorsal surface of the band-like portion of the alimentary canal.

Comparing the conditions in this embryo with those in the earlier one above described, the first impression is that the anterior prolongation of the alimentary canal of the older embryo is simply an extension of the cavity of that canal in the line of tissue that I have considered to represent the preoral gut together with the naso-hypophysial fold. This is however evidently improbable, for if it were so the mouth of *Hippocampus* would correspond to the so-called primitive mouth of v. Kuppfer's description of *Bdellostoma*. It is therefore quite certain that the fore-gut has simply shifted forward to the same extent as the related portions of the visceral arches, and that the line of tissue that, in the earlier embryo described, apparently represented the preoral gut together with the naso-hypophysial fold has either been crowded forward to the anterior end of the snout, or broken down and dispersed. The bucco-pharyngeal plate would then lie immediately anterior to the ventral ends of the mandibular mesodermal arches, the tissue of the premandibular arches would lie anterior to this, and the conditions would be, in principle, as in the other fishes above considered. In later stages a small buccal depression develops in the external layer of the ectoderm and when it breaks through, the definitive bucco-pharyngeal opening is formed.

In a 49-day old embryo of *Salmo salar* described by Lundborg (1894) the brain is shown prolonged anteriorly considerably beyond the notochord, and a deep head fold extends posteriorly beneath it and meets and fuses with what has the appearance of being the anterior wall of the alimentary canal, but is certainly, as in the other fishes above considered, the anterior portion of the ventral surface of the fore-gut. The plate so formed extends from below dorso-posteriorly, instead of dorso-anteriorly, and is called by Lundborg the lower jaw, but it is certainly, the bucco-pharyngeal plate and is so designated (Rachenhaut) by B. Haller, as described immediately below. The long dorsal wall of the head fold later becomes the roof of the buccal cavity, and slightly anterior to the bucco-pharyngeal plate, and directly beneath the infundibulum, two pocket-like invaginations of the deeper layer of the ectoderm are said by Lundborg to develop, one on either side of the median line and close to it. The external layer of the ectoderm is said to later break through, the cavities of the two pockets then opening directly to the exterior. These two invaginations then fuse with each other and form the hypophysis, the ectoderm becomes continuous beneath it, and the hypophysis is connected with the deeper layer of the ectoderm by a solid stalk which later breaks down and becomes dispersed. No preoral gut is either described or shown in the figures, but a line of scattered cells is said to extend forward from the hypophysis, thus corresponding to what I have considered to be the naso-hypophysial fold of Dohrn's descriptions of his earliest embryo of *Hippocampus.*

In a 4 mm. embryo of *Salmo irideus* B. Haller (1896) describes a head fold similar to that in *Salmo salar*, and the hind end of the fold, where it abuts against and fuses with the wall of the alimentary canal, is called by him the Rachenhaut (bucco-pharyngeal plate). The hypophysis is said to first appear as a thickening of the ectoderm that forms the dorsal wall of the head fold, at a point slightly anterior to the dorsal edge of the bucco-pharyngeal plate, but it soon separates completely from that ectoderm excepting where a short and solid stalk connects the two. No invagination of the ectoderm is described, the latter always remaining even and unbroken. A short diverticulum is said to extend forward from the dorsal wall of the alimentary canal immediately posterior to the dorsal end of the bucco-pharyngeal plate and to closely approach both the hypophysis and the infundibulum, but not to come into contact with either of them.

Dohrn says that in the Teleostei examined by him the mandibular clefts first broke through laterally and that these two openings were extended ventrally until they met and fused with each other in the median line; and Platt (1891) describes similar conditions in *Batrachus tau.* Lundborg, however, did not find these lateral openings of the clefts in any of the Teleostei examined by him, and he thinks that those described by Dohrn were artifacts due to the reagents used. If the walls of the mandibular visceral pouches take some part in the formation of the bucco-pharyngeal plate, as seems quite probable, there would be nothing improbable in the plate breaking through at its lateral edges before it did in the median line.

There is in the Teleostei, as in *Amia*, a maxillary breathing valve and, as also in the latter fish, the palatine processes of the palatoquadrates are directed anteriorly instead of transversely beneath the trabeculae.

Comparing the conditions in these fishes with those in the other fishes above considered, it seems practically certain that there was primarily in them, as in *Acipenser* and *Amia*, a naso-hypophysial canal or strand, and that its development has simply been slurred over or completely suppressed in ontogeny. The connection of the hypophysis with the dorsal wall of the alimentary canal of *Hippocampus* and with the dorsal wall of the buccal cavity in *Salmo* would then be of secondary origin.

SUMMARY AND CONCLUSIONS

The hypophysis develops in the deeper part of what is primarily either an open fold of the external ectoderm (Plagiostomi), a pocket-like extension of such an open fold (*Bdellostoma*), or a pocket or solid strand that arises as an infolding or ingrowth of the deeper layer only of the ectoderm, the external layer of the ectoderm passing over it unbroken (*Petromyzon, Acipenser*, Teleostomi). The hypophysis never arises, in any of the fishes here considered, in relation to a simple pit-like invagination of both layers of the ectoderm.

This fold, pocket or strand may be called the naso-hypophysial. It extends, when fully developed, from the lobus olfactorius impar (neuropore) to the hind end of the infundibulum, and lies, throughout its entire extent, in close proximity to that part of the cranial wall. It never extends posteriorly beyond the infundibulum and may be said to present two regions, a hypophysial and prehypophysial, the line between the two lying somewhere in the region between the recessus preopticus and the anterior end of the infundibular depression. The hypophysial portion, when it reaches the ventral surface of the infundibulum, there receives a nervous strand that grows outward from the latter.

The dorsal wall of the deeper portion of the fold, pocket or strand always lies, in all of the fishes considered, immediately beneath the ventral surface of the infundibulum.

The morphologically ventral surface of the deeper portion of the fold, as found in the Plagiostomi, lies against the ventral surface of the preoral portion of the alimentary canal. This type of fold and the related hypophysial pit (Rathke's pocket) are only developed when, in early embryonic stages, the head is lifted sufficiently above the dorsal surface of the egg to permit the swinging downward and backward of the anterior surface of the brain around the anterior end of the preoral gut. There is never, in any of the Plagiostomi here considered, any communication between the cavities of the fold and the canal. An apparently secondary and indirect communication is, however, said to occur in *Torpedo*, where there is a pair of so-called proboscis pores, each of which extends from Rathke's pocket to the premandibular head cavity of its side.

The conditions in early embryos of the Crossopterygii are not known. In all of the other non-elasmobranchian fishes considered the head is not sufficiently lifted above the dorsal surface of the egg in early embryonic stages to permit the swinging downward and backward of the infundibulum around the anterior end of the alimentary canal, and furthermore the infundibulum does not shift forward beyond the anterior end of the canal. The ventral surface of the deeper portion of the hypophysial pocket or strand of these fishes accordingly lies actually or morphologically dorsal to the preoral gut and the cavities of the pocket and gut may be, at certain stages of development, directly continuous with each other (*Bdellostoma, Acipenser*).

The tip of the hypophysial fold, pocket or strand apparently always lies at the point where the cranial and visceral ectoderms meet and are continuous with each other.

The prehypophysial portion of the naso-hypophysial fold is always either completely fused with the dorsal surface of the related portion of the head fold, or separated from that fold by the bucco-pharyngeal upper lip which is, in the Cyclostomata, of secondary origin. In the Chondrostei and Teleostomi this lip is found *in situ* in the earliest embryos described.

Considering the conditions in these several fishes the suggestion is evident that there was primarily a visceral cleft in the median line between the premandibular arches of opposite sides, and whether there were one or more of these premandibular arches is unimportant in so far as this is concerned. This unpaired premandibular cleft is later reduced and finally suppressed as a result of the development of the fore-brain and the related descent of the infundibulum. A bucco-pharyngeal opening is then developed in the floor of the alimentary canal between the ventral ends of the mandibular and premandibular mesodermal arches, the hypophysis developing in some relation to the premandibular cleft.

The polar cartilage of either side is the pharyngeal element of the related mandibular arch, the trabecula and the palatine process of the palatoquadrate apparently being, respectively, the entire dorsal and ventral halves of the premandibular arch.

The descent of the infundibulum compresses the underlying premandibular (preoral) portion of the alimentary canal and causes its ultimate breakdown and dispersion. As a result of this, the related portion of the notochord is greatly reduced or completely suppressed, and the dorsal end of the premandibular arch (trabecula) loses its connection with the axial skeleton and acquires connection with the distal end of the polar cartilage (pharyngo-mandibula).

When in early embryos the anterior portion of the head is embedded in the dorsal surface of the egg, the polar cartilage fuses with the anterior end of the related parachordal, but when the head is raised above the surface of the egg and prolonged anteriorly beyond it, the polar cartilage fuses with the ventral surface of the parachordal.

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