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ON THE ORIGIN OF THE CENTRAL NERVOUS SYSTEM OF VERTEBRATES.

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Of the three possible methods—anatomical, physiological, and embryological—of investigating the nature of the invertebrate nervous system from which the vertebrate sprang, the last is in great favour at the present day partly because it is a novelty and partly because it is considered to be a fact that ontogeny reproduces more or less the phylogenetic history. If we glance at the theories which have been held about the origin of the central nervous system we find a distinct difference of view corresponding with the incoming of embryological teaching. The older ideas, based on anatomical and physiological comparisons, before the birth of embryological conceptions, pointed directly to the evolution of the vertebrate nervous system from such invertebrates as the Arthropoda; such comparisons are well exemplified by the writings of Newport in the *Phil. Trans.* of 1834 and 1843, and were defended and extended by Leydig¹ even as lately as 1864.

The newer school of morphologists have disregarded these comparisons and attempted to find the origin of the vertebrate in such forms as the Tunicates, the Nemertines, Balanoglossus, &c. The reason for the change of view has been not only the embryological evidence leading to the transmu-

¹ F. Leydig., *Bau des thierischen Körpers*, Tübingen, 1864.

nation of Vertebrata into a group of the Chordata, but also the difficulty of reconciling the homologies which apparently exist between the different parts of the nervous system in Vertebrata and Arthropoda, with the complete failure of any attempt to discover in the vertebrate any trace of an invertebrate alimentary canal passing between the supra- and infra-œsophageal ganglia.

Yet it appears to me that the resemblances, both anatomical and physiological, between the central nervous system of Arthropoda and Vertebrata, not only as given by Leydig, but as discovered since, are too strong to be lightly disregarded.

Leydig¹ looks upon the vertebrate brain as corresponding not only to the supra-œsophageal ganglia of the Arthropoda, but to the supra- and infra-œsophageal ganglia taken together, so that the parts of the vertebrate brain correspond to the parts of the invertebrate, if we imagine that the brain was pierced by an œsophagus between the crura cerebri. With this idea as groundwork, he then attempts to follow out the resemblances between the brains of Arthropoda and Vertebrata, in the same manner as, but more fully than, Treviranus, Newport and others had already done, without however attempting to account for the disappearance of the original œsophagus; he comes to the following conclusions.

In insects the brain consists of a number of swellings, all of which are paired; the foremost pair are the lobes from which the antennæ spring—these are equivalent to the lobi olfactorii of vertebrates; the next pair are the main cerebral ganglia, from which the optic lobes can separate as special lobes. The œsophageal commissures are the crura cerebri, and the infra-œsophageal ganglia correspond to the cerebellum and medulla oblongata, from which arise the nerves for the mouth parts.

He then asserts that not only does this resemblance of position exist, but also that Bergmann and Leuckart are wrong in considering the supra-œsophageal ganglia as structurally the same as the lower ganglia of the ventral chain; on the contrary, the structure of the nervous system becomes

¹ *Op. cit.* p. 185.

more complicated as we pass from the ventral chain of ganglia into the infra-oesophageal and supra-oesophageal ganglia, and in the latter especial structural peculiarities exist, so that a structural difference exists between the brain and ventral chain of the Arthropoda, just as between the brain and spinal cord of vertebrates.

Further¹ he points out that physiological as well as anatomical resemblances have been shown to exist; thus he quotes Faivre, who, working on *Dytiscus*, says, if the brain lobes are removed the animal can walk and swim, but the will to move and the power of regulating the direction are gone. If further the infra-oesophageal ganglia be removed as well, then the animal can still move all its legs but cannot co-ordinate or regulate its movements, so that it can no longer carry out any proper walking or swimming movements.

According then to Leydig in 1864, the brain of the arthropod corresponds to that of the vertebrate in that they both consist of three separate parts which correspond in anatomical position and in physiological significance. They both possess special paired ganglion masses, in the absence of which the will to execute movements is lost. These might in both cases be called the cerebrum or fore-brain. They both possess special paired ganglion masses connected with vision; these might in both cases be called the optic lobes, if we include in that term the optic thalami, and speaking generally, this part might be called the mid-brain. They both possess special nerve structures, in the absence of which co-ordination of movements for such acts as walking or swimming is no longer possible; these might in both cases be called the hind-brain.

Since this time evidence has been accumulating to confirm and strengthen the position taken up by Treviranus, Newport, Leydig and others. Thus to give one or two examples, I would refer to Bellonci's² paper on the brain of *Spharoma serratum*, where he describes the supra-oesophageal ganglia as consisting of a superior segment, a

¹ *Op. cit.* p. 187.

² 'Archiv. Ital. de Biologie,' vol. i., p. 176. (See Fig. 1, Pl. 1.)

middle segment, and an inferior segment. The superior segment constitutes the cerebrum and may be looked upon as the cerebral hemispheres or fore-brain; the middle segment gives origin to the optic nerves and to the olfactory nerves, and may be looked upon as the mid-brain and optic thalami; the inferior segment is not strictly speaking supra-oesophageal, but is situated on the oesophageal commissures and consists especially of a ganglion on each commissure which is the stomatogastric ganglion and gives origin to the nerves of the alimentary canal; in addition the nerves of the external antennæ arise from this region. Upon the assumption that the crura cerebri represent the oesophageal commissures, then, as I have pointed out in my last paper, we may perhaps compare the stomato-gastric ganglion with the cells of the *substantia nigra*, and may look upon the infra-oesophageal ganglia, together with this inferior segment of Bellonci, as constituting the hind-brain.

We see then that not only the more ancient but also the more modern researches indicate an anatomical separation of the brain of a crustacean into three parts, which correspond in relative position to the fore-brain, mid-brain with optic thalami, and hind-brain of the vertebrata.

From the physiological side the evidence is still stronger; if we take first the fore-brain or cerebral hemispheres we may use the phraseology of Hughlings Jackson and speak of them as connected with the spinal cord nervous system by a well-defined system of nerve tracts or commissures which are extrinsic to the level of the spinal cord system; now one of the most striking peculiarities of this higher level system is its inhibitory power over the activity of the lower centres.

Taking next the second division, *i.e.*, the optic lobes with the optic thalamus, we see clearly that here is the centre for the nerves of vision, and that also in the past history of the vertebrate there existed in connection with that part of the optic thalamus known as the ganglion habenulæ an extra visual organ of an invertebrate type, *viz.*, the pineal eye; also if Hill¹ is right the ultimate origin of the olfactory nerves is to be found in the optic thalamus.

¹ Hill 'Plan of the Central Nervous System,' Cambridge, 1885.

In the third place the cerebellum with the pons varolii and the semi-circular canals are recognised universally as that part of the brain which is especially concerned in the maintenance of the equilibration of the body and in the co-ordination of such complicated movements as walking, swimming, &c.

Evidence as to the seat of the corresponding functions in the brain of Arthropods is given in a most able paper by Ward¹ upon the brain of the crayfish, in which he shows that section of the œsophageal commissures not only removes the power of the will over the movements of the animal, but also removes powerful inhibitory influences which normally pass down from the supra-œsophageal ganglia to the lower centres, as is evidenced by the unceasing rhythmical movement of the appendages after separation of the supra-œsophageal ganglia. Such influences may pass from the superior segment of Bellonci, which I have compared to the cerebral hemispheres, or from the middle segment which corresponds to the optic lobes and optic thalami. At present we cannot separate these two with respect to their inhibitory power. Physiologically, then, the superior segment of the supra-œsophageal ganglion corresponds to the cerebral hemispheres, especially if we take into account at the same time the function of the closely-connected optic part of the brain. So also the middle segment, which gives rise to the optic and olfactory nerves, clearly corresponds to the optic lobes and optic thalami as far as function is concerned.

Ward's experiments also confirm Leydig's view as to the functions of the sub-œsophageal ganglia; he concludes that the second or sub-œsophageal ganglia have functions so nearly equal in importance to the supra-œsophageal as to justify Leydig's comparison of the two together with the brain of a vertebrate pierced by an œsophagus between the crura cerebri, and he proves that the sub-œsophageal ganglia are the centres *par excellence* for co-ordinating the movements of the limbs. We see then that Bellonci's inferior segment together with the sub-œsophageal ganglia, correspond physiologically to the region of the cerebellum and pons varolii;

¹ Ward *Journ. of Physiol.*, vol. II.

nor is this all, for so close is the parallelism between the two that even the curious part played by the semi-circular canals in the maintenance of the equilibrium of the body finds its counterpart in the functions of the otocysts of the crustaceans. This observation has been made by Delage¹ who has found that the removal of the otocysts at the base of the antennæ in various decapods is followed by distinct disturbances of equilibration.

Delage goes so far as to draw a direct comparison between the otocyst and the membranous labyrinth of the vertebrate ear. He says,² "The otocysts represent in a stage of imperfect development, the membranous labyrinth of the vertebrates. We see in fact that in the latter the semi-circular canals and cochlea exist only in the higher classes; as we descend in the scale we see that the cochlea becomes simpler and simpler and finally disappears, while the semi-circular canals are greatly reduced in the lowest fishes (Myxine). It is therefore clear that in spite of its complication the membranous labyrinth of the vertebrates is derived from a single vesicle with smooth walls, in all respects similar to an otocyst; a further proof of this is given by the evidence of the ontogenetic development of that organ."

He then goes on to say in what way he imagines that the double function of the auditory organ may have arisen phylogenetically. "The function of the simple auditory vesicle of the primitive vertebrate, like the otocyst of the invertebrate, must have been for the purpose of perceiving noises (bruits), and of regulating locomotion. It would then become separated into two parts, each of which was told off for one of these functions, the saccule for the first, the utricle for the second. Then little by little diverticula would be developed from the central parts: the cochlea to perceive sounds (sons), with their qualities of pitch (hauteur) and timbre, no longer mere noises differing from each other only in intensity; and the semi-circular canals, perhaps for the purpose of co-ordinating the movements of the eyes with those of the head, so as to get rid of the visual illusions,

¹ Delage, "Archiv. de Zoolog. experiment. et generale," vol. v. 1887.

² *Op. cit.* p. 22.

which are produced upon movements of the head when the eyes are immoveable."¹

So far we may sum up as follows: the nervous systems of the Crustacea and Vertebrata resemble each other in the following particulars. In both cases the fore part of the brain forms a distinct cerebrum, removal of which removes the will power of the animal and makes it a more or less elaborate reflex machine. In both cases this cerebrum has special inhibitory power over the lower centres. In both cases a special part of the brain, in close connection with the cerebrum, is set apart for the origin of the nerves of sight and smell. In both cases this fore-part of the brain is connected with the hind-part of the brain by means of commissural tracts known respectively as the œsophageal commissures and the crura cerebri. In both cases the hind-part of the brain is concerned in the maintenance of the equilibrium of the animal. In both cases the auditory capsule contains not only the organ of hearing but special apparatus subservient to the maintenance of the equilibrium of the animal.

Further if we consider those nervous elements which we have classed together as being of the same level as the elements of the spinal cord, we find in the vertebrate, as I have pointed out previously,² that we are dealing with nerve structures which form the origin of a series of segmental nerves, and also the central inter-segmental communications of such neuromeres. I will not here give again in detail the arguments which I have already used, to show how the segmental cranial nerves are built up on the same plan as the spinal, how the nerve cell groups in the two regions correspond in position and function, but will refer my reader to my two previous papers.³ Here I will only state the conclusion to which I have arrived, which is the same as has been taught by Schwalbe and others for many a long day—viz., the spinal cord, and its continuation cranialwards, constitutes a well-defined nervous system which is formed by a bilateral series of ganglia, connected together transversely and intersegmentally, which give rise to a series of segmental

¹ *Op. cit.* p. 23.

² *Journ. of Physiol.*, vol. 10, p. 153.

³ *Journ. of Physiol.*, vols. 7 and 10.

nerves, all of which are built up on the same plan ; the whole forms a uniform system which is connected with the system of the brain, already described, by a number of well-defined commissural tracts, described by Hughlings Jackson as being extrinsic to the level of the spinal cord.

Here then we see a direct parallelism in both anatomic arrangement and subordination of function to higher centres between the spinal cord of vertebrates and the ventral chain of ganglia, in the crustacean with their transverse and intersegmental connections, and their connecting commissural fibres with the cerebral nervous system.

The parallelism, according to Leydig, is still closer, for he believes that the segmental nerves of the crustaceans show a division at their origin into two parts, corresponding to the anterior and posterior roots of the vertebrate.

We see then that no difficulty exists in the comparison between the nervous matter of the crustacean and that of the vertebrate central nervous system, both in its anatomic and physiological relations.

Indeed the consideration of the phylogenetic development of the nervous system in the Vertebrata enables us to compare in still more minute detail than in the sketch I have just given the nervous system of the two classes ; at the end of this paper I will point out how the origin of the vertebrate nervous system from one of a crustacean type not only gives an explanation of a number of obscure anatomic appearances in the brain of the Vertebrata, but at the same time helps to fix homologous parts in the two nervous systems.

I conclude then that there is no difficulty in tracing the parts of the most highly developed central nervous system from a system of an arthropodan type. This would doubtless have been long since accomplished as the continuation of Leydig's work, but for the difficulty of the invertebrate alimentary canal.

The attempts which have been made by Dohrn and others to locate the original mouth in the neighbourhood of the fourth ventricle, and then to pass the œsophagus through the infundibulum by way of the pituitary body into the alimentary

anal, and so to make the vertebrate derived from an invertebrate ancestor, whose dorsal surface has become ventral, have conspicuously failed, and have indeed been given up by Dohrn himself. With this failure it has been supposed to be hopeless to pierce the anterior part of the vertebrate central nervous system with an œsophageal canal, and in consequence the comparison of the nervous system of the vertebrate with that of the arthropod has been given up.

In my paper published in the *Journal of Physiology*, vol. x., and in a paper which I read before the Neurological Society in the summer of 1888, I have explained how in my opinion the remains of the old invertebrate alimentary tract is still existent in the vertebrate nervous system. I will not again here repeat what I have already published, but will briefly indicate the nature of the arguments used and the conclusions arrived at.

We find throughout evidence of a non-nervous tube, which is mixed up with the formation of the nervous system proper.

This non-nervous tube is the remains of the old alimentary canal, and was of the type of the crustacean canal, with large cephalic stomach, and a straight, simple intestine opening into an anus. The straight, simple intestine forms the canal of the spinal cord, and its walls have become modified to form the supporting tissue or myelo-spongium of the nervous elements of the cord; it passes free from admixture with nervous elements, as the neurenteric canal of the embryo, into the anus.

The remains of the non-nervous cephalic stomach are well seen in the cephalic region of the nervous system in the shape of the non-nervous epithelial structures, which are so freely found there, as part of the walls of the central tube, and which, by being thrown into folds, form on the dorsal side the choroid plexuses, and on the ventral side the saccus vasculosus. The remains of the mouth and œsophagus are found as a folded-down tube, which passes from the third ventricle, forms the infundibulum with the lobi infundibuli, when remaining dilated and epithelial in character, forms in the fishes the saccus vasculosus, and finally is bent down on

to the surface of the brain to near the exit of the third nerve being occluded by the compression of its walls, and by degenerative modification of the cells of its terminal portion. The pituitary body is situated on the anterior lip of this tube against the dilated portion known as the saccus vasculosus. In this way not only does the arrangement of the nervous material in the two classes remain the same, but an explanation is given of the non-nervous structures found in connection with the nervous tube of the Vertebrata.

By this explanation of the relation between the non-nervous and nervous material, the crustacean merges insensibly into the vertebrate without any shifting of dorsal and ventral surfaces; the supra- and infra-oesophageal ganglia remain the same in position and in function; the oesophageal commissures remain; mouth, oesophagus, intestine, anus, &c. all there in the same position, with respect to the nervous elements, as in the crustacean ancestor.

Hitherto no explanation has been given of the reason for the non-nervous epithelial structures in the brain of the vertebrate: in the pre-Darwinian days it was possible to say that these epithelial parts of the roof of the nervous tube in the cranial region were potential nervous matter, were formed for the purpose of enabling the development of the brain to take place as the vertebrate rose in the scale of creation; now however such an explanation is recognised as unmeaning and yet no other is given in its place. We cannot say that it is nervous material which has thinned down and degenerated for all the evidence of comparative anatomy goes to show that the lower the animal in the scale of evolution, the more conspicuous is this epithelial bag, and the less is it obscured by the growth of nervous matter. In fact we are driven to conclude that the epithelial bag is pre-existent and that the nervous matter is situated in definite places on the outside of it, as I have already said.

Again, it is significant in connection with the comparison between the nervous system of the vertebrate and the combined nervous and alimentary systems of the crustacean, to find that the cephalic stomach of the crustacean is a non-glandular, simple epithelial bag, for the purpose of holdi-

food and not for digesting it; in this respect also the non-nervous membranous structures of the vertebrate brain, with their well-known simple epithelial character, agree with the theory which I have put forward. So also the simple, straight intestine of the crustacean is free from any digestive glandular structures, and is simply either an excretory duct, or perhaps absorbent in function.

In the crustacean however in addition to the intestine and stomach, and in connection with the latter, there exists a large and most important organ, the so-called liver, and it is in the cells of this gland that the digestive ferments are formed, and by means of its secretion the food taken into the stomach is rendered capable of absorption, either by the intestine, or perhaps partly by the liver itself. It is a large, symmetrically bilateral gland, spreading over the whole of the cephalic region; its ducts enter into the alimentary canal at various places, or else combine as a single duct to enter the stomach near its pyloric end on the ventral surface.

Seeing then the large size and great importance of this organ in the crustacean, it follows that if the theory set forth in these pages is a true one then some vestige of this important adjunct of the crustacean alimentary canal ought most certainly to be found in connection with the canal of the vertebrate nervous system in the cranial region.

A comparison of the cranial cavity of the lowest and highest vertebrates brings prominently forward the great difference in the extent of space occupied by the brain mass at the two extremities of the vertebrate kingdom: on the one hand in man the nervous matter so closely packed within the cranium as to leave its impress upon the bony walls of the cavity; on the other hand in the fishes a brain so small lying in a cranial cavity so much out of proportion that the greater part of the cavity is unoccupied by nervous matter. Here again, just as in the case of the membranous parts of the brain tube, the explanation which might have been given, and indeed was given in pre-Darwinian days can no longer be accepted now—the explanation, viz., that in the lowest vertebrates a small brain was designedly contained in a large cavity in order to allow room for the increase of

the brain material as the animal ascended in the scale of creation; yet no other is put in its place, no explanation as far as I know is given why the large space between brain and brain case in the lowest vertebrates is occupied by a mass of peculiar jelly-like tissue, while in the highest vertebrates nothing of the sort is to be found. The reasonable argument appears to me to be not that this mass of gelatinous-looking tissue has been formed for the purpose of supporting and steadying a brain which is too small for its case, but rather that it represents some pre-existing organ which, together with the brain, filled up the cranial cavity, and that having lost its original function it has become converted into a mass of soft jelly-like material. The pre-existing organ is in my opinion the so-called cephalic liver of the crustacean ancestor. My reasons for this opinion are based on the study of this structure in the ammocœte and I am at present engaged in writing out a paper on the brain of the ammocœte in which I intend to discuss fully the nature of the evidence which has led me to this conclusion. It will be sufficient here to say that this tissue is composed of large closely packed glandular-looking cells which are arranged so as to form a distinct organ symmetrically placed on each side of the middle line of the brain; this organ extends as a compact mass in front of the cerebral hemispheres, and extends in the shape of scattered cells into the region of the spinal cord. At one place this tissue forms an apparent hilus and here in the nervous matter the remains of a tube passing from the commencement of the fourth ventricle to the surface are to be found; this spot is the region of the *ganglion interpedunculare* or the *conus post-commissuralis* (Fritsch). That this *conus post-commissuralis* contains within itself the remains of a diverticulum from the central cavity of the nervous system is recognised by Ahlborn¹ and in confirmation of the view that it represents the rudiment of the duct of the original cephalic liver of the crustacean ancestor we find that it opens into the central canal at the lower limit of the fourth ventricle—*i.e.*, according to the theory here put forward, into the pyloric end of the original

¹ Ahlborn, *Zeitschrift f. Wissent. Zoolog.*, vol. xxxix., 1883.

stomach; that it comes to the surface of the brain on the ventral side at the spot where the gelatinous tissue converges to form a hilus, just as in the crustacean ancestor the original liver duct must have entered into the so-called liver at this point

In this way then it seems to me do we obtain a good and sufficient reason in accordance with modern evolutionary ideas, for the apparent emptiness of the brain case in the lowest vertebrates; the large space in question was filled by that large and important organ of digestion, the so-called liver, which occupies so great a space in the crustacean economy. With the loss of function of the original alimentary canal and the increasing growth of the nervous system, this organ also lost its function and its cells became converted by that curious mucilaginous degeneration into the so-called arachnoidal fat tissue which is not real fat tissue, and is therefore called by Ahlborn "*Arachnoidale Füll-gewebe*."¹ After it had lost its original function this tissue still remained well-supplied with blood vessels and according to Sagemehl² perhaps took on the function of lymph tissue; with the increase and growth of the brain it was gradually compressed out of existence altogether until at last in the human brain the cranial cavity is filled with nervous matter, and the remains of the old original cephalic liver are perhaps to be seen in the so-called *Glandulæ Pacchioni*.

We see then that by this theory of mine a perfectly straightforward and reasonable explanation is given of two hitherto insoluble anatomical problems, the one the reason for the existence of the choroid plexuses, and the other the reason why the cranial cavity in the lower vertebrates is so largely filled up with a non-nervous gelatinous semi-fluid mass of tissue. The truth of a theory however depends not only upon its being able to explain one or two striking difficulties but even in small details its correctness ought to appear. This appears to me to be the case. In the brain of the vertebrate or in connection with it, are many peculiar structures, the function of which is unknown and which are apparently the remains of originally important structures,

¹ F. Ahlborn, *loc. cit.* p. 287.

² *Morphol., Jahrbuch.* vol. ix. p. 457.

for they are found with great constancy throughout the vertebrate kingdom. Such are the hypophysis and epiphysis, the ganglia habenulæ and Meynert's bundle, the tænia thalami, the ganglion interpedunculare and the substantia nigra. Of these there is no evidence that the hypophysis is of the nature of a sense organ; on the contrary, its glandular character is manifested both by histological and pathological investigations. It is in some animals, according to Dohrn, a paired organ; there is no evidence that it communicates with the central canal of the nervous system. It is in all probability the remains of a primitive glandular structure, and its interpretation is so closely bound up with the question whether or no it is a paired organ, that it is better to wait until that question is settled before speaking with any certainty about its homologies.

The epiphysis is clearly, as the result of recent investigations shows, the rudiment of a median eye; such eye is usually spoken of as having been vesicular, and it has been suggested to me that it is difficult to obtain a vesicular eye from a crustacean ancestor. In my paper on the ammocæte brain I propose to give the appearances presented by the eye in the young lamprey and to show that its structure is not vesicular, but closely resembles the median eye of *Limulus* as described by Ray Lankester.¹ In fact the position of this pineal eye, its relation to the ganglia habenulæ and its structure, all fit in well with the supposition that it represents the median eye of a crustacean ancestor of an antique type, such as is represented by the king-crab.

With respect to the *substantia nigra*, I have already suggested that it may represent the primitive stomato-gastric ganglia, partly from its position on the crura cerebri, partly from the deeply pigmented character of its cells, which points directly to a loss of function, and partly from its apparent connection with the degenerated tissue in the roots of the oculomotor nerve. The rest of the structures which I have mentioned at the beginning of this section, viz., the ganglia habenulæ, tænia thalami, Meynert's bundle and ganglion interpedunculare, form a group of considerable interest from the

¹ *Quarterly Journ. Microp. Science*, vol. xxv.

point of view of this paper; for the lower we descend in the scale of evolution of the vertebrate the more do these structures become prominent, the more evident is it that they represent distinctly very primitive parts of the nervous system.

We see that the phylogenetic development of the nervous system in vertebrates largely consists in the great increase of those parts which correspond to the supra-oesophageal ganglia and their connections with the subordinate system of the spinal cord. Thus the superior segment of Bellonci, viz., the cerebral hemispheres, increases enormously in size and complexity.

The optic thalami which overshadow and include the ganglia habenulæ in the higher vertebrates, are in the ammocœte but small in comparison with the conspicuous and important ganglia habenulæ.

The optic lobes vary in size according to the perfection of the visual apparatus, and in the ammocœte, before transformation takes place, they can hardly be said to exist, although at this time both the pineal eye and the ganglia habenulæ are well developed. In the primitive crustacean-like ancestor of the vertebrates, then, it appears to me that the superior segment of the supra-oesophageal ganglia was represented by the cerebral lobes, while the middle segment was represented essentially by the ganglia habenulæ and the optic thalami. It follows then, that the *tænia thalami*, which according to Ahlborn are well represented in the ammocœte and form an extensive system of peculiarly coloured fibres which pass symmetrically on each side from the *tubercula intermedia* (ganglia habenulæ) into the cerebral hemispheres, represent the original connection between the superior and middle segments, while the Meynert's bundles represent the connections between the middle segment and some part of the sub-oesophageal ganglia.

Whether Meynert's bundles are connected with the ganglion interpedunculare or not Ahlborn was unable to assert definitely; they come to the ventral surface of the brain near that region but their ultimate destination is not yet settled.

If I understand rightly the part of the brain recognised by Ahlborn as the ganglion interpedunculare, then this so-called ganglion represents in my opinion the occluded termination of the duct of the cephalic liver, as I have already said; the details of its structure in the ammocœte upon which this opinion is based will be given in the paper already alluded to.

Further in considering the hind-brain it is very instructive as already pointed out in my former paper, to observe the growth of the cerebellum, so large and important in the highest vertebrates, so small and insignificant in the ammocœte that Ahlborn could only recognise it with difficulty. In its inception it must be looked upon, as Osborn¹ has shown, as a band of nervous tissue stretching over the dorsal side of the neural tube, in close contiguity to the fourth nerve. Then before the cerebellar hemispheres are formed, we find this band of nervous material surrounding a loop of the membranous roof, and so forming the worm of the cerebellum. By this solidification of the walls of the pinched-up loop it follows that two lateral bags of the membranous roof are formed; on the external surface of the floor of these two bags two ear-shaped ridges of nervous tissue are found, called the *fimbriæ*, which ultimately by further growth form the cerebellar hemispheres, as I have explained in my last paper.²

We see then that the evolution of the cerebellum not only shows in a most instructive manner how the enlargement of the brain is formed by the steady growth of nervous material over the original non-nervous epithelial tube, but also points directly to the conclusion that in the primitive condition the nervous material which corresponded in function with the cerebellum, and from which by gradual increase of growth the cerebellum has been evolved, was situated on the ventral and not on the dorsal side of the original neural tube. In other words the cerebellum and semi-circular canals are both concerned in the function of equilibration, just as are the sub-œsophageal ganglia and the otocysts, because in each case they are the direct lineal descendants of these parts of the crustacean nervous system.

¹ *Journ. of Morphol.*, vol. ii.

² *Jour. of Physiol.*, vol. x., p. 194.

Again, in the spinal cord it is easy to see how the evolution of the nervous system has brought about the marked separation between the exits of the anterior and posterior roots, which is so marked a characteristic of the cord of the higher vertebrates; for we see that with the growth of the cerebral hemispheres and cerebellum we must have an increasing growth of the long commissural tracts which connect the lower centres of the spinal cord, or ventral chain, with these two great masses of brain matter. This means essentially an increase in the pyramidal and cerebellar tracts, and it is clear that if the crossed pyramidal tract and the direct cerebellar tract be either removed or very much diminished, then the anterior and posterior horns, with the exits of the corresponding roots, must approximate to each other more and more closely.

Finally, this theory explains, as I have already pointed out in my former paper, what has always been hitherto without explanation, viz., the meaning of the formation of the cerebral vesicles in the embryo. If we keep steadily in view the conception that the nervous system is formed around and on the outside of a pre-existing non-nervous epithelial tube, the anterior dilated part of which was the original cephalic stomach, then we see how the evidence of ontogeny confirms this conception and how far it indicates the line of phylogenetic descent. At first the neural tube is formed with a simple dilated anterior extremity, indicating its origin from a simple intestinal tube with a dilated anterior cephalic stomach. Then as it continues to grow into a vesicular form it ceases to dilate uniformly, a constriction appearing on its dorsal surface at one particular place so as to divide it into an anterior and posterior vesicle; this constriction denotes the growth of the nervous matter of the ganglia habenulæ and posterior commissure and indicates the position of the optic portion of the supra-oesophageal ganglia upon the original cephalic stomach.

The posterior vesicle now becomes divided into two portions by a constriction which again corresponds to the formation of nervous matter upon the non-nervous tube, viz., the fourth nerve and commencing cerebellum. By this

means the brain tube is divided into the three cerebral vesicles, the dorsal walls of which are membranous except at the place of the constrictions.

Then again the first cerebral vesicle becomes divided into two to form the fore-brain and thalamencephalon, while the third cerebral vesicle is also divided into two to form the cerebellum and medulla oblongata.

In this way then we see the formation of five cerebral vesicles, viz., prosencephalon, thalamencephalon, mesencephalon, cerebellum and medulla oblongata, and it is clear, as Osborn¹ has pointed out, that the divisions between these vesicles are formed by a series of commissural bands of nervous matter. Of these the limiting nervous strands between the thalamencephalon and mesencephalon, and between the mesencephalon and the hind-brain are of primary importance; while the separation into prosencephalon and thalamencephalon, and into cerebellum and medulla oblongata, are of subordinate importance.

Not only the posterior commissure and ganglia habenulæ, but also Meynert's bundle are most constant throughout the vertebrate kingdom, and it is instructive to note how prominently these latter fibres stand out in sections of such low forms as *Petromyzon* in its young state. I suggest therefore that the primary constriction which separates the thalamencephalon from the mesencephalon is an indication of the formation of the ganglia habenulæ, posterior commissure and Meynert's bundle, *i.e.*, of the middle segment of the supra-œsophageal ganglia with its connecting tract with the subœsophageal ganglia. There is nothing new in the suggestion that Meynert's bundle on each side is in the position of the lateral constriction which separates the thalamencephalon from the mesencephalon; it has been already made by Paul Mayser, and in Ahlborn's paper² a discussion of Mayser's view is given, to which I must refer my reader.

Again, the next most important constriction is the place where the valvula cerebelli is found in the adult and indicates the separation between mid-brain and hind-brain; here we

¹ *Op. cit.*

² *Op. cit.*, p. 235.

find again in all vertebrates the crossing over of a nerve tract from the ventral to the dorsal side, viz., the fourth nerve; and in close connection with this is the original commissural band of fibres which constitutes, according to Osborn, the rudiment of the cerebellum. The meaning of this crossing over of the fourth nerve and of the formation of these bands of nervous material in this region I must leave until the discussion of the meaning of the cranial nerves as a whole, in connection with the origin of vertebrates from a crustacean-like ancestor.

With respect to the other two divisions, the separation between cerebellum and medulla oblongata is clearly an indication of the hinder limit of the formation of the cerebellum itself, and depends therefore for its distinctness mainly upon the extent to which the cerebellum is developed in the adult condition. Thus in the lamprey Ahlborn¹ was unable to satisfy himself of the existence of this constriction.

The division of the fore-brain into prosencephalon and thalamencephalon is recognised now as a constant and important division, but it does not appear to be absolutely settled what the dorsal constriction corresponds to in the adult state. The most generally held view is that the anterior commissure marks the position of the dorsal limit between these two parts of the brain. Osborn however considers that his superior commissure is the true limit, and not the anterior.

The difference comes to this: on the first view the prosencephalon forms the cavity of the cerebral hemispheres and the nervous matter overlying them, while the thalamencephalon forms the cavity of the third ventricle with its membranous roof which forms the choroid plexus of the third and lateral ventricles and its lateral nerve masses the optic thalami together with the pineal gland. According to Osborn's view, seeing that his superior commissure separates the supra-plexus (i.e., the choroid plexus of the third and lateral ventricles) from the pineal gland, it follows that his prosencephalon includes this choroid plexus as well as the cerebral hemispheres, while his thalamencephalon consists

¹ *Op. cit.*

on the dorsal side only of what is included between the superior and posterior commissures, *i.e.*, the pineal body, with I presume the optic thalami forming its lateral walls.

Of these two views it seems more reasonable to look upon the supra-plexus (choroid plexus of third and lateral ventricles) as belonging to the thalamencephalon, so that the anterior commissure would in this case represent the limit of the first vesicle or prosencephalon. This commissure is said to be very constant among vertebrates; it forms a connection between the two cerebral hemispheres, and is said to be the first transverse commissure of the cerebrum (Quain) which is developed in the embryo. It represents probably the intercommunication between the two lobes of Bellonci's superior segment, and forming the posterior boundary of the cerebral hemispheres causes a well-defined constriction in consequence of the growth of the cerebrum forwards.

The increasing study of this question convinces me more and more that the view herein expressed is right. I have however thought it best to bring out my investigations bit by bit as they are ready for publication, rather than to wait some years and then publish the results of my investigations as a whole. I propose then to publish a series of papers in support of the view here expressed, dealing with the question of the origin of vertebrates from the crustacean from every point of view, both anatomical and palæontological. I reserve to myself the right of following up this investigation and propose after the publication of my paper on the central nervous system of the ammocete to deal with the meaning of the cranial nerves, and therefore with the formation of the present vertebrate alimentary canal; for as I have pointed out in my last paper it is clear that the hindmost group of cranial nerves which arise from the medulla oblongata possess peculiarities of origin and distribution which are due to the formation of the present alimentary canal, just as the peculiarities of the foremost group of cranial nerves are due to the loss of function of the old alimentary canal and the parts connected with it.

Cambridge, June 1st, 1889.