ON THE RELATION BETWEEN THE STRUCTURE, FUNCTION, DISTRIBUTION AND ORIGIN OF THE CRANIAL NERVES; TOGETHER WITH A THEORY OF THE ORIGIN OF THE NERVOUS SYSTEM OF VERTEBRATA. BY W. H. GASKELL, M.D., F.R.S.

(Plates XVI.—XX.)

A preliminary account of the first part of this paper is published in the Proceedings of the Royal Society, Vol. 43, *p.* 382, *and in the Medico-chirurgical Transactions, Vol.* 71, *p.* 363; *and a condensed account of the second part in a paper read before the Anatomical Society on June* 23, 1888, *and published in the Journal of Anatomy and Physiology, Vol.* 23.

PART I.

ON THE RELATION BETWEEN THE STRUCTURE, FUNCTION, DISTRIBUTION AND ORIGIN OF THE CRANIAL NERVES.

IN a former paper[1] I pointed out that the conception of a spinal nerve as described there, removed many of the difficulties which have hitherto hindered the comparison of the cranial with the spinal nerves; in this paper I propose to compare structure and centres of origin as regards the cranial with the spinal nerves, more closely than I was able to do at that time. In order to make such a comparison with any chance of success, it is necessary in the first place to have a clear conception of the elements composing a typical spinal nerve; in addition it is most essential to understand as far as possible the centres of origin of these different elements, for I am convinced that the true morphological meaning of the segmental arrangement of nerves whether spinal or cranial is bound up with the arrangement of the groups of nerve cells in the central nervous system, rather than with the exits of the different nerves from the central nervous system. It is therefore advisable to

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[1] This *Journal*, Vol. VII. p. 1.

commence the study of the cranial nerves with a sketch of the way in which I consider a typical spinal nerve to be built up.

The conclusions to which I came in my former paper were, that in addition to the well-known division into afferent and efferent groups of fibres, two other divisions existed in the nervous system; the one, a division of nerve fibres and their centres of origin into somatic and splanchnic groups; and the other, a division into anabolic and katabolic groups. The most essential division of the nervous system is that expressed by the terms splanchnic and somatic, for it embraces the minor divisions of afferent and efferent and of anabolic and katabolic. The characteristics of this division are to be found equally well in the cranial as in the spinal nerves. The division is a natural one which includes not only the nervous system but the whole organism, for by somatic nerves are meant those nerves which supply structures derived from the epiblast and from that part of the mesoblast which forms the mesoblastic somites, and by splanchnic nerves those which supply structures derived from the hypoblast and the rest of the mesoblast; in accordance with this phraseology we find in the body two separate segmentations, the one "somatic" (called by Ahlborn Mesomerie), which corresponds to the "dorsal segmentation" of v. Wijhe and Gegenbauer, and is characterised by the formation of somites, and the other "splanchnic" (called by Ahlborn Branchiomerie), the "ventral segmentation" of v. Wijhe and Gegenbauer, more local in situation characterized by the formation of gill clefts.

In my former paper I have pointed out how the splanchnic nerves are divisible from the somatic in so far as the structure and origin of their efferent fibres are concerned; the separation of the afferent somatic and splanchnic nerves is a more difficult matter and one which will require a large amount of time for its successful accomplishment. Leaving the afferent fibres for future consideration, we see that the fibres of an efferent root are divisible into a ganglionated and a non-ganglionated group of which the former belongs to the splanchnic system, while the latter is partly splanchnic and partly somatic.

The somatic efferent nerves, which contain the large medullated motor fibres of those striated muscles which arise from the muscle plates, spring from groups of nerve cells (A in Fig. 1) situated in the anterior horn; the characteristic appearance of these nerve cells is shown in the Figure on p. 352 of Schwalbe's *Neurologie*, where also it is asserted that they vary in size from 67—135 μ.

The splanchnic efferent nerves on the other hand are in all probability connected with the cells of Clarke's column (C in Fig. 1), the cells of the lateral horn (B and E in Fig. 1), and with the solitary cells of the base of the posterior horn (D in Fig. 1).

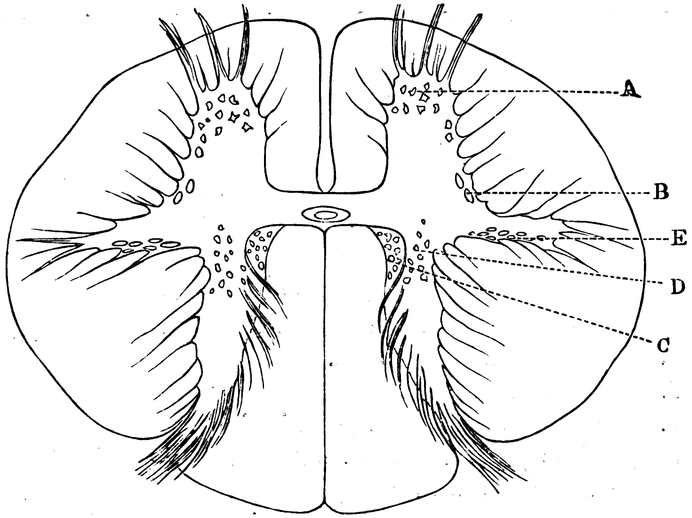

FIG. 1. Section of the spinal cord in the thoracic region. (*Slightly modified from Schwalbe.*)

The characteristic appearance of the cells of Clarke's column is well shown in the Figure on p. 58 of Henle's *Nervenlehre des Menschen* (2nd Edition). They measure from 45—90 μ, according to Stilling and Schwalbe.

The cells of the lateral horn in the thoracic region, i.e. the cells of the intermedio-lateral tract (E in Fig. 1), are described by Schwalbe (p. 349) as consisting of groups of spindle-shaped multipolar cells which are smaller than those of the anterior horn and are arranged for the most part with their long axis in the direction of the lateral horn.

The solitary cells of the base of the posterior horn are figured in Schwalbe (p. 350) as elongated spindle-shaped multipolar cells of a size much smaller than those of the anterior horn, possessing a marked axis cylinder process the direction of which is nearly at right angles to the long axis of the cell.

We see then that these different groups of nerve cells present marked characteristics and (see Fig. 1) are arranged in a definite manner in the spinal cord; those groups of nerve cells which in this paper are supposed to give origin to the splanchnic efferent nerves being collected together around the central canal, while the centres for the somatic efferent nerves are situated in the outlying anterior horns of grey matter.

Further, in order to understand the origin of the cranial nerves it is advisable to consider somewhat more closely the meaning of the different groups of nerve cells situated in what I may now call the splanchnic region of the grey matter, and as unfortunately these different groups of cells have not been traced directly into nerve fibres of definite function the only evidence for their function must of necessity be indirect and consequently somewhat speculative. I do not therefore look upon the following remarks as anything more than suggestions which may help to the elucidation of the difficult problem before us.

We have to consider the nerve cells of three different groups, viz.:

1. Cells of Clarke's column.
2. Cells of lateral horn.
3. Solitary cells of base of posterior horn.

In my previous paper I pointed out (1) that the cells of Clarke's column were associated with the presence in the anterior roots of bundles of very fine medullated fibres forming the splanchnic ganglionated efferent nerves; (2) that the solitary cells of the base of the posterior horn increased in number to form part of the vagus nucleus, and (3) that the cells of the lateral horn belonged to the same group as those of the nucleus of the facial &c., and formed the motor nerve cells of those splanchnic non-ganglionated nerves which supplied the voluntary muscles derived from the lateral plates of mesoblast,—muscles which correspond closely with A. Schneider's group of "visceral muscles."

Cells of Clarke's column.

We can I think go further than this by means of the process of elimination. Thus, the cells of Clarke's column are found in the cranial, thoracic, and sacral splanchnic regions; consequently they do not give origin to the vasoconstrictor nerves,—i.e. the katabolic nerves of the muscles of the blood vessels,—which arise only in the thoracic region, and with the vasoconstrictor nerves the katabolic glandular nerves are in all cases closely associated, so that these two categories of nerves may be eliminated from the consideration of Clarke's column. Further, Clarke's column is most developed from the 9th dorsal to the 3rd lumbar nerves, therefore it is associated with the abdominal splanchnics rather than with the cervical splanchnics. Moreover, if we remove from the abdominal splanchnics the katabolic nerves of the glands and blood vessels, we have left all the anabolic nerves and the katabolic nerves of the muscles of the alimentary tract. We know however that the vagus nerve is the great provider of these latter nerves, i.e. the viscero-motor nerves, and that it is not easy to prove that the abdominal splanchnics contain any nerves which cause contraction of the muscles of the alimentary canal; we know on the other hand that the great function of these splanchnic nerves is to inhibit the movements of the alimentary tract. The natural conclusion is that the cells of Clarke's column are associated with anabolic rather than katabolic nerves and that they give origin to the inhibitory or anabolic nerves of the muscles of the alimentary canal, and perhaps also to the corresponding nerves of the vascular and glandular systems. This conception is in harmony with their presence in the sacral region in connection with the *n.n. erigentes*, and at the upper part of the cervical region where the inhibitory cardiac nerves are given off. Again, the observations of Mott show that the cells of Clarke's column are not all alike, but are divisible into two groups, of different sized cells, which suggests that the nerve fibres arising from these two groups of nerve cells supply more than one special structure.

Solitary cells of base of posterior horn.

We come next to the solitary cells of the base of the posterior horn which I was inclined in my former paper on the strength of Schwalbe's suggestion to classify as splanchnic sensory nerve cells. The evidence for their connection with sensory nerves as given by Schwalbe (p. 353) is not strong, being based mainly on the observation of Freud that the posterior cells (Hinterzellen) of Petromyzon which he considers to be homologous with these solitary cells, send their axis cylinder processes into the posterior roots. Against this observation is to be reckoned in the first place that no posterior root fibres in the higher vertebrata are known to arise as axis cylinder processes of ganglion cells in the central grey matter; secondly, as Schwalbe points out, the observations of Gerlach show that the axis cylinder processes of these solitary cells pass direct into the anterior horn and so form anterior root fibres and not as Deiters thought fibres of the posterior roots. Finally the observations of Freud are not necessarily contrary to the motor character of these cells even if they are homologous with the Hinterzellen of Petromyzon, for the observations of **Ransom**[1] and **D'Arcy Thompson** show that the posterior root of the Petromyzon contains the small fibres with their ganglia which correspond to the so-called sympathetic system in other vertebrata, in other words contains ganglionated splanchnic nerves closely corresponding to those which are in the higher vertebrata essentially efferent in character. **Freud's** observation therefore harmonises with the motor character of these ganglion cells on the possible assumption that in Petromyzon the nerve roots are arranged not as afferent and efferent but as ganglionated and non-ganglionated; the ganglionated containing both afferent and efferent ganglia.

Again, if the observations of **His**[2] are confirmed, it is very significant that the jugular ganglion should in the embryo be connected only with the nerve fibres forming the ascending root of the vagus or *fasciculus solitarius*, while the fibres arising from the cells of the vagus nucleus pass not into this ganglion but into the ganglion trunci vagi and so to the vagus nerve trunk. In accordance with my previous observations this means that the afferent vagus fibres all arise from the ascending root of the vagus, just as all the afferent fibres of the trigeminal arise from the ascending root of the trigeminal; that therefore the cells of the vagus nucleus give origin to efferent and not to afferent nerves.

A similar conclusion has been arrived at by **Osborn**[3] in a recent paper on the internal structure of the Amphibian brain in which he gives reasons for considering the nucleus of the vagus in the floor of the 4th ventricle as motor; the sensory fibres of the vagus and glossopharyngeal arising from the *fasciculus solitarius*, *fasciculus communis* and the large sensory nucleus in the dorsal folds of the medulla oblongata. Moreover the functions of the vagus nerve point clearly to the conclusion that this nerve is very largely if not mainly an efferent nerve rather than an afferent and that therefore in its centre of origin, including in this centre that of the medullary fibres of the spinal accessory, motor nerve cells must exist in sufficient quantity to give origin not only to the motor nerves of the striated muscles of the larynx, pharynx and œsophagus, but also to the motor nerves of the unstriated muscles of the alimentary tract.

Now a comparison of the function of the vagus with that of the abdominal splanchnics shows that a great split has taken place in the centres of origin of the katabolic and anabolic nerves of the same

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[1] *Zoolog. Anzeig.* No. 227, 1886.

[2] *Archiv. f. Anat. u. Physiol.* Anat. Abtheil 1887, p. 368.

[3] *Journ. of Morphol.*, Vol. II. p. 51.

muscular tissue of the alimentary canal; in the vagus we find the great mass of motor fibres, in the splanchnics the great mass of inhibitory fibres. If therefore a difference exists in the nerve cells which give origin to the motor and inhibitory fibres of these muscles, that difference ought to manifest itself in these two regions and we ought to find that the solitary cells of the base of the posterior horn increase largely when the vagus nucleus is reached, just as the cells of Clarke's column increase at the origin of the abdominal splanchnic nerves.

Judging from the description given by Schwalbe[1] and from what I myself have observed in the case of the spinal cord of the pigeon, there can be no doubt but that the formation of the vagus nucleus is associated with a large increase of cells at the base of the posterior horn. The point however which requires further investigation is the respective shares taken in that increase by the cells of Clarke's column and the solitary cells of the base of the posterior horn. As far as I know no such investigation has been as yet published, so that at present we are hardly justified in concluding that the split which has taken place in the nerves of opposite function which govern the muscles of the alimentary tract has its counterpart in the central nervous system in the shape of a corresponding separation of the centres of those nerves, i.e. of the cell groups of Clarke's column and the solitary cells of Schwalbe respectively. At present all we can say is that taking these two sets of cells together we may look for the origin of both motor and inhibitory nerves of the alimentary tract in them, and that it is possible that further investigation will prove the truth of the suggestion here made, viz. that the solitary cells of the base of the posterior horn give origin to the motor fibres of the muscles of the alimentary canal while some of those of Clarke's column are the centres of the inhibitory fibres of the same muscles.

Cells of lateral horn.

In my former paper I spoke somewhat vaguely as to the meaning of these cells, because I did not sufficiently realize that the term lateral horn does not mean quite the same thing in different parts of the cord. Thus the lateral horn of the cervical region is not necessarily the same as that of the thoracic region either in structure, position or function. In the thoracic region the lateral horn or intermedio-lateral tract is in the case of the dog situated somewhat on the dorsal side of the middle line of the cord and is well pronounced; in the cervical region any

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[1] *Op. cit.* See x in Fig. 362, p. 609.

projection that may be defined as a lateral horn is on the ventral side of the middle line in close proximity to the cells of the anterior horn.

This intermedio-lateral tract is according to Schwalbe most distinct in the upper part of the thoracic region, disappears gradually at the lower limit of the thoracic region and is absorbed into the cervical swelling, reappearing again as a distinct part of the anterior horn in the upper cervical region.

It is therefore conspicuous only in the thoracic region and contains there a well-marked group of nerve cells (E in Fig. 1) which as seen in the figure are in close connection with the solitary cells of the base of the posterior horn and the cells of Clarke's column. This group of cells is situated on the dorsal side of the intermedio-lateral tract. In addition to these cells some of the sections of the thoracic cord in man show on the ventral side of the tract (B in Fig. 1) the occurrence of other cells which are markedly larger, resembling much more the cells of the anterior horn, and which are very few in the thoracic region in comparison with the large number of the smaller cells already described. These large cells on the ventral side of the intermedio-lateral tract appear to me to form a connecting link between the somatic area of the anterior horn and the splanchnic area around the central canal.

It is this part of the lateral horn group of cells which forms, as I believe, the whole or greater part of the lateral group of cells in the cervical region; it is this group therefore which in all probability gives origin to the phrenic nerves, to some if not all of the large motor fibres of the spinal accessory; it is the continuation of this group which forms the *nucleus ambiguus* or so-called motor nucleus of the vagus and glossopharyngeal, which forms the nucleus of the facial and the motor nucleus of the trigeminal.

In this group of nerve cells we have in my opinion the origin of the motor nerve fibres belonging to the non-ganglionated group of splanchnic nerves—motor nerves which supply voluntary muscles derived not from the muscle plates but from the lateral plates of mesoblast—structures which segmented in the region of the head give rise to the voluntary muscles of the jaws and the gills but unsegmented in the trunk give rise to the diaphragm and transversus abdominis muscles.

What then is the function of the smaller cells which form the main portion of the intermedio-lateral tract in the thoracic region? Although we have no direct evidence to go upon I venture to suggest that these nerve cells give origin to the katabolic or motor nerves of the vascular and glandular systems, for in contradistinction to the cells of

Clarke's column they are most numerous in the upper part of the thoracic region and are therefore concerned in the formation of the cervical splanchnic nerves as well as of the abdominal splanchnics; they correspond in fact closely to the distribution of the motor nerves of the heart and blood vessels as given by me in my former paper. Again it is a significant fact that in the medulla oblongata a group of nerve cells exists known by the name of the antero-lateral nucleus, which is an isolated clump of nerve cells apparently belonging to the lateral horn, separate from the motor nuclei of the IXth, Xth and XIth nerves; as far as is known this group of nerve cells does not give origin to any outgoing nerve fibres of that region; the only function which has been suggested for it is based upon the experiments of Owsjannikow and Dittmar in Ludwig's laboratory, by means of which it was shown that the vasomotor centre in the medulla oblongata was confined to the position of this antero-lateral nucleus. The experiments also of Miescher in the same laboratory render it highly probable that the nerve fibres which spring from this group of nerve cells pass along the cervical region of the cord in the lateral columns in order to be distributed in the thoracic outflow of visceral nerves to the blood vessels which they supply. I am inclined to look on this antero-lateral nucleus as serially homologous with the smaller cells of the intermedio-lateral tract in the thoracic region and to consider this chain of nerve nuclei as giving origin to the motor or katabolic nerves of the vascular system.

I have ventured to put towards these suggestions of the meaning of these different groups of nerve cells in the hope that they may prove of assistance to others who are endeavouring to bring into harmony the relations between the structure and functions of the spinal cord. The arguments which I have used are I think, as far as they go, good; but I am ready to confess that they do not go very far. For the purposes of this paper it is a matter of no great importance whether the division of function of these four groups of cells—viz. those of Clarke's column, the solitary cells of the base of the posterior horn, and the two groups of the lateral horn—corresponds to the suggestions above enunciated; the important point is that these four groups of cells taken together give origin to the splanchnic efferent fibres, both ganglionated and non-ganglionated, that therefore the centres of the efferent nerves both somatic and splanchnic fall into two separate groups, of which the latter is situated in the neighbourhood of the central canal while the former is confined to the outlying anterior horn. If then the cranial nerves are comparable to the spinal, we must find in the cranial region groups of nerve cells serially homologous with these splanchnic and somatic efferent spinal centres.

Definition of a complete segmental nerve.

Turning our attention now to the arrangement of the fibres composing a complete segmental spinal nerve, the results arrived at in my previous paper show that we must look upon both afferent and efferent roots as ganglionated, for the whole argument in my former paper as to the meaning of the sympathetic system was to prove that the sympathetic ganglia are the ganglia belonging mainly to the fine medullated fibres of the anterior roots, so that we must look upon a spinal nerve as possessing efferent or motor ganglia as well as afferent or sensory ganglia. These efferent ganglia have according to the observations of Onodi travelled away from the original ganglionic mass situated on the roots of the spinal nerve, so that we may term these motor ganglia "vagrant" in contradistinction to the "stationary" sensory ganglia on the posterior root; it follows then that a spinal nerve must be defined as formed by

1. A posterior root composed of afferent fibres, both somatic and splanchnic, the ganglion of which root is stationary in position and is always situated near the entrance of the fibres into the central nervous system.
2. An anterior root composed of (1) efferent non-ganglionated splanchnic and somatic fibres, and (2) efferent ganglionated splanchnic fibres characterised by the fineness of their calibre, the ganglion of which is vagrant and has travelled to a variable distance from the central nervous system.

Also it must be remembered that the anterior root fibres need not necessarily leave on one side the ganglion of the posterior root, for as pointed out previously both anterior and posterior roots pass into the spinal ganglion in the case of all the thoracic nerves of such an animal as the tortoise and also of the first two cervical nerves of the dog.

The essential characteristics therefore of a segmental spinal nerve are as follows:

1. Afferent nerve fibres, splanchnic and somatic, both in connection with a ganglion situated near the exit of the nerve from the central nervous system.
2. Efferent fibres which may either pass through the afferent

ganglion or may pass on one side of it and which are divisible into large fibred and small fibred groups, the latter of which is connected with a vagrant ganglion.

3. The efferent fibres, both somatic and splanchnic, may be traced to certain definite groups of nerve cells in the spinal cord; but no such groups are known in connection with the afferent fibres.

The cranial segmental nerves.

Having thus defined the nature of a fully formed spinal segmental nerve, we are able now to discuss more fully than in my previous paper the nature of the cranial nerves and see whether or no they conform in structure, origin, and function to the above definition of a complete segmental nerve. I propose to consider the cranial nerves seriatim, and seeing that the optic and olfactory nerves clearly do not conform to the above type I will commence with the consideration conjointly of the oculomotor and trochlear nerves[1].

Nerves of mid-brain, IIIrd and IVth cranial nerves.

The functions of the oculomotor nerve are well defined, it supplies a number of somatic muscles of the eye with motor fibres and it is also the motor nerve for the sphincter muscle of the iris and for the ciliary muscle; it is therefore purely an efferent nerve in existing animals, whatever it may have been originally.

It arises from a large number of rootlets which unite to form a single nerve trunk within the cranium; section of the nerve here shows that it is composed of both large and fine medullated fibres; the large fibres varying in size from 14·4—18 μ while groups of fine fibres varying in size from about 3—5 μ are to be found strongly resembling the groups found in the anterior roots of the thoracic nerves; in fact the structure of the nerve strongly resembles a typical anterior root. By means of a series of sections it is easy to see how the large fibres pass off to supply the eye muscles belonging to this nerve and how as we approach the oculomotor ganglion the small fibres separate out from the fibres forming the nerve supplying the internal rectus muscle and pass off as a separate group, forming the radix brevis, into the oculomotor ganglion.

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[1] In order to compare these observations with those of my former paper, all measurements of size of fibres are taken from the dog unless expressly stated otherwise.

Here they enter into a large number of ganglion cells resembling those of a spinal ganglion and issue forth to form the short ciliary nerves, i.e. the motor nerves of the sphincter and ciliary muscles.

Fig. 1, Pl. XVI, is a small portion of one of a series of sections taken through an osmic preparation of the IIIrd nerve of the dog. The sections were cut from the roots of the nerve towards the periphery and the section of which Fig. 1 represents a part was through the nerve just before the oculomotor ganglion was reached. Great numbers of the smallest fibres are seen coming to the periphery of the nerve, preparatory to entering into the oculomotor ganglion. Soon after this section the cells of the oculomotor ganglion begin to appear and Fig. 2, Pl. XVI, represents a portion of one of the sections through the middle of the ganglion; all the fibres in among the ganglion cells are of the smallest size to be found in the IIIrd nerve. The continuation of the series of sections shows the formation of the short ciliary nerves from the ganglion, and as is seen in Fig. 3, Pl. XVI, the fibres of which these nerves are composed are all very small and very uniform in size.

In this way by far the largest portion of the ganglion is formed; in addition however to the mass of fibres coming from the IIIrd nerve, one or two fine nerves are found entering into the ganglion which come apparently from the naso-ciliary branch of the Vth and from the so-called sympathetic system. These small nerves considered as a whole are made up of very fine medullated fibres, of non-medullated fibres and of larger medullated fibres; all their large fibres pass away into the muscular branches of the oculomotor nerve and do not enter the ganglion, while the rest of the fibres pass into the ganglion and lose themselves in a small group of cells which appear to me to resemble in form and appearance those of the sympathetic system rather than spinal ganglion cells.

Neither part of this ganglion then is connected with any large fibred sensory nerves from the Vth, it is connected only with very fine efferent nerve fibres which come mainly from the IIIrd nerve; it is in fact as typical a motor vagrant ganglion as any in connection with the spinal nerves. We see then that Schwalbe is right in looking upon this ganglion as essentially belonging to the IIIrd nerve; that van Wijhe would have been right in considering it as wholly sympathetic if he had only known the true meaning of a sympathetic ganglion. Those observers are wrong who have endeavoured to force the IIIrd nerve into the position of a segmental nerve by making this ganglion into a posterior root ganglion. This confusion has doubtless arisen as Gegenbauer[1] has pointed out by mixing up that part of the Gasserian ganglion, which forms the ganglion of the *ram. ophthalm. profundus,* with the oculomotor ganglion. In a recent paper by Beard[2] the distinction between the ganglion belonging to the Vth (meso-cephalic ganglion, Beard) and the true oculomotor ganglion has been pointed out.

It may be argued that the structure of the nerve cells points to a close relationship of the main portion of this ganglion with a spinal ganglion; this by no means necessarily follows, for the difference between a spinal ganglion cell and a so-called sympathetic ganglion cell depends probably upon the structure and number of the nerve fibres which enter and pass from it rather than upon their function; thus in the spinal ganglion the unipolar and bipolar cell is found associated with fibres which are medullated in both directions while the multipolar cell belonging to the efferent nerves of the vascular and glandular systems, i.e. the so-called sympathetic nerve cell, is according to the arguments given by me in my previous paper associated with a medullated fibre only in one direction, the other processes giving rise to a number of non-medullated fibres. The reason then why the nerve cells with which the fine fibred motor nerves of the sphincter and ciliary muscles are connected are of the spinal type is because the fibres do not lose their medullary sheath in their passage through the ganglion; as is seen in Fig. 3, Pl. XVI, the short ciliary nerves are medullated as much as the small fibres in the roots of the oculomotor nerve which give origin to them.

This then is in my opinion the reason why the cells of this vagrant efferent ganglion resemble the cells of a spinal ganglion, and it is a matter of great interest to inquire why some motor nerve fibres lose their medullary sheath in their passage through an efferent ganglion while others do not; it would lead too far away from the main purpose of this paper if I were to enter into this subject here, so I will simply suggest that the peculiarity of the sphincter and ciliary muscles consists in this:—that their action is to a certain extent voluntary and that in certain animals, e.g. birds, they are composed of striated muscle fibres; I hope however in a separate paper to treat especially of the relation which subsists between the structure and function of different muscles and their nerve supply.

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[1] *Morphol. Jahrbuch,* 1887, p. 1.

[2] *Anatom. Anzieger,* 1887, p. 565.

Up to this point we can say that the oculomotor nerve conforms to the type of a spinal segmental nerve in that its efferent fibres are composed of a large fibred and a small fibred group of which the latter is in connection with a vagrant efferent ganglion.

Turning our attention now to the IVth nerve we see that its structure is very similar to that of the IIIrd; here also the nerve is efferent in function and is divisible into a large fibred and small fibred part, the large fibres supply the sup. obliq. muscle and vary in size from 14·4—18 μ. The small fibres which are more or less grouped together in the roots of the nerve vary in size from 3·6—5·4 μ, but as yet their destination is unknown; what structures they supply or whether they are in connection with any definite group of efferent ganglion cells requires a more special investigation of the nerve than I have as yet been able to give. We can however say this much that the IVth nerve so closely resembles in its structure the IIIrd as to allow the assertion that it too conforms to the type of the efferent portion of a segmental spinal nerve.

Where then are the afferent fibres of these two nerves? In the various schemes put forward by morphologists to explain the peculiarities of the cranial nerves some portion of the Vth nerve has generally been dislocated from the rest and forced to do duty as the afferent root of the IIIrd and IVth cranial nerves; attempts have been made for instance to look upon the *ram. ophthalmic. profund.* as a separate nerve which is the separated off posterior root of the IIIrd nerve; the history of such attempts together with a criticism upon them is given fully in Gegenbauer's[1] paper and need not detain us here. In my opinion no such supposition is necessary, for both these nerves possess within themselves structures which appear to me to have been originally the nerve cells and nerve fibres corresponding to the cells and nerve fibres of the stationary ganglion on a posterior root of a spinal nerve; so that in the possession of afferent fibres with a stationary ganglion as well as in the possession of efferent fibres these two nerves conform each to the type of a complete segmental nerve.

These structures I have found in their greatest perfection in the nerves of man; and the following description refers to osmic acid preparations of the cranial nerves of a woman aged 29 who died of perforation of the intestines. The roots of the nerves were taken out 24 hours after death with portions of the brain attached to them and

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[1] *Op. cit.*

immediately placed in osmic acid 1 % solution. Each nerve was cut into a series of sections from its exit at the brain for some distance peripheralwards.

In Pl. XVII, Fig. 2, I give three sections of the IVth nerve selected out of the whole series. The section (2*a*) is through the root of the nerve close to its exit from the valve of Vieussens, and it shows that the nerve fibres are surrounded by a thick sheath of peculiar connective-tissue-like material; while section (2*c*) taken more towards the periphery shows that this sheath of peculiar tissue no longer exists. An examination of the sections between 2*a* and 2*c* shows that the manner of disappearance of this thickened sheath is very peculiar, it does not remain on the outside of the nerve fibres but forms roundish masses of the same peculiar material in between the nerve fibres themselves as is seen in (2*b*), so that the sections with a low power possess a remarkable resemblance to a section through a ganglion. At the peripheral side of this ganglion like formation these round masses of fibrillar-like material cease somewhat abruptly and the sections appear as in 2*c*.

Again in the IIIrd nerve the same formation is seen; here we have a nerve composed of a great number of rootlets and the sections show that the ganglion-like structure makes its appearance on the separate rootlets before they join together to form the conjoint root. Very striking indeed is the sight of a number of these rootlets each presenting in a greater or less degree the appearance represented in Fig. 1, Pl. XVII. Here too we see another point of resemblance between this structure and a spinal ganglion. In the latter it is of common occurrence to find that the formation of the ganglion has thrown many nerve fibres out of their previously parallel course, so that on transverse section of the ganglion many fibres are cut in a more or less longitudinal direction; the same deviation is found, as is seen in Fig. 1, in many of the large fibres of the IIIrd nerve, which are thrown out of their direct course in consequence of the formation of these rounded fibrillar masses in a way precisely similar to what occurs in the spinal ganglion. In fact if we imagined the living protoplasm of both the cells and the sensory fibres of such a spinal ganglion as that found in the thoracic region of the tortoise to have degenerated and disappeared so that only the envelope of these structures, so to speak, was left, we should have an appearance very like what is seen in the IIIrd and IVth nerves of man; the intact fibres of the anterior root in the tortoise, which as already mentioned do not in this animal run separately from the ganglion, would correspond to the intact motor fibres of the IIIrd and IVth nerves in man.

When I first observed this peculiarity of structure in the roots of certain of the cranial nerves I imagined that the observation was entirely new; it was however pointed out to me later on that a paper had been written on the subject by Thomsen[1] working with Westphal; from his figures and description he evidently has seen the same structures which I have described, and although he does not recognize anything of the nature of a ganglion in the roots of such a nerve as the IIIrd yet he says that he has convinced himself that this fibrillar material is of phylogenetic importance and represents the remains of nerve cells; further that in the new-born infant he has found ganglion cells in connection with these circumscribed spots. If then we put together the observations of Thomsen which led him to the conclusion that these fibrillar masses were the remains of isolated nerve cells and mine which have shown that such masses are not isolated but are arranged just like the cells of a spinal ganglion, we must I think come to the conclusion that in these strands and clumps of fibrillar tissue found in the IIIrd and IVth nerves we have the remnants of nerve fibres and nerve cells which in by-gone animals were once of functional importance, but which have become useless and so lost their living protoplasmic contents, leaving the mere husk to show us still that these two nerves originally possessed nerve fibres and groups of ganglion cells corresponding in position and doubtless also in function with the nerve fibres and nerve cells of the stationary ganglia on the afferent root of a spinal nerve.

Any arrangement then of cranial nerves according to cranial segments must in the future reckon the IIIrd and IVth cranial nerves as completely or rather almost completely formed segmental nerves.

I say almost completely because in one respect only they do not apparently conform to the complete segmental type, viz. the large medullated fibres of their efferent roots supply muscles which are all somatic, being formed according to van Wijhe from the muscle plates of the first two cranial somites; they ought in addition to possess large medullated motor nerve fibres belonging to the non-ganglionated splanchnic group. Clearly such fibres do not exist in the nerves themselves, it however by no means follows that such fibres do not

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[1] Virchow's *Archiv*, Vol. CIX.

spring from centres of origin belonging to the same metamers as those of the IIIrd and IVth nerves but pass out at a different level, for it cannot be too often insisted upon that the position of the cell groups in connection with the nerve fibres is the true criterion of what forms a nervous metamer rather than the position of the exits of the nerve fibres. When I come to the consideration of the structure of the VIIth nerve I will deal with the evidence for the existence of non-ganglionated splanchnic efferent nerves belonging to the same metamers as the IIIrd and IVth cranial nerves (see p. 175).

Finally before passing on to the consideration of the other cranial nerves it is perhaps worth while to indicate how my view of the meaning of these two nerves differs from the views generally held as put forward by Gegenbauer in his recent paper. According to v. Wijhe both IIIrd and IVth cranial nerves are the ventral roots of two segmental nerves of which the *ram. ophthalm. profundus* and the rest of the Vth nerve form the respective dorsal roots. Against this Gegenbauer urges (1) that the *ram. ophthalm. profundus* bears no trace of being a separate nerve, it is only a branch of the Vth and therefore will not do for the dorsal root of the nerve of the 1st somite, and (2) that the IVth nerve is something separate and possesses sensory branches both in Amphibians and Selachians. The view which I put forward is this, both IIIrd and IVth nerves are in themselves complete segmental nerves of the type which Balfour[1] supposes to have been the original type "when mixed motor and sensory posterior roots were the only roots present"; that then owing to some change which occurred during the past history of the vertebrate the sensory parts of these two nerves degenerated and their place was taken by the sensory elements of the Vth nerve which, arising from segments behind, supplied those parts which have replaced the original sensory surfaces. Thus the *ram. ophthalm. profundus* is not a separate dorsal root but is a part of an extraordinary group of nerves, viz. those constituting the sensory root of the Vth nerve, which as we shall see have come up from hinder segments for the purpose of replacing the lost sensory nerve roots of a series of primarily fully formed segmental nerves.

These two nerves then form the primitive segmental nerves of the 1st and 2nd segments.

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[1] *Comp. Embryol.*, Vol. II. p. 380.

Nerves of the hind-brain, Vth and VIth cranial nerves.

These two nerves are in reality made up of 3 nerves, viz. two efferent nerves and one afferent; the function of the VIth nerve is purely motor, it supplies only one muscle, *m. externus rectus,*—a muscle belonging to the somatic system being derived according to v. Wijhe from the muscle plate of the 3rd somite; the structure of the VIth nerve shows that it is composed of large medullated fibres varying in size from $14{\cdot}4\mu$—18μ together with a few smaller ones, but there is no sign of any distinct group of small fibres as in the IIIrd and IVth nerves.

The function of the so-called motor part of the Vth nerve is also very largely motor but it in all probability contains also fibres for the lachrymal gland as well as fibres which dilate the pupil and relax the ciliary muscle and possibly also vaso-dilator fibres; in accordance with its function the structure of the nerve is composed of large medullated fibres and of groups of small fibres which are doubtless in connection with the various vagrant ganglia such as the spheno-palatine found in connection with this nerve.

The muscles which are supplied by the large fibres of the motor part of the Vth nerve are derived from the ventral group of mesoderm segments according to v. Wijhe, i.e. from the lateral plates of mesoblast, so that these fibres belong to the group of non-ganglionated splanchnic efferent nerves and it follows that the motor part of V contains no somatic elements; if then we take together the two nerves VI with its somatic fibres and the motor part of V with its splanchnic fibres we obtain all the elements necessary for the construction of a complete spinal nerve as far as the efferent fibres are concerned.

If we ask next, Where are the afferent fibres with their root ganglion belonging to this nerve? the natural answer would be in the sensory root of the Vth with the Gasserian ganglion; and yet I venture to think such answer would be wrong, for the roots of the motor part of the Vth contain within themselves the remains of nerve fibres and ganglia of precisely the same character and in the same position as those already described on the roots of the IIIrd and IVth nerves. In the VIth nerve I have not found any sign of a regular ganglion formation, only a few scattered round masses of the same fibrillar material which are apparently the remains of isolated ganglion cells; I conclude therefore that primitively the motor part of V and the VIth nerve taken together form a complete segmental nerve which does not require the sensory part of V to make it complete. It is possible that some portion of the sensory part of V which is in close connection with the origin of the motor part may belong to this segment. All that I desire to emphasise is the independence of the ascending root of V from this segment. In order to understand the meaning of the sensory root of V with its Gasserian ganglion, it will be better to consider it with the nerves of the medulla oblongata rather than in the present place; it will suffice here to say that the nerve fibres and ganglion cells of this root are all functional, there is no sign here of any degenerated ganglion cells or nerve fibres.

The primitive segmental nerve then of the 3rd or mandibular segment is represented by the 3rd branch or motor part of the Vth nerve together with the VIth nerve and the *ramus maxillaris superior* of the Vth nerve, i.e. the 2nd branch of the Vth has replaced the lost sensory elements of the original nerve just as the *ram. ophthalmicus* has replaced those of the two first segments. This is in accordance with the observations of Marshall and Spencer and v. Wijhe who all, as quoted by Gegenbauer, look upon the *ram. maxillaris sup.* as arising secondarily to the *ram. mandibularis.* As to the position of the VIth nerve the main fact is that it supplies the *m. rectus externus* which is derived from the 3rd somite; it is however by no means so clear that it therefore belongs to the 2nd ventral segment or hyoid segment rather than to the 1st or mandibular, for neither Marshall's nor v. Wijhe's arguments are sufficient to convince Gegenbauer that the VIth is the anterior root of the VIIth. The investigations of Ahlborn seem to show that in Petromyzon this nerve is much more closely connected with the Vth than with the VIIth; and the investigations of v. Wijhe show that the 1st gill-pouch is situated mainly under the 3rd somite, its anterior portion only lying under the posterior portion of the 2nd somite. In order to make his dorsal and ventral segments fit each other, and because he considers that the 2nd somite belongs to the mandibular segment, v. Wijhe is obliged to suppose that the hyoid segment is really double and that the ventral portion corresponding to the 3rd somite is not developed. Gegenbauer has however shown that such an assumption is not warranted; we have no reason to suppose that the hyoid segment is double and v. Wijhe's difficulty no longer exists if the VIth nerve belongs in reality to the mandibular rather than to the hyoid segment.

Nerves of the hind-brain, VIIth and VIIIth nerves.

In the VIIth nerve we find again an essentially motor nerve as far as function is concerned, for it supplies the muscles of the face; in addition it supplies efferent fibres to glandular structures, dilator nerves to blood-vessels by means of its well known branches chorda tympani &c. Like the motor part of the Vth nerve it is essentially a splanchnic efferent nerve, for the striated muscles it supplies all belong to the visceral group of muscles, being derived according to v. Wijhe from the ventral mesoderm segments, i.e. from the lateral plates of mesoblast. Examination of its structure shows again a division into large fibred and small fibred groups of nerves; the larger fibres passing off as the motor nerves of the facial muscles, while the fine fibres in the main separate out to enter into the geniculate ganglion and from thence to pass to their destination in the *chorda tympani, petrosus superficialis major* &c.

In man it can be very plainly seen that the majority of these fine fibres do not belong to the roots of the facial proper, but compose a series of rootlets situated between the facial and the auditory and known by the name of the *n. intermedius.* The contrast between the structure of the *n. intermedius* and that of the facial roots proper is very striking, and it is worthy of mention that although the *n. intermedius* is essentially a small fibred formation a few very much larger fibres stand out conspicuously among the smaller ones. I draw attention to this fact simply because it is possible that the further investigation of these larger fibres may throw light on the vexed question of the existence of nerves of taste in connection with the VIIth nerve. In neither dog nor rabbit can a distinct *n. intermedius* be spoken of; in both cases however, when the sections of the rootlets of the VIIth nerve are examined close to the exit of the nerve from the brain substance, it is found that many of the separate bundles are composed entirely or nearly entirely of the smallest fibres, of fibres in the case of the dog varying in size from about 3μ—4μ.

These bundles have a strong tendency to be grouped together apart from the rootlets containing the large fibres of the VIIth nerve; such bundles represent I imagine the *n. intermedius* of human anatomy and their fibres pass directly into the geniculate ganglion. Undoubtedly the cells of the geniculate ganglion are mainly connected with these small fibred groups and equally undoubtedly such nerves as the *chorda tympani* and *petros. superficialis major* which are known to be largely efferent in function spring from this ganglion, so that we have very good grounds for looking upon this ganglion as a vagrant efferent ganglion of the same kind as the oculomotor ganglion. It may however be more than this, for I have not been able as yet to convince myself that it is free from connection with any group of large fibres as is the case in the latter ganglion. It is difficult to obtain a really good series through this ganglion, owing to the great difficulty of combining really good osmic staining with freedom from splinters of bone, so that I can only say that my present sections point to the conclusion that this ganglion is not wholly efferent, for it appears to be in connection with a small group of large fibres which are probably afferent in nature. Whether this group if it exists comes from the *n. intermedius* or not I cannot at present say; it is one of the numerous points of interest in connection with the relation between the size of a nerve fibre and its function which requires investigation. One point however is worthy of mention, viz., that according to the universal agreement of morphologists, the VIIth nerve in the lower vertebrates possesses a ganglion which is in connection with sensory nerves; in man, and in the higher vertebrates, it would appear that the region supplied by such sensory nerves is innervated by the Vth and not by the VIIth, so that, considering the intimate relationship which is known to exist between the VIIth and Vth in these lowest classes of vertebrates, it is possible that a remnant of sensory fibres should still exist in the VIIth nerve of the higher vertebrates which would belong to the same system as the sensory fibres of the Vth nerve, and therefore as we shall see later on to the system of ascending roots.

The large fibred rootlets of the VIIth nerve contain a few fibres of the smallest size, but are mostly composed of the motor fibres of the facial muscles, which are very uniform in size and measure about 10·8μ. In addition to these there are also a very large quantity of fibres which measure between 7μ and 8μ.

The evidence then of the structure and function of the VIIth nerve shows that it corresponds to a complete segmental nerve, in that its efferent root contains a large fibred non-ganglionated splanchnic portion and a small fibred ganglionated splanchnic portion with its vagrant ganglia in the shape of the geniculate ganglion, submaxillary ganglion, &c.

As far as its stationary ganglion belonging to its afferent root is concerned we find here, as in the other motor cranial nerves already considered, evidence of a degenerated ganglionic structure close to the exit of the nerve from the brain. In Fig. 3, Pl. XVII, I give a picture of a section through this primitive ganglion of the VIIth nerve. In my opinion, then, the VIIth nerve is similar to the IIIrd, IVth and *pars mandibularis* of the Vth in that it has lost its primitive stationary ganglion and the afferent fibres in connection with that ganglion; I would therefore look upon the existing sensory distribution of the nerve as belonging to the same system as that of the Vth, i.e., as already mentioned, a system of sensory nerves which has taken the place of the lost sensory elements of the primitive group of segmental nerves.

One component of a fully formed segmental nerve still remains for consideration, viz. the somatic efferent portion. In my previous paper[1] I called attention to the remarks of Schwalbe, that many observers considered that some part of the fibres of the VIIth arose from the nucleus of the VIth nerve, and also that the *m. orbicularis palpebrarum* and *m. frontalis* often remain unaffected in cases of bulbar paralysis when the nucleus of the VIIth nerve has been destroyed by disease. I imagined then that possibly these muscles might be supplied by fibres from the nucleus of the VIth nerve.

Now I had noticed that the motor fibres supplying the somatic muscles of the eye were very much larger than those supplying the facial, pharyngeal and laryngeal muscles, i.e. in these cases a distinct difference in size, between somatic motor and splanchnic motor non-ganglionated nerve fibres, the former varying from $14{\cdot}4\mu$—18μ, the latter from 9μ—$10{\cdot}8\mu$. A similar difference in size of fibres is very evident in the formation of the phrenic nerve. In Fig. 5, Pl. XVI, I give a section through the 4th cervical nerve of the rabbit at the point where the fibres of the phrenic are separating out from the rest of the fibres of the 4th cervical nerve; as is seen the fibres of the phrenic nerve (B) are very uniform in size and much smaller than the large motor fibres of the somatic muscles supplied by the 4th cervical nerve (A). If then any somatic fibres from the nucleus of the VIth passed out in the VIIth nerve they ought to be conspicuous by their size among the smaller motor fibres of the VIIth. Reasoning in this way I was much struck to find that in the roots of the VIIth nerve of the dog a small group of large fibres stands out most conspicuously; the size of the fibres being the same as those of the large motor nerves of the eye muscles, viz. 16μ—18μ. In Fig. 4, Pl. XVI, these fibres are shown in the rootlets

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[1] *Op. cit.* p. 68.

as they are found. Here then appeared to be positive evidence of the existence of somatic motor fibres in the roots of the VIIth nerve. Upon examination, however, of the nerves supplying the orbicularis and frontalis muscles I was unable to find that their fibres were different in size to those of the other facial muscles, and, indeed, section of the branches of the VIIth nerve after they had passed out of the stylomastoid foramen failed to show the presence of any group of especially large fibres.

There is then no evidence that any one of the muscles of expression is innervated differently from the rest, they all belong to the same group, they are all supplied by splanchnic non-ganglionated fibres. Yet the fact remains that certain muscles escape paralysis when the rest are paralysed by disease situated centrally. During the last year an explanation of this peculiarity has been given by the observations of Mendel[1], who found that the *m. orbicularis palpebrarum* was innervated by fibres which arose from the posterior portion of the oculomotor nucleus and travelling along the posterior longitudinal bundle passed out with the roots of the VIIth nerve to reach their destination. In fact in these muscles and their nerve supply we have the missing splanchnic non-ganglionated efferent portion of the oculomotor and trochlearis segments to which reference was made on p. 169.

Still firmly convinced in my own mind that these large fibres represented the somatic efferent elements of the facial nerve, I dissected out the whole facial from its origin to its exit from the stylomastoid foramen, stained it with osmic and cut sections of it at intervals, and found that at a certain point in the nerve all the very large fibres which were present in the nerve at that point came together to the periphery of the nerve, and forming a distinct though small nerve branch disappeared out of the series of sections. It is clear then that these large fibres have a very definite meaning, for they go off by themselves to form a separate nerve; I was unable to trace this slender nerve to its destination but it seemed to me at the time that the only muscle it could possibly supply was the *m. stapedius*, and as the rest of the very large fibres left the main trunk in one of the branches from the geniculate ganglion I imagined that they probably were intended for the supply of the *m. levator palati*, which according to all the text-books is innervated from the VIIth nerve. That such were the actual or probable destinations of these large fibres I have stated in the preliminary

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[1] "Ueber den Kern-Ursprung des Augen-Facialis." *Neurolog. Centralblatt*, 1887, p. 537.

communication[1] to this paper; in both cases that statement is unfortunately erroneous, for in the first place I determined before the full paper was published to trace this fine nerve into the *m. stapedius*, and one of the students, Mr Waggett, kindly undertook to dissect out the facial nerve and the stapedius muscle and to make sections; this he has done and has proved to me conclusively that the large fibres do not supply the stapedius muscle and do not leave the main trunk until nearer the exit of the facial from the bone; as yet he has not determined their ultimate destination. I beg here to thank him for pointing out to me the erroneous conclusion to which I had come from my own imperfect observation. In the second place, the observations of Beevor[2] and Horsley which have recently been published show that the text-books of anatomy are wrong with respect to the *m. levator palati*, for that muscle is innervated by the spinal accessory nerve and not by the facial, so that the large fibres of the facial cannot supply that muscle.

At present, then, I must confess that I have no evidence to offer as to the existence of the somatic efferent nerves of the hyoid segment, and can only point out that v. Wijhe's 4th somite aborts and does not form any muscles, which, if v. Wijhe is wrong, as Gegenbauer thinks, in supposing that the hyoid segment is double, may mean that the somatic muscles of the hyoid segment have for some reason or other ceased to be developed. The other supposition would be that the VIth nerve is all that remains of the somatic efferent nerves of both the mandibular and hyoid segments.

As to the VIIIth nerve, I do not think it advisable at present to offer any definite opinion upon its position; for I do not as yet know sufficient about its structure or the origin of its nerve fibres to enable me to speak with any confidence with respect to it. I can therefore only repeat that it is not necessary to look upon it as part of the VIIth, and that it occupies a special position as a nerve of special sense, which may possibly justify its claim to an independent position. I am pleased to find that I am supported in this view by the observations of Osborn[3], who from his investigations into the brain of the Amphibia is inclined likewise to place the auditory nerve in a separate category.

Summing up the results of our investigation into the nature of the

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[1] *Proceedings of the Roy. Soc.* Vol. XLIII. p. 389.

[2] *Proceedings of the Roy. Soc.* Vol. XLIV. p. 269.

[3] *Op. cit.* p. 71.

cranial nerves considered up to this point we see that they form a natural group, all the members of which possess the same characteristics.

In this group of motor cranial nerves formed by the IIIrd, IVth, VIth and motor part of Vth, and VIIth nerves we find at least 4 fully formed segmental nerves, which for some reason or other have lost a certain portion of their original components.

Nerves of the Medulla Oblongata.

In the next group of cranial nerves, viz. those which arise from the medulla oblongata, we again find all the components which make up a fully formed spinal nerve or rather group of nerves; here however there is no sign of any degeneration of any special group of fibres, but rather of a dislocation and scattering of the different components, so that the cranial nerves of this group form parts of a number of segmental nerves instead of each one forming a single nerve; thus the somatic efferent nerves are collected together in the hypoglossal nerve; the somatic afferent fibres of this region do not pass out with the nerves of the medulla oblongata, but help to form part of the sensory root of the Vth nerve, the only other somatic sensory nerves in the mammal being the auricular branches of the vagus; the splanchnic nerves, both afferent and efferent, form the glossopharyngeal, vagus and medullary portion of the spinal accessory. Taking then these nerves in order we must examine first the glossopharyngeal or IXth cranial nerve.

By the general consent of all morphologists this nerve holds a perfectly definite position among the cranial nerves; it is the nerve of the 1st branchial segment and supplies only the ventral portion of that segment; i.e. it is a purely splanchnic nerve and contains no somatic elements. Further, it is the foremost of a series of nerve roots, viz. those of the vagus and the medullary portion of the spinal accessory which are all built up on the same plan, are all splanchnic nerves and supply the ventral portions of the rest of the branchial segments. The nature of the fibres which form the nerves of this group has already been largely considered in my former paper, so that it is not necessary to dwell upon them here. I will however briefly recapitulate. The IXth and Xth each possess two ganglia, the *ganglion jugulare* and *ganglion petrosum* on the one hand, and the *ganglion jugu-*

lare and *ganglion trunci vagi* on the other[1]. In connection with the *ganglion petrosum glossopharyngei* we find efferent nerves such as those forming part of the *n. tympanicus* and supplying the parotid gland with both secretory and vaso-dilator fibres. In connection with the *ganglion trunci vagi* we find, as pointed out in my former paper, the motor fibres of the alimentary tract.

The structure of the roots of the IXth and Xth nerves resemble each other in the fact that they are composed mainly of very small fibres varying in size from 1·8 μ to 3·6 μ. They also contain large fibres the size of which does not exceed 10·8 μ. Such fibres however are very sparing in the glossopharyngeal root, but more numerous in the roots of the vagus and the medullary roots of the spinal accessory. With respect to the function of the different fibres we are met with the difficulty, that at present no criterion exists in the structure of a nerve fibre by which we can decide whether a nerve fibre of any particular size is afferent or efferent; we cannot therefore as yet decide by the mere inspection of sections of the roots of the IXth nerve the disputed point as to the existence in this root of nerve fibres which are motor to striated muscles. The large fibres may be motor to such muscles as the *m. stylo-pharyngeus* or they may be sensory fibres to some tract supplied by the nerve.

In the case of the Xth and XIth nerves it is easy to determine the size of the large motor nerve fibres of the laryngeal muscles by section of the vagus nerve at the place where the inf. laryngeal is just leaving the nerve, and it is very instructive to see how a number of the largest fibres in the nerve (about 10·8 μ in size) sort themselves out into a group at the periphery of the nerve trunk and so form the inf. laryngeal. These large fibres probably come partly from the medullary roots of the spinal accessory nerve, in which fibres of that size are freely found. Such medullary roots however merge imperceptibly into the roots of the vagus proper.

In accordance with the arguments used in my former paper and in this paper, I consider that the two jugular ganglia represent the stationary afferent ganglia of the IXth and Xth nerves, while the *ganglion petrosum glossopharyngei* and the *ganglion trunci vagi* represent their

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[1] The roots of IX, of X, of the medullary portion of XI and that rootlet which springs from XI to pass over to XII and to form its ganglionated root, all have their fibres imbedded in a peculiar matrix somewhat resembling the degenerated material of the 1st group. This is however not arranged so as to form ganglia, and cannot be interpreted as in the first case.

vagrant efferent ganglia. In the higher animals the stationary ganglia are in connection almost entirely with splanchnic afferent fibres, for, with the exception perhaps of the auricular branch of the vagus, the somatic afferent nerves of this region have all passed away into the ascending root of the Vth nerve. In fishes, however, a marked sensory nerve, belonging I imagine to the somatic system, viz. the *r. lateralis,* arises from the vagus; and section of this nerve in the skate shows that it is composed mainly of large fibres which are in marked contrast to the small fibred structure of the *r. intestinalis.*

An interesting point in connection with the vagrant or efferent ganglion of the vagus is the fact that its nerve cells belong to the so-called spinal type of ganglion cell, and not to the so-called sympathetic type, although as I have already explained[1], the fine motor fibres of the alimentary tract lose their medullary sheath after passing through the ganglion. Here then apparently we have connected with ganglion cells motor fibres which are intermediate in type between the motor fibres of the iris muscles and those of the muscles of the vascular system; and I imagine that the reason why these nerve cells are of the spinal type is because, as in the case of the oculomotor ganglion already discussed, only one nerve fibre leaves the cell and only one enters it, that in fact the difference between the non-medullated fibres of the vagus trunk and those of the so-called sympathetic system may be explained by supposing that the multiplication of fibres takes place differently in the two cases: in the former the nerve fibre divides some time after it has left the cell, in the latter the division takes place in the cell itself. In osmic preparations of the vagus nerve near the diaphragm I have often thought that the outlines of the separate nerve fibres showed more distinctly than is usual in a mass of non-medullated fibres, and many of the students who attend my lectures to whom I have shown the specimens have thought that a very fine medullated sheath existed round each axis cylinder, so that the loss of medulla was not absolutely complete; I have not, however, been able to convince myself that such is the case, in the dog at all events, and I find that Ranvier[2] in the recently issued number of his Histology also looks upon the vagus as largely composed of non-medullated fibres. On the other hand, the great mass of fibres which leave the *ganglion trunci vagi* of the crocodile are medullated; and in connection respectively with the retention and loss of the motor

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[1] *Op. cit.* p. 24.

[2] *Traité technique d'Histologie, 7th Fascic.* Paris, 1888, p. 1022.

functions of the nerve according as it was cut above or below the ganglion, it is to be noticed that in the former case most of the medullated fibres showed no signs of degeneration, while in the latter case the most noticeable feature was the marked degeneration of these fibres.

Seeing that, as already mentioned, I propose in a future paper to discuss the exact differences in size of fibre, loss of medulla and connection with ganglion cells which exist in the motor nerves of the same animal according to the nature of the muscle supplied I will not dwell longer on this point now. I would simply desire to impress upon my readers the necessity of recognising that the vagus is very largely if not mainly a motor or efferent nerve. It is the motor nerve not only of the laryngeal and pharyngeal muscles but also of the unstriped muscles of the bronchi, and of the muscles of the whole alimentary tract as far as the hind gut and its appendages. In accordance with its motor character we see that a large number of its fibres pass on one side of the *ganglion jugulare* and enter directly into the motor ganglion called the *ganglion trunci vagi.*

The Spinal accessory Nerve.

This was the nerve the consideration of which led me to the conception of the division of the nerve roots into the two great somatic and splanchnic divisions. It is clearly an efferent nerve, it is equally clearly, as I have already shown in my previous paper, mainly composed of two kinds of fibres, the one large in size, and the other very small; the large ones arise in all the roots of the nerve, the groups of small fibres are confined to the medullary and upper cervical roots and pass into the *ganglion trunci vagi.* In this nerve we have, then, clearly a separated group of motor fibres which take origin from the same metamers as the vagus and the upper cervical nerves. This group of motor nerves is clearly composed of a ganglionated splanchnic part, i.e. the small fibred portion and a non-ganglionated part; and the interesting question arises, Are these non-ganglionated large-fibred nerves splanchnic or somatic? According to the suggestions of my former paper the voluntary muscles supplied by this nerve belong to Charles Bell's system of respiratory muscles, and the nerve therefore is a purely splanchnic nerve. If this suggestion is a true one we have the very important fact that the efferent splanchnic fibres of the upper cervical region, both ganglionated and non-ganglionated, have separated out from the rest of the components, with which they ought to be associated to form a complete nerve, and thus have formed a separate nerve root. It is necessary then to consider the position of the muscles supplied by this nerve. In the first place, we see that the large motor fibres of the medullary roots of this nerve, together with those of the vagus proper, supply the laryngeal and pharyngeal muscles; these are clearly splanchnic muscles, and not somatic[1]. The main bulk of large fibres supply the trapezius and sterno-cleido-mastoid muscles, of which the latter muscle is recognised as an isolated portion of the former; the question for discussion therefore resolves itself into this. Does the *m. trapezius* or *m. cucullaris*, as it is called in the lower animals, belong to the splanchnic or somatic muscular systems? For the answer to this question I am indebted to my friend Dr H. Gadow, whom I beg here to thank for this and other assistance. He tells me that the evidence of comparative anatomy distinctly points to the conclusion that the cucullaris group of muscles was originally a visceral or splanchnic group belonging to the same set of muscles as the mylohyoid, platysma, and perhaps the digastric. He argues that the original visceral muscles of the branchial region have been largely invaded and superseded by the ventral longitudinal somatic muscles, so that only portions of them have remained on each side of the median ventral muscles. These portions then have in their turn spread over the invading somatic muscles ventralwards and so formed the mylohyoid, platysma, trapezius and sterno-cleido-mastoid muscles. If this be the case then all the large fibres of the spinal accessory supply splanchnic muscles, so that this nerve is to be looked upon as the separated out splanchnic portion of the efferent roots of the upper cervical nerves, and contains all their splanchnic efferent fibres, both ganglionated and non-ganglionated, with the exception of those fibres which form the phrenic nerve.

The Hypoglossus Nerve.

It is unnecessary to add anything to my previous description of this nerve; it is a purely motor nerve, it is motor to the longitudinal ventral muscles, i.e. it is a somatic motor nerve. It clearly represents the separated somatic efferent nerves of this region, and cannot be

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[1] In the pharyngeal muscles supplied by this nerve the levator veli palati ought to be included according to the observations of Horsley and Beevor; we have not at present sufficient evidence to enable us to judge of the position of this muscle.

looked upon as a separate segmental nerve any more than the anterior roots of the 1st or 2nd cervical nerves. As to the so-called ganglionated root of the XIIth nerve noticed by Froriep, no difficulty appears to me to arise. It is easily seen in the dog, and I have shown the structure of it in my former paper[1]. I have also in the figures on Pl. III. of the same paper indicated the nature of its origin; it is simply one of the rootlets of the medullary portion of the XIth nerve which runs with the XIIth nerve instead of with the Xth. Its presence no more indicates a posterior or afferent root to the XIIth nerve than the *ganglion trunci vagi*, and the small ganglia found on some of the other rootlets of the XIth nerve make this latter nerve an afferent as well as an efferent nerve.

Summing up, then the peculiarities of this second group of cranial nerves, viz. IX, X, XI and XII together with the sensory part of V, we see that they represent a primitive group of at least five segmental nerves which unlike those of Group I. have not lost any particular component, but have become broken up and split into various portions, doubtless in connection with the making good of those parts, the loss of which caused the degeneration of nerve structures observed in Group I.

This group of cranial nerves is further characterised by the extensive distribution of its peripheral nerves both somatic and splanchnic, for not only is the whole of the alimentary canal and its adjuncts with the exception of the hind gut and its appendages, innervated by the vagus nerve, but also in the nerve of the lateral line we have the somatic sensory elements of this group extending along the whole length of the body. Further, this group is characterised not only by the extensive distribution of its peripheral nerves but also by the extensive origin of its nerve fibres in the central nervous system, as will appear in the following section.

Origin of the Efferent Fibres of the Cranial Nerves.

As far as the origin of the cranial nerves is concerned I can add little to what is already known and described in the anatomical textbooks, the substance of which was epitomised by me in my former paper; this is amply sufficient to show that the groups of cells which give origin to the cranial nerves belonging to the two groups treated of

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[1] *Op. cit.* Pl. I. Fig. 5.

in this paper are the direct continuation of the corresponding cell groups found in the spinal region, that in fact the spinal nature of these cranial nerves is shown in the groups of cells from which their fibres arise just as clearly as in the correspondence between the structure and function of their peripheral nerve-fibres already treated of. In the first place, the centres of origin of the somatic efferent nerves are absolutely well-known in the groups of cells forming the nuclei of the IIIrd, IVth, VIth and XIIth nerves, which are in structure and position undoubtedly the continuation of the cell groups of the anterior horn. They show clearly the very significant fact, which is by no means confined to the cranial region, that this group of cells does not form a continuous column, but that the separate groupings point strongly to an original metameric arrangement of the centres of origin as well as of the peripheral distribution of these somatic nerves. It is worthy also of notice that the nuclei of the IIIrd and IVth nerves are so close together as to be continuous, while that of the VIth is some distance removed from them; as though the metamers supplied by III and IV were more closely related to each other than to that supplied by VI. Again, considering the smallness and compactness of the region supplied by the XIIth nerve the extent of its nucleus is most striking, for it extends along the whole length of the medulla oblongata; and considering that this nerve represents the somatic efferent part of the vagus nerve, i.e. of a nerve supplying a number of splanchnic segments, it is most probable that this extended nucleus of origin indicates a corresponding number of somatic centres which have coalesced to form one long nucleus.

In the description of the nuclei of origin of the cranial nerves given in the text-books of human anatomy, such as Schwalbe and Rauber, it is clearly pointed out and indeed has long been known that the cranial motor centres are divisible into two groups; the one the group already considered, and the other a lateral group corresponding to the lateral horn in the spinal region which gives origin to the motor nerves of the trigeminal, facial, vagus and spinal accessory. The morphological importance of this division was recognised and emphasised by Hill[1], who however failed to understand its true import as he had not read v. Wijhe's paper[2]. My work on the true meaning of the sympathetic system in combination with v. Wijhe's discovery that the muscles

[1] Plan of central nervous system. Cambridge, 1885.

[2] *Ueber die Mesoderm segmente u. die Entwickl. der Nerven des Selachierkopfes.* Amsterdam, 1882

supplied by these two sets of motor fibres arise from the dorsal and ventral mesoblastic segments respectively, enabled me to recognise the true meaning of this separation of the motor nuclei of the cranial nerves into two well-defined groups, of which the one gave origin to the somatic efferent nerves and the other to the splanchnic non-ganglionated efferent nerves. In his last paper His[1] has also begun to appreciate the importance of this separation of cranial motor nuclei into two groups; as however he has apparently not read my former paper he has failed to understand its full significance.

The centres then of the splanchnic non-ganglionated efferent nerves form the well defined group of cranial nuclei known as the motor nucleus of the trigeminal, the nucleus of the facial, the motor nucleus of the vagus group, and the nucleus of origin of the spinal accessory fibres. In connection with these nuclei various important questions arise which are of interest but which, since they are subsidiary to the main argument of this paper, it is not necessary to discuss here; such questions are the meaning of the upper nucleus of the trigeminal, the exact origin of the fibres of the facial which supply the *m. orbicularis palpebrarum*, and the limits of the spinal accessory nucleus. The main point is that the striated muscles which arise from the ventral mesoblastic segments, i.e. from the splanchnic segments, are innervated by nerves which not only leave the central nervous system separately from the nerves which innervate the muscles of the somatic segments, but also have in the central nervous system itself separate centres of origin from those latter nerves. These centres of origin are the continuation of the large celled groups in the lateral horn of the spinal region (see p. 160). Here too we find that these nuclei of origin are distinctly arranged metamerically, and it is worthy of notice that these metameric nuclei extend far into the cervical region, and by the formation of a long-ascending root give origin to a single nerve trunk, viz. the spinal accessory.

We come next to the origin of the splanchnic ganglionated efferent nerves of the cranial region, i.e. to the continuation of the groups of Clarke's column, the solitary cells of the base of the posterior horn, and the small cells of the intermedio-lateral tract. According to the conjectures already made we should not expect to find the small cells of the intermedio-lateral tract, i.e. the centres of katabolic nerves of the vascular and glandular systems, prolonged beyond the antero-

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[1] *Archiv f. Anat. u. Physiol. Anat. Abtheil.* 1887, p. 379.

lateral nucleus in the medulla oblongata. Of the other two groups the nerve cells of Clarke's column are most easily followed, owing to their shape; they form part of the nucleus of the vagus and glosso-pharyngeal and terminate apparently in the large group of cells forming the *locus cœruleus.* These latter cells as pictured in Henle[1] resemble most closely the cells of Clarke's column.

With respect to the continuation cranialwards of the solitary cells of the base of the posterior horn I do not know of any observations which would enable us to follow them further than the vagus and glosso-pharyngeal nucleus; I have already given my reasons for believing that the vagus nucleus on the floor of the 4th ventricle (see Fig. 1. Pl. XVIII) is essentially a motor nucleus giving origin to the gangli-onated motor fibres of the alimentary tract; and I feel that we cannot at present attempt to differentiate in the higher cranial regions between the origins of the ganglionated efferent anabolic and katabolic nerves or between the two contiguous groups of nerve cells which are known in the spinal cord as the cells of Clarke's column and the solitary cells of the posterior horn respectively. It is, however, possible to make certain suggestions for future investigations in this direction. Thus we find that, according to Henle[2], the descending root of the trigeminal nerve consists at its commencement of fine fibres only; soon however large fibres mix with them, which increase in number as the descending root approaches the nucleus of the trigeminus, until at last the root appears to consist almost entirely of large fibres; along the whole length of its course the root is accompanied by large bladder-shaped cells in strong contrast to the pigmented cells of the *locus cœruleus,* which latter are situated in close contiguity to it. If then, as is most probable, the observations of Henle and Forel that this descending root is composed of motor fibres are correct, it is possible that the three groups of nerve cells which give origin (1) to the small fibres of this root, (2) to the large fibres of this root, and (3) which form the cells of the *locus cœruleus* correspond to the three groups of nerve cells which in the spinal region give origin to the splanchnic ganglionated and non-ganglionated efferent fibres respectively. The nerve cells of the *locus cœruleus,* although strongly pigmented, are probably not entirely devoid of function, for according to Schwalbe[3] they are not pigmented in children or in mammalia generally.

The origin of the ganglionated small-fibred motor nerves of the

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[1] *Op. cit.* p. 256.
[2] *Op. cit.* p. 253.
[3] *Op. cit.* p. 678.

sphincter muscles of the iris and of the ciliary muscles is, as far as I can find out, not clearly known; Hensen and Voelcker's experiments seem to point to an origin for these nerves in front of and separate from the origin of the nerves which supply the striated muscles of the eye. The arrangement of the nerve fibres in the rootlets of the IIIrd nerve at their exit from the central nervous system appears to me to suggest a separate origin for these fibres, for certain of these very fine rootlets are almost entirely composed of the smallest fibres to be found in this nerve. This is especially noticeable in the case of the rabbit, and is strongly suggestive of the commencement of an intracranial separation of the small and large fibres. We are in fact reminded here of the same kind of separation as is seen clearly in the case of the VIIth nerve, where groups of the smallest fibres mixed with a few large ones separate out to form the *n. intermedius.*

The origin of this latter nerve is most interesting if the observations of Sapolini[1] are correct, for this observer asserts that the *n. intermedius* arises as a long-ascending root of the same character as the ascending root of the vagus. If this be so we find then here at the border of the two groups of cranial nerves an ascending root composed largely of splanchnic ganglionated efferent fibres as the companion of the ascending root of the spinal accessory, which is composed mainly of splanchnic non-ganglionated efferent fibres.

The origin of the Afferent Fibres of the Cranial Nerves.

It is impossible to trace the centres of origin of the afferent fibres in the same way as we have been able to do for the efferent fibres, and to compare them directly with the corresponding centres in the spinal cord, because even in the spinal cord itself no well-defined groups of nerve cells exist with which it has been proved that afferent nerves have connection.

The two main characteristics of the spinal afferent fibres are the presence of the ganglion on the posterior root and the presence of the substantia gelatinosa Rolandi with its scattered small cells in the posterior horn. Of these two the former has already been considered, and it has been shown that the cranial nerves correspond to the spinal in this respect. As far as the substantia gelatinosa Rolandi is concerned this is found in the cranial nerves, as is well known, only in close con-

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[1] Quoted by His.

nection with the ascending root of the vth nerve. As to the degenerated nerve fibres of Group I. of the cranial nerves I have not attempted at present to trace them into the central nervous system. I can only say that the nerve cells of the *substantia nigra* appear from their position and from the direction of the long axis of many of their cells to have been originally connected with some of these nerve fibres belonging to the IIIrd nerve; I do not however think that such nerve fibres were afferent, for it is improbable that such a group of nerve cells as we find forming the *substantia nigra* should give origin to afferent nerve fibres. As, however, I propose to discuss the meaning of the cells of the *substantia nigra* later on I will not dwell further on this question here.

The afferent nerves of Group II. are most interesting in their distribution in the central nervous system, for not only are they distinctly separated into somatic and splanchnic groups but also both groups arise from the cervical region of the spinal cord as well as from the medulla oblongata. Thus all the sensory nerves of V forming the somatic afferent nerves arise from the ascending root of V, a bundle of fibres which has been traced as far as the middle of the cervical region; so also the ascending root of X or *fasciculus solitarius* or respiratory bundle formed by fibres of the IXth and Xth nerves is afferent in function, and, as has been already pointed out, contains if His is right all or nearly all of the afferent fibres of the latter nerve. This bundle of fibres has not been proved to arise from any groups of nerve cells in the medulla oblongata and has been traced into the spinal cord as far as the origin of the phrenic nerves.

Further, according to His[1] these afferent ascending roots of both the trigeminal and vagus nerves are in an embryo of 4½ weeks old quite superficial in position; so that we have evidence of a series of ascending roots in the cervical region of the cord of the same type as the spinal accessory. Including the spinal accessory itself these ascending roots respectively consist of (1) somatic afferent fibres, *i.e.* the ascending root of the trigeminal; (2) splanchnic afferent fibres, *i.e.* the ascending root of the vagus; (3) splanchnic non-ganglionated efferent fibres, *i.e.* the cervical portion of the spinal accessory; (4) splanchnic ganglionated efferent fibres, *i.e.* the *n. intermedius.* These form in fact a series of roots arising from spinal as well as cranial regions, which taken together contain all the elements of a complete segmental nerve or group of nerves with the exception of the somatic efferent

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[1] *Op. cit.* p. 374.

fibres. Although these latter fibres do not form an ascending root yet they evidently are not missing from this system, for the whole argument of Gegenbauer, as already pointed out, goes to show that the hypoglossal nerve may be looked upon as the remnant of a system of somatic efferent roots which were spinal as well as cranial.

Summary.

In order to put clearly before my readers the results of the previous pages, I have endeavoured in Pl. XVIII to express in the form of diagrams the views therein expressed. In Fig. 1, Pl. XVIII, I have copied a section of the medulla oblongata from Edinger[1], and on the one half of the section I have lettered the groups of nerve cells *A*, *B*, *C*, *D*, *E*, to correspond with the lettering of the section of the spinal cord given in Fig. 1, p. 155. In both cases the letters have the same signification viz.

A (Cells of ant. horn)
= nucleus of efferent nerves to somatic muscles.
B (Large cells of lat. horn)
= nucleus of efferent nerves to striated splanchnic muscles.
C (Cells of Clarke's col.)
= nucleus of anabolic (inhibitory) nerves to splanchnic glandular system and to muscles of viscera and of vascular system.
D (Solitary cells of post. horn)
= nucleus of motor nerves to muscles of viscera.
E (Small cells of lat. horn)
= nucleus of katabolic (motor) nerves to splanchnic glandular system and to muscles of vascular system.

On the other half of the figure, I have lettered the groups of cells in the same way as Edinger has done and in addition have coloured the different groups of motor cells red, yellow, and green and the two tracts of sensory fibres blue and purple; the signification of the colours is as follows:—

Red (nucleus of XII) = somatic efferent.
Green (so-called motor nucleus of X, &c.) = splanchnic non-ganglionated efferent.
Yellow (part of nucleus of X and XI) = splanchnic ganglionated efferent.
Blue (ascending root of X) = splanchnic afferent.
Purple (ascending root of V) = somatic afferent.

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[1] *Bau der nervösen Centralorgane*, Leipzig, 1885, p. 118.

On the same plate, Fig. 2, I have made an attempt to express diagrammatically the formation of the two great groups of cranial nerves and to indicate the arrangement of the different segments. For this purpose I have not attempted to give an accurate representation of any particular brain, but only to indicate by means of different colours the main peculiarities of the segmental cranial nerves. The colours have the same meaning as given above, and in addition I have marked out the degenerated ganglia of the 1st group of cranial nerves with black lines. The outline of the brain itself and the arrangement of its cavity is drawn from a longitudinal section of the brain of a young dog-fish and is represented somewhat diagrammatically for the purpose of illustrating Part II of this paper. Thus the cerebellum and optic lobes are not intended to be accurate in size but are put in simply for the purpose of indicating their position. For the purpose of comparison with the cranial nerves I have drawn and coloured two typical segmental spinal nerves from the thoracic region as the continuation of the same diagram.

I conclude then that the cranial nerves, with the exception of the optic, olfactory and auditory, are formed from a series of segmental nerves of the same type as in the spinal region, but have been modified so as to form two distinct great groups, of which Group I consists of at least four complete segmental nerves each of which has lost certain components owing to the loss of the parts which they originally supplied; these nerves are—1st segment, oculomotor; 2nd segment, trochlear; 3rd segment, motor part of trigeminal with abducens; 4th segment, facial.

Group II. consists of at least five complete segmental nerves which are both cranial and spinal in origin. The characteristic of this group is not the loss of any particular component but the splitting up of the different components to form the separate nerves known as the vagus, glosso-pharyngeal, hypoglossal, spinal accessory nerves, together with the sensory part of the trigeminal; and a further characteristic of this group is the remarkable and extensive peripheral distribution of its nerves, a distribution which is partly at all events for the purpose of replacing the lost elements of Group I.

In order then to understand the present arrangement of the vertebrate nervous system some explanation must be found for the formation of these two characteristic groups. I propose then in the second part of this paper to put forward what seems to me a probable explanation of the peculiarities of Group I. of the cranial nerves.

PART II.

A THEORY OF THE ORIGIN OF THE CENTRAL NERVOUS SYSTEM OF VERTEBRATES, TO EXPLAIN THE DEGENERATION OBSERVED IN THE FOREMOST GROUP OF CRANIAL NERVES.

The central nervous system of the vertebrate considered anatomically and morphologically suggests two modes of origin which are apparently antagonistic to each other. On the one hand the segmental arrangement of the nerves, the evidence that not only the nerves but also the groups of nerve-cells from which these nerves arise are arranged not in a continuous chain but metamerically, point directly to the conclusion that the nervous tissue of the animal from which the vertebrates took their origin was arranged in a distinctly segmental manner. On the other hand, the embryological evidence of the formation of the central nervous system, as the folding over of the medullary plate so as to form a simple tube, gives no evidence in favour of any origin from a primitive segmentally arranged nervous system. Any theory then of the origin of the nervous system must take into account not only its segmental arrangement but also its tubular formation.

In all the more recent text-books of human anatomy and physiology great stress is laid on the anatomical and physiological metamerism of the spinal cord, and as is seen in Schwalbe, p. 351, evidence exists to show that the ganglion cell groups of the cord are arranged metamerically.

He quotes Schiefferdecker, who has shown that longitudinal sections in the lumbar region of the dog show that the ganglion cells of the median and lateral groups of the anterior horn are arranged after the fashion of a rosary in such manner that the broad parts, where the ganglion cells are thickest, correspond to the places of exit of the corresponding anterior roots.

He points out also that Freud has noticed that the posterior cells in the lamprey (Hinterzellen), which are supposed by him to give origin to sensory fibres (see p. 157), are arranged in distinct groups separated by considerable distances from each other; and that Stieda noticed the number of nerve cells was very variable in sections of the spinal cord of the eel, many sections being free from nerve cells. Schwalbe concludes that the evidence points to the origin of the spinal cord from a bilateral chain of ganglia connected together by means of transverse and longitudinal commissures.

This conclusion is strongly confirmed by the evidence given by the origin of the cranial nerves. For in the case of the segmental cranial nerves, which I have already shown are built up on the same plan as the spinal nerves, it is clear that the different groups of cells from which they arise are arranged segmentally. Nothing can be more evident than the groups of cells which give rise to the somatic motor nerves of the IIIrd, VIth and XIIth nerves, in fact the very expressions used to describe these groups as nuclei of the different cranial nerves shows how clearly the discontinuous character of the cell groups of this the most primitive part of the nervous system has been recognised.

The clearest case of segmentation in the cord which I have come across is found in the Sauropsida, for both in crocodiles and birds at the very surface of the lateral region of the cord a group of nerve cells exists which is as strictly metameric as the ganglion cells on the posterior roots of the spinal nerves. I have described this lateral group of cells in the cord of the crocodile in a former paper[1]; and Fig. 5, Pl. XIX illustrates their situation in the cord of the chick.

As far then as that part of the central nervous system is concerned which is connected with the spinal and cranial segmental nerves, we may I think without hesitation consider it as formed by a bilateral chain of ganglia which give origin to a series of segmental nerves and are bound together by connecting fibres both transversely and longitudinally. This forms one uniform system both anatomically and physiologically: a system the members of which, to use Hughlings Jackson's phrase, we may speak of as being on the same level; in addition this system is connected by another set of fibres—fibres spoken of by Hughlings Jackson as extrinsic to this level—to a nervous system of a different character, of higher function, that connection being recognised by the name of the pyramidal tracts, direct cerebellar tracts &c. This nervous system of higher function is not represented in the spinal cord and does not give origin to any outgoing nerves except such nerves of special sense as the optic and olfactory nerves.

If then we fix our attention exclusively upon the nervous elements of the central nervous system, we can describe it as a system composed of a bilateral chain of ganglia connected together by means of longitudinal and transverse commissures,

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[1] *Proc. Physiol. Soc.* Dec. 12, 1885. This *Journ.* Vol. VII.

which gives origin to a series of segmental nerves and is connected by means of well-defined commissural tracts with another nervous system of higher function which gives origin to no outgoing nerves except such nerves of special sense as the optic and olfactory nerves.

In addition however to the nervous elements the spinal cord and its extension cranial-wards contains an elaborate system of non-nervous structures, viz. the supporting structures of the cord, and it is here that the significance of the embryological formation of the central nervous system comes prominently forward. If we suppose all the nerve cells, nerve fibres and blood vessels of the spinal cord to be removed we should still have left a tube composed of the supporting structures of the spinal cord and lined by the epithelium of the central canal. In the adult this tube would form a meshwork with nuclei imbedded here and there, the meshes and nuclei becoming closer in the regions of the *substantia gelatinosa centralis* and *Rolandi*, until at the central canal the network becomes compact and forms the epithelial lining of that canal. The formation of this meshwork has been well described by His[1], who points out that it is formed by the modification of layers of epithelial cells of the same kind as those lining the central canal. The protoplasm surrounding the nucleus of the original cell thins out and elongates, forming long threads connecting together the nuclei which are now nearly denuded of their surrounding protoplasm. In Fig. 1, Pl. XIX I reproduce His' figure, which shows clearly the formation of this meshwork, to which he gives the name of myelospongium.

I also (Fig. 2, Pl. XIX) give a drawing of a portion of the substance lining the central canal in the neighbourhood of the infundibulum of a puppy, in which the limbs were fully formed and the groups of nerve cells in the cranial and spinal regions were well defined. It shows clearly the formation of the *substantia gelatinosa centralis* from the original layers of epithelial cells.

Again, Corning[2] has pointed out how the peculiarities of the *substantia gelatinosa Rolandi* are due to the persistence in this position of a concentrated and comparatively unaltered portion of the original embryonic cell formation.

Clearly then the folding over of the medullary plate gives origin not merely to nervous material but also to a tube of

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[1] *Op. cit.*

[2] *Archiv f. mikroscop. Anat.* Vol. XXXI.

supporting tissue which was originally formed of compact layers of epithelial cells arranged symmetrically around the central canal.

In the course of development this compact tube becomes broken up into a loose meshwork by the invasion, increase and growth of the nervous elements.

What is the connection between these two structures? If I understand rightly the view which has been held by many embryologists, it is that all the cells of the embryonic tube formed by the folding over of the medullary plate are capable of being converted into nervous tissue, that therefore in the non-nervous parts of this tube we have structures which are potentially nervous, the cells remaining in the embryonic condition although of exactly the same nature as those which have become nervous material.

The view which seems to me the correct one is that in the embryological development of the central nervous system we are observing the simultaneous development of two different organs, the one the nervous system, and the other the tube of supporting tissue the formation of which is not necessarily involved with that of the nervous system. In certain parts of the central nervous system the sole structure formed by the folding over of the medullary plate is the supporting tube which is not nervous and never was nervous, while in other parts the simultaneous formation of nervous material with that of the supporting tube has so complicated the problem that it is difficult to decide which of the embryonic cells form supporting structure and which nervous material.

The evidence both ontogenetical and phylogenetical appears to me to lead to the conclusion that the central nervous system of the higher vertebrates has been formed by the spreading and increase of nervous material over the walls of an original non-nervous tube the cellular elements of which tube, whatever may have been its original function, have been utilised as supporting structures for the nervous elements in those parts where the latter have invaded its walls; while in other parts where no such invasion has taken place the walls of the tube have retained their primitive simple cellular structure or have undergone gelatinous degeneration.

To take first the phylogenetic evidence; the striking characteristic of the evolution of the vertebrate central nervous system is the increase in amount and complexity of that part of the system which forms the brain, so that in the evolution of this part of the nervous system especially we may expect to find evidence which will enable us to decide whether that increase of nervous material has taken place by the continual growth of nervous matter over an original non-nervous substratum, or whether all parts of it were originally composed of nervous material which has thinned down in places and become non-nervous.

The comparison of the brain of the lowest vertebrate, such as Petromyzon especially in its Ammocœte form, with that of a mammal shows how striking in these two cases is the difference in the extent of the nervous masses situated on the dorsal side of the brain tube. In the former the whole of the dorsal wall is composed of a non-nervous membranous bag which if expanded would be of considerable size, but which by being thrown into a complicated system of folds forms the series of choroidal plexuses described by Ahlborn[1] and other writers and gives to this brain so characteristic and puzzling an appearance. This non-nervous roof to the brain of the lamprey is interrupted by nervous matter in two places corresponding to the two places where the two original constrictions in the brain tube took place by which the three cerebral vesicles are formed, viz. a small band of nervous matter which according to Ahlborn is the commencement of cerebellum and optic lobes and another in the region of the posterior commissure forming the ganglia habenulæ and optic thalami.

On the other hand in the mammal we have the large masses of the cerebellum, corpora quadrigemina, and optic thalami roofing over the brain tube, so that nothing is left of the original membranous roof except the thin roof of the 4th ventricle, the remains of the non-nervous choroid plexuses being enclosed in the 4th, 3rd and lateral ventricles.

In the Elasmobranch, as for instance the dog-fish, we find again that parts of the walls of the brain tube are conspicuously membranous in character; thus we find in the infundibular region a membranous sac known as the *saccus vasculosus*, the membranous roof of the 4th ventricle is more extensive than in the mammal, the choroid plexuses are very conspicuous as is shown in the diagram Fig. 2, Pl. XVIII., and what is especially instructive, we find here on each side of the central cerebellar mass or worm a lateral membranous bag continuous with the roof of the 4th ventricle, the ventral surface of which forms the lining membrane of the two masses of nervous tissue often called the *corpora restiformia* but which G. Fritsch[2] calls the *fimbriæ* and recognises as the commencing formation of the cerebellar hemispheres.

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[1] *Zeit. f. wissens. Zool.* Vol. XXXIX. p. 191.

[2] *Bau des Fischgehirns*, Berlin, 1878.

In Fig. 8, Pl. XIX I give a dorsal view of the medulla oblongata and cerebellum of a large dog-fish to show the thin membranous roof of the 4th ventricle and its continuation into the two membranous lateral bags which overlie the fimbriæ. In Fig. 7, Pl. XIX I give the appearance of a transverse section through one of the fimbriæ with its overlying membranous roof, to show how the epithelial lining of that roof does not follow the course of the pia mater, but passes into, blends with, and forms the lining of the nervous matter of the fimbria itself; as is also seen, proliferation of these epithelial cells appears to take place where the membranous bag comes into close relation with the nervous substance.

I will not go further into a detailed description here of the manner in which in the lowest vertebrates this membranous non-nervous tube has been folded and compressed in the cranial region by the growth of the nervous material within and around its walls, but will leave that to be dealt with in a subsequent paper upon the central nervous system of the Ammocœte, in which I intend to show how the study of the lowest vertebrate nervous system confirms and strengthens the conclusions to which the study of the highest vertebrate nervous system has led me.

I can see no evidence to show that the thin membranous portions of the roof of the brain are the thinned down remnants of some pre-existing nervous material, and I cannot conceive that a non-nervous epithelial bag should be formed in the lower vertebrates only for the purpose of being converted into nervous material as the animal rose in the scale of evolution. The reasonable explanation therefore appears to me to be what I have already suggested, viz. that the nervous material of the vertebrate central nervous system is situated in definite places outside but in close contact with the walls of a pre-existing non-nervous tube, and that the elements of this non-nervous tube, which is formed by the folding over of the medullary plate, become utilised as the supporting tissue or myelo-spongium wherever the nervous matter comes in contact with it.

Again the evidence of embryology appears to me to point to the same conclusion, for we find that in all classes of vertebrates the nervous matter, both nerve cells and nerve fibres, makes its appearance first on the ventral side of the original tube, so that, as is seen in Fig. 2, reproduced from Kölliker, in the cervical region of the spinal cord of a rabbit 14 days old the dorsal portion of the walls of the original central canal still retains its original character and has not been invaded by nervous material; the same thing is seen in Fig. 3, representing a section through the 4th ventricle of the embryo of the sheep. In the first case, by the invasion of nervous tissue, the dorsal portion of the original canal is subsequently converted into the posterior fissure, the walls of the canal forming especially the substantia gelatinosa centralis and Rolandi; in the second case they remain as modified epithelial structures to form the membranous roof of the 4th ventricle.

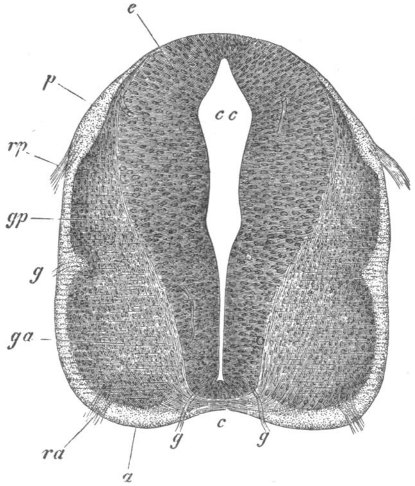

Fig. 2. Section of spinal cord from cervical region of embryo of rabbit (14 days old). (From Kölliker).

In Kölliker's description the letters in the figures have the following meanings. *c.c.* central canal, *a.* and *p.* anterior and posterior columns respectively, *ra.* and *rp.* anterior and posterior roots, *ga.* and *gp.* motor and sensory grey nuclei respectively, *c.* anterior commissure, *e.* apparent epithelium of the central canal.

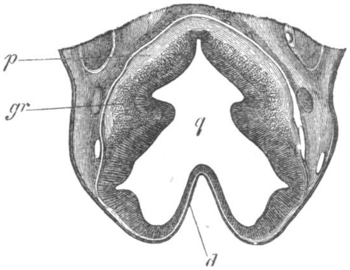

Fig. 3. Section of the brain of a sheep embryo (15 mm. long) through the 4th ventricle. (From Kölliker). *d.* thin roof of 4th ventricle, *q.* 4th ventricle, *p.* white fibres of pyramid (?), *gr.* ganglion-cell masses on the floor of the 4th ventricle.

The same method of formation, with the same structure, is found in the membranous portions of the brain already spoken of, such as the infundibular sacs of the skate and the membranous enclosures of the fimbriæ of the dog-fish, and the comparison of Fig. 3, Pl. XIX, which represents a section through a part of the *saccus vasculosus* of the skate, with Fig. 1 on the same Plate, shows that the membranous structure formed is in all cases the same in character as the myelo-spongium described by His, which was, as we have seen, formed from the walls of the same embryonic tube. Especially instructive is the evidence given by the formation of the rhomboidal sinus in birds.

At first the embryonic tube is formed in the same manner in this part of the nervous system as in other places, so that Kölliker's picture of the cord of the rabbit, Fig. 4, Pl. XIX, may be used to illustrate the original relation between the nervous and non-nervous parts of the tube here as elsewhere. At a later stage we see as represented in Fig. 5, Pl. XIX, that the white matter of the cord remains separated in the dorsal region by the original layers of embryonic cells; the result being that in the course of growth this mass of embryonic tissue which is not invaded by nervous elements forms a wedge-shaped mass in between the nervous elements on each side.

This tissue is at first composed of the same kind of epithelial cells as those forming the lining of the central canal, each cell possessing a well-defined nucleus in the midst of its protoplasmic contents so that at a period (about eight days) when the nerve cell groups of the anterior horn, the white matter of the cord and the central canal are all well formed, the appearance of a section through this region is as given in Fig. 5, Pl. XIX. Later on a peculiar degeneration takes place in these cells, which consists in the formation of a large quantity of gelatinous material which apparently, just as the fat globules in a fat cell, push the nucleus and the remainder of the protoplasm of the cell to one side, so as to give the appearance of a nucleated mesh-work, the interspaces of which are filled up with gelatinous material. This is represented in Fig. 6, Pl. XIX. At the same time in consequence of the large amount of gelatinous material, this wedge-shaped altered portion of the dorsal wall of the original tube presents the appearance in the adult bird of a jelly-like mass lying upon the spinal cord in this region.

Here it seems to me we see the formation of a modified form of the myelo-spongium of His, which on the one hand has not formed a supporting structure for nervous tissues because it has not been invaded by nervous elements, and on the other hand for some reason or other has not thinned down like the corresponding structures in the cranial region, but on the contrary has increased in thickness and undergone gelatinous degeneration.

The difference between this part of the nervous system as seen in birds and that seen in other vertebrates is clearly not due to atrophy in the case of the former of any special nerve tissues which are developed in the latter, for birds are supplied in the lumbar just as much as in other spinal regions with the same nerve structures, possessing the same functions, as other warm-blooded animals. There is no evidence here of any loss of nervous mechanism, but only a difference of arrangement of the nervous material in consequence of which the dorsal wall of the original tube has been left free from the admixture of nervous matter, and having lost its original function has undergone gelatinous degeneration.

The whole evidence then, embryological as well as phylogenetical, appears to me to point to the conclusion that the spinal cord is formed of a non-nervous tube, the walls of which have become invaded with nervous material.

Again, the embryological evidence of the order in which this nervous material makes its appearance is very striking and very suggestive.

According to the account given by Balfour, the white matter appears first in Elasmobranchs as a layer on the ventral and lateral parts of the spinal cord, but does not extend to the dorsal surface; at the same time the anterior white commissure is formed. About the same time two large bilateral ventral masses of nerve cells appear which are formed on the outer anterior part of the original thick walled tube as seen in Fig. 4, Pl. XIX, so that at this time, before the dorsal coalescence of the walls of the canal to form the posterior fissure, the nervous elements are represented by a series of symmetrically situated bilateral ganglion masses connected together by longitudinal and transverse commissures, the whole being situated within the walls of, but ventrally to, the non-nervous tube already spoken of. With the formation of the posterior fissure the nervous material spreads round to the dorsal side of the tube, and finally the chief evidence of the original tube is to be found in the peculiar structure of the *substantia gelatinosa centralis* and *Rolandi.*

The difficulty of deciding which of the elements of the original embryonic tube will form nervous material and which will form supporting structure consists in the absence of any histological means of discriminating between the two structures at an early time of development: much has been written about the first development of nerve cells and nerve fibres in the spinal cord, but I doubt very much whether we can go much further than the observations of His[1], viz. (1) that all the cells of the embryonic tube do not form nervous material; (2) that all the motor nerve fibres arise as prolongations of the motor nerve cells; and (3) that the motor nerve cells as soon as they can be recognised are always situated in a perfectly definite place in the embryonic tube, viz. in the outer part of the tube (Mantelschicht) and not in the inner part (Innenschicht).

Up to this point I would submit the following possible explanation of the ancestral history of the spinal cord.

It was originally composed of a bilateral chain of ganglia, situated ventrally to a non-nervous tube, the parts of each chain being connected together by commissures also situated ventrally to this tube. By the increase and spreading round of the nerve cells and nerve fibres to the dorsal side the original tube was so invaded with nervous elements as to have lost its original character and become the supporting structure of the spinal cord; leaving as the most marked indication of its original character the epithelial lining of the central canal and the peculiar structure of the *substantia gelatinosa centralis*.

Tailwards this tube emerges free from its encasing mass of nervous matter as the neurenteric canal and its walls are continuous with those of the alimentary canal. Headwards this tube passes into the 3rd ventricle and has apparently no anterior opening.

In the cranial region the formation of the original tube by the folding over of the medullary plate is of the same character as in the spinal region, the main difference being the larger size of the cavity formed. The cavity, as in the spinal region, is throughout lined with the epithelium of the central canal and the *substantia gelatinosa centralis* is formed in the same way as in the spinal region. We see then in the cranial region that the tube of supporting tissue exists of the same character and formed in the same way as in the spinal region.

What then about the nervous elements, are they the same here as in the region of the spinal cord? To my mind clearly not. In this part

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[1] *Anat. Anzeig.* 1888, p. 499.

of the nervous system we find, as already pointed out, both physiologically and structurally, two different nerve systems bound together. On the one hand the continuation of the metameric groups of nerve cells with their connecting fibres and their outgoing segmental nerves, which we have found to constitute the essential part of the spinal cord, forming a nerve system of the same level as that of the cord, a nerve system which we may call the cranial portion of the spinal cord nervous system; on the other hand a nerve system of different structure and higher function, which is connected by well-defined nerve tracts with the nervous system of the spinal cord; this nervous system of higher function, which we may term the brain proper, is not found at all in the spinal cord but only the tracts such as the direct cerebellar, the pyramidal &c., which connect the spinal cord nervous system with this brain.

How are these two different systems situated in the cranial region? We see that both embryologically, anatomically and physiologically the spinal cord nervous system in the cranial region arises in the same way as in the spinal region and is directly continuous with the nerve tissue of the spinal region; the metameric ganglion masses with their investment of nerve fibres arise here in pairs, connected by a ventral commissure on the ventral side of the original tube just as in the spinal cord. The nervous matter spreads laterally just as in the spinal cord, but the great distinction between the two places is found in this, viz. that the elements of this nervous system do not as in the spinal cord invade the dorsal side of the tube; they remain on the ventral and lateral sides of the tube forming the floor of the medulla oblongata and of the hind- and mid-brains. Further, the anterior limit of this system is very clearly defined; the nucleus of the IIIrd nerve is the limit of the groups of nerve cells connected with segmental nerves built up on the spinal nerve type; the tuber cinereum and infundibulum mark clearly the limit of spinal cord structure in the cranial region. In the diagram Fig. 2, Pl. XVIII I have represented the manner in which the spinal cord structure becomes limited in the cranial region to the ventral side of the central canal. If then we speak of the continuation of the spinal cord structure up to the infundibulum as the floor of the original tube in the cranial region, we have left on the dorsal side forming the roof of the tube special nervous structures forming the brain proper.

These masses of nervous structures formed in the roof form a separate chain of ganglion masses separated from each other by the thin membranous, almost non-nervous, walls of the original tube. Thus we see firstly the membranous roof of the IVth ventricle passing into the *velum posterius*, then the ganglionic mass of the cerebellum connected with the rest of the nervous system by means of the inferior middle and superior peduncles; then the semi-membranous *velum anterius* or valve of Vieussens, upon which, as a sign of the striking nature of the change which has occurred in the past history of the vertebrate, the IVth nerve has become fixed; then the ganglionic masses of the optic lobes, then again a thinned-out portion where in the past history of the vertebrate the invertebrate eye now known as the pineal gland took its rise; close to this, situated laterally, the two conspicuous most primitive ganglionic masses known as the optic thalami, and then anterior of all the cerebral hemispheres. In fact we find this striking fact, that the nervous matter formed in the roof of the original tube in the cranial region is composed of 4 separate paired masses of nervous tissue of different structure and higher function than the nervous system formed on the floor of the tube; the different ganglion masses are connected with each other and with the spinal cord nervous system by a perfectly well recognised system of commissures, already spoken of as the nerve tracts extrinsic to the level of the spinal cord. Further, it is to be noticed that the increase in the size of these nerve tracts coincidently with the great increase and development of these groups of dorsal ganglion masses constitutes the most striking feature of the development of the vertebrate nervous system.

We see then that it is possible to look upon the central nervous system as being built up around and within the walls of a tube somewhat as follows. The nervous system from which the vertebrate system was formed was originally composed of a bilateral chain of ganglia situated on the ventral side of this tube, the nervous material of which has subsequently grown round and enveloped the tube both dorsally and ventrally along its whole length with the exception of its anterior end; here the ventral chain of ganglia instead of spreading round to the dorsal side of the tube is connected by means of strong encircling commissures, forming a commissural collar around the tube, with a series of ganglia lying on the dorsal side of the tube whose function is of a higher character than that of the ventral chain and which give rise to no outgoing nerves except those of such special senses as sight and smell.

Clearly this description is the description of the typical form of nervous system found among invertebrates in which the dorsal ganglion masses of the cranial region with their connections with the optic and olfactory nerves are the supra-œsophageal ganglia; the nervous matter which gives origin to the segmental cranial nerves and to the spinal cord forms the infra-œsophageal ganglia and ventral chain; and the crura cerebri, peduncles of the cerebellum, and the other tracts which are extrinsic to the level of the ventral ganglionic chain form the œsophageal collar. The necessary conclusion to this comparison is that the tube of supporting tissue around and within which the nervous system is formed, with its extraordinary continuation as the neurenteric canal into the present alimentary canal, was originally the whole or part of the alimentary canal of the invertebrate from which the vertebrate ancestor arose; and it still further follows that this tube must have had an anterior opening as well as a posterior one, the œsophagus must have ended in a mouth just as the intestine in an anus. Examination of the region in which the mouth was most likely to have been situated, viz. the infundibular region, where the notochord and the nervous tissue which corresponds to the infra-œsophageal ganglia terminate, has led me to the discovery of what I believe to be the remains of the terminal œsophageal tube. My original discovery was made on the brains of adult sheep which were taken out of the animal immediately after death, and the portion of the base of the brain which contained the infundibulum with the pituitary body attached and the tuber cinereum was cut out and placed in 1 °/$_0$ osmic acid; the pituitary body being turned up towards the optic chiasma and the piece of tissue hardened in that position. In this way the region of the tuber cinereum was well exposed to view and it was easy to cut a whole series of sections transverse to the long axis of the brain, beginning at the cavity of the infundibulum and passing onwards to the corpus mamillare. These sections showed the existence of a canal leading from the cavity of the infundibulum towards the corpus mamillare; a canal which lies quite on the surface of the brain and occupies the greater portion of the length of the tuber cinereum. This canal is lined with epithelium continuous with that of the IIIrd ventricle and of the infundibulum; its walls are composed of substance similar to the substantia centralis gelatinosa; the further away from the infundibulum the more is its cavity closed by the approximation of its walls, and the nearer it comes to the surface, until at last, when completely closed, it vanishes at the very surface where a number of blood vessels from the pia mater pass in to the brain substance. Its appearance is exactly that of an open tube which has been bent down on the surface of the brain and so its open extremity been obliterated by the coming together of its walls; the appearance of a tube lying flat is much enhanced by the presence of a row of blood vessels between it and the brain proper. In Fig. 3, Pl. XX, I represent a series of sections through this canal at different distances from the infundibulum.

The examination of other cases is very instructive. Thus in the skate the series of sections through this region shows how the terminal portion of this tube has been fixed down and partially obliterated while the next portion has been distended and folded to form the saccus vasculosus. I have also found the same appearance in the brain of the dog-fish; the diagram on Pl. XVIII is drawn from one of the series of longitudinal sections through the brain of a young dog-fish and is a fairly accurate representation of the shape of the brain cavity; the dorsal masses of nervous matter are not drawn to scale but simply indicated so as to show roughly the relation of parts. In that figure the position of this folded down tube is clearly shown.

In Fig. 1, Pl. XX, I give a sketch of the ventral surface of the brain of a dog-fish to show the position of this folded down tube and the position in which the brain was hardened for the purpose of making a series of sections through this tube. The pituitary body, the saccus vasculosus and the lobi infundibuli were all turned back on to the optic chiasma as far as possible; the brain was then placed in picric acid, hardened, stained, and a series of sections cut through the part indicated by the lines drawn across Fig. 1.

Fig. 2, Pl. XX, represents a selection out of the whole series of transverse sections through this part of the brain. They disclose clearly the fact that the cavity of the infundibulum not only forms the cavity of the lobi infundibuli and of the saccus vasculosus but is continued on the surface of the brain backwards beyond the limits of the saccus vasculosus as a tube which becomes more and more superficial. An examination of the separate sections shows that this tube forms a distinct projection on the surface of the brain and at first it possesses a conspicuous lumen lined with epithelial cells of the same character as those lining the rest of the central canal. In the 3rd section represented the last remains of the cells lining the lumen is seen, but as is seen in the 4th, 5th and 6th sections the walls of the tube not only continue to appear in each section but come to lie more and more outside the nervous matter, so that in the last two sections the continuation of the walls of this tube is seen as a small mass of peculiarly structureless tissue entirely surrounded by pia mater and blood vessels and so lying freely on the surface of the contiguous nervous matter. Examined with a high power this tissue presents the appearance of a remarkably homogeneous gelatinous-looking material free from nuclei in which a meshwork of fine lines is seen.

Again, in the young lamprey this folded down tube is most conspicuous and beautifully shown in the series of sections which I have made. As however I propose to deal in a separate paper with the evidence which the investigation of the lamprey has given in confirmation of the views expressed in this paper, I will only mention the fact of the existence of this tube here, in order to point out that this same structure is found in both the highest and the lowest vertebrate. My suggestion then is that the terminal part of the œsophagus has been obliterated by being folded down on the infra-œsophageal ganglia while the next portion of the œsophagus has been dilated to form the infundibulum with the glands of the pituitary body lying on the anterior lip of the original mouth and œsophagus. In order to illustrate my meaning, I here reproduce, Fig. 4, Pl. XX, Dohrn's picture[1] of the nervous system of a young Limulus in which, as is seen, the mouth and œsophagus are lying on the chain of infra-œsophageal ganglia in exactly the same way as this tube in the vertebrates of which I have been speaking.

If this tube be really, as I have suggested, the remains of the original mouth and œsophagus, then I believe that the vertebrate nervous system is brought into complete harmony with that of the invertebrate, and although I know that my view will meet with strenuous opposition from many morphologists who hold very different views upon the origin of the vertebrate nervous system, yet I am emboldened to put it forward not only because it appears to me to follow legitimately from the anatomical and physiological facts which I have brought forward, but also because so many previous investigators have felt the necessity of harmonising the vertebrate and invertebrate nervous systems. Thus Balfour is strongly in favour of looking upon the fore-brain of the vertebrate as the pre-oral ganglion of the invertebrate; Dohrn was so anxious to pierce the brain with an œsophagus that he at one time suggested that the original mouth was situated dorsally and that the old œsophagus passed through the roof of the 4th ventricle and so into the alimentary canal through the infundibulum, thus turning over the ancestor of the vertebrate and making him crawl on his back. It is unnecessary to mention the names of other morphologists

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[1] *Jenaische Zeitschr.* Bd. VI. Taf. XV. Fig. 10.

who have made attempts in this direction, for the desire of piercing the brain of the vertebrate with an œsophagus has been expressed again and again in the writings of many distinguished comparative anatomists from Owen downwards.

I recognise fully the many difficulties which require explanation before this view can receive general acceptance, and especially the difficulty of accounting for the present alimentary canal. I beg therefore of my readers to abstain from criticism upon this point until I have published my paper to explain the peculiarities of the hindmost group of cranial nerves; for in that paper I shall endeavour to explain the formation of the present alimentary canal just as in this paper I have endeavoured to account for the old invertebrate alimentary canal. So also I have not touched upon the embryological difficulties which apparently stand in the way of the acceptance of this view of mine; for I consider that their discussion ought to come, and will come best, after some conclusion upon the ancestor of the vertebrate has been arrived at upon anatomical, physiological and phylogenetic grounds, and by that time, if we may judge from the change of opinion which is now going on, the embryological standpoint will have changed so much that perchance many of the present difficulties will be found to have vanished.

I ought perhaps to mention here that in a paper published during this last summer Bland Sutton[1] has suggested that pathological cystic malformations of the spinal cord point to the cord as being a modified gut. The view which I have put forward in this paper was in no way suggested by this paper of Bland Sutton's, for I had already worked out and written out a manuscript embodying my views during the Christmas Vacation of 1887; and indeed the opinions which I held were well known to my friends and many students at Cambridge during the summer and autumn of 1887. On the advice however of friends I determined not to publish the whole manuscript at that time but only the part concerning the structure of the cranial nerves which appeared in the *Proceedings of the Royal Society.*

Sutton's paper is to me most valuable because it confirms, from an entirely different method of investigation, the importance of looking upon the non-nervous elements of the spinal cord as possessing a separate individuality from the nervous elements.

Finally, we see that a self-evident and straightforward reason for the degeneration of certain components of the foremost groups of cranial

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[1] "Brain," Vol. x. p. 429.

nerves, *i.e.* nerves which arise from the original infra-œsophageal ganglia, is afforded by the loss of function of the invertebrate alimentary canal and the mouth parts in connection with it. It is to my mind very suggestive that a part at all events of the degenerated material in the IIIrd nerve is apparently in direct connection with the large group of cells known as the *substantia nigra*, for the direction of the processes of many of these cells is parallel to the direction of the fibres of the IIIrd nerve, and the cells themselves are imbedded in the continuation of the degenerated material belonging to the IIIrd nerve.

The groups of cells known as the substantia nigra have long been a stumbling block to anatomists; their strongly pigmented character points directly to a cessation of function on their part; they have not been traced into connection with any definite tracts of nerve fibres; and their position on the crura cerebri is a peculiar one and is not homologous with any of the groups of nerve-cells which are in connection with the spinal and cranial segmental nerves. If however we look upon the nervous system from the point of view suggested in these pages, we see that the crura cerebri form the main commissures connecting the supra- and infra-œsophageal ganglia, and that a group of cells situated upon these œsophageal commissures belonging neither to the supra-œsophageal or infra-œsophageal systems would correspond exactly to the stomato-gastric ganglion which in crustaceans forms the main nervous supply of the mouth and alimentary tract. If then it be allowable to speak of the parts of the vertebrate nervous system in invertebrate phraseology, I would suggest that with the alteration of function of the original invertebrate alimentary canal is associated the pigmentation of the cells of the stomato-gastric ganglion which supplied that canal with nerves, and therefore may perhaps still supply the myelo-spongium with nervous elements, and also the degeneration of certain parts of the nerves which arise from the infra-œsophageal ganglia.

I have mentioned the word Crustacean in connection with the nerve supply of the invertebrate alimentary canal, and it appears to me that the theory which I have put forward fits in best with an original alimentary canal of the crustacean type. Thus in Fig. 3A, Pl. XVIII, I give a diagram of the relation between the nervous system and the alimentary canal of the Crustacean with its turned down œsophagus, large cephalic simple stomach and straight simple intestine. In such an animal as *Sphæroma* we find according to Bellonci[1] that the supra-

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[1] *Archiv Ital. de Biolog.* Vol I. p. 176.

œsophageal ganglia are separable into 3 segments: 1. a superior segment or cerebrum; 2. a middle segment which gives origin to the optic and olfactory nerves; and 3. an inferior segment which is situated upon the œsophageal commissures and forms the stomato-gastric ganglion and gives origin to the nerves of the external antennæ. Such an arrangement I have represented diagrammatically in Fig. 3 A.

In the vertebrate the folding over of the medullary plates in the cranial region forms first a simple large bag in connection with the straight narrow tube of the spinal cord. This stage then of embryological development corresponds to Fig. 3 A. The next important occurrence embryologically is the formation of the 3 cerebral vesicles. At first the cephalic bag is constricted in one place so as to form two lobes, and later on another constriction appears in the posterior lobe by which 3 instead of 2 vesicles are formed. The first constriction takes place at that spot which afterwards forms the posterior commissure, and here we see the ganglia habenulæ are formed in the lamprey, ganglia which are clearly in connection with the pineal eye. From the ganglia habenulæ across to the ventral side of the brain in the lamprey run two well-marked nervous commissures known by the name of Meynert's bundles.

Upon the view put forward in this paper this first constriction represents simply the formation and growth in this position of nervous matter which is homologous with the middle segment of the supra-œsophageal ganglia of *Sphæroma*; which therefore is in connection with the original organs of sight, i.e. with the pineal eye.

The 2nd constriction, which occurs subsequently to the first, is in the position of the valvula cerebelli or valve of Vieussens, and is therefore associated with the crossing over of the IVth nerve from the ventral to the dorsal side; here at first according to Ahlborn[1] in Ammocœtes a deep inward projecting fold of the membranous roof of the brain is the only indication of the position of cerebellum and optic lobes. If then we imagine in the Ammocœte the 3 choroid plexuses inflated so as to get rid of their folds and creases, Fig. 3 B would represent not only the embryological stage of the formation of the 3 cerebral vesicles but also the corresponding phylogenetic stage as shown by the brain of the Ammocœte.

From this stage to that represented by the Elasmobranch brain and so on to the mammal the steps are easy; owing to the increase of the nervous material and to the limited space in the cranial cavity, the free

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[1] *Op. cit.*

portions of the original cephalic stomach are thrown into folds forming the choroid plexuses and the other membranous parts of the brain already spoken of in this paper. Thus, as is seen in Fig. 3 C or Fig. 2, Pl. XVIII, a loop of the bag of the 3rd vesicle forms the internal lining of the worm of the cerebellum. This very formation of the worm of the cerebellum in the Elasmobranch produces of necessity the two lateral membranous folds shown in Fig. 8, Pl. XIX. These in their turn become surrounded with nervous matter and then form the cerebellar hemispheres. In front of the valvula cerebelli the nervous matter grows over the membranous walls of the 2nd vesicle and forms the optic lobes.

By the growth of the cerebral hemispheres and the increase in size of the two lateral masses known as the optic thalami, the membranous portion of the 1st cerebral vesicle is thrown into folds which project into the 3rd ventricle and form the choroidal plexuses of the 3rd and lateral ventricles, as is seen in Fig. 2, and Fig. 3 C, Pl. XVIII. In this way it appears to me perfectly possible to construct the vertebrate nervous system from one of the Crustacean type.

Before however it is possible or advisable to speculate further upon the changes associated with the loss of the old alimentary canal, it is necessary to have some conception of the manner in which the present alimentary canal arose; in other words to attempt to explain the peculiarities of the hindmost group of cranial nerves, for it is evident that their peculiarities are associated with the formation of the new, *i.e.* the present alimentary canal, just as much as those of the foremost group were associated with the loss of the old canal. Such an attempt may well form the subject of a separate paper, which I hope before very long to be able to publish.

CAMBRIDGE,
March 20, 1889.

DESCRIPTION OF FIGURES. PL. XVI—XX.

PLATE XVI.

Fig. 1. Portion of a section through the IIIrd cranial nerve of the dog, to show how the smallest fibres in the nerve congregate together at the periphery, preparatory to passing out into the oculomotor ganglion.

Fig. 2. Portion of a section through the middle of the oculomotor ganglion, to show that there are no large nerve fibres in the ganglion. (From the same series as Fig. 1.)

Fig. 3. Section through some of the short ciliary nerves immediately after their exit from the oculomotor ganglion. (From the same series as Figs. 1 and 2.)

Fig. 4. Section through some of the rootlets of the VIIth cranial nerve of the dog, to show the presence of the large fibres in these rootlets.

Fig. 5. Section through the IVth cervical nerve of the rabbit at the origin of the phrenic nerve, to show the fibres of the phrenic nerve (B) separating out from the larger fibres of the IVth cervical nerve (A).

PLATE XVII.

The sections are all carefully drawn from osmic acid preparations of the nerves of man.

Fig. 1. Transverse section of rootlet of IIIrd cranial nerve to show degenerated ganglion. (Zeiss A, Oc. 4.)

Fig. 2. Three transverse sections of IVth cranial nerve. (Zeiss A, Oc. 2):

a. Section near exit of nerve from valve of Vieussens, showing degenerated tissue arranged so as to form a sheath around the functional medullated nerve-fibres.

b. Section of nerve farther away from point of exit, showing the formation of the degenerated ganglion.

c. Section of nerve peripheral to the ganglion. The degenerated tissue has almost entirely disappeared.

Fig. 3. Transverse section of VIIth cranial nerve to show degenerated ganglion. (Zeiss A, Oc. 2.)

Fig. 4. Longitudinal section of a rootlet of IIIrd cranial nerve to show the structure of the degenerated material. (Zeiss D, Oc. 2.)

PLATE XVIII.

Fig. 1. Section of the medulla oblongata (after Edinger). The letters A, B, C, D, E have the same meanings as in the diagram of the spinal cord on p. 155.

Fig. 2. Diagrammatic representation of the arrangement of the segmental cranial nerves. The diagram represents roughly a longitudinal section through the brain of a young dog-fish, upon which the general plan of arrangement of the cranial nerves has been drawn as explained in the text.

Fig. 3. These three diagrams illustrate the possible origin of the vertebrate nervous system as suggested in the text.

3 A. Diagram of the relation between the Crustacean alimentary and nervous systems.

3 B. Diagram of relation between the nervous and non-nervous parts of the central nervous system in the Ammocœte. It illustrates also the formation of the three cerebral vesicles from the simple stage represented in Fig. 3 A.

3 C. Diagram of relation between the nervous and non-nervous parts of the central nervous system in the Elasmobranch and in the higher vertebrates generally. It illustrates the formation of the choroid plexuses and the increasing invasion of the walls of the original cephalic stomach by the increase in the amount and complexity of the nervous material.

PLATE XIX.

Fig. 1. The supporting tissue or myelospongium of the spinal cord (copied from His).

Fig. 2. Portion of a section of the lining of the central canal in the region of the infundibulum of a puppy, to show how the original compact layers of epithelial cells spread out to form the substantia gelatinosa centralis.

Fig. 3. Section of the wall of the saccus vasculosus in the adult skate.

Fig. 4. Reproduction of Kölliker's drawing of the spinal cord of the embryo of the rabbit, to show how at this stage the dorsal part of the tube is free from the admixture of nervous material.

Fig. 5. Section of cord in chick (about 8 days) through the rhomboidal sinus to show the position of the groups of motor ganglia, and the manner in which a wedge-shaped mass of the original epithelial embryonic tissue remains on the dorsal side of the central canal free from admixture with nervous material.

Fig. 6. Appearance of this wedge-shaped dorsal mass of embryonic

tissue in the more adult condition. The spaces formed by the nucleated meshwork are filled with a homogeneous gelatinous material.

Fig. 7. Section through the nervous matter forming the fimbria of a dog-fish, with its overlying membranous roof. The epithelial layer of the membranous roof is seen to be continuous with and to form the lining epithelium of the projections of nervous matter, while the pia mater as shown by the thin lines does not follow the course of the epithelial layer.

Fig. 8. Dorsal view of the medulla oblongata and cerebellum of a dog-fish. *cb.* worm of the cerebellum, *l.* the two lateral membranous pouches which form the roof of the commencing cerebellar hemispheres or fimbriæ, *d.* membranous roof of the IVth ventricle which is continuous with the two lateral membranous pouches.

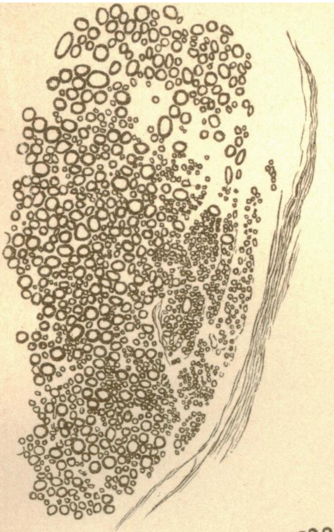
PLATE XX.

Fig. 1. Ventral surface of the brain of a young dog-fish; the pituitary body and saccus vasculosus are turned back on to the optic chiasma. The lines drawn across the figure indicate the position of the series of sections from which the drawings in Fig. 2 were made.

Fig. 2. A selection out of the whole series of sections indicated in Fig. 1, to show how the cavity of the saccus vasculosus is continued as a tube on the surface of the brain; the last three sections show how the continuation of this tube at its termination is separated from the brain by pia mater and blood vessels.

Fig. 3. A selection out of a series of sections through the tuber cinereum of the sheep, to show the existence of a tube, the walls of which gradually close, which lies on the surface and passes from the infundibulum towards the corpus mammillare.

Fig. 4. Diagram of the arrangement of the nervous system and of the alimentary canal in the young Limulus. (Copied from Dohrn.)



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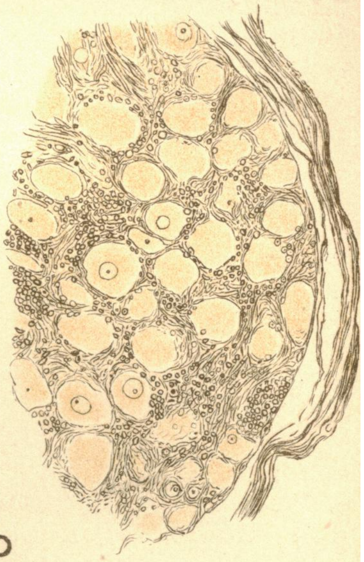

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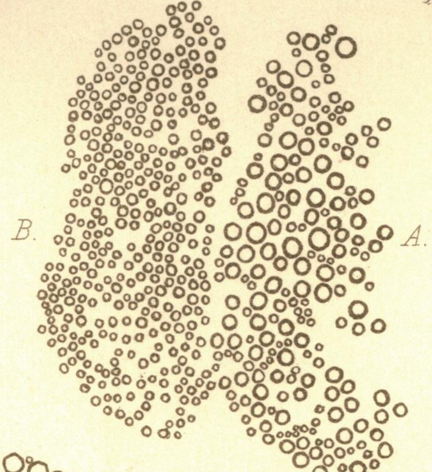

Fig 5

Fig. 4.

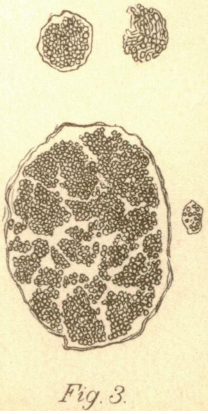

Fig. 3.

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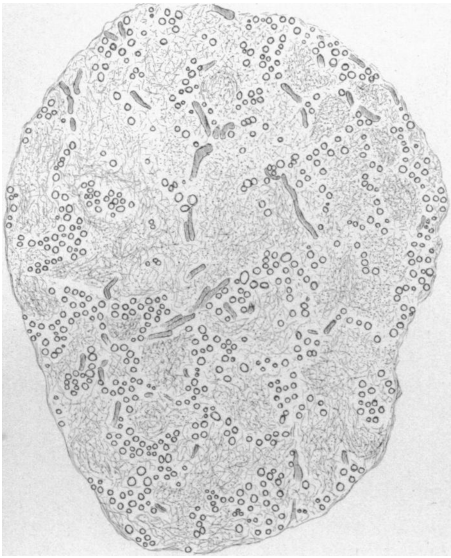
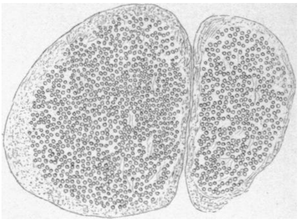


Fig.1.



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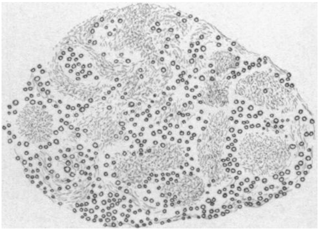

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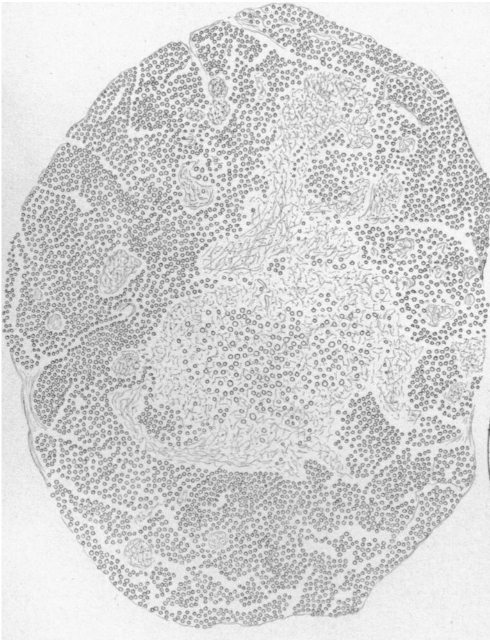

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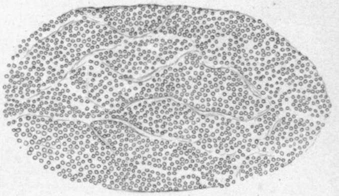

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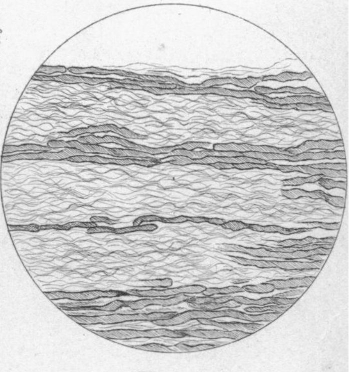

Fig.4.

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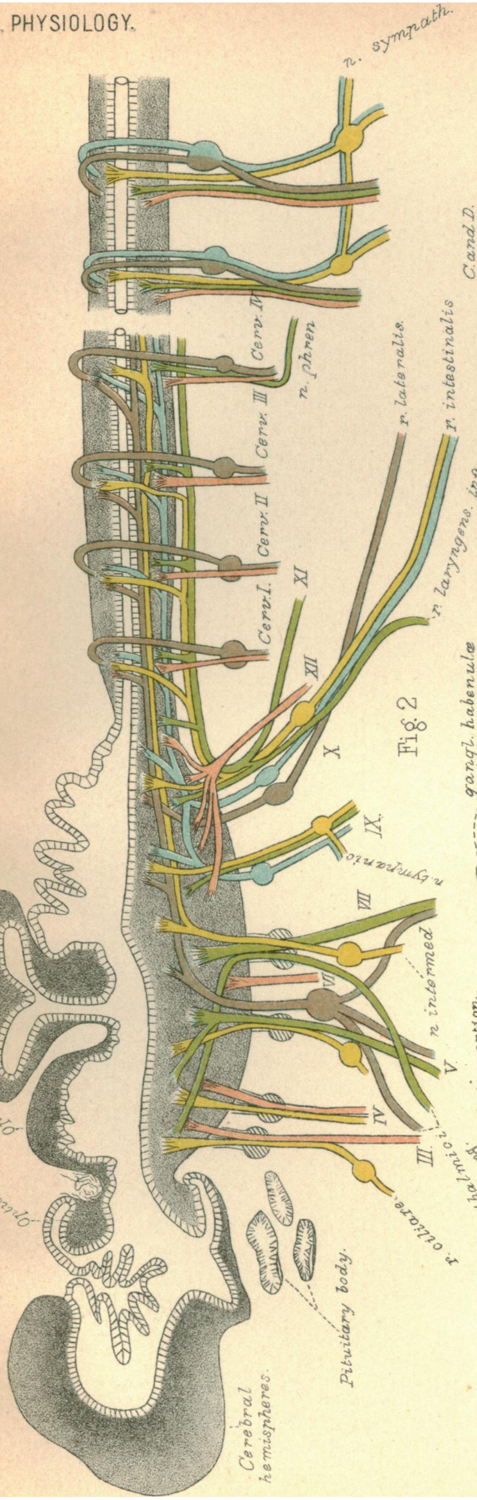

Fig 2

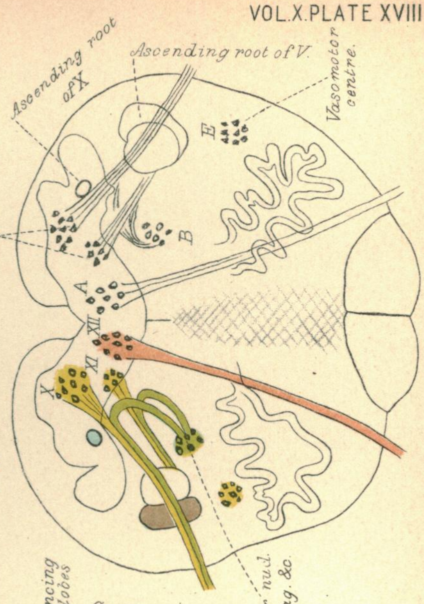

Fig. 1.

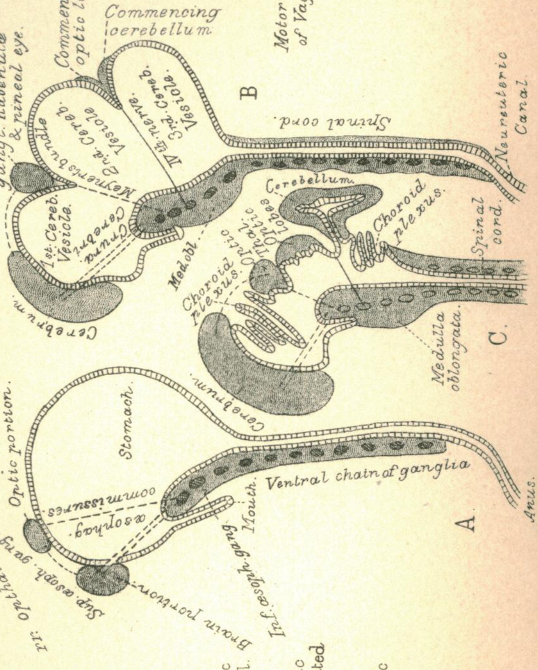

Fig. 3.

🟥 Somatic efferent.
🟫 Somatic afferent.
🟩 Splanchnic non. gangl. efferent.
🟨 Splanchnic ganglionated efferent.
🟦 Splanchnic afferent.

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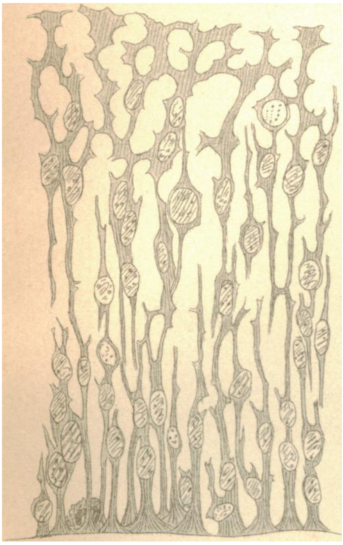

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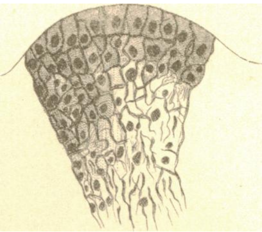

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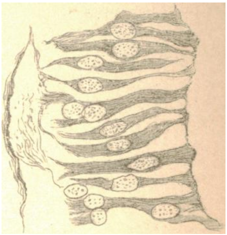
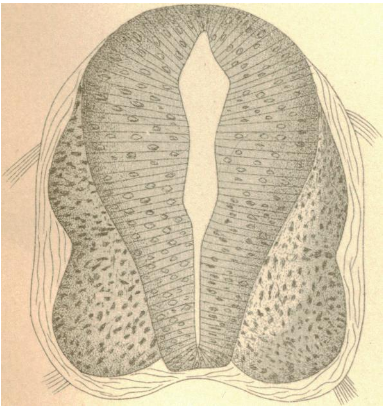


Fig. 3.

Fig. 7.



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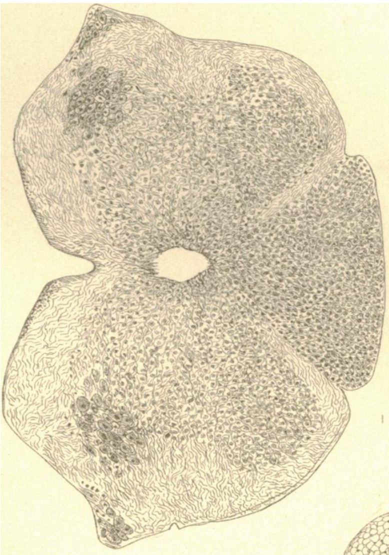

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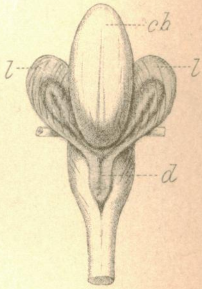

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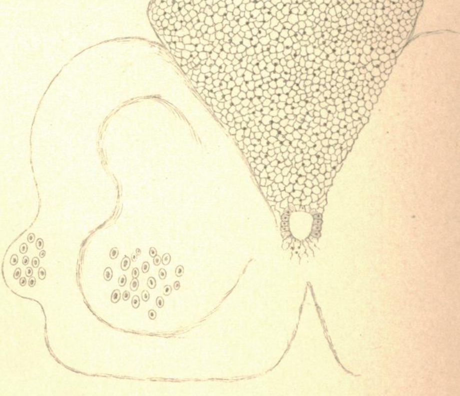

Fig. 6.

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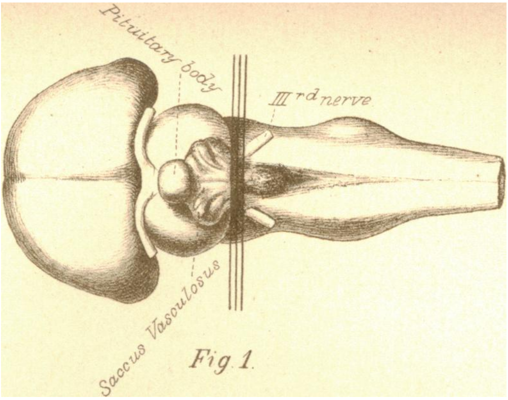
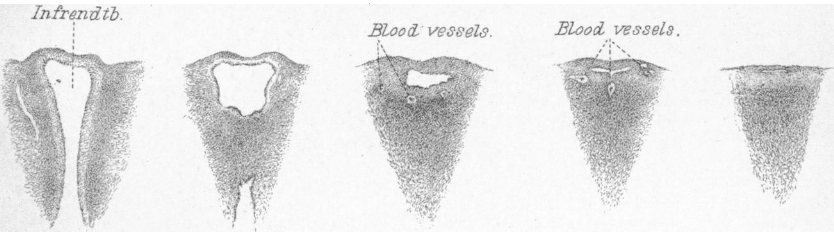


Fig. 1.

Fig. 2.



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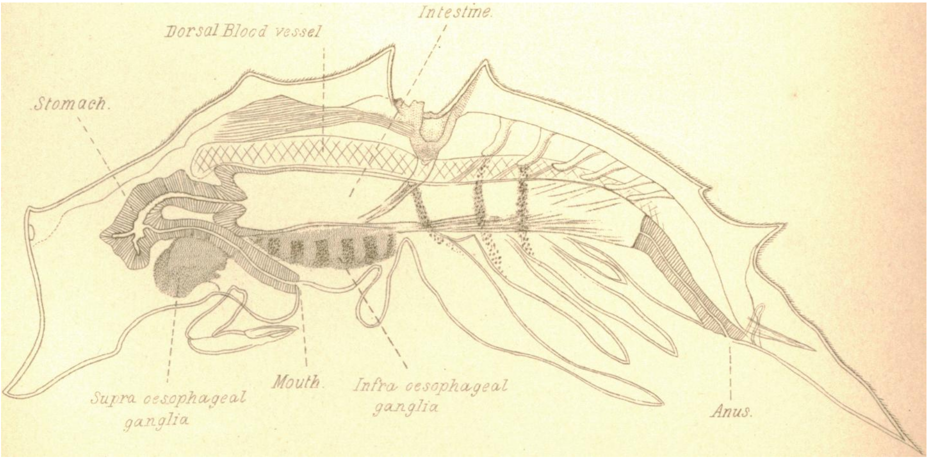

Fig. 4.

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