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Anatomy. — "*Further contributions to our knowledge of the brain of Myxine glutinosa.*" By P. RÖTHIG (Berlin) and C. U. ARIËNS KAPPERS (Amsterdam). (Communicated by Prof. L. BOLK).

(Communicated in the meeting of March 28, 1914).

The former of us has given a description of the motor roots and nuclei in Myxine glutinosa and in some Amphibia in Vol. XVI of these Proceedings (p. 296).

For Myxine the topography of the V—VII nucleus and the spino-occipital column has been discussed, and mention was made of the absence of the eyemuscle-nuclei and the motor glossopharyngeus.

For the discussion of the vagus roots reference was made to further researches not yet completed at that time, which we should accomplish in conjunction.

It is known that the vagus of Myxine glutinosa has caused many difficulties, and before giving our own results we wish to review the opinions of former authors, because such a review clearly shows the points which give rise to different interpretations.

It is obvious that in doing so we shall be obliged to deal again with other roots of the cranial nerves in Myxine.

The first description of the central nervous system of Myxine glutinosa was given by ANDERS RETZIUS [1]), who mentions three nerves of the Oblongata, the Vagus, a nerve of the labyrinth (Table VI l. c. Fig. 7), a cutaneous branch of this labyrinth nerve (Table VI, Fig. 8) and several branches of the V (p. 397, 400 and 401.)

After A. RETZIUS, JOHANNES MÜLLER [2]) gave an elaborate description of the origin and periferal course of the cranial nerves in Petromyzon, Bdellostoma and Myxine. For Myxine he gave a description of the Trigeminus, Facialis, Acusticus and Vagus (comp. Fig. 4, 4 and 6 on Table III l. c. 1838).

It is interesting that he mentions a cutaneous branch of the VII (p. 193 l. c. 1838), which still wants affirmation, specially since Miss WORTHINGTON [3]) could not find any but visceral sensory and

[1]) A. RETZIUS, Beitrag zur Anatomie des Ader- und Nervensystems der Myxine Glutinosa (Lin.) (Aus d. Abhandlg. d. Königl. Schwedischen Akademie der Wissen schaften Jahrgang 1822 H. 2) Meikel's Archiv für Anatomie u. Physiologie 1826 S. 386—404.

[2]) J. MÜLLER, Ueb. d. eigentümlichen Bau des Gehörorgans bei den Cyclostomen, mit Bemerkungen über die ungleiche Ausbildung der Sinnesorgane bei den Myxinoiden Abhandlg. d. Kgl. Akad. d. Wissensch. Berlin 1837 (25. IV. 1836), und: Vergleichende Neurologie d. Myxinoiden, ibidem, 1838 (15. II. 1838).

[3]) J. WORTHINGTON: Descriptive Anatomy of the Brain and cranial nerves of Bdellostoma dombeyi (p. 169) Quart. Journ. Miscr. Science Vol. 49, 1906.

motor fibres in the facial nerve of the American Myxinoid Bdellostoma dombeyi.

After JOH. MÜLLER, GUSTAF RETZIUS [1]) gave very valuable contributions which appeared abundantly illustrated in 1881 and 1893. It is just the excellent descriptions given by G. RETZIUS that show how difficult the interpretation of this brain is, for G. RETZIUS himself emphasizes at the end of his elaborate description of 1893 (p. 63) that — though he had been gathering the data concerning the brain of this animal for several years, he had not yet succeeded in obtaining a complete idea of its exact relations.

G. RETZIUS mentions, as did P. RÖTHIG in his contribution (l. c.), the absence of the trochlearis, oculomotorius and abducens. The most frontal nerve roots, according to him, are two trigeminal branches (p. 60 and Table 24, Fig. 1—3) each provided with a spindleshaped ganglion.

Following on this he finds a small nerve without ganglion (a motor nerve consequently) which he considers to be — like JOH. MÜLLER — the facial nerve. Close to this nerve he finds a third ganglionated root, which he supposes to be a third trigeminus root, and behind these the two roots of the octavus occur which he had already described before (1881): the Ramus anterior and ramus posterior acustici. Much more backward the vagus roots appear without ganglion. Dorsally from these he, however, finds a small sensory root with an oval ganglion, which he considers to be a sensory vagus root (p. 59).

After G. RETZIUS SANDERS [2]) took up this subject. Since this work was not available for us, we can only quote from it what HOLM has cited (l. c. infra).

According to this author SANDERS found the V, VII, VIII and X nerves, but differs in so far from G. RETZIUS that he considers some roots entering the brain behind the vagus of RETZIUS still as vagus roots, whilst the latter mentions them as spino-occipital nerves.

It is SANDERS' merit to have first given a detailed description of the oblongata-nuclei, which he divides into two cellgroups of which one has an entirely central position near the dorsal raphe: "ganglia centralia", and another near the perifery of the bulb: "ganglia latero-

[1]) G. RETZIUS. Das Gehörorgan d. Wirbeltiere Bd. I, Stockholm, 1881; Ueb. d. Hypophyse von Myxine Biolog. Untersuchg. Bd. VI; Das Rückenmark von Myxine Biolog. Untersuchg. N. F. Bd. W. 1891; Das Gehirn und das Auge von Myxine Biolog. Untersuchg. N. F. Bd. V 1893.

[2]) SANDERS. Researches on the nervous system of Myxine glutinosa. 1894, Williams and Norgate, London.

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ventralia", the latter of which extending (varying in size) from the entrance of the V to the X.

In GEGENBAUR's Festschrift FÜRBRINGER [1]) describes the spinal, occipito-spinal and vagal roots (p. 616 et seq.) and gives a drawing of the roots of the American Myxinoid : Bdellostoma (Text figure 1). According to him the vagus leaves the brain with 1—4 rootlets (he draws 2) and possesses a prevailing motor character (p. 619).

FÜRBRINGER states that this also holds good for Myxine. He considers the glossopharyngeus — not mentioned by preceding authors — as represented by elements of the nervus pharyngeus X, although he states that a branchial sack innervated by the IX is failing in Myxinoids. In other words he grants the absence of an independent IX, but supposes that elements of it are included in the pharyngeus branch of the X! [2])

FÜRBRINGER emphasizes that the spino-occipital roots are shifted in a frontal direction in Myxine. This holds good as well for his first sensory spino-occipital root as for his second spino-occipital root. The first in his opinion enters the brain on the level of the ramus acusticus posterior, the second near the level of the vagus roots. FÜRBRINGER points out that, in contrast to Myxine, in Petromyzon the spino-occipital roots are located on a fairly large distance behind the vagus roots.

This difference between Myxine and Petromyzon, according to him, can be explained in two ways, either the first spino-occipital root of Myxine is lacking in Petromyzon, or the spino-occipital roots are shifted forward in Myxine. FÜRBRINGER believes that the

[1]) FÜRBRINGER, Ueber die spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie. Festschrift für GEGENBAUR Teil III 1897 p. 349-766.

We do not deal here with the paper of RANSOM and D'ARCY THOMPSON (quoted by FÜRBRINGER) because it contains very little on our subject. Compare: On the spinal and visceral nerves of Cyclostomata. Zoölogischer Anzeiger No. IX, 1886 p. 421.

[2]) We may add here that Miss WORTHINGTON, to whom we owe such an excellent series of papers on the American Myxinoid Bdellostoma, considers this branch as a real IX (l. c. p. 172), "lying so close to the X that it is difficult to distinguish one from the other". She also mentions that they have a common foramen and that (p. 173) "the glossopharyngeus runs in the same sheath with the vagus as far as the second branchial arch". Consequently — as far as these points are concerning — the presence of a real glossopharyngeus is not very conspicuous either in Bdellostoma nor in Myxine — Since its periferal territory also is fairly well atrophied — (see the following pages) these arguments for the presence of a IX seem to be open to criticism, though in a very rudimentary way it may be present.

first is true, and that consequently the first sensory spino-occipital root of Myxine is lacking in the Lamprey.

We may remark here that, in our opinion, FÜRBRINGER is mistaken when he considers the first root here mentioned as being a spino-occipital one. We are more inclined to believe that in Myxine the same relation is found as in Bdellostoma, for which Miss WORTHINGTON has pointed out that FÜRBRINGER's first spino-occ. root is the Acusticus *b*, i. e. a lateralis root. [1])

The topographical difference in the spino-occipital roots between Myxine and Petromyzon consequently is not so considerable as FÜRBRINGER thought, since the spino-occipital roots of Myxine do not reach as far frontally as the acusticus.

Still there is a conspicuous frontal displacement of spino-occipital elements in Myxine, as appears from a comparison of Fig. 2 with Fig. 1. In our opinion the transitory region between oblongata and cervical cord is shifted in a frontal direction.

The vago-spino-occipital region of the oblongata has approached the trigemino-facial region, the otic and postotic part of the bulb being reduced. This frontal shifting of the vago-spino-occipital region of the brain is accompanied by a frontal displacement of the spino-occipital nucleus and roots, but the vagusroots (see fig. 2) are not so much displaced as their nucleus and remain behind, perhaps on account of their lying on the ear capsula.

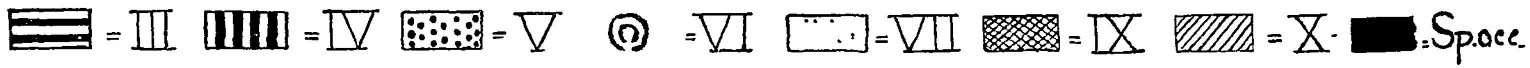
In consequence the spino-occipital and vagus roots have considerably approached and the vagusroots appear crowded together on the level of the caudal extremity of the nucleus, instead of being divided fairly regularly over the level of the whole nucleus as is the case in Petromyzon.

That the whole vago-spino-occipital region of the bulb has shifted frontally and not only the spino-occipital region, appears from the fact that the spino-occipital column does not overlap the vagal column in Myxine more than in Petromyzon.

As already said, this process is accompanied, if not partly caused, by a reduction of the acoustic region of the brain. That the acoustico-lateral system in Myxinoids is not very much developed results also from the researches of AYERS and WORTHINGTON [2]) (see further below). We shall now proceed to the description of the nuclear topography of the bulb and discuss at the same time the paper published by

[1]) Compare: Quarterly Journal of Microscopical Science Vol. 49, 1906 p. 171 and 175.

[2]) AYERS and WORTHINGTON: The finer anatomy of the brain of Bdellostoma dombeyi I. The acustico-lateral system. American Journal of Anatomy vol. VIII, 1908.



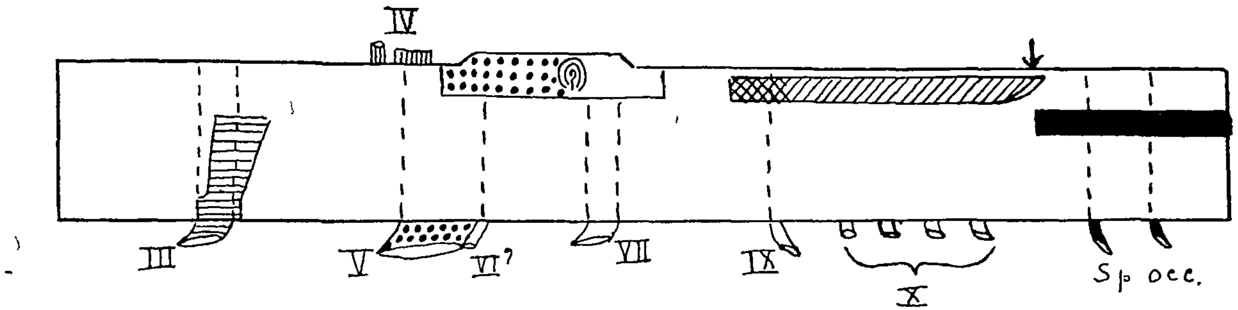


Fig. 1. Petromyzon.

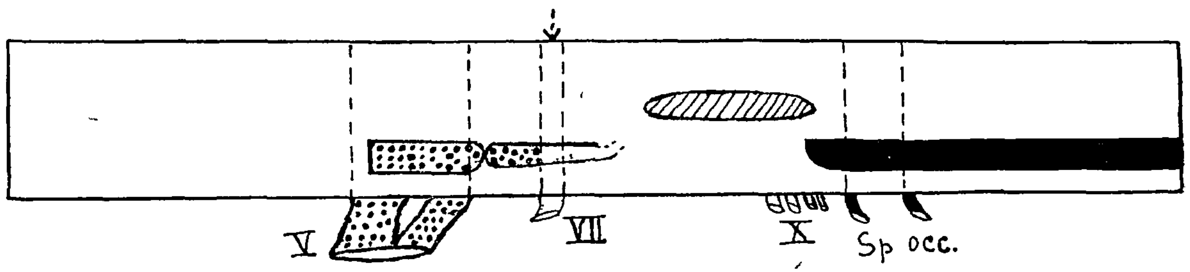


Fig. 2. Myxine.

Holm[1]) on this subject in 1902, which is certainly the best description as yet given of the motor nuclei in Myxine glutinosa.

Holm points out that the motor column of the spinal cord (comp. our Fig. 10) can be traced frontally in the bulb.

Laterally from it lies the posterior extremity of what Sanders has called the lateral or latero-ventral cell group (comp. our. Fig. 9).

Holm divides this latero-central column of the bulb, which we shall call the viscero-motor column, into two divisions, a frontal and a caudal one.

He again divides the frontal division into two, the caudal one into three subdivisions.

We can only follow him in so far as we also divide the visceromotor column into two divisions (see Fig. 2 and Fig. 3) of which however only the frontal one is again divided into two subdivisions. The caudal viscero-motor division, in our opinion, is continuous (see Fig. 2 and 3 nucl. X mot.) and does not exhibit subdivisions

Apart from this column Holm mentions a group of cells located next the ventricle in the rostral part of the oblongata from which he thinks that a part of the motor trigeminus originates. Another part of the motor trigeminus should originate from a nucleus in the lateral part of the oblongata on the level of the acusticus ganglion.

The nuclei of the trigeminus thus would be located at a fairly great distance from each other, one lying near the ventricle, the other near the perifery of the bulb. (Comp. his Fig. 20 on Plate 21: Nc I m. N V and Nc II m N V).

We do no agree with this description, nor with his statements concerning the motor facialis.

Also the facialis — according to Holm's opinion — should have two nuclei (l. c. p. 389) and from his description it clearly appears that he considers our frontal motor V nucleus as a VII nucleus, for the axones of this nucleus — as shown in his drawings — (Fig. 21 Plate 21) constitute the most frontal root of the bulb.

No doubt the two VII roots described by Holm (VII*a* and VII*b*) are V roots, since only this nerve leaves the bulb with two motor roots[2]), whereas the motor VII root is single and very small. Our opinion is confirmed by his description of the corresponding nuclei.

The first VII nucleus described by this author lies in the frontal part of the bulb near the perifery, and consists of large cells. His

1) J. F. Holm. The finer Anatomy of the nervous system of Myxine glutinosa. Morpholog. Jahrbuch Bnd. 29, 1902.

2) This separation of the motor V in two roots is only visible near the entrance. Soon after it they unite.

second V nucleus according to his description is located in the caudal elongation of the first, is not completely separated from it and consists of smaller cells, which description is perfectly in accordance with the two V nuclei (see Fig. 3) of which the second, consisting of smaller cells and not completely separated from the frontal nucleus, gives also rise to the VII root. (Comp. also Fig. 4—7).

Like HOLM we were first inclined to consider the second (caudal) nucleus only as a VII nucleus, but a more scrutinous examination of the V fibres showed that in this nucleus also the second motor V root found its origin.

Summarizing we state that the motor V nuclei mentioned by HOLM are no motor V nuclei, and that of the two VII nuclei mentioned by this author the frontal one is a pure V nucleus, whilst the caudal more parvocellular one contains root cells of the V and VII.

This union of motor V cells and VII cells is in perfect harmony with the condition found in Petromyzon (comp. Fig 1), where the motor VII cells also form the caudal continuation of the V nucleus and are a little smaller.

Since we only wish to deal with the motor nuclei in this description, we shall pass the acustico-lateral system, which for the American Myxinoid Bdellostoma dombeyi has been so minutely described by AYERS and WORTHINGTON [1]) and proceed to the motor X nucleus of Myxine.

It is obvious that, without an examination of the periferal nervous system and its muscles, the question of the presence or absence of a motor glossopharyngeus cannot be settled.

We can only state that our researches show a reduction of the number of root fibers of the motor X group, which in Myxine only consists of 3 of 4 rootlets, whereas in Petromyzon it contains together with the glossopharyngeus at least 5 rootlets.

This combined with the fact that the posterior visceromotor column has suffered a reduction in its frontal part is in harmony with the opinion defended by JOHNSTON [2]) that the glossopharyngeus and perhaps even the first motor X root sensu strictiori are either very much reduced or absent. A comparison of Fig. 1*a* and 2*a* shows that this reduction is only probable for the frontal pole of the column,

[1]) AYERS and WORTHINGTON: They finer anatomy of the brain of Bdellostoma dombeyi I. The acustico-lateral system. American Journal of Anatomy Vol. VIII, 1908.

[2]) JOHNSTON: Note on the presence or absence of the glossopharyngeal nerve in Myxinoids. Anatomical Record Vol. II, 1908.

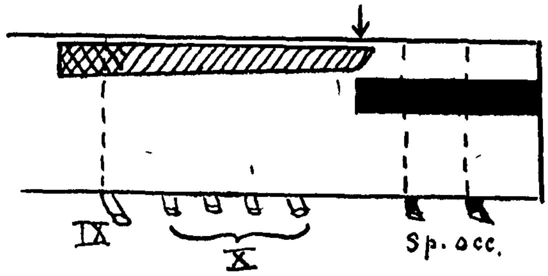


Fig. 1*a*.

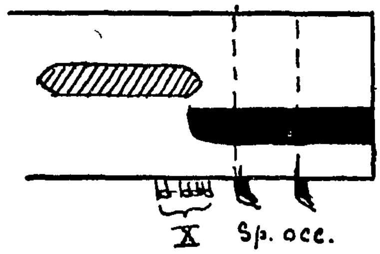


Fig. 2*a*.

Showing the reduction in the frontal part of the vagal column.

since the overlapping of the caudal part of the vagal column and spino-occipital column, as well as the topography of the posterior extremity of the vagal column to the spino-occipital roots, are the same in both Petromyzon and Myxine.

The reduction of the roots and of the frontal part of the vagal column in Myxine is also in harmony with STOCKARD's observation that in Myxinoids, at least in its American form Bdellostoma, the branchial sacks behind the hyomandibular arch are atrophied.[1])

The vagal column begins fairly near the posterior extremity of the mixed V—VII nucleus, lying in a somewhat more dorsal position (Comp. Fig. 3, 7 and 8). A few scattered cells lie between them, thus constituting a sort of broken link.

The size of the vaguscells is considerably smaller than that of the frontal V nucleus, more like the cells of the mixed V—VII nucleus, specially the smaller caudal cells of the latter.

In its frontal part the vagus nucleus is rather small and the cells do not attain their largest size here. The nucleus as well as the cells attain their maximum development in the middle part. We have not been able however, to state a division of the nucleus in three parts as HOLM did.

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1) STOCKARD: The development of the Mouth and Gills in Bdellostoma Stouti. American Journal of Anatomy Vol. V 1906, specially p. 511 and fig. 33—36. Compare also for further knowledge of these animals:

AYERS. Bdellostoma dombeyi. Woodshole lectures for 1893.

WORTHINGTON. Contribution to our knowledge of the Myxinoids. American Naturalist Vol. 39, 1905.

On the other hand we agree with HOLM that the small ventro-lateral root that leaves the bulb in the posterior part of the vagal region and is considered by SANDERS to be a vagalroot, is certainly a spino-occipital one (Cf. HOLM p. 395), as much on account of its position as on account of its central connection.

That the spino-occipital column extends for a short distance in the vagal region is a general feature in vertebrates and has been shown before to occur also in Myxine by EDINGER [1]) (l. c. p. 28).

We also agree with HOLM that the dorsal sensory root entering on this level is a sensory spino-occipital or spinal root and not a sensory Vagusroot, as results from the facts 1. that the size of its fibres corresponds with those of the sensory spinal rootfibres, 2. that the line of entrance and the ascending character of the fibres during their intramedullary course are the same as in the spinal sensory roots and 3. because they are joined by the latter during this course.

Finally we wish to call attention to the fact that not only the topography of the nuclei, but also the general morphology of this brain shows the compression which the brain has suffered.

Similar to the other ventricles of the brain the 4[th] ventricle is reduced to a minimum. This is complicated by the peculiarity that the caudal end of the midbrain (a cerebellum does not occur in this animal) protrudes a considerable distance between the dorsolateral walls of the oblongata and is so closely adjacent to it that only the pial membrane can follow it. Behind the caudal extremity of the midbrain the dorsolateral walls of the oblongata unite.

One cannot speak here of a real calamus scriptorius caused by a widening of the ventricle itself. The lateral deviation of the walls takes place only under the influence of the midbrain, but the 4[th] ventricle itself remains a small split underneath it. The dotted arrow in figure 2 indicates the place of this pseudo-calamus. Since in this animal, with atrophic eyes, there is no question of an enlargement of the midbrain being the cause of this telescoping, the only reason of it can be found in the compression of the whole brain in its longitudinal axis, which is also exhibited by the approach of the vago-occipital part of the oblongata to the trigemino-facial part.

This longitudinal compression probably finds its chief reason in the pressure exercised on the frontal part of the brain by the olfactory pit and dorsal lip, the influence of which on the form

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1) EDINGER: Das Gehirn von Myxine glutinosa. Abhandlungen der Preussischen Akademie der Wiss. 1906.

P. RÖTHIG (Berlin) and C. U. ARIËNS KAPPERS (Amsterdam). Further contributions to our knowledge of the brain of Myxine glutinosa.

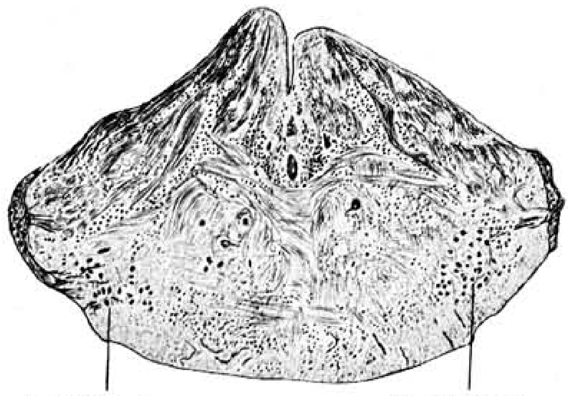

Fig. 6.
Myxine glutinosa. Magn. 20 : 1.
Frontal Section through the mot. V—VII-nucleus.

Fig. 7.
Myxine glutinosa. Magn. 20 : 1.
Frontal Section through the mot. VII nucl., caudally from Fig. 6.

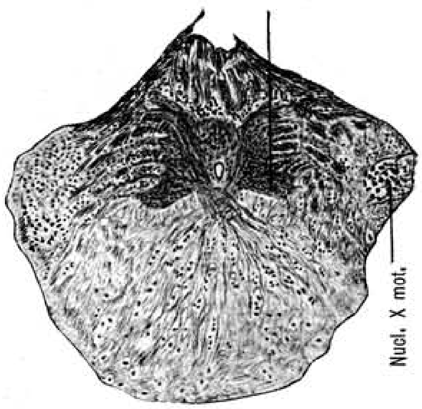

Fig. 8.
Myxine glutinosa. Magn. 20 : 1
Frontal Section through the mot. X nucl.

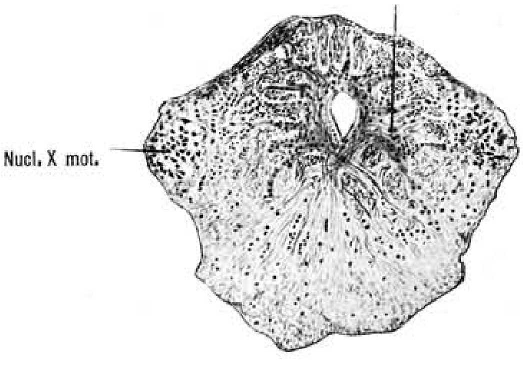

Fig 9.
Frontal Section through the Nucl. X mot.
Magn. 20 : 1 (caudally from Fig. 8).

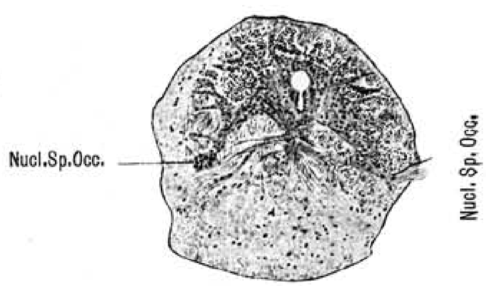

Fig. 10.
Myxine glutinosa. Magn 20 : 1.
Frontal Section through the spino occip. column.

of the brain in Cyclostomes is already mentioned by SCOTT [1]) in Petromyzon.

As stated above, the telescoping is the more obvious in the oblongata on account of the reduction in the acustico-lateral system of the bulb.

Everything indeed shows that in Myxine we have to do with considerable secondary modifications.

Also the topography of the motor nuclei is by no means a primitive one.

The primitive location of the V, VII, and X nuclei in Cyclostomes is near the ventricular ependyma where the matrix of the nerve cells is, and where they are still found in Petromyzon. In Myxine, however, the V—VII nucleus has a ventro-lateral periferal position and the X nucleus a lateral periferal position, a condition that can only be caused by secondary influences originating in the functional reflectory relations of this animal.

The influence which has caused this secondary position is certainly the considerable development of the descending sensory V, which has a dominating influence on the structures of the oblongata, an influence which is the more prevailing since the other sensory and reflectory paths are either atrophied or poorly developed in this animal. We know that in animals with a well-developed dorsal viscero-sensory nucleus the motor vagal column generally has a dorsal position, adjacent to its sensory grey (Selachians), which is still the case even in Petromyzon.

On account of these facts we cannot agree with HOLM in his statement that Myxine has a more primitive character than Petromyzon.

Summarizing our results we conclude.

In Myxine the eye-muscle nuclei are absent.

The motor V nucleus is incompletely divided into two parts corresponding to the central division of the motor root into two parts.

In the continuation of the caudal V nucleus also the motor VII cells are found, as is also the case in Petromyzon. These nuclei have a ventrolateral position very near the concomitating grey substance of the sensory root. A central V nucleus (HOLM) has not been found.

The posterior viscero-motor column, and also the spino-occipital motor column has shifted considerably frontally. By the adjacency of the earcapsule this shifting could only be partly followed, by the motor X roots, which are crowded together on the earcapsula.

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[1]) SCOTT The embryology of Petromyzon. Journal of Morphology Vol. 1, 1887

The spino-occipital roots have, however, followed the shifting of their nucleus and have come very near the vagus roots.

The posterior viscero-motor column is considerably shortened at its frontal extremity, which most probably results from the absence or extreme reduction of the motor IX, and perhaps even of the frontal motor X root (JOHNSTON) in connection with the absence or reduction of the two posthyomandibular branchial sacks (STOCKARD).

Physics. — *"Further experiments with liquid helium. J. The imitation of an* AMPÈRE *molecular current or of a permanent magnet by means of a supra-conductor."* Communication N°. 104*b* from the Physical Laboratory at Leiden. By Prof. H. KAMERLINGH ONNES.

(Communicated in the meeting of April 24, 1914).

§ 1. *Introduction.* If a current is generated in a closed supraconductor, from which no other work is required than what is necessary to overcome the possible remaining micro-residual resistance of the conductor, it follows, from the small value that the micro-residual resistance can have at the most, that the current will continue for a considerable time after the electromotive force that set it in motion has ceased to work. The time of relaxation τ in which the current decreases to e^{-1} th of its value is given by the ratio $\frac{L}{r}$ of the self-induction L and the resistance r of the circuit. When r approaches zero, this period may rise to very high values. Whereas the time of relaxation is extremely small in ordinary cases (for the coil with which we are about to deal for instance, of the order of a hundredthousandth of a second) when the resistance in the supra-conducting condition becomes say 1,000,000 or even 1,000,000,000 times smaller it may increase so much, that the disappearance of the current can be observed; it may even take place extremely slowly.

From the moment that I had found in mercury a supra-conductor at the lower temperatures which can be obtained with liquid helium, I was desirous to demonstrate the persistence of a current in a conductor of this kind, and amongst other things to take advantage of it in the further investigation of the microresidual resistance of the supra-conductor [1]). But it was only after the previous study of various

[1]) For the sake of brevity we use the word resistance here in the sense of quotient of potential difference and current strength. In supra-conductors (see Comm. No. 133) we can at present only speak of current and potential difference; whether the relation between these two can be expressed by means of the conception of specific resistance, has still to be investigated. (Comp. note 1 § 3).