Anatomy. — *"The cerebellum of fishes. 2. The cerebellum of Megalops cyprinoides (Brouss.) and its connections."* By C. J. VAN DER HORST, (Communicated by C. U. ARIËNS KAPPERS.) (Central Institute for Brain Research, Amsterdam.)

(Communicated at the meeting of November 26, 1925).

In Teleosts great variability is found in the shape and the seize of the cerebellum. Dimensions and form of the cerebellum are in close relation to the phylogenetical position of the particular fish and to no less a degree to the habits of the animal. This has been studied by V. FRANZ in a great number of Teleosts. Also ADDISON accurately studied and compared the fiber connections of the cerebellum of three Teleosts with different habits, viz. Gadus, Arius and Pleuronectes in the Institute for Brain Research at Amsterdam.

In general the cerebellum is small in fishes that move slowly, like Hippocampus, Pleuronectes, Cyclopterus, Scorpaena and Lophius. On the other hand the cerebellum is large in good swimmers like Clupea, Gadus and Thynnus.

All the different stimuli that reach the central nervous system by way of the sense organs do not have the same influence on the development of the cerebellum. No doubt the most important sense organ for the cerebellum is the lateral line system together with the vestibular organ which is closely related with the former. Direct fibers of the N.N. laterales and the N. octavus end in the cerebellum which also forms an unity with the endnuclei of these nerves in the oblongata. From this as also from the ontogenetic development, it is clear that in the cerebellum originally only ended the octavo-lateralis fibers. It is only later on that secundary and tertiary connections of other centra reach the cerebellum.

Also very important for the cerebellum is the degree of development of the optic system. The tectum opticum is in direct connection with the cerebellum by the tractus tecto-cerebellaris which is one of the largest afferent tracts of the cerebellum.

Of importance also is the general sensibility of the body. Sensory stimuli can reach the cerebellum by way of the tractus spino-cerebellaris which ascending from the spinal cord and the oblongata ends also in fishes in the cerebellum. The taste and olfactory organs seem to be of small importance. Only by way of tracts of higher order taste and olfactory stimuli may reach the cerebellum probably by means of the tractus lobo-cerebellaris.

So it is not surprising that the cerebellum of Megalops is very large. As a pelagic fish Megalops is a strong swimmer. The lateral line system is greatly developed and the name of the fish indicates already that it is provided with large eyes. On the contrary the general sensibility of the skin is poorly developed in keeping with the habits of the animal, at least judging from the small seize of the ascending spinal tracts compared with those of Lophius, Trigla etc.

But before discussing the peculiarities shown by this cerebellum in relation with its great development, I should like to call attention to a few particular points that show, that this cerebellum has retained original characters notwithstanding its great development.

At first the ventriculus cerebelli is large (fig. 1). This must be looked

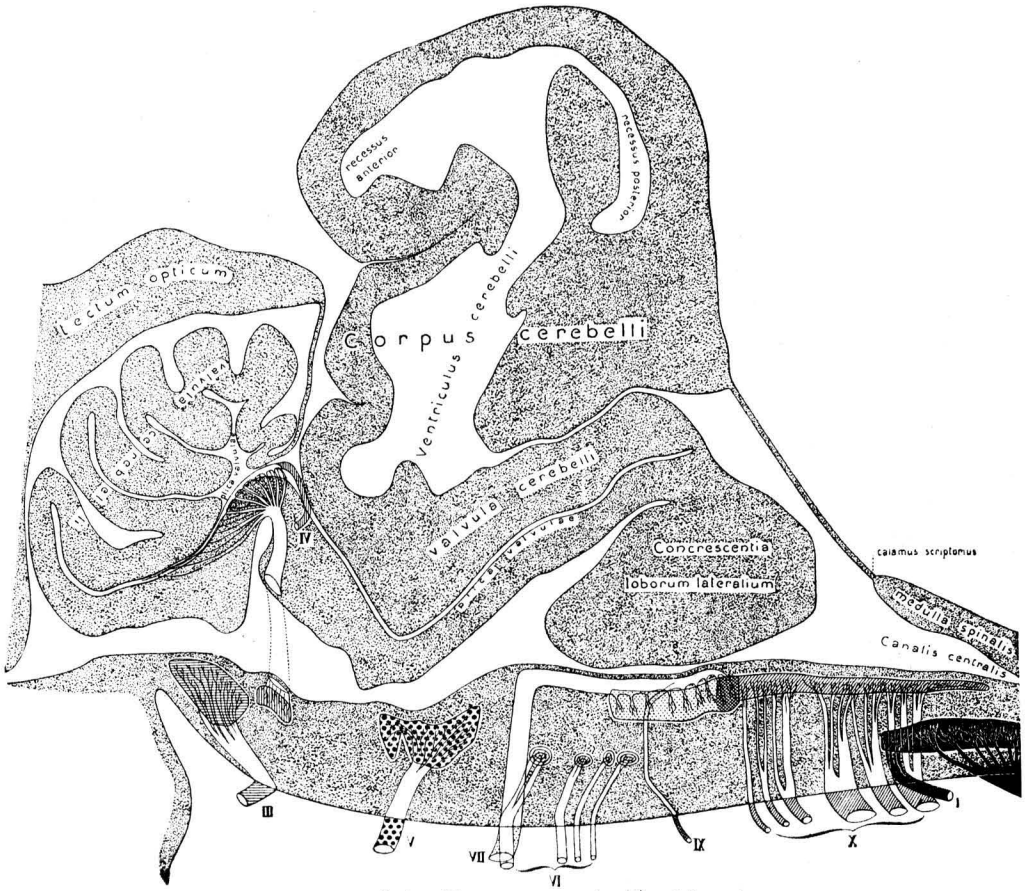

fig 1 - Megalops cyprinoides (Brouss.)

upon as a primitive character, because the cerebellum has a bilateral origin according to SCHAPER. Whereas in most Teleosts the two halves totally unite, in other more primitive forms among them the lateral halves remain more or less separated by a narrow sagittal, fissurelike ventricle. In the corpus cerebelli of Megalops the right and the left granular masses are

almost entirely separated from each other. A union occurs only in the middle of the dorsal part, by which the ventricle is divided in a recessus anterior and a recessus posterior. To be sure the ventricle in Megalops is also fissurelike, however this fissure is for the greater part strikingly broader than in other Teleosts (fig. 2).

Another primitive character of this cerebellum is the occurrence of a well defined auricle. In a previous communication I tried to make clear, that the auriculus cerebelli is absent in Teleosts or only indicated by a slight accumulation of granular cells. On the contrary the auricle is very clear in Megalops and it is separated from the corpus cerebelli by a deep fissure, comparable with the sulcus para-auricularis described by VOORHOEVE in Selachians. Even a recessus lateralis of the fourth ventricle is present, though this is very small (fig. 3).

Also the ventral part of the granular mass, pushed away by molecular substance in other Teleosts is still a rather compact mass of granules in

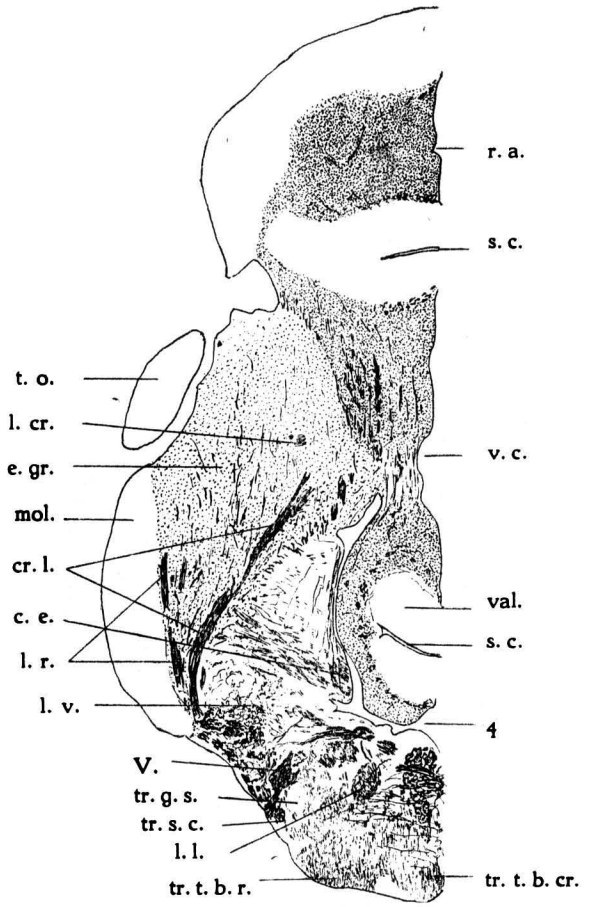

Fig. 2. Crosssection of the frontal part of the corpus cerebelli.

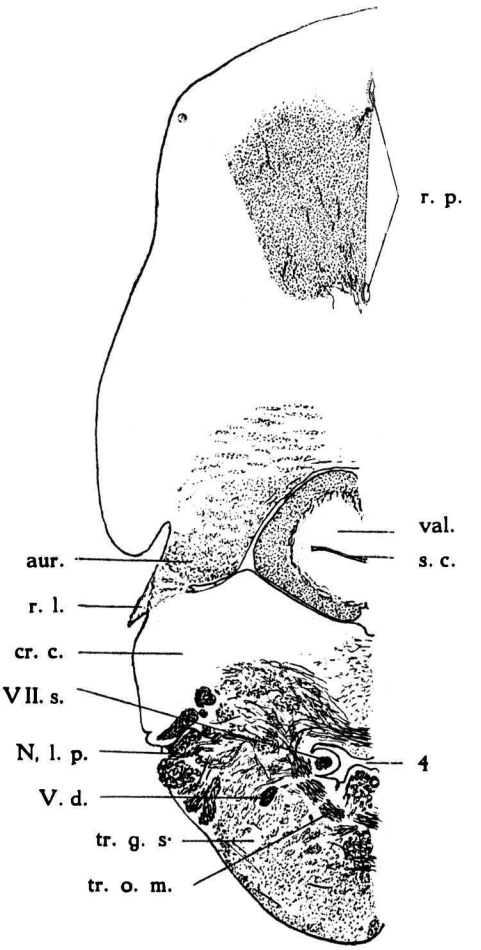

Fig. 3. Crosssection of the caudal part of the corpus cerebelli.

the caudal part of the cerebellum of Megalops. Of course, fibers of the commissura vestibulo-cerebellaris pass through this mass, but in general the granular cells lie densely packed in the whole breadth between the two auricles (fig. 3).

Finally I should like to call attention to the fact that the valvula cerebelli has a simple shape and has no lateral lobes, though it is very large and shows a peculiarity that I have not seen in any other Teleost (fig. 5).

The progressive development of the cerebellum of Megalops is, as we have seen, principally influenced by the lateral line system. Both the N. lateralis anterior and the N. lateralis posterior are very large. It was not possible for me to separate the N. octavus from the N. lateralis anterior with certainty, because the nerves were cut off near the brain surface. In correspondence with the seize of the nerves, the lobus liniae lateralis is very large as is also the crista cerebellaris; the latter is situated at the dorsal side of the lobus. It is not only in the crosssection that they are very large but they also extend in caudal direction farther than I have found in any other bony fish, viz. a little beyond the calamus scriptorius, thus in fact into the spinal cord (fig. 4). The two lobes have fused above

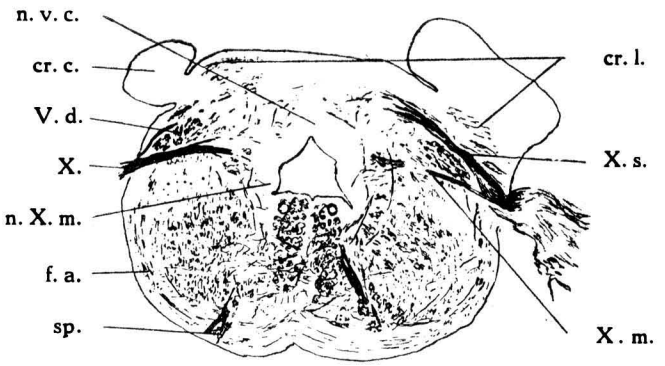

Fig. 4. Crosssection of the spinal cord immediately behind the calamus scriptorius.

the fourth ventricle over a long extend (fig. 1). Such a concrescentia loborum lateralium occurs generally in Teleosts, in which the lateral line system is well developed. A great number of crossing fibers is found here, for the greater part direct lateralis fibers (fig. 3). A very few fibers cross over in the commissura infima (fig. 4). In Anguilla, in which the lateral lobes do not fuse, a great number of lateralis fibers cross over here according to HERRICK.

Near their entrance the two roots split into ascending and descending fibers. It may be that the entering fibers split in two parts. I have not seen it in my crosssections, but I take it for probable, because this dichotomy has been found in other fishes. These fibers intermingle in such a way in the lobe, and also numerous fibers of the lateralis posterior ascend till in front of the lateralis anterior, that it is not possible to

distinguish a lobus anterior and a lobus posterior as BERKELBACH VAN DER SPRENKEL was able to do in Silurus.

But not all lateralis fibers end in the lobe. A great number of them ascends to the cerebellum to spread in the eminentia granularis which, as I have shown before, is in close relation with the lobus liniae lateralis. Among these are also numerous fibers of the lateralis posterior. ADDISON stated, that only fibers of the lateralis anterior reach the cerebellum in Gadus. These fibers end in the eminentia of the same side or they unite to a compact bundle that crosses over in the cerebellum and ends in the eminentia of the other side (fig. 2). TELLO found this decussation in the velum ; in Megalops it is found in the middle of the cerebellum.

These crossing fibers do not end in the valvula in Megalops ; in Gadus they do according to ADDISON.

The eminentiae granulares are very large, but only present in the frontal part of the cerebellum. The caudal part consists only of the corpus cerebelli proper. So in Megalops the eminentiae are stretched out in dorso-ventral direction, as this is in fact the case with the whole corpus cerebelli.

The two eminentiae granulares are connected with each other by a great number of commissural fibers that, united in a compact bundle, cross over in the frontal part of the concrescentia loborum lateralium (fig. 2). I take this commissure to be homologous with the commissura interauricularis of WALLENBERG, which has been described by KAPPERS as a small commissure in Gadus but as a very large one in Arius. But there is a striking difference. In Arius this commissure is situated near the peripheral surface of the brain, the decussation is quite ventral. It also curves in a frontal direction. In Megalops on the contrary the fibers take a shorter way. They leave the eminentia at its medial side and run from there directly to the median plane curving only in a caudal direction.

As I have given evidence in a previous communication, the Teleosts in general have no auricle. The commissure, mentioned above, in fact does not connect the two auricles, but the eminentiae granulares ; so I think it better to call it the commissura eminentiae granularis. There could be discerned a ventral commissure, as found especially in Arius, and a dorsal one like Megalops has. I think it probable, that the tractus or commissura trigemino-cerebellaris, found by V. FRANZ very well developed in Silurus, and also the decussating bundle that has been described by MAYSER in Cyprinidae as Pons Varoli, are both the same as the commissura eminentiae granularis.

It is selfevident, that also the lateral lemniscus, which, ascending from the oblongata, conducts the octavo-lateral stimuli, is well developed and, in correspondence to this, also its endnucleus, the torus semicircularis, is very large (fig. 6). But these are not the only fibers that end in the torus semicircularis. At first fibers of the N. opticus enter the torus along its whole length and end in the ventral part of the torus (figs. 5 and 6). I have never found these direct opticus-fibers in any other fish.

Secundly also of the secundary fibers that leave the tectum opticum some pass through the torus with which they are probably connected. These secundary fibers are arranged in three superposed systems (figs. 5 and 6). The most ventrally situated fibers form the tractus tecto-bulbaris cruciatus, which curving around the dorsal side of the commissura transversa runs in median direction. The fibers lying in the middle are more diffusely scattered or form small bundles. They unite farther caudally to the very large tr. tecto-bulbaris rectus. The third, most dorsally situated system of fibers runs in the caudal part of the mid-brain through the torus semicircularis and parallel its surface (fig. 6). In the most caudal part these fibers can not be distinguished from those of the tr. tecto-bulbaris rectus, which also makes a dorsally directed curve in the torus. I think it probable, that many of these last mentioned fibers end in the torus or at least have

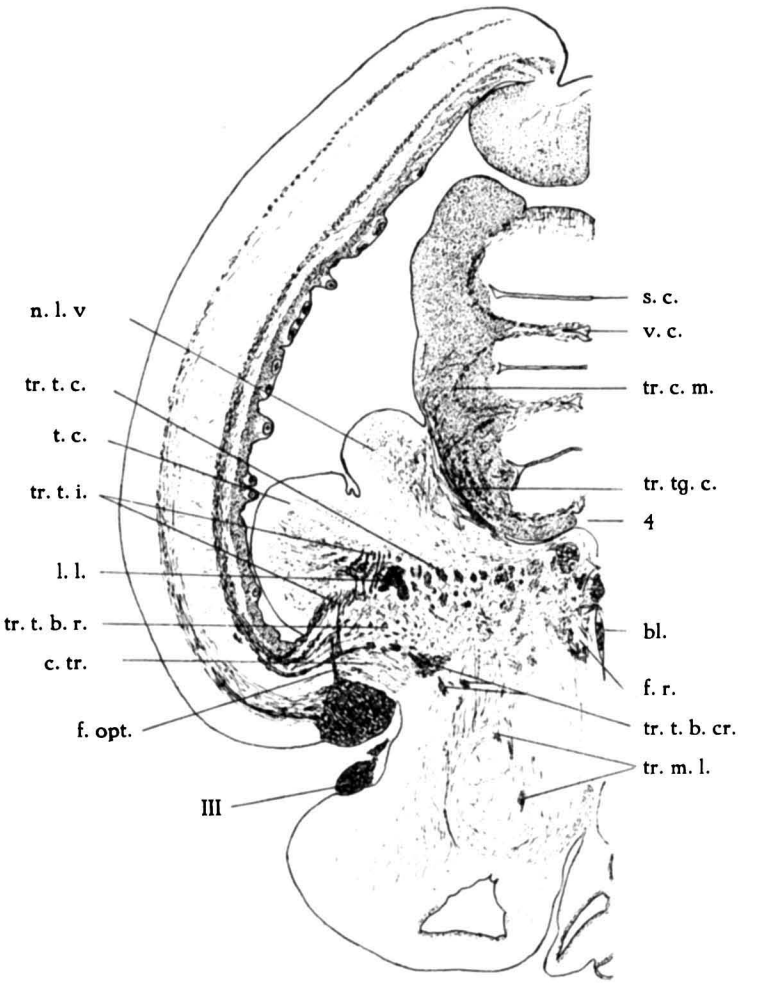

Fig. 5. Crosssection of the middle part of the tectum opticum and of the valvula cerebelli.

connections here. They end in a row of glomerulilike arborisations, which lie at the median border of the torus and caudally to the nucleus lateralis valvulae (fig. 6.) Farther frontally these fibers run directly, without curving through the torus semicircularis, to the glomeruli, piercing through the lemniscus lateralis (fig. 5). I suppose these fibers which come as the most dorsal ones from the tectum opticum to constitute the tr. tecto-isthmicus and then the glomeruli with the surrounding cells are the ganglion isthmi.

It is very difficult to trace the afferent connections of the nucleus lateralis valvulae. I agree with KAPPERS, when he supposes that this nucleus is closely related with the torus semicircularis, so that octavus and lateralis stimuli will reach it. But also it receives optic stimuli from the torus and the ganglion isthmi, also direct fibers from the tectum opticum reach this nucleus. Many fibers from the nucleus lateralis valvulae run along the ventricle at the dorsal side of the fasciculus longitudinalis posterior in a

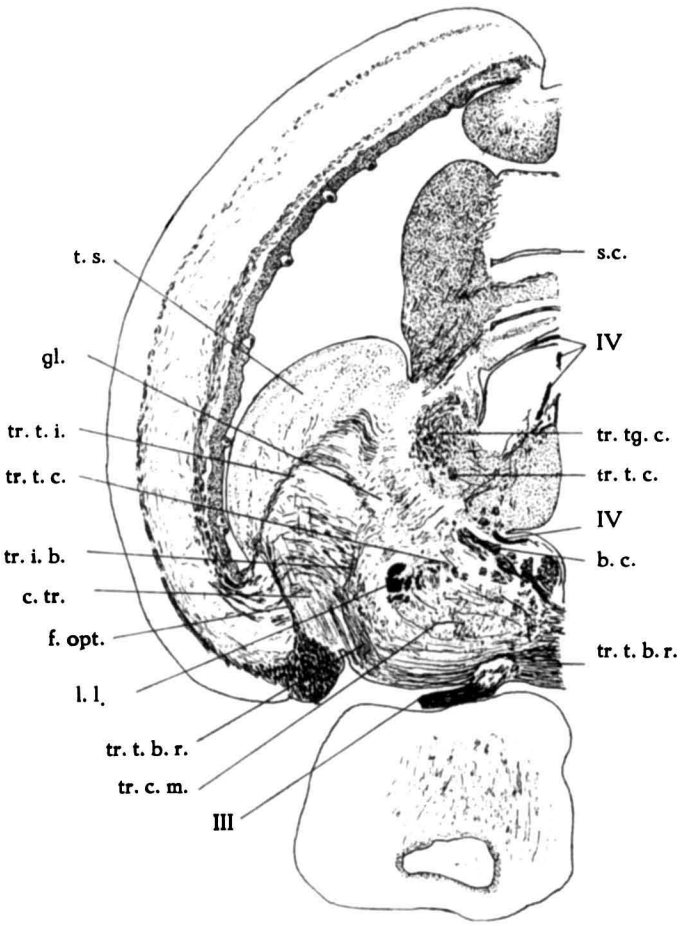

Fig. 6. Crosssection of the caudal part of the tectum opticum and of the valvula cerebelli.

median direction and seem to decussate. I could not state the origin of these fibers, but I suppose that they are crossing fibers from the torus semicircularis, because also many fibers from the torus take the same direction (fig. 5).

The large tractus mesencephalo-cerebellaris posterior or tegmento-cerebellaris runs from the nucleus lateralis valvulae to the cerebellum. At its caudal side follows the tractus mesencephalo-cerebellaris anterior or tecto-cerebellaris. This latter bundle has a different course in Megalops to that usually met with in Teleosts. Generally it leaves the tectum opticum where, at its frontal end, the median part of the tectum fuses with the tegmentum. From here the tract runs as a compact bundle through the tegmentum at the median side of the lemniscus (fig 5), it bends towards the corpus cerebelli just behind the tractus mesencephalo-cerebellaris posterior and runs here near the midline to its endings in the caudal part of the corpus. The number of fibers leaving the tectum at its frontal end near the midplane is very small in Megalops. These fibers are joined by numerous other ones that, arising in the frontal part of the tectum, reach the tegmentum by way of the lateral attachment of the tectum and, arranged in small bundles, they run in a caudal direction.

These fibers leave the tectum in the same way as, on a more caudal level, the fibers that run to the ganglion isthmi do (fig. 5). Also in the cerebellum these fibers have not the course otherwise met with, but are situated quite laterally in connection with the tractus tegmento-cerebellaris.

Whereas the tractus tecto-cerebellaris spreads wholly in the corpus cerebelli, the tractus tegmento-cerebellaris sends the greater part of its fibers to the valvula. This bundle is a very large one in Megalops. In correspondence with this the valvula is also very large. As said before the valvula has a comparatively simple form, but only in that the lateral lobes are absent (fig. 5). But the rather narrow midpart is very long and lies in many curves under the roof of the midbrain. A simple shaped valvula makes only one curve in general, sometimes a secundary curve can be added like in Gadus and Perca. I found in Megalops no less than six secundary curves.

A striking peculiarity of the valvula of Megalops is, that it is not only situated below the tectum opticum, but it stretches also caudally in the fourth ventricle like a fingershaped organ untill near the caudal side of the corpus cerebelli (figs. 1, 2 and 3). This part has the typical structure of a valvula with the granular layer at the outside and the molecular layer, in which extends the skullcavity, at the innerside. It is situated in the ventricle quite free, but for a possible superficial fusion with the concrescentia loborum lateralium. I found this fusion in one series but not in the other. No fibers enter the valvula from the concrescentia.

The other afferent systems are slightly developed. The tractus spino-cerebellaris and olivo-cerebellaris are very thin and have the normal course for these tracts (fig. 2). The tractus lobo-cerebellaris is not present as a well

defined bundle. Numerous isolated fibers join the tractus tecto-cerebellaris, where this enters the cerebellum. These fibers come from the ventral part of the bulbus to which part run also fibers from the lobi inferiores.

The tractus cerebello-motorius leaves the cerebellum along the mediocaudal side of the very small gustatory nucleus. The more medially situated fibers, which originate all in the corpus cerebelli, form a compact bundle that, piercing through the fasciculus longitudinalis posterior, decussates just behind the oculomotor nucleus (fig. 6).

Also the more laterally situated fibers decussate at this level. So the decussation is not drawn out in Megalops as FRANZ found it in other Teleosts, but it is limited to a small area. The lateral fibers, which run to the midline more in a curve, arise principally in the valvula ; they form a great number of small bundles which partly pierce through the tractus tecto-cerebellaris.

Megalops is one of the most primitive Teleosts. In correspondence to this the cerebellum shows several primitive characteristics and to a greater number and more primitive than the simple cerebellum of Osmerus, and even, as to the auricle, than that of Amia. On the other hand the cerebellum is greatly developed in connection with the habits, whereby especially the valvula shows particular peculiarities.

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LIST OF ABREVIATIONS

aur.	auriculus cerebelli.	cr. c.	crista cerebellaris.
b. c.	brachium conjunctivum.	cr. l.	primary lateralis fibers before the decussation.
bl.	blood vessel.		
c. e.	commissura eminentiae.	c. tr.	commissura transversa.

e. gr.	eminentia granularis.
f. a.	fibrae arcuatae.
f. opt.	fibers of the Nervus opticus.
f. r.	fasciculus retroflexus.
gl.	glomeruli.
l. cr.	primary lateralis fibers after the decussation.
l. l.	lemniscus lateralis.
l. r.	non crossing lateralis fibers.
l. v.	lobus liniae lateralis ventralis.
mol.	molecular mass.
N. l. p.	Nervus lateralis posterior.
n. l. v.	nucleus lateralis valvulae.
n. v. c.	nucleus visceralis commissuralis.
n. X. m.	nucleus vagi motorius.
r. a.	recessus anterior of the ventriculus cerebelli.
r. l.	recessus lateralis of the fourth ventricle.
r. p.	recessus posterior of the ventriculus cerebelli.
s. c.	skull cavity.
sp.	Nervus spinalis.
t. c.	torus semicircularis.
t. o.	tectum opticum.
tr. c. m.	tractus cerebello-motorius.
tr. g. s.	tractus gustatorius secundarius.
tr. i. b.	tractus isthmo-bulbaris.
tr. m. l.	tractus mesencephalo-lobaris.
tr. o. m.	tractus octavo-motorius.
tr. s. c.	tractus spino-cerebellaris.
tr. t. b. cr.	tractus tecto-bulbaris cruciatus.
tr. t. b. r.	tractus tecto-bulbaris rectus.
tr. t. c.	tractus tecto-cerebellaris.
tr. tg. c.	tractus tegmento-cerebellaris.
tr. t. i.	tractus tecto-isthmicus.
t. s.	torus semicircularis.
val.	valvula cerebelli.
v. c.	ventriculus cerebelli.
III.	Nervus oculomotorius.
IV.	Nervus trochlearis.
V.	Nervus trigeminus.
V. d.	trigeminus descendens.
VII. s.	Nervus facialis sensibilis.
X.	Nervus vagus.
X. m.	motor vagus root.
X. s.	sensory vagus root.
4.	fourth ventricle.