

Anatomy. — C. J. VAN DER HORST : "*The Cerebellum of fishes. I. General morphology of the cerebellum.*" (Central Institute for Brain research. Amsterdam). (Communicated by Dr. C. U. ARIËNS KAPPERS.)

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

Concerning the general structure of the cerebellum of fishes three quite different lines of development can be distinguished which in their final stages, as found in Selachians, Chondrosteans and Teleosts, deviate to such a degree that it makes a direct comparison of these cerebella very difficult and has been the cause of erroneous interpretations.

To comprehend the development and morphological significance of the different parts of the cerebellum of fishes it is necessary to begin with a simple shaped and yet well developed cerebellum like that of *Ceratodus*. This cerebellum has been fully described by HOLMGREN and VAN DER HORST. It has practically the shape of a thick plate, but for a ridge in its middle part which protrudes downward into the fourth ventricle, and extends almost the total length of the cerebellum. It is rather flat in longitudinal direction but in crosssection it is crescentshaped, which is especially apparent in the middle part, at the level of the entrance of the trigeminus. Here two longitudinal furrows, one at the side of the ventricular and one on the outer surface, clearly indicate the boundary between the cerebellum and the oblongata. The granular mass is found at the side of the ventricle over the whole breadth of the cerebellum at this level, whereas the outer surface wholly consists of molecular matter.

The caudal border of the cerebellum of *Ceratodus* is convex. In cross-section the cerebellum has here the shape of a flat plate consisting of a granular and a molecular layer, which covers the fourth ventricle. On both sides this plate is connected with the dorsal border of the oblongata by means of the choroid membrane. Further frontad this plate is more and more curved until its edges fuse with the dorso-lateral margins of the oblongata. Where the fusion takes place, the granular mass curves outward and in this way the small but well defined auricles are formed.

The granular mass of the auricle continues in a caudal direction, though it can be clearly distinguished from it, into the lobus liniae lateralis anterior. This lobe forms the most dorso-lateral part of the oblongata and extends in a caudal direction to about the level where the first vagus roots leave the brain. I consider it better to call this nucleus which belongs to the dorsal root of the anterior lateral line nerve lobus liniae lateralis dorsalis and I will do so in this article. At the ventral side of this dorsal lobe the crista

cerebellaris is found, which stretches far more in caudal direction than the lobe. At the frontal end it continues with the molecular layer of the

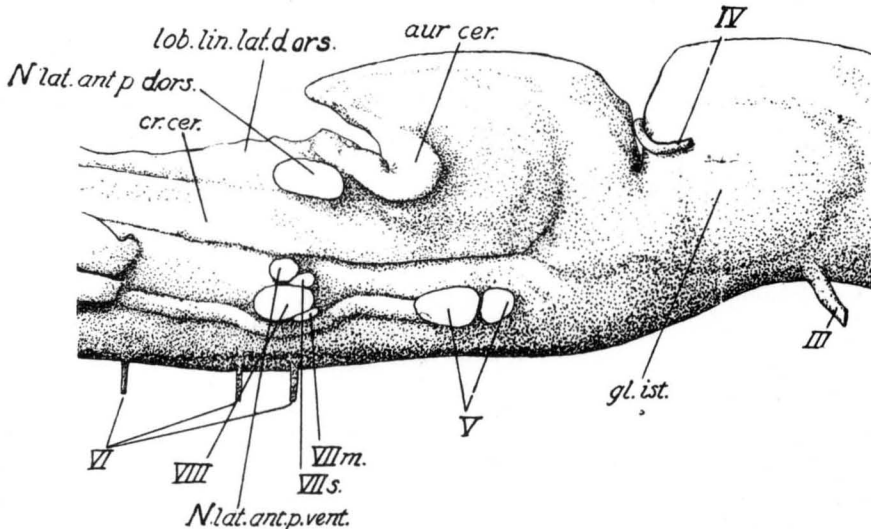


Fig. 1. Cerebellum and medulla oblongata of *Ceratodus* from the lateral side.
After HOLMGREN and VAN DER HORST.

cerebellum. The lobus lineae lateralis posterior is situated ventral to the crista, being the nucleus of the N. lateralis posterior and also of the ventral root of the anterior lateralis. Herefore I think it is better to call this nucleus lobus ventralis.

In the frontal part of the cerebellum on both sides of the ventricle the granular layer becomes considerably thicker and the molecular layer at the outside becomes gradually thinner. Finally the granular mass reaches the surface of the lateral sides of the cerebellum, so that the molecular layer forms then only the dorsal surface. The lobus lineae lateralis ventralis is connected with this lateral granular mass, and this mass continues in a frontal direction along the lateral side of the midbrain to the level where the oculomotorius leaves the brain.

In the chapter about the cerebellum, principally compiled by me, HOLMGREN and VAN DER HORST identified this lateral granular mass with the ganglion isthmi. It is possible that the frontal part, covering the lateral side of the midbrain, is homologous with the ganglion isthmi, but the caudal part of this granular mass, situated in the frontal part of the cerebellum, certainly can not be identified with this ganglion. It is the eminentia granularis of teleosts, as will be explained later on. In the meantime I will call this granular mass in this article the eminentia granularis.

Because of the fact that the dorsal lateralis nucleus is connected with the auricle and the ventral lateralis nucleus with the eminentia granularis, it follows, that these two parts of the cerebellum have a similar function. Especially does HERRICK call attention to this fact, but because of this

functional similarity HERRICK did not see the morphological difference between these parts. According to him the eminentia granularis is homologous with the auricle.

In connection with this I should call attention to the fact, that in *Ceratodus* the two frontal lateralis roots exchange a great number of fibers, before they enter the brain. In this way the functional similarity between auricle and eminentia granularis is still increased. The only difference is, that the ventral lateralis nucleus is in close connection with the nucleus of the N. octavus, even to such an extent that it is impossible to distinguish these two nuclei.

The auricle belongs almost wholly to the area of the N. lateralis, whereas the eminentia granularis is not only in connection with the lateralis but also with the octavus. On the other hand the middle part of the cerebellum is principally the endnucleus of secondary tracts arising from the mesencephalon or which ascend from the spinal cord and the oblongata and which carry somato-sensory stimuli.

Starting from such a simple and yet well developed cerebellum, as is found in *Ceratodus*, it is possible to understand the morphological significance of the different parts of the cerebellum, as it has developed in different directions in the other orders of fishes.

In Selachians we find the middle part, the corpus cerebelli, enormously developed and the same is the case with the auricles, as has also been explicitly described by VOORHOEVE for a great number of sharks and rays. The auricle extends frontad along the total length of the cerebellum, so that the place, where the eminentia granularis might be expected, is covered by the auricle. In embryo's, in which the auricles are still smaller, the eminentia granularis is plainly visible, but during further development it is included more or less within the auricle. So we see, that the lobus liniae lateralis ventralis of Selachians is connected with the auricle, namely with the frontal part of it. But I will not enter into details here about the morphology of the cerebellum of Selachians.

Whereas the cerebellum of Selachians, upon becoming too large to form a flat plate, curves upwards in the middle part, in Crossopterygians it curves downwards in the ventricle (VAN DER HORST). In the median sagittal plane the skull cavity deeply penetrates into the cerebellum, so that the two lateral halves, forming the cerebellum, are connected in these fishes only by the ependyma and a thin layer of crossing fibers.

In Chondrosteans (*Acipenser*, *Polyodon*) the cerebellum is formed principally in the same manner, but for a few differences, by which this curving inwards of the cerebellum is less striking in Chondrosteans than in Crossopterygians. The main difference in this respect is, that the median fissure which remains in Crossopterygians between the two lateral halves of the cerebellum, disappears in Chondrosteans for the greater part, so that the curved in part is almost a solid mass. The second difference is, that the auricles in Crossopterygians are very small or lacking altogether,

whereas in Chondrosteans they are very large and furthermore they are situated far dorsally, so that they cover the lateral surface of the corpus cerebelli. So when comparing Chondrosteans with Teleosts one gets the impression, that the corpus cerebelli is not curved inwards into the ventricle, but only that the auricles are situated far dorsally.

This dorsal position of the auricles is a result of the curving inwards of the cerebellum. This makes it necessary for the ventricle to enlarge, and this enlargement occurs by the stretching out of the lateral sides of the fourth ventricle in a dorso-ventral direction. This becomes clear upon comparing fig. 2 of *Calamoichthys*, showing a section slightly caudal of the cerebellum, with fig. 3 of the same animal showing the most caudal

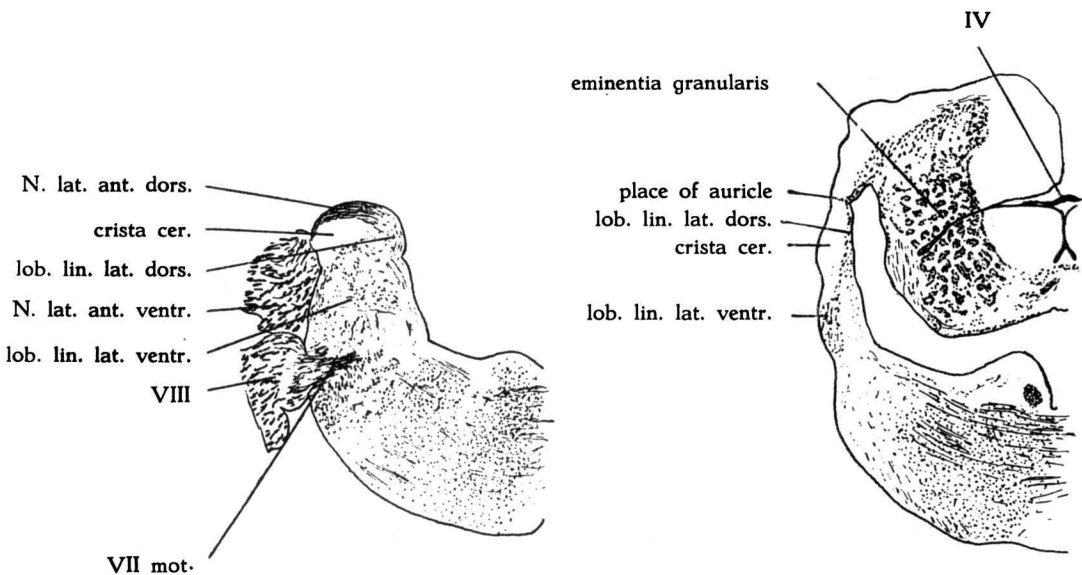


Fig. 2. *Calamoichthys calabaricus*.

Fig. 3. *Calamoichthys calabaricus*.

section, in which the corpus cerebelli is connected with the dorso-lateral border of the oblongata.

Figure 4 shows a similar section of the brain of *Polypterus* and here we see a striking difference between the two Crossopterygians. In *Polypterus* the granular mass reaches the lateral surface at the place, where the caudal border of the cerebellum unites with the dorso-lateral margin of the oblongata. Here a distinct, though small, auricle is present. The choroid plexus had been removed from this brain, so that the lateral recess, that otherwise covers the auricle externally, is not visible in the sections. On the other hand in *Calamoichthys* the auricle is lacking absolutely, the crista cerebellaris being directly combined with the molecular layer of the cerebellum.

This slight development or total absence of the auricle in Crossopterygians is in close relation to another remarkable fact. In Chondrosteans and

Selachians, as in *Ceratodus*, the dorsal root of the lateralis anterior is much thicker than the ventral root. But in *Crossopterygians* the dorsal root is

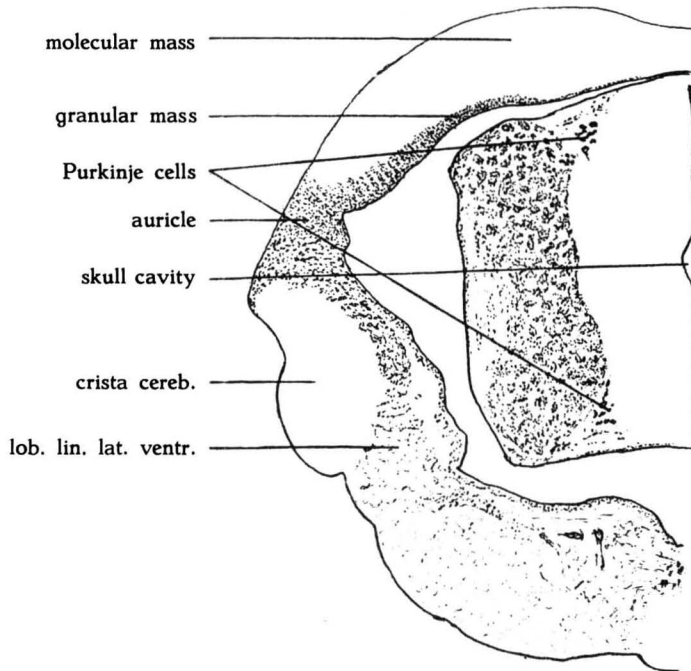


Fig. 4. *Polypterus bichir*.

small and the greater part of the lateralis fibers enters ventrally (fig. 2). So we see, that the dorsal lateral line lobe in *Crossopterygians* is relatively much smaller than in the other fishes mentioned above. And as the auricle is in close relation with the lobus liniae lateralis dorsalis, we need not be surprised, that also the auricle is here very small, or absolutely wanting. It is not necessary that this reduction of the dorsal lateralis root indicates, that the whole lateral line system is less developed in *Crossopterygians*, and as we will see still more in *Teleosts*, than in *Chondrosteans* and *Selachians*. As I mentioned above, in *Ceratodus* an important exchange of fibers is found between the two roots of the anterior lateralis before they enter the oblongata. In *Crossopterygians* the small dorsal root combines with the large ventral root directly outside the brain. It is quite certain, that fibers entering dorsally in *Chondrosteans* and *Selachians* will do so ventrally in *Crossopterygians*.

The eminentia granularis of the *Crossopterygians* and *Chondrosteans* has shifted in dorsal direction in the same way as the auricle. We find this eminentia quite at the dorsal surface of the cerebellum and in *Crossopterygians* it reaches the surface even in the median fissure. In *Chondrosteans* the eminentia is more distinct than in *Crossopterygians*.

A third line of development of the cerebellum is found in *Holosteans*

and Teleosts. We find the most simple condition which is easiest to be compared with that of *Ceratodus* in *Amia*. I was unable to obtain suitable material of *Lepidosteus*. The cerebellum of *Amia* shows principally the same structure as that of *Ceratodus*. It covers as a curved plate the frontal part of the oblongata. The caudal border is convex and forms here the roof of the fourth ventricle. Also the ependyma, forming a distinct lateral recess, is attached in the same place as in *Ceratodus*.

Whereas in *Ceratodus* the freely projecting caudal part of the cerebellum consists of an outer molecular and an inner, ventricular, granular layer, this caudal part in *Amia* is formed only by molecular substance (fig. 5). Only at the ventricular side and especially near the attachment of the ependyma scattered granular cells are found between the fibers. When studying the brain from this level in frontal direction, we see that soon a real granular mass appears in the sections (fig. 6), not at the ventricular side but in the middle of the molecular mass. The molecular substance situated at the dorsal side of this granular mass is the same as found in *Ceratodus*, whereas the ventral molecular mass consists of crossing fibers

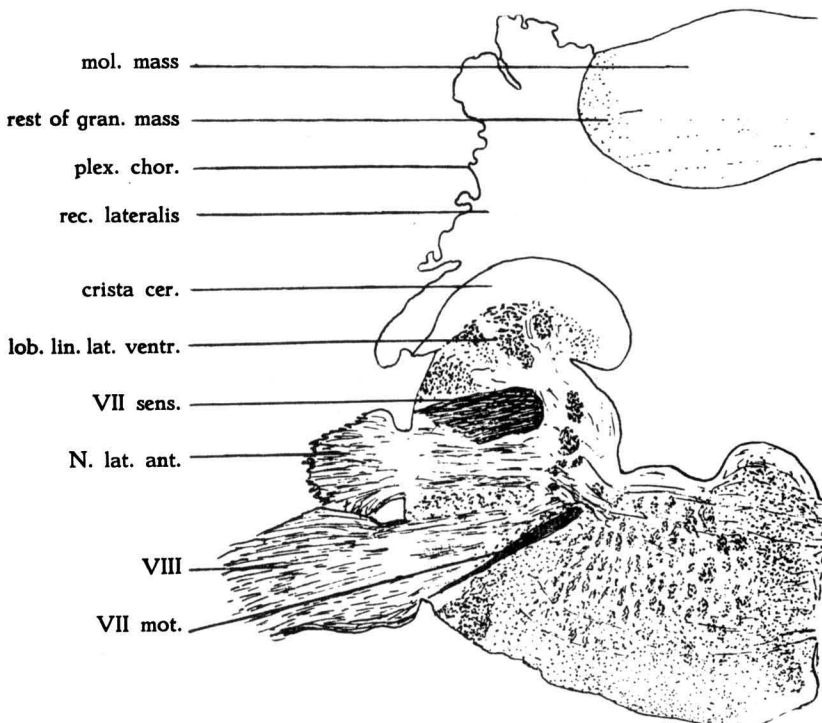


Fig. 5. *Amia* calva.

arising from the crista and forming the tractus vestibulo-cerebellaris. The fact, that groups of granular cells are scattered between the fibers shows, that the fibers have pushed away the granular substance, which was situated originally at the ventricular side.

Running from the crista to the cerebellum the fibers curve in caudal direction to cross over near the caudal border of the cerebellum. So we

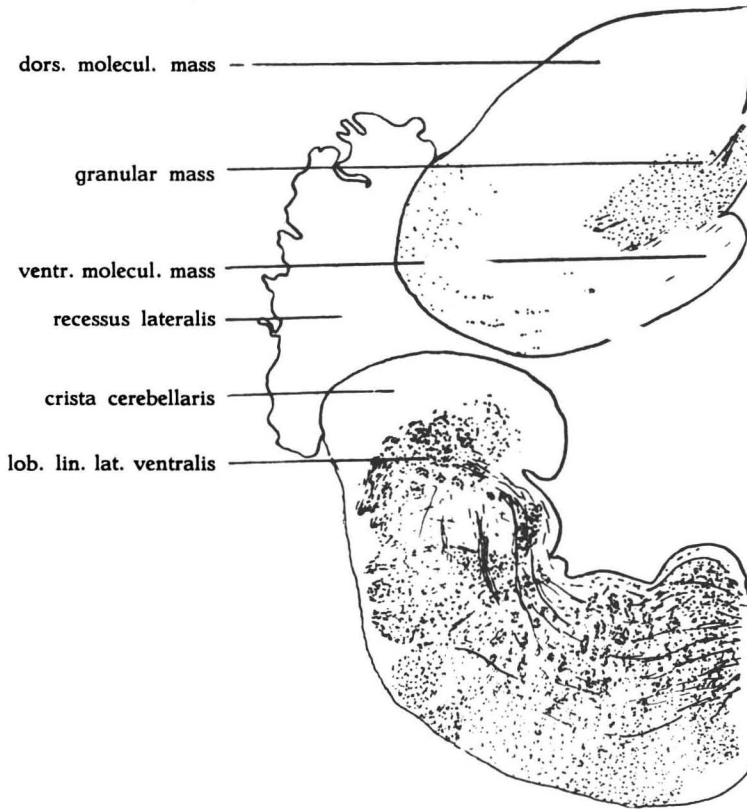


Fig. 6. *Amia calva*.

see, that the ventral molecular layer soon splits, in the median sagittal plane, into two parts (fig. 6), which, running in a frontal direction, are separated more and more. The two parts disappear wholly at the level, where the molecular mass combines with the crista cerebellaris (fig. 7).

Because the vestibulo-cerebellar fibers run from the crista along the ventricular side of the cerebellum and here push away the granular substance, it goes without saying, that an auricle cannot be present. Only the granules that are scattered through the whole ventral molecular mass, are a little more densely packed at the place, where cerebellum and oblongata unite and where the auricle might be expected. This accumulation of granules may be looked upon as a rest of the auricle. In *Amia* only a few granular cells are found here, in some Teleosts, e.g. *Esox*, by far more. The granules may also form a small compact group like in *Osmerus* (fig. 9).

As mentioned before, the dorsal root of the lateralis anterior is much smaller than the ventral root in Crossopterygians. This root is absolutely lacking in *Amia* and Teleosts. All lateralis fibers enter ventrally to the crista cerebellaris (fig. 5). BERKELBACH VAN DER SPENKEL mentions a

dorsal root of the lateralis anterior in *Silurus*, but this root is a bundle of fine lateralis fibers, forming the most frontal part of the entering nerve

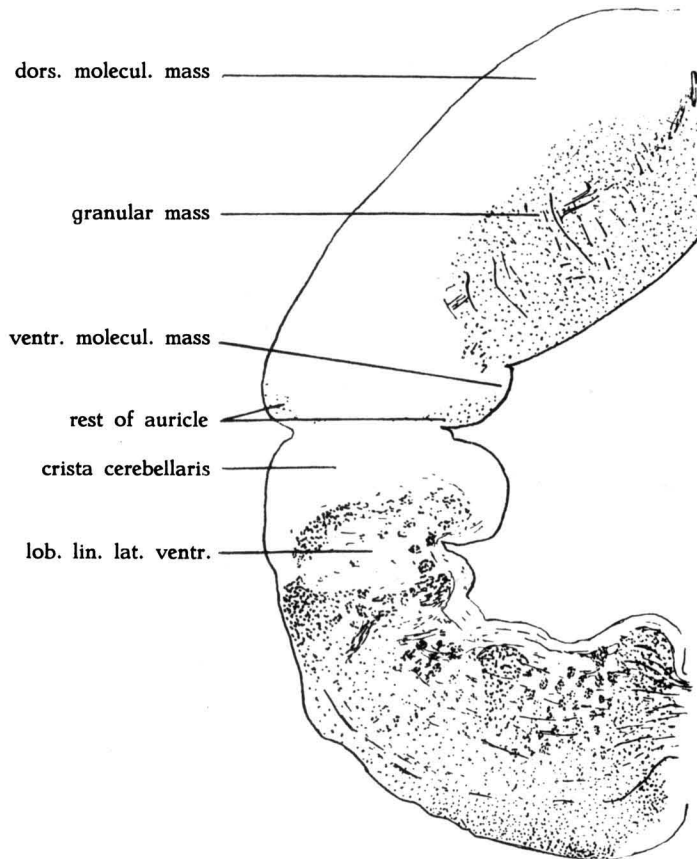


Fig. 7. *Amia* calva.

and ascending directly to the cerebellum. The fact that this ventral root consists of coarse and thin fibers, makes it apparent that the dorsal lateralis root is inserted in the ventral root in Teleosts.

According to SCHEPMAN in Cyclostomes the dorsal root consists only of coarse fibers and the ventral of thin ones, whereas in Teleosts both types of fibers occur in the ventral root.

If we continue our study of the cerebellum in *Amia* in a frontal direction, we see that the granular mass extends more and more in lateral direction, untill finally it reaches the lateral surface of the cerebellum. In figure 8 the granular mass is still covered by a thin layer of molecular substance, but this layer disappears a few sections more frontally. Here we find the molecular layer only at the external surface of the middle part of the cerebellum or the corpus cerebelli. The lateral mass of granular substance, found in the same way in Teleosts (fig. 11), has been described by FRANZ as *eminentia granularis*. In *Ceratodus* this lateral extension of granular substance occurs in quite the same way. So here it ought to be called

also eminentia granularis. The ventral lateralis nucleus passes over into this eminentia granularis.

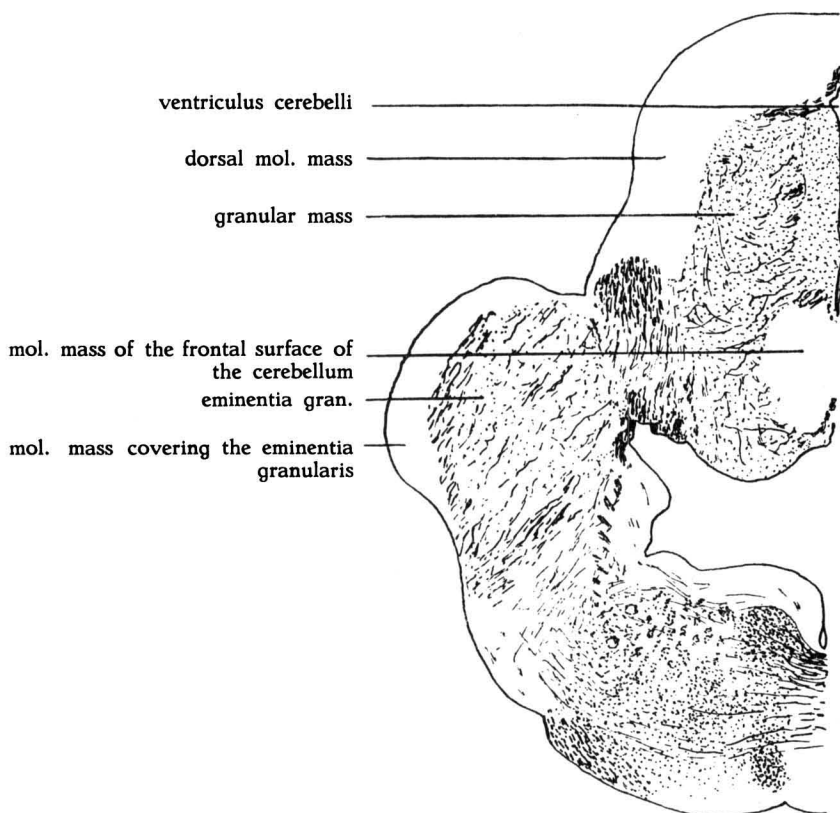


Fig. 8. *Amia calva*.

In the frontal part of the cerebellum the two eminentiae granulares are connected by a band of granular cells, which, situated along the roof of the fourth ventricle, form the most ventral part of the corpus cerebelli. In *Amia* the eminentiae can be clearly distinguished from this band of granules. In this fish the frontal extremity of the eminentia is seen some sections in front of that figured in fig. 8, whereas the band of cells above the ventricle reaches farther frontally and passes over in the granular mass of the valvula. But in different Teleosts the two eminentiae granulares cannot be separated from the granular mass between them nor from the granular substance of the valvula. Moreover it is known also by the fiber connections, that the valvula cerebelli belongs to the acustico-lateral area.

In *Ceratodus* the granular mass of the eminentia extends as a tongue far frontally along the lateral side of the midbrain (fig. 1) HOLMGREN and VAN DER HORST have called this part the ganglion isthmi. It is not impossible, that this granular mass really is the ganglion isthmi, because also this ganglion is related to the acustico-lateral area. But it may also

be possible, that this mass is the homologue of the valvula cerebelli which in this case should have extended along the lateral surface of the midbrain instead of curving into the ventricle of this brain part.

In Teleosts almost the same relations are found as in *Amia*; what was still in a rudimentary state in *Amia*, has developed farther in Teleosts. This concerns in particular the ventral molecular mass. Compared with *Amia* this mass extends by far more frontally and covers the whole ventricular side of the cerebellum. Also the place of attachment of the choroid plexus, covering the fourth ventricle, has shifted frontally, so that the caudal part of the cerebellum projects quite independently to the exterior.

In *Osmerus* the conditions are nearly the same as in *Amia*. Here also the cerebellum has the form of a thick curved plate (fig. 9). The ventral molecular mass extends here farther frontally (fig. 10), but still it disappears soon, when the cerebellum is attached to the dorso-lateral border of the oblongata. But in the more specialised Teleosts this ventral molecular layer extends below the whole corpus cerebelli. Moreover the cerebellum has increased in size considerably and it shows a different form in the different orders of Teleosts. It may grow high up as a solid mass, as is often the case in *Acanthopterygii* (fig. 11), or it remains more or less flat; it may be situated above the fourth ventricle as in *Gadidae*, or it may bend in frontal direction above the tectum opticum as in *Siluridae*.

Also the *eminentia granularis* varies greatly in development. This all has been described by FRANZ for a great number of Teleosts.

I only will call attention here to the relation met with in *Anguillidae* (fig.

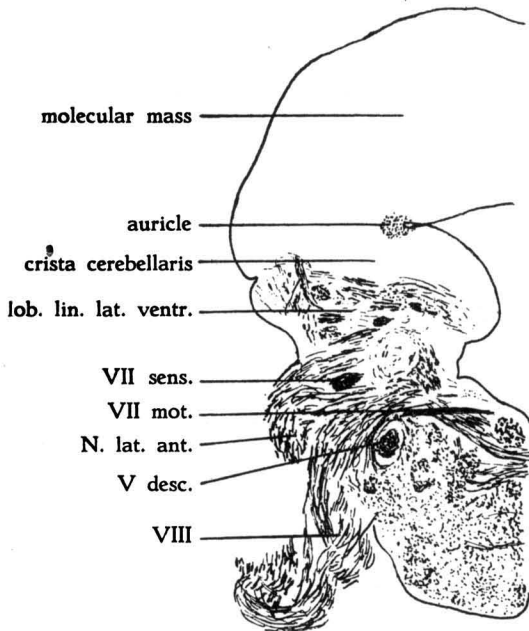


Fig. 9. *Osmerus eperlanus*.

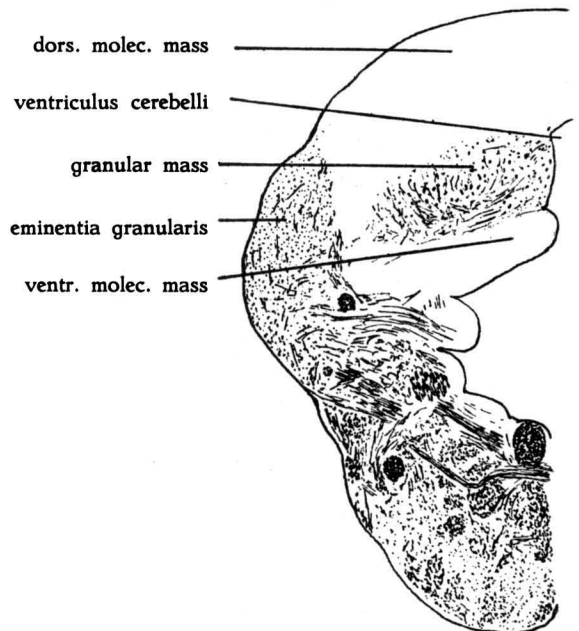


Fig. 10. *Osmerus eperlanus*.

12). Here the granular layer reaches the lateral surface along the whole length of the cerebellum. Also the granular mass consists clearly of two layers, the ventral one of which is in connection with the eminentiae granulares. These two layers are separated by a furrow on the lateral surface. According to FRANZ this is a primitive condition and it proves, that the cerebellum of Teleosts has developed from a plate-like state by curving upwards. This should correspond to a selachian cerebellum being so much flattened in fronto-caudal direction, that the ventricle should have quite disappeared. Only in some cases as in *Anguilla*, a limit between the dorsal and ventral granular layer should be visible.

In my opinion the cerebellum of *Anguilla* must be explained as follows: The eminentiae granulares are greatly developed and extend along the whole length of the cerebellum. Also the granular layer, which otherwise in Teleosts connects the two eminentiae only in the frontal part of the cerebellum, has enlarged in caudal direction. In this way two granular layers are visible externally over the total length of the cerebellum, the ventral one

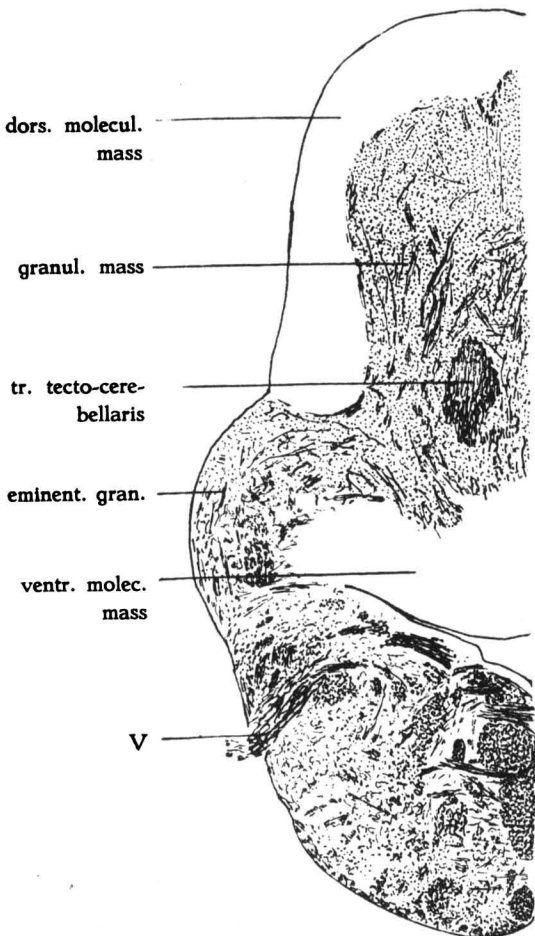


Fig. 11. *Trachinus draco*.

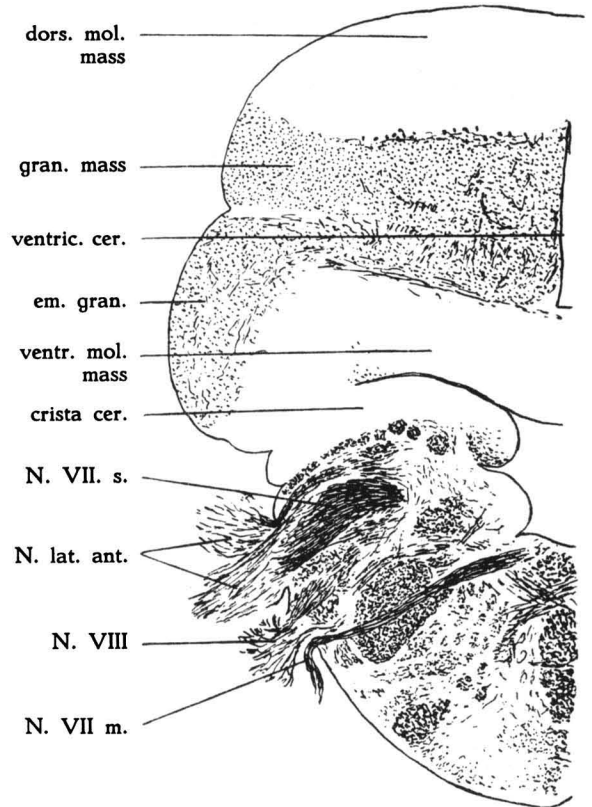


Fig. 12. *Anguilla anguilla*.

belongs to the eminentiae granulares, the dorsal one is the real granular substance of the corpus cerebelli. Also the latter granular substance reaches the surface in Anguillidae in contradistinction to the other Teleosts, and this may be in relation with the great depression of the cerebellum.

Finally I may show, that the ventriculus cerebelli in *Amia* and different primitive Teleosts, is not homologous to the ventriculus cerebelli in Selachians. In Teleosts this ventricle is a very narrow sagittal fissure, being a last remnant of the bilateral origin of the cerebellum as described by SCHAPER. If the opinion of FRANZ were correct, we might expect a horizontal or a transverse fissure instead of a sagittal one. The cerebellum of Selachians arises by folding upwards of a plate-like rudiment which is found in embryo's. So the ventriculus cerebelli in these animals is a part of the fourth ventricle separated from the rest by the folding upwards of the cerebellum. The only part of this ventricle which may be compared with the ventriculus cerebelli of Teleosts is the sagittal fissure between the two granular ridges.

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