Zoology. — *"The Fore-brain of Synbranchidae"*. By Dr. C. J. V. D. HORST, Amsterdam. (Communicated by Prof. MAX WEBER).

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The Synbranchidae are distinguished from all other Teleosts by a secondary coalescence of the two halves of their fore-brain.

In the rich collection of the Central Institute for Brain Research at Amsterdam, which includes almost all the suborders of the Teleostei, I found several representantives of other suborders of Teleosts in which the hemispheres of the fore-brain are pressed together, but where no coalescence has occurred.

In only one of the three series of Hippocampus in the Institute the two hemispheres partially have grown together in the midline, dorsal from the commissura anterior. This, however, must be regarded rather as an abnormality in this specimen caused by the presence of parasites in the brain cavity, whereby the fore brain has become totally changed in form.

Of the suborder of Synbranchii, I was able to examine the brains of Monopterus albus (Zuiew) received from Dr. SUNIER of Batavia, and of Synbranchus marmoratus Bl., which I obtained from the Aquarium of the Royal Zoological Society "Natura Artis Magistra" at Amsterdam. The brains of these fishes were cut in series of sections 20μ thick, treated by the WEIGERT-PAL method and contra-stained with paracarmine.

Monopterus and Synbranchus are exactly alike as regards the formation of the brain, as I have pointed out in a previous paper (2). The coalescence of the two hemispheres is therefore not an abnormality here as in the above-mentioned specimen of Hippocampus, but is a typical characteristic of the family of Synbranchidae, and, if it also occurred in Amphipnous, even of the whole order of Synbranchii.

The outer form of the fore-brain.

The fila olfactoria are collected in a short nervus olfactorius which forms a fairly sharp boundary with the bulb.

As in most of the Teleostei the bulbi olfactorii in Monopterus and Synbranchus are sedentary; an elongated tractus olfactorius is not found here.

Further back the bulbi, which in comparison with the fore-brain are considerably big, decrease in size according as the fore-brain becomes larger. On the median side they are separated by a deep groove. Whereas in most Teleosts with sedentary bulbs, this groove extends over the dorsal and lateral side of the bulbus, so that the front point of the fore-brain projects in the ventricular cavity above the bulbi; this is not the case in the Synbranchidae; the foremost point of the telencephalon has already united with the bulb.

On this boundary between the bulb and the fore-brain the ependyma, which forms the roof of the fore-brain, is attached to the dorsal and lateral sides of the olfactory bulb, while on the medial side the place of attachment lies on the bulb rather before this boundary (see fig. 2). Except for a small fold on the front, the membranous roof lies flat over the whole fore-brain. To the ventro-lateral side of the hemispheres in the fissura endorhinalis (not lateral from it, as in many other Teleosts), the tela choreoidea is attached and the ependyma passes over into the subventricular ependyma, which even extends over the hemispheres themselves.

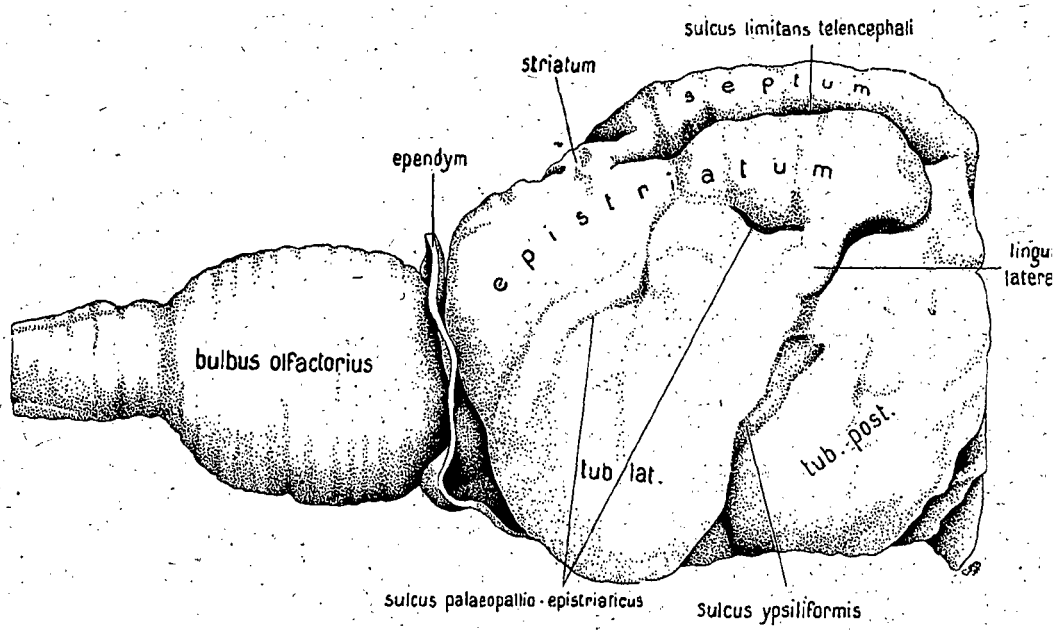
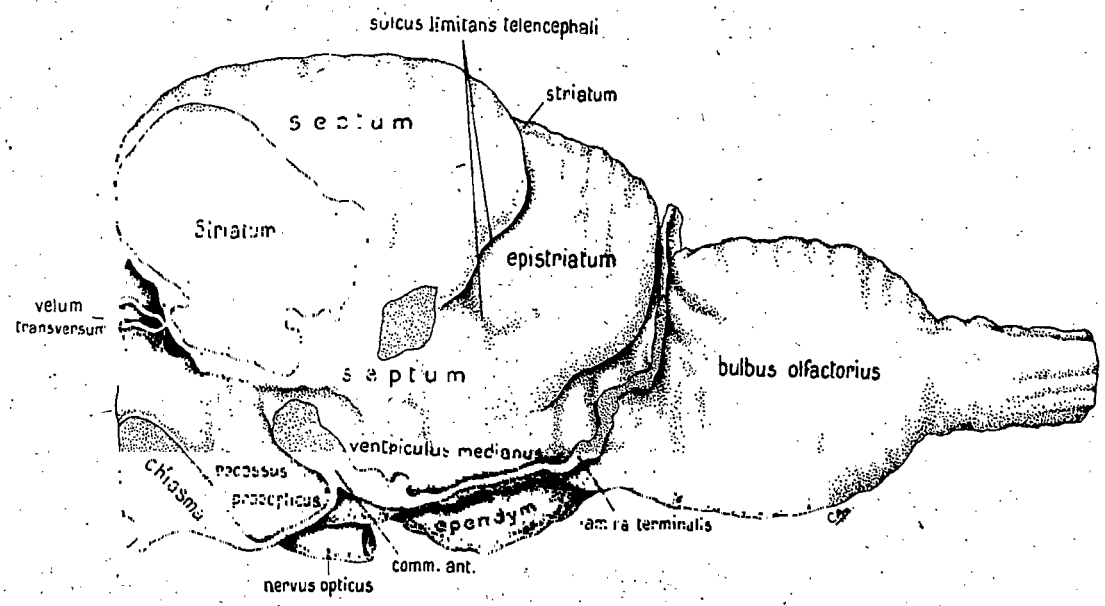


Fig. 1. Monopteus albus. Wax model of the fore-brain Lateral side.

The fissura endorhinalis is very deep owing to the great development of the lateral portion of the fore-brain (tuberculum laterale and tuberculum posterius of SHELDON (6)). As SHELDON has described of the carp, so also in Monopterus this fissure deviates at the place of the sulcus ypsiliformis rather decidedly in a lateral direction.

Thus seen from the ventral side, the fissura endorhinalis is shaped like two half arcs, which form an obtuse angle with each other. The anterior of these bounds the tuberculum laterale, the posterior the tuberculum posterius.

Not only latero-ventrally, but also caudally the tuberculum posterius is strongly developed like the median portion of the fore-brain. The caudal portion in these fishes thus covers a greater part of the thalamus. One consequence of this is that the posterior fold of the velum transversum points forwards instead of backwards (fig. 2). Whereas the dorsal sack (pulvinar epiphyseos) usually lies on the roof ependyma of the fore-brain, here we see just the reverse; the richly folded dorsal sack is covered by the ependyma of the fore-brain which bends backwards over it.



– Fig. 2. Monopterus albus. Wax model of the fore-brain Median side.

A short distance behind the middle of the hemispheres, in a rather frontal position consequently the sulcus ypsiliformis of GOLSTEIN (1) begins at the place where the fissura endorhinalis forms the aforementioned obtuse angle (fig. 1). The sulcus, very deep at this place, proceeds at first perpendicularly upwards, but later on bends in a somewhat caudal direction. As in Cyprinus, according to SHELDON's description, the groove then divides. The two grooves then formed run along the whole dorso-lateral side of the hemispheres. They constitute the boundary between the lateral part of the fore-brain, the palaeopallium (tuberculum laterale and tuberculum posterius),

and the more dorsal epistriatum. These two grooves together may thus very justly be termed the sulcus palaeopallio-epistriaticus, as this has been described by KAPPERS and THEUNISSEN (5) in Thynnus.

The most posterior portion of this groove is very deep and narrow; the boundary between the palaeopallium and the epistriatum can therefore be drawn very sharply there. The direction of this portion is almost caudo-frontal. Towards the front, the groove becomes shallower and wider. It then deviates in a ventral direction and reaches the fissura endorhinalis on the front of the hemispheres, getting gradually fainter.

Dorsally from this sulcus palaeopallio-epistriaticus there lies a body which I take to be the epistriatum (the primordium hippocampi of SHELDON). At least the posterior portion, limited by the deep grooves, corresponds exactly in form to the epistriatum of Gadus, Silurus and other fishes, as has been described by KAPPERS. Thus it shows clearly a lingua lateralis descending in the sulcus ypsiliformis, as well as a lingua posterior projecting backwards. The latter is especially distinct in Synbranchus (fig. 6). This part too receives secondary olfactory fibres from the tractus olfactorius medialis pars lateralis, just as the lateral part of the hemispheres lying caudally from the sulcus ypsilliformis. To this very pronounced part of the epistriatum an anterior portion joins, which is connected with it by a narrow strip lying rather deeper, so that one might say that it is separated from it by a broad and shallow groove. Viewed through the microscope, these two parts merge invisibly into each other. I therefore believe that this front portion must also be considered as a part of the epistriatum. Like the caudal portion it is closely connected with the palaeopallium. Both receive secondary olfactory fibres from the tractus olfactorius lateralis. On the other hand, it is fairly sharply divided from the striatum, over which it lies like a hood.

The epistriatum is bounded on the median side by the sulcus limitans telencephali, which has been described by SHELDON, and which forms the boundary between the corpus precommissurale (septum mihi) and the primordium hippocampi of this author (epistriatum mihi) (figs. 1, 2, 3, 4, 5, 6). This sulcus in Monopterus is very narrow and deep, as is seen in figs. 3, 4, and 5, specially the posterior portion of the epistriatum (the lingua posterior) is sharply separated by it from the other parts of the hemispheres. In Synbranchus the sulcus is not so deep, but this is secondary compared with Monopterus, since, here and there in Synbranchus a series of ependyma cells is found lying between the epistriatum

and the septum at the same place as where in Monopterus the sulcus cuts deep into the hemispheres. From this it is evident that the sulcus limitans telencephali is present at first in Synbranchus in the same form as in Monopterus, but that later it grows together in a similar way as in the posterior portion of the central canal of the spinal cord, where only a septum ependymale remains. In consequence of this the sulcus is only indicated by a very faint groove in Synbranchus.

In Cyprinus, where SHELDON has described this groove, the sulcus limitans runs entirely on the median side of the hemispheres and only at its caudal end does it reach the dorsal surface of the fore-brain then lying on the dorso-median side of the hemispheres. In most of the specimens of Teleosts, which I examined as to this, the groove is found at the same place as in the carp. But in the Synbranchidae the course of the sulcus limitans is entirely modified owing to the enormous development of the septum. This body, in most Teleosts, covers the entire median wall of the hemispheres ventrally from the sulcus limitans. Whereas it is comparatively small at the front of the fore-brain there covering only the ventral half of the median wall of the cerebrum, it grows out caudally in a dorsal direction and finally covers the whole median side of the hemispheres.

In Monopterus the frontal end of the sulcus limitans lies at the same place as in other Teleosts, about half way up the median wall of the hemispheres. From here this groove runs slightly caudally, but then makes a sharp bend and further proceeds in a dorso-frontal direction to the upper surface of the brain (fig. 2). Here the groove curves gradually in a caudal direction and then runs backwards almost parallel to the median line. (Fig. 1).

This course of the sulcus limitans is, as has been said, caused by the enormous increase of the septum. As in Cyprinus the frontal termination of this body occupies only the ventral half of the median side of the hemispheres. But the greater part of it has developed strongly in a dorsal direction. The whole median side of the hemispheres and a part of the dorsal side are covered by it. Moreover it protrudes there somewhat in a frontal direction covering the striatum, in consequence of which the sulcus limitans is bent here in a dorso-frontal direction (fig. 2). This dorsal growth also explains why the sulcus limitans cuts so extremely deep into the fore-brain. This groove also proceeds over the posterior side of the cerebrum and forms there, caudally from the epistriatum, the boundary between the septum and the tuberculum posterius.

In many Teleosts a large part of the surface of the hemispheres is formed by the corpus striatum. KAPPERS (4) has described this in Gadus and Hippoglossus. On the other hand, in Synbranchidae the corpus striatum is almost completely pushed away from the surface, owing to the septum growing over it from the median side, and the epistriatum from the lateral side. Only a small portion of the striatum remains on the surface, viz. on the dorsal side of the hemispheres, lateral from the frontal point of the septum.

As was already remarked (pag. 217), the cerebra of Monopterus and Synbranchus are specially remarkable owing to the two hemispheres having partially united (fig. 2).

This junction has an important influence on the relation of the ventricular cavities.

The ventricular cavity dorsal and lateral from the two hemispheres has been called ventriculus lateralis by GOLDSTEIN (1), and the slit between the hemispheres has been termed ventriculus medianus by the author. This nomenclature may very suitably be employed here, now that the two ventricle portions have been separated by the growth. Ventrally from the coalescence between the hemispheres lies the ventriculus medianus, for in spite of the growth the median ventricle remains still clearly visible in these fishes, owing to the fact that the hemispheres of the forebrain always deviate slightly from each other on the ventral side above the lamina terminalis and the commissura anterior. Behind the commissura anterior the median ventricle is connected with the recessus praeopticus, while at the frontal pole of the cerebrum the lateral and median ventricles are continuous. For the rest, the two ventricles are completely separated, also in the front portion of the cerebrum. Here the two halves of the fore-brain lie closely pressed together, each indentation in the one half being filled out by the other half, and we frequently see a blood-vessel passing from the one side to the other (fig. 3). Locally too the two halves have frequently grown together; such a coalescence is rather larger immediately caudad from the bend in the sulcus limitans (fig. 2).

The caudal parts of the hemispheres have completely united. The frontal boundary of this coalescence is not constant. In Monopterus it runs differently from that in Synbranchus; very probably in individual cases it will not be constant either, and this is not surprising, considering the local coalescence, which can also be found in the frontal portion. On the other hand, the boundary behind the level of the commissura anterior is sharply defined (fig. 2).

Between the two hemispheres, on the dorsal side, is a deep groove,

which penetrates to where the hemispheres lie against each other or are connected with each other. This groove grows shallower and fainter in a caudal direction and finally disappears altogether (Cf. figs. 3–6).

The coalescence of the hemispheres is by no means a superficial one, since it is accompanied by radical changes in the position of the nuclei and in the course of the fibre tracts. Some of the fibres, indeed, which in other fishes decussate in the commissura anterior, here decussate above the ventriculus medianus. The small size of the ventral commissura anterior of these fishes as compared with that of other Teleosts, is hereby explained.

I wish to point out that it is a common feature that a part of a commissure may cross more dorsally if a suitable commissure-bed is present (c.f. the development of the psalterium in reptiles and of the corpus callosum in mammals).

The nuclei and tracts in the fore-brain.

The nuclei and tracts of the fore-brain have been frequently described, and SHELDON in particular has given a most minute and accurate account of it. It is therefore not my intention to describe them all again here, the more so as the position of the nuclei has already been spoken of in discussing the morphology. I will only say a few words concerning some fibre-tracts which differ from the normal type in their course, and concerning the corpus striatum which has been almost quite pushed away from the surface by the other portions of the fore-brain (vide supra).

At the frontal part of the telencephalon, the corpus striatum is seen for a short distance on the medio-dorsal side of the hemispheres between the septum and the epistriatum (fig. 1). Further caudally the growth of the septum pushes it quite away from the surface. Its shape then is oval, in consequence of which in a cross section through this region the septum appears narrowest in the middle (fig. 3). Further caudally the striatum becomes broader; it spreads further in a median direction, dislodging the two septa. This spreading of the striata goes so far that at the level of the posterior boundary of the commissura anterior, they grow together over the median line, whereby the septum becomes divided into a dorsal and a ventral part (fig. 4). We can here distinguish a median and two lateral portions in the striatum.

Further caudally the median connecting portion of the striata is separated from the lateral parts more or less. This separation is

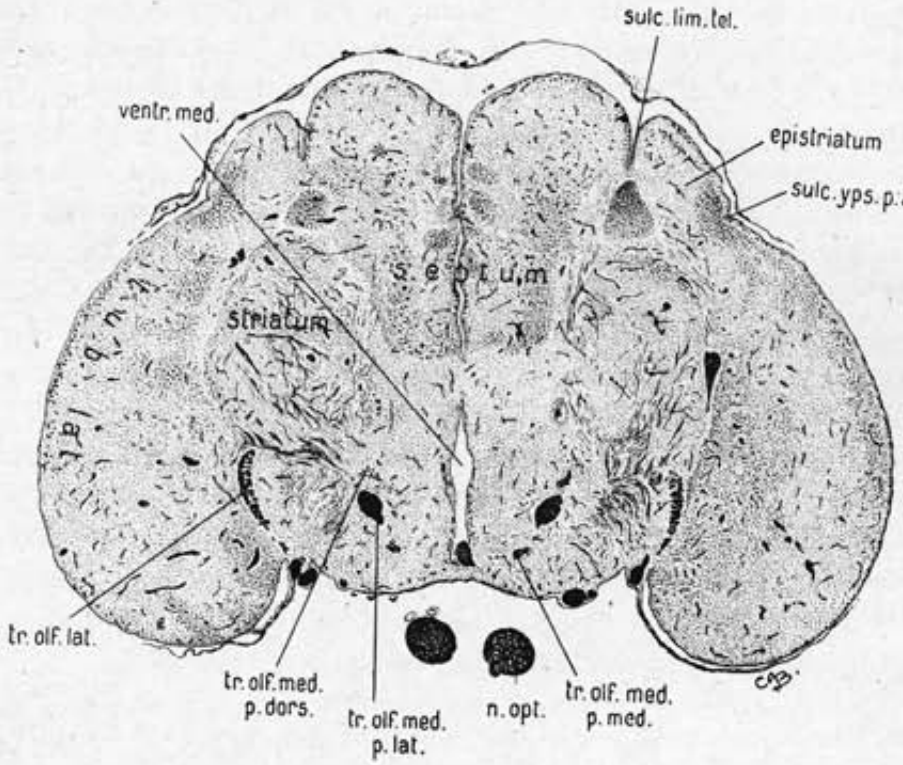


Fig. 3. Monopterus albus.

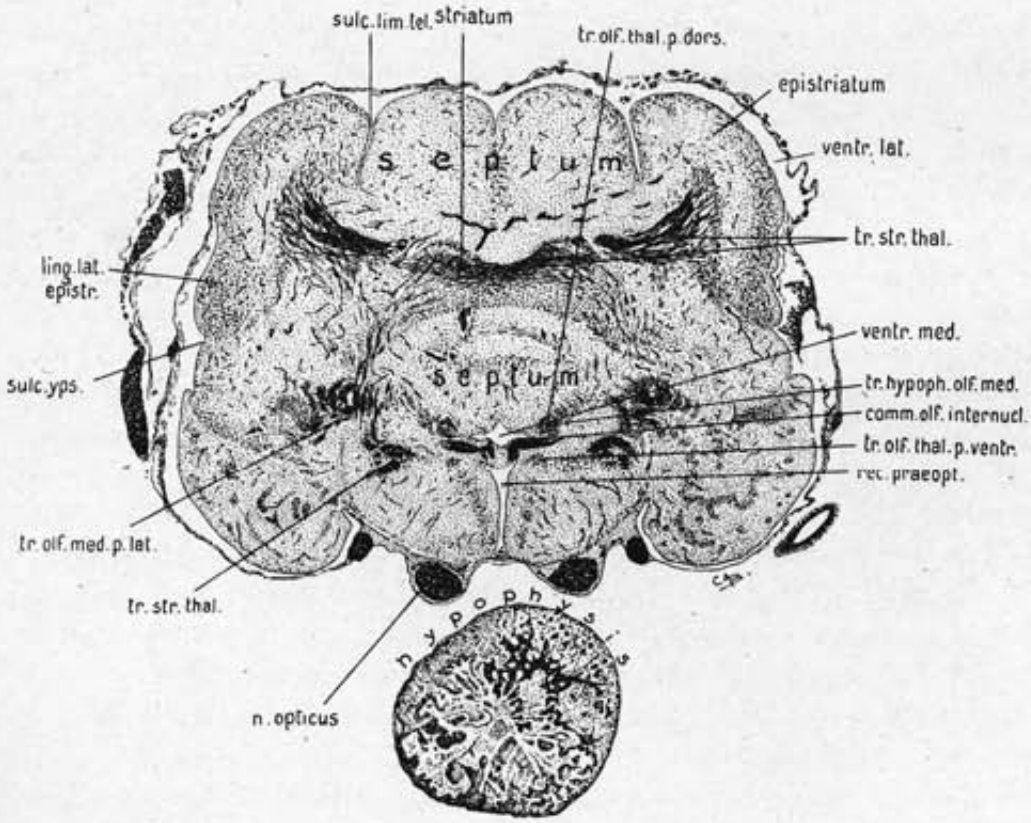


Fig. 4. Monopterus albus.

carried further in Synbranchus than in Monopterus, just as in the former the whole curious development of the fore-brain has reached a further stage than in the latter, as was already pointed out in discussing the sulcus limitans telencephali. The same thing is also clear in considering the caudal end of the striata. In Monopterus the striatum is still separated by a part of the septum from the ventriculus medianus and the recessus praeopticus. The lateral portions of the striata extend equally far caudally as the median portion; in the series of sections the striatum is therefore seen to disappear entirely simultaneously, and at the back it is covered by the septum and the lateral portions of the cerebrum, which meet here.

In Synbranchus, on the contrary, the striatum in the middle pushes away the ventral portion of the septum, so that the striatum lies directly dorsally from the recessus praeopticus (fig. 6). This median portion of the striata extends further in a caudal direction than the lateral parts. At the back of the fore-brain the striatum is not

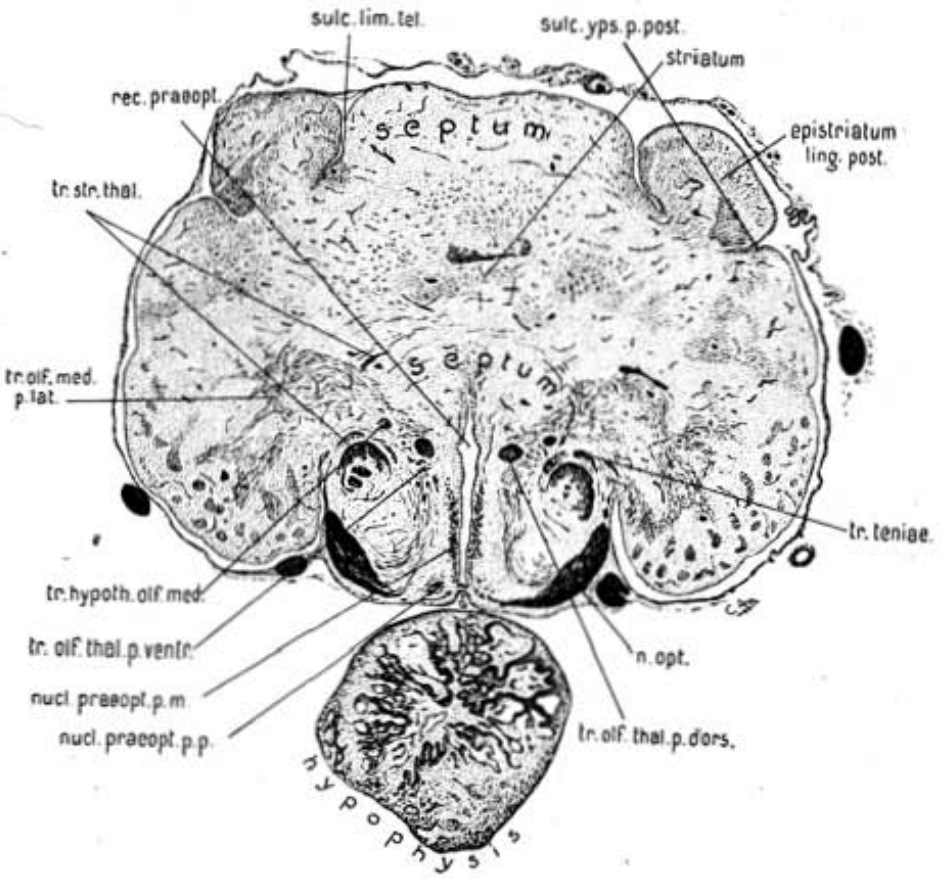


Fig. 5. Monopterus albus.

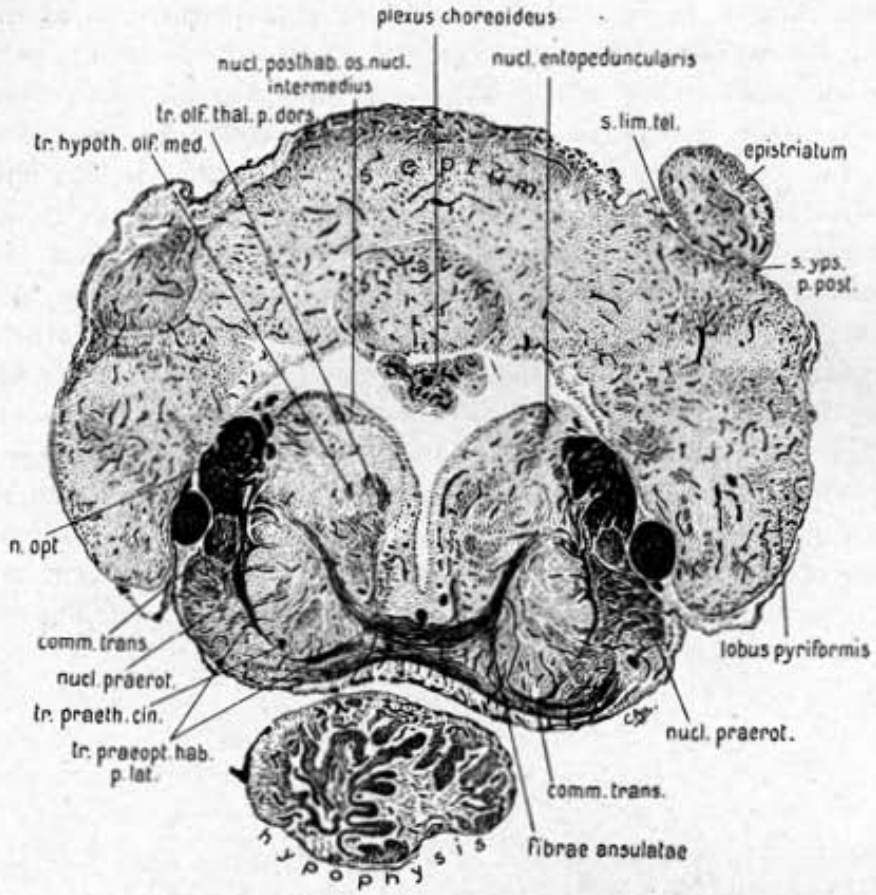


Fig. 6. Synbranchus marmoratus.

entirely surrounded by other parts of the cerebrum, though the dorsally situated septum reaches rather further caudally.

Of the fore-brain tracts the tractus olfactorius claims our attention first.

The lateral olfactory tract (tractus olfactorius lateralis) is found in its usual position near the fissura endorhinalis. It sends its fibres into the lateral olfactory regions, the area olfactoria lateralis of KAPPERS and THEUNISSEN (5). In the level of the sulcus ypsiliformis this olfactory tract has entirely disappeared. It is my opinion therefore that in Synbranchidae only that part of the lateral olfactory region which lies in front of the sulcus ypsiliformis is provided with olfactory fibres from the tractus olfactorius lateralis. According to SHELDON in the Cyprinidae the nucleus piriformis and the nucleus taeniae also receive fibres from the lateral olfactory tract.

In the tractus olfactorius medialis I can distinguish three bundles. One, non-medullated, connects the septum with the bulb and is probably the same as SHELDON describes as tractus olfactorius ascendens (running frontally).

The course of the very small tractus olfactorius medialis pars medialis does not differ from that in Cyprinus, while on the other hand, the thick medullated tractus olfactorius medialis pars lateralis takes a different course. According to SHELDON (6), KAPPERS (4), GOLDSTEIN (1), and others, this bundle decussates with the commissura anterior in at least the large majority of cases among Teleosts. In Synbranchus and Monopterus, however, nothing is to be seen of this decussation. The tract here runs somewhat in a lateral and dorsal direction, on to the commissura anterior, and then penetrates between the various bundles of the tractus strio-thalamicus (fig. 4). When slightly lateral from this, i. e. dorsal from the fissura endorhinalis, the bundle dissolves into a dense network of fibres which lie nearly on the boundary of the nucleus piriformis, the striatum and the ventral portion of the septum (fig. 5). The fibres of this network then spread into the nucleus piriformis and the nucleus taeniae, which are not clearly distinguishable from each other here, and further into the caudal part of the epistriatum. This region, behind the sulcus ypsiliformis, is thus provided with olfactory fibres only by the lateral part of the median olfactory tract.

Very slightly caudal from the place where the tractus olfactorius medialis pars lateralis merges into the aforesaid network, medullated fibres from the nucleus piriformis gather (GOLDSTEIN's commissura olfactoria internuclearis, described as a non-medullated bundle by SHELDON under the name of tractus olfactorii mediales partes laterales). These fibres, forming a considerable bundle, decussate with the most posterior part of the commissura anterior (fig. 4). It is possible that in this bundle there are still a few decussating fibres of the tractus olfactorius medialis pars lateralis; but this I could not determine with certainty.

In connection with the coalescence of the two halves of the fore-brain, the course of a part of the so-called tractus strio-thalamicus is very remarkable. The majority of the fibres which form this bundle congregate, as in all Teleosts, from nearly every part of the fore-brain and, after having decussated partly in the commissura anterior, run medially from the fissura endorhinalis to the mid-brain. From the most posterior part of the epistriatum (the lingua posterior), however, a great number of medullated fibres join to a thick bundle, which decussates somewhat further frontally in the median striatal portion connecting the two halves of the telencephalon. (fig. 4). After the decussation this bundle runs a short distance forward in the dorso-lateral portion of the striatum. On the frontal level of the commissura anterior this bundle bends at a right angle

in a ventral direction, and joins the rest of the tractus striothalamicus.

The fore-brain of the Synbranchidae is remarkable, because it forms, as it were, the final stage in the series of development of the telencephalon of Ganoids and Teleosts. For, according to SHELDON, the septum originally forms the ventro-mēdian part of the fore-brain. In Polypterus, which forms the first stage in this series of development, this part still lies at its original place. The septum now gradually grows on the median side past the striatum, whereby the striatal portion of the ventricle wall is more and more restricted. This process going on, in some Teleosts the striatum disappears altogether from the ventricular wall, and the sulcus limitans telencephali forms the boundary between the septum and the dorsal part of the cerebrum, the epistriatum. At the caudal end of the fore-brain this process is further advanced than at the frontal end; the sulcus limitans thus lying in front on the median side, at the back on the dorso-median side of the hemispheres.

Only in the Synbranchidae however, this process goes so far that the septum reaches the dorsal surface of the cerebrum, whereby the epistriatum is pushed aside and the sulcus limitans comes to lie on the dorsal, or even dorso-lateral, surface of the hemispheres.

The coalescence of the hemispheres may also be regarded as a final stage in the development. In the Ganoids the two hemispheres are far apart and the ventriculus medianus is broad. This is also the case in primitive Teleosts, such as Salmo. In other Teleosts the hemispheres approach each other more and more, and in most Acanthopterygii they lie right against each other; the ventriculus medianus only being open in the ventral part above the lamina terminalis and above the commissura anterior. In the Synbranchidae the hemispheres, at least as regards their caudal half, have almost entirely coalesced, and of the ventriculus medianus only a narrow split remains, ventrally from this junction.

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