Anatomy. — "*Contributions to the knowledge of the brain of bony fishes.*" By Prof. KYOZO KUDO, Mukden (Manchuria). (Communicated by Dr. C. U. ARIËNS KAPPERS).

(Communicated at the meeting of January 27, 1923).

1. *The Tr. olfactorio-opticus.*

NILS HOLMGREN found in Osmerus eperlanus with the CAJAL-method, but also with methylene-blue colouring, a bundle which, long before the middle of the telencephalon, separates from the tr. olfactorius lateralis, then, following the sulcus externus, extends as far as the opticus, into which it enters, and can be traced (in the opticus) for some distance towards the eye. He called the bundle *tr. olfactorius lat. optici* (op. cit., p. 188). With Callionymus lyra he found a similar bundle, but lying in the medial olfactory tract (l.c., p. 188, Anmerkung).

This discovery should be considered most remarkable. Being able to test and confirm the latter case (the fibres in the tr. olfactorius med.) with various Teleosts also by WEIGERT-preparations, I will describe it here more fully.

With the WEIGERT-colouring these fibres, connecting the tr. olfactorius with the tr. opticus, seem fairly coarse; they are nearly always scattered and mixed only with the tr. olfactorius medialis, never with tr. olfactorius lateralis. In the bony fishes, which I examined they run always the same way. As these relations are the most distinct in Ammodytes tobianus, I take this fish as example.

With this fish the tr. olfactorius med. consists of two sorts of medullary fibres, a thin one and a much coarser one. The fibres divide into three parts

The *pars dorsalis* is that part of the tr. olfactorius med. that on a quite frontal level turns towards dorsal. It consists for the greater part of thin fibres that radiate in dorso-lateral direction and disappear rather soon, already on the level of commissura anterior. A few coarse fibres, however, also belonging to this portion, run further caudad, always following laterally the tr. olfacto-hypothalamicus med., but strongly contrasting with these by their coarseness. They cannot be traced accurately from the place where they medially

pass the fibrae ansulatae of BELLONCI, caudo-ventrally descending by and by with the accompanying tractus olf.-hypothal. med.

These fibres form the *dorsal* group of the coarse olfactory fibres.

The *pars intermedia* of the tr. olfact. med. consists half of the thinner, and half of the coarser fibres. The first form a small bundle and cross in the commissura anterior (the so-called comm. interbulbaris).

The *pars ventralis* is formed by coarse fibres exclusively. They at first join to a bundle, but gradually they separate into several small bundles. These, together with the fibres from the pars intermedia form the *ventral* group of the coarse olfactory fibres. The bundles soon arrange in regular order dorso-ventrally in the praethalamus, thereby dorsally touching the tr. olfacto-hypothalamicus med., ventrally the tr. opticus, into which they are taken up gradually (fig. 1). A few fibres that are in an exceptional dorsal position, enter into the just rising commissura minor.

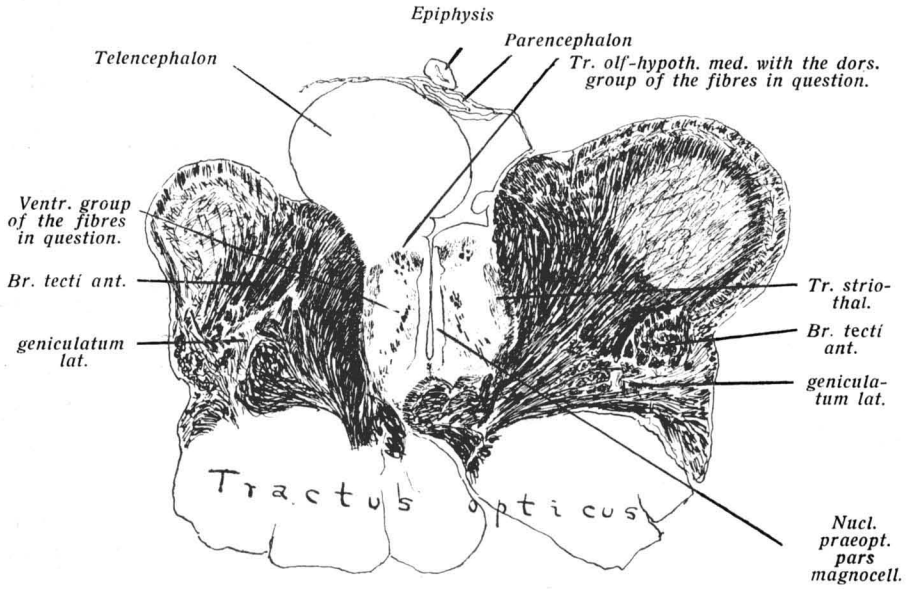

Fig. 1. Ammodytus tobianus.
(Preparation of the Central Institute for Brain-rescarch, Amsterdam).

With other bony fishes the course of these coarse olfactory fibres is nearly the same. Only the relation to the commissura minor (and to the fasciculus medialis n. optici) does not always exist, this being most distinct, besides in Ammodytes, with Rhombus, Hippocampus and Morone.

I have been able to find these fibres with Catostomi, Percesoces,

Acanthopterygii and Plectognathi, but not with Malacopterygii, Ostariophysi, Symbranchii and Haplomi. They probably are neither to be found with Anacanthini and Pediculati (at least not medullated).

The quantity of the fibres varies according to the kind of fishes. It often is so small that the fibres can be easily counted. In any case the fibres are generally not very numerous. The *ventral* group is always superior in number to the *dorsal*, which I even cannot find in Solea and Cottus.

With Callionymus lyra, the very bony fish that HOLMGREN examined, the matter is somewhat different.

Inasfar as it may be judged by WEIGERT-PAL series these fishes show no tr. olfactorius lat. The tr. olfactorius med. is fairly coarse and is found as usual on the medio-ventral side of the frontal half of the brain. Caudally it soon descends a little ventrally already before the level of the commissura minor, and comes in touch with the opticus fibres and especially with those that arrive here from lateral. I think it fairly probable that fibres are being exchanged between these two tracts, that is to say that tr. olfactorius gives away a part of its fibres to the tr. opticus, but in exchange receives more fibres from the latter tract during its descension (see below) and so becomes visibly coarser. The fibre tract now runs medially along the dorsal opticus root in a ventral direction. [1]) More frontal a small part of the tr. olfactorius is separated from the chief bundle on the spot where this tract begins to descend in order to come into touch with the tr. opticus. This separated little bundle runs independently in the praethalamus also ventrad, about in the middle of the inner and outer surface of same, and finally joins again the principal bundle. [2])

When the thus formed olfacto-optic bundle has at last left the tr. opticus, it runs lateral, viz. between the tr. strio-thalamicus med. and the nucl. anterior thalami? [3]). More caudally it wedges between the nucl. praerotundus? [3]) and the tr. tubero-dorsalis of GOLDSTEIN. A little way back nerve cells begin to appear in the bundle and finally take up the area of the bundle nearly entirely. This nucleus takes its place quite superficially of the lateral surface of the hypothalamus, close above the lobus inferior (see fig. 87 of HOLMGREN's

[1]) The formation of the very extensive tectum plate and accordingly the topography of the opticus roots are in this bony fish different from others.

[2]) So with Callionymus nearly all medullary olfactory fibres seem to run as far as into the praethalamus.

[3]) I have not yet succeeded in identifying these nuclei free from objection with this fish.

work, showing the nucleus in question, medial of "tr. olf. tect. sem."). The cells of this nucleus are small.

From this nucleus proceeds a new fibre tract, running in a curve in the torus semicircularis, parallel to and inward of the tr. isthmo-tectalis mihi (see below), yet it seems to end in the torus itself. That besides this, fibres should come from the said tract in the path of the tr. tecto-bulbaris or tr. tecto-isthmicus into the tectum, as HOLMGREN seems to presume, is improbable to me[1]).

As to the origin and the end of my coarse olfactory fibres, I am quite unable yet to say anything definite. That frontally they are connected with the bulbus olfactorius is undoubtedly sure, but their caudal destination remains quite uncertain. HOLMGREN seems to hold the opinion that his tr. olfactorius lat. optici runs centrifugally in the opticus (l.c., p. 188). I myself am more inclined to believe that the fibres of the *ventral* group tend through the path of the commissura transversa towards the tectum or, less probable, towards the nucl. praerotundus of the other side, the spot where they penetrate into the opticus root just corresponding with the most frontal level of this commissure. This, however, is a mere supposition.

It is harder still to say anything of the *dorsal* group of my fibres.

Concerning the curious olfacto-optic bundle in Callionymus, it can only be said that the part of tr. olfactorius med., that enters frontally into the opticus, corresponds fairly certainly with the *ventral* group of my fibres. But about the other part of the tract, the associating opticus fibres, the peculiar nucleus and the bundle originating from it, I cannot give an opinion, as — till now — I have not seen anything similar with the other bony fishes.

Summarizing we find in the brain of the Teleosts a remarkable fibre system, connecting the tr. olfactorius with the tr. opticus, consisting in the more primitive forms (Osmerus eperlanus) of thin fibres (that can only be exposed by the impr̊egnation method) running in the tr. olfactorius lat., whereas in the more highly organised forms it has coarse, medullary fibres as components and is mixed between the fibres of the tr. olfactorius med. At the present I must be content with confirming HOLMGREN's finding, leaving the arising questions to later investigations.

II. *The Tr. tecto-praerotundus.*

I think I have discovered in the brain of bony fishes a medul-

[1]) HOLMGREN, namely in fig. 87 of his work, has indicated this newly forming fibre tract as „tr. olfacto-tectalis et semicircularis", without further referring to it in the text.

lary fibre tract, not yet described as far as I know, which probably connects the tectum with the nucleus praerotundus. This tract appears in transverse sections on the level where the fasciculus medialis nervi optici, swinging across the tr. strio-thalamicus, joins the lateral opticus root. It there appears as a bundle, running dorso-ventrally, medially along the dorsal opticus root. Dorsally it lies in separate bundles between the just-mentioned opticus root and those fibres that branch off (more frontally) from the tr. opticus, run dorsad in the post-habenular region and finally lateral into the deep medullary layer tectum. From these fibres (probably corresponding to the fibrae tectales n. optici of KRAUSE) the tract is distinguished by the smaller caliber of its fibres and its steeper course. Somewhat more caudally it bends in a lateral direction and enters also into the deep medullary layer of the tectum.

Ventrally it crosses with the fasciculus med. n. optici directly medially to the praetectal nucleus, then runs laterally down from the tr. strio-thalamicus, to finally join the fibres of the commissura transversa (see fig. 2).

Often, however, it does not run laterally to the tr. strio-thalamicus but medially, together with the fasciculus med. n. optici towards medioventral, consequently in this case delusive of a commissura minor in the sense of ARIËNS KAPPERS (one-sided in a specimen of

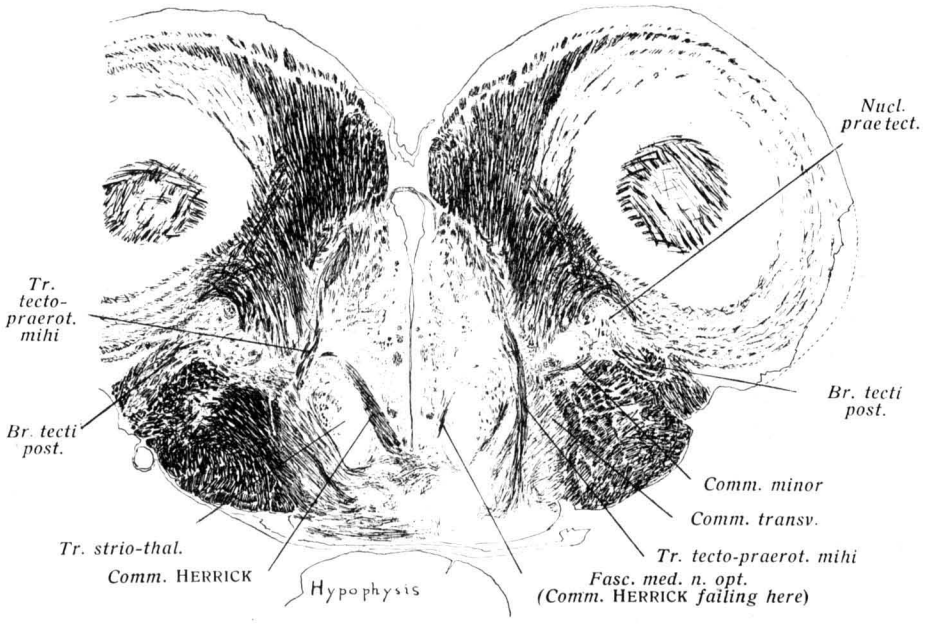

Fig. 2. Mugil chelo.
(Preparation of the Central Institute for Brain-research, Amsterdam).

Gasterosteus (see fig. 3), double-sided in a specimen each of Belone and Exocoetes). However, I want to consider this course as aberrating, for in another specimen of Gasterosteus and also of Exocoetus it runs laterally to the tr. strio-thalamicus, as with the other Teleosts.

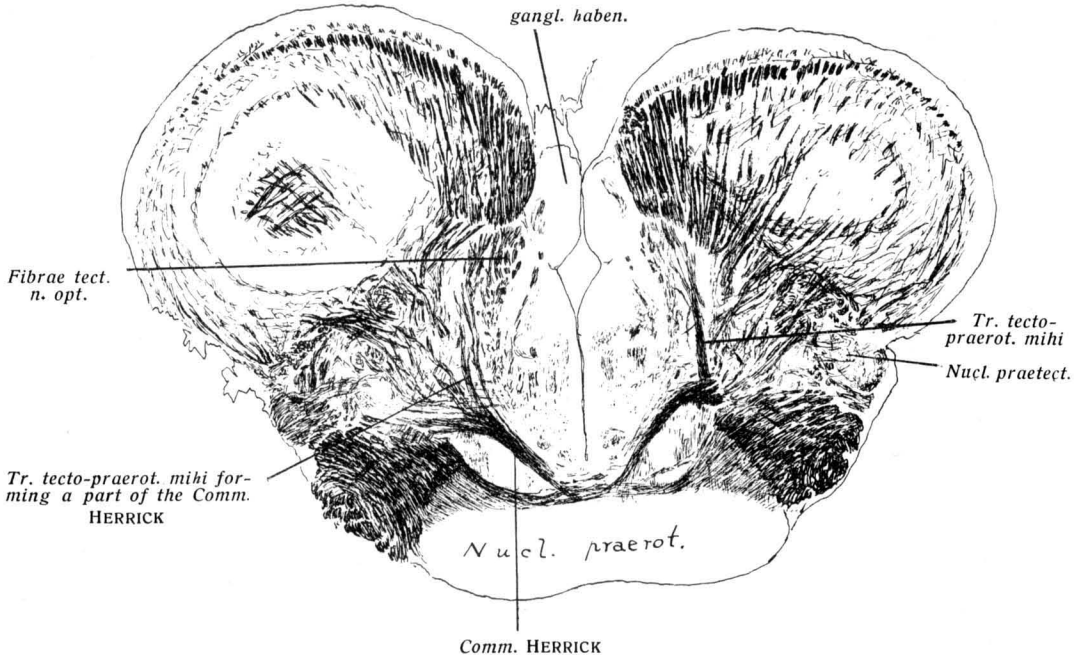

Fig. 3. Gasterosteus aculeatus.
(Preparation of the Central Institute for Brain research, Amsterdam).

Ventrally it mixes, as mentioned, among the fibres of the commissura transversa, in two ways. One time it runs nearly horizontally towards medial as the most caudal part of this commissure, close to the ventral periphery of the midbrain. Here it soon cannot be traced any further among the commissure fibres. Yet it seems plausible to me that here it crosses the medial line. This I find with Trutta, Syngnathus?[1]), Ammodytes?[1]), Mugil, Ophiocephalus, Morone, Osphremenus, Pleuronectes platessa?[1]), Rhombus, Hippoglossus?[1]), Solea?)[1]), Cyclopterus, Agonus?[1]), Trachinus and Tetrodon.

Another time it forms the most dorsal part of the commissura transversa and crosses directly under the ventricle. I was able to ascertain this course, besides in the cases where it is delusive of the commissura minor (Gasterosteus, Belone and Exocoetus), with

[1]) The question-marks denote that with these Teleosts I do not find the matter quite clear.

Clupea?[1]) and Pleuronectes limanda. Also with Gadidae this tract can easily be traced from the subventricular crossing as far as the deep medullary layer of the tectum.

FRANZ has erroneously indicated this bundle in Gadus, in fig. 6 of his work, as "fibrae tect. n. opt." The correctness of my observation, however, can be tested not only in Gadus itself, but very easily in Lota and Motella. In fig. 24 of the same work FRANZ has called the same tract correctly "ascending decuss. transversa" (the upper line of his reference, at the bottom, left hand).

Although the exact way of origin and termination of this bundle is not yet clear to me, I should like to call it provisionally *tr. tecto-praerotundus* and introduce it under this name.

III. *Tr. isthmo-praetectalis.*

FRANZ describes the course of his *tr. isthmo-opticus* as follows (op. cit., p. 414): "a tract which, together with the opticus, first appears ventrally to the midbrain roof, ascends on the inside of the midbrain roof, reaches the torus semicircularis and here curves round to the ganglion isthmi — here often difficult to distinguish from the fibres of the commissura transversa. It may be possible that part of the fibres remains already in the torus semicircularis."

He further is of opinion, supported by experiments (on which fishes?) that the fibre tract arises undoubtedly from cells of the ganglion isthmi and sends its neurites centrifugally into the eye (l.c., p. 415).

My investigation confirms the presence of such a bundle and its caudal course, as described by FRANZ. I only want to remark that I could not find this bundle with all bony fishes. A few fishes, such as Salmonids, Siluroids, Misgurnus, Symbranchidae, Esox, Ammodytes?[1]), Gadidae, Lophius?[1]) and Tetrodontidae?[1]) seem not to possess such a fibre tract.

Its further frontal course, however, is not as supposed by FRANZ, but different according to the Teleosts examined.

FRANZ seems to be right, in so far as the bundle, after its characteristic curve in the torus semicircularis, gathers its fibres at the lateral basal ridge of the midbrain, then by bundles enters into the lateral opticus root and disappears from examination under the fibres of the latter, as is the case with Megalops (with all)[2]), Gastero-

[1]) The question-marks indicate here that the matter concerned is not quite clear in these fishes.

[2]) The brackets refer to the quantity of fibres, entering into the opticus root.

steids (few)[2]), Scombresocids (part)[2]), Mugil (the greater part)[2]), Ophiocephalus (the greater part)[2]), Morone (greater part)[2]), Osphromenus (part)[2]), Cottids?[1]), Cyclopterus?)[1]), Agonus?)[1]) and Trachinus (with the smaller part of the fibres)[2]).

On the other hand there are bony fishes in which the bundle in question can be distinctly followed as far as the frontal tectum section, as Clupea, Cyprinidae, Syngnathidae, Osphromenus, Pleuronectidae (Solea excepted) and Callionymus. I therefore will give here a minute description of the course of this fibre tract in some specimens of fishes.

Just with Pleuronectes, where FRANZ believed to have his tr. isthmo-opticus fully established, we can clearly prove that the bundle in question actually enters frontally into the tectum, in the most superficial medullary fibre layer of it. The small bundles namely gather on the lateral surface of the midbrain to a roundish bundle that protrudes into the optic ventricle and then takes a wholly sagittal course. (see fig. 6 of Hippoglossoides). At first it runs ventrally to the bundles of tr. tecto-bulbaris and directly dorsal of the ventral point of the tectum plate. Some way more frontal it takes the shape of a curved medullary plate and encircles about half of the nucl. praetectalis from the lateral side. During this course its position corresponds to the bottom of the tectal furrow characteristic of this fish and, situated caudally deep inside, it frontally more and more approaches the outer surface; at last, quite frontal on the level of the geniculatum, it comes close under the molecular layer[3]) of the tectum. Till there it never touches the opticus root. Now part of the bundle radiates caudo-laterally of the geniculatum, towards mediodorsal into the dorsal part of the tectum[4]), whereas the other part runs further frontad and finally enters latero-ventrally into connection with the ventral part[4]) of the tectum, which extends a little further frontad than the dorsal one. At this radiation of the bundle I could quite clearly distinguish its small bundles from those of the brachium tecti (KAPPERS) and the optic root, and prove that the most superficial narrow layer of the so-called opticus fibre layer of the tectum consists of the little bundles of the fibre tract in question and the next much broader layer of medullary fibres (of the opticus

[1]) See note 1 p. 71.

[2]) See note 2 p. 71

[3]) This designation has its explanation in the above-mentioned treatise „On the torus longitudinalis etc.".

[4]) The frontal part of the tectum plate is divided into two parts by the aforementioned furrow.

fibre layer), separated from the first by a strand of grey substance, consists of the small bundles of the brachium tecti and the tr. opticus (see fig. 4).

Also with Clupea, examined likewise by FRANZ and drawn by him in fig. 9 of his treatise, I could trace the fibre tract as one or two coarsefibred bundles above and partly through the lateral opticus root, lateral of the praetectal nucleus and the geniculatum, as far as in the upper fibre layer of the most frontal tectum (fig. 5).

With the Cyprinidae its course is about the same as with Clupea. The small bundles gather medio-dorsally to the lateral root in one or two bundles, then run frontad, at first between the nucl. praetectalis and the lateral opticus root, then between the nucl. anterior thalami and the ganglion geniculatum. Here a part of the fibres branches off into the tectum, but the remainder runs, dorsally to the geniculatum, further frontad, then turns medio-dorsad and finally also reaches the tectum.

By the way I want to remark that with these Teleosts (Pleuronectids, Clupea and Cyprinids) the bundle in question is accompanied in its entire frontal course by the tr. geniculo-myelencephalicus of HOLMGREN. The two bundles, however, can easily be distinguished, the fibres of the first bundle being far coarser than those of the latter.

With Osphromenus the bundle shows a peculiarity. Part of its fibres enter, as mentioned above, already caudally into the lateral opticus root. Here again I expected to be able to trace the small bundles through the complex of the opticus fibres right into the upper fibre layer of the tectum. The other part, however, turns in the subependymal layer gradually medio-dorsad, above the comm. horizontalis fibre group[1]), and finally enters into the fibre system of the most medio-frontal tectum part.

Therefore I am fully convinced that there is no doubt but the bundle in question, that is to say what FRANZ calls tr. isthmo-opticus, does not run in the opticus to the eye, as FRANZ presumes, but to the frontal tectum, and there becomes part of the opticus fibre layer. Also in those cases where the fibres concerned enter already caudal into the lateral opticus root, it may be assumed that we have the same state of affairs as I have been able to prove in Osphromenus. In the following I shall call the bundle provisionally *tr. isthmo-tectalis*, although the direction of its course (ascending or descending) is not have proved yet.

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[1]) Complex of commissura horizontalis and tr. tecto-cerebellaris (cf. fig. 5).

This *tr. isthmo-tectalis* mihi was traced already fairly minutely by MAYSER, the sharp observer. He called it "the outer (back) layer of the stratum zonale" of the torus semicircularis; but made it originate frontal in the corpus geniculatum externum (nucl. praetectalis of the authors) and terminate caudally between "numerous

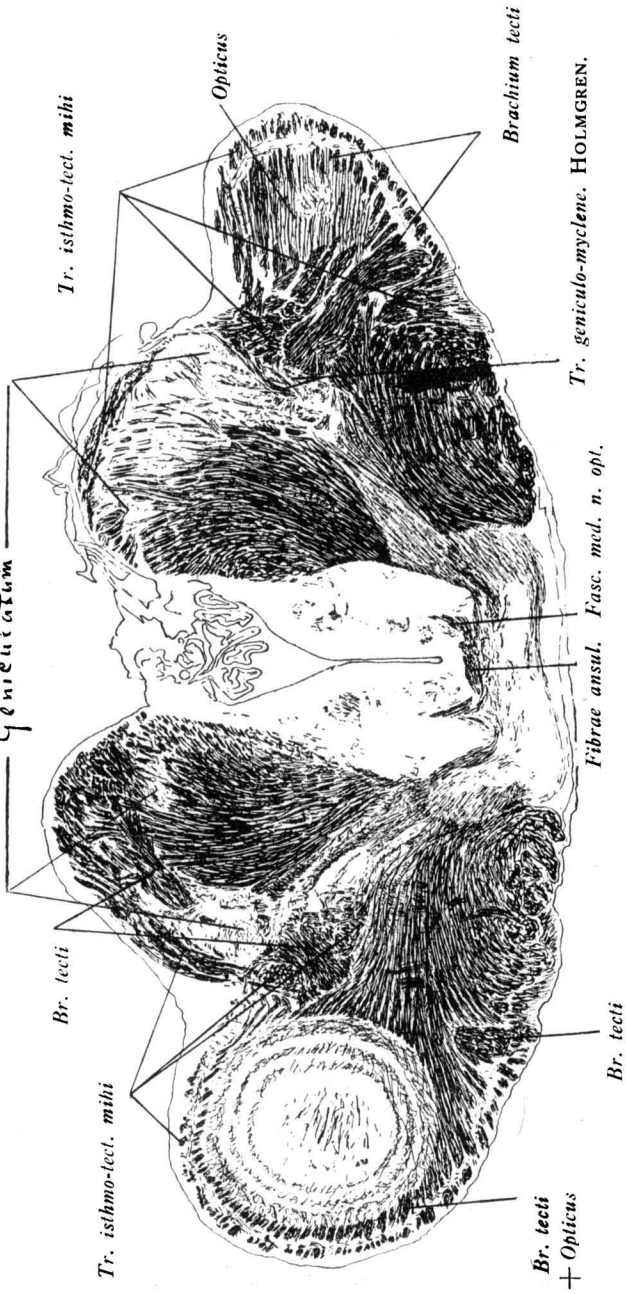

Fig. 4. Pleuronectes platessa.
(Preparation of the Central Institute for Brainresearch Amsterdam.)

small nerve cells chiefly in the caudal and upper part of the torus" (op. cit., p. 342—343 and 348), without yet having applied to the latter a special name (ganglion isthmi).

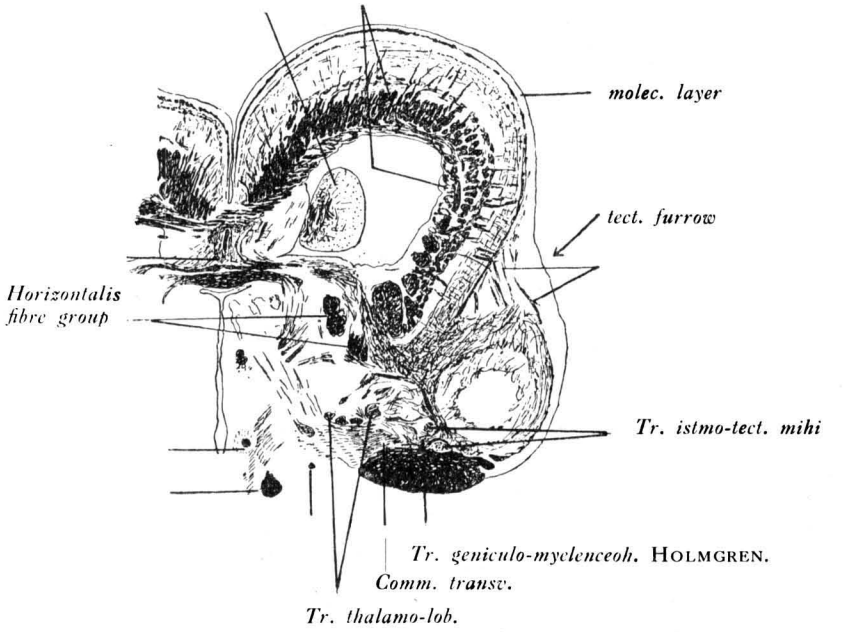

Fig. 5. Clupea harengus.
(Preparation of the Central Institute for Brain research, Amsterdam.)

After MAYSER no authors had occupied themselves, as far as I know, with this interesting fibre bundle, till FRANZ discovered it again.

Through the result of this investigation the relation between the tectum opticum and the ganglion isthmi with Teleosts gets closer. The connection is twofold, one time through the tr. tecto-isthmicus of FRANZ, another time through the tr. isthmo-tectalis of myself, and we may presume that the first leads tectofugal, the latter tectopetal.

Although MAYSER's opinion that the bundle in question originates from the corpus geniculatum externum s. l. (i.e. from nucl. praetectalis of the authors) cannot be confirmed by me as to the Cyprinoids (s. above), yet I saw in a specimen of Exocoetus a small part of the fibres of my tr. isthmo-tectalis end in the nucl. praetectalis, the other larger part running further frontad past this nucleus. The same I have been able to find with Cyclopterus, Trachinus, with some doubt also with the Gasterosteids, Syngnathidae, Belone and Solea. As just on the spot where these fibres should enter and end

in the nucl. praetectalis, the brachium tecti, whose fibres are as coarse as the others, leaves this nucleus, it is quite possible that a misinterpretation can arise. All the same I can maintain this point as being quite certain, at least with Exocoetus. When this is the case, these fibres correspond with those of CATOIS from the nucl. praetectalis, of which he writes: "Les autres (fibres)[1]) descendent presque verticalement de la partie inférieure du noyau prétectal, se recourbent ensuite en arrière et se dirigent vers la région basale du mésencéphale" (op. cit., p. 97). But when he supposes "qu'elles doivent servir à établir des connexions entre le thalamus et la moelle spinale" (l.c., p. 97—98), this remains a mere supposition, for according to my investigations we can say for certain that they are connected with in the ganglion isthmi and consequently form a *tr. isthmo-praetectalis*, [2]) (or *praetecto-isthmicus*).

IV. *Pars praetectalis Comm. posterioris.*

The component part of the so-called "*stratum zonale*" of the torus semicircularis, (for convenience' sake I here use this long abandoned nomenclature) is not at all exhausted with the above tr. isthmo-tectalis mihi and the commissura transversa. With most bony fishes there is namely a fibre connection between this stratum and the commissura posterior. One bundle from about the middle of this commissure runs latero-ventrally and at the same time frontad, joins the tr. isthmo-tectalis in the most caudal level of the nucl. praetectalis (fig. 6) or, if this is missing, directly the commissura transversa and then joins in the characteristic curved course of the torus semicircularis. To the first category, where there is a tr. isthmo-tectalis, belong the Gasterosteids, Belone, Mugil, Ophiocephalus, Morone, Osphromenus, Pleuronectids, Gobius, Cottus, Cyclopterus, Agonus, Trachinus and Callionymus, to the latter, where the tr. isthmo-tectalis is not present, belong Symbranchidae?, Esox, Ammodytes, Gadids, Solea, Lophius and Tetrodontidae. The fibres of the latter bundle are thinner than those of the tr. isthmo-tectalis. On the other hand there are fishes that have no such connection, e.g. Megalops?, Clupea, Cyprinoids, Syngnathidae, Exocoetus and Zoarces?.

This bundle differs from the other components of the commissura posterior by its finer fibres and mostly also by its compactness. As to its position it is about in the middle of the commissure, in sagittal

[1]) Bracketed by myself.

[2]) Cf. also HOLMGREN's drawings of Callionymus: fig. 87, 88 and 89: Tr. ist.-praet.

as well as in dorso-ventral direction. In WEIGERT-preparations it often has a greyish colour, which makes me suppose that it consists of medullary as well as unmedullated fibres.

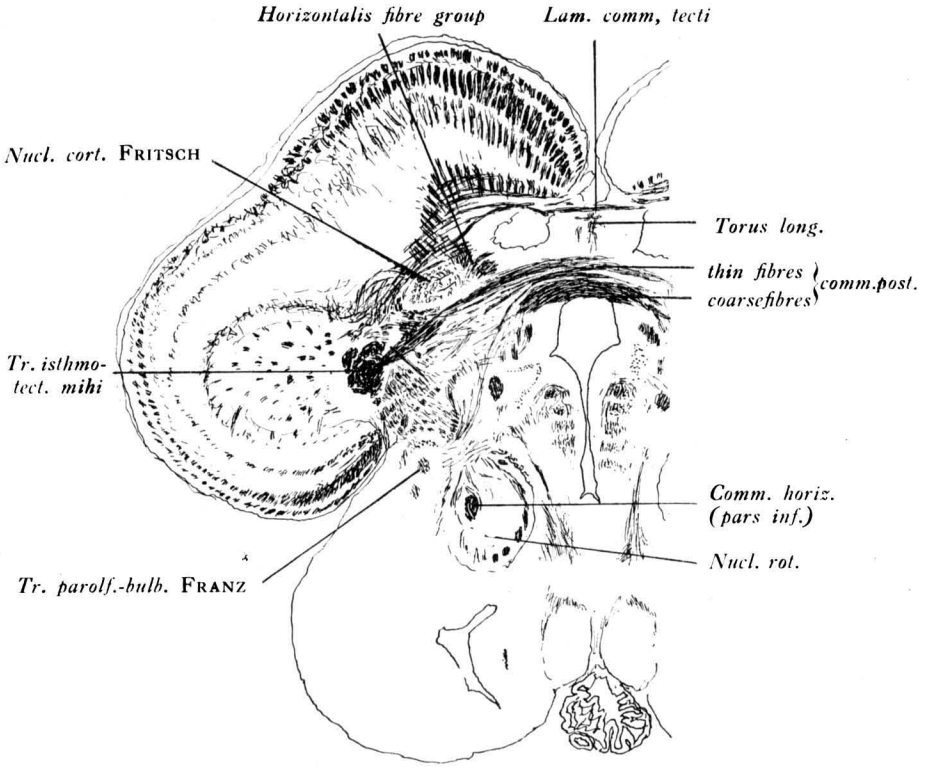

Fig. 6. Hippoglossoides platessoides.
(Preparation of Prof. RÖTHIG's Collection, Berlin.)

ARIËNS KAPPERS in his work on Ganoids (op. cit., p. 475) has expressed the supposition that the middle part of the commissura posterior partly enters into a connection with the geniculatum (i.e. the nucl. praet-ectalis of the authors), partly passes over this nucleus, bends backwards and ends in the tegmental region, just under the torus semicircularis. Also in his treatise on the brain of Chimaera (p. 158) and of late in his manual (p. 818) he considers it as highly probable that this "lateral part" of the commissura posterior originates in the geniculatum (i.e. in the nucl. praetectalis) of the one side and extends caudad on the other side (extremely clear with Pleuronectidae, as he emphasizes).

HOLMGREN calls the relative part of the commissura posterior after EDINGER commissura praetectalis, but is also of opinion that it is "not excluded that praetectalis fibres, that were traced till in the

commissura posterior, may go on the other side to an other final station than in the nucleus praetectalis" (op. cit., p. 262).

In my opinion one of the two formations is to be considered as the caudal destination of this bundle, viz. the torus semicircularis or the ganglion isthmi, the first with greater probability than the latter. About its frontal extremity I cannot express an opinion for the present, although the nucl. praetectalis of the other side seems to be the most probable. In any case further investigations on this point are most desirable.

It is difficult yet to say anything about the relation of the bundle concerned, to the commissura praetectalis (or pars praetectalis of the commissura posterior) of EDINGER. However, I have been able to state with a specimen of Leuciscus rutilis that, although with no other of the Cyprinoids which I examined, I could prove a well-marked fibre connection between the commissura posterior and the tr. isthmo-tectalis mihi or even the "stratum zonale" of the torus semicircularis, with the said fish there existed a well characterized, closed commissura bundle between the nuclei praetectales of both sides.

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